Effect of Various Water Application Strategies on Root Development of *Opuntia ficus-indica* and *O. robusta* Under Greenhouse Growth Conditions[♦]

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ABSTRACT

This study aimed at determining the influence of different water applications on the root/cladode ratio and water-use efficiency (cladode or root dry-mass production per unit of water used) of one-year-old *Opuntia ficus-indica* (L.) Miller (cultivar Morado – green cladode) and *O. robusta* Wendl. (cultivar Monterey – blue cladode) plants. The one-year-old cactus-pear cladodes were planted in pots (210-mm diameter and 550-mm-deep soil) and grown in the greenhouse at day/night temperatures of 25-30^{o}C/15-18^{o}C. The water treatments applied were 0-25%, 25-50%, 50-75% and 75-100% depletion of total plant-available water. Root mass and root length decreased significantly with water stress over the three months for both *Opuntia* species. The finer root system of *O. robusta* showed a lower root mass than *O. ficus-indica*. Although the influence of water stress on root die-back was clearly observed, it was less striking in *O. robusta* than in *O. ficus-indica*. The dry-mass-based root/cladode ratio decreased significantly with water stress for all three months for both species. The roots comprised only 11% and 12% (average of all months and water treatments) of the total plant biomass for *O. ficus-indica* and *O. robusta*, respectively. The water-use efficiency expressed in terms of cladode mass decreased with water stress for *O. ficus-indica* and increased with water stress for *O. robusta*. A water application of only 13.63 mm and 11.64 mm was enough to fill up the cladodes for *O. ficus-indica* and *O. robusta*, respectively, at the lowest water treatment. It seems that *O. robusta* is less sensitive to water stress conditions than *O. ficus-indica*. The quick reaction to water makes the cactus pear plant adaptable to very low rainfall conditions.

Keywords: Cactus pear, cladode mass, root/cladode ratio, root length, root mass, root thickness, water-use efficiency

INTRODUCTION

In the arid and semiarid regions of southern Africa drought is a normal phenomenon and seriously limits the agricultural potential (Snyman, 1998). Therefore, when farming under rain-fed conditions, it is important for the available water to be used in the most efficient way. There is a need for more research on drought-tolerant fodder plants, such as *Opuntia* species. Cactus pear features prominently in the agriculture of less-developed countries, especially in their marginal areas (areas that are infertile and not used for crop production) (Mondragón-Jacobo and Pérez-Gonzáles, 2000). It is used mainly as animal feed in times of droughts as it provides water and some vital nutrients, such as carbohydrates (Le Houérou, 1996). It can also be used as a fruit crop for two to three months of the year (Brutsch, 1988). Their young cladodes are consumed as vegetables (Florez-Valdez, 1995). It is also used in the control of soil erosion, since it is easily established inexpensively with little labour (Le Houérou, 1996; Felker and

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Inglese, 2003). It does not compete with other rangeland species (Le Houérou, 1994) and, therefore, deserves more attention as one of the most valuable promising crops (Snyman, 2004). Over the last ten years there has been an increased interest worldwide in the spineless cactus pear as both fodder and a fresh-fruit crop (Felker and Inglese, 2003; Felker *et al*., 2005). In South Africa specifically, very competitive prices for cactus pear fruit are obtained at the national fresh-fruit market compared to apples, peaches, and oranges (Snyman, 2003).

Despite the large range of commodities cactus pear could provide in areas with little available resources, it has received scant attention by horticultural research (Inglese *et al*., 1995; Inglese and Pace, 2002). Most of the research in plant physiology and ecology originates in the USA, while Israeli, Italian, and South African researchers produce most of the horticultural research. Advancing desertification, coupled with the urgent need for appropriate technologies and crops capable of developing sustainable and valuable production in arid and semiarid areas, has raised new interest for the environmental role and the potential production of cactus pear. There is, therefore, a need for increased farmer interest and knowledge of production and adaptability of cactus pear through published information and more research. Increasing knowledge of environmental influences on cactus-pear productivity and quality will also allow more profitable production (Oelofse, 2002; Felker *et al.* 2005). Although relevant information on the above-ground growth and development of the cactus-pear plant is available (Brutsch and Zimmerman, 1990; Galizzi *et al*., 2004), very limited studies have been done on *Cactaceae* roots (Hills, 1995). They certainly differ from that of other plants, as they develop xeromorphic characteristics (Hills, 1995).

Water availability is the most important environmental factor limiting plant growth and survival in arid areas (Snyman, 1998; Nobel and Huang, 1992). Root systems of these plants can be subjected to prolonged droughts that are interrupted by sporadic and often light rainfall (Nobel, 1977, 1991). The root system of the succulent cactus pear occurs predominantly in the upper layers of the soil, where the soil-water content is both temporally and spatially heterogeneous (Drennan and Nobel, 1998; Nobel, 2001). Lateral root primordia of *Opuntia* species are formed during periods of soil drying where lateral roots emerge in response to rainfall and abscise as soil dries (Nobel *et al*., 1991). As for other species, seasonally high temperatures limit root proliferation near the soil surface (Nobel, 1988). Cactus pear is, therefore, well adapted to arid and semiarid conditions with high evaporation following rain where it can tolerate drought to such an extent that the smallest amount of water being absorbed can be used efficiently (Hills, 1995; Brutsch, 1979; Reynolds and Arias, 2001; De Kock, 2001; Han and Felker, 1997). The cactus pear can utilise drier areas to its full potential because of its Crassulacean Acid Metabolism (CAM) photosynthesis pathway (Nobel, 1995; Lahsasni *et al*., 2004) which is about four times more efficient in water use than C_4 plants, such as maize (Felker and Russell, 1988). The aim of this study was, therefore, to determine the response of roots and cladodes to different water applications of two *Opuntia* species in terms of root/cladode ratio and water-use efficiency.

PROCEDURE

Methods

The research was conducted during the 2002/2003 growing season (September 2002 to March 2003) in the greenhouse. The temperatures were regulated between 25^{o}C and 30^{o}C during the day and 15^{o}C to 18^{o}C during the night over the trial period. According to Nobel (2001) the ideal day/night temperatures for *Opuntia* are 25^{o}C/15^{o}C. Asbestos pots of 210-mm diameter and 550-mm deep were filled with the same amount of dry, fine, sandy-loam soil after which each was weighed. The clay, silt, and sand content of the soil were 14%, 2%, and 84%, respectively. It has a pH (KCL) of 4.5 and EC_s of 21 mSm^{-1}. The exchangeable Ca, Mg, K, and Na contents of the soil were respectively 468 mg kg^{-1}, 235 mg kg^{-1}, 148 mg kg^{-1} and 42 mg kg^{-1}. The extractable N and P contents were 54 mg kg^{-1} and 7 mg kg^{-1}, respectively. The bulk density of the soil was 1,260 kg m^{-3} after filling the pots. The soil was taken from the top 100 mm of the A-horizon of a Bloemdal Form (Roodeplaat family -3200) (Soil Classification Working Group, 1991). Forty millimetres crushed stone covered the bottom of each pot. The pots have three holes of 7-mm diameter at the bottom to ensure free water movement through the pot. In total, 53 pots were prepared of which five were used to determine the soil-water depletion intervals, which will be discussed later.

One-year-old cladodes of *Opuntia ficus-indica* (L.) Miller (cultivar Morado) (green cladodes) and *O. robusta* Wendl. (cultivar Monterey) (blue cladodes) were obtained from the farm Waterkloof approximately 20 km west of Bloemfontein. The cladodes of *O. ficus-indica* were, on average, 506 ±46 mm long, 183 ±15 mm wide, 20 ±3 mm thick and 1,406 ±170 g fresh mass (means ±SE, n = 10). The cladodes of *O. robusta* were 261 ±46 mm long, 244 ±15 wide, 15 ±2 m thick, and 1,354 ±130 g fresh mass (means ±SE, n = 10). The cladodes were dried for four weeks in the shade to allow healing of the cutting area and then planted in the pots with one quarter of *O. robusta* (50 mm to 60 mm) and *O. ficus-indica* (100 mm to 120 mm) of the cladode in the soil. Each cladode was weighed before planting. The cladodes were placed North/South in the greenhouse. The planting was done on 4 September 2002.

Treatments

Four water treatments, namely, T_1 = 0 to 25% depletion of plant available soil water (PAW), T_2 = 25% to 50% depletion of PAW, T_3 = 50% to 75% depletion of PAW and T_4 = 75% to 100% depletion of PAW, were applied. In determining the soil-water depletion intervals, five pots (19,058 cm^3 each) were filled with the same mass of dry soil, which was spread out and dried in the sun beforehand. These values were taken as permanent wilting point (PWP) of the soil. In determining field water capacity (FWC), the pots were saturated with water and left for 48 hours before being weighed again. At FWC the soil-water content was 0.263 mm water mm^{-1} soil depth or 26.3% volumetric soil water. At PWP, the soil-water content was 0.075 mm water mm^{-1} soil depth or 7.5% volumetric soil water. The total PAW was, therefore, 0.188 mm mm^{-1} or 94 mm water pot^{-1}. Therefore, weighing the planted pots monitored the depletion of PAW within the specific water treatment. The mass of the planted cladodes was considered when calculating the water increments per pot.

The plants were allowed to establish for five weeks before water treatments were initiated. To keep the soil-water content of the different treatments to the correct level, the pots were periodically weighed and watered to the specific levels before reaching the lower limits of PAW. The amount of water needed to reach the upper limit for the specific water treatments was then added. Each planted pot was kept in the weight range of the water treatments for one of the following periods, namely: one, two, or three months before being washed out and root and cladode measurements took place. These were done to measure the plant development at the different water treatments over time (three months).

Data Collection

Data collected after applying the different water treatments included root and cladode mass, root length, root/cladode ratio, water-use efficiency, water content in each cladode, and water needed to fill up a cladode after lifting water stress.

The roots of the plants were sieved through a 2-mm and 0.5-mm mesh after being removed from the cladodes. The roots and the cladodes were dried at 100°C for 24 and 72 hours, respectively, for reaching a constant weight.

The length of the washed roots was measured by using a modified infrared root length counter (Rowse and Philips, 1974). The root counter was first calibrated by using 10 pieces of string being cut at different well-known lengths (ranging from 0.5 m to 5 m). The string pieces were more or less of the same thickness as the roots. The cut string pieces (approximately 20) for each length were spread over the counter and six replications of the readings were taken. Before each replication the string pieces were moved around over the counter. The counts from the root-length counter were regressed against the length of the string. The regression function used to calculate the root length from the root-counter readings was y = 0 + 45.349x, where y = root-counter reading and x = root length (m) (R^2 = 0.9406 and n = 20). The averages of six readings were taken from each plant. The lengths of all roots in each pot were measured.

The thickness at the end of the root where die-back took place, as well as the thickness of the tap roots, was measured at 30-mm intervals with a vernier caliper. The length of the roots from the top up to where die-back took place was measured and also the number of side roots per tap root was determined. Twenty roots, randomly selected, were measured in each pot.

Water-use efficiency (WUE) is defined as the amount of plant material (dry matter) produced (roots and cladodes) per unit of water used (evapotranspiration). The water-use efficiency of the cladodes was calculated in two ways. First, only the newly formed cladodes were taken into account and, second, the increase in mass of the mother cladode (planted cladode) was also included. In the last mentioned case the mass of both newly formed cladodes and the increased mass of the mother cladode were added and used in the calculation of the total dry matter (DM) of the cladodes. The DM value for the mother (planted) cladode was obtained from 10 extra cladodes, although not planted but more or less the same size as the planted ones. Those 10 cladodes were weighed before and after drying at 100^{o}C for 72 hours. All other cladodes planted in the pots were done the same day. The obtained average DM was used to work back to the expected DM values for each cladode when planted. These values were then used to correct the DM content for each planted cladode when the pots were washed out. This DM increase was included in calculating the WUE. The average water content of the 10 cladodes for *O. ficus-indica* and *O. robusta* was 88.13% and 87.29%, respectively.

The amount of water needed to fill up the cladodes after the plants were stressed was also measured. This was done by weighing the potted plants when the different water treatments were reached, after which they were again watered up to field capacity and left overnight to settle down. The soil was covered to avoid evaporation overnight. The next day, the potted plant plus the soil were weighed again, as well as the cladodes alone after being washed.

The water uptake, or water needed to fill up the cladodes, was then calculated by the following equation:

$$[(d + c) – e] – b = a \text{ and}$$

$$d – a = \text{water uptake by the cladodes overnight}$$

where:

a = mass of cladodes when stressed (at specific water treatment),
b = mass of soil when dry,
c = mass of watered soil,
d = mass of cladodes after watering and washed out, and
e = mass of water added to the pot.

Data Analysis

A 2 x 4 (*Opuntia* species and water treatments) factorial experiment, with fully randomised design, was conducted. There were two replications for each water treatment. The pots were washed out monthly over a three-month period (18 pots each month). The data collected was analysed by SAS (DOS program, 6.04 version) (Cary, 1988). The one-way analysis of variance at 95% confidence interval was conducted to determine any significant difference in root mass, length, thickness, root/cladode ratio, water-use efficiency, and percentage water in the cladodes. The Tukey test was used to find where, exactly, the difference is (Mendenhall and Sincich, 1996). Data for different months and/or over three months were analysed separately. In determining least significant difference (LSD), the method of Fisher (1949) was used.

RESULTS AND DISCUSSION

Root Mass

The root mass decreased ($P \leq 0.05$) with water stress for both *Opuntia* species within each month, with the exception of *O. ficus-indica* during month 1 for the two lowest water treatments (Figure 1). In all four water treatments the root mass for *O. ficus-indica* was higher ($P \leq 0.05$) than that of *O. robusta*. The highest root mass of *O. ficus-indica* ranged between 25 g plant^{-1} and 27 g plant^{-1} and the lowest was between 10 and 15. Although not physically measured, the root system in general for *O. robusta* visually showed a finer structure than that of *O. ficus-indica* with its thicker appearance. The finer root system of *O. robusta* than that of *O. ficus-indica* could be responsible for the lower root mass obtained for *O. robusta*, while *O. robusta*'s highest mass was 20 g plant^{-1} and the lowest was 8 g plant^{-1}. The root mass response to water treatments within a month was almost the same ($P > 0.05$) for both species. For both species the root mass remained nearly the same ($P > 0.05$) within a water treatment between the three months.

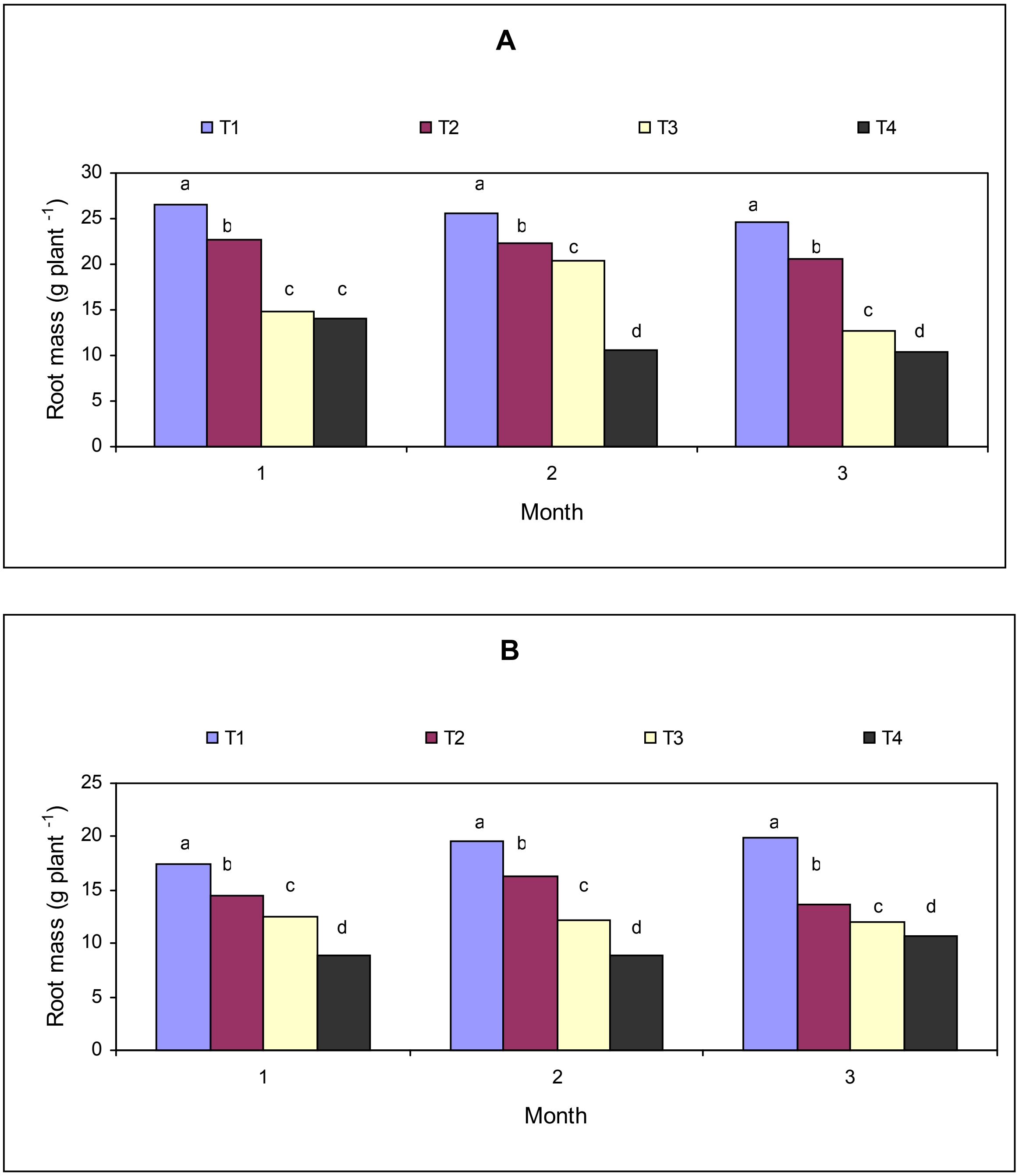


Figure 1. Root mass (g plant^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75%, T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly (P<0.01). $LSD_{0.01}$: species = 1.0208 and water treatment = 1.9146.

According to most researchers, the roots of cactus pear are typically shallow (50-mm to 150-mm deep) and, even for a large arborescent cactus, occur chiefly in the upper 300 mm of the soil (Gibson and Nobel, 1986). Irrigation water is generally applied only to the usual rooting depth, but excessive irrigation can force roots to lower soil layers. As the soil dries, fine lateral roots generally die, while larger roots become covered with a corky layer (periderm) (Nobel, 1995, 2001). In this study the influence of water stress on root dieback was also clearly observed (Table 1). With increased water stress, the average thickness over the three months where die-off of the tap roots took place increased ($P \leq 0.05$) for *O. ficus-indica* with 0.43 mm, it decreased ($P \leq 0.05$) at the top with 0.68 mm and with 30-mm intervals also decreased ($P \leq 0.05$) with 0.67 mm. In contrast for *O. robusta*, the average thickness of the tap roots where die-off over the three months took place with water stress increased ($P \leq 0.05$) with 0.30-mm and at 30-mm intervals decreased ($P \leq 0.05$) with 0.47 mm and also decreased ($P \leq 0.05$) at the top with 0.70 mm. It is clear that in most cases the decrease in root thickness due to water stress was less for *O. robusta* than for *O. ficus-indica*. This finding is an indication that *O. robusta* is less sensitive to water stress than *O. ficus-indica*. No significant ($P > 0.05$) differences for all root thickness measurements were observed between the three months for both species (data not shown). *Opuntia robusta* also has a finer root system according to the root thicknesses.

Table 1. Root thickness (mm) and length (mm) for the *Opuntia* species at different water treatments. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Data are means of three months and SE of 20 roots per plant. Least significant difference (LSD) is calculated at 1% level.

Measurement	**Water treatments**				
	T_1	T_2	T_3	T_4	LSD
O. ficus-indica					
Thickness of tap root (mm):					
At top	2.25	2.21	1.74	1.57	0.21
	(±0.96)	(±0.84)	(±0.74)	(±0.62)	
At end where dieback	0.37	0.55	0.60	0.80	0.11
	(±0.09)	(±0.08)	(±0.09)	(±0.08)	
At 30-mm intervals	1.40	0.93	0.83	0.73	0.21
	(±0.61)	(±0.44)	(±0.41)	(±0.31)	
Average root length (mm):	295.27	446.67	456.67	401.67	92.16
Tap roots not die-back	(±92.16)	(±111.12)	(±123.17)	(±126.57)	
	270.00	256.67	166.67	136.67	101.20
Tap roots from top to dieback	(±91.26)	(±91.24)	(±66.66)	(±69.14)	
	150.00	200.00	243.33	313.67	111.11
Side roots	(±23.14)	(±31.22)	(±36.14)	(±36.26)	
O. robusta					
Thickness of tap root (mm):					
At top	1.21	1.24	1.48	0.51	0.20
	(±0.61)	(±0.64)	(±0.61)	(±0.63)	
At end where dieback	0.20	0.30	0.50	0.50	0.10
	(±0.08)	(±0.07)	(±0.06)	(±0.06)	
At 30-mm intervals	0.77	0.73	0.70	0.30	0.19
	(±0.41)	(±0.11)	(±0.12)	(±0.09)	
Average root length (mm):	300.00	300.00	250.00	170.00	121.26
Tap roots not dieback	(±66.66)	(±66.66)	(±60.14)	(±41.26)	
	160.00	146.67	130.00	76.67	81.00
Tap roots from top to dieback	(±41.22)	(±40.16)	(±22.14)	(±10.10)	
	200.00	200.00	200.00	130.00	36.66
Side roots	(±42.16)	(±24.15)	(±26.12)	(±25.14)	

Lateral roots branching from main roots could account for about 70% of the total root length for cacti (Huang and Nobel, 1993) and have a higher hydraulic conductivity than tap roots (Nobel and Sanderson, 1984). However, little attention has been paid to lateral roots, especially to their hydraulic and anatomical changes with distance from the root tip and with soil-water availability (Huang and Nobel, 1993). Interestingly, the study showed that for *O. ficus-indica*, on average over the three months, the individual root lengths for the tap and side roots increased ($P \leq 0.05$) with water stress with 106 mm and 164 mm, respectively (Table 1). In contrast for *O. robusta* the root lengths for the tap and side roots decreased significantly ($P \leq 0.01$) with water stress with 130 mm and 70 mm, respectively. The root length of the tap root from top up to where die-back took place decreased ($P \leq 0.05$) with water stress with 133 mm and 83 mm for *O. ficus-indica* and *O. robusta*, respectively. These findings again highlight the lesser sensitivity of *O. robusta* to water stress. The root lengths within a water treatment did not differ significantly ($P > 0.05$) for both species between the three months (data not shown).

Root Length

Root length increased ($P \leq 0.05$) from month 1 to month 3 in all treatments for both species (Figure 2). Root length decreased ($P \leq 0.05$) with water stress in each month for both *Opuntia* species with the exception of T_3 for all months and also with the exception of treatment T_2 in month 2 for *O. ficus-indica*, which confused the trend. In general, the conclusion can be made that root length is the function of both soil-water content and growth stage. In both species the roots were longer at T_1 and T_3 than T_2 and T_4. For most water treatments the root length between the species did not differ much ($P > 0.05$).

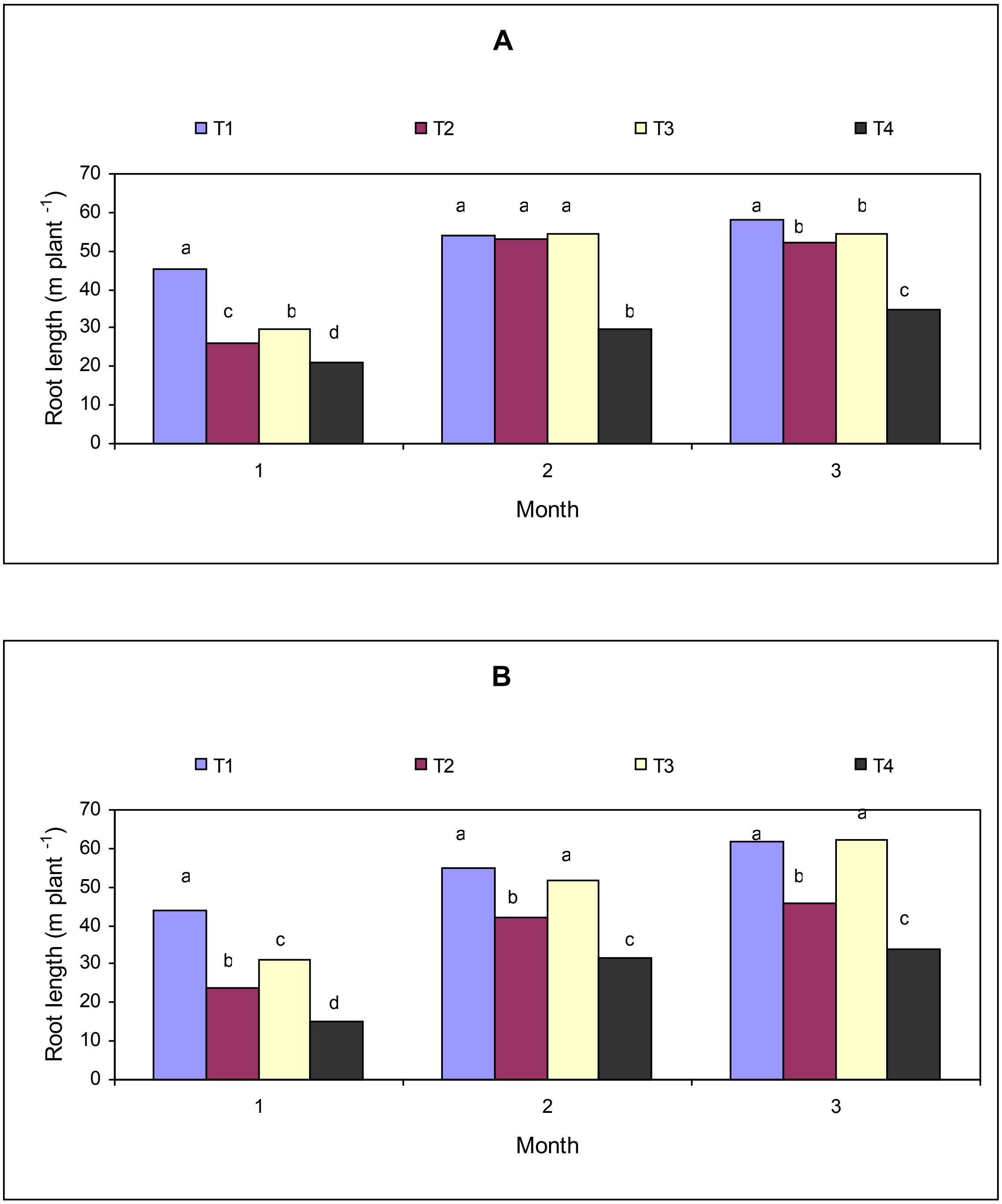


Figure 2. Root lengths (m $plant^{-1}$) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly (P<0.01). $LSD_{0.01}$s: species = 3.4232 and water treatment = 4.4206.

Root-Length/Root-Mass Ratio

The root-length/root-mass ratio increased ($P \leq 0.05$) with water stress for *O. ficus-indica* over the last two months, with the exception of water treatment 2 (Figure 3). In contrast for *O. robusta*, the root length/root mass ratio decreased for the first and the third months, with the exception of T_2 and T_3 . It also increased with time from the first month to the third month in both species.

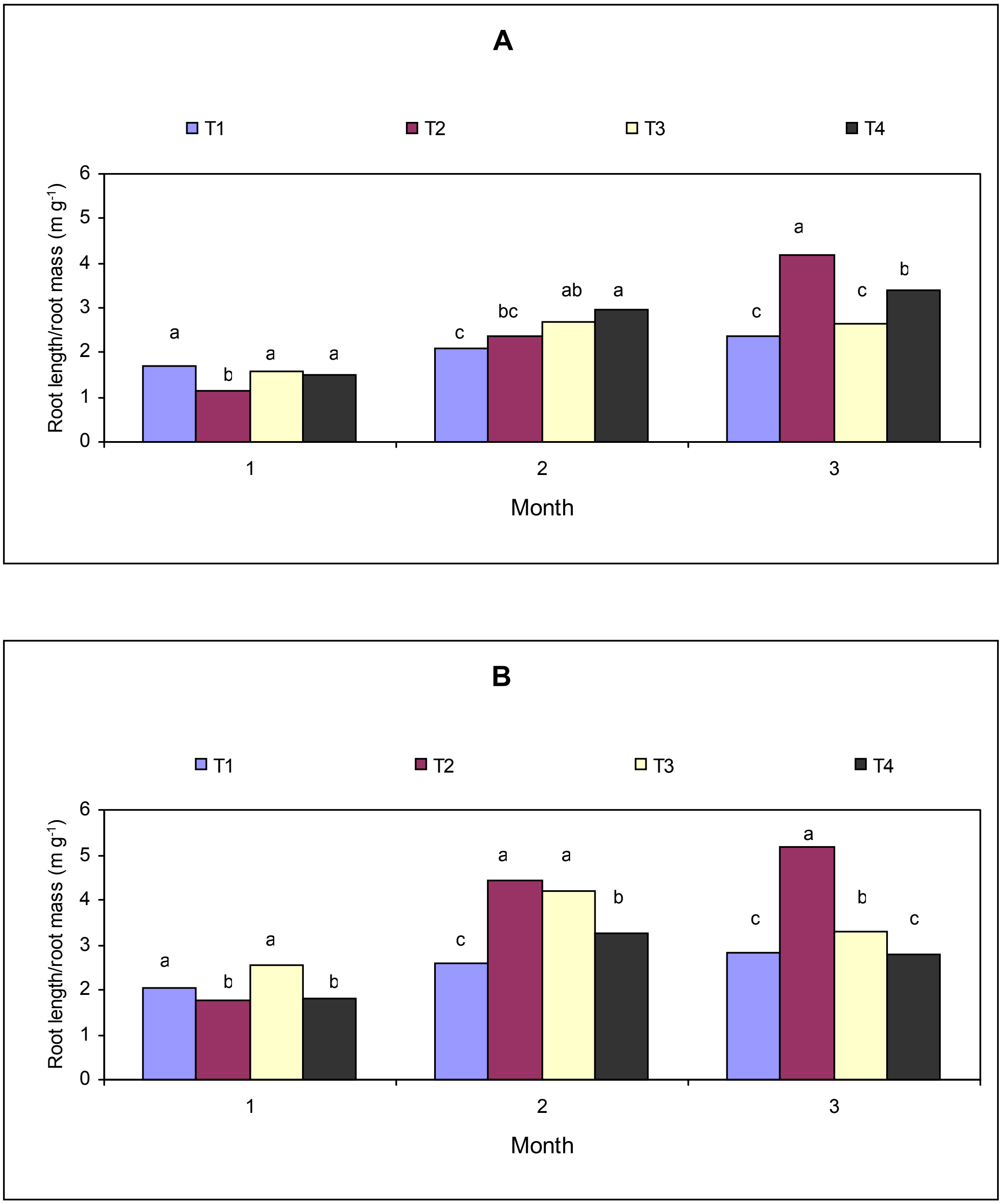
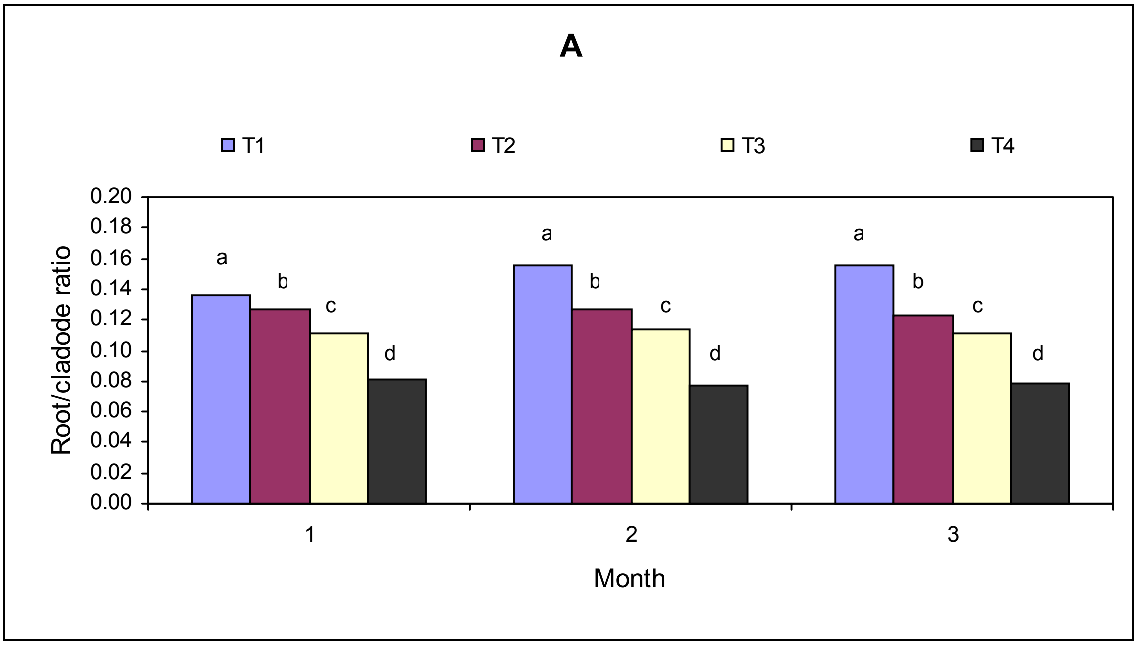


Figure 3. Root-length/root-mass ratio (m g^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil-water. Means within a month with different superscripts differ significantly ($P<0.01$). $LSD_{0.01}$: species = 0.3680 and water treatment = 0.6284.

Root/Cladode Ratio

Based on dry mass, root/cladode ratio decreased ($P \leq 0.05$) with water stress for all three months for both *Opuntia* species, with the exception of T_3 and T_4 over month 3 for *O. robusta*. (Figure 4). It increased ($P \leq 0.05$) from month 1 to month 3 for both species, which is an indication of a greater increase in root mass over time than cladode mass. The root/cladode ratio for *O. ficus-indica* of 0.07 to 0.14 as found by Drennan and Nobel (1998) and Nobel (1995, 2001) supported the very low values found in this study, regardless of the water application or over time.



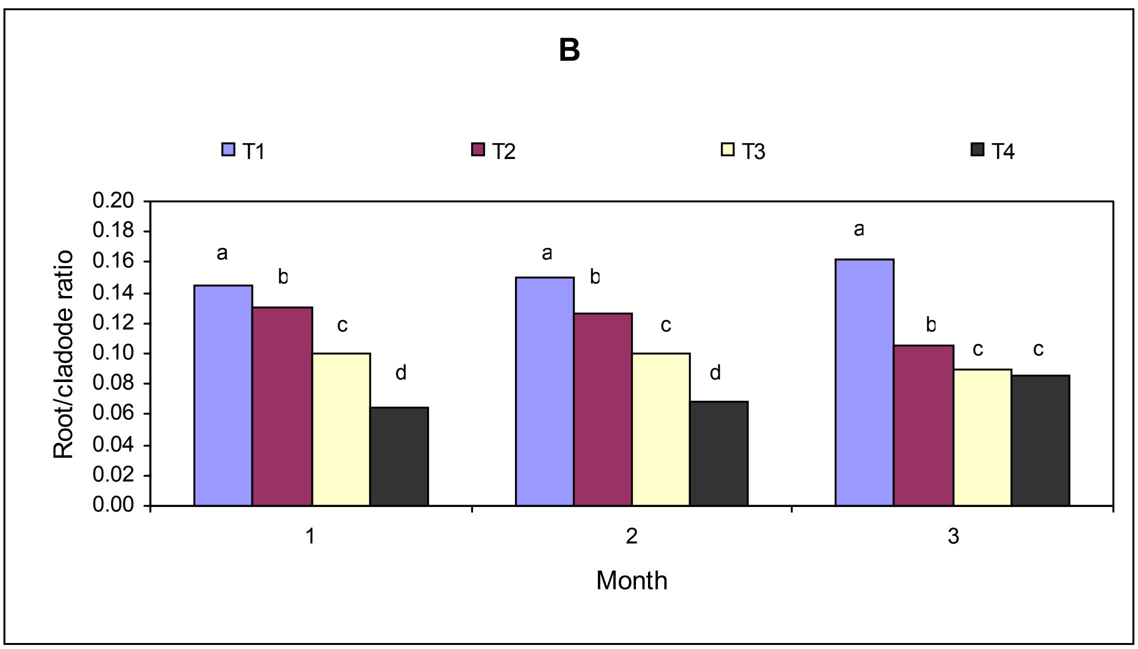


Figure 4. Dry-mass root/cladode ratio for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly ($P<0.01$). $LSD_{0.01}$: species = 0.0059 and water treatment = 0.0112.

The root/cladode ratio differed significantly ($P<0.01$) for each species among water stress treatments within each month. The average roots of *O. ficus-indica* composes 11% of the total plant biomass for all the water treatments and months, compared to the 12% for *O. robusta*, which perhaps could be due to the finer root system of the last-mentioned species.

Water-Use Efficiency

Although the water-use efficiency expressed in terms of roots for both *Opuntia* species decreased with water stress (Figure 5) over the three months, it was only not significantly ($P>0.05$) different between water treatments, for *O. robusta* during the first and second months and for *O. ficus-indica* during the last months. The water-use efficiency of *O. ficus-indica* decreased ($P\leq0.05$) with time, from the first to the third month. In contrast, the WUE for *O. robusta* showed a more constant trend within a water treatment over time. In general *O. ficus-indica* used water more efficiently than *O. robusta*.

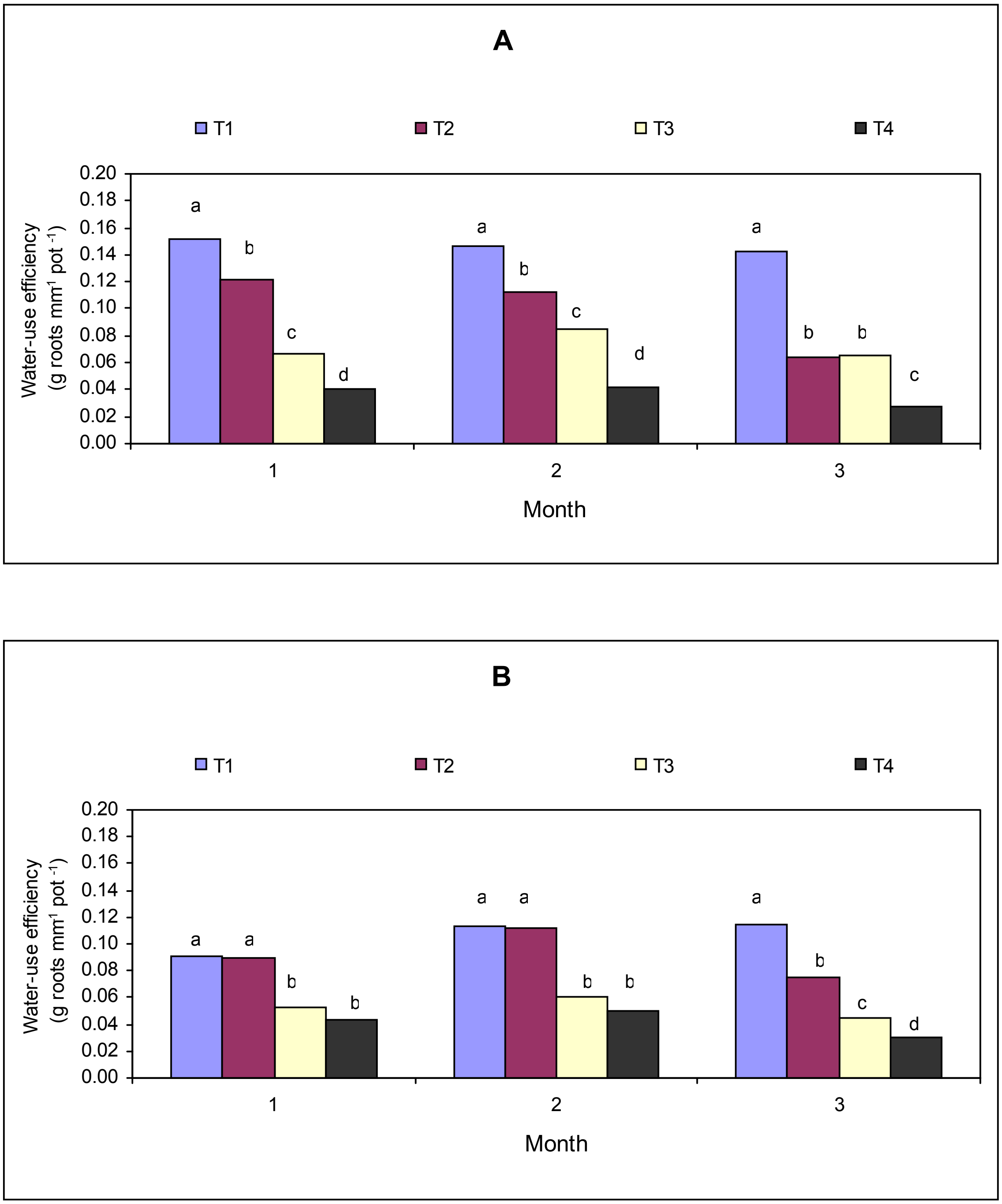


Figure 5. Water-use efficiency (g roots mm^{-1} pot^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly ($P<0.01$). $LSD_{0.01}$ species = 0.0059 and water treatment = 0.0112.

Water-use efficiency expressed in terms of cladode mass generally decreased with water stress for *O. ficus-indica* and increased with water stress for *O. robusta* for all months (Figure 6) because of the exceptions that are mentioned afterwards. *O. robusta*, therefore, used water more efficiently with water stress than *O. ficus-indica*. The WUE between water treatments for *O. ficus-indica* differed not significantly (P>0.05) only for the third month. During this month the WUE for T_1 was significantly (P<0.01) higher than that of the other water treatments. In contrast, for *O. robusta* the WUE between water treatments was not significantly (P>0.05) different during both the second and third months. Within a water treatment, the WUE differs not significantly (P>0.05) for both species during the last two months (Figure 6). The water application has, therefore, a greater influence on WUE than the growth stage of the plant. The WUE presented in Figure 6 also included the increase in mass of the mother cladode over time. These values did not differ significantly (P>0.05) when the mother cladodes mass increase was not included (data not shown). According to Han and Felker (1997), who worked on three- and four-year-old *Opuntia ellisiana* plants, the cactus pear is among the greatest water-use efficient of any plant species (including C_3 and C_4) that has been measured under long-term field conditions. Various other researchers (Felker and Russell, 1988; Le Houérou, 1994; Nobel, 1988, 1995; De Kock, 2001; Guevara and Estevez, 2001) also have shown that the conversion efficiency of water to dry matter from matured plantations to be, in general, greater for *Opuntias* than either C_3 or C_4 plants. Unfortunately, there is a lack of WUE results from one-year-old plants.

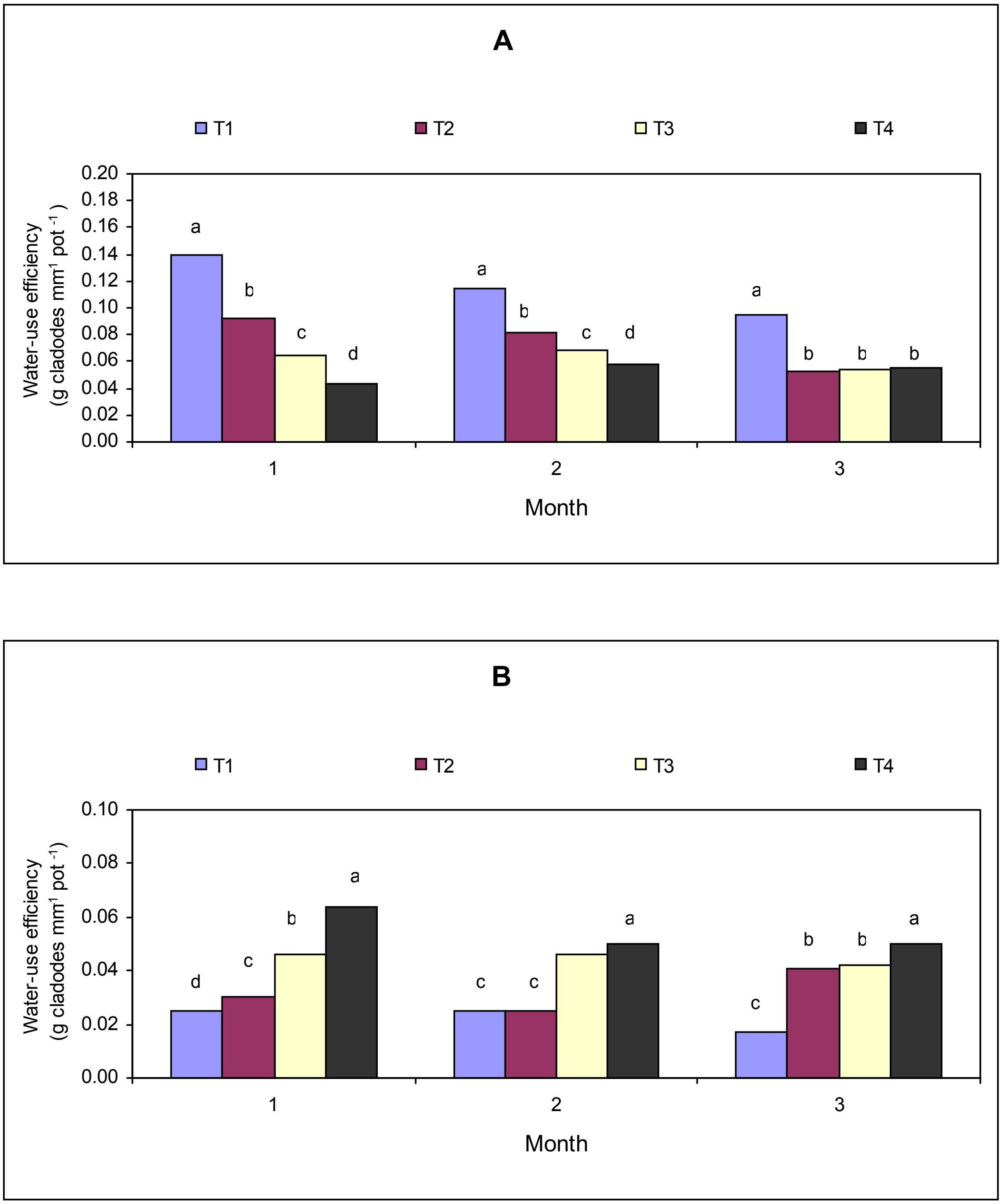


Figure 6. Water-use efficiency (g cladodes mm^{-1} pot^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly ($P<0.01$). $LSD_{0.01}$: species = 0.0083 and water treatment = 0.0056.

Amount of Water to Fill the Cladode

The cladodes of T_4 showed signs of water stress throughout the three-month trial period, although not so prominent in *O. robusta* than *O. ficus-indica*. These signs include decreasing firmness of the cladodes more than those of other water treatments. Although not measured, the cladodes of T_4 appeared thinner than that of other water treatments. These visible water stress signs were less prominent in *O. robusta.*

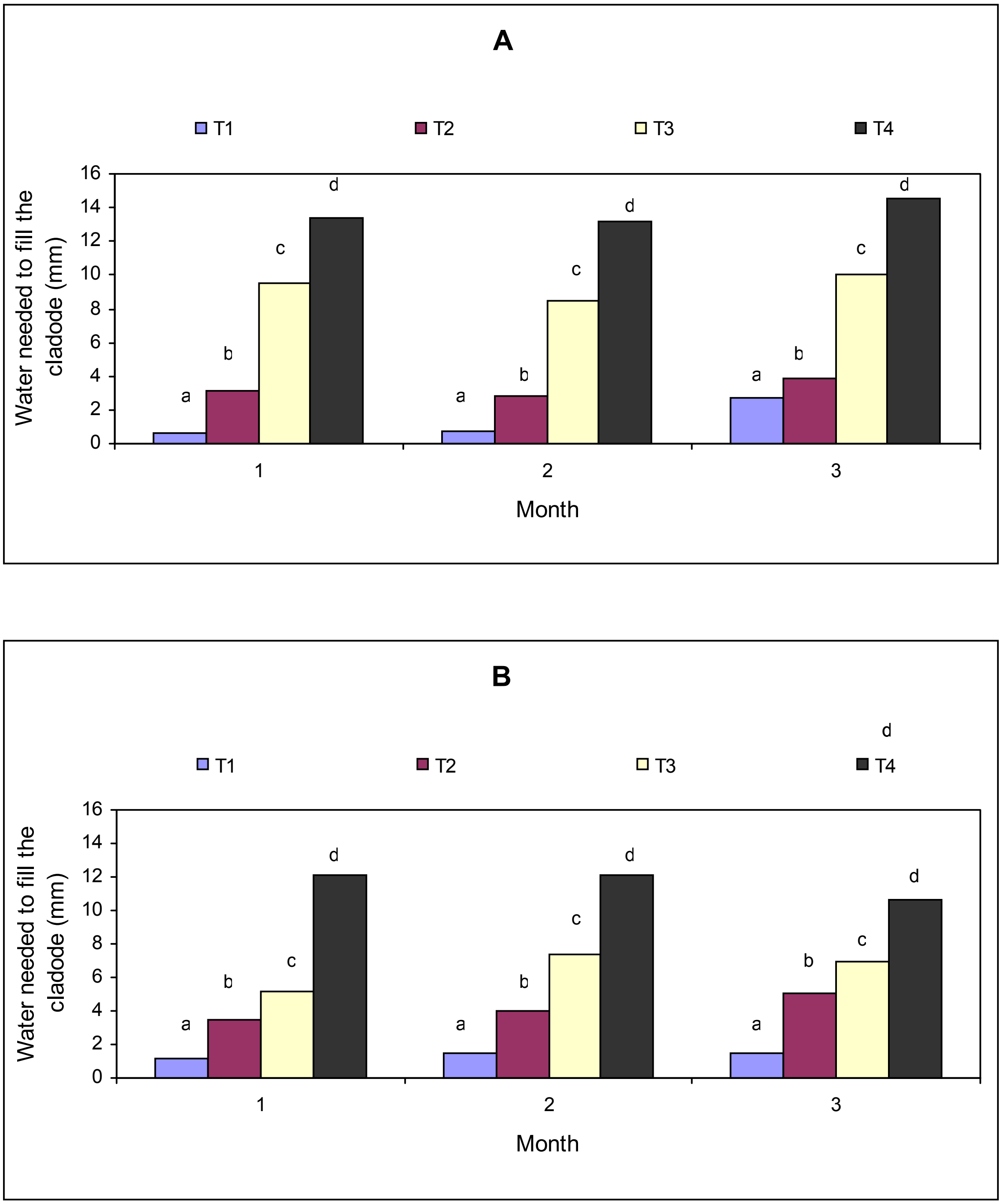
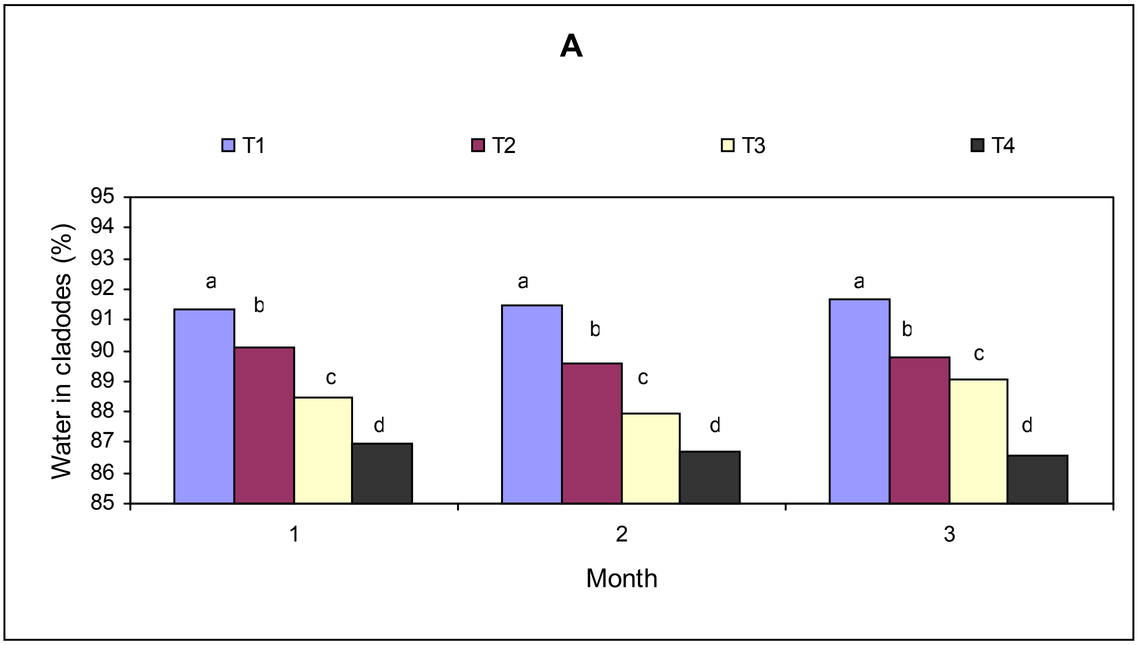


Figure 7. Amount of water (mm) needed to fill up the cladode for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly (P<0.01). $LSD_{0.01}$ species = 0.4133 and water treatment = 0.7751.

The amount of water needed to fill up the cladodes increased ($P \leq 0.05$) with water stress as expected in all the months for both species (Figure 7). Therefore, the higher the plant available water, the less water is needed to fill up the cladode. Both species responded the same ($P > 0.05$) toward the water treatments in each of the three months. The water needed to fill up the cladodes showed a constant trend between the different months for both species. On average over the three months, *O. robusta* needed less water to fill up the cladodes than *O. ficus-indica*, which could be due to the finer root system and smaller cladodes of *O. robusta*. Also interesting is that with increased water stress the cladodes of *O. ficus-indica* needed more water to fill up the cladodes than *O. robusta*. On average over the three months, a water application of only 13.63 mm and 11.64 mm was enough to fill up the cladodes for *O. ficus-indica* and *O. robusta*, respectively, at the lowest water treatment. Han and Felker (1997) reported as much as 17 mm water stored in the cactus cladode after a rain shower.

Percentage of Water in Cladodes

The percentage of water in the cladodes decreased ($P \leq 0.05$) with water stress for *O. ficus-indica* (Figure 8). As expected the more the plant is stressed the less amount of water in the cladodes of *O. ficus-indica.* In contrast, it seems that *O. robusta* retained water more than *O. ficus-indica* during water stress treatments, especially during the last two months. During the third month the water percentage in the cladodes for this species was significantly ($P < 0.01$) higher for the lowest water treatment than that of the other water treatments. *Opuntia robusta* also took longer in reaching the level of the lowest soil-water treatment. Also according to Lopez-Garcia *et al*. (2001), the total amount of water stored in the cactus cladodes depends upon species and varieties.



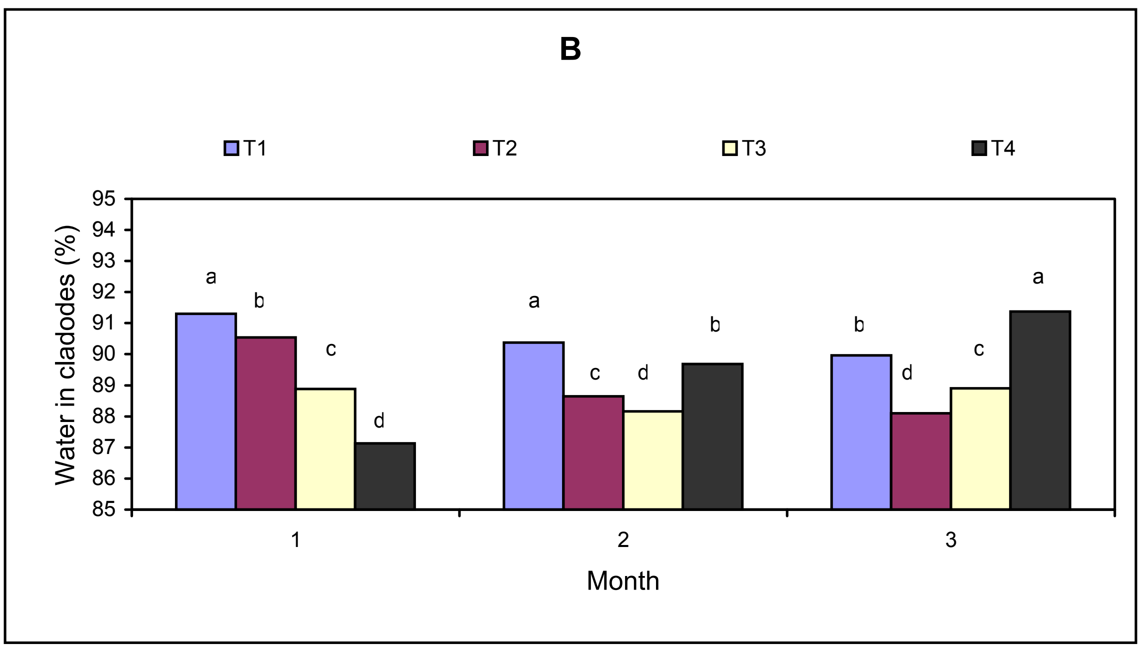


Figure 8. Water (%) in the cladodes for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. Means within a month with different superscripts differ significantly ($P < 0.01$). $LSD_{0.01}$: species = 0.2481 and water treatment = 0.4653.

As the soil dried out, the cladodes were a little bit softer (more noticeable in *O. ficus-indica*) although it was not much as the lowest water percentage for both species was 86.55%. The highest percentage water in the cladodes of *O. ficus-indica* was 92%. This is supported by Lopez-Garcia *et al.* (2001) that the water content in the cladodes, which can range between 70% and 92%, is strongly influenced by environmental conditions. From this it can be concluded that the cactus-pear cladodes hold a lot of water even during drought. According to most researchers, cactus cladodes aged 1 to 3 years are high in water (75% to 85%) in summer and early fall and (85% to 90%) in winter and spring (Monjauze and Le Houérou, 1965; Felker, 1995; Nefzaoui and Ben-Salem, 1996; Ramakatane, 2003). During a drought lasting three months, the chlorenchyma in the stem of *O. ficus-indica* can decrease in thickness by 13%, while the water-storage parenchyma can decrease in thickness by 50%, indicating a greater water loss from the latter tissue (Nobel, 2001).

CONCLUSION

Although research is in progress to obtain a better understanding of the response of spineless cactus pear to different climatic conditions and irrigation in South Africa, there is still a lack of knowledge on the dynamics of the root system of these plants. The results from this study are of the few where the development of the roots under different water applications was quantified. The common opinion that cactus pear needs low inputs to give high yields has been so misconceived that very limited scientific information is available to farmers and the importance of appropriate orchard management has been largely neglected.

Looking at the enormous root dieback taking place with water stress, one can conclude that the root system of cactus pear is not as stable as one would expect but is perhaps more adaptable to different environmental conditions. The decrease in root mass and length for both species with water stress showed the drastic impact of water stress on the root dieback. It was also clear that more tap root dieback took place with soil drying than side roots and also an increase in side-root development with water stress. These cactus-pear root characteristics make it a valuable crop in improving the productivity in arid and semiarid regions of the world. The root system of cactus pear is very complex and may exhibit different kinds of roots. As a multifunctional crop (fruit and fodder) it can be of great value in both developed and underdeveloped countries. In South Africa the full potential of cactus pear has not been realised yet.

The cactus pears' various water-conserving strategies lead to a need for a small root system. Indeed, according to these results, roots compose only about 11% and 12% of the total plant biomass for *O. ficus-indica* and *O. robusta*, respectively. As one would expect, there was clearly a greater increase in root mass over time than cladode mass. Root length is a better indication of root distribution and absorbing activity than root mass; therefore, these results are valuable in future management planning. In the past, most root studies on *Opuntias* only included root-mass measurements and, therefore, fewer root-length indications are available under different environmental conditions.

Although *O. ficus-indica* may have a higher WUE, it could be slightly less tolerant to drought, in contrast to *O. robusta*. The finer root system (more side roots) of the last-mentioned species and less root dieback, make it more adaptable to drier conditions. It is well-known that side roots can take up soil water at lower levels than tap roots. The species *O. robusta* also took longer to reach the lowest water treatment and did not show such noticeable signs of stress as *O. ficus-indica* does. *Opuntia robusta* needed less water to fill up the cladodes after a period of water stress. It was also interesting that *O. robusta* retained more water in the cladodes during a water-stress period than *O. ficus-indica*. It is clear that cactus pear cladodes hold a lot of water even during low soil-water contents. Unfortunately, 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.

In this study, only visual observations were made of the water stress levels of the cactus pear. The softer or firmer feeling of the cladodes with water stress, as well as the visual observation of its thickness, although not significantly correct, gave at least a good indication of when the plant is in a critical stage. In the future, more in-depth studies have to be done on identification criteria for water-stress indications in cactus pear.

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