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Root distribution with changes in distance and depth of two-year-old cactus pears *Opuntia ficus-indica* and *O. robusta* plants

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Abstract

Opuntia is a drought tolerant crop and even the smallest amount of water is absorbed efficiently through the shallow and horizontally spread root system. However, there is a lack of knowledge on the root dynamics of cactus pear for sustainable production of fodder and fruit in the drier areas. This study, conducted during the 2003/2004 growing season on two-year-old *Opuntia ficus-indica* (L.) Miller (cultivar Morado–green cladode) and *O. robusta* Wendel. (cultivar Monterey–blue cladode) plants in the field was therefore aimed at quantifying root distribution with distance and depth from the stem. Root growth was expressed in terms of both mass and length, and water-use efficiency (WUE) was defined as the cladode dry mass production per unit of evapotranspiration. In both species most roots were concentrated in the first 150 mm soil layer. After only two growing seasons the roots spread as far as 2.5 m from the stem for both species. The total root dry weight production calculated per plant up to a depth of 1200 mm, was 239 and 316 g per plant or kg ha⁻¹ for *O. ficus-indica* and *O. robusta* respectively. The thickest roots developed directly from the planted cladode and were 9.1 mm thick for *O. ficus-indica* and 6.3 mm for *O. robusta*. *Opuntia robusta* showed a finer root system than that of *O. ficus-indica*. After two growing seasons 3407 and 2702 kg ha⁻¹ aboveground dry mass was produced by *O. ficus-indica* and *O. robusta* respectively. The WUE of *O. ficus-indica* (6.52 kg ha⁻¹ mm⁻¹) was significantly higher than that of *O. robusta* (5.39 kg ha⁻¹ mm⁻¹). The roots comprised only 11% of the total biomass for *O. robusta* and 7% for *O. ficus-indica*. Such root adaptations of this species are in addition to the classical physiological and structural modifications of CAM plants to tolerate prolonged drought.

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1. Introduction

In both natural and agricultural plant communities, the environment is seldom optimally fit for plant growth. Moreover, plant growth in most natural environments is limited by one or more environmental parameters, such as water and nutrient availability (Chapin III, 1991; Le Houérou et al., 1993; Snyman, 2004a). *Opuntia* is a drought tolerant crop, since even the smallest amount of water it absorbs is used efficiently (Le Houérou, 1996; Felker et al., 1997; Han and Felker, 1997; Snyman, 2003). It is able to do this due to its relatively shallow and horizontally spread root system and the ability to still withdraw water from the soil at a stage when other crops are not able to (Singh and Singh, 2003; Snyman, 2004b). These traits

make it highly promising as a crop for soils poor in nutrients and with limited water supply (Silva and Acevedo, 1985). It can survive in regions with 200 to 300 mm rainfall, which are common in less developed countries (Brutsch, 1988). The specialized photosynthetic system in cacti, known as Crassulacean Acid Metabolism (CAM), provides greater water to dry matter conversion than the C₃ and C₄ photosynthetic pathways (Nobel, 1988; Han and Felker, 1997) and results in great potential for the production of flat stemmed *Opuntias* in arid lands (Mizrahi and Nerd, 1999; Galizzi et al., 2004; Felker et al., 2005).

The cultivation of *Opuntia* species (cactus pear), which requires little or no irrigation, may assume greater agronomic importance in the future, since a large fraction of the land area of southern Africa is destined to become arid or semi-arid due to global warming (Snyman, 2004b). The common opinion that cactus pear needs low inputs to give high yields have been so

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misconceived that very limited scientific information is available to farmers and the importance of appropriate orchard management has been largely neglected (Inglese et al., 1995). Cactus pear is capable of establishing a sustainable production system that will increase the efficiency and economic viability of small and medium sized farms of lower income farmers (Pimienta-Barríos et al., 1993). The complexity of cactus pear species, together with the relevance of their different uses, deserve more attention (Inglese et al., 1995; Felker and Inglese, 2003). The decade of the 1990's has seen a great expansion in national and international cooperative research and development on cactus, including plant physiology and orchard management (Felker and Inglese, 2003).

In order to obtain a clearer picture of the dynamics of the root system development in cactus pear, more intensive research on the root distribution in plantations of different ages and different soil types have to be carried out. Studies on water-use efficiency of CAM plants at plant community level under field conditions over a whole growing season is of great agronomic significance, both in theory and in practice (Han and Felker, 1997). The aim with this study was, therefore, to determine the root distribution pattern of two two-year-old cactus pear species in the field from in situ rooting profiles. Water-use efficiency was also quantified for these two spineless species (*Opuntia ficus-indica* and *O. robusta*) during the 2003/2004 growing season.

2. Materials and methods

2.1. Site description

The research was conducted in Bloemfontein (28°50'S, 26°15'E, altitude 1350 m), in the semi-arid, summer rainfall (annual average 530 mm) region of South Africa. Rain falls almost exclusively during summer (October to April), with an average of 78 rainy days per year. Mean annual temperatures range from 17 °C in July to 33 °C in January. It has 119 average frost days per year (Schulze, 1979).

The soil in which the plants were cultivated is a fine sandy, loam soil of the Bloemdal Form (Roodeplaat family — 3200) (Soil Classification Working Group, 1991). Clay content increases down the profile from 10% in the A horizon (0–300 mm) to 24% in the B1 horizon (300–600 mm) and 42% in the B2 horizon (600–1200). The pH (KCl) was 4.5 over the first 0 to 300 mm layer. Bulk densities of the soil after cultivation were 1260 kg m⁻³ for the A horizon, 1563 kg m⁻³ for the B1 horizon and 1758 kg m⁻³ for the B2 horizon (Snyman, 2000). Planting took place during August 2002 under dry land conditions and the soil was well cultivated (300 mm deep) before planting. No additional fertilisation or cultivation took place over the trial period (2003/2004 season) or the preceding season (2002/2003 season). Weed control was done chemically.

2.2. Treatments

Three plants each of *O. ficus-indica* (L.) Miller (cultivar Morado) (green cladode) and *O. robusta* Wendl. (cultivar

Monterey) (blue cladode) were studied. Planting (one-year-old cladodes) took place on 4th August 2002 in two lines, with 10 m spacing between rows and 10 m within a row. The test plants were randomly placed over the area.

One-year-old cladodes of the two species were obtained from the farm Waterkloof approximately 20 km west of Bloemfontein. Cladodes of *O. ficus-indica* were on average 506±46 mm long, 183±15 mm wide and 20±3 mm thick with an average fresh mass of 1406±170 g (means±SE, *n*=10). Cladodes of *O. robusta* were on average 261±46 mm long, 244±15 mm wide and 15±2 mm thick with an average fresh mass of 1354±130 g (means±SE, *n*=10). The cladodes were dried for 4 weeks in the shade to allow healing of the wound surface and then planted upright with one quarter of the cladode in the soil. The cladodes were facing North/South.

2.3. Data collection

The root mass and length of plants two years after planting were estimated at 50 mm intervals to a depth of 1200 mm from a sample of three soil cores obtained randomly over a distance of 2500 mm from the stem of each plant at 100 mm intervals. The soil cores were collected with an auger (70 mm diameter) at the end of the growing season. After collecting these samples, the soil between the sampling rows was washed out in the field to determine root distribution visually.

Roots obtained from washing the cores were sieved through a 2 mm mesh sieve followed by a 0.5 mm mesh sieve. Most of the roots were extracted after successive washings of the core. No attempt was made to distinguish between live and dead roots. The roots were then dried at 100 °C for 24 h. The length of the washed roots was measured by using a modified infrared root length counter (Rowe and Phillips, 1974) calibrated by using 10 pieces of string cut at different lengths ranging from 0.5 to 5 m. The regression function used to calculate the root length was $y=0+43.126x$, where y =root counter reading, x =root length (m) and $R^2=0.9555$. An average of six readings were taken from each core. The thickness of 10 randomly selected roots that developed from the planted cladodes, were measured with a vernier caliper.

Water-use efficiency (WUE) is defined as the amount of plant material (dry matter of cladodes) produced per unit of water used (evapotranspiration). Water-use efficiency was calculated as described by Snyman (2005).

Evapotranspiration (Et) was determined by the soil–water balance equation (Hillel, 1971). Rainfall (P) was measured daily with rain gauges. The change in soil water (ΔW) was calculated according to Moore et al. (1988), where (+) indicated an increase and (–) a decrease in the quantity of water within the root zone. The soil–water content was determined gravimetrically by means of a Veihmeyer tube (Snyman et al., 1985) at 50 mm intervals down to a depth of 1 m every month. Due to the low rainfall input of the study area, it is very difficult to obtain

drainage (D) and hence it can be discarded as a term in calculating the water balance (Snyman, 1998). Evapotranspiration was therefore calculated as follows:

$$Et = P \pm \Delta W$$

2.4. Statistical analysis

The experimental layout was a fully randomised design consisting of two *Opuntia* species and three replicates of each. The data collected was analysed by SAS (DOS program 6.04 version) (Cary, 1988). A two-way of variance (ANOVA) at 95% confidence level (depth \times distance) was computed for root mass and root length (Mendenhall and Sincich, 1996). Data on cladode mass and water-use efficiency was analysed using a one-way ANOVA (Winer, 1974). The method of Fisher (1949) was used to calculate LSD_T .

3. Results and discussion

3.1. Root production

For both species, significantly more ($P \leq 0.01$) roots were found in the first 150 mm soil layer than deeper into the soil (Fig. 1). In both cases most roots were found at a depth of 50–100 mm and a distance of 0–200 mm from the stem. This finding is supported by Sudzuki (1995) who found the bulk mass of roots up to a depth of 300 mm. In the 0–50 mm soil layer root mass increased up to a distance of 600 mm from the stem in *O. ficus-indica* and 400 mm in *O. robusta*. At all other depths the root mass decreased with distance from the stem. Over a distance of 2.5 m from the stem, an average of 90% the roots for *O. ficus-indica* and 88% for *O. robusta* were distributed in the top 150 mm soil layer. After two years of growth only a few deep roots were detected directly underneath the stem for species, showing a more shallow and horizontal

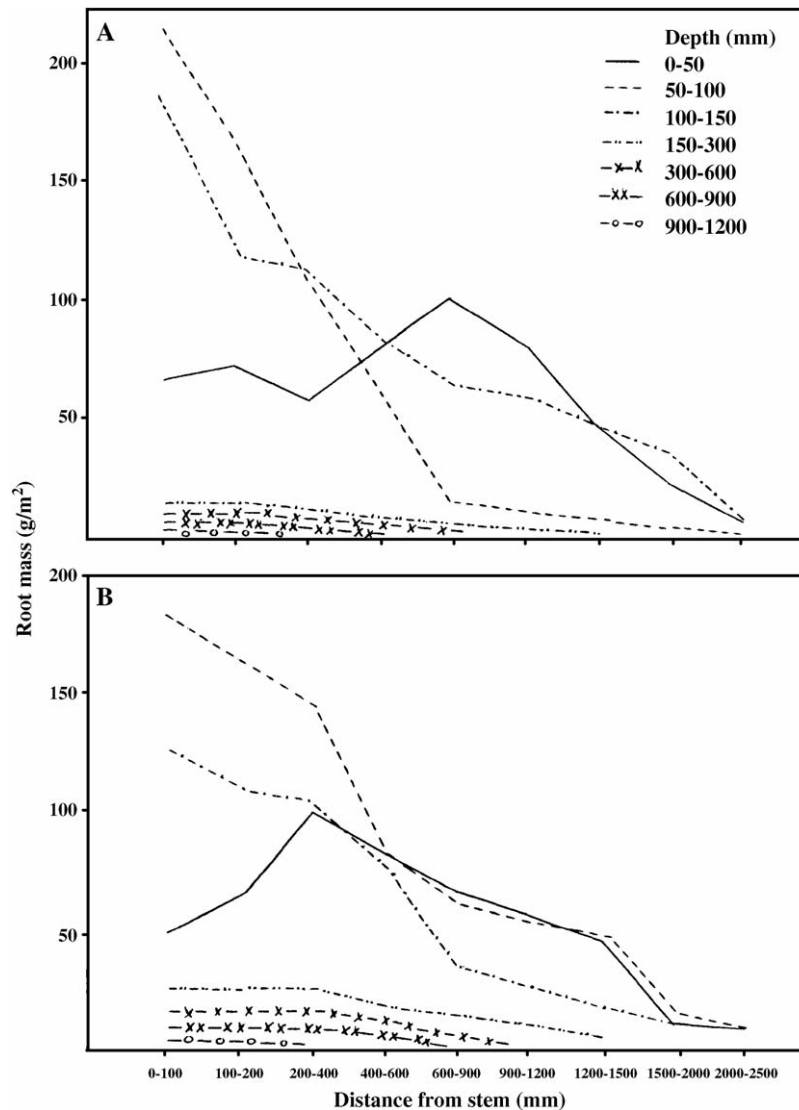


Fig. 1. Root mass (g m^{-2}) for *Opuntia ficus-indica* (A) and *O. robusta* (B) at a depth of 0–1200 mm and distance ranging from 0–2500 mm from the stem. $LSD_{0.01}$: species=1.32, depth=5.41 and depth \times distance=3.16.

root spread. In both species, the root spread in the first 100 mm soil layer extended up to 2500 m away from the stem.

After two years the total root mass, up to a depth of 1200 mm, was calculated to be 239.06 g per plant or kg ha^{-1} for *O. ficus-indica* and 316.62 g per plant or kg ha^{-1} for *O. robusta*. The 32% higher ($P \leq 0.01$) total root mass found in *O. robusta* plants can be attributed to a denser and finer root system (Snyman, 2004a,b, 2005). In the same study area and soil, Snyman (2005) reported a total root mass per plant of 107.5 and 131.6 g or kg ha^{-1} for one-year-old *O. ficus-indica* and *O. robusta* plants respectively. The root mass more than doubled from the first to the second growth season.

It is clear from Fig. 1 that, up to a depth of 100 mm, the roots must have spread further than the 2500 mm from the stem. Efficient chemical weed control is, therefore, important to ensure effective water and nutrient uptake by the cactus pear (Ratsele, 2003). This is confirmed by the observations made after washing out the soil between the sampling rows. It appears that a two-year-old cactus pear plant is not a deep rooted plant. The root system of *O. robusta* generally showed a finer structure than that of *O. ficus-indica* (Snyman, 2005).

3.2. Root thickness

The average diameter of the thickest roots developing directly from the cladodes in the top 150 mm of the soil was 9.1 mm for *O. ficus-indica* and 6.3 mm for *O. robusta*. In the same soil and study area, Snyman (2005) found the largest root diameter for one-year-old plants of *O. ficus-indica* and *O. robusta* to be 3.3 and 3.3 mm respectively, indicating that root diameter could increase two to three times during the second year of growth. The average diameter of all the roots developing from the cladodes was 3.5 mm for *O. ficus-indica* and 2.5 mm for *O. robusta*. The higher root mass in the 50–100 mm soil layer (Fig. 1) could be ascribed to the fact that the thickest roots are found at this depth. According to Snyman (2005) the roots of *O. ficus-indica* were thickest near the stem at a depth of 50–100 mm, while that of *O. robusta* were thickest at a depth of 0–50 mm.

3.3. Root length

As in the case of root mass, the longest roots were found in the 50–100 mm soil layer at distances up to 200 and 400 mm from the stem for *O. ficus-indica* and *O. robusta* respectively (Fig. 2). Snyman (2005) found most roots from one-year-old plants at a depth of 0–50 mm on the same study area. This is an indication that roots spread deeper during the second season. Down to a depth of 150 mm, 81% of the roots were distributed over a distance of 2.5 m from the stem for *O. ficus-indica* and 83% for *O. robusta*. These findings agree with that of most researchers that the roots of cacti are typically shallow (50 to 150 mm deep) and even for a large arborescent cactus occurs chiefly in the upper 300 mm of the soil (Gibson and Nobel, 1986; Nobel, 1995; Snyman, 2005, 2006). Irrigation water is generally applied only to the usual rooting depth, but excessive irrigation can force roots to lower soil layers (Nobel, 2001).

It is well known that cactus pear is a shallow-rooted crop with a fleshy root system, which can spread horizontally from 4 to 8 m from the mother plant after a few years (Nobel et al., 1992; Sudzuki, 1995; Drennan and Noble, 1998). From this study it was clear that the root spread more than 2.5 m from the stem after only two years. For one-year-old plants the roots spread 1.8 m from the stem for *O. ficus-indica* and 1.7 m for *O. robusta* (Snyman, 2005).

In general, the roots of *O. robusta* were longer ($P \leq 0.01$) than that of *O. ficus-indica*, with the exception of the 50–100 mm soil layer. This could be ascribed to fewer lateral roots in *O. robusta* in comparison to *O. ficus-indica* (Snyman, 2004a, b), which allows better adaptation of the latter species to lower rainfall conditions. Lateral roots branching from main roots could account for up to 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).

4. Aboveground biomass production

4.1. Cladode mass

The rainfall over the study period was 392 mm, which is 40% lower than the long-term average for this area. Especially the first half of the growing season received abnormally low rainfall.

The percentage water in the cladodes did not differ significantly ($P > 0.05$) between the two species and ranged between 88.14% and 87.41% for the one and two-year-old cladodes (Table 1). More or less the same values were obtained for the two species by Snyman (2005). According to Lopez-Garcia et al. (2001) the total amount of water stored in the cladodes varies between species and varieties. The water content is also strongly influenced by environmental conditions such as rainfall and can range between 70% and 93% (Lopez-Garcia et al., 2001). According to most researchers cactus cladodes aged 1 to 3 years, are high in water content during summer and early fall and during winter and spring (Monjauze and Le Houérou, 1965; Le Houérou, 1994; Felker, 1995; Nefzaoui and Ben-Salem, 1996; Ramakatane, 2003). Ramakatane (2003) found a decrease of the water content in the cladodes of *O. ficus-indica* with water stress, but it appears that *O. robusta* retained more water under water stress conditions.

The aboveground biomass production is presented separately for the one and two-year-old cladodes in Table 1. *O. ficus-indica* produced on average seven cladodes during the previous season and 17 new cladodes during the studied season, with an average fresh mass of 1268.14 g per cladode. This is 8% higher than that obtained for the same cultivar by Oelofse (2002). *Opuntia robusta* formed six cladodes during the previous season and 16 new ones during the study period with an average fresh mass of 1057.61 g per cladode. The fresh mass of the previous season's production was 94.00 g per cladode higher than that of the studied season for *O. ficus-indica* and 113.10 g per cladode higher for *O. robusta*. After two growing seasons *O. ficus-indica* and *O. robusta* produced 28.65 and 21.59 kg per plant or ton per hectare fresh mass respectively. This much higher than

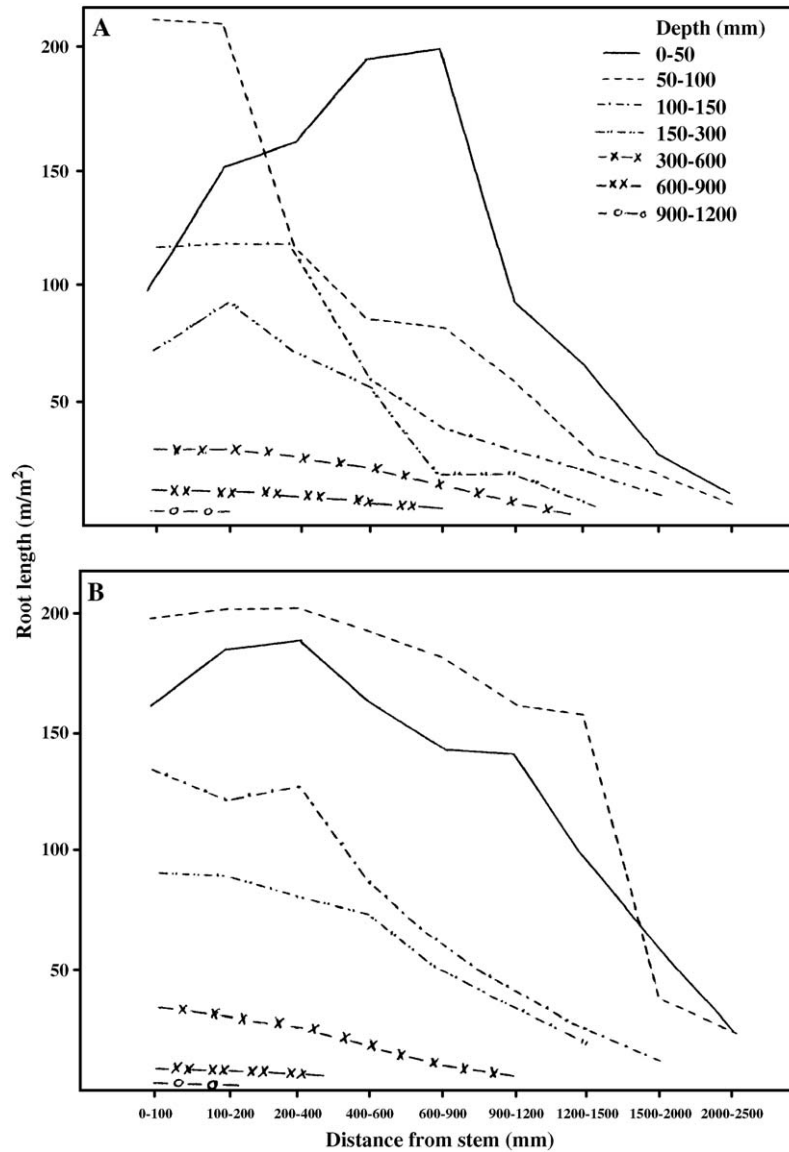


Fig. 2. Root lengths (m m^{-1}) for *O. ficus-indica* (A) and *O. robusta* (B) at a depth of 0–1200 mm and distance ranging from 0–2500 mm from the stem. $\text{LSD}_{0.01}$: species=11.37, depth=10.22 and depth \times distance=4.19.

the 5.26 ton per hectare obtained from two-year-old *O. robusta* (cultivar Monterey) plants in the Karoo (De Kock, 1980, 2001). Oelofse (2002) reported a fresh mass production of 78.84 kg per plant for five-year-old *O. ficus-indica* (cultivar Morado) plants.

Although *O. robusta* had the longest and heaviest roots, its aboveground dry mass was lower ($P < 0.01$) than that of *O. ficus-indica*. This could be ascribed to a strategy of *O. robusta* that favours survival rather than vegetative growth and is therefore

Table 1
Average fresh and dry weight and water content for one- (1) and two-year-old (2) cladodes, as well as the water-use efficiency (WUE) of *O. ficus-indica* and *O. robusta*

Species	Cladode mass				Water content in cladodes (%)		WUE ($\text{kg ha}^{-1} \text{mm}^{-1}$)
	Fresh (g cladode^{-1})		Dry (g plant^{-1} or kg ha^{-1})		1	2	
Age (years)	1	2	1	2	1	2	2
<i>O. ficus-indica</i>	1315 \pm 106	1221 \pm 101	945 \pm 81	2462 \pm 81	88.02 \pm 1.11	88.14 \pm 1.02	6.52
<i>O. robusta</i>	1114 \pm 98	1001 \pm 90	701 \pm 71	2000 \pm 72	87.41 \pm 1.01	87.51 \pm 1.26	5.39
LSD	55.14	54.12	43.15	42.16	3.21	3.05	0.39

Data are means of seasonal growth and S.E. of 3 plants. Least significant differences (LSD) was calculated at a 1% level.

more adaptable to prolonged drought conditions than *O. ficus-indica*. Although extremely high (50 ton dry mass per hectare per year) productivity is possible for *O. ficus-indica* under ideal conditions, the predicted productivity of 5 to 6 ton per hectare per year under water-limited conditions can still surpass productivity of C_3 and C_4 species used traditionally for forage (Nobel, 2001). The production of 3407.38 g per plant obtained in this study for *O. ficus-indica* and 2701.88 g per plant for *O. robusta*, compared well with the fodder production results obtained by Oelofse (2002) and Potgieter (1998, 2000). Most researchers argued that the fodder production of cactus pear is variable over the first three years before obtaining a more constant production (Potgieter, 1995, 1998; De Kock, 1998; Potgieter and Carstens, 1996). Cactus pear is able to produce up to 5 to 10 ton aboveground dry mass per hectare per year in arid zones, 10 to 20 ton in semi-arid areas and 20 to 30 ton in sub-humid zones, under close to optimum intensive cultivation (Monjauze and Le Houérou, 1965; Franclét and Le Houérou, 1971; De Kock and Aucamp, 1970; De Kock, 1980; Steynberg and De Kock, 1987; Nobel, 1988; Le Houérou, 1992a,b). Under such conditions, productivity is about 10 times higher than in standard rangelands (Le Houérou, 1994). In less than optimal soil and management conditions (no cultivation, no fertilisation) yield is still 3 to 5 times higher than in standard rangelands (De Kock, 1980; Le Houérou, 1984; Le Houérou et al., 1988). No fruit production was obtained over this study period from any of the two species.

4.2. Water-use efficiency (WUE)

The WUE of *O. ficus-indica* was significantly ($P \leq 0.01$) higher than that of *O. robusta* (Table 1). This finding is in spite of the fact that vesicular arbuscular mycorrhizal fungi could enhance water uptake in *O. robusta* (Pimienta-Barríos et al., 2002). The WUE after two years was calculated to be $6.52 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for *O. ficus-indica* and $5.39 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for *O. robusta*. Rain-use efficiency was in the order of 2 to $5 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ in unspoilt (good ecological condition) arid rangelands (Le Houérou, 1994; Snyman, 1998, 1999, 2000; Guevara et al., 2000; Holm, 2000; Ingram, 2002), compared to 10 to $15 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ of full grown cactus pear plantations under average standard deep soil and management conditions (Le Houérou, 1994, 1996). Guevara and Estevez (2001) reported a WUE of only $7.4 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ from cactus pear in a 300 mm rainfall area in Argentina. According to them, this low WUE was probably due to a lack of proper weed control. Water-use efficiencies as low as $3.5 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ were also reported on a silty sand soil with a rainfall slightly higher than 200 mm (Guevara and Estevez, 2001). Han and Felker (1997), who studied three- and four-year-old plantations, argued that the water-use efficiency of cactus pear is among the highest of any plant species (including C_3 and C_4) that has been measured under long-term field conditions. The high WUE ($62 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$) from a four-year-old plantation recorded by Han and Felker (1997) was the result of the high biomass production in the fourth year. Maximum WUE's of 40 to $60 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ have been attained with cactus pear in semi-arid and sub-humid climates under irrigation and cultiva-

tion with fairly high levels of fertilizing and/or manuring close to the biological limit for CAM species (Le Houérou, 1984; Nobel, 2001; Fisher and Turner, 1978). The high WUE values for cactus pear under rain-fed conditions in the arid Karoo of up to $43 \text{ kg DM ha}^{-1} \text{ mm}^{-1}$ found by De Kock and Aucamp (1970) and De Kock (1965, 1980, 1998, 2001) in arid areas, are questionable due to the fact that it is close to the biological limit for CAM species. According to Felker and Russell (1988) cactus pear is about 3 to 5 times more efficient in water-use than C_3 and C_4 plants such as maize, due to its Crassulacean Acid Metabolism (CAM) pathway (Nobel, 1995, 1997, 2001) and can therefore be cultivated with great success in drier areas.

4.3. Root/cladode ratio

The calculated root/cladode ratio (dry mass based) for *O. robusta* of 0.11, was significantly ($P \leq 0.05$) higher than the 0.07 for *O. ficus-indica*. The root/cladode ratios for *O. ficus-indica* (ranging from 0.07 to 0.14) obtained by Drennan and Noble (1998) and Nobel (2001) for mature plants, supported the very low values found in this study. In one-year-old plants Snyman (2005) calculated root/cladode ratios of 0.21 for *O. robusta* and 0.13 for *O. ficus-indica*. The roots comprise 11% of the total plant biomass for *O. robusta*, compared to only 7% for *O. ficus-indica*, which could be due to the finer root system of the former species.

5. Conclusion

The cactus pear with its shallow root system, occurring predominantly in the upper soil layers (0–150 mm) where soil–water content is heterogeneous, is well adapted to arid and semi-arid areas. It can take up water efficiently after light rain showers and therefore has the potential of improving the productivity of arid and semi-arid regions. After two years no deep tap root system developed in and both species was characterized by a shallow, horizontally spread root system. A deeper root system might develop after a few years depending on the type of soil and cultivation management.

After only two years the root systems of both species can spread as far as 2.5 m from the stem. Cultivation in-between rows must therefore be carefully planned to avoid root damage. Due to the shallow root distribution, cultivation around the plants must be avoided and for sustainable production chemical weed control is preferable. These practices are especially important during the early stage of plant development. Fertiliser must also be applied in small quantities over the season to avoid damage to the shallow root system. *Opuntia robusta* has a finer root system, higher root mass and longer roots than *O. ficus-indica*, which makes it more adaptable to drier conditions. Its various water-conserving strategies lead to a need for a small root system; indeed roots comprised only about 7% and 11% of the total plant biomass for *O. ficus-indica* and *O. robusta* respectively.

Cactus pear is useful not only because it can withstand drought, but also due to its efficient water-use and high productivity. In this study the aboveground dry mass production

of two-year-old plants was already 3407 kg ha⁻¹ for *O. ficus-indica* and 2702 kg ha⁻¹ for *O. robusta*. The WUE of cactus pear can be about three times higher than that of C₃-plants and five times higher than C₄-plants. After only two years *O. ficus-indica* already produced 6.52 kg ha⁻¹ for each mm water used, compared to 5.39 kg ha⁻¹ mm⁻¹ by *O. robusta*. Cactus pear is therefore particularly attractive as an animal feed in arid zones because of its efficient use of water in relation to biomass production.

References

- Brutsch, M.O., 1988. The role of prickly pear in less developed agriculture. First National Symposium on Fruit Production from Spineless Prickly Pear. University of Pretoria, South Africa.
- Cary, N.C., 1988. SAS Institute Inc. SAS DOS Program 6.04, USA, p. 1089.
- Chapin III, F.S., 1991. Integrated responses of plants to stress. *Bioscience* 41, 29–36.
- De Kock, G.C., 1965. The management and utilization of spineless cactus (*Opuntia* spp.). Proceedings of the IX International Grassland Congress, Sao Paulo, Brazil, pp. 1471–1474.
- De Kock, G.C., 1980. Drought resistant fodder shrub crops in South Africa. In: Le Houérou, H.N. (Ed.), *Browse in Africa, the Current State of Knowledge*. International Livestock Centre for Africa, Addis-Ababa, pp. 399–410.
- De Kock, G.C., 1998. The use of cactus pear (*Opuntia* spp.) as a fodder source in the arid areas in South Africa. Proceedings of the International Symposium on Cactus Pear and “Nopalitos” Processing and Uses. Universidad de Chile, Santiago, and International Cooperation and Network on Cactus pear, pp. 83–95.
- De Kock, G.C., 2001. The use of opuntia as a fodder source in arid areas of Southern Africa. In: Mondragón-Jacobo, C., Pérez-González, S. (Eds.), pp. 101–105. Cactus (*Opuntia* spp.) as forage, FAO Plant protection and production paper 169, pp. 146.
- De Kock, G.C., Aucamp, J.D., 1970. Spineless cactus, the farmer’s provision against drought. Leaflet, vol. 37. Agricultural Research Institute of the Karoo region, Department of Agriculture, Pretoria, South Africa, p. 11.
- Drennan, P.M., Noble, P.S., 1998. Root growth on soil temperature for *Opuntia ficus-indica*: influences of air temperature and in doubled CO₂ concentration. *Functional Ecology* 12, 959–964.
- Felker, P., 1995. Forage and fodder production and utilization. In: Barbera, G., Inglese, P., Pimienta-Barrios, E. (Eds.), pp. 144–154. Agro-ecology cultivation and uses of cactus pear. FAO Plant production and protection paper 132, pp. 213.
- Felker, P., Inglese, P., 2003. Short-term and long-term research needs for *Opuntia ficus-indica* utilization in arid areas. *Journal of the Professional Association for Cactus Development* 5, 131–151.
- Felker, P., Russell, C.E., 1988. Effects of herbicides and cultivation on the growth of *Opuntia* in plantations. *Journal of Horticultural Science* 63, 149–155.
- Felker, P., Singh, G.B., Parcek, O.P., 1997. Opportunities for development of Cactus (*Opuntia* spp.) in arid- and semi-arid regions. *Annals of Arid Zone* 36, 267–278.
- Felker, P., Rodriguez, S. de C., Casoliba, R., Filippini, P., Medina, D., Zapata, R., 2005. Comparison of *Opuntia ficus-indica* varieties of Mexican and Argentine origin for fruit yield and quality in Argentina. *Journal of Arid Environments* 60, 405–422.
- Fisher, R.A., 1949. *The Design of Experiments*. Oliver and Boyd Ltd., Edinburgh.
- Fisher, R.A., Turner, N.P., 1978. Plant productivity in the arid and semi-arid zones. *Annual Review of Plant Physiology* 29, 277–313.
- Francllet, A., Le Houérou, H.N., 1971. Atriplex and cactus pear in South Africa. FAO plant protection and production paper. Rome 32, 249–253.
- Galizzi, F.A., Felker, P., González, C., Gardiner, D., 2004. Correlation between soil and cladode nutrient concentrations and fruit yield and quality in cactus pears, *Opuntia ficus-indica* in a traditional farm setting in Argentina. *Journal of Arid Environments* 59, 115–132.
- Gibson, A., Nobel, P., 1986. *The Cactus Primer*. Harvard University Press, Cambridge.
- Guevara, J.C., Estevez, O.R., 2001. *Opuntia* spp. for fodder and forage production in Argentina: Experiences and prospects. In: Mondragón-Jacobo, C., Pérez-González, S. (Eds.), pp. 66–69. Cactus (*Opuntia* spp.) as forage FAO. Plant protection and production paper 169, pp. 146.
- Guevara, J.C., Stasi, C.R., Estevez, O.R., Le Houérou, H.N., 2000. N and P fertilization on rangeland production in Midwest Argentina. *Journal of Range Management* 53, 410–414.
- Han, H., Felker, P., 1997. Field validation of water-use efficiency of the CAM plant *Opuntia ellisiana* in south Texas. *Journal of Arid Environments* 36, 133–148.
- Hillel, D., 1971. *Soil and Water. Physical Principles and Processes*. Academic Press, New York, p. 242.
- Holm, A.M., 2000. A study of degradation processes at patch to landscape scale within the arid shrubland of Western Australia. PhD Thesis, University of Western Australia, Perth, pp. 192.
- Huang, B., Nobel, P.S., 1993. Hydraulic conductivity and anatomy along lateral roots of cacti: changes with soil water status. *New Phytologist* 123, 499–509.
- Inglese, P., Barbera, G., La Mantia, T., 1995. Research strategies and improvement of cactus pear fruit quality and production. *Journal of Arid Environments* 29, 455–468.
- Ingram, L.J., 2002. Growth, nutrient cycling and grazing of three perennial tussock grasses in the Pilbara Region of NW Australia. PhD Thesis. University of Western Australia, pp. 280.
- Le Houérou, H.N., 1984. Rain-use efficiency, a unifying concept in arid land ecology. *Journal of Arid Environments* 7, 213–247.
- Le Houérou, H.N., 1992a. The role of *Opuntia Cacti* in the agricultural development of Mediterranean arid zones. 2nd International Congress on Cactus Pear and Cochinille, Santiago, Chile, pp. 315–329.
- Le Houérou, H.N., 1992b. Feeding shrubs to sheep in the Mediterranean arid zone: intake, performance and feed value. Proceedings of the IV International Rangeland Congress. Montpellier, France, pp. 623–628.
- Le Houérou, H.N., 1994. Drought-tolerant and water-efficiency fodder shrubs (DTFS): their role as drought insurance in the agricultural development of arid and semi-arid zones in Southern Africa. Report to the Water Research Commission of South Africa. WRC Report, vol. 65/94, p. 436.
- Le Houérou, H.N., 1996. The role of cacti (*Opuntia* spp) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean Basin. *Journal of Arid Environment* 33, 135–159.
- Le Houérou, H.N., Bingham, L.R., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15, 1–18.
- Le Houérou, H.N., Popov, C.F., See, L., 1993. Agro-bioclimatic classification of Africa. FAO Agrometeorology Working Papers Series 6, 221–241.
- Lopez-Garcia, J.J., Fuentes-Rodriguez, J.M., Rogriguez, R.A., 2001. Production and use of *Opuntia* as forage in northern Mexico. In: Mondragón-Jacobo, C., Pérez-González, S. (Eds.), pp. 29–36. Cactus (*Opuntia* spp.) as forage, FAO Plant protection and production paper 169, pp. 146.
- Mendenhall, W., Sincich, T., 1996. *Principles of experimental design, A Second Course in Statistics*, Fifth edition. Prentice-Hall, Incl, New Jersey, pp. 582–595.
- Mizrahi, Y., Nerd, A., 1999. Usage of various cactus species as fruit and vegetables crop in Israel. VIII National Congress on Cactus Pear, Mexico, pp. 514–522.
- Monjauze, A., Le Houérou, H.N., 1965. Le rôle des Opuntias dans l’Economie Agricole Nord Africain. *Bulletin de l’Ecole Supérieure d’Agriculture de Tunis* 8–9, 85–164.
- Moore, A., Van Eck, J.A.J., Van Niekerk, N.P., 1988. Evapotranspirasie in drie plantgemeenskappe van ‘n *Rhygosum trichotomum* habitat te Upington. Proceedings of the Grassland Society of Southern Africa 5, 80–84.
- Nefzaoui, A., Ben-Salem, H., 1996. Nutritive value of diets based on spineless cactus (*Opuntia ficus-indica* var. *inermis*) and Atriplex (*Atriplex nummularia*). Native and Exotic Fodder Shrubs in Arid and Semi-Arid Zones. Regional Training Workshop, Tunisia, p. 562.

- Nobel, P.S., 1988. Environmental Biology of Agaves and Cacti. Cambridge University Press, Cambridge New York, USA, p. 270.
- Nobel, P.S., 1995. Environmental biology. In: Barbera, G., Inglese, P., Pimienta-Barrios, E. (Eds.), pp. 36–48. Agro-ecology, cultivation and uses of cactus pear, pp. 36–48. FAO Plant production and protection paper 132, pp. 213.
- Nobel, P.S., 1997. Recent ecophysiological findings for *Opuntia ficus-indica*. Journal of the Professional Association for Cactus Development 2, 89–96.
- Nobel, P.S., 2001. Ecophysiology of *Opuntia ficus-indica*. In: Mondragón-Jacobo, C., Pérez-González, S. (Eds.), pp. 13–19. Cactus (*Opuntia* spp.) as forage. FAO plant production and protection paper 169, pp. 146.
- Nobel, P.S., Sanderson, J., 1984. Rectifier-like activities of roots of two desert succulents. Journal of Experimental Botany 35, 727–737.
- Nobel, P.S., Alm, D.M., Cavelier, J., 1992. Growth respiration, maintenance respiration and structural-carbon costs for roots of desert succulents. Functional Ecology 6, 79–85.
- Oelofse, R.M., 2002. Characterization of *Opuntia ficus-indica* cultivars in South Africa. Unpublished MSc Thesis, University of the Free State, Bloemfontein, South Africa, pp. 128.
- Pimienta-Barrios, E., Barbera, G., Inglese, P., 1993. Cactus pear (*Opuntia* spp., Cactaceae) international network: an effort for productivity and environmental conservation for arid and semi-arid lands. Cactus and Succulent Journal 65, 225–229.
- Pimienta-Barrios, E., González del Castillo-Aranda, M.E., Nobel, P.S., 2002. Ecophysiology of a wild platyopuntia exposed to prolonged drought. Environmental and Experimental Botany 47, 77–86.
- Potgieter, J.P., 1995. The cactus pear (*Opuntia ficus-indica*) in South Africa: cultivation and research in the Northern Province (review paper). 6th National and 3rd International Cactus Pear Congress, 3–10 November 1995, Guadalajara, Mexico, pp. 352–362.
- Potgieter, J.P., 1998. Evaluation of spineless cactus pear (*Opuntia* spp.) varieties for environmental adaptation in the Northern Province of South Africa (research poster). Eight Congress of the Southern African Society for Horticultural Science, 24–27 January 1998, Stellenbosch, South Africa, p. 398.
- Potgieter, J.P., 2000. Riglyne vir die verbouing van doringlose turksvye vir vrugteproduksie. Group 7 Printers BK, P.O. Box 14717, Sinoville 0129, South Africa, p. 16.
- Potgieter, J.P., Carstens, K., 1996. The cactus pear (*Opuntia* spp.): a matter of identity (research poster). 4th International Cactus Pear Congress, 30 January–1 February 1996, Midrand, South Africa.
- Ratsele, C., 2003. Production evaluation of *Opuntia robusta* and *O. ficus-indica* cultivars in the Central Free State. Unpublished MSc Thesis, University of the Free State, Bloemfontein, South Africa, pp. 110.
- Ramakatanane, E.M., 2003. Root dynamics and water studies on *Opuntia ficus-indica* and *O. robusta*. Unpublished MSc Thesis, University of the Free State, Bloemfontein, South Africa, pp. 94.
- Rowse, H.R., Phillips, D.A., 1974. An instrument for estimating the total length of root in sample. Journal of Applied Ecology 11, 309–314.
- Schulze, E.R., 1979. Climate of South Africa. Part 8. General Survey. Weather Bureau, Pretoria, South Africa, p. 158.
- Singh, R.S., Singh, V., 2003. Growth and development influenced by size, age and planting methods of cladodes in cactus pear (*Opuntia ficus-indica*). Journal of the Professional Association of Cactus Development 5, 47–54.
- Silva, H., Acevedo, E., 1985. Introducción y adaptación de *Opuntia* spp. en el secano mediterráneo árido de la IV Región. Informe final. Proyecto 0065. Fondo Nacional de Desarrollo Científico y Tecnológico (FONDOECYT), p. 136.
- Snyman, H.A., 1998. Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of South Africa. Journal of Arid Environments 39, 645–666.
- Snyman, H.A., 1999. Quantification of the soil–water balance under different veld condition classes in a semi-arid climate. African Journal of Range and Forage Science 16, 108–117.
- Snyman, H.A., 2000. Soil–water utilisation and sustainability in a semi-arid grassland. Water South Africa 26, 331–341.
- Snyman, H.A., 2003. Root dynamics of cactus pear. Agri TV. <http://www.agriTV.co.za>, 25 October 2003, pp. 1–6.
- Snyman, H.A., 2004a. Effect of various water applications on root development of *Opuntia ficus-indica* and *O. robusta* under greenhouse growth conditions. Journal of the Professional Association for Cactus Development 6, 35–61.
- Snyman, H.A., 2004b. Effect of water stress on root growth of *Opuntia ficus-indica* and *O. robusta*. South African Journal of Animal Science 34, 101–103.
- Snyman, H.A., 2005. A case study on in situ rooting profiles and water-use efficiency of *Opuntia ficus-indica* and *O. robusta*. Journal of the Professional Association for Cactus Development 7, 1–21.
- Snyman, H.A., 2006. A greenhouse study on root dynamics of cactus pears, *Opuntia ficus-indica* and *O. robusta*. Journal of Arid Environments 65, 529–542.
- Snyman, H.A., Van Rensburg, W.L.J., Opperman, D.P.J., 1985. Grond- en afloopverliesbepalings vanaf natuurlike veld, met behulp van 'n reënvalna-bootser. Journal of the Grassland Society of Southern Africa 2, 35–40.
- Soil Classification Working Group, 1991. Soil Classification: A Taxonomic System for South Africa. Department of Agriculture Development, Pretoria, South Africa, p. 262.
- Steynberg, H., De Kock, G.C., 1987. Aangeplante weidings in die vee-produksiestelsels van die Karoo en ariede gebiede. Karoo Agriculture 3, 4–13.
- Sudzuki, F., 1995. Anatomy and morphology. In: Barbera, G., Inglese, P., Pimienta-Barrios, E. (Eds.), pp. 28–34. Agro-ecology, Cultivation and Uses of Cactus Pear, FAO plant production and protection paper 132, pp. 213.
- Winer, B.J., 1974. Statistical Principles in Experimental Design. McGraw-Hill, London, p. 218.