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Water requirements and use of Buttonwood (*Conocarpus erectus*) seedlings grown under arid conditions

A.E. Moftah and A.I. AL-Humaid

College of Agriculture and Veterinary Medicine, The University in Al-Qassim, Saudi Arabia. P.O. Box: 1482 Burida E.mail: ansary80@yahoo.com

Abstract

Six-month-old buttonwood (*Conocarpus erectus* L.) seedlings were grown in containers under different soil water potentials (Ψ_{soil}), 1) to determine the minimum soil water potential at which *Conocarpus* trees can survive and grow fairly well, 2) to study the soil-plant water relationship at different irrigation regimes, and 3) to examine the capacity of *Conocarpus* seedlings for osmotic adjustment via solute accumulation. Seedling growth was not affected significantly until soil water potential was lower than –0.1 MPa (between 40 and 30% FC), after which, plant height, leaf area and shoot and root dry weights became disrupted by severe water deficit. Water stress decreased osmotic potential (Ψ_{π}) of leaves and roots. Leaves tended to osmoregulate their cell sap through osmotic adjustment process as their content of soluble sugars increased. The positive survival under low Ψ_{soil} could be related to increased osmotic adjustment. Ψ_{soil} values seem more useful tool than FC values to estimate water requirements and use over an extended period of time, for plant grown under different soil types and different environmental conditions. The study indicate that *Conocarpus* seedlings can withstand reasonable water stress and can survive at moderately low water potential but, in contrast to other studies, can not be classified as a high drought tolerant or resistant species.

Key words: Water stress, *Conocarpus*, growth, osmotic adjustment, osmotic potential, arid conditions

Introduction

Buttonwood (*Conocarpus erectus* L.), an evergreen tree of family *Combretaceae*, was found to tolerate extreme desert heat where summer temperature may reach 47ºC and grow in soil of very low fertility (Branney, 1989). This tree deserves attention because it grows fairly rapidly and can endure the unrelenting fierce tropical sun and can survive in the high salinity levels if it is adequately supplied with water. It provides food and cover for wildlife, protects the soil during storm surges and helps fix dunes (Popp *et al.*, 1989). It is widely planted as ornamental evergreen in yards, parking lots, streets, parks, and potted plants are used to form bonsai (Gliman and Watson, 1993). The wood is durable and is used to make railroad ties, posts, boat building, fuel, and charcoal (Nelson, 1996). The bark and leaves have been used in tannery and folk medicine (Liogier, 1990). Also, it is an excellent reforestation and ornamental tree.

Unfortunately, there is little information on the water use and requirements of Buttonwood, as the case in other isolated landscape trees. Most of the information on *C. erectus* water use in Saudi Arabia as the case in many other arid regions is based on low-water-use trees recommended by various organizations such as Environmental Protection Agency (Garbesi, 1992) and reported in some literature (Levitt *et al.*, 1995, Nardini *et al.*, 2000). Lists of these tree species are usually based on empirical observations and the their native habitat, due to the lack of data on actual tree water use and requirements. They are also largely based on the observations of minimum water requirements and drought survivability, rather than actual water use (Levitt *et al.*, 1995). Therefore, some drought-resistant tree species on these lists may actually be moderate or high water users when water is nonlimiting. Buttonwood (*Conocarpus* sp.), for example, is reported to be highly drought tolerant (Gliman and Watson, 1993; Little, 1983; Nelson, 1996; Stevens *et al.*, 2001), but its actual water use and requirement is not known.

Most methods of estimating water use of isolated trees consist of direct gravimetric measurements such as measuring water consumption or transpiration. Soil moisture readings and potential are useful tools to determine how much water is available for the crop, when to start irrigating, and how much water to apply. The objectives of this study were: 1) to determine the minimum soil water potential at which *Conocarpus* trees can survive and grow fairly well, and 2) to find the relationship between soil water potential and plant water potential at different irrigation regimes, and finally 3) the comparison of variations in plant osmotic potentials and osmotic adjustment of *Conocarpus erectus* seedlings in response to water stress.

Materials and methods

Field experiments were conducted at the Research Station of the College of Agriculture and Veterinary Medicine in Al-Qassim, Saudi Arabia during May 2 to September 15, 2003. The weather during the experiment was characterized by sunny, hot, dry days and warm nights. The average daily maximum temperature was 37.6ºC with little variation. The daily minimum temperature during the experiment ranged from 15.6 to 28.5. No rain was observed during the experimental period.

Six-month old buttonwood (*Conocarpus erectus* L.) seedlings were transferred from nursery soil in the greenhouse to 30 l plastic containers filled with 40 kg sandy soil each. The seedlings,

averaged 75 ± 4.5 cm tall with a caliper of 2.5 ± 0.3 cm at the soil line, were grown outdoors under natural conditions in a shade-free location. Containers were sunken in the ground such that the surface of the potted soil was at approximately the same level of the surrounding ground surface. Empty containers were used as sleeves to line the holes so that the plant-holding containers could be removed and replaced easily. The tops of the containers were covered with white polyethylene film to minimize evaporation. A completely randomized design with 10 replicates for each treatment was used in this experiment. Seedlings of uniform height (one seedling per pot) were located in lines with spacing of 2 m between lines and 1 m between pots to avoid mutual shading. The ground surface between and surrounding the trees consisted of bare soil. At the time of transplanting, all trees were fertilized with the complete water-soluble fertilizer "Sangral" (William Sinclair Horticulture LTD, England) compound fertilizer (20N-20P-20K, plus micronutrients) at the rate of 600 kg ha^{-1}. Each tree received 10 g of fertilizer.

For the first 4 weeks, all the seedlings were watered to field capacity (FC), supplying an amount of water equal to transpiration losses as pots were weighed every other day, to ensure the establishment of seedlings and to allow adaptation to the field conditions before drought treatments were imposed. By the end of this period, pots received an amount of water equal to 100, 80, 60, 40, 20, or 10% of the field capacity and allowed to grow for 4 more weeks. The field capacity was determined gravimetrically and found to be 12%; each water treatment consisted of 10 seedlings. At the time of transplanting, five seedlings identical to those used in the experiment were separated to roots, stems, and leaves, then oven-dried at 70°C until constant weight, and weighed separately.

Measurements

Soil measurements: At each water regime, soil water potential was measured using tensiometers, and soil water content was measured gravimetrically using an electronic balance (Mittler EB60, Hightstown, NJ) as described by Ranney *et al.* (1991) and calculated as:

$$\text{Moisture}(\%) = \frac{(\text{Soil wet weight} - \text{Soil dry weight}) \times 100}{(\text{Soil dry weight})}$$

The relation between amount of soil moisture and soil water potential (Fig. 1) was established by the pressure plate apparatus as described by Shock *et al.* (2002). Briefly, saturated soil samples were set on a plate composed of a porous membrane. The membrane was then placed in a pressure cooker type chamber and sealed. The soil was then subjected to a selected series of pressures. The pressure in the chamber forced the water out the soil through the membrane. After equilibrium was established at each pressure step, a soil sample was taken from the chamber and the amount of water in the soil is determined gravimetrically.

Plant water relations: Predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential was determined in eight randomly chosen leaves from each irrigation regime, using a pressure chamber (PMS Instrument Co., Corvallis, OR, USA) as described by Scholander *et al.* (1965). The sampled leaves were enclosed in a polyethylene bag just before detaching them from the plant and conserved in a thermal isolated box. The measurements were made as soon as possible using a pressure increment of 0.1 MPa per 2 or 3 s.

Osmotic pressure was determined as described by Ranney *et al.* (1991). Terminal-fully-expanded and middle leaf and root samples were collected before dawn to minimize variation in solute accumulation during the light period. Roots were excised at a point where the root diameter was 5 mm and included the portion of the root system distal to the excision. Excised tissue was hydrated by recutting under water and holding for 2 h, covered with plastic, in the dark, with the cut end submerged. This method was sufficient to fully rehydrate tissue, *i.e.*, result in a water potential of 0 MPa. Osmotic potential (Ψ_π) was determined on expressed sap from fully hydrated tissue after freezing and thawing. Osmolality of expressed sap was determined using a vapor pressure osmometer (Wescor model 5100C, Logan, Utah). Ψ_π potential of the expressed sap was then calculated for 20°C, based on the van't Hoff relation as given by Nobel (1999):

$$\Psi_\pi\,(\text{MPa}) = 0.002437\ (\text{m3.MPa.mol}^{-1}) \times \text{osmolality}\ (\text{mol.m}^{-3})$$

Turgor potential (Ψ_p) were calculated by subtracting Ψ_π from Ψ_w and osmotic adjustment was calculated as the difference in osmotic potential at full turgor between control (100% FC) and stressed plants (Blum, 1989).

Soluble sugar analysis: Total soluble sugars were analyzed in terminal leaves, mature leaves and roots after 30 days of irrigation treatments. Soluble sugars were determined using the phenol-sulfuric acid method described by Dubois *et al.* (1956) and developed by Buysse and Merckx (1993). Fifty milligrams of dry leaf powder were extracted with 80% (v/v) ethanol for three times (20 ml). The total volume of the combined and filtered extracts was adjusted to 100 ml using deionized water. One milliliter of samples was transferred into a glass tube, and 1 ml 18% (w/v) phenol solution was then added. Immediately afterwards, 5 ml of concentrated sulphuric acid were added, the solution in the tube was mixed using a vortex mixer. The tubes were allowed to stand for 20 min, and cooled to room temperature before absorbance was measured with a spectrophotometer at 490 nm (Genesys, Spectronic Instruments, Inc., Rochester, NY, USA). The contribution of soluble sugars to the osmotic potential of the expressed sap was calculated based on the relative dry weight (RDW) at saturation [dry weight/ (saturated weight – dry weight)], the solute concentration, and the van't Hoff relation.

Transpiration: Cumulative transpiration was measured gravimetrically and water use efficiency (WUE) was determined by dividing total dry matter production by the cumulative amount of water used throughout the growth period.

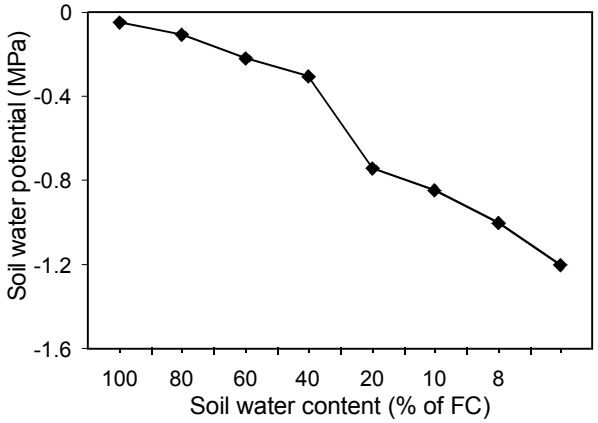

Fig. 1. Relationship between soil water content and soil water potential (Mpa)

Growth analysis: Shoot length, leaf area per plant (measured with a leaf area meter LI-COR Model 3100, Lincoln, NE), and dry weight of plants were recorded at harvest. The decision to harvest any particular treatment was based on the need to do so at the beginning of death symptoms and before death began to occur. Dry weights were determined after drying at 70°C till constant weights. Leaves dropped during water-stress treatment were included.

Relative growth rate (RGR) was measured according to the equation: $RGR = (\ln W_2 - \ln W_1)/ (t_2 - t_1)$

where ln is the natural log and W_1 and W_2 are total dry wt at times (t) 1 and 2, respectively. The experiment was arranged in a completely randomized design and was analyzed by analysis of variance. All data were statistically analyzed according to Snedecor and Cochran (1980) with the aid of COSTAT computer program for statistics. Differences among treatments were tested with LSD at 5% level of significance.

Results and discussion

It is well known that expression of soil moisture status in terms of soil water potential tells much more than just the amount of moisture. Soil water at field capacity is readily available to plants and sufficient air is present for root and microbial respiration. The optimum water content for plant growth and soil microbial respiration is considered to be close to field capacity (FC). Thus, high growth rate is expected to occur at or near FC. Data in Fig. 1 show that, at FC, sandy soil used in this experiment was found to be holding water at a tension of about –0.015 MPa.

Based on our observation, permanent wilting and symptoms of death didn't appear until soil water potential reached about –1.5 MPa, below which, plants were not able to tolerate severe drought or resurvive after rewatering. In contrast to Gliman and Watson (1993), who reported that *Conocarpus* is a highly drought tolerant trees, the present results indicate that *Conocarpus* seedlings can withstand reasonable soil water stress (less than –1.5 MPa) and can survive at moderately low Ψ_{soil}, but can not be classified as a highly drought tolerant or drought resistant species which can survive at much more lower Ψ_{soil} (Kramer and Boyer, 1995). The differences between the early and the present studies may be attributed to the differences between environmental conditions. Vapor pressure deficit (VPD) between leaves and air is highly depending on environmental parameters that might be differing in both studies.

Seedling growth was not affected significantly until soil water potential was lower than –0.1 MPa (between 40 and 30% FC), after which, plant height, leaf area and shoot and root dry weights became disrupted by the interruption in water status as they were severely reduced by soil water deficit (Figs. 2 and 3). Leaf area per plant was the most affected growth parameter by low soil-water potential causing a considerable reduction in the rate of leaf production, which, in part, accounted for the effect of drought on leaf biomass production. The reduction in leaf area per plant was about 70% at soil water potential of –0.3 MPa (20% FC) compared to that at 100% FC (-0.015 MPa). The corresponding reduction in shoot dry weight was about 40% at same soil water potential.

It is well known that reduction in plant growth is one of the most

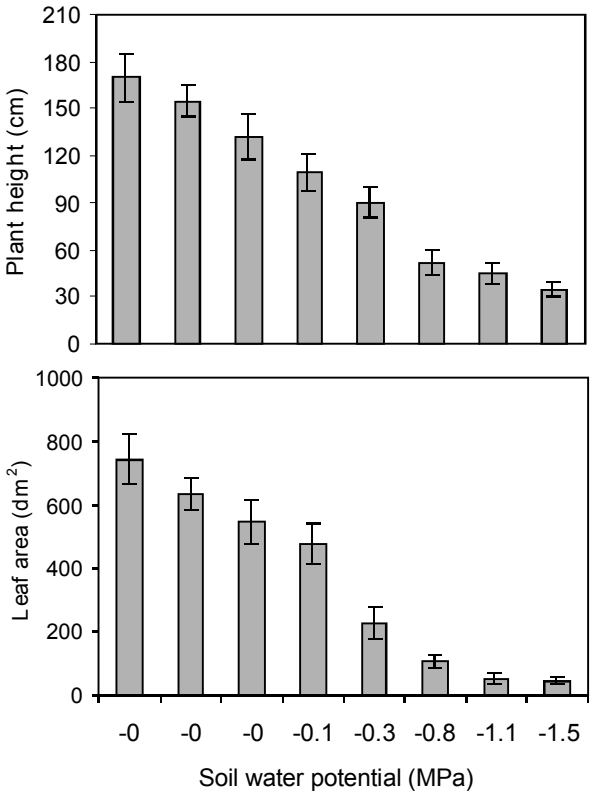

Fig. 2. Effect of soil water potential on plant height and leaf area per plant (n=6)

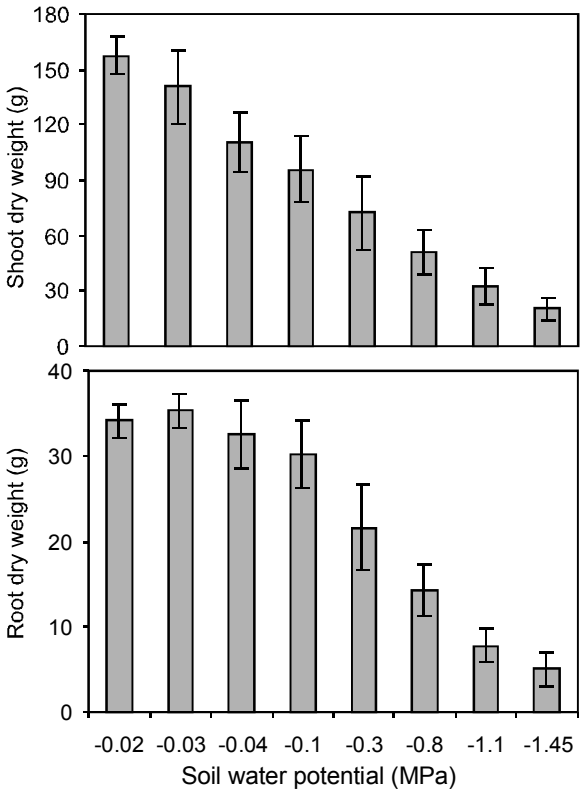

Fig. 3. Effect of soil water potential on shoot and root dry weights (n=6)

conspicuous effect of water deficit on the plant and is mainly caused by inhibition of leaf expansion and stem and root elongations when water potential decreases below a threshold which differs among species (Kramer and Boyer, 1995; Younis *et al.*, 2000). Because turgor reduction is the earliest significant

biophysical effect of water stress, turgor-dependent activities such as leaf expansion and cell elongation are the most sensitive to water deficit. This reality is based on the fact that cell expansion is a turgor-driven process and is extremely sensitive to water deficit according to the equation, $GR = m(\Psi_p - \gamma)$, where GR is the growth rate, Ψ_p is the turgor, γ is the pressure below which the cell wall resists deformation, and m is the wall extensibility. Therefore, a small decrease in plant water content and turgor can substantially decrease the relative growth rate (Fig. 4) and slow down or fully stop growth (Taiz and Zeiger, 2002).

Moreover, water deficit episodes in field conditions are frequently associated with high radiation, thus water deficit is an important limitating factor to plant growth and production in arid and semi-arid regions (Tambussi *et al.*, 2000; Delperee *et al.*, 2003). Typically, as the water content of the plant decreases by water deficit, its cells shrink. This decrease in cell volume results in lower turgor pressure and the subsequent concentration of solutes in the cell. Because growth is dependent mainly on cell turgor (Leuschner *et al.*, 2001) and turgor pressure is very sensitive to water deficit, it decreases sharply with little change in plant water content. So small decrease in water content and turgor can slow down plant growth. In an early study, Nilsen and Orcutt (1996) pointed out that the quantity and quality of plant growth depend on cell division, enlargement, and differentiation, and all these parameters are affected by water deficit because all of them are dependent on turgor pressure. Lowering turgor potential and consequent inhibition of cell expansion as a result of water deficit conditions was reported to slow plant growth and to reduce the number of leaves as plants became shorter (Taiz and Zeiger, 2002).

Also, root mass production decreases progressively with decreasing soil water potential (Fig. 3). This decrease in root growth was associated with decreased root osmotic potential and, consequently, decreased turgor pressure (Fig. 5). It appears that osmotic adjustment in roots occurred at soil water potential lower than –0.40 MPa (Fig. 5). Over a range in soil water potential of –0.015 (FC) to nearly –1.0 MPa, root osmotic potential fell about 0.37 MPa (35%) whereas P fell about 0.75 MPa (60%).

The increase in root/shoot ratio with decreasing water potential indicated more severe reduction in shoot than root growth with decreasing soil water potential (Fig. 4). It is frequently observed that drought increases allocation to roots (Kramer and Boyer, 1995). It may be that ABA plays a role in inhibiting shoot growth, while maintaining root growth (Hsiao and Xu, 2000). Finally, the reduction in leaf growth leaves more assimilates free to go to roots (Leuschner *et al.*, 2001).

Water stress decreased Ψ_π of *Conocarpus* leaves and roots (Table 1). It is clear that fully expanded upper leaves have higher Ψ_π than lower (older) leaves. Interestingly, when

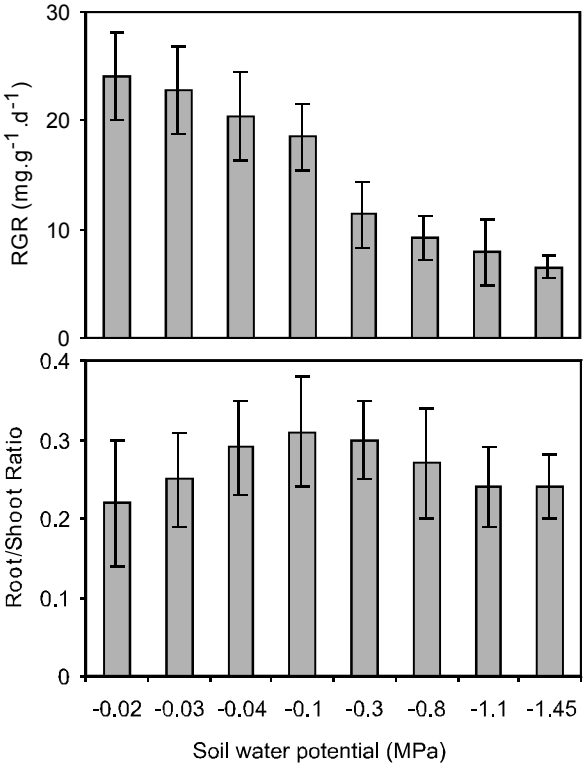

Fig. 4. Effect of soil water potential on relative growth rate (RGR) and root/shoot ratio (n=6)

stressed, all leaves tended to osmoregulate their cell sap as leaves adjusted osmotically. As soil water potential fell from –0.015 MPa (100% FC) to –1.0 MPa (40% FC) the upper leaves showed the greatest decrease in osmotic potential (0.60 MPa), while lower leaves showed less decrease *i.e.* 0.47 MPa (Table 2). The roots had substantially higher Ψ_π than leaves, with an osmotic

Table 1. Effect of water regime on total soluble sugar concentration (mmol.kg^{-1} dry wt), and calculated osmotic potential (Ψ_π) for fully expanding upper and lower leaves and roots of *Conocarpus* seedlings

Water regime (% FC)[1]	Upper leaves		Lower leaves		Roots	
	mmol sugar	Ψ_π (MPa)	mmol sugar	Ψ_π (MPa)	mmol sugar	Ψ_π (MPa)
100	365.3 c[2]	-0.26 c	415.2 d	-0.41 d	114.5 c	-0.12 d
80	410.7 b	-0.53 b	488.3 c	-0.75 c	165.5 b	-0.14 c
60	482.7 a	-0.88 a	531.5 b	-0.94 b	196.2 b	-0.18 b
40	513.4 a	-0.92 a	622.3 a	-1.22 a	250.1 a	-0.21 a

[1] FC = Field capacity.

[2] Values represent means of 3 measurements. Means followed by the same letter(s) within a column are not significantly different using $LSD_{(0.05)}$ comparisons.

Table 2. Effect of water regime on the contribution of soluble sugars to the measured osmotic potential (Ψ_π) of *Conocarpus* leaves and roots

Water regime (% FC)[1]	Upper leaves		Lower leaves		Roots	
	Measu. Ψ_π (MPa)[2]	%Calc. */ Measu.	Measu. Ψ_π (MPa)	%Calc./ Measu.	Measu. Ψ_π (MPa)	%Calc./ Measu.
100	-1.24 c[3]	21 c	-1.45 c	28 c	-0.44 d	27 a
80	-1.46 b	36 b	-1.77 b	42 b	-0.55 c	25 b
60	-1.76 a	50 a	-1.94 a	48 b	-0.64 b	28 a
40	-1.84 a	50 a	-1.92 a	64 a	-0.83 a	25 b

[1] FC = Field capacity.

[2] Calc. = calculated, Measu. = measured.

[3] Values represent means of 3 measurements. Means followed by the same letter(s) within a column are not significantly different using $LSD_{(0.05)}$ comparisons.

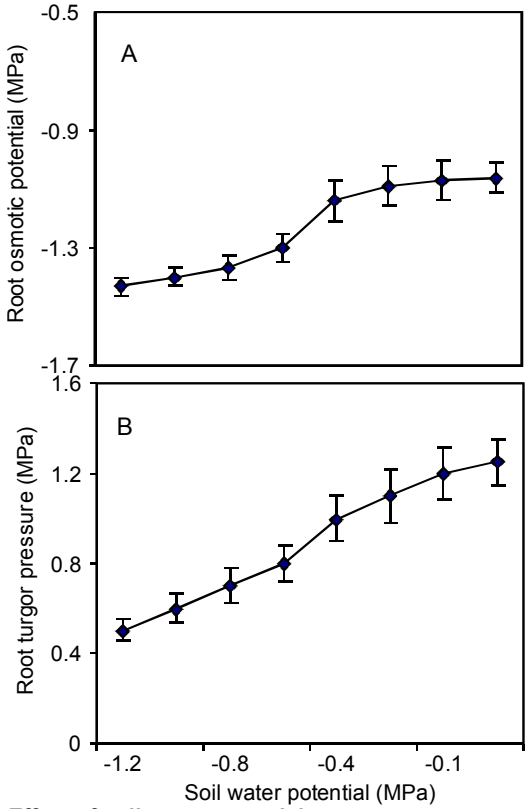

Fig. 5. Effect of soil water potential on root turgor potential and root osmotic potential (MPa). Vertical bars indicate standard error of the mean (n=6 roots)

potential of –0.44 and –0.80 MPa at 100 and 40% FC treated plants, respectively. The higher osmotic potential of roots than of leaves is consistant with work done on other woody species, including *Juglans nigra* (Parker and Pallardy, 1985), *Quercus* spp. (Parker and Pallardy, 1988), and *Prunus avium* (Ranney *et al.*, 1991). But it should be noticed that, although Ψ_π is typically higher in roots than leaves, the greater elasticity of root tissue can contribute to decreased water content and increased solute concentration as tissue water potential declines, resulting in similar water potential at the turgor loss point for both leaves and roots (Ranney, 1991; Salisbury and Ross, 1992).

Total soluble sugars increased in response to water stress in leaves and roots. Estimates of the contribution of total soluble sugars to the Ψ_π of the expressed sap of leaves and roots showed that sugars accounted for a large percentage when plants exposed to severe drought conditions. The contribution reached about 50-60% in leaves and about 25% in roots (Table 2). Generally, the stress-induced reduction in Ψ_π could be accounted for by increasing levels of soluble sugars. The capacity for osmotic adjustment via solute, including soluble sugars, accumulation has been reported for many woody plants (Jones *et al.*, 1985; Parker and Pallardy, 1988; Ranney *et al.*, 1991). Higher sugars and other solute concentrations contribute to lower tissue osmotic potential, maintenance of turgor potential, and improved tolerance of low tissue water potentials (Tyree *et al.*, 2001).

In early studies, Loescher *et al.* (1982) and Ranney *et al.* (1991) found that osmotic potentials of expanding terminal leaves of water-stressed apple and cherry trees, respectively, were higher than that of older leaves. Other studies have found that soluble sugars and sorbitol (a sugar alcohol) are synthesized primarily in older leaves, suggesting that osmotic adjustment in expanding leaves resulted either from increased translocation of soluble sugars and sorbitol to young leaves or from a decreased rate of the metabolism of both compounds, resulted in their accumulation in young leaves under water stress conditions without being disruptive to cell organelles, enzymes, and membrane-bound processes (Salisbury and Ross, 1992; Taiz and Zeiger, 2002). Water soluble sugars have been found to be associated with osmotic adjustment in response to water stress in some plant species (Tan *et al.*, 1992; Zhang and Archbold, 1993; Wang *et al.*, 2003). In the present study, soluble sugar content was higher under prolonged and severe drought stress conditions than under wet conditions. Barathi *et al.* (2001) found that increases in soluble sugar content during prolonged drought stress was accompanied by decreases of starch, protein, and nucleic acids, which indicates drought injury.

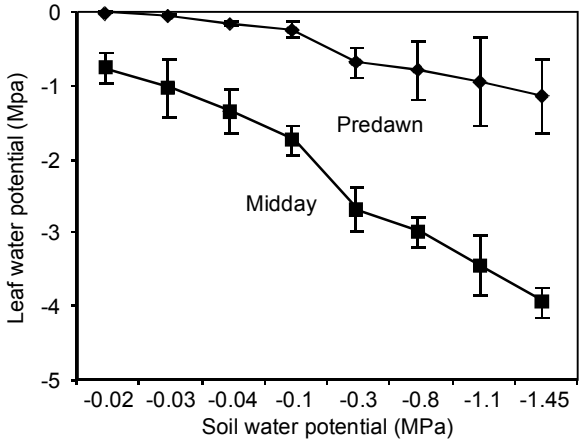

Fig. 6. Effect of soil water potential on predawn and midday water potentials (MPa) of Conocarous plants. Vertical bars indicate standard error of the mean (n=6 leaves)

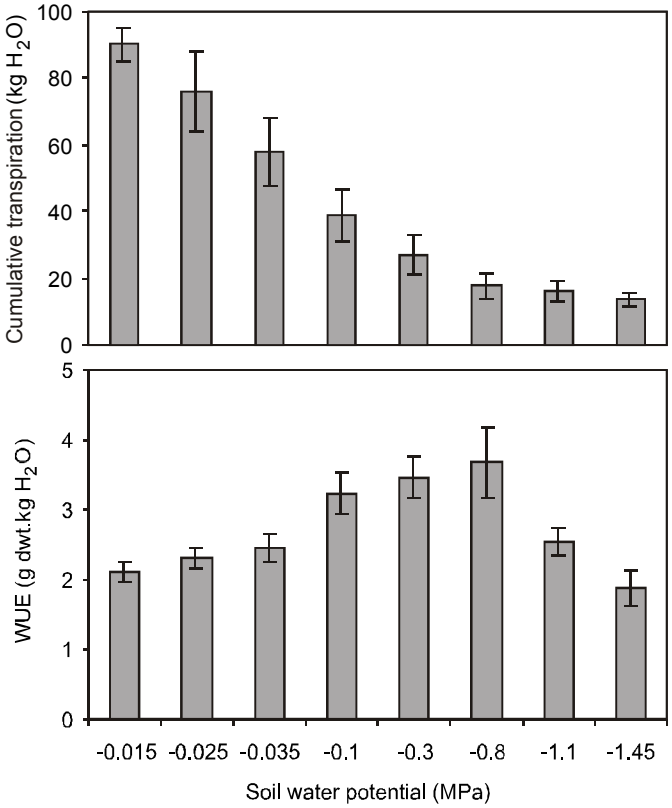

Fig. 7. Effect of soil water potential on cumulative transpiration and water use efficiency of *Conocarpus* (n=6)

Data in Fig. 6 shows that when the soil was held close to field capacity (- 0.015 MPa) leaf water potential (Y_{leaf}) fell from –0.05 MPa in the morning to -0.8 MPa in the middle of the day. During drying, Y_{leaf} progressively decreased with decreasing Y_{soil} to reach its minimum (-0.75 MPa) as soil became severely dry (Y_{soil} = -1.45 MPa). The corresponding value of midday Y_{leaf} was –2.8 MPa. Menzel *et al.* (1986) reported that 85% of the variation in Y_{leaf} could be attributed to some extent to the negative response to leaf-air vapor pressure deficit (VPD). It is not likely to be much response to soil water potential or irrigation when the air is dry. Wet soil alone did not prevent development of low leaf water potential when air is dry. (Menzel *et al.*, 1986) on lychee trees.).

In this concern, Scholander *et al.* (1965) gave a good survey of the water potential ranges of species from different habitats. They found no values below –2.5 MPa for forest trees. Richter (1997) also listed the minimal water potentials of species from contrasting environments for woody species from temperate regions and gave a range between –1.5 and -2.5 MPa. *Conocarpus* showed fairly low Ψ_{leaf} that reached about –2.8 MPa at midday and survived at rewatering. This low Ψ_{leaf} is comparable with the minima found on Chaparral shrubs (-3 to –4 MPa) as reported by Bowman and Roberts (1985). This means that the hydraulic conductivity of the roots can be maintained even as the soil water potential fell below –1.4 MPa during drought periods. For water stress sensitive species, total blockage of sap flow might occur at –1.2 MPa (Kramer and Boyer, 1995; Vogt, 2001). Therefore, only small fluctuations of field water potential are tolerable for these species to maintain vitality. So, *Conocarpus* may be considered as a drought-moderately-tolerant species.

Data in Fig. 7 show that cumulative transpiration was reduced with decreasing Ψ_{soil} particularly at severe drought conditions. The decrease in cumulative water loss may be attributed to the decrease in transpiration rate under water deficit (Kramer and Boyer, 1995). It should be understood that the water potential of the trees was kept relatively high by quite sensitive stomatal control of transpiration (Vogt and Losch, 1999), and this may contribute to drought survival. The suppression of transpiration at severely low Ψ_{soil} may be a reason for diminishing the differences between Ψ_{soil} and the morning Ψ_{leaf} (Ni and Pallardy, 1991).

The results showed a tendency of increasing values of water use efficiency (WUE) with a decrease in the soil water content (Fig 7). It is clear that WUE increased as Ψ_{soil} decreased to –0.8 MPa followed by a decline at lower water potential. These results agree well with those reported by Mielke *et al.* (2000) on *Eucalyptus grandis*. It seems that, under moderately drought condition *Conocarpus* can regulate stomata without prejudicing the amount of water ultimately transpired. It may maintain higher stomatal conductance and thus probably enables high dry matter accumulation and, as the soil was allowed to dry behind a critical value, both photosynthesis and conductance decreased causing a marked decrease in WUE. Similar relationships were also found on *Quercus alba* (Ni and Pallardy, 1991) and *Eucalyptus* trees (Tuomela *et al.*, 1993; Li, 2000). In a study by Morvant *et al.* (1998), they found that Poinsetta plants had acclimated to the water limitation by increasing their photosynthetic WUE. They reported that with an increase in WUE, the drought-treated plants were better able to utilize internal CO_2 for photosynthesis.

Li (2000) explained the influence of WUE on plant growth and stated that, increasing WUE could theoretically either increase or decrease biomass productivity. When water is limited, plants that use a finite water supply more efficiently would grow more rapidly, in this situation, high WUE would positively affect plant growth. Another case increasing WUE is to close stomata partially, thus restricting photosynthesis relative to plants whose stomata are fully open. This strategy would result in a negative correlation between WUE and plant biomass productivity (Cowan, 1982; Makela *et al.*, 1996). In the present study *Conocarpus* followed the latter strategy, as did those in a study by Tuomela (1997) and Li (2000), who also found that increasing WUE could decrease plant dry matter production.

Based on the results of this experiment, the use of soil water potential values seems to be more useful tool than field capacity values for estimating water requirements and use in *Conocarpus* seedlings over an extended period of time.

Conocarpus was found to tolerate a moderate soil water stress over a long period of time than a severe stress for a short time. Growing plants at Ψ_{soil} of –0.1 to –0.2 MPa had only a slight effect on the height, the leaf area, and the dry weight of *Conocarpus* seedlings, and the effect was quickly reversed on rewatering. While, severe drought caused a substantial reduction in the leaf production, which in part account for the effect of drought on plant biomass production. Root elongation decreased progressively with decreasing Ψ_{soil} and was associated with decreased Ψ_{π} and decreased turgor pressure. Osmotic adjustment occurred at Ψ_{soil} of less than -0.4 MPa. Decreased Ψ_{π} in roots was caused by accumulation of osmotica, particularly soluble sugars, in the root cells. The relationship between plant growth and WUE may provide a basis for selecting genotypes with improved drought adaptation and biomass productivity. Midday plant water potential measurements may be a relevant and applicable indicator for irrigation scheduling in *Conocarpus* trees.

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