ROOT DYNAMICS AND WATER STUDIES ON *Opuntia ficus-indica* AND *O.robusta*

by

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Dedication

This work is dedicated to my beloved husband Mokhethi Peter Ramakatane and my two lovely kids, Reitumetse and Maphali.

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Declaration

I declare that the thesis hereby submitted by me for the partial fulfillment of the requirements of the M.Sc. (Agric.) degree (Grassland Science) at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I furthermore cede copyright if the dissertation in favour of the University of the Free State.

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Table of contents

Chapter 1

Introduction

South Africa is one of the dry African countries and due to its relative dryness or aridity (mean annual precipitation/potential evapotranspiration ratio), 55 % of the land area lies within the arid zone (aridity index of 0.05 to 0.2) and 39 % is semi-arid (aridity index of 0.2 to 0.5) (Le Houérou *et al.* 1993; Rutherford &Westfall 1994; Hoffman & Ashwell 2001). In these areas the phenomenon of annual or shorter seasonal droughts is an inherent characteristic (Fouché 1992; Snyman 1998). Therefore when farming under dryland conditions (without irrigation), it is important for the available water to be used in the most efficient way (Snyman & Fouché 1991). The cactus pear, with its adaptability to such water stressed environmental conditions and its relatively low water requirements (De Kock 1965; Lahsasni *et al.* 2004)) is an important drought resistant crop (Lahsasni *et al.* 2003). Although it is well adapted to arid and semi-arid conditions, in arid regions it will nevertheless respond favourably to light supplementary irrigation (Vander Merwe *et al.* 1997; Pretorius *et al.* 1997; Guigliuzza *et al.* 2000).

The roots of cactus pear, which are extensive and dense close to the soil surface, also have a high capacity for storing water (Hills 1995). The root system has the ability to take up water at very low soil-water contents (Noble & Huang 1992; Oelofse 2002). It can therefore utilise light showers of only few millimetres, more efficiently than other fodder plants (De Kock 1965, 1967; Noble 1991; Snyman 2003). The cactus pear leaves, which are modified stems, also assist photosynthesis. They consist of water-storage tissue (mesophyll), which contains cell mucilage with a high water-binding ability (Oelofse 2002). The cladodes also have an outer wax layer and thick epidermis, which limits evaporation (Hills 1995). The stomata are sunken and remain closed for the greater part of the day when temperatures and light intensity are high (Brutsch & Zimmerman 1992). An important adaptation of a desert plant is to maximise water uptake and minimise water loss (Huang & Nobel 1992; Lahsasni *et al.* 2003).

Cactus pear is well adapted to arid and semi-arid 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). According to De Kock (1967), the cactus pear, due to its Crassulacean Acid Metabolism (CAM) pathway can therefore be cultivated in drier areas (Nobel 1995; Lahsasni *et al.* 2004)) which is about four times more efficient in water-use than C_4-plants such as maize (Felker & Russel 1988).

Over the last ten years there has been an increased interest in the spineless cactus pear as both fodder and fresh fruit crop. Very competitive prices for cactus pear fruit are obtained at some of the national fresh fruit markets compared to apples, peaches and oranges (Snyman 2003). In poor socio-economic and arid countries, the high productivity and fruit quality of some species such as the *Opuntia ficus-indica* can be used to reduce famine (Oelofse 2002). According to estimates, the cactus pear ranges from 687 000 to 2.3 million ha worldwide (Mondragon-Jacob & Pérez-Gonzàlez 2000). Even though the idea of planting cactus pear is being resisted because it is considered to be a weed, especially in non-native habitats, it is an ideal crop for semi-arid zones especially during drought periods (Brutsch 1997a). The spiny cactus pear plant is referred to as prickly pear in South Africa to distinguish it from the cultivated spineless cactus pear forms, although both are *O. ficus-indica* cultivars (Brutsch & Zimmerman 1993).

Due to regular drought occurrence in Southern Africa (Snyman 1998), there is a need for more research on drought tolerant and valuable plant species 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). It is used mainly as animal feed in times of droughts as it provides water and other vital nutrients. 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. It is adapted to a wide range of soils and climatic conditions (Brutsch 1988). It does not compete with other rangeland species

(Le Houérou 1994) and therefore deserves more attention as one of the most valuable promising crops.

There is a need for increased farmer interest and knowledge on 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). Although relevant information on the aboveground growth and development of the cactus pear plant is available (Brutsch & Zimmerman 1990), 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). Most people could be of the opinion that the cladodes with their sunken stomata and outer wax layer to limit evaporation are the most important adaptations to arid areas, but the contribution of the effective root system must not be underestimated. Sound knowledge on the root dynamics of this plant under different soil-water conditions is therefore important in understanding the adaptations of the plant to be implemented in management practices. The aim of this study was therefore to determine the response of roots and cladodes to different soil water levels of two *Opuntia species* namely *Opuntia ficus-indica* (cultivar Morado) and *Opuntia robusta* (cultivar Monterey). The objectives were:

- to determine the root/cladoses ratio and water-use efficiency under different soil-water contents,
- to quantify the dynamics of different root types and
- to have a thorough knowledge of cactus pear root development and distribution to serve as guidelines in management practices.

Chapter 2

Literature review

2.1 Introduction

Cactus pear (*Opuntia* species) is a dicotyledonous perennial with cladodes, which are modified stems (Lahsasni *et al.* 2003). The spines are modified leaves. This plant is an example of a xerophyte. The cladodes have an outer wax layer and thick epidermis, which limit evaporation. The stomata are sunken and remain closed for the greater part of the day when temperatures and light intensity are high. The absorbed water combines with hydrophilic mucus compounds in the cladodes, slowing down water evaporation. This compound is stored in the mesophyll cells of the cladodes (Brutsch & Zimmerman 1992).

It is one of the CAM (Crassulacean Acid Metabolism) plants, with a nocturnal carbon–dioxide uptake and diurnal fluctuation of organic acid. This type of plant transpires more during the night than the day. This is because their stomata open during the night and close during the day. The photosynthetic organs have an increase in acid content at night with a decrease during the day. Carbon dioxide diffuses inwards during the day and is bound as organic acid, called oxalo–acetic acid. During the day, when stomata are closed, the 4–C organic acid breaks down (dicarboxilised) and CO_2 is released, which is then reduced into carbohydrates through the Calvin Benson Cycle (C_3-cycle) (Galton *et al.* 1980).

This plant is characterised by a shallow, fleshy root system with horizontal root spreading, so that a 500 mm soil depth is adequate. The root distribution may also depend on type of soil and cultivation. Taproots that develop can penetrate nearly 300 mm into the soil under favourable soil-water conditions (Hills 1995). Under drought conditions in semi-arid and arid areas, fleshy side roots develop from the taproot to take up soil-water at levels inaccessible for the taproots. In all soil forms the bulk mass of absorbent roots is found in the first few centimetres with a maximum depth of

300 mm and a spreading of 4 to 8 m from the stem (Hills 1995). The roots develop xeromorphic characteristics enabling the plants to survive prolonged periods of drought.

Opuntia is a drought tolerant crop, since even the smallest amount of water it absorbs is used efficiently (Le Houérou 1996), and withstand dry periods and extreme heat. These traits make them highly promising 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). Higher yields are obtained in areas with lower rainfall. The water percentage in the cladodes can be as high as 90.9% in winter and 85.9% in summer (Le Houérou 1994). Most of the cactus pear plantations are established at altitudes from 1400 to 1600m and used mostly as fodder banks. It is also abundant at altitudes below 1400m in summer rainfall areas with mean rainfall of 400 to 600 mm. The aridity in winter rainfall regions, freezing temperatures, high altitudes and deep sandy areas limit the distribution of cactus pear (Brutsch 1997b; Dean & Milton 1999).

2.2 Utilisation of cactus pear

Cactus pear is one of the most useful fodder crops especially during the critical periods, such as winter and droughts, in semi-arid areas (Brutsch 1997b). It provides animals with energy, water and nutrients (Monjouze & Le Houérou 1965; Le Houérou 1996;). However, it is poor in protein content and fibre (Table 2.1; Le Houérou 1994) and therefore needs high protein supplements such as lucerne hay, cottonseed and other supplementations (Monjouze & Le Houérou 1965).

Utilisation of cactus pear as fodder complement to range animals in periods of critical nutrition constitutes a real 'drought insurance' since it prevents destocking and therefore decreases economic loss in such periods (Monjauze & Le Houérou 1965; Brutsch 1997b). The cactus pear cladodes are used as fodder and provide a good diet to animals except for being very low in crude protein (De Kock 1980; Le Houérou 1994; Felker 1995; Nefzaoui & Ben- Salem 1996). In some cases, cactus pear can be more economical than lucerne or maize as emergency stock feed in times of droughts.

Thirty-five spineless varieties were developed and promoted from 1906 to 1915 for feeding purpose (Brutsch 1988; Gathaara *et al.* 1988). Approximately 2600 ha of grazing land have been planted with spineless cactus pear on commercial farms in the Karoo in South Africa and serve as a source of fodder bank for the animals (De Kock 1974; Brutsch & Zimmerman 1993; Felker 1995; Brutsch 1997b). Brutsch and Zimmerman (1993) pointed out that the cladodes, when supplemented with cottonseed meal, provide all the nutrients needed by an animal. When fed to dairy stock, the cladodes impart a distinctive flavour to milk and butter, and these products are highly desired (Brutsch 2000).

Table 2.1 Chemical composition (dry matter %) for *Opuntia* species cladode ranges (Le Houérou 1994; Felker 1995; Nefzaoui & Ben Salem 1996).

NUTRIENT	DRY MATTER (%)
Water	85-90
Crude protein (CP)	5-12
Ash	20
Crude fiber (CF)	10-43
Calcium (Ca)	1.4-4.2
Phosphorus(P)	0.2
Sodium (Na)	0.1
Potassium (K)	2.3
Magnesium (Mg)	1.4

Spineless cactus pear contributes substantially to the diet of large, mainly peasant populations during summer months in countries such as Mexico, Peru and North African states (De Kock 1974; Mizrahi *et al.* 1997). Nowadays South Africa is one of the countries interested in cactus pear cultivation, as there is an increasing interest in the major markets for the fruits of these plants. The fruits compete well with some of the better-known traditional fruits (Table 2.2) like apples, peaches and oranges on the national fruit market of South Africa (Brutsch & Zimmerman 1993; Cantwell 1994; Snyman 2003).

The naturalised cactus pear fruits, in South Africa, are harvested by rural people for local consumption or for sale along the roadside and in smaller urban centres in those areas (Brutsch 1988). Informal trading in prickly pear fruits takes place in most parts of South Africa such as Eastern Cape, Ciskei and Port Elizabeth, from January to March (Brutsch 1988). Therefore the demand for good quality fruit can be expected to increase fairly rapidly. In 1990, the price of cactus pear fruits was high and is expected to increase as many South Africans come to realise that they can earn substantial income from this drought tolerant crop (Brutsch & Zimmerman 1993). Apart from fruits, cladodes and flowers are also utilised as food in most of the developing countries.

Table 2.2 Comparison of the composition of the pulp of cactus pears, orange and papaya fruits (Cantwell 1994).

COMPONENTS	CACTUS PEAR	ORANGE	PAPAYA
Water (%)	85.0	87.8	88.7
Total Carbohydrates (%)	11.0	11.0	10.0
Crude Fibre (%)	1.8	0.5	0.8
Lipids (%)	0.1	0.1	0.1
Protein (%)	0.5	0.4	0.6
Ash (%)	1.6	0.4	0.6
Calcium (mg $100g^{-1}$)	60	40	20
Vitamin C (mg $100g^{-1}$)	30	50	50
Vitamin A (IU)	50	200	1100

Cactus pear is utilised in various ways apart from being a fodder, fruit crop or vegetable. It can be used as a hedge or a fence by planting it a meter apart. Cactus pear planted on contours is an efficient tool in water and soil conservation in most countries, including South Africa (Le Houérou 1994). Most of the developing countries are experiencing the problem of desertification, so cactus pear is still a solution since it can easily be established, tolerates drought and uses water efficiently (Le Houérou 1996). Therefore it can be used to reclaim eroded areas such as the eroded volcanic ash soils in the Central Mexico highlands (Brutsch 1988, Martin

1993). It competes less with other rangeland plants so there are no land problems. Sixty-five percent of the natural pasture of South Africa falls within the semi-arid areas, where moderate to severe droughts are a common occurrence (Brutsch 1988). These areas are considered to be ecologically suitable for the cultivation of cactus pear.

The cactus pear can also be used as medicine for various diseases such as diabetes (Sáenz-Hernández 1995). It has been found to increase sensitivity to insulin, in addition to possibly delaying the absorption of glucose. It has also been proven to decrease cholesterol levels in the body. The high fibre content and water absorption capacity of the mucilage can explain the current use of capsules of dried napol, to control obesity (Sáenz-Hernández 1995; Mizrahi *et al.* 1997). The cactus mucilage is also used by small farmers to purify drinking water (Sáenz *et al.* 2004). The sap from the pads can be used in the same way as *Aloe vera* for first aid. The sap is squeezed from the cladode onto a cut, burn or bruise, where it soothes the wound. The young cladodes can also be used as a laxative (Family Farm Series 1989). Ground or pureed young cladodes are used as a laxative and also as a remedy for diabetes. In Central Africa, the sap from the cladodes serves as a mosquito repellent (Sáenz *et al.* 2004).

Cactus pear sap from the pads can also be utilised in the manufacturing of candles, chewing and cotton stiffening agent (Family Farm Series 1989). It is also useful as a mosquito repellent in Central Africa. In the rural areas of Mexico, the sap is boiled and mixed with white wash and mortar to increase the durability of buildings (Sáenz-Hernández 1995; Sáenz *et al.* 2003).

The pads can also be pounded and dried to make strong fibre woven into mats, baskets, fans and fabrics. Pressed fibre can be used to make paper. The spines are used for toothpicks, needles and pins (Sáenz-Hernández 1995). The red coloured fruits supply red pigment for food colouring (Brutsch & Zimmerman 1993). Edible oils can be obtained from the seeds, with yields of between 5.8 and 23.6% (Sáenz-Hernández 1995). A variety of cosmetics, which are napol-based such as shampoos, astringent lotion, body lotion and soaps are found on the markets (Sáenz-Hernández 1995). Its nutritional value, hardiness, ease of cultivation, low establishment and production costs, as well as high potential yields, makes it worthy to feature in the agricultural economy of South Africa (Brutsch 1979).

Cactus pear, as a drought and erosion tolerant plant, can be used to slow and direct sand movement, enhance the restoration of the vegetation cover and avoid the water destruction of the land terraces built to reduce run-off. The cactus pear plant can be used in combination with cement barriers or cut palm leaves to stop wind erosion and sand movement. It will fix the soil and enhance the restoration of the vegetative plant cover (Brutsch and Zimmerman 1993). Cactus pears are often used as defensive live hedges for protection of gardens and orchards throughout North Africa and parts of Italy and Spain. Cactus pear hedges play an important role in landscape organisation when established in double rows. Cactus hedges also play a major role in erosion control and land–slope partitioning, particularly when established along contours. Moreover, hedges are physical obstacles to run-off favouring silting and thus preventing regressive erosion (Monjauze and Le Houérou 1965). Another role of cactus pear plantation is for run-off and erosion control and watershed management. Planting cactus pear in degraded arid and semi-arid lands is one of the easiest, quickest and fastest ways of rehabilitating them (Le Houêrou 1982). Recently, a cactus cladodes extract was tested to improve water infiltration (Sáenz et al. 2004).

2.3 Historical background and distribution

Cactus pear originated in Central Mexico and some parts of the Caribbean region (Mondragon-Jacob & Perez-Gonzalez 1996). Some are native to Canada and others to Patagonia. It was widely distributed and is naturalised in all the continents (Brutsch 1988). Cactus pear (with spines) was introduced to South Africa during the early European settlement of the Cape in the seventeenth century (Brutsch & Zimmerman 1992). It has become a serious weed in some regions and is one of the nine plant species that have been declared as invader plants according to the Conservation of Agricultural Resources Act number 43 of 1983 in South Africa (Brutsch & Zimmerman 1992).

More or less 50 years ago, approximately 9 000 ha of the Eastern Cape and Karoo was infested with cactus pear. It has been found that *Opuntia ficus–indica* has established itself in the Karoo rangelands, with highest densities below the telegraph and transmission lines and along the wire fences than in the open rangelands (Dean & Milton 1999). This dispersal seemed to be through crows because seeds are regurgitated together with other indigestible parts of the food and appear still viable (Dean & Milton 1999). Since 1980, the first intensive and specialised plantations have been set up, mostly in the Transvaal and Ciskei regions (Barbera 1995).

Spineless cactus pear now covers some 1 500 ha in South Africa and one of the main targets is to reach the northern hemisphere market during the highly favourable period from an economic viewpoint (that is December to March) (Barbera 1995). Today cactus pear covers as much as 50 000 ha in Mexico. It is produced worldwide, mostly in countries such as Italy, Sicily, Chile, other American countries, Mexico, other European countries and South Africa, North Africa and Middle East (Barbera 1995).

Due to the fact that it has been considered a weed, there is still a resistance to the planting of cactus pear. However the biological control of this plant, whereby a population of cactus pear moth (*Cactoblastis coctorum*) or cochineal (*Dactilopius opuntia*) was introduced to the plantation, was launched in 1932 and it has been successful in many countries like Australia, South Africa, Malagasy Republic and others (Brutsch 1988; Brutsch & Zimmermann 1995). The spineless cacti planted in South Africa had been imported from America as fodder plants from Burbank's selection in about 1914 (Mondragon-Jacob & Perez-Gonzalez 1996).

Although cactus pear is widely spread through the drier areas of South Africa, it is not common in the western interior of the karoo. It is limited by aridity in the winter-rainfall region, freezing temperatures at high altitudes and by sandy substrates in the Kalahari area of South Africa (Fabbri *et al.* 1996). The Kalahari region of the Northern Cape Province similarly has many small plantations of cactus pear and low densities of self-established plants because of coarse sand.

Even though cactus pear has been declared a weed throughout South Africa, the spineless cactus pear (mainly *Opuntia ficus- indica*) is increasingly forming the basis of the cultivated cactus pear industry in many countries including South Africa. Commercial production started in the 1960's (Mondragon-Jacob and Perez-Gonzalez 1996). In 1989, large commercial plantations thrived in Mediterranean areas and the fruit was an important agricultural crop of Sicily (Family Farm Series 1989). Cactus pear trials on commercial scale started near Brits in Bophuthatswana even though it was neglected until 1987 when renewed interest was shown as a result of a study indicating definite market potential for its fruits (Brutsch 1988).

2.4 Cactus pear as CAM plant

Cactus pear takes up carbon dioxide at night and this is related to the gas exchange pattern known as Crassulacean-Acid Metabolism (CAM). These plants have high water-use efficiency and that might explain their success in invading semi-arid areas. They are viewed as slow growers. In the morning their leaves have a very acidic taste, which gradually lessen during the daytime (Nobel 1995; Mizrahi *et al.*1997).

The low productivity of CAM plants is not an inherent character and does not apply to the CAM species *Opuntia ficus-indica*, which is cultivated in about 30 countries for its fruit, young cladodes (vegetables) and mature cladodes (forage and fodder) (Hills 1995). Succulent plants tend to be native to arid and semi-arid regions, or to microhabitats that are periodically dry such as beaches, rock outcrops and tropical sites (Hills 1995). These plants represent 6 to 7% of the nearly 300 000 species of plants (Hills 1995).

The characteristics of the CAM plants are as follows:

- they transpire more at night than during the day under natural conditions because the stomata of these plants open at night and close during the day,
- because of their photosynthesis the acid content in the photosynthetic organs of the plant increases during the night and decreases during the day,

- carbon dioxide (CO_2) diffuses inwards at night and it is bound as organic acid, called oxalo-acetic acid and
- during the day when stomata are closed the 4-C organic acid is broken down (dicarboxilised) and CO_2 is released. The released CO_2 is reduced into carbohydrates in the Calvin-Benson Cycle (Galston *et al.* 1980; Nobel 1995; Mizrahi *et al.* 1997).

2.5 Establishment of cactus pear

Cactus pear has become successfully established in many parts of the world and is suitable as a subsistence dryland crop in drier areas of less developed countries, which are considered marginal for rain fed food crops such as maize (Brutsch 1988). It can also be successfully produced under irrigation and become popular in developed countries, especially for fodder and fresh fruit production. It can easily be established and survives a wide range of temperatures, water levels and soils. It is a shallow-rooted crop, which can do well in at most 500 mm soil depth (Martin 1993). Cactus pear can be propagated both by seed and vegetatively.

2.5.1 Vegetative propagation

In vegetative propagation, six months old cladodes can be cut and allowed to form callouses, which take a week or two in warm weather and longer when air is moist. This period must rather be longer than shorter to avoid rotting (Family Farm Series 1989). The cladodes are stored upright during this time so that they will not curl. They might be dipped in Bordease mixture to further protect them from fungal infections (Family Farm Series 1989). The cladode is planted upright only about one third deep in soil with good drainage. Planting deeply encourages rotting. The cladodes must be positioned in such a way that sunlight can pass along their narrow side during the hottest time of the day to avoid sunburn (Family Farm Series 1989).

The cladodes can be anchored in place with rocks to keep them upright but should not be watered, because they can sprout roots by themselves and excess water may cause rot. After 3 to 7 days the first roots develop and enough roots have sprouted after a month so the cladode will stand firmly by itself in the soil (Snyman 2003). They must be watered once and left to dry out before watering again (Family Farm Series 1989). The second or third cladode to form will bear flowers and fruits, but a cladode from an old plant may flower and set fruits sooner (Family Farm Series 1989).

Rows are usually established 2 to 6 m apart and 1 to 2 m apart in the rows. Density may vary from 850 to 5 000 plants per hectare (Le Houérou 1994). Spacing of the plants depends on the plant usage, for instance, if the plant is going to be used for grazing, then 1.2 to 1.8 m and 2.7 m are sufficient between rows. In the case where cladodes and fruits are going to be picked and transported to the feeding place or home, the rows should be 4.5 m apart to allow vehicles to pass between them (De Kock 1965). Cactus pear is unable to stand very low temperatures of as much as –12°C. The best time for planting is early spring. At this stage the cladodes for propagation are strong and ready to sprout. (De Kock 1965).

2.5.2 Seed propagation

Seeds are obtained from whole, healthy and ripe fruits, which are handwashed and sieved. They are then sun-dried to reduce exterior moisture (Mondragon-Jacob & Pimienta-Barrios 1995). Fruits have viable and aborted seeds. Fully developed seeds are darker, larger and have one to three embryos. Seeds have hard–lignified coats that serve for protection from adverse, environmental factors and also prevent germination (Mondragon-Jacob & Pimienta-Barrios 1995).

The seed coat can be broken in different ways, namely:

- mechanically,
- immersing of seeds in giberellic acid (GA_3),
- immersion of seed in water at temperatures of close to 100^0C for 5 to 20 minutes and

- immersion of seed in concentrated sulphuric acid and then washed and imbibed in giberellic acid at 100mg litre^{-1}.

The seeds can be treated against root rot organisms with an application of Captain or Thiran after scarification (Mondragon-Jacob & Pimienta-Barrios 1995).

2.5.3 Seed storage

Seeds can be stored in small plastic containers, such as film containers or paper bags, under fresh and dry conditions. Long-term storage reduces seed germination rates with recorded values of under 50% for seed stored for nine years. Short-term storage increases germination rates for over 80% after nine months of harvest, in contrast with low rates of germination by seeds stored for less than four months (Mondragon- Jacob & Pimienta-Barrios 1995). According to De la Barrera & Nobel (2002), 85% germination occurred in seeds that were 11 to 28 months old. Seeds should be kept at cool temperatures (13 to 20^{0}C) and under diffused light conditions, to induce germination (Mondragon- Jacob & Pimienta-Barrios 1995).

2.5.4 Seed germination

Seed germination studies, carried out on different *Opuntia* spp collected in western Texas, revealed that scarification with sulphuric acid consistently increased germination (Mondragon-Jacob & Pimienta-Barrios 1995). Optimum constant temperatures for germination were generally between 25°C and 35°C and alternating temperatures enhanced germination (Reinhardt *et al.* 1999). Seed germination was higher at higher water potential (Barrera & Nobel 2002). There was a trend towards increased germination following leaching in water for 12 hours, which suggests the presence of chemical germination inhibitors. Seeds that have passed through the digestive tract of cattle, exhibited an average germination percentage of 1.5 times greater than in seeds removed from ripe fruits (Mondragon-Jacob & Pimienta-Barrios 1995).

Seeds can be used for propagation but take a long time to grow. Three to four years may pass before flowers and fruits appear. The second or third cladodes to form will bear flowers and fruits (Family Farm Series 1989). Therefore vegetative propagation is preferred to seed propagation.

2.6 Root types

Very limited studies have been done on cactus roots so far and this area needs more attention. Cactus pear is a shallow rooted crop with a fleshy root system spreading horizontally up to 4 to 8m from the mother plant (Hills 1995). The root distribution pattern depends on soil type and cultural management. The cactus pear grows best on sandy loam soils. However cactus pear is adapted to many soil types and climatic conditions and it is easily established with low labour requirements.

There are four kinds of cactus pear roots, namely skeletal roots or main roots, absorbing roots, root spurs and roots developing from the areoles (Hills 1995).

- Skeletal roots: these are the primary skeletons of scarcely fibrous roots, which are 200 to 300 mm long. The lateral roots grow from the skeletal roots.
- Absorbing roots (rain roots): These roots grow rapidly from the lateral roots in response to soil water. They grow from the hidden latent bud in the cortex of the older roots.
- Root spurs: This type of root develops as a cluster from the bulkiest mass of roots. There are no glochids present. They are short, gross and fleshy with plenty of root hairs.
- Roots developing from the areoles: These roots develop when the areoles come in contact with the soil. At the onset of their development, they are gross and without root hairs. The young roots grow rapidly. They become slender with a cortex of three to four cells thick and are covered by many root hairs. In time, all the roots developing from the areoles make up a real root system.

2.6.1 Root formation in the areoles

The roots develop from the areoles once the cladodes come in contact with the soil or any other growth media. The root primordia originate from phloem cells located below the areoles. Primordia emergence takes as short as two weeks. The stimulus to cell differentiation and multiplication may occur very early, within the first 48 hours (Fabbri *et al.* 1996).

The primordia never penetrate the areoles but rather turn around them and run parallel to the areolar cavity to emerge through the cladode tissue adjacent to the areolar cavity. The areole surface appears to be somehow impenetrable to the primordia. It is eventually crushed by root growth. The adventitious rooting process, with the emergence of several roots per areole, may take up to 2 to 3 months (Fabbri *et al.* 1996).

Early mitotic divisions in the phloem cells, initial development and primordial growth take place simultaneously within the same areole. *Opuntia* stem cuttings do not respond to excision and subsequent favourable rooting conditions with a stimulus to the cambium to resume activity. Only some well-differentiated tissues such as phloem and inner parenchyma, display in the first days, a localised mitotic activity that soon leads to root regeneration (Fabbri *et al.* 1996).

2.6.2 Root characteristics

As has been mentioned above, cactus pear is a shallow rooted crop with a fleshy root system. Normally the main roots develop 300 mm deep in the soil, but during droughts more lateral roots develop to ensure efficient water uptake around 100 mm soil depths. The periodically fertilised cactus pear develops succulent and unbranched roots (Hills 1995).

Cactus roots have xeromorphic characteristics, which help the plant to tolerate drought in different ways.

- Firstly the fine roots are covered with a layer, which is relatively impermeable to water.
- The roots abscise by a cicatrization layer to avoid water loss in dry soil.

There are three ways in which cactus roots contribute towards drought tolerance.

- Firstly the roots restrict their surface contact with the soil and decrease their permeability to water.
- The rain roots develop to rapidly absorb small quantities of water supplied by the light rains.
- Cladodes transpiration is decreased through high negative water potentials, leading to high hydraulic resistance, which in turn decrease water flow to the shoots.

The root water conductivity decreases about 10 times during soil drying after which water loss is reduced from the plant tissue to the soil (Nobel 1997). The lateral roots and rain roots develop when the soil is wet and the absorption of water and nutrients increase. Root regeneration takes place easily in cactus pear but the period varies with species and temperature, but can however be accelerated by externally applied hormones. Cacti are relatively tolerant to waterstress but are highly sensitive to salinity. The taproots die back as they avoid Na^+ uptake (Nobel 1997). *Oputia*'s high water use efficiency makes it more efficient in converting water into dry matter than other traditional crops (Murilo-Amador *et al.* 2001).

Root volume of *Opuntia* species can be related to canopy development. Both cladodes size and number can also decrease linearly with container size if planted in pots (Inglese and Pace 2000). The effect of root confinement can still be significant after transplanting plants into the field, with vegetative growth and cladodes size lower for plant coming from the smallest containers

Root/cladodes ratio decreases with increasing salinity. The higher the salinity, the lower the cladodes fresh weight, the succulence of the cladodes and root fresh weight, dry weight and root length (Murillo-Amador *et al.* 2001). Root growth of cacti can also drastically be inhibited by seawater concentrations (Murillo-Amador *et al.* 2001). As salinity increases, the cladodes' osmotic pressure increases and is then associated with tissue dehydration. *Opuntia ficus-indica* has been reported to reduce its growth by half when continually exposed to NaCl (1/10 seawater) (Murilo-Amador *et al.* 2001).

2.6.3 Effect of low temperature on roots

Cladode thickness, cladode water content and water potential decreased with low temperatures (Cui & Nobel 1991). The osmotic pressure increases with low temperatures. Transpiration decreases gradually with lower temperatures and root water uptake decrease immediately and to a greater extent. Stomata open more for cacti and other CAM plants at low temperatures (Cui & Nobel 1991). Lower temperatures can change membrane configuration in root cells, which could substantially decrease its permeability to water (Cui & Nobel 1991). Root hydraulic conductivity decrease more than their transpiration as temperatures decrease towards freezing, leading to desiccation of the cladodes (Cui & Nobel 1991).

2.6.4 Effect of drying and rewetting on root hydraulic conductivity and sheath formation

Root hydraulic conductivity decreased with root age for *F. acanthodes* and *O. ficus-indica* under wet conditions. Changes in root hydraulic conductivity were accompanied by changes in root structure. For young, 1-month-old roots of *Ferocactus acanthodes* and *O. ficus-indica* hydraulic conductivity (L_p) decreased only slightly in response to drying. Rewetting restored conducting completely for 1-month old roots but only partly for 3- and 12- month old roots (Cui & Nobel 1991).

The reduced L_P can help restrict water loss to dry soil yet the recovery upon rewetting can re-establish substantial water uptake when soil water is restored (Cui & Nobel 1994). An increase in abscisic acid concentration during droughts can influence hydraulic conductivity. For 1-month-old roots of *Opuntia* species, root hairs were more numerous at 7 and 30 days of drying than at 0 days. After about 2 days of drying, soil particles adhered to the root surface in the root hair zone, forming soil sheaths (North & Nobel 1991). Anatomically, 12-month old roots of *F. acanthodes* and *O. ficus-indica* were essentially unchanged throughout 30 days of drying. Structural changes in response to rewetting were slight for 1-month old roots of both species (North & Nobel 1991).

For 1-month old roots, the slight decrease in hydraulic conductivity during drying followed by an increase to nearly its original value is accompanied by the development of persistent soil sheaths (North & Nobel 1991). For several species in the field, dry soil and poor roots/soil contact increase the production of both root hairs and mucilage. Soil sheaths, while not impermeable to water, might restrict water movement from root surface to a drier bulk soil (North & Nobel 1991).

The apparent dehydration of cortical cells in 1-month old roots at 7 and 30 days of drying could cause the roots to shrink, leading to an air filled gap between the sheath and the bulk soil. The permeability to water of suberised cell walls can decrease markedly and irreversibly upon drying or exposure to air. A drought induced decrease in the permeability of the periderm could have contributed not only to the decline in Lp that occurred for 3- and 12- month old roots of *F. acanthodes* and *O. ficus-indica* but also to their limited recovery after rewetting (North & Nobel 1991).

Water movement into and out of roots depends on the water potential difference from the bulk soil to the root xylem and the conductivity of three root-soil pathways: the root, the root-soil air gap and the soil (Huang & Nobel 1992). As the roots of these succulents shrank during the next 13 days of soil drying, water movement was limited mainly by the root-soil air gap (Nobel & Cui 1991). The increasing of the air gap around the roots would then help prevent water loss to the drying soil (Nobel & Cui 1991).

The water available to roots in a wet region of soil can be transferred by the root system to drier regions of the soil, especially at night (Nobel & Cui 1991). During drying, soil particles in the sheaths aggregate more tightly, making the sheaths less permeable to water and possibly creating air gaps. The soil sheaths of *O. ficus-indica* thus reduce water loss from the roots to a drying soil (Huang *et al.* 1993). Soil sheaths developed around 2-week old roots of *Opuntia ficus –indica*, except near the root tip where few soil particles adhered (Huang *et al.* 1993).

The mucilage covering the surface of the root hairs and adjacent soil particles apparently helped maintain the integrity of the sheath. Similar soil sheaths develop around the roots of species, including *Ferocactus acanthodes*, *Glycine max*, *Oryzopsis hymenoides* and *Zea mays* (Huang *et al.* 1993). The sheathed roots of *O. ficus-indica* had a higher water potential, a lower rate of water loss, and a more turgid appearance compared with unsheathed roots, especially at low soil-water potential (Huang *et al.* 1993).

The dehydration and contraction of mucilage also cause the overall soil sheath to contract, leading to an increase in the air space between the roots and bulk soil. Water movement can be greatly restricted by the low hydraulic conductivity of an air gap as the root shrink. For instance, when the soil is rewetted, unsheathed roots of *O. ficus-indica* swell, the air gaps are eliminated and root hydraulic conductivity is the primary limiter of water movement (Huang *et al.* 1993). Also upon rewetting the mucilage increases greatly in volume, which should increase the space between soil particles in the sheath, thereby increasing its permeability to water. Rewetting of the sheath should also eliminate the air gap created by its contraction during drying (Huang *et al.* 1993).

The morphological characteristics of lateral roots of *Ferocactus acanthodes* and *Opuntia ficus–indica* can vary with soil-water status. Under wet conditions, the elongation rate decreases with root age. Drought caused some of the primary lateral roots to abscise in *F. acanthodes* and to die in *O. ficus–indica*. The root surface area increased after rewetting as a result of the development of new lateral roots, especially in *O. ficus–indica* (Huang & Nobel 1992).

Important adaptive strategies for desert plants include to maximise water uptake and to minimise water loss to dry soil. Such morphological and physiological responses of lateral roots to soil-water availability are important for desert plants that face long periods of drought and sporadic rainfall, as well as presumably for other plant species growing in less severe environments, but still with seasonal soil-water content variations (Huang & Nobel 1992).

Chapter 3

Effect of various water application strategies on root development under glasshouse growth conditions.

3.1 Experimental layout

A 2×4 (*Opuntia* species and water treatments) factorial experiment, with fully randomised design was conducted. There were two replications for each water treatment.

3.2 Methodology

The research was conducted during the 2002/2003 growing season (September 2002 to March 2003) in the glasshouse. The temperatures were regulated between 25 and 30^0C during the day and 15 to 18^0C during the night over the trial period. 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 soil consists of 16 % clay + silt, a pH (KCl) of 4.5 and 53.8 ppm nitrogen. 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 millimetres crashed 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 107 planted pots were prepared of which 80 were randomly selected and used as described in this chapter. The rest of the pots will be described in the next chapters. Five of the pots were used to determine the soil-water depletion intervals, which will be discussed under 3.3.

One-year-old cladodes of *Opuntia ficus-indica* (cultivar Morado) (green-cladodes and *O. robusta* (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 1406 ± 170 g fresh mass (means ± SE, n = 10). The 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 and then planted in the pots with one quarter (50 to 60 mm) of the cladode in the soil. Each cladode was weighed before planting. The cladodes were placed North/South in the glasshouse (Fig. 3.1). The planting was done on the 4th September 2002.

Figure 3.1 The cladodes of *Opuntia robusta* after planting in the pots.

3.3 Treatments

Four water treatments namely, T1 = 0 to 25 % depletion of plant available soil water (PAW), T2 = 25 to 50 % depletion of PAW, T3 = 50 to 75 % depletion of PAW and T4 = 75 to 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 permanent wilting point (PWP) of the soil. In determining field water capacity (FWC) the pots were then saturated with water and left for 48 hours 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 were then added.

Each planted pot was kept in the weight range of the water treatments for different periods. These different treatments or periods studied include:

- Root and cladodes measurements took place at one, two and three months after being kept at different water levels. Forty-eight pots were used. This was done to measure the plant development at the different water treatments over time (3 months).
- The pots were filled to FWC and then the root and shoot component was monitored after reaching each water treatment level. Sixteen pots were used and randomly selected from the rest of the pots. The remaining 16 pots were also stressed after filling to FWC.
- The remaining 16 pots were watered for the second time to FWC after it was stressed to PWP (as described above) and then roots and cladodes were measured.

The last two treatments were done to get an idea of the plants' response to water stress and the recovery thereafter over the short-term.

3.4 Data collection

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

3.4.1 Root and cladodes mass

The roots of the plants were sieved through a 2 mm and 0.05 mm mesh after it was removed from the cladodes. The roots and the cladodes were dried at 100^0C for 16 hours and weighed.

3.4.2 Root Length

The length of the washed roots was measured by using a modified infrared root length counter (Rowse & Philips 1994). The root counter was first calibrated by using ten pieces of string being cut at different well-known (range from 0.5 to 5 m) lengths. 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 surface from where 6 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, x = root length (m) and $R^2 = 0.9406$. The averages of 6 readings were taken from each plant. The lengths of all roots in each pot were measured.

3.4.3 Root thickness and number of side roots per taproot

The thickness at the end of the root where die back took place as well as the thickness of the tap roots at 30 mm intervals were measured by a vanier calliper. 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 taproot was determined. Ten roots, randomly selected, were measured in each pot.

3.4.4 Water-use efficiency

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 was calculated in two ways for the cladodes. Firstly, only the newly formed cladodes were taken into account and secondly, 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 ten cladodes were weighed before and after drying at 100 °C for 16 hours. All other cladodes were planted the same day.

The obtained average DM was then used to work back 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 then included in calculating the WUE. The average water content of the ten cladodes for *O. ficus-indica* and *O. robusta* was 88.13 % and 87.29 % respectively.

3.4.5 Water needed to fill up the cladode

When the plants were ready for data collection, the plant and pot were weighed and then watered up to field capacity again and left overnight to settle down. The soil was then covered to avoid evaporation. The next day, the potted plant plus the soil were weighed again and the cladodes alone (after washing) were also weighed.
The water up-take was calculated by the following equation:

$[(d + c) - e] - b = a$

$d - a$ = 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.

3.5 Data analysis

The data collected was analysed by SAS, which is a statistical software analysis program. The one-way analysis of variance at 95 % confidence interval was conducted to determine any significant difference. Tukey test was used to find out where exactly the difference is (Mendenhall & Sincich 1996). In determining least significance difference (LSD), the method of Fisher (1949) was used.

3.6 Results and discussion

As discussed above, the study was divided into three experiments so the results are also going to be presented and discussed under three different sub headings (Table A.2).

3.6.1 The influence of four water levels over a three monthly period

3.6.1.1 Root mass

The root mass decreased ($P \leq 0.05$) with water stress for both *Opuntia* species during the three months growth (Fig.3.3). 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 and 27 g plant^{-1} and the lowest was between 10 and 15. 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* (Fig.3.2), 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. Root mass remained nearly the same ($P > 0.05$) for all water treatments for all three months.

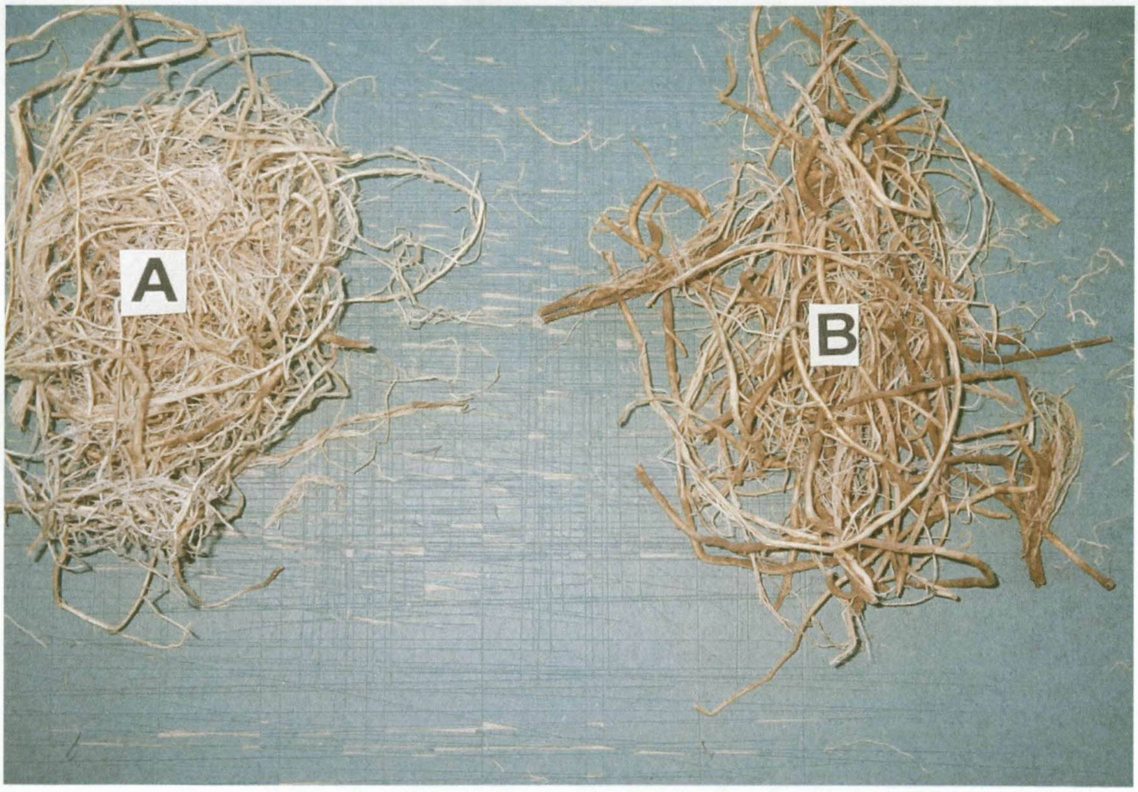
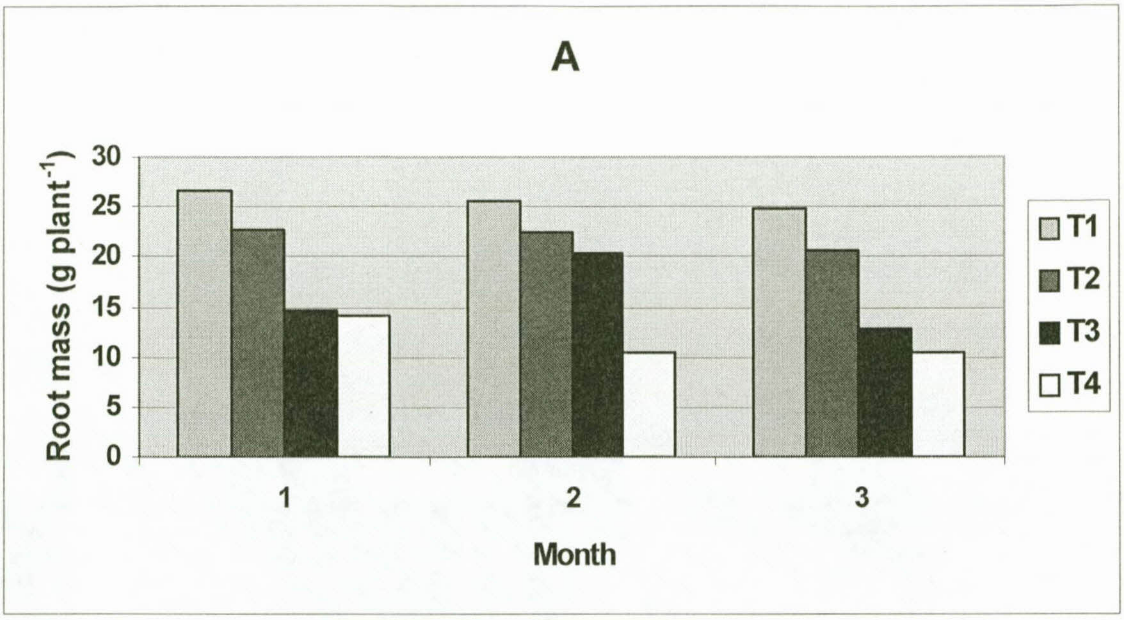


Figure 3.2 Roots of *O.ficus-indica* (B) and finer roots of *O. robusta* (A) after washing.



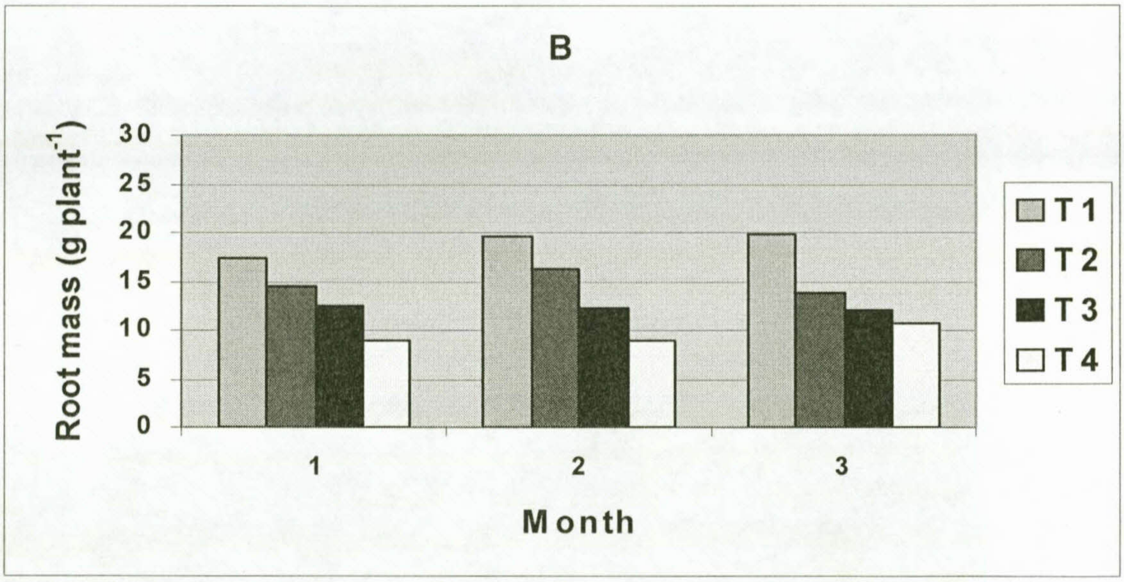


Figure 3.3 Root mass (g plant $^{-1}$) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 =50 to 75 % T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 1.0208 and treatments = 1.9146.

3.6.1.2 Root length

Root length increased (P<0.05) from month 1 to month 3 in all treatments for both species (Fig. 3.4). Root length decreased (P<0.05) with water stress in each month for both *Opuntia* species with the exception of T3 for all months, 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.

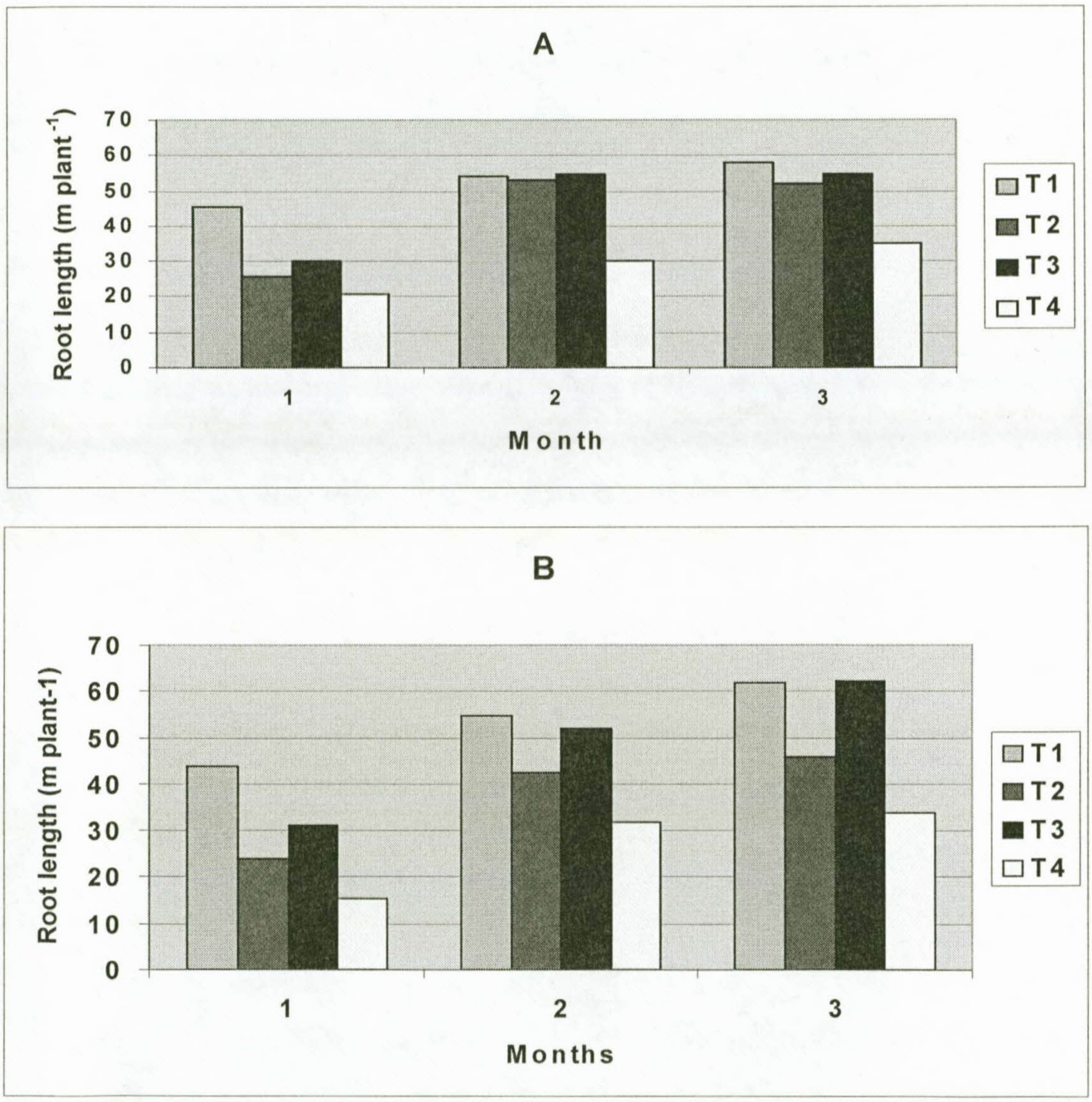


Figure 3.4 Root lengths (m plant^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2, and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species =3.4232 and treatments = 6.4206.

In both species the roots were longer at T1 and T3 than T2 and T4. For most water treatments the root length of the species differed not much ($P>0.05$).

3.6.1.2 Root length/root mass ratio

The root length/root mass ratio increased ($P<0.05$) with water stress for *O. ficus-indica* over the last two months (Fig. 3.5). In contrast for *O.robusta* the root length/root mass ratio decreased for the first and the third month. It also increased with time from the first month to the third month in both species.

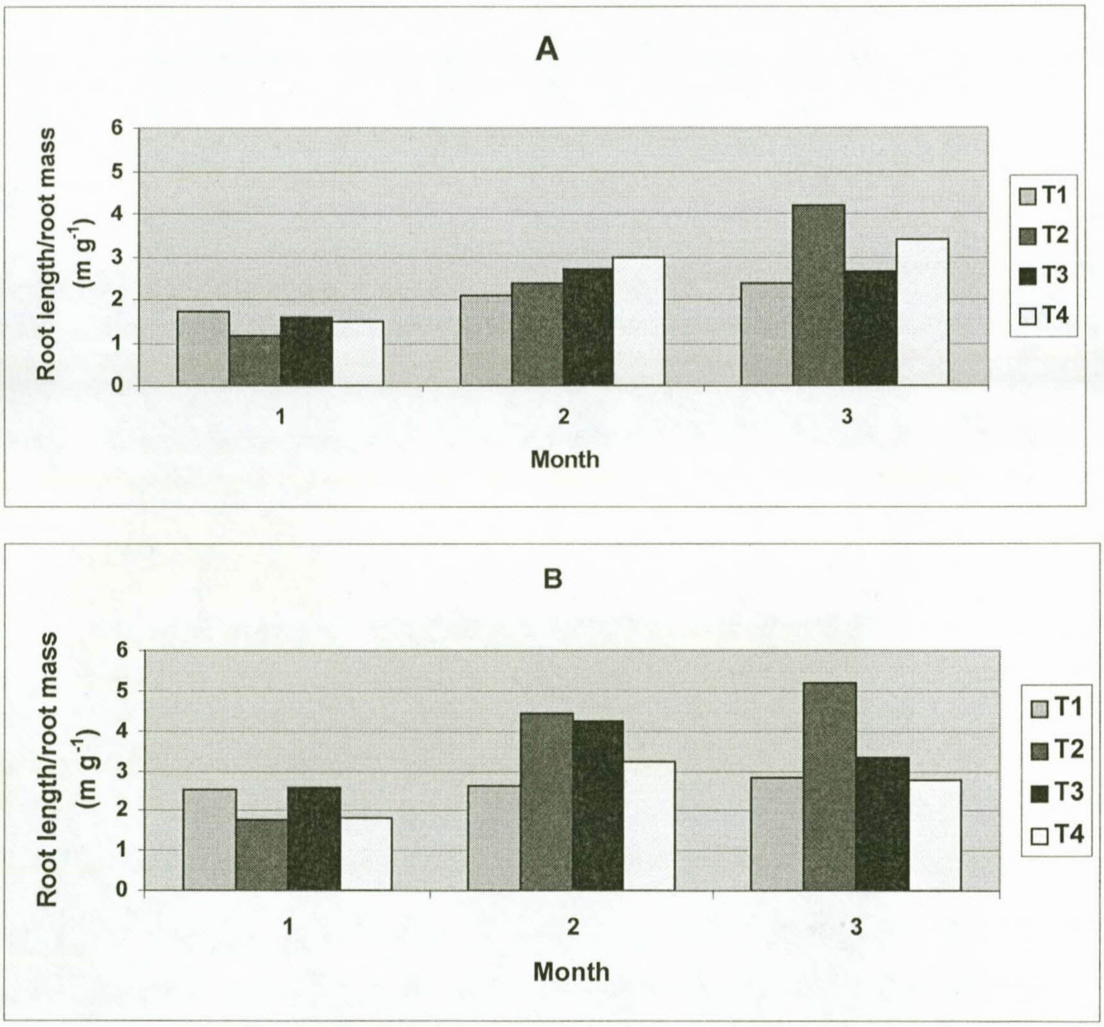
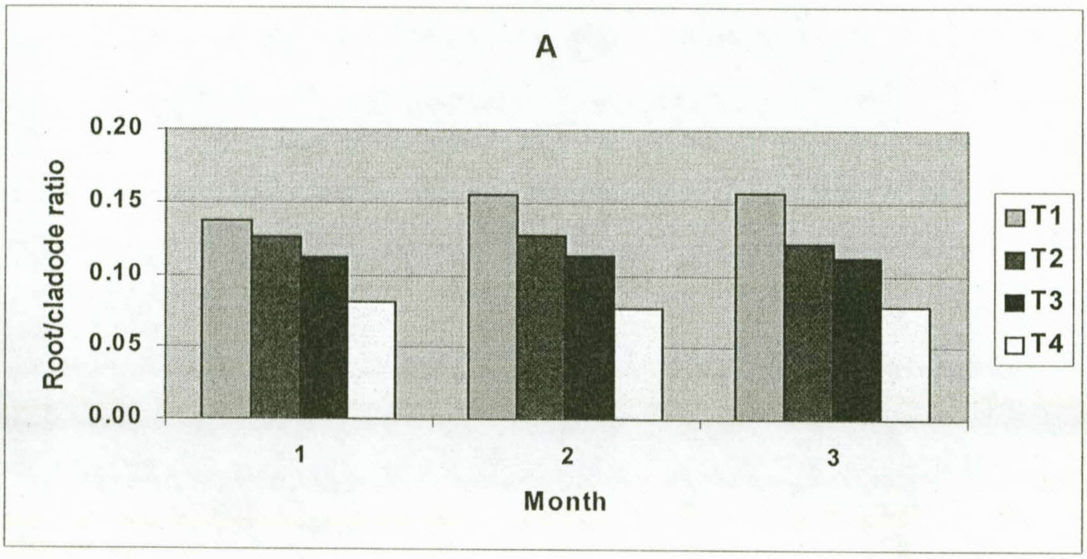


Figure 3.5 Root length/root mass ratio (m g $^{-1}$) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1; 2; and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil-water. LSD $_{0.01}$: species = 0.3680 and treatments = 0.6284.

3.6.1.4 Root/cladodes ratio

Mass based, root/cladodes ratio decreased ($P<0.05$) with water stress for all three months for both *Opuntia ficus-indica* and *Opuntia robusta* (Fig. 3.6). It also increased ($P<0.05$) from month 1 to month 3 for both species. The root/cladodes ratio for *O.ficus-indica* of 0.14 as found by Drennan & Nobel (1998), supported the very low values found in this study regardless of the water application or over time.



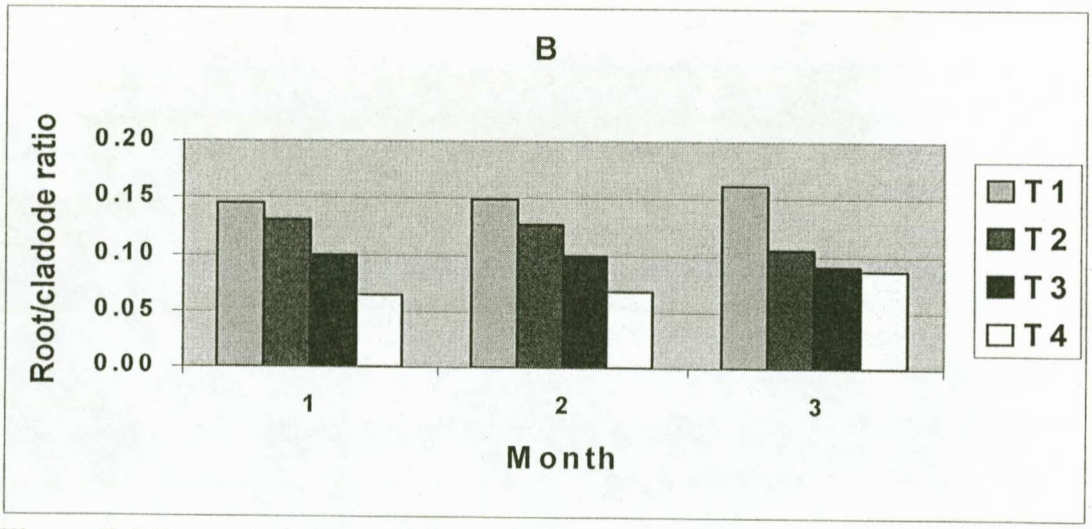


Figure 3.6 Root–cladode ratio for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1; 2; and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.0059 and treatments = 0.0112.

3.6.1.5.1 Water–use efficiency (roots)

Water-use efficiency of both *Opuntia* species decreased ($P<0.05$) with water stress (Fig. 3.7) over the three months. The water–use efficiency of *O. ficus-indica* decreased ($P<0.05$) with time, from the first month 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.*

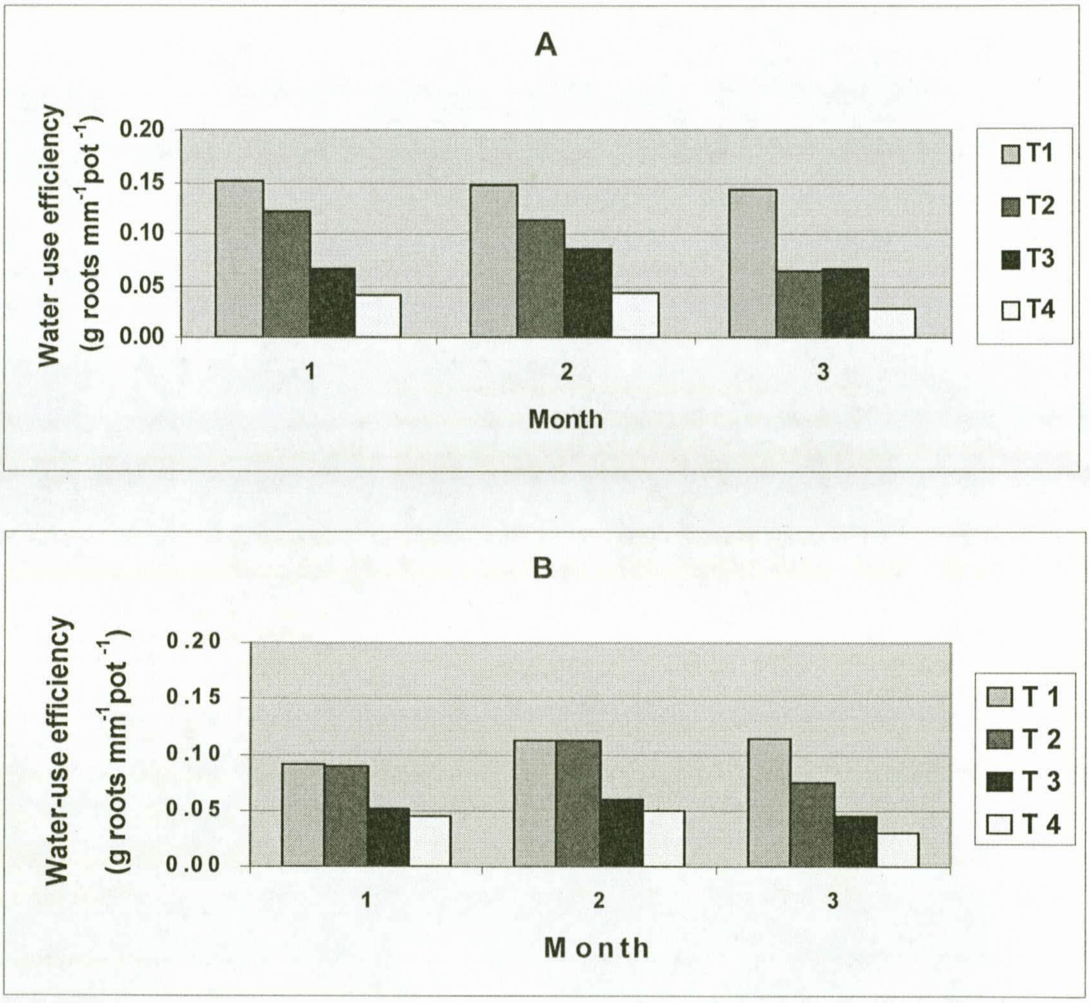


Figure3.7 Water–use efficiency (g roots mm^{-1} pot^{-1}) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1; 2; and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. $LSD_{0.01}$: species = 0.0059 and treatments = 0.0112.

3.6.1.5.2 Water-use efficiency (cladodes)

Water–use efficiency decreased ($P<0.05$) with water stress for *O. ficus-indica* and it increased ($P<0.05$) with water stress for *O. robusta* for most months (Fig.3.8).

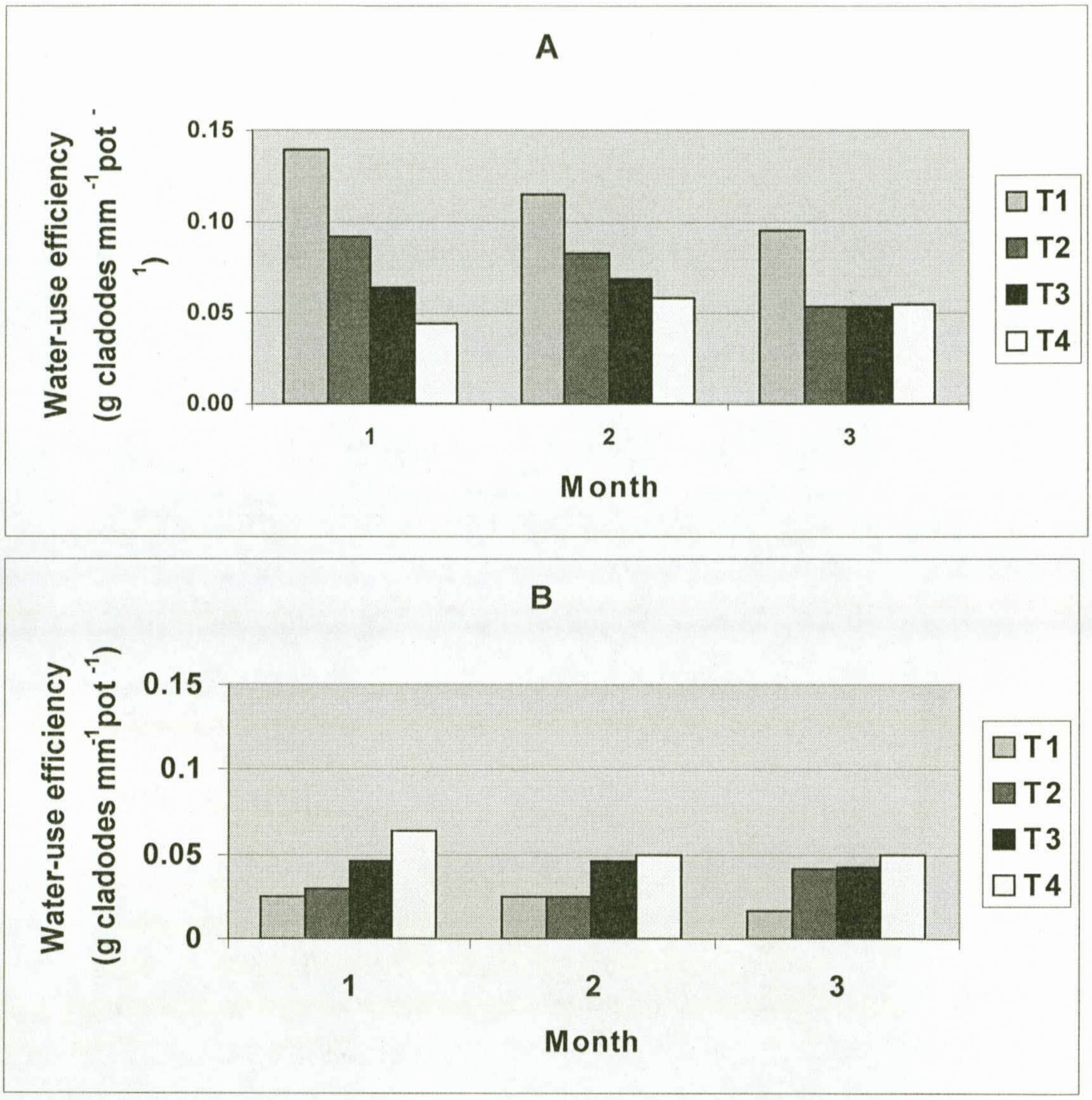


Figure 3.8 Water-use efficiency (g cladodes mm^{-1} pot $^{-1}$) for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1; 2; and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.0083 and treatments = 0.0156.

There was no difference ($P>0.05$) in water–use efficiency in the last two months for each species. The water application has therefore a greater influence on WUE than the growth stage of the plant. The WUE presented in Figure 3.8 included the increase in mass of the mother cladode over time. These values did not differ much (P>0.05) when the mother cladodes mass increase was not included.

3.6.1.6 Amount of water to fill the cladode

The cladodes of T4 showed signs of water stress throughout the three months trial period. These signs include decreasing firmness of the cladodes than those of other water treatments. Although not measured, the cladodes of T4 appeared thinner than that of other water treatments.

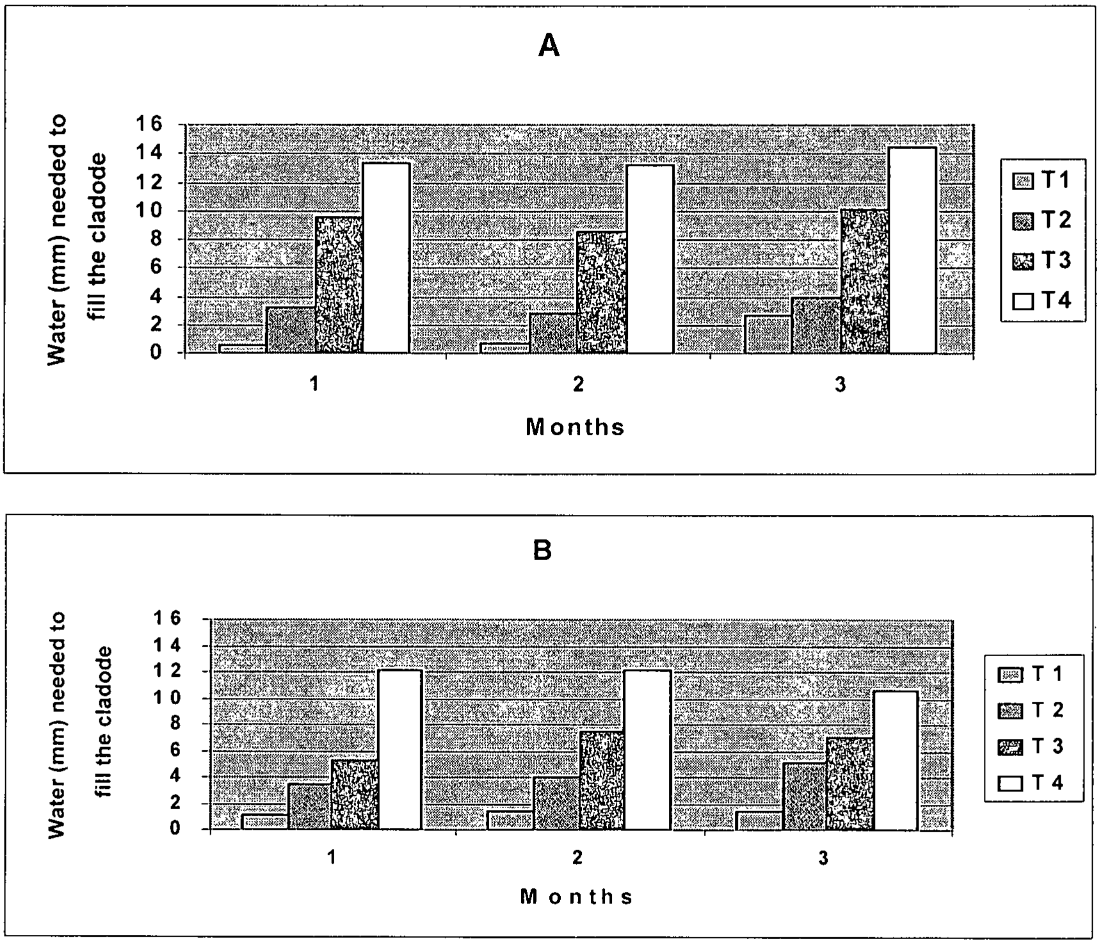


Figure 3.9 Amount of water (mm) needed to fill up the cladode for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1; 2; and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.4133 and treatments = 0.7751.

The amount of water needed to fill up the cladode increased ($P<0.05$) with water stress in all the months (Fig. 3.9). The higher the plant available water, the less water needed to fill up the cladode. Both species responded the same ($P>0.05$) towards the 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.

3.6.1.7 Percentage water in cladodes

The percentage water in the cladodes decreased ($P<0.05$) with water stress for *O.ficus-indica* (Fig.3.10). 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.

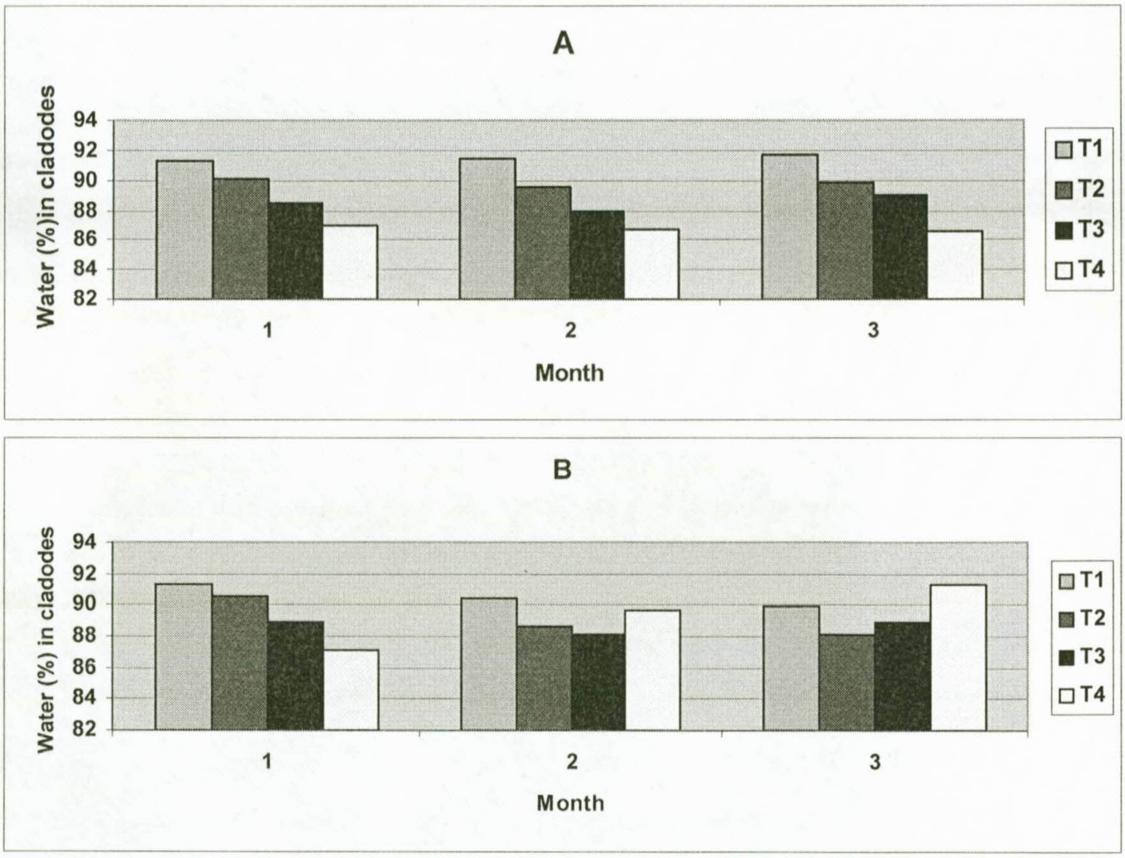


Figure 3.10 Water (%) in the cladodes for *Opuntia ficus-indica* (A) and *Opuntia robusta* (B) under the different water treatments measured after 1, 2 and 3 months. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.2481 and treatments =0.4653.

As the soil became dry, the cladodes were a little bit softer even though it was not much as the lowest water percentage for both species was 86.55 %. The highest percentage water obtained in the cladodes of O. *ficus-indica* was 92. From this it can be concluded that the cactus pear cladodes hold a lot of water even during drought.

3.6.2 Influence of water stress

3.6.2.1. Root mass

The root masses of *O. ficus-indica* and *O. robusta* decreased ($P \leq 0.05$) with water stress (Fig. 3.11). Root mass of *O. ficus-indica* for all water treatments was higher ($P \leq 0.05$) than that of *O. robusta.* The finer root system of *O. robusta* could be the reason for this (Fig. 3.2). The average thickness at the end of the roots for *O. ficus-indica* where die back took place was 0.9 mm T4 compared to that of only 0.3 mm for the less stress treatment. In contrast, for *O. robusta* the average thickness at the end of the roots where die back took place was 0.3 mm for both T1 and T4 water treatments. There could be a contributing factor to the higher root mass of *O. ficus-indica.*

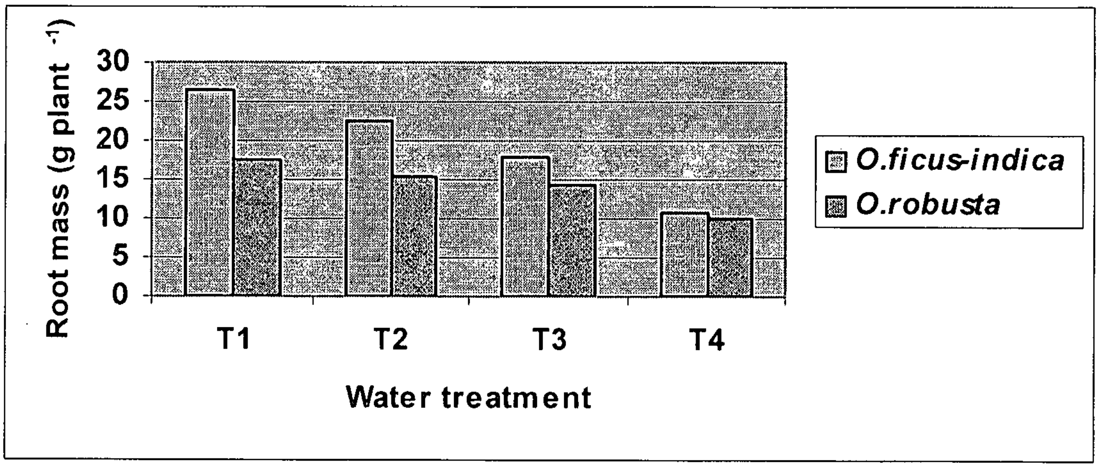


Figure 3.11 Root mass (g plant $^{-1}$) for the *Opuntia* species at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments =1.0672 and species = 2.0959.

The higher the water stress the smaller the difference in root mass between the two species.

3.6.2.2 Root length

In contrast to root mass, the root length increased ($P \leq 0.05$) with water stress in both species (Fig. 3.13). The average length of the roots up to where die off took place decreased with water stress from 300 to 200 mm for *O. ficus-indica* and from 270 to 120 mm for *O. robusta.* This finding explains to some extent the increase in root length with increased water stress. Another reason for the increase in root length with water stress can be the more side roots developing with water stress (Fig. 3.12)

The root length of *O. ficus-indica* was high at T3 and declined to T4 due to root die back. Drought caused some primary lateral roots to die in *O. ficus-indica* (Huang & Nobel 1992; Nobel 1997). The two *Opuntia* species responded almost the same ($P \geq 0.05$) to the water treatments although the root length was higher for *O. ficus-indica* for most water treatments. The combined effect of treatment and species on root length was not significant ($P \geq 0.05$).

Figure 3.12 Roots of *O.ficus-indica* after washing for water treatment T1 (left) and finer roots (more side roots) for T4 (right).

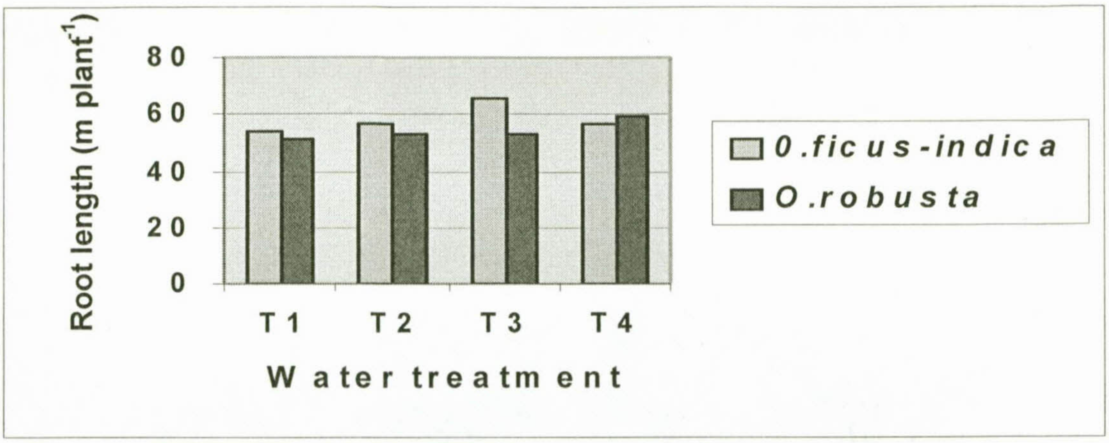


Figure 3.13. Root length (m plant^{-1}) for the *Opuntia* species at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 2.5152 and species = 4.9397.

3.6.2.3 Root length/root mass

The root length/root mass ratio increased (P<0.05) with water stress (Fig. 3.14). This is mainly because the root length increased with water stress (Fig. 3.13) while root mass decreased as well as soil dried out (Fig. 3.11).

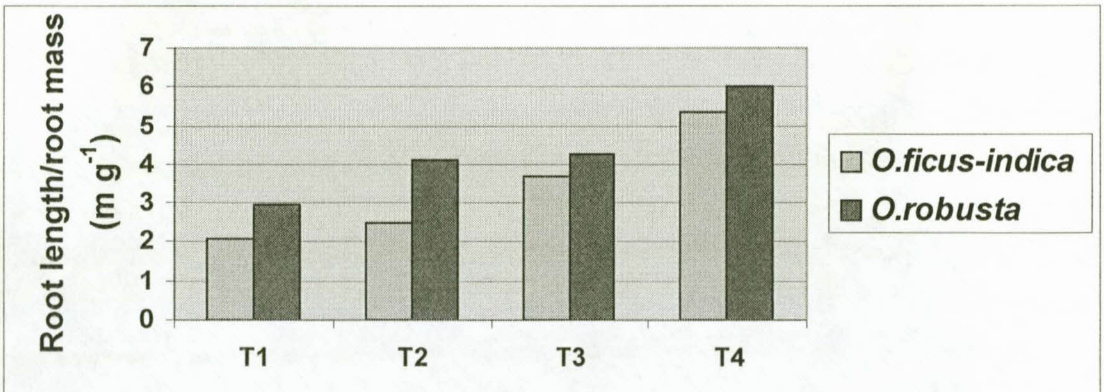


Figure 3.14 Root length/root mass ratio (m g^{-1}) for the *Opuntia* species at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.9823 and species = 0.5.

3.6.2.4 Root/cladodes ratio

For all water treatments *O. robusta* had the lowest ($P \leq 0.05$) root/cladodes ratio (Fig.3.15). The greatest difference in root/cladodes ratio between the two species was at the water treatment T4. With water stress the difference in root/cladodes ratio was not significant ($P > 0.05$) between the two species.

The low root/cladodes ratio for *O. ficus-indica* and *O. robusta* obtained in this study is supported by the 0.14 found by Noble (1988) and Drennan & Noble (1998) on *O. ficus-indica.* Also according to Noble (1995) the root system of *Opuntia* represents only 7 to 12 % of the dry (non-water) weight of a mature plant.

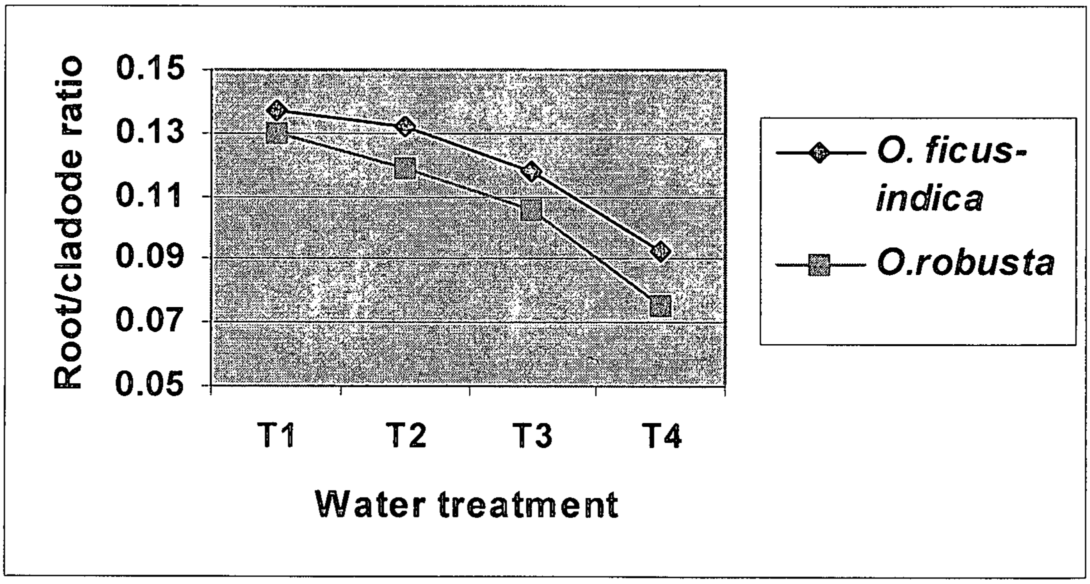


Figure 3.15 Root/cladodes ratio for two *Opuntia* species at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %,T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.0051 and species = 0.0101.

3.6.2.5 Water–use efficiency (WUE)

3.6.2.5.1 Roots

With water stress both *Opuntia* species used water less efficiently ($P \leq 0.05$) if expressed in terms of roots produced per unit of water used (Fig.3.16). Although *O. ficus-indica* used water more efficiently ($P<0.05$) than *O. robusta* under high soil-water content, it became more or less the same ($P>0.05$) with water stress. This must be seen also against the background that the taproots decrease in length with water stress from 680 to 450 mm for *O. ficus-indica* and from 520 to 390 mm for *O. robusta.* On the other hand the side roots increased with water stress from 380 to 480 mm for *O. ficus-indica* and from 220 to 360 mm for *O. robusta.*

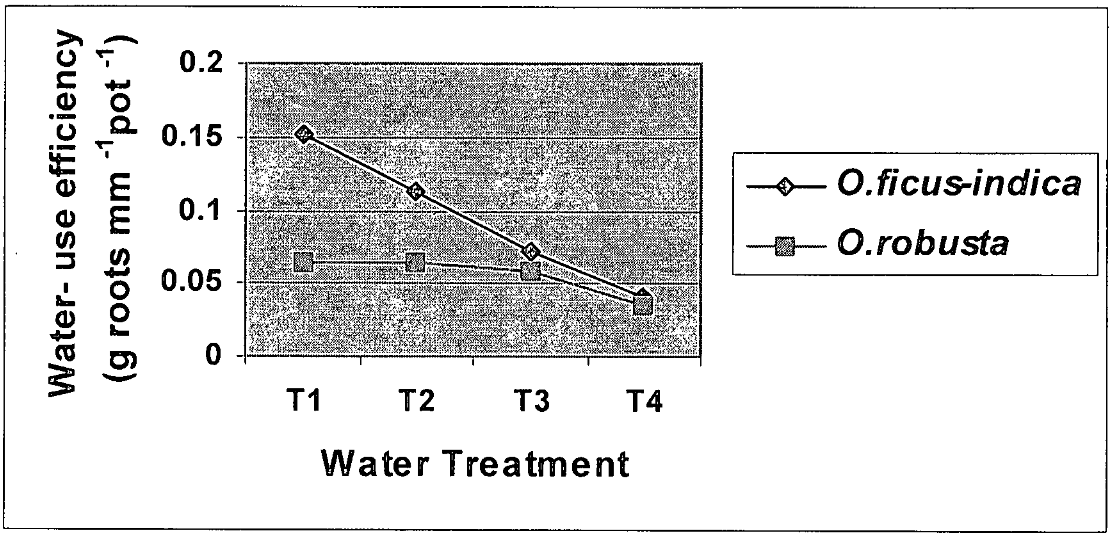


Figure 3.16 Water–use efficiency (g roots mm^{-1}pot $^{-1}$) for the *Opuntia ficus-indica* and *O. robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25%, T2 = 25 to 50%, T3 = 50 to 75% and T4 = 75 to 100% depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.0058 and species = 0.0115.

3.6.2.5.2 Cladodes

The WUE expressed in terms of cladode production per unit of water used, decreased ($P \leq 0.05$) from T1, T2 and T3 to T4 for *O. ficus-indica* (Fig. 3.17). At high soil-water content, *O. ficus–indica* used water more efficiently ($P \leq 0.05$) than the other species, but its water–use efficiency was not significantly (P>0.05) different with water stress. At T4 the water–use efficiency of *O. robusta* was higher (P≤0.05) than that of *O. ficus-indica*. The WUE for *O. robusta* increased (P≤0.05) with water stress, which could be due to the more fine roots of this species (Fig. 3.2).

The number of side roots per tap root also increased with water stress from 24 to 59 for *O. ficus-indica* and from 21 to 91 for *O. robusta*, which can explain the above-mentioned findings to a great extent. With these increases in side roots with water stress the plants are better prepared for taking up water under these lower soil-water potential conditions. Under drought conditions, the succulent cladodes of *Opuntia* have a relatively high water potential of –0.3 to –0.6 Mpa. Some water is lost from the stem but the cladodes and the root water potentials still remain high when compared with non-succulent C_3 or C_4 plants (Nobel, 1995).

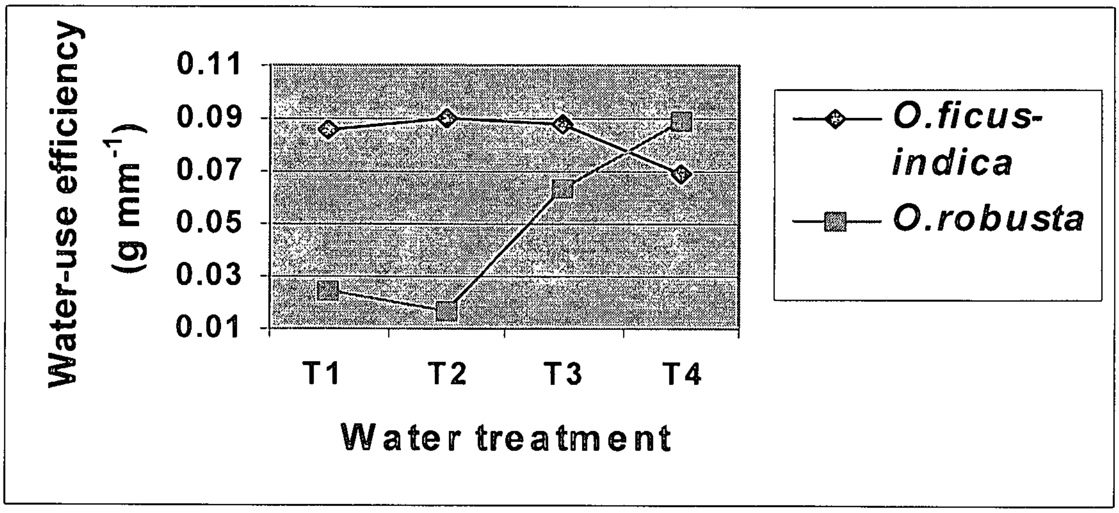


Figure 3.17 Water–use efficiency (g mm^{-1}) for the two *Opuntia* species cladodes at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.0045 and species = 0.0089.

The WUE presented in Figure 3.17 is calculated in such a way as to include the increase in mass of the mother cladode in cladodes dry matter production. There was no big difference (P>0.05) when the mass increase of the planted cladode was not included.

3.6.2.6 Water needed to fill a cladode

Interesting to note that cladodes of both species grow softer and less firm with water stress. The most visible changes in firmness of the cladodes were found at T4. Although not measured the cladodes at T4 also looked visually thinner than that of the other water treatments. In all water treatments the cladodes were restored overnight after watering. From Figure 3.18 it is clear that for both species more ($P \leq 0.05$) water was needed to fill the cladode with water stress. The amount of water needed to fill up a cladode did not differ much ($P > 0.05$) between the two *Opuntia* species within a water treatment. A water application of only 11 mm is enough to fill the cladodes of both species at the lowest water stress, which makes it very adaptable to the drier areas.

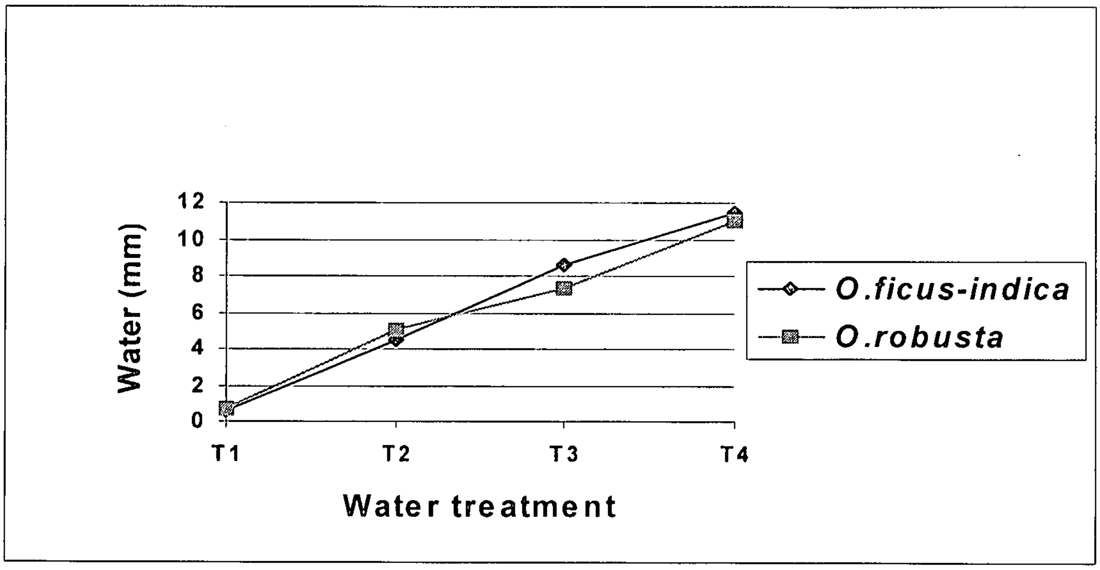


Figure 3.18. Water (mm) needed to fill up a cladode for the *Opuntia ficus-indica* and *O. robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.5776 and species = 1.1344.

A 10 mm water application is sufficient to wet the soil in the root zone of *Opuntia* according to Noble (1995) and raise the soil-water potential above the root water potential and hence leading to water up-take. If such a rainfall occurs on a dry sandy loam, the type of soil in which *Opuntia* commonly grow, the soil-water potential generally remains above the root potential for fewer days. At the lowest water treatment *O. robusta* showed the less water in the cladodes, while it was the same at T1.

3.6.2.7 Percentage water in cladodes

The percentage water in cladodes decreased ($P<0.05$) with water stress for both species. As the soil dried, the percentage water in cladodes also decreased (Fig. 3.19).

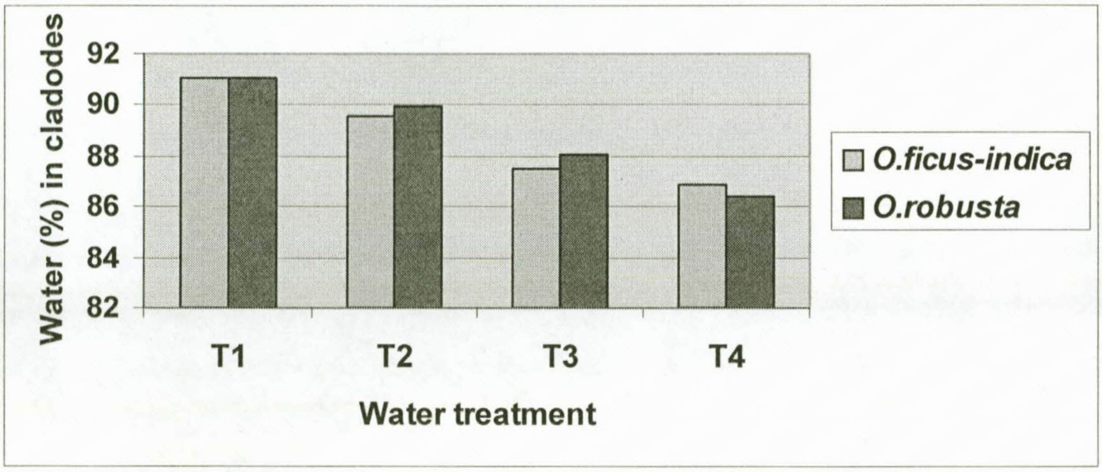


Figure 3.19 Water (%) in the cladodes for the *Opuntia ficus-indica* and *O robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.8323 and species = 0.4238.

3.6.3 Influence of a second water stress after recovery

As discussed in the previous section, at T4 the cladodes were also less firm. The cladodes of the other water treatments also appeared thicker than that of T4. With stress lifting, all cladodes recovered firmness overnight and also visually looked thicker.

3.6.3.1 Root mass

The root mass increased ($P<0.05$) with water stress for both species from T1 to T3 and decreased slightly from T3 to T4 (Fig.3.20). The reason for this decrease might be due to the taproot die back with higher water stress. The thickness of the taproots, measured at 30 mm intervals, increased with water stress from 0.70 to 1.04 mm for *O. ficus-indica* and from 0.4 to 0.9 mm for *O. robusta*. This is an indication that the roots grow shorter with water stress. An explanation for the increase in root mass with water stress, in contrast to the decrease in Figure 3.11, could be that root development had not recovered before the second stress. In most cases the root mass of *O. ficus-indica* was higher than that of *O. robusta*. The reason for this could be the finer root system of *Opuntia robusta* (Fig.3.2).

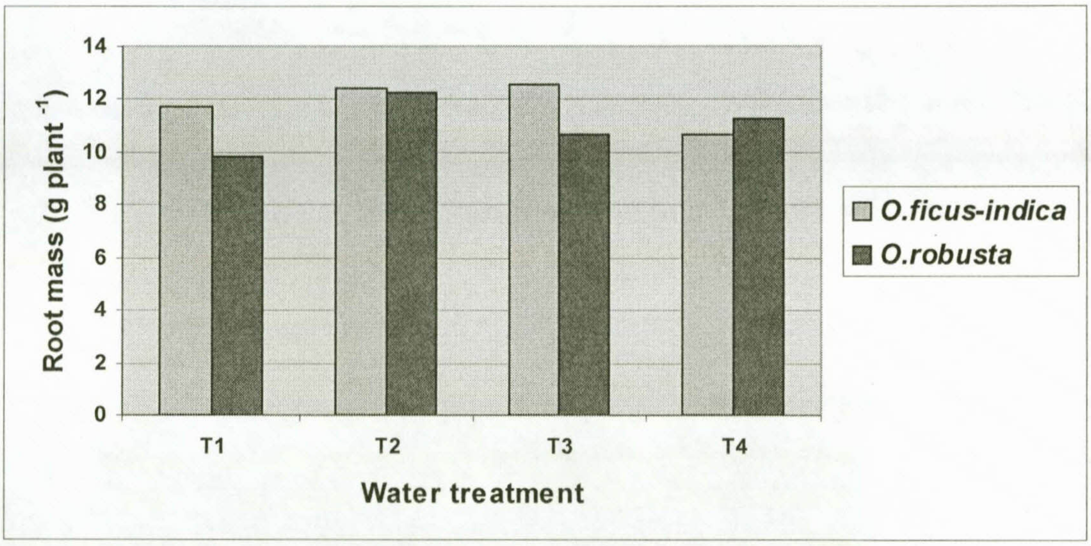


Figure 3.20 Root mass (g plant^{-1}) for *Opuntia ficus-indica* and *O. robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.8443 and species = 6581.

3.6.3.2 Root length

Root length increased ($P<0.05$) with water stress from T1 to T3 and decreased slightly from T3 to T4 for both species (Fig. 3.21). The decrease from T3 to T4 might be due to root die back, which occurs when the plant is highly stressed. This is supported by the finding that the thickness of the roots at the ends where die back occurred increase with water stress from 0.3 to 0.9 mm for *O. ficus-indica* and only from 0.3 to 0.4 mm for *O. robusta*.

The length of the roots up to die back also decreased with water stress from 350 to 100 mm for *O. ficus-indica* and from 220 to 100 mm for *O. robusta*. On the other hand the number of side roots per taproot increased with water stress from 10 to 33 for *O. ficus indica* and from 12 to 31 for *O. robusta*, see also Figure 3.12.

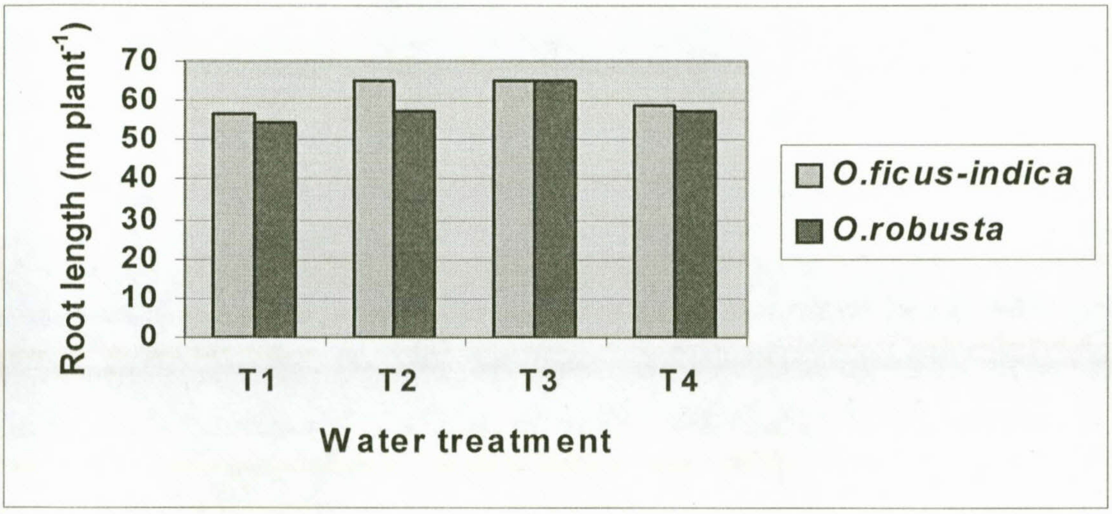


Figure 3.21 Root length (m plant^{-1}) for the *Opuntia ficus-indica* and *O. robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 1.7850 and species = 3.5057.

3.6.3.3 Root length/root mass ratio

The root length and root mass ratio increased ($P<0.05$) with water stress (Fig. 3.22). *Opuntia ficus-indica* showed lower root length/root mass ratio than *O. robusta* in all the treatments except in T2 where it is lower (Fig. 3.22).

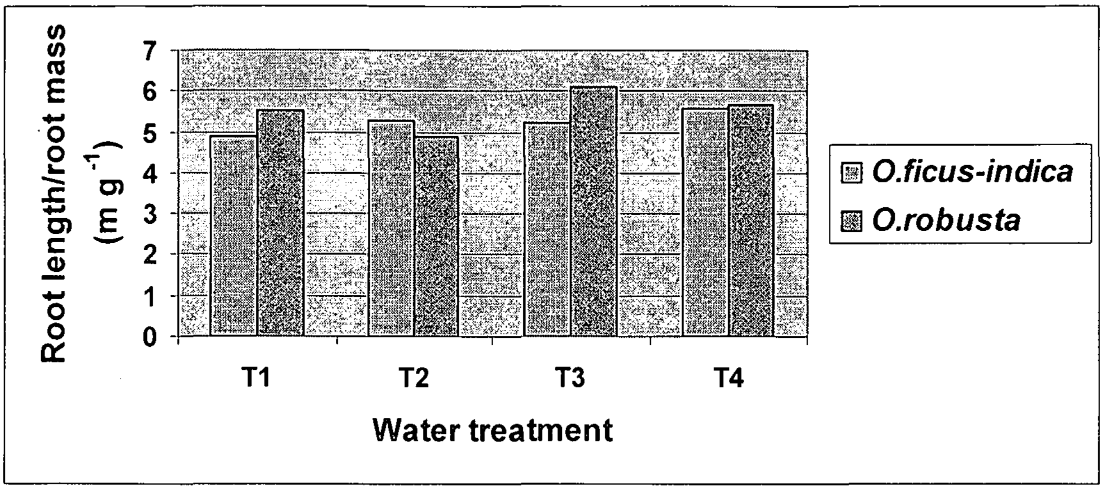


Figure 3.22 Root length/root mass (m g $^{-1}$) for the *Opuntia ficus-indica* and *O.robusta* roots at different water treatments. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.5898 and species = 0.2728

3.6.3.4 Root/cladode ratio

The root/cladode ratio for *O. robusta* increased (P<0.05) with water stress while it decreased (P<0.05) with water stress for *O. ficus–indica* (Fig.3.21).

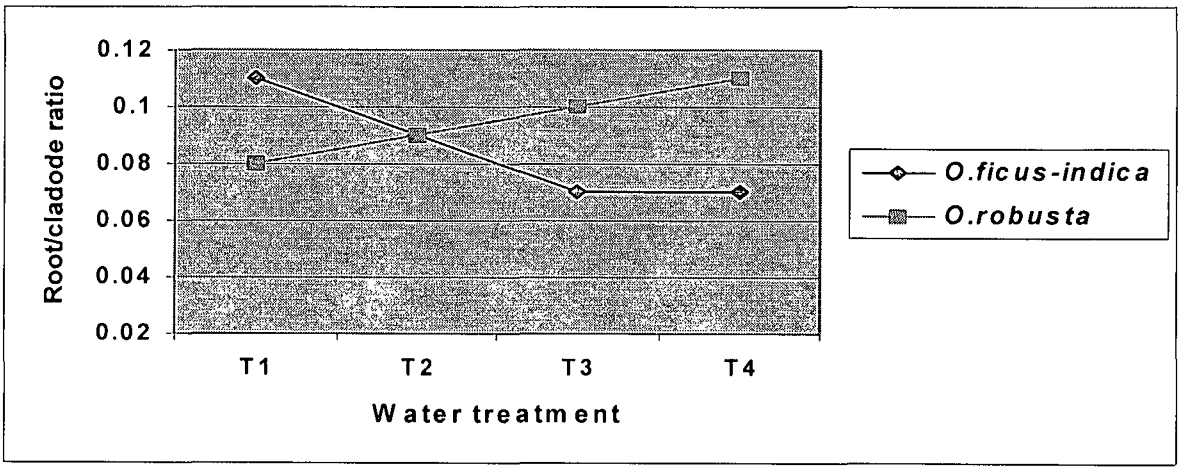


Figure 3.21 Root/cladode ratio for the *Opuntia ficus-indica* and *O. robusta*. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: treatments = 0.0090 at species level and LSD = 0.0177.

With the exception of T1 the root/cladode ratio for *O.ficus-indica* was lower than that of *O. robusta*. The increase in root/cladodes ratio for T2 and T3 could also be due to the fact that with the first water stress the plant was still recovering. At T4 the second water stress affects the plants and therefore the decrease in root/shoot ratio again.

3.6.3.5 Water-use efficiency (WUE)

3.6.3.5.1 Roots

The water-use efficiency expressed in terms of roots decreased with water stress for both species (Fig. 3.22). These lower WUE than that obtained for the first stress (Fig. 3.16) could be due to the plant roots not having recovered after the first water stress and therefore used water not so efficiently. *Opuntia robusta* used water less efficient for all water treatments than *O.ficus-indica*.

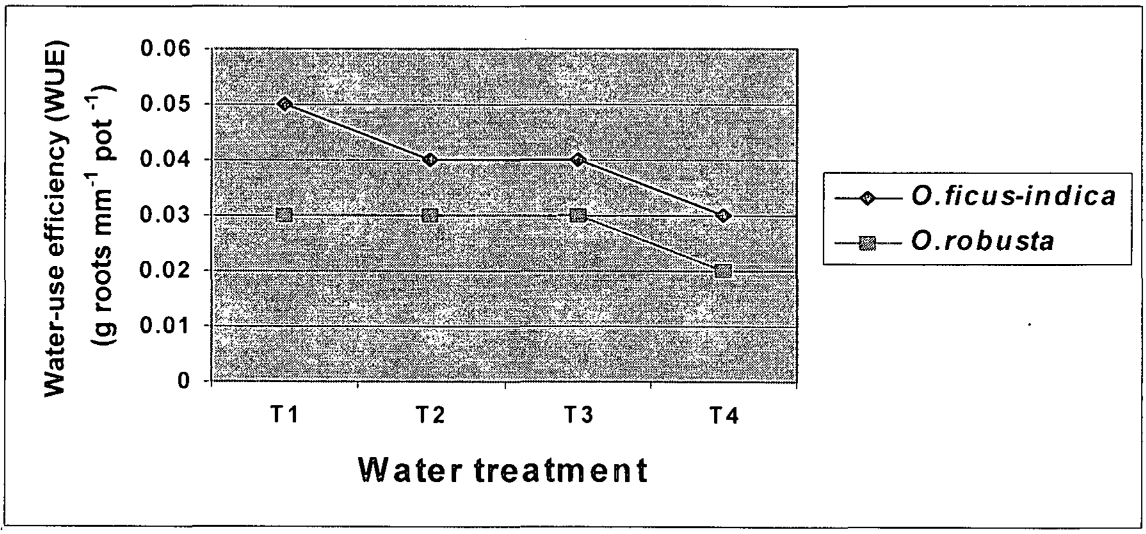


Figure 3.22 Water-use efficiency (g roots mm^{-1} pot $^{-1}$) for *O. ficus-indica* and *O. robusta*. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.0042 and treatment = 0.0084.

3.6.3.5.2 Cladode

The water–use efficiency of the cladodes decreased ($P<0.05$) with water stress for *O. robusta* (Fig. 3.23). Opuntia ficus-indica showed a n increase in WUE from T1 to T2 and again from T3 to T4, while it decreased only from T2 to T3. The water–use efficiency for *O. ficus-indica* cladodes was higher ($P<0.05$) than that of *O. robusta*. This might be due to the different sizes of the cladodes of these two *Opuntia species*. There is no significant difference ($P>0.05$) between root and shoot water-use efficiency in this study.

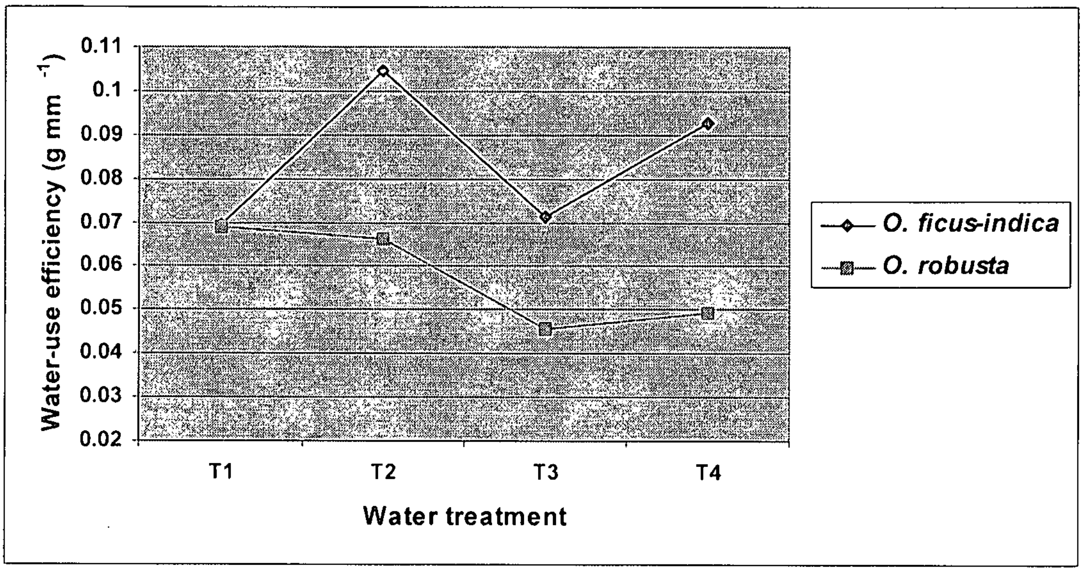


Figure 3.23 Water-use efficiency (g mm^{-1}) for *O. ficus-indica* and *O. robusta*. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.0038 and treatments = 0.0075.

3.6.3.6 The amount of water needed to fill the cladode

The amount of water needed to fill the cladode increased ($P<0.05$) with water stress as expected for both *Opuntia* species (Fig. 3.24). The fact that *O. ficus-indica* needed less water for cladode filling than *O. robusta* in spite of its smaller cladodes is of great interest here. In this case a water application of 12 to 14 mm is needed to fill up the cladodes of the two *Opuntia* species, which is nearly the same as that found with the first water stress.

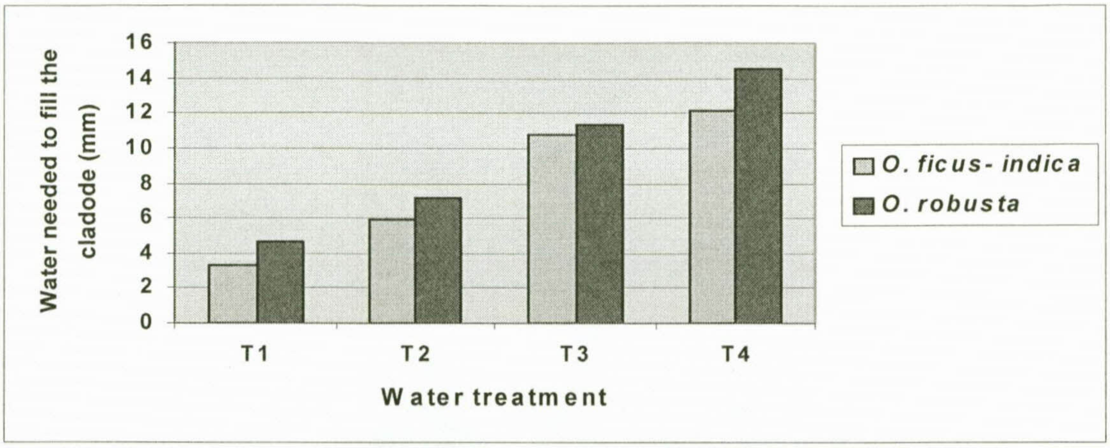


Figure 3.24. Amount of water (mm) needed to fill the cladode for *O. ficus- indica* and *O. robusta.* Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.6362 and treatment = 1.2493.

3.6.3.7 Percentage water in cladodes

The percentage water in the cladodes decreased ($P<0.05$) with water stress for both *Opuntia* species (Fig. 3.25). As plant available water decreased, the water in the cladodes also declined and therefore the amount of water needed to fill up the cladodes increased as shown in Figure 3.24 above.

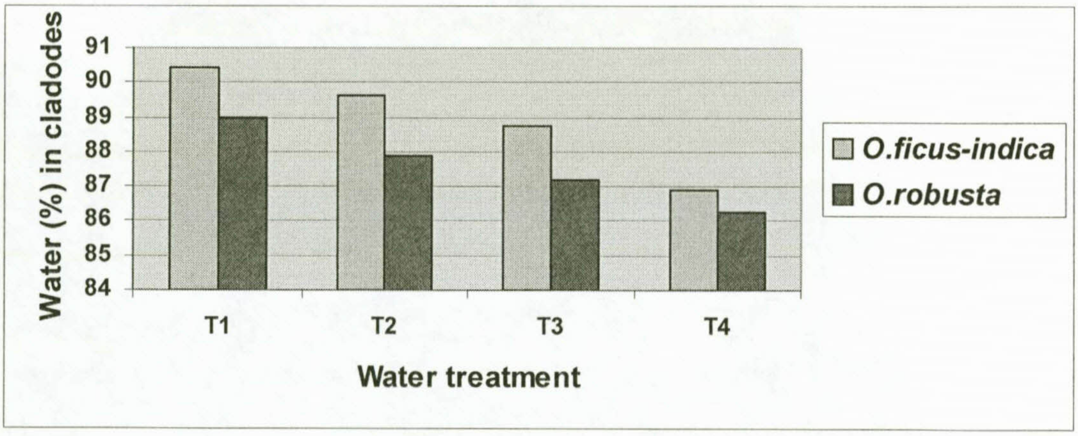


Figure 3.25 Water in the cladodes for *O. ficus-indica* and *O. robusta*. Water treatments are: T1 = 0 to 25 %, T2 = 25 to 50 %, T3 = 50 to 75 % and T4 = 75 to 100 % depletion of plant available soil water. LSD $_{0.01}$: species = 0.3147 and treatments = 0.6180.

3.7 Conclusion

Root mass for both *Opuntia* species decreases with water stress. This might be due to the die back of some taproots and side roots as the plant experiences severe water stress (Huang & Nobel 1992). However the root mass of *O. ficus-indica* is higher than that of *O. robusta*, which consists of mainly smaller side roots than thick taproots. The finer root system of *O. robusta* could also be the reason for lower root mass of this species.

The root length of *O. ficus-indica* and *O. robusta* increased with water stress and decreased slightly due to root die back when the plant is severely stressed. Root/cladode ratio decreased as the plant was stressed. However, as the plant grew older the root/shoot ratio increased. Root length is a better indication of root distribution and absorbing activity than root mass and therefore these results are valuable in future management. Although there is a lack of root studies on cactus pear, the only information is on root mass and not root length.

The water–use efficiency decreased with water stress in *O. ficus-indica* and increased as the plant is stressed in *O. robusta*. This might be due to finer roots of *O. robusta,* which are able to absorb even the little soil water available. These results have shown that strategically placed irrigation is definitely an option for some cactus pears in obtaining better and more constant productions.

In this study only visual observations were made of the 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 it is not significantly correct, gave a good indication of when the plant is in a critical stage. In future more in-depth studies have to be done on identification criteria for water-stress indications in cactus pear.

This information is important in deciding when and how to irrigate this plant for higher water-use efficiency and therefore a better and constant production. This study again showed the effective root system of cactus pear and its ability to absorb small amounts of water very quickly. A water application of only 11 to 14 mm is enough to fill up the cladodes and therefore survive another drought period, as is common in the arid and semi-arid areas. The above-mentioned water up-take can take place overnight and make the plant very unique in the drier areas. The study also showed the fast and rapid recovery of the plant after being severely stressed.

Chapter 4

Dynamics of different root types

4.1 Experimental layout

The experimental layout of the root boxes was a fully randomised design consisting of two treatments (*Opuntia* species) and six replications. The aerial root layout was a 2×3 (2 *Opuntia* species and 3 planting methods) factorial experiment with fully randomised design. There were 10 replications for each planting method.

4.2 Methodology

The planting was conducted in the glasshouse during the 2002/2003 season (September 2002 to March 2003). The glasshouse temperatures were as described in Chapter 3, as well as the soil, cactus pear species and cultivars. The same procedures were followed preparing the cladodes before planting.

4.3 Treatments

4.3.1 Root development from the areoles

The cladodes of both species (*Opuntia ficus-indica* and *Opuntia robusta*) were planted in twelve asbestos pots (100×100 mm and 200 mm deep). Five plants were randomly planted in each pot. The soil was kept between the field water capacity and permanent wilting point over the three weeks study period. The cladodes were planted in three ways to determine the percentage root development from the areoles. The different ways of placing the cladodes included the whole cladode flat on the soil, placed vertically (50 to 60 mm deep) and the last one was placed horizontally (20 mm deep) into the soil. Thirty cladodes of each species were used (ten for each treatment) and were measured over a three-week period.

4.3.2 Root development in the boxes

A cladode was planted into the soil (one quarter, 50 to 60 mm) in each of 12 root boxes of 650 mm length, 100 mm width and 900 mm deep. The boxes were placed at a 15% slope so that the roots growing down could easily be seen through the glass covered by a steel plate that could be removed from time to time for measuring root development (Fig. 4.1).

Figure 4.1 The cladodes planted in root boxes, in the glasshouse. The glass plate can be seen in front of the left box and the steel cover on the right box.

Half of the boxes were planted with each species and faced north/south. The boxes were also filled with dry soil as described under Chapter 3. The total plant available water (PAW) was 11.00 ℓ per root box or 169.23 mm water per box.

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

When the lower point of PAW is reached, the cladodes grow softer and less firm, the same characteristic shown in water treatment T4 (75 to 100% depletion of PAW) in Chapter 3. According to these observations one can be sure of a definite soil-water gradient over the last month when measurements took place. After two months with the soil at a low point of PAW or near permanent wilting point, it was again filled up to total PAW level. This was done to measure the recovery of the plants and especially the rain root development.

4.3.3 Rain root growth

Cladodes of both species were planted in 38 of the same pots as described in Chapter 3. After growing the cladodes for 8 weeks in the pots at water treatment T1 (0 to 25% depletion of plant available water (PAW) (see Chapter 3)), it was stressed up to T4 (75 to 100% depletion of PAW) and kept there for two weeks. All the pots were then filled with water up to T1 after which two pots per species (randomly selected) were first washed each hour, then every second hour and lastly daily to determine the rain roots.

4.4 Data collection

4.4.1 Root from the areoles

The number of areoles from where roots developed was counted for the different treatments after three weeks of planting.

4.4.2 Root development in root boxes

The different root types namely tap roots and side roots were measured hourly and daily over a period of one month. Three main roots per cladode or root box were measured and also three side roots on each of the main roots. The rate of main root growth was observed daily as well as each hour, which also included at day and night.

The measurements took place over a soil-water gradient. The root lengths were marked on the glass after which it was accurately measured (Fig 4.2).

Figure 4.2 Root measurements in root boxes on the glass.

The rain roots were measured after lifting the water stress. Three rain roots on each of the three main roots were measured daily for each species.

4.4.3 Rain root growth

After washing each pot the rain roots were measured with a caliper. Over the first six hours it was done hourly but after that every second hour up to 12 hours. During the next 12 hours pots were washed only every third hour. The rain roots were therefore intensively measured over a 24-hour period and thereafter only daily for the next three 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. Ten roots randomly selected within each pot were measured.

4.5 Data analysis

The data collected was analysed by SAS, which is a statistical software analysis program. The one-way analysis of variance at 95% confidence interval was conducted to determine any significant difference. Tukey's test was used to find out where the difference is (Mendenhall & Sincich 1996). In determining least significant difference (LSD), the method of Fisher (1949) was used.

4.6 Results and discussion

4.6.1 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 4.1) with an average of only 3.4% areole not rooting (Table A.1). The number of areoles in contact with the soil differs ($P<0.05$) 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 to 100 mm in the soil (vertically) both species had an average of 11 areoles in contact with the soil, of which mostly all of them, rooted (Table 4.1). In general most areoles in contact with the soil formed roots in both species after three weeks regardless of planting method. First roots developed three days after planting which is in agreement with the findings of Hills (1995). Each areole formed an average of three roots. Roots developed first on the lower side of the cladode and later at the top for both species. This might be due to more reserves being available at the bottom than at the top.

Table 4.1 Average number of areoles (cladode^{-1}) where roots developed under different ways of planting for the two *Opuntia* species (n =10). Numbers in brackets are percentage of areoles where roots did not develop.

Species	**Planting method**		
	Flat	50 to 100 mm deep (vertically)	20 mm deep (horizontally)
O. ficus-indica	43.7 (3.0)	11.4 (5.3)	18.0 (10.0)
O. robusta	31.6(4.1)	10.8 (3.7)	14.4 (8.3)
LSD $_{0.01}$	5.4986	1.1292	1.3723

4.6.2 Root development over a soil-water gradient

4.6.2.1 Taproot growth (day and night)

The taproot measurements taken during both day and night times every hour are presented in Figure 4.3 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 for every seventh day. As most of the taproots grow to a great extent horizontally, it was difficult to follow root growth after 22 days because most marked (measured) roots reached the sides of the root boxes.

It is clear from Figure 4.3 that root length increased in the morning with water stress for both species. The reason for this could be the building up of growth reserves during the night by this CAM plant and usage of them in the morning. The opposite happened during the afternoon where root length decreased with water stress for both species. This could also be due to the decrease in carbohydrates available due to the low soil-water and perhaps also the greater sensitivity of the roots to soil temperatures building up due to lower soil-water. Daytime CO_2 uptake was observed when soil-water content was high, with a progressive reduction in daytime CO_2 uptake which correlated with a decrease in soil-water content (Hanscom, III & Ting 1978). At night both species showed an increase in root growth with water stress, which could be due to more efficient water use during the cooler part of the day. According to Noble & Huang (1992) new roots can be 5 mm long about 6 hours after rewetting a cactus plant. The highest daily taproot growth for *O. ficus-indica* and *O. robusta* was 42 and 36 mm respectively. This daily growth is in agreement with the findings of Noble & Huang (1992) of 5 mm growth after 6 hours for two desert succulents. Regardless of water stress both species attained a relatively high daily taproot growth.

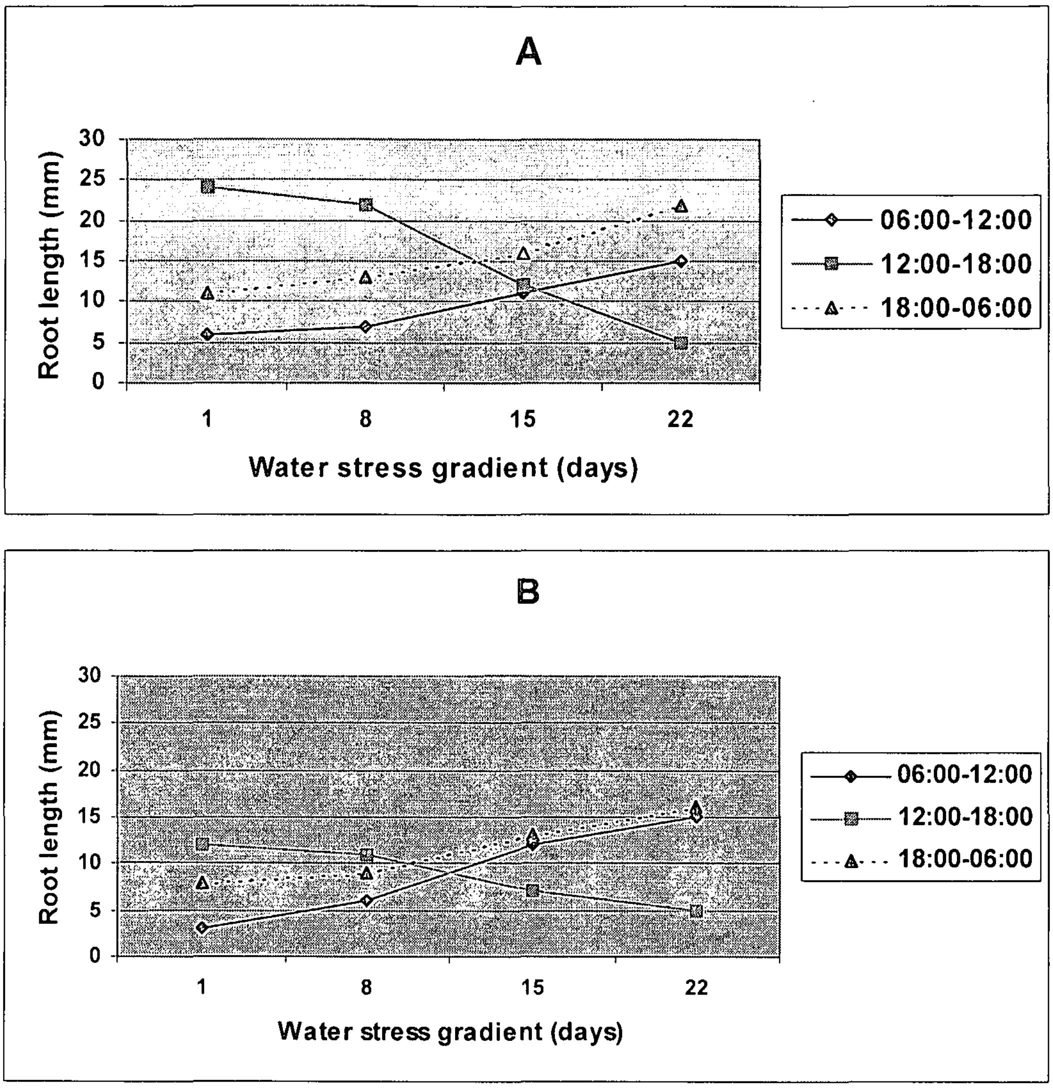


Figure 4.3 Daily taproot growth (mm) during both day and night times for *O. ficus-indica* (A) and *O. robusta* (B) measured over a soil-water gradient with seven day intervals.

4.6.2.2 Number of side roots per taproot

When the first side root development was noted through the glass cover, the side root per taproot measurements started. These observations started a month after planting and were measured over a soil-water stress gradient for two weeks, after which it became difficult to distinguish between the massive root developments. As water stress increased the side roots increased more and more, which made them difficult to identify. The side roots per taproot are presented for both species in Figure 4.4, as measured over a two weeks period. Only the measurements for every fourth day are presented in Figure 4.4

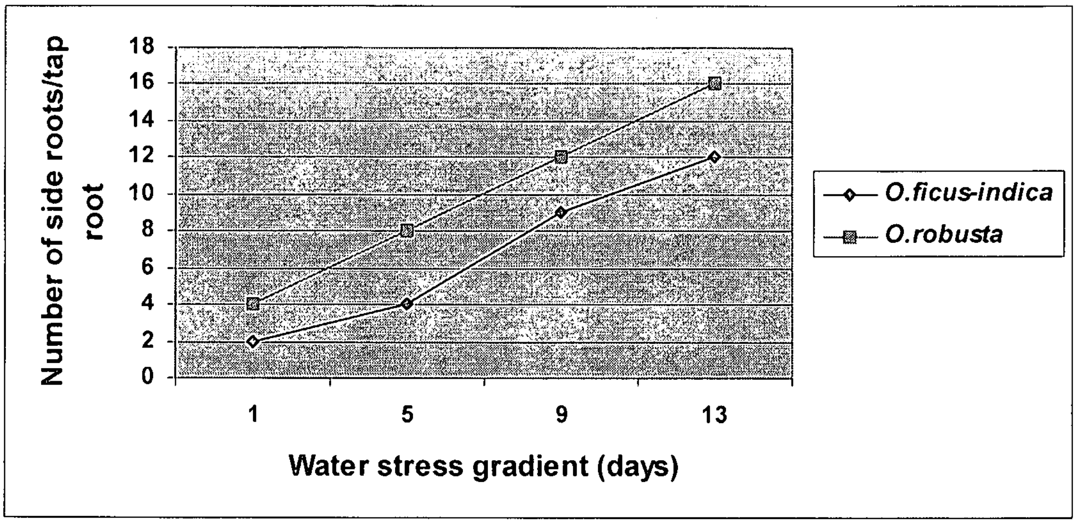


Figure 4.4 Number of side roots per taproot for *Opuntia ficus-indica* and *O. robusta* measured over a soil-water gradient or drying cycle with four intervals. LSD $_{0.01}$: species = 0.967.

Opuntia robusta has got more ($P<0.05$) side roots for each taproot than *O. ficus-indica* (Table A.4), which again explains the finer root system of this species (Fig.3.2 in chapter 3). For both species side roots per tap root increased with water stress (Fig.3.12 in chapter 3). This is supported by Hills (1995) who stated that in drier areas or with water stress, side roots developed from the taproots to take up soil-water at lower levels. Lateral root branching from taproots could account for about 70% of the total root length for *Opuntias* and have a higher hydraulic conductivity than the main roots (Huang & Nobel 1993).

4.6.2.3 Side root growth

The daily side root growth over a soil-water stress gradient or drying cycle is presented in Figure 4.5. In both species side root length increased rapidly over time and therefore with water stress (Fig. 3.12). The side root length was higher ($P<0.05$) in *O. ficus-indica* than *O. robusta* (Table A.3). After a day of water stress lifting, the side roots grew as much as 8 and 5 mm for *O. ficus-indica* and *O. robusta* respectively. Up to day five 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* (Fig. 3.2).

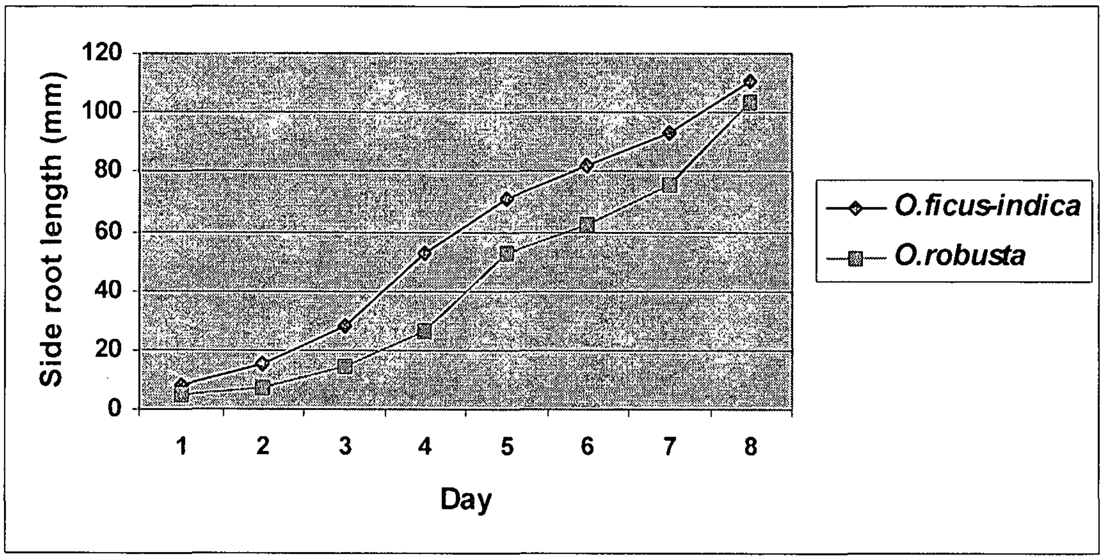


Figure 4.5 Cumulative average side root length (mm) after lifting water stress for the two *Opuntia* species measured over an 8-day period. (n = 54) LSD $_{0.01}$: species = 0.0337.

4.6.3 Root development with water stress

4.6.3.1 Rain root development per day

Before watering the plants, the cladodes were softer, but the next day they filled with water and became firm again. The rain roots grew up to 7 and 5 mm within a day for *O. ficus-indica* and *O. robusta,* respectively (Fig. 4.6), when water stress was lifted. According to Hills (1995), the rain roots are formed within a few hours as the lateral buds rapidly respond to the soil-water. The rain root length increased ($P<0.05$) rapidly from the first day to the third day for both species (Table A.5). After three days the length of the rain roots remained constant for both species and with no further growth. As time passes, the rain roots grew thinner after six days and lost their typical characteristic white colour, making them easy to identify. Hills (1995) also reported the rain roots dying as the soil dries.

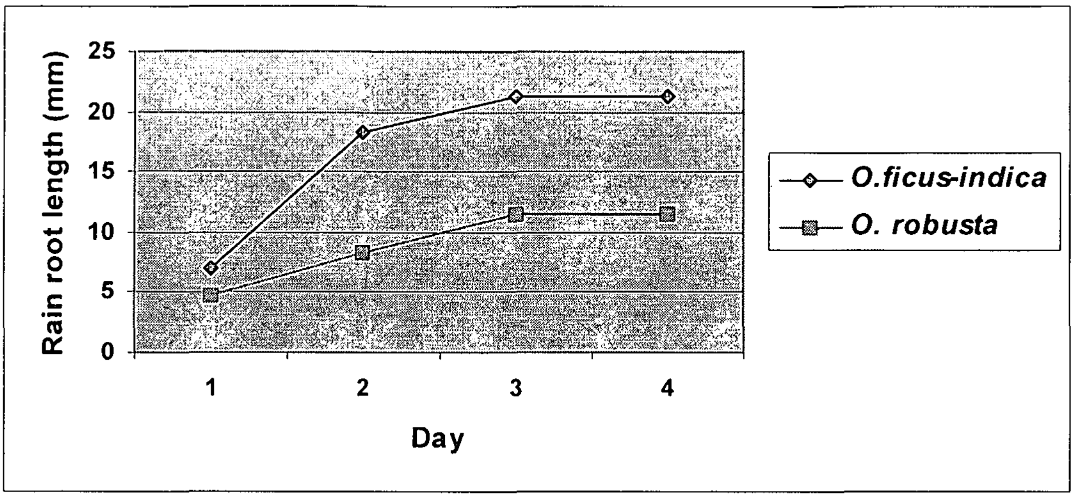


Figure 4.6. Cumulative average rain root length (mm) after lifting water stress for the *Opuntia* species (n = 54). LSD $_{0.01}$: species = 3.3398.

After a few weeks of stress lifting the rain roots could hardly be identified. New rain roots developed after the lifting of a next water stress period. The function of the rain roots is therefore to take up water as quickly as possible after a dry period and fill the cladodes rapidly. The species *O. robusta*'s rain roots developed significantly ($P<0.05$) slower than *O. ficus-indica*.

A general conclusion could be made that due to the fact that *O. robusta* has a finer root system (Fig. 3.2), the rain roots must also be smaller. After six days the soil was again brought to field water capacity to check whether the rain roots stopped growing or not due to water stress. There is therefore no doubt that rain roots grow only over a three-day period after water stress lifting.

4.6.3.2 Rain root growth per hour

The rain roots started growing within the first two hours after rewetting the soil in both species (Fig. 4.7). The same tendency is described by Hills (1995) with rain root development after a few hours. After 24 hours, the average rain root length of *O. ficus-indica* was 6 mm and 4.5 mm for *O. robusta*. The shorter rain roots of *O. robusta* compared to that of *O. ficus-induca* can be attributed to the finer type of root system (Fig. 3.2) of *O. robusta*. *Opuntia ficus-indica* showed rapid rain root growth over the first nine hours and then slower growth, while the growth for *O. robusta* increased more evenly. Smoother curves could be obtained with more roots measured. The average rain root length two and three days after lifting water stress was 18 and 21 mm respectively for *O. ficus-indica.* For *O. robusta* the rain root length two and three days after lifting water stress was 8 and 12 mm respectively. These end values for both species are more or less the same as that described in Figure 4.6. No further rain root growth took place four days after stress lifting for both species.

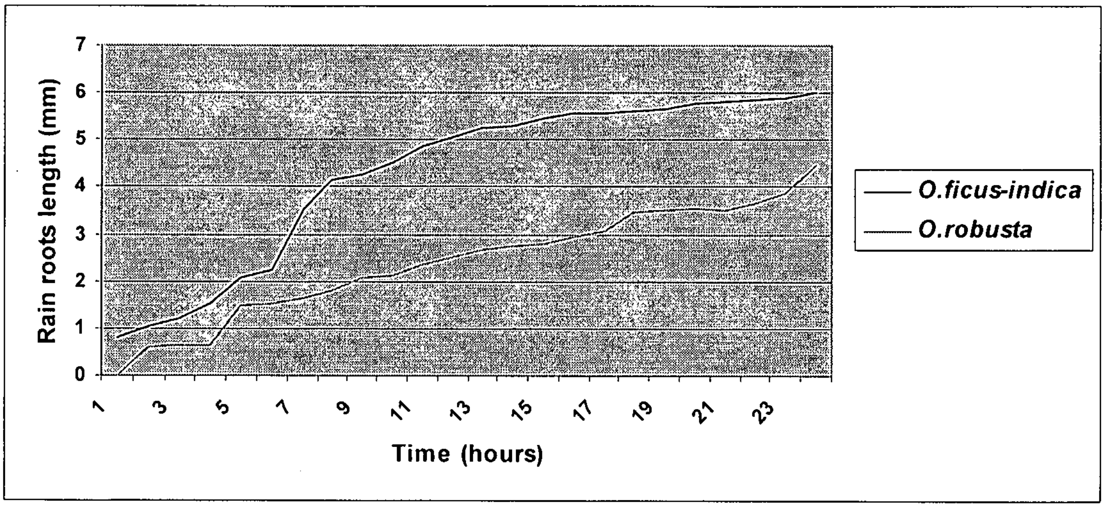


Figure 4.7. Cumulative average rain root growth (mm) for two *Opuntia* species in hourly intervals measured over a day. (n = 10); LSD $_{0.01}$: species = 1.3352.

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

4.7 Conclusion

Due to the extensive and dense root system near the soil surface, the plant has a high water uptake ability. This unique adaptation makes the plant ideal for production systems in areas with low rainfall. This type of root system can utilise drier areas to its full potential. The unique rain roots can fill the cladodes very quickly with water after a rain shower, which is essential for dry areas where evaporation is high. There is no other fodder plant with this characteristic of such fast root development. The fact that rain roots only grow for three days again showed the efficient root system following a drought. The root system of the cactus pear is not as generally expected but very adaptable under a great variety of soil-water conditions in the drier areas.

The side roots that developed with water stress also allow the plant to take-up water more efficiently and ensure survival under dry conditions. The die off of great parts of the taproots during a drought or water stress was surprising but again showed the adaptability of this plant to different environmental conditions. The fact that it is also a CAM plant makes it more adaptable to water usage during day and night times.

The easy establishment of the plant makes it suitable for farming in both developing and developed agriculture. It seems that the species *O. robusta* with the finer root system is the most adaptable to lower water conditions.

Chapter 5

A case study on in situ rooting profiles

5.1 Experimental layout

Three cactus pear plants, for each of the species *Opuntia ficus-indica* (cultivar Morado) and *O. robusta* (cultivar Monterey) were studied. The planting took place August 2002 in two lines, with 5 m spacing between rows and 5 m within a row. The plants were randomly placed over the area. The experimental layout is a fully randomised design consisting of two treatments (*Opuntia* species) replicated thrice on the cultivated area.

5.2 Methodology

The research was conducted in the district of Bloemfontein, (28°50′S and 26°15′E and altitude 1 350 m), in the semi-arid, summer rainfall (annual average 560 mm) region of South Africa. Rain falls almost exclusively during summer (October to April), with an average of 78 rainy days per year. The mean annual temperatures range from 17°C in July to 33°C in January. It has 119 average frost days per year.

The soil 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 after cultivation were 1 260 kg m^{-3} for the A horizon, 1 563 kg m^{-3} for the B1 horizon and 1 758 kg m^{-3} for the B2 horizon (Snyman 2000). The planting that took place during August 2002 was under dryland conditions and cultivated well (300 mm deep) before planting. No fertilisation or cultivation took place over the trial period. Weed control was done chemically.

5.3 Data collection

The root mass and length were estimated at 50 mm intervals to a depth of 900 mm from a sample of 3 soil cores systematically distributed from the stem of each plant. This was done over a distance of 1 500 mm from the stem of each plant with 100 mm intervals. The soil cores were collected with an auger (70 mm diameter) at the end of the growing season (April 2003). Data collection took place from nine month old plants, which grew over a full growing season. After monitoring root length and mass with depth and over distance, the soil between the sampling rows was washed out to determine root distribution.

5.3.1 Root mass and length

Sieving was through two sieves, a 2 mm mesh followed by a 0.05 mm mesh. Most of the roots had been extracted via successive washings of the core. The roots were then dried at 100°C for 16 hours. Root length was measured using the infrared root length counter (Rowse & Philip 1996). Root length was determined from the equation as described in Chapter 3 and expressed in terms of roots per m^{-2} for each 50 mm soil layer.

5.3.2 Root thickness

The root thickness was measured in mm with a vanier calliper. The thickness of 10 roots, randomly picked from each depth and distance was measured. The average measurement of each root taken at the top and end, was used.

5.4 Statistical analysis

The data collected was analysed by SAS, which is a statistical software analysis program. A two-way of variance (ANOVA) at 95% confidence level (depth × distance) was computed for root mass, root length and thickness (Mendenhall &

Sincich 1996). In determining least significant difference (LSD), the method of Fisher (1949) was used.

5.5 Results and discussion

5.5.1 Root mass

The root mass decreased ($P<0.05$) with distance from the mother plant as well as with depth for both *Opuntia* species (Fig.5.1). At a distance of 400-1 500 mm from the mother plant, there were no roots at a depth of 300-900 mm for *O. ficus-indica,* while *O. robusta* had no roots at a depth of 600-900 mm from a distance of 200-1 500 mm from the mother plant. At 1 200-1 500 mm away, there were no roots in a depth of 300-900 mm for both species. More ($P<0.05$) roots were found at the topsoil layer (0-100) than any other level in both species (Table A.6). Most roots were found 100-200 mm away from the mother plant in both species. However, *O. robusta* seems to have a constant root distribution into the soil and from the mother plant than *O. ficus-indica.* This shows that after a year of establishment there is only few roots exactly underneath the mother plant. According to the literature the cactus pear also develops a deep root system after a few years (Noble 1988; Hills 1995).

From Figure 5.1, it is clear that for both species more roots were distributed over the first 100 mm soil depth than the 1 500 mm depth in this study. If one could lengthen the pattern in Figure 5.1, the distance from the plant where roots can still be found would be 1.6 and 1.7 m respectively for *O. ficus-indica* and *O. robusta.* It is clear from Figure 5.1 that for both species the root distribution over the first 100 mm soil depth must have spreaded further than the 1 500 mm measured in this study. If one extrapolated Figure 5.1, the distance from the plant where roots could still be found can be predicted as 1.6 and 1.7 m respectively for *O. ficus-indica* and *O. robusta.*

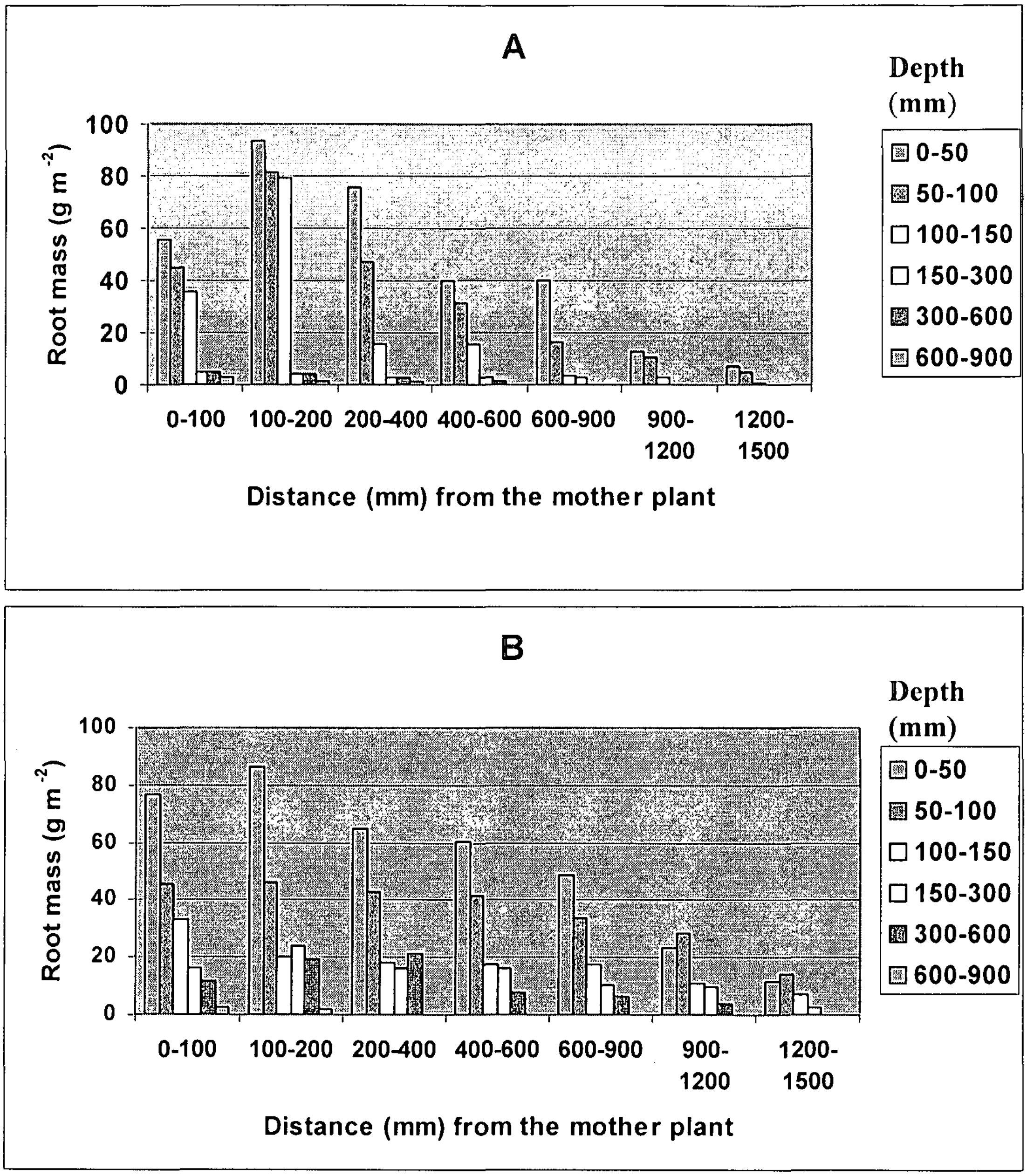


Figure 5.1 Root mass (g m^{-2}) for *Opuntia ficus-indica* (A) and *O. robusta* (B) with depth and distance from the mother plant. LSD $_{0.01}$: species = 1.9255 and depth = 5.1119.

5.5.2 Percentage of root mass in each layer

From Table 5.1 it is clear that most of the roots are found in the first 100 mm for both species. The percentage of root mass decreased with depth in both *Opuntia* species. Over a distance of 1.5 m from the mother plant, an average 75 and 68% of the roots of

O. ficus-indica and *O. robusta* respectively, were distributed over the top 100 mm soil layer. Also the fact that for both species the roots distribution was relatively constant over the first 100 mm soil layer and increased in some instances away from the mother plant is of interest here. The average thickness of the roots at the top developing from the cladodes after one season's growth were 3.3 and 3.2 mm for *O. ficus-indica* and *O. robusta* respectively after the first season's growth. The conclusion can be made that one year old cactus pear is not a deep-rooted plant as shown in Figure 5.2.

Table 5.1 Root mass (%) distribution per depth for increase distance from the mother plant for *Opuntia* species.

Opuntia ficus-indica

Depth (mm)	**Distance from the mother plant (mm)**						
	0-100	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**	**1200-1500**
0-50	37.27	35.46	52.14	44.87	64.22	50.21	53.71
50-100	30.23	30.78	32.54	34.44	25.42	39.83	40.31
100-150	23.83	30.04	10.84	17.49	6.22	9.96	6.98
150-300	3.47	1.52	1.79	2.87	4.14	0	0
300-600	3.47	1.71	1.78	0.333	0	0	0
600-900	1.73	0.49	0.89	0	0	0	0
Total	100	100	100	100	100	100	100

Opuntia robusta

Depth (mm)	**Distance from the mother plant (mm)**						
	0-100	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**	**1200-1500**
0-50	41.30	43.57	39.65	42.28	41.69	30.57	32.31
50-100	24.50	23.23	26.18	29.02	28.74	37.39	40.59
100-150	17.85	10.18	11.20	12.05	15.12	14.58	19.80
150-300	8.62	12.18	9.88	11.19	8.89	12.66	7.30
300-600	6.33	9.92	13.09	5.46	5.56	4.80	0
600-900	1.40	0.98	0	0	0	0	0
Total	100	100	100	100	100	100	100

Figure 5.2 Root distributions over the first 0 to 100 mm soil layer as washed in the field.

5.5.3 Root length

Cactus pear is a shallow rooted crop with a fleshy root system, which can spread horizontally up to 4-8 m from the mother plant after a few years (Hills 1995; Drennan & Nobel 1998). The root length decreased ($P<0.05$) with depth and distance from the mother plant for both *Opuntia* species (Fig. 5.3). Most roots were found at a depth of 0-50 mm and 100-200 mm away from the mother plant for both species. As the case with root mass, further from the mother plant, root lengths decreased with depth. The fact that the root length of *O. robusta* is higher ($P<0.05$) over all depths the further away from the mother plant than that of *O. ficus-indica,* is of great interest (Table A.6). This could be due to the fewer root hairs or side roots found in this species.

The conclusion could therefore be made that *O. robusta* generally has a more constantly spread root system with depth and distance than *O. ficus-indica*. This can allow better adaptation of this species to lower rainfall conditions. It can be predicted by extrapolating Figure 5.2 that for both species beyond 1 500 mm there could still be roots as is the case with *O. robusta,* which could have roots spreading over a distance of 1.7 and 1.8 for *O. ficus-indica* from the mother plant after one year of establishment (Fig. 5.2).

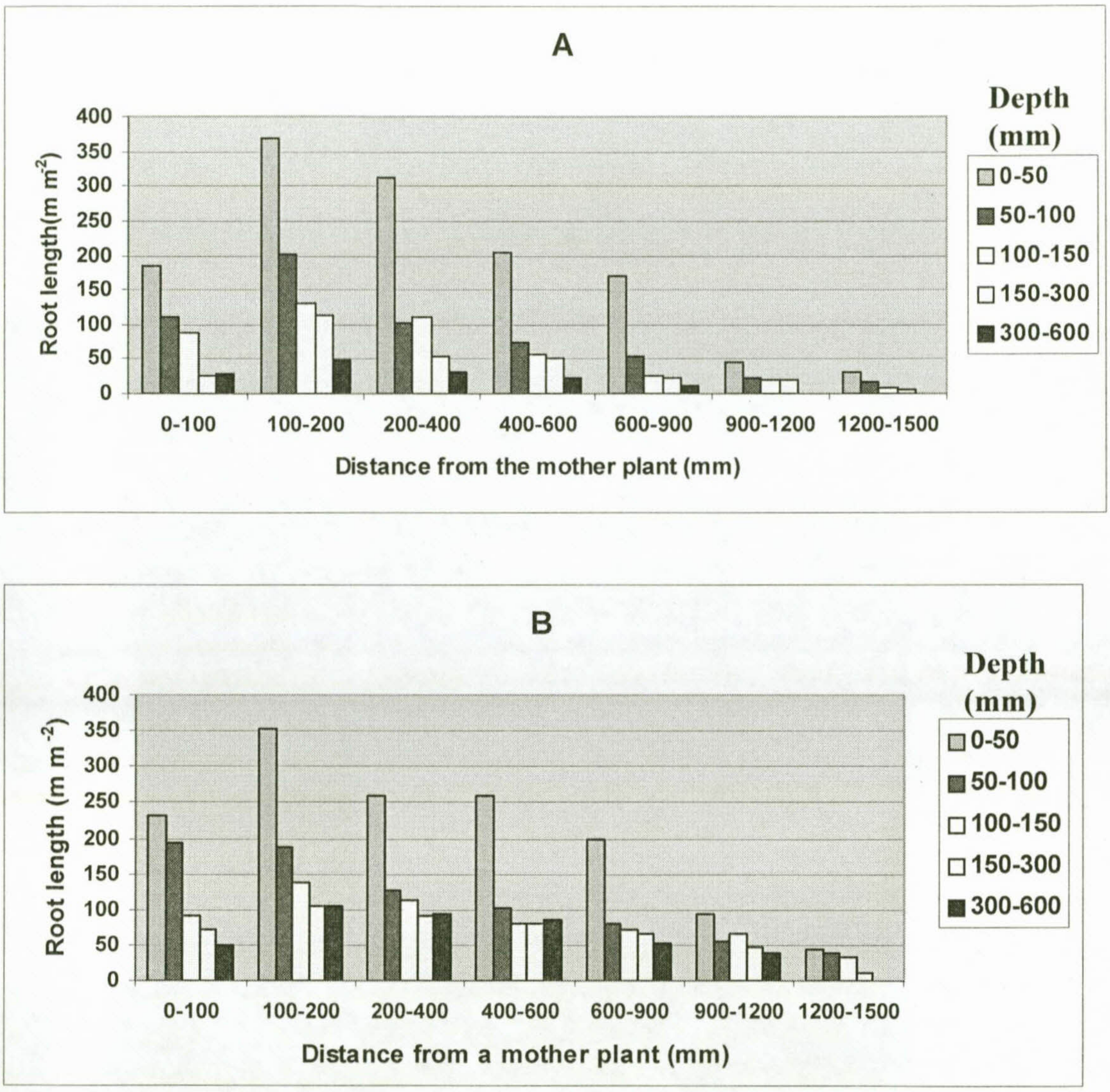


Figure 5.2 Root lengths (m m^{-2}) for *O. ficus – indica* (A) and *O. robusta* (B) at adepth of 0-600 mm and distance of 0-1 500 mm from the mother plant. LSD $_{0.01}$: species = 11.3663.

5.5.4 Percentage of root lengths in each layer

As shown in Table 5.1, most roots are distributed within the 0-100 mm soil layer. When growing deeper and further away from the mother plant the root mass and length decreased. On average 68 and 55% of the roots over a distance of 1.5 m from the mother plant for *O. ficus-indica* and *O. robusta* respectively, were distributed over the top 100 mm soil layer. Already over the first 50 mm depth 47 and 35% of the roots of *O. ficus-indica* and *O. robusta* respectively were found over a distance of 1.5 m from the mother plant. Over the first 100 mm soil layer, the root distribution is relatively high and remains constant away from the mother plant.

Table 5.2 Root length (%) distribution per depth for increase distance from the mother plant for both *Opuntia* species

Opuntia ficus-indica

Depth	**Distance from the mother plant (mm)**						
(mm)	**0-100**	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**	**1200-1500**
0-50	41.39	42.79	47.07	49.94	60.51	41.56	50.00
50-100	24.96	23.38	15.61	17.98	18.98	23.38	28.57
100-150	20.10	15.09	16.70	14.10	8.72	18.18	11.90
150-300	6.97	13.27	16.05	12.69	8.20	16.88	9.52
300-600	6.48	5.47	4.56	5.29	3.20	0	0
Total	100	100	100	100	100	100	100

O. robusta

Depth	**Distance from the mother plant (mm)**						
(mm)	**0-100**	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**	**1200-1500**
0-50	37.94	37.91	37.87	42.90	42.25	31.36	30.73
50-100	29.45	20.63	18.62	16.92	17.02	18.33	26.72
100-150	13.82	17.32	16.32	13.11	15.20	22.20	23.75
150-300	11.18	11.49	13.39	13.11	14.28	15.92	18.87
300-600	7.68	11.65	13.81	13.96	11.25	12.54	0
Total	100	100	100	100	100	100	100

5.5.5 Root mass and root length relationship

Root length is regressed against root mass and the relationships for two *Opuntia* species are presented in Figure 5.3. The root length for *O. ficus-indica* and *O. robusta* can be determined with an accuracy of 72 % and 77 % respectively if the root masses are known. These regressions imply that a root mass of 1 g m^{-2} is equal to a root length of 3.17 and 3.79 m m^{-2} for *O. ficus-indica* and *O. robusta* respectively. As the root mass increased the root length also increased (Fig. 5.3) for both *Opuntia* species.

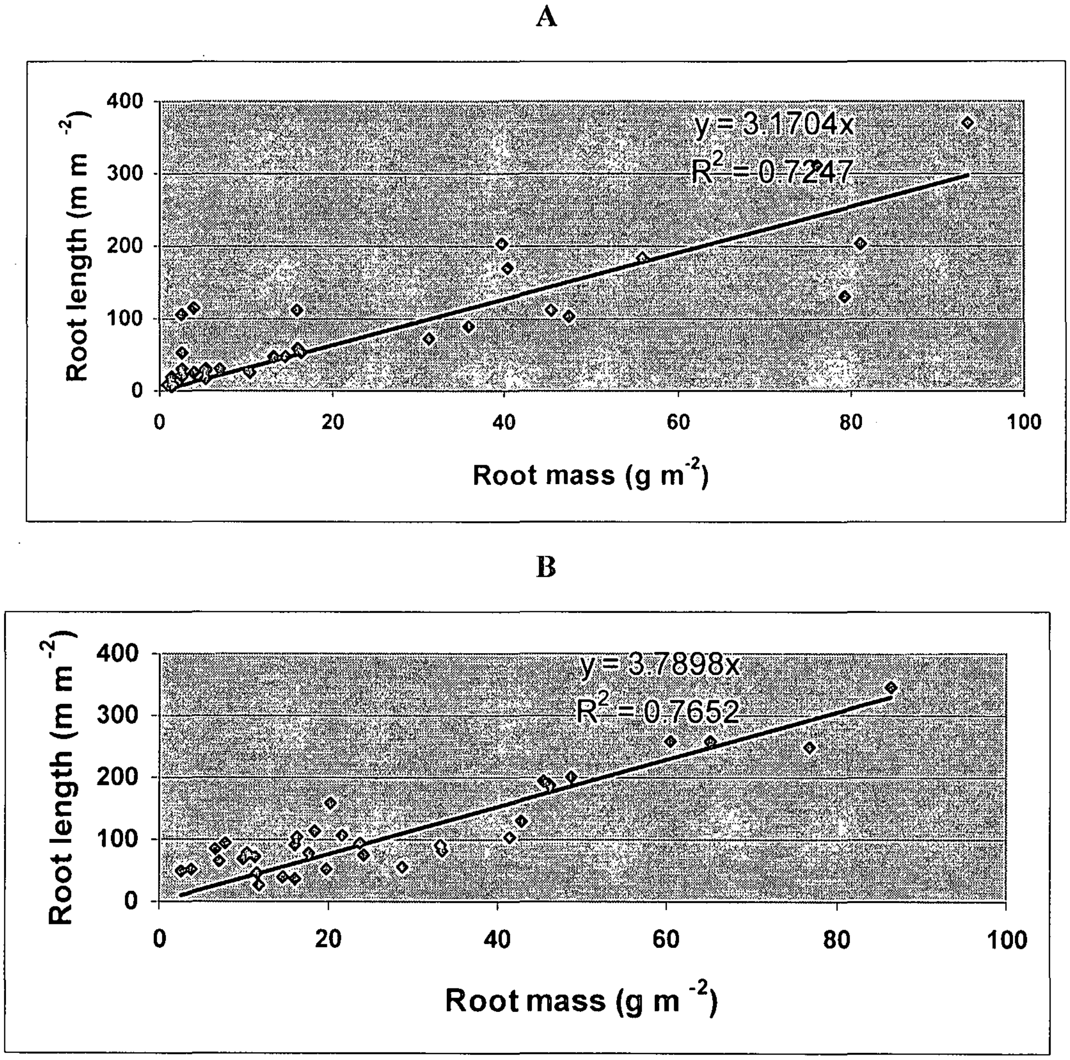


Figure 5.3 Relationship between root mass (g m^{-2}) and root length (m m^{-2}) for *Opuntia ficus-indica* (A); $y = 0 + 3.1704x$ ($R^2 = 0.7247$; n = 33) and *O. robusta* (B); $y = 0 + 3.7898x$ ($R^2 = 0.7652$; n = 33).

5.5.6 Root thickness

The root thickness also decreased ($P<0.05$) with distance from the mother plant (Table A.7; Appendix A). *Opuntia ficus-indica*'s roots were thicker near the stem at a depth of 50-100 mm, while that of *O. robusta* were thicker for most distances at 0-50 mm depth. From Figure 5.4 it is clear that the roots of *O. robusta* are still thick though spread far away from the mother plant in all depths. The roots of *O. ficus-indica* on the other hand showed a slight decrease in thickness with distance from the stem.

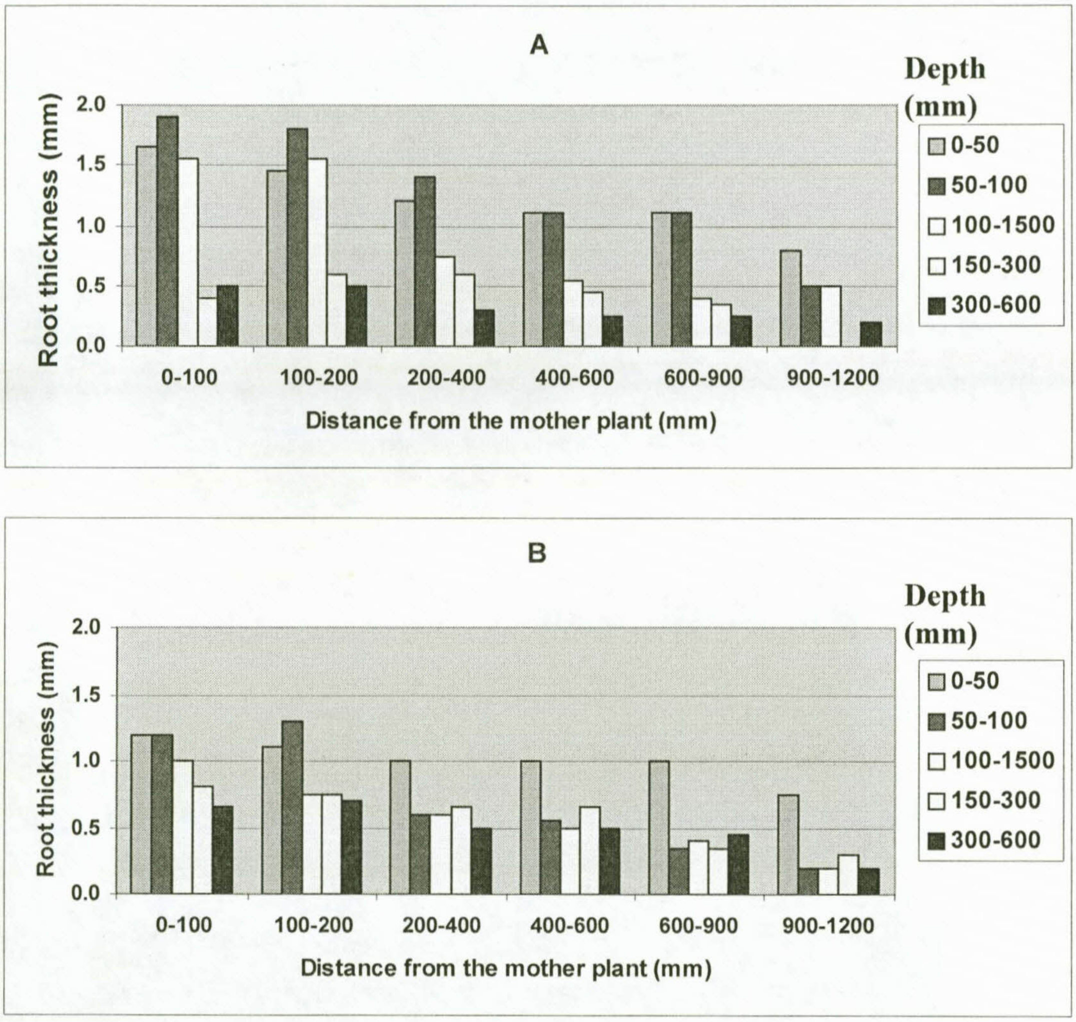


Figure 5.4 The thickness (mm) of roots with distance from the mother plant and depth for *Opuntia ficus-indica* (A) and *O. robusta* (B). (n =10). $LSD_{0.01}$: species = 0.2673.

It is very clear that the roots of *O. ficus-indica* for most depths and over distances were thicker than that of *O. robusta*. Figure 5.4 again illustrated the finer root system of last mentioned species as discussed in detail in Chapters 3 and 4.

5.6 Conclusion

It was clear from this study that after only the first season of planting the roots can spread as far as 1.5 to 1.7 m from the plant. Hills (1995) and Drennan and Nobel (1998) observed with mature plants that cactus roots could spread horizontally from 4 up to 8 m from the mother plant. More roots were found in the 0-100 mm soil depth for both *Opuntia* species in this study. According to Hill (1995), the bulk mass of roots is found in the first few centimetres with a maximum depth of 300 mm therefore according to Ratsele (2003), efficient weed control is very important. The further away from the plant the less roots there are.

It can also be concluded that *O. robusta* had more constant root distribution with depth and distance from the mother plant than *O. ficus-indica*. It was also clear that after one year of establishment *O. ficus-indica* had shallower and shorter root system than *O. robusta*. This might be due to *O. robusta's* more and fine side roots than *O. ficus-indica* as also shown in Figure 5.4 and Figure 3.2.

From this study one can also learn that root distribution can be studied well in the field than in the glasshouse, as there is a lot of space where roots can spread as much as they could and freely than in the pot or root box. It would be interesting if root distribution for different depths could also be studied in future for various soil types with different clay contents. This study must also be repeated, but with older plants in future.

Chapter 6

General conclusions and recommendations

The cactus pear, as a CAM plant, can tolerate water stress or drought. Its succulent leaves or cladodes with sunken stomata, which regulate water loss through transpiration by closing for most of the day, and shallow root system occurring predominantly in the upper layers (0 to 100 mm) of the soil, where soil-water content is heterogeneous, make it well adapted to arid and semi-arid areas.

In this study the response of roots of *Opuntia ficus-indica* and *O. robusta* to water stress has been observed and the functions of the different root types were also identified. The root mass decreased ($P<0.05$) with water stress in both species, which is possibly because of taproots die back. In contrast, root length increased ($P<0.05$) with water stress even though a slight decrease occurred when the plant is severely stressed due to root die back. The increase in root length might be due to more side root development for efficient water uptake as the soil dries up. The root-shoot ratio also decreased ($P<0.05$) as the plant available water declined. These results show in principle, adaptability of cactus pear plant to different soil-water contents and ability for surviving under drought conditions

In both species, lateral root primordia develop as the soil dries up and emerge rapidly in response to soil rewetting and abscise with water stress. The rain roots develop in response to rewetting and grow for only three days after which they remain constant from the fourth day onwards. On the other hand side roots continue to grow until they die back in very dry soil conditions. Something interesting about the rain roots is that they have started to develop within the first hour after rewetting the soil. This makes cactus pear unique because there are no other fodder plants that can develop roots as quickly as it does. The main function of the rain roots is for quick water uptake after lifting of water stress, which can fill the cladode overnight with only 10 to 14 mm water added to the soil. These cactus root characteristics make it more efficient to use cactus pear as a valuable crop in arid and semi-arid areas. Light rain showers of only a few millimetres, which is not always of value to other fodder plants, the cactus pear can utilizes very efficiently. With this shallow root system, it is adaptable to drier areas and takes up water rapidly after a rain shower when evaporation is high.

Although the taproots can grow as much as 5 mm a day, the average thickness at the end of the roots for *O. ficus-indica* for example where die back took place was up to 0.8 mm for the highest water stress. In contrast, the die back for *O. robusta* was not so high and can handle water stress conditions better than the other species. One should expect that due to its adaptability to drier areas, it should have a very stable root system, but is not the case according to this study's results. The whole root system is therefore adaptable to different soil-water conditions. The fact that tap roots grow more in the night than during the day, still needs clarification and in depth research in future.

In general cactus pear is water-use efficient because of its unique features mentioned above. However, it differs to some extent from other species. *Opuntia ficus-indica*'s water-use efficiency declined as the soil got drier while *O. robusta* became more water-use efficient with an increase in water stress as a result of its more and finer roots which helps in efficient water uptake despite the low soil-water content. From these results one can conclude that strategically, irrigation could be of great importance for higher production in some species such as *O. ficus-indica* during dry periods. It might also be concluded that *O. robusta* is drought resistant.

As mentioned, cactus roots are extensive and shallow. Most roots are found in the first 100 mm soil layer and decrease lower down in the soil. Therefore, for sustainable cactus pear production, chemical weed control is important, especially during the early stage of plant development to avoid competition for water and minerals. Cultivation in-between rows to loosen the soil for better water infiltration must be avoided or carefully planned to avoid root damage. Fertiliser applications must also be done in small quantities over the season to avoid burning the shallow root system. From the study on root distribution with distance and depth, it was clear that after only one season of establishment, the root distribution can be as far as 1.6 m and 1.7 m from the stem for *O. robusta* and *O. ficus-indica* respectively. The root length and mass also decreased slightly with distance from the stem for both species. As expected the thickness of the roots also slightly decreased ($P<0.05$) with distance and depth.

In order to obtain a clearer picture of the whole dynamics of the root system of the cactus pear, more intensive research on the root distribution in older plantations have to be carried out in future. This must also be done under soils with different clay contents to see how root distribution will vary under such conditions. It is recommended to grow cactus pear in shallow, eroded areas for reclamation as it establishes easily with low labour costs.

Summary

Over the last few years a great interest in cactus pear was shown in terms of both fresh fruit and fodder production. However, there is a lack of knowledge on roots and therefore this study aimed at determining the root dynamics in relation to soil-water content and to quantify or characterise the different root types for two *Opuntia* species namely *Opuntia ficus-indica* (cultivar Morado) and *O. robusta* (cultivar Monterey). This was carried out in the glasshouse (pots and root boxes) as well as in the field.

Cactus pear planted in asbestos pots were used to determine the impact of soil-water content on root development and also their short time of recovery after rewetting the soil. The water treatments included 0 to 25% depletion of plant available (PAW) (not stressed), 25 to 50% depletion of PAW (mildly stressed), 50 to 75% depletion of PAW (moderately stressed) and 75 to 100% depletion of PAW (severely stressed). The root mass and root/shoot ratio decreased ($P<0.05$) with water stress for both species. Water-use efficiency decreased for *O. ficus-indica* and increased for *O. robusta* with water stress. The root length, root length/root mass ratio and amount of water needed to fill the cladodes increased ($P<0.05$) with water stress for both species.

The root boxes were used for observation and characterising the different root types and their response to soil drying and rewetting. Main roots grow up to 42 and 36 mm per day for *Opuntia ficus-indica* and *O. robusta* respectively. The rain roots, which develop after only one hour of rewetting the soil, grow only for three days until dying due to soil drying. The side roots also emerge in response to soil-water but differs from rain roots in that they continue to grow until they die back as soil dries. Only 10 to 14 mm water is needed to fill the cladodes after a water stress. The rain roots therefore play an important role in rapid water up-take, which can fill the cladodes overnight.

The root distribution with depth and distance was studied in the field, where root mass, root length, root length/root mass relationship and root thickness were measured at different depths and distances for each species. It has been found that most roots were concentrated over the first 100 mm soil layer for both *Opuntias*. After only one season of establishment the root distribution can spread as far as 1.6 and 1.7 m from the stem for *O. robusta* and *O. ficus-indica* respectively. The root mass, root length and root thickness decreased (P<0.05) with depth and distance.

In conclusion, the cactus pear is characterised by a shallow and extensive root system, which contributes a lot to its water-use efficiency. These characteristics make it more appropriate for arid and semi-arid crop production. The marginal drier areas with shallow soils can therefore be utilised to their full potential by the cactus pear plant.

Key words: Cactus pear, water stress, taproots, side roots, rain roots, root mass, root length, water-use efficiency, root/cladodes ratio, root distribution.

Opsomming

Die afgelope aantal jare het daar 'n geweldige belangstelling in die turksvybedryf ontstaan, wat beide vrugte en voerproduksie aanbetref. Ongelukkig bestaan daar 'n groot gebrek aan kennis oor die wortelontwikkeling van die turksvyplant en daarom was die doel met hierdie studie om die dinamika van wortelontwikkeling in verhouding tot grondwater status te ondersoek. Die verskillende worteltipes is gekarakteriseer en die wortelontwikkeling gekwantifiseer vir twee *Opuntia* spesies naamlik *Opuntia ficus-indica* (kultivar Morado) en *O. robusta* (kultivar Monterey). Hierdie navorsing is in die glashuis (potte en wortelkaste), asook in die veld uitgevoer.

Turksvyplante gevestig in asbespotte is gebruik om die impak van grondwaterinhoud op wortelontwikkeling, asook hulle herstel na opheffing van waterstremming oor die korttermyn te ondersoek. Die waterbehandelings het ingesluit 0 tot 25% onttrekking van plantbeskikbare water (PBW) (nie gestrem), 25 tot 50% onttrekking van PBW (matig gestrem), 50 tot 75% onttrekking van PBW (redelik gestrem) en 75 tot 100% onttrekking van PBW (erg gestrem). Die wortelmassa en wortel/blad verhouding het afgeneem ($P<0.05$) met waterstremming vir beide spesies. Die watrverbruiksdoeltreffendheid het afgeneem vir *O. ficus-indica*, maar is verhoog vir *O. robusta* met waterstremming. Die wortellengte, wortellengte/wortelmassa verhouding en die hoeveelheid water benodig om 'n blad te vul, het toegeneem ($P<0.05$) met waterstremming vir beide spesies.

Die wortelkaste is gebruik vir die monitering en karakterisering van die verskillende worteltipes en dié se reaksie op gronduitdroging en herbenatting van die grond. Die hoofwortels groei soveel as 42 en 36 mm per dag vir onderskeidelik *O. ficus-indica* en *O. robusta*. Die reënwortels wat na slegs 'n uur na opheffing van waterstremming begin ontwikkel, groei vir slegs drie dae totdat dit weens gronduitdroging verkurk. Die sywortels wat ook ontwikkel in reaksie tot waterstremming, verskil van die reënwortels in die sin dat dit aanhou verleng totdat dit begin afsterf weens gronduitdroging. Slegs 10 tot 14 mm water is nodig om die blaaie weer te vul na 'n

waterstremming. Die reënwortels speel dus 'n belangrike rol om vinnig water op te neem en die blaaie oornag met water te kan vul.

Die wortelverspreiding met diepte en oor afstand is in die veld bestudeer waar wortelmassa, -lengte, wortellengte/wortelmassa verwantskappe en worteldiktes oor verskillende afstande en dieptes vir elke spesie bepaal is. Daar is bevind dat die meeste wortels oor die eerste 100 mm grondlaag by beide *Opuntia* spesies voorkom. Die wortelmassa, -lengte en –dikte het afgeneem ($P<0.05$) met diepte en oor afstand. Na slegs een seisoen van vestiging was die wortelverspreiding reeds 1.6 en 1.7 m vanaf die stam vir onderskeidelik *O. robusta* en *O. ficus-indica*.

Samevattend kan gesê word dat die turksvyplant gekarakteriseer word deur 'n oppervlakkige en uitgebreide wortelstelsel wat bydra tot die waterverbruiksdoeltreffendheid daarvan. Hierdie eienskappe maak dit 'n ideale gewas vir verbouing in ariede en semi-ariede gebiede. Die marginale ariede gebiede met vlak grond kan gevolglik tot hulle volle potensiaal deur die turksvyplant benut word.

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Appendix A

Table A. 1 Number of areoles (cladode^{-1}) where roots developed for two *Opuntia* species namely *O. ficus-indica* (A) and *O. robusta* (B). (The numbers in brackets are the areoles where no roots developed).

Cultivar	**Cladodes**	**Flat**	**50-60 mm depth**	**20 mm depth**
A	1	48 (1)	12 (2)	20 (4)
A	2	33 (2)	12 (0)	18 (4)
A	3	51 (0)	12 (0)	16 (0)
A	4	51 (0)	10 (2)	20 (0)
A	5	35 (1)	12 (0)	18 (4)
A	6	56 (2)	10 (0)	16 (2)
A	7	36 (2)	14 (0)	20 (0)
A	8	42 (2)	12 (0)	16 (4)
A	9	43 (3)	10 (2)	18 (0)
A	10	42 (0)	10 (0)	18 (0)
B	1	27 (1)	12 (0)	14 (2)
B	2	30 (2)	10 (2)	16 (4)
B	3	31 (0)	10 (0)	14 (0)
B	4	32 (0)	12 (0)	12 (2)
B	5	36 (0)	10 (0)	16 (0)
B	6	36 (0)	12 (0)	16 (0)
B	7	34 (2)	10 (0)	14 (0)
B	8	32 (3)	12 (0)	14 (0)
B	9	30 (2)	10 (0)	14 (2)
B	10	28 (3)	10 (2)	14 (2)

Table A.2 The P-Values for the different water treatments (trmt) and root development for two *Opuntia* species (spp). ($P<0.05$ = significant difference at 95 % confidence interval and $P>0.05$ = non-significant difference).

Study	**Sources**	**Cladodes wet mass (g)**		**Cladodes dry mass (g)**		**Root mass (g)**	**Root length (m)**	**Root /shoot ratio**	**Root length/ root mass ratio**	**% water**	**Water-use efficiency (WUE) (g m^{-1})**		**Water (mm) to fill the cladodes**
		big + small	**small**	**big**	**small**						**roots**	**shoots**	
Diff. water levels & washed over 3 months.	Species	0.0001	0.1389	0.0001	0.0572	0.0001	0.6681	0.4983	0.0190	0.7106	0.0414	0.0002	0.0111
	Trmt	0.0002	0.6904	0.6094	0.2929	0.0001	0.0001	0.0001	0.3686	0.0001	0.0002	0.8262	0.0001
	Spp*trmt	0.0617	0.8966	0.6252	0.3587	0.3471	0.7607	0.9294	0.2437	0.6465	0.7090	0.0141	0.0033
First water stress	Spp	0.0042	0.8325	0.0081	0.0117	0.0001	0.2299	0.0390	0.0043	0.4769	0.0001	0.0001	0.6342
	Trmt	0.0009	0.0603	0.0188	0.0012	0.0001	0.0423	0.0001	0.0001	0.0001	0.0001	0.0014	0.0001
	Spp*trmt	0.0224	0.2537	0.0388	0.0203	0.0162	0.3912	0.1394	0.3062	0.5498	0.0078	0.0001	0.5853
Second water stress	Spp	0.1286	0.3934	0.3139	0.0001	0.2447	0.0711	0.7785	0.5639	0.0037	0.0005	0.0001	0.0269
	Trmt	0.0364	0.1755	0.2272	0.0001	0.3950	0.0067	0.6511	0.6608	0.0011	0.0001	0.0016	0.0001
	Spp*trmt	0.0154	0.2701	0.2483	0.0001	0.4945	0.2528	0.1753	0.5928	0.6598	0.0006	0.0042	0.6664

Table A. 3 The P-values for growth of side roots per day over 8 days.

Sources	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Replication	0.4226	0.1859	0.0001	0.6667	0.8399	0.0001	0.2697	0.4226
Treatment	0.0033	0.0167	0.0001	0.9850	0.0030	0.0001	0.2692	0.5000

Table A. 4 The P-Value for number of side roots /main roots at four day intervals

Sources	**1**	**5**	**9**	**13**
Replication	0.0001	0.1835	0.0547	0.4226
Treatment	0.0001	0.1250	0.0284	0.0106

Table A. 5 The P-Values for the rain root growth per day over 3 days.

Sources	**1**	**2**	**3**
Species	0.0168	0.0041	0.0041
Treatment	0.0404	0.0135	0.0474

Table A. 6 The P-Values for root distribution (root mass and root length) with distance and depth

	Sources	**0-100**	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**	**1200-1500**
Root mass	Trmt	0.0021	0.0002	0.0485	0.0005	0.0001	0.0014	0.0044
	Spp	0.0001	0.0001	0.0001	0.0001	0.0001	0.0003	0.0001
	Trmt*Spp	0.0075	0.0001	0.0004	0.0716	0.0466	0.03570	0.0979
Root length	Trmt	0.0001	0.1115	0.0370	0.0004	0.0123	0.0012	0.0018
	Spp	0.0001	0.0001	0.0001	0.0001	0.0001	0.0006	0.0001
	Trmt*Spp	0.0002	0.0008	0.0006	0.0817	0.7002	0.3286	0.0440

Table A.7 The P-Values for root distribution (root thickness) with distance and depth.

Sources	**0-100**	**100-200**	**200-400**	**400-600**	**600-900**	**900-1200**
Species	0.0256	0.0667	0.2254	0.5487	0.2840	0.4519
Depth	0.0027	0.0017	0.0365	0.0130	0.0067	0.0397

Table A. 8 Regression analysis for root mass and root length relationship for *Opuntia ficus-indica.*

Regression Statistics	
Multiple R	0.897696
R Square	0.805858
Adjusted R Square	0.774608
Standard Error	9.456491
Observations	33

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	11878.18	11878.18	132.8281	9.74E-13
Residual	32	2861.607	89.42522		
Total	33	14739.79			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.244619	0.01213	20.16707	9.31E-20	0.219912	0.269326	0.219912	0.269326

A. 9 Regression analysis for the root mass and root length relationship for *Opuntia robusta*

Regression Statistics	
Multiple R	0.871698
R Square	0.759857
Adjusted R Square	0.728607
Standard Error	13.46386
Observations	33

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	18354.82	18354.82	101.2537	2.76E-11
Residual	32	5800.815	181.2755		
Total	33	24155.63			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	0	#N/A	#N/A	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.27161	0.019282	14.08605	2.87E-15	0.232334	0.310887	0.232334	0.310887