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ARTICLE *in* JOURNAL OF ARID ENVIRONMENTS · JUNE 2006

Impact Factor: 1.64 · DOI: 10.1016/j.jaridenv.2005.10.004

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ELSEVIER
Journal of Arid Environments 65 (2006) 529–542
Journal of Arid Environments
www.elsevier.com/locate/jnlabr/yjare

A greenhouse study on root dynamics of cactus pears, *Opuntia ficus-indica* and *O. robusta*

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Received 9 February 2005; received in revised form 29 July 2005; accepted 4 October 2005

Abstract

Over the last 10 years a great interest in spineless cactus pear was shown in the drier areas in terms of both fresh fruit and fodder production. However, there is a lack of knowledge on quantitative data on root dynamics of these plants needed to fully understand its potential under water limiting conditions. This study aimed at quantifying the effects of water stress on the growth of tap roots, side roots and rain roots of the species *Opuntia ficus-indica* (L.) Miller (cultivar Morado—green cladode) and *O. robusta* Wendl. (cultivar Monterey—blue cladode). One-year-old cladodes were planted in root boxes and pots (2002/2003 season) that were kept in the greenhouse at day/night temperatures of 25–30 °C/15–18 °C. Placing the cladodes flat on the soil, more areoles came in contact with the soil and therefore more roots developed in both species with an average of only 3.4% areole complexes not rooting. Each areole complex formed on average 3 roots. The highest daily tap root growth was 42 and 36 mm for *O. ficus-indica* and *O. robusta*, respectively. Tap root growth increased in the morning with water stress for both species but decreased in the afternoon. Side root growth increased with water stress, with that of *O. robusta* more per tap root than *O. ficus-indi*ca. *O. robusta* showed a finer root system than *O. ficus-indica*. The side roots grew as much as 8 and 5 mm per day for *O. ficus-indica* and *O. robusta*, respectively. Whitish rain roots developed on the established roots within the first hour after rewetting the soil and grew for only 3 days. Rain roots grew up to 7 and 5 mm within a day for *O. ficus-indica* and *O. robusta,* respectively. Considering all studied aspects of their roots systems, *O. robusta* appears to be better adapted to drought (less sensitive to water stress) than *O. ficus-indica*.

Keywords: Areoles; Cactus pear; Rain roots; Root boxes; Root length; Side roots; Tap roots; Water stress

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doi:10.1016/j.jaridenv.2005.10.004

1. Introduction

Various species of *Opuntia* provide an important source of fodder especially in arid and semi-arid environments. The fruits of the plant are also useful to humans (Snyman, 2004). Species of *Opuntia* (cactus pear) grow in all parts of the American continent, from Canada to Patagonia and in the course of time have been cultivated in different areas of Europe, particularly in the Mediterranean countries, as well as in Africa and Australia (Le Houérou, 1994, 1996; Lahsasni et al., 2004). Due to its ability to adapt to different environmental conditions (Silva and Acevedo, 1985), the cactus pear grows in plains, coastal regions, plateaus and among diverse vegetation (Lahsasni et al., 2003). This plant exhibits crassulacean acid metabolism (CAM), is able to withstand drought (Nobel, 1995, pp. 36–48; Felker et al., 1997) and extreme heat (Sudzuki, 1995, pp. 28–34) and is highly efficient in the use of water (Nobel, 1995; Han and Felker, 1997; De Kock, 2001, pp. 101–105; Reynolds and Arias, 2001, pp. 1–4; Snyman, 2004, 2005). CAM plants are commonly considered as drought avoid, because they store considerable amounts of water in their shoots as well as fix CO_2 at night, thereby reducing transpiration as air temperatures, and hence the force for water loss, are lower at knight than during the daytime (Nobel, 1994, 1995).

The root systems of desert plants can be subjected to prolonged droughts that are interrupted by sporadic and often light rainfall (Nobel and Huang, 1992). The root distribution of cactus pear may also depend on the type of soil and cultural management (Snyman, 2005). Under favourable soil conditions a tap root develops, penetrating nearly 300 mm into the soil, while under drought conditions, like those experienced in arid and semi-arid regions, fleshy side roots develop from the tap roots to take up soil water at lower levels (Sudzuki, 1995). In contrast with the shoot (cladode) system, the roots of Cactaceae have received little attention (Nobel, 1995, 2001, pp. 13–19; Snyman, 2004). The root system differs from that of other plants as they develop xeromorphic characteristics which enable the plant to survive prolonged periods of drought (Sudzuki, 1995). Roots can, according to Sudzuki (1995), contribute to drought tolerance in 3 ways, namely: (1) by restricting the root surface and decreasing their permeability to water; (2) by rapidly absorbing the small quantity of water supplied by light rains via "rain roots", which develop within a few hours after a shower and disappear as soon as the soil dries up, or via a reduction in the root surface from which water flows off; (3) by decreasing shoot transpiration due to high root negative potential. On the basis of the above, these drought-resistant water savers may have high hydraulic resistance (Passioura, 1988), which would in turn decrease water flow to the cladodes. The root system of cactus pear is very complex (Sudzuki, 1995; Snyman, 2004, 2005).

Studies on adaptations to drought under field conditions are scarce in the native habitats of *Opuntias* (Pimienta-Barrios et al., 2002). Various responses of specific *Opuntia ficus-indica* to the environment and literature on its physiology has become quite rich in the last decades, a sign of the increasing economical importance (fruit and fodder) of the crop (Pimienta-Barrios et al., 1993; Inglese et al., 1995; Fabbri et al., 1996; Le Houérou, 1996; Nobel, 1997; Mizrahi et al., 1997; Felker and Inglese, 2003; Galizzi et al., 2004; Felker et al., 2005). It was hypothesized that the fact that *Opuntia's* grow and survive in infertile and shallow soils, with a highly efficient water use, reflect a unique root adaptation strategy. Sound knowledge of the root dynamics of *Opuntia* under different soil-water conditions is important in understanding the adaptations of the plant to be implemented in management practices for both fruit and fodder production. This study therefore contributes to the understanding and quantification of the different root types of *O. ficus-indica* (both fruit and fodder production) and *O. robusta* (fodder production) in relation to soil-water content.

2. Materials and methods

2.1. Experimental conditions

The research was conducted during the 2002/2003 growing season (September 2002–March 2003) in greenhouse. Greenhouse temperatures were regulated between 25 and 30 °C during the day and 15–18 °C during the night over the trial period. According to Nobel (2001) the ideal day/night temperatures for *Opuntias* is 25 °C/15 °C.

2.2. Cultivation of Opuntia cladodes

One-year-old cladodes of *O. ficus-indica* (L.) Miller (cultivar Morado)—(green cladode) and *O. robusta* Wendl. (cultivar Monterey)—(blue cladode) 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±55 mm wide, 20±3 mm thick and 1406±170 g fresh mass (means±SE, $n = 10$). Cladodes of *O. robusta* were 261±46 mm long, 244±15 mm wide, 15±2 mm thick and 1354±130 g fresh mass (means±SE, $n = 10$). The cladodes were dried for 4 weeks in the shade to allow healing of the cutting area.

2.3. Root development from the areoles

The cladodes of both species (*O. ficus-indica* and *O. robusta*) were planted in 12 asbestos pots (100 × 100 mm and 200 mm deep filled with soil). Five plants were randomly planted in each pot. The clay, silt and sand content of the soil were 14%, 2% and 84%, respectively, with pH (KCI) 4.5 and EC_s 21 m S m^{-1}. The exchangeable Ca, Mg, K and Na content of the soil were, respectively 468, 235, 148 and 42 mg kg^{-1}. The extractable N and P contents were 54 and 7 mg kg^{-1}, respectively. The bulk density of the soil was 1260 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 millimeters crushed stone covered the bottom of each pot. The pots have 3 holes of 7 mm diameter at the bottom to ensure free water movement through the pot. The soil was kept between field water capacity (FWC) and permanent wilting point (PWP) over the 3 weeks study period. The cladodes were planted in 3 ways to determine the percentage root development from the areoles, which included the whole cladode flat on the soil, placed vertically (50–60 mm deep) and the last one was placed horizontally (20 mm deep) into the soil. Thirty cladodes of each species were used (10 for each treatment) and were measured over a 3-week period.

2.4. Rain-root growth in pots

Cladodes of both species were planted in 38 asbestos pots of 210 mm diameter and 550 mm deep and were filled with the same amount of dry, fine, sandy, loam soil after which each was weighed. The cladodes were planted upright with one quarter of *O. robusta* (50–60 mm) and *O. ficus-indica* (100–120 mm) of the cladode in the soil. Each cladode was weighed before planting. The cladodes were placed North/South in the greenhouse and planted in September 2002. The same soil, crushed stone and pot preparation as described was used to fill these pots.

Four water treatments namely, $T1 = 0-25\%$ depletion of plant available soil water (PAW), $T2 = 25-50\%$ depletion of PAW, $T3 = 50-75\%$ depletion of PAW and $T4 = 75-100\%$ depletion of PAW, were applied. In determining the soil water depletion intervals, 5 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 PWP of the soil. In determining FWC the pots were then saturated with water and left for 48 h before weighing 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}. Weighing of the planted pots therefore 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 5 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. After growing the cladodes for 8 weeks in the pots at water treatment T1 (0–25% depletion of plant available water (PAW), it was stressed up to T4 (75–100% depletion of PAW) and kept there for 2 weeks. All the pots were then filled with water up to T1 after which 2 pots per species (randomly selected) were first washed each hour, then every second hour and lastly daily to determine the rain roots.

2.5. *Root development in root boxes*

The cladodes were planted the same depths (one quarter) into the soil as described for the pots, in each of 12 root boxes. The root boxes were 650 mm long, 100 mm wide and 900 mm deep. The boxes were placed at a 15% angle so that the roots growing down could easily be seen through the glass side of the box, covered by a steel plate that could be removed for measuring root growth. The root lengths were marked on the glass after which they were accurately measured with a vanier caliper.

Half of the boxes were planted with each species on 4 September 2002 and faced north/south. The boxes were filled with the same dry soil as described for the rain roots and areoles in the pots. The total PAW was 11.00 l per root box or 169.23 mm water per box.

After planting the cladodes in the dry soil, they were watered to FWC or to the total PAW level as described above, after which no additional water was added over a 2-month period. The first tap and side root measurements were taken a month after watering. As the plants became stressed and the soil reached the lower point of PAW at the end of the 2 months, this monitoring period can be taken as soil-water uptake over a water stress gradient or a drying cycle.

When the lower point of PAW was reached, the cladodes grew softer and less firm, the same characteristic shown in water treatment T4 (75–100% depletion of PAW) in the pots. According to these observations one can be sure of a definite soil-water gradient over the last month when measurements took place. The cladodes of *O. robusta* took longer reaching this point than *O. ficus-indica*. After 2 months with the soil at a low point of PAW or near PWP, it was again filled up to a total PAW level. This was done to measure the recovery of the plants and especially the rain root development.

2.6. Data collection

The number of areoles from where roots developed was counted for the different treatments after 3 weeks of planting. After washing each pot the rain root lengths were measured with a caliper. Over the first 6 h it was done hourly but after that every second hour up to 12 h. During the next 12 h pots were washed only every third hour. The rain roots were therefore intensively measured over a 24-h period and thereafter only daily for the next 3 days. The rain root length per species was measured each time. The thickness of the roots was also measured at the top and where the roots die back due to water stress, with a caliper. Twenty roots randomly selected within each pot were measured.

The length of the different root types namely tap roots and side roots were measured hourly and daily in the root boxes over a period of one month. Three tap roots per cladode or root box were measured and also 3 side roots on each of the tap roots. The rate of tap root growth was observed daily as well as hourly, which included day and night. The measurements of tap and side roots took place over a soil-water gradient. The rain root lengths were measured after lifting the water stress. Three rain roots on each of the 3 main roots were measured daily for each species.

2.7. Statistical analysis

The experimental layout of the root boxes was a 2 (*Opuntia* species) × 3 (time of the day) × 4 (number of days since watering) factorial experiment with 6 replications for each species. The aerial root layout was a 2×3 (2 *Opuntia* species and 3 planting methods) factorial experiment with fully randomized design. There were 10 replications for each planting method. The experimental layout for the rain roots in the pots was also a fully randomized design consisting of 2 treatments (*Opuntia* species) and 2 replications.

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 length and areole number. Tukey's test was used to find determine the difference (Mendenhall and Sincich, 1996). In determining least significant difference (LSD), the method of Fisher (1949) was used.

3. Results

3.1. Root development from the areoles

When placing the cladode flat on the soil, more areoles came in contact with the soil and therefore more roots developed in both species (Table 1) with an average of only 3.4% areole complexes not rooting. The number of areoles in contact with the soil differed ($P\leqslant 0.05$) with species when placing the cladode flat and 20 mm in the soil (horizontally) due to their different shapes and sizes. When planting the cladodes 50–100 mm in the soil (vertically) both species had an average (±S.E.) of 11.13 ± 1.11 areole complexes in contact

Table 1
Average number of areoles (cladode^{-1}) where roots developed under different ways of planting for the two *Opuntia* species

Species	Planting method		
	Flat	50–60 mm deep (vertically)	20 mm deep (horizontally)
O. ficus-indica	43.7 (3.0) ± 3.32	11.4 (5.3) ± 1.06	18.0 (10.0) ± 1.22
O. robusta	31.6 (4.1) ± 3.15	10.8 (3.7) ± 1.11	14.4 (8.3) ± 2.14
LSD	5.4986	1.1292	1.3723

Numbers in brackets are percentage of areoles where roots did not develop.Data are means and S.E. of 10 areoles. Least significant difference (LSD) is calculated at 1% level.

with the soil, with mostly all rooted (Table 1). In both species, most areoles in contact with the soil formed roots after 3 weeks regardless of the planting method. First roots developed 3 days after planting. Each areole complex formed an average of three roots. Roots developed from areole complexes first on the lower side of the cladode and later at the top for both species.

3.2. Tap root growth (day and night)

Although not physically measured, the root system in general for *O. robusta* showed a finer structure visually than that of *O. ficus-indica* with its thicker occurrence. The tap root measurements taken hourly during both day and night are presented in Fig. 1 for the two *Opuntia* species a month after watering and a water stress gradient noted. This water stress gradient was followed over a 22-day period and the average daily growth was presented in Fig. 1 for every seventh day. As most of the tap roots grew horizontally (0–300 mm depth), it was difficult to follow root growth after 22 days because most marked (measured) roots reached the sides of the root boxes.

Root length increased during the morning with increasing water stress for both species (Fig. 1). The opposite happened during the afternoon when root length decreased with water stress for both species. At night both species showed an increase in root growth with water stress. The highest average (±S.E.) rate of daily tap root growth for *O. ficus-indica* and *O. robusta* was 42 ± 2.1 and 36 ± 2.1 mm, respectively. Regardless of water stress both species attained a relatively high daily tap root growth.

3.3. Number of side roots per tap root

When the first side root development was noted through the glass cover in the root boxes, the side root per tap root measurements started. These observations started a month after planting and were measured over a soil-water stress gradient for 2 weeks, after which it became difficult to distinguish between the massive root developments over the 0–300 mm depth. As water stress increased the side roots increased more and more, which made them difficult to identify. The side roots per tap root are presented for both species in Fig. 2, as measured over a 2-week period. Only the measurements for every fourth day are presented in Fig. 2.

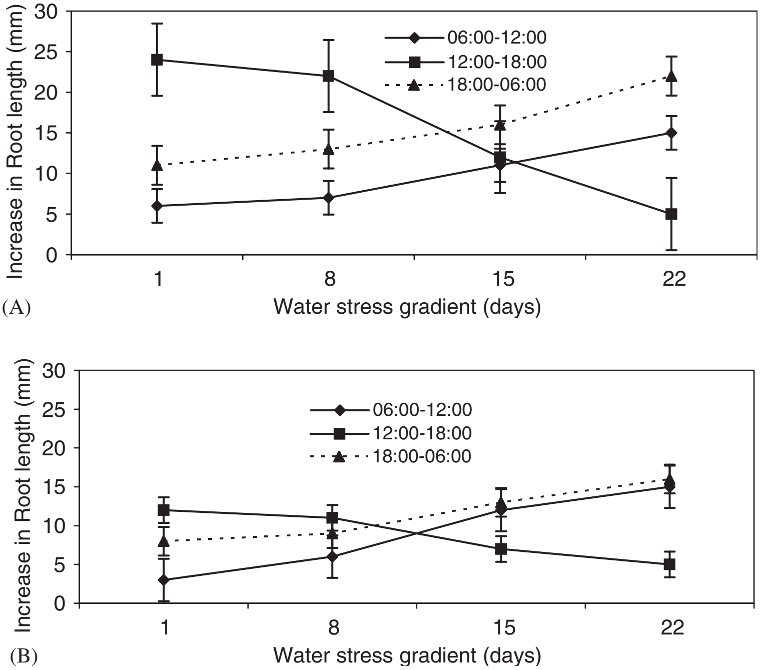

Fig. 1. Daily tap root growth (mm) during both day and night times for *O. ficus-indica* (A) and *O. robusta* (B) measured over a soil-water gradient at 7-day intervals. $LSD_{0.01}$ days (A): 1 = 3.16, 8 = 3.22, 15 = 3.21 and 8 = 3.44. (B): 1 = 2.14, 8 = 1.66, 15 = 1.78 and 18 = 2.21.Vertical bars are standard errors of means.

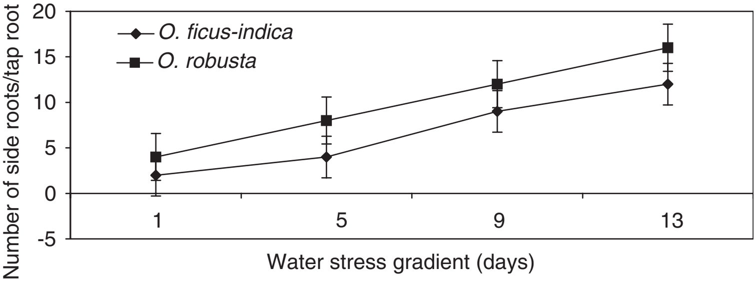

Fig. 2. Number of side roots per tap root for *Opuntia ficus-indica* and *O. robusta* measured over a soil-water gradient or drying cycle with four intervals. $LSD_{0.01}$: species = 0.967. Vertical bars are standard errors of means.

O. robusta has got more (4.61 ± 0.51, $P \leqslant 0.05$) side roots for each tap root than *O. ficus-indica* (2.21 ± 0.41), which explains the finer root system of this species. For both species side roots per tap root increased with water stress.

3.4. Side root growth

The daily side root growth over a soil-water stress gradient or drying cycle is presented in Fig. 3. Side root length increased rapidly in both species over time and therefore with

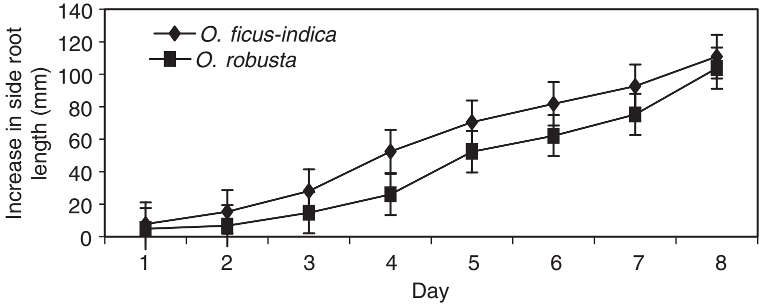

Fig. 3. Cumulative average side root length (mm) after lifting water stress for the two *Opuntia* species measured over an 8-day period ($n = 54$). $\mathrm{LSD}_{0.01}$ species = 0.0337. Vertical bars are standard errors of means.

water stress. The side root length was higher ($P \leqslant 0.05$) in *O. ficus-indica* than *O. robusta*. After a day of restoring FWC the side roots grew as much as 8.24±0.53 and 5.11±0.41 mm per day for *O. ficus-indica* and *O. robusta*, respectively. Up to day 5 the fastest growth took place for both species. The finer root system of *O. robusta* could be the reason for the shorter side root length as compared to that of *O. ficus-indica*.

3.5. Rain root development per day

Before watering the plants in the root boxes again, when reaching the lowest point of the soil-water gradient, the cladodes were softer, but the next day they were filled with water and became firm again. The finer root system of *O. robusta* compared to that of *O. ficus-indica* was again visually noted when washing out the pots. The rain roots grew up to 7.11±0.41 and 5.22±0.32 mm within a day for *O. ficus-indica* and *O. robusta*, respectively (Fig. 4), when water stress was lifted. The rain root length increased ($P \leqslant 0.05$) rapidly from the first day to the third day for both species. After 3 days the length of the rain roots remained constant for both species and with no further growth. The species *O. robusta*'s rain roots developed significantly ($P < 0.05$) slower than that of *O. ficus-indica*.

After 6 days the rain roots lost their typical characteristic whitish colour, but are still easy to identify. After a few weeks of the lifting of water stress the rain roots could hardly be identified. New rain roots developed after the lifting of a next water stress period.

One could argue that due to the fact that *O. robusta* has a finer root system, the rain roots must also be smaller. Unfortunately the thickness of the rain roots could not be measured. After 6 days the soil was again brought to FWC to check whether the rain roots stopped growing or not due to water stress. Therefore, there is no doubt that rain roots grow only over a 3-day period after water stress lifting.

3.6. Rain root growth per hour

The rain roots started growing within the first 2 h after rewetting the soil in the pots in both species (Fig. 5). After 24 h, the average (±S.E.) rain root length of *O. ficus-indica* was 6.11±0.41 and 4.51±0.31 mm for *O. robusta*. The shorter rain roots of *O. robusta* compared to that of *O. ficus-indica* can be attributed to the finer type of root system of *O. robusta. O. ficus-indica* showed rapid rain root growth over the first 9 h and then slower

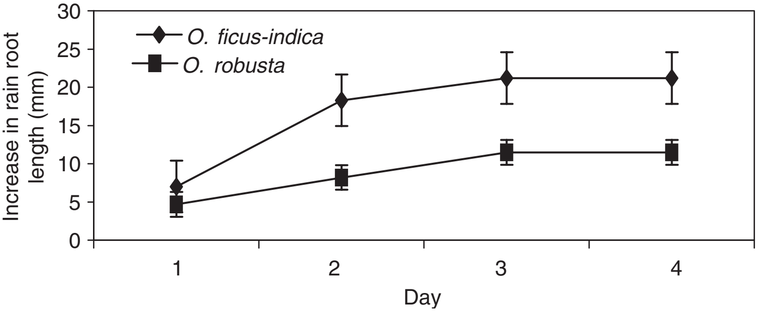

Fig. 4. Cumulative average rain root length (mm) after lifting water stress for the *Opuntia* species ($n = 54$). $LSD_{0.01}$ species = 3.3398. Vertical bars are standard errors of means. Vertical bars are standard errors of means.

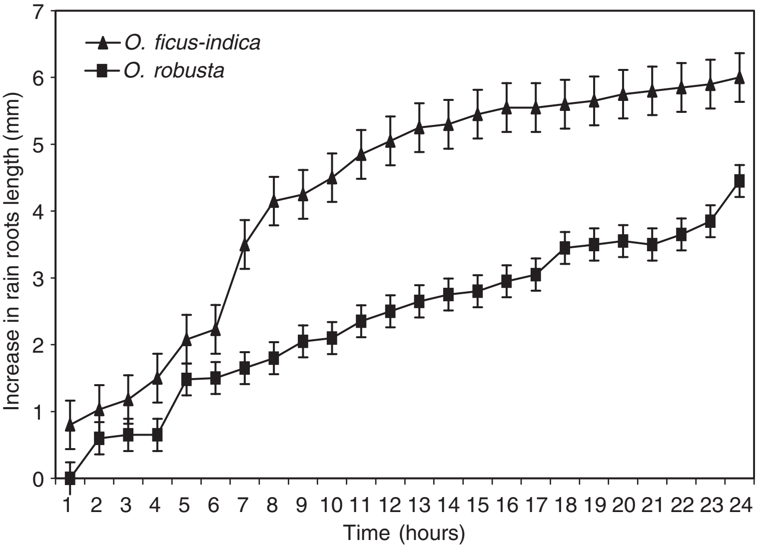

Fig. 5. Cumulative average rain root growth (mm) for two *Opuntia* species in hourly intervals measured over a day ($n = 20$); $LSD_{0.01}$: species = 1.3352. Vertical bars are standard errors of means.

growth, while the growth for *O. robusta* increased more evenly. Smoother curves could be obtained with more roots measured. The average (±S.E.) rain root length 2 and 3 days after lifting water stress was 18.12±2.14 and 21.22±2.66 mm, respectively for *O. ficus-indica*. For *O. robusta* the rain root length 2 and 3 days after lifting water stress was 8.12±0.42 and 12.22±0.51 mm, respectively. These end values for both species are more or less the same as that described in Fig. 4. No further rain root growth took place 4 days after stress lifting for both species.

The major die back of the tap roots due to water stress is conspicuous when pots were washed. The thickness at the end of the tap roots where die back took place was as much as 0.4 and 0.9 mm for *O. robusta* and *O. ficus-indica*, respectively. The average thickness of the tap roots at the top was 1.3 mm for *O. robusta* and 2.2 mm for *O. ficus-indica*.

4. Discussion

The axillary's buds in cactus are represented by oval areoles, 2 mm below the skin surface, which function like meristemic buds (Buxbaum, 1950). Under appropriate environmental conditions, new cladodes, flowers or roots will arise from the meristematical tissue of the areoles (Sudzuki, 1995). In *O. ficus-indica*, the areoles are distributed in a helical way, and according to Sudzuki (1995) they develop spines rather than leaves, as most plants do. In general in this study most areoles in contact with the soil formed roots in both species after 3 weeks, regardless of planting method (Table 1). Due to the different shapes and sizes of the cladodes of the two species, *O. ficus-indica* had more areoles in contact with the soil than *O. robusta*, regardless the way of planting. First roots developed 3 days after planting which agreed with the findings of Sudzuki (1995). The role of season and methods of planting could also affect productivity. According to Singh and Singh (2003), the upright planting of full-size cladodes of *O. ficus-indica* (12-months-old, 8–150 mm width) significantly influenced the relative growth rate and dry weight. Higher cladode yield was also recorded from planting 12-month-old cladodes as compared to 6-month-old cladodes (Singh and Singh, 2003).

Most researchers argue that root distribution of cactus pear may depend on the type of soil and cultivation management. In this study it was clear that under favourable soil conditions a tap root developed, penetrating nearly 300 mm into the soil and grew as much as 42 and 36 mm per day for *O. ficus-indica* and *O. robusta*, respectively. This daily growth is in agreement with the findings of Nobel and Huang (1992) of 5 mm growth after 6 h for two desert succulents. It was also clear from the study that tap root length increased in the morning (06:00–12:00 h) with water stress for both species (Fig. 1). The reason for this increase could be the building up of reserves during the night and use of them in the morning. Pimienta-Barrios et al. (2002) and Nobel and De la Barrea (2002) also reported the highest rates of net CO_2 uptake by *O. robusta* during water stress periods towards the end of the night. The opposite happened during the afternoon in this study when root length decreased with water stress for both species. At night both species showed an increase in root growth with water stress. Regardless the time of the day and water stress, the tap root growth of *O. ficus-indica* was higher ($P \leqslant 0.01$) than that of *O. robusta*. Research done on *O. ficus-indica* also showed that it can tolerate prolonged drought by extending carbon gain during periods of low soil water availability, as stem succulence acts as an important buffer to main turgescence in the photosynthetic tissue (Nobel, 1995; Pimienta-Barrios et al., 2000) A root-soil air gap that develops as the roots of *O. ficus-indica* shrink in response to drying conditions also could help retard water loss to the soil in the initial phases of drought, with cellular changes affecting the root hydraulic conductivity playing a secondary role and decreases in soil hydraulic conductivity becoming dominant after a few weeks of draught (Nobel, 1997).

This study showed that under drought conditions, like those experienced in arid and semi-arid regions, fleshy side roots developed from the tap roots to take up soil water at lower levels. A bulk mass of absorbent roots found in the first few millimeters with a maximum depth of 300 mm. Side roots per tap root also increased with water stress, which grew as much as 8 and 5 mm for *O. ficus-indica* and *O. robusta* respectively after water stress lifting. Also according to Szarek et al. (1973) and Nobel (1977) existing roots of cacti quickly respond to rewetting and permitting water uptake. The higher amount and shorter side roots for each tap root experienced in *O. robusta* than *O. ficus-indica*, could be explained by the finer root system of first mentioned species (Snyman, 2004). Vesicular arbascular mycorphizal fungi which are associated with the roots of *O. robusta* (Barcikowski and Nobel, 1984; Pimienta-Barrios and Nobel, 1998), can improve the water uptake in environments where water availability is the main environmental factor limiting productivity. Therefore, its various water-conserving strategies lead to a need for a small root system where roots compose only about 12% of the total plant biomass for *O. robusta* (Snyman, 2004).

The side roots per tap root increased with water stress for both species, which is supported by Sudzuki (1995) who stated that in drier areas or with water stress, side roots developed from the tap roots take up soil-water at lower levels. According to Huang and Nobel (1993) lateral root branching from tap roots could account for about 70% of the total length of *Opuntia*'s roots 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). Nobel (1997) found that a root-soil air gap, that develops as the roots of *O. ficus-indica* shrinks in response to drying conditions, helps retard water loss to the soil in the initial phases of drought, with cellular changes affecting the root hydraulic conductivity playing a secondary role and decreases in soil hydraulic conductivity, becoming dominant after a few weeks of drought. Regardless water stress, the side root length in this study was higher in *O. ficus-indica* than *O. robusta*.

One of the most important adaptations of cactus pear to drought tolerance is the development of whitish rain roots on their established roots, which develop within the first hour after rewetting the soil (Fig. 5), and disappear as soon as the soil dries up again (Sudzuki, 1995). The same tendency is described by Sudzuki (1995) and Nobel (1991, pp. 839–866) that rain roots are formed within a few hours after rewetting as the lateral buds rapidly respond to soil water. Rain roots, whose periodic shedding can represent a large loss of carbon (Smucker, 1984, pp. 27–48), have higher respiratory rates and higher hydraulic conductivities than do established roots (Caldwell, 1979; Hunt and Nobel, 1987). After 3 days the length of the rain roots remained constant for both species. The daily and hourly rain root development of *O. ficus-indica* was higher ($P \leqslant 0.01$) than that of *O. robusta*. Interestingly, despite the quick rain root development, over 90% of the water taken up during the first 24 h after rewetting the dry plants, took place through existing, established roots that became dehydrated (Nobel, 1991). Until 4 days after the soil had been rewet, the rain roots with their relatively high hydraulic conductivities, made a contribution equal to that of the dehydrated established roots (Nobel, 1991). Therefore, according to Nobel (1991) the qualitative explanation that rain roots lead to the observed water uptake by desert succulents immediately after rainfall must be replaced by a quantitative assessment of contribution of both established and rain roots, which indicates that over 75% of the water taken up by cacti for the first 4 days, after rainfall interrupts a drought, is by the established roots.

5. Conclusions

The response of root formation was evaluated in one of the most important domesticated varieties of *Opuntias* (*O. ficus-indica*) that regularly thrives in deep alluvial soils, and one of the most important wild species (*O. robusta*) that grows in infertile and shallow soils. It was clear from this study that regardless of planting method, *O. ficus-indica* had more areoles in contact with the soil than *O. robusta*. Also, differences in root development from the areoles can be attributed to the different shapes and sizes of the cladodes of the two *Opuntia* species. Although the tap roots which develop from the areoles, can grow as much as 42 and 36 mm per day for *O. ficus-indica* and *O. robusta*, respectively, the average thickness at the end of the tap roots, for example where die-back took place due to water stress, was up to 0.9 and 0.4 mm, respectively, supporting the adaptability of their unique root system. While the average daily tap root growth of *O. robusta* was lower than that of *O. ficus-indica*, it seems that the finer root system, the larger number of side roots per tap root (which can take up soil-water at lower levels) and the mycrophizal fungi associated roots of *O. robusta*, would make this species less sensitive to water stress than *O. ficus-indica*.

The extensive and dense roots near the soil surface, as well as the rapid absorption of small quantities of water by the rain roots, which grew for only 3 days up to 7 and 5 mm/day were found for *O. ficus-indica* and *O. robusta*, respectively. The rain roots of *O. ficus-indica*, for example, can grow as much as 1 mm within the first hour of rewetting the soil. The cactus pear, one of the few arid-adapted crops that can be used both as human food and cattle feed, has therefore great potential to improve productivity in arid and semi-arid regions, since its root system can utilize drier areas to its full potential and provide feed for livestock when it may be urgently required.

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