

Spatial and temporal variability of soil water in drylands: plant water potential as a diagnostic tool

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Abstract Arid and semi-arid regions are characterized by low rainfall and high potential evaporative demand. Here, water is the major limiting factor for plant growth and productivity. Soil and surface hydrology properties (e.g. field capacity, infiltration rates) effectively control the water re-distribution in the ecosystem, a fact that is aggravated in arid environments. Information of the spatial and temporal accessibility of soil water in desert ecosystems is limited. The purpose of the studies is the application of plant water potential to estimate the spatial and temporal variations of soil water availability in different arid ecosystems of the Negev (Israel) and southern Morocco. As model plants the evergreen shrubs *Retama raetam*, *Thymelaea hirsuta* and trees (*Acacia tortilis*) were chosen. Seasonal and spatial variations of the pre-dawn water potential (ψ_{pd}) were examined as diagnostic tool to determine water availability on the landscape level. The seasonal differences in the pre-dawn water potential were less pronounced on the dune compared to the interdune. This showed a better water availability on the dune slope. Also in the investigated wadis systems spatial differences of the water potential could be detected and related to the vegetation pattern.

Key words soil water, pattern, pre-dawn potential, deserts, Nizzana, Negev

1 Introduction

In arid and semi-arid ecosystems water is the major limiting factor for plant growth and determines the vegetation pattern. A pronounced spatial variability of soil water availability is well recognized in dryland research. Besides precipitation, the hydrological soil properties are important for soil water availability. Accumulation of fine grain material on the topsoil and surface crusting lowers infiltration and increases surface runoff along slopes. Re-distribution of water locally leads to an improved water supply for the vegetation (Yair, 1983, 2001). The detection of the spatial heterogeneity of the water requires a high number of sensors to evaluate the water availability on the landscape level. However, the use of tensiometers in drylands is limited mainly due to low soil water content in the upper soils. Therefore, phanerophytes are good indicators for water resources in these heterogenetic ecosystems. Desert perennials develop an extensive root system and are able to explore the soil for water also in deeper soil layers (Evenari et al., 1982; Adar et al., 1995; Batanouny, 2001; Groom, 2003, 2004). Especially shrubs and trees in desert environments depend on sufficient water resources during the entire year. This information is important for a successful

planning of forestry, design of shelterbelts and rehabilitation measures in drylands in the context of soil water resources (Littmann and Veste, 2005; Veste et al., 2006).

Water uptake by the roots depends on the water potential gradients in the soil-plant-atmosphere continuum. The whole plant water fluxes (J_{H_2O}) are estimated with an equation following Ohm's law (Eq. 1):

$$J_{H_2O} = G_{plant} \times (\psi_{soil} - \psi_{min}) \quad (1)$$

where J_{H_2O} is the plant transpiration, G_{plant} is the plant hydraulic conductivity, ψ_{soil} is the soil water potential and ψ_{min} the minimum diurnal leaf water potential. The plant water potential can be easily and rapidly determined with pressure-chambers (Scholander et al., 1965) or by thermocouple psychrometers (von Willert et al., 1995). Commonly used parameters for plant water stress characterization are the minimum water potential (ψ_{min}) and the pre-dawn water potential (ψ_{pd}). During the night the water potential of a non-transpiring plant will equilibrate with the "wettest" water potential of the substrate around the roots and ψ_{soil} becomes ψ_{pd} in Eq. 1 (Ritchie and Hinckley, 1975; Hinckley et al., 1978; Richter, 1997). Therefore,

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ψ_{pd} will be a good estimate of the soil's water availability in many cases.

However, several authors have questioned the equilibrium of plant and soil water potentials. In desert shrubs, investigated in the Great Basin, pre-dawn water potentials were up to 2.1 to 2.7 MPa lower than the substrate water potential. The differences between ψ_{pd} and ψ_{soil} are more important in wet than in dry soils (Havranek, 1980; Donovan et al., 1999; 2001).

Hence, a critical re-evaluation of the pre-dawn water potential as a measure to rapidly estimate soil water availability in drylands is needed. Information on the spatial and temporal accessibility of soil water in desert ecosystems is limited. The purpose of the present studies is to evaluate the potentials of the application of plant water potential to estimate the spatial and temporal variations of soil water availability in drylands. In this context the measurements of ψ_{pd} are used as a diagnostic tool to rapidly determine water availability on the landscape level. As model plants we choose the characteristic shrubs and trees, e.g. *Acacia tortilis*, *Retama raetam* and *Thymelaea hirsuta*. This information of the water accessibility on the ecosystem level is useful for the design of shelterbelts and rehabilitation measures in degraded lands as well in agro-forestry systems in drylands. Sand dunes and rocky areas are characteristic for many deserts. Therefore, the investigation were carried out in the north-western Negev and compared with a wadi systems in southern Morocco.

2 Materials and methods

2.1 Study sites

Sand dunes, North-western Negev, Israel The sand dunes of the north-western Negev are the eastern most part of the sand field covering the northern part of the Sinai Peninsula and the north-western Negev (Veste, 2004). The studies were carried out at the southern most experimental site Nizzana (Fig. 1A, 30°56'N, 34°23'E) at an altitude of 185 m a.s.l. The dunes reach a height of approx. 8–12 m. The climate is determined by a sharp gradient from the moister north to the arid south and average annual rainfall decreases from around 170 mm at the northern edge of the sand field near Yevul to approx. 90 mm near Nizzana. The rainfall is limited to the winter season (October to March). At the Nizzana experimental site the average annual rainfall is approx. 90 mm and varies between 30 mm (1997) and 141 mm (1995/1996). Vegetated linear dunes with mobile crests characterize the study site. Arenosols are the major soil types (Blume et al., 1995). Dominating shrubs at the investigation site are *Anabasis articulata*, *Artemisia monosperma*, *Thymelaea hirsuta*, *Convolvulus lanatus*, *Moltkiopsis ciliata*, *Echiochilon fruticosum* and *Retama raetam* (Veste et

al., 2005). Mean vegetation cover is around 20% in the interdune and 20%–25% on the slopes.

Central Negev Highlands, Sede Boqer, Israel The Sede Boqer experimental site (30°51'N, 34°47'E) is located in the Negev Highlands at an altitude of 480 m a.s.l (Fig. 1A). Rainfall is limited to winter season with an average of 97 mm and varied between 31 mm and 167 mm (Yair and Shachak, 1987; Veste, 2004). The upper slopes are rocky and composed of limestone and flinty limestones. Characteristic plants of the area are *Artemisia herba-alba*, *Retama raetam*, *Thymelaea hirsuta* and *Zygophyllum dumosum* (Evenari et al., 1982).

Wadi El Miyit, Southern Morocco The wadi of El Miyit (30°21'N, 5°37'W) is situated in a basin in the east of the city of Zagora in southern Morocco at an altitude between 720 and 750 m (Fig. 1B). Annual precipitation in the area is highly variable and ranging from 14 mm (1983) to 300 mm (1988) with an average of approx. 70 mm (IMPETUS, 2002). The basin is surrounded by protero- to Paleozoic sedimentary quartzite rocks of the Jebel Tadrart, covering Precambrian granites. The vegetation is dominated by *Acacia tortilis* ssp. *raddiana*, *Retama raetam* and *Ziziphus lotus*.

2.2 Investigated plant species

***Retama raetam* (Forsskal) Webb. (Fabaceae)** The white weeping broom is a stem-assimilating shrub with a height up to 2.5 m. It has a wide ecological range, reaching from Mediterranean coastal dunes to the dry Saharo-Arabian deserts of North Africa. In the Negev *R. raetam* is a common species of the loessial northern Negev, the central Negev highlands, the stony southern Negev and the arid Arava-Valley (Evenari et al., 1982). In the sand dunes of the Nizzana site *R. raetam* growth in the interdune and on stable dune slopes. In the stony Negev Highlands as well as in Wadi El Miyit (southern Morocco) *Retama* grows only within the wadi systems.

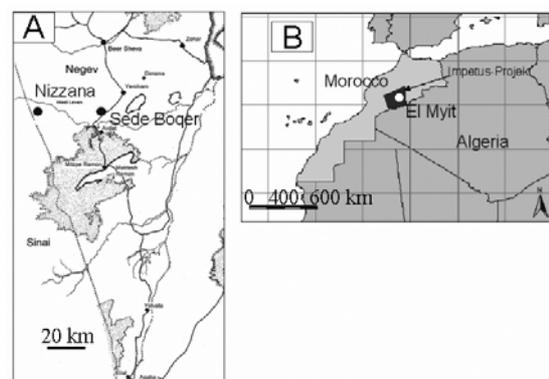


Fig. 1 Location map of the investigation sites Nizzana and Sede Boqer in the Negev desert (Israel) (A) and El Miyit in Morocco (B)

***Thymelaea hirsuta* (L.) Endl. (Thymelaceae)** This evergreen small leaved shrub can reach up to 2 m height. It has a Mediterranean and Saharo-Arabian distribution. *T. hirsuta* is characteristic for the coastal dunes of the northern Sinai and Israel and the inland dunes of the north-western Negev. In the Northern Negev and the adjacent areas this shrub occurs in areas where the annual rainfall is 180 to 300 mm mostly in a diffuse pattern (Danin, 1978). In drier areas it is found in mesic habitats as wadis or at the foot of limestone slopes.

***Artemisia monosperma* Delile (Asteraceae)** *A. monosperma* is 0.5–1.5 m high and a typical plant of semi-stable sands of the northern Sinai, the north-western Negev and of the Coastal Plain in Israel. It tolerates modest sand movement.

***Acacia tortilis* ssp. *raddiana* (Fabaceae)** *A. tortilis* is a typical tree of the African savannas. Subspecies *raddiana* is confined to the northern part of its area from the northern Sahara to the Middle East. In southern Morocco it is the dominant tree species.

***Ziziphus lotus* (L.) Lam. (Rhamnaceae)** A spiny shrub with a wide distribution from Mediterranean to sudanian Africa and occurs also in Spain and Anatolia.

2.3 Plant water potential

Plant water potential (ψ_w) was determined by an Scholander-type pressure chamber (Plant Water Status Console 3000, Soilmoisture Inc., Santa Barbara, CA, USA) after Scholander et al. (1965) and Turner (1988). Terminal shoots were covered with aluminium foil to prevent transpirational lost and cut off with a razor blade. Pre-dawn water potentials (ψ_{pd}) were measured starting 1–2 h before sunrise. The studies in the Negev were carried out between October 1994 and October 1997 and in the Moroccan deserts in May 2002. In El Miyit individuals of *A. tortilis* ssp. *raddiana* ($n = 30$), *R. raetam* ($n = 39$) and *Z. lotus* ($n = 8$) were measured. The position of each individual in El Miyit was mapped by a differential GPS system (Trimble, Sunnyvale, CA, USA) and combined with a three-dimensional relief model of the El Miyit watershed using ArcView Vers. 3.2 (ESRI, Redlands, CA, USA).

3 Results

Figure 2 shows the diurnal changes of leaf water potential in the investigated shrub species in the interdune and at the dune slope after the end of the rainy season. After sunrise the leaf water potential dropped down due to increasing plant transpiration, but it rapidly starts to recover after sunset. No significant variation of leaf water potential between the different species as well as between the plants growing on the dune

and in the interdune area could be measured after winter rainfall.

However, seasonal variations of the pre-dawn water potential of shrubs were more pronounced in the interdune area than on the dune slopes (Fig. 3). At the end of the dry season the pre-dawn water potential of shrubs in the interdune was between -2.42 MPa in *T. hirsuta* and -1.95 MPa in *R. raetam*. In the same dry

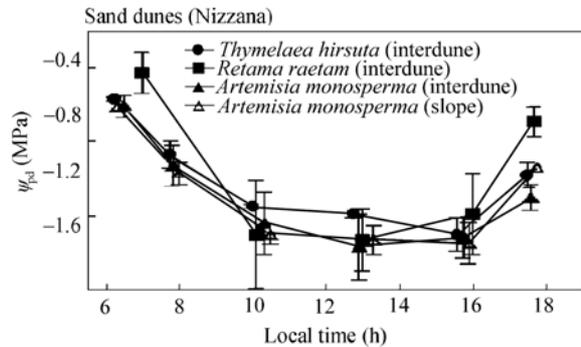


Fig. 2 Diurnal courses of plant water potential of *T. hirsuta*, *R. raetam* and *A. monosperma* growing in the interdune (closed symbols) and on the slope (open symbols) at the end of the rainy season (April 4, 1995)

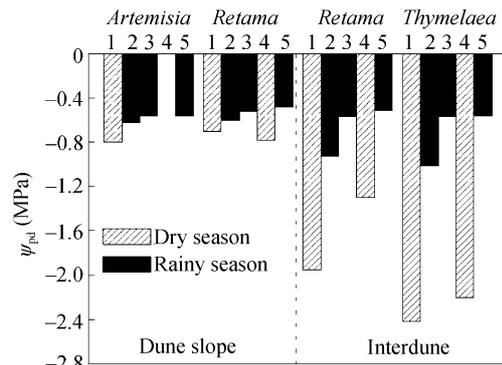


Fig. 3 Spatial and seasonal variations of pre-dawn leaf water potential of *A. monosperma*, *R. raetam* and *T. hirsuta* growing on the slope and in the interdune in the Nizzana sand dunes. 1: Oct. 1994; 2: Nov. 1994; 3: April 1995; 4: Sept 1996; 5: March 1997.

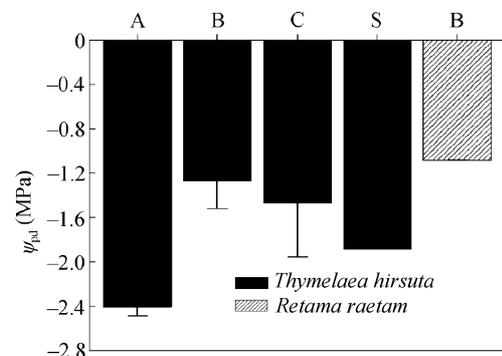


Fig. 4 Spatial variation of the pre-dawn water potential of individuals of *T. hirsuta* along a watershed in Sede Boqer. A: rocky surface; B: terraced wadi; C: non-terraced wadi; S: slope.

season, pre-dawn water potential of the slope growing plants was only -0.7 MPa in *R. raetam* and -0.8 MPa in *A. monosperma* (Fig. 3). After rain pre-dawn water potential increased within a few days in all investigated species. Similar spatial and seasonally changes of the pre-dawn water potential could be observed in the following years (Fig. 3).

Spatial variations of pre-dawn water potential of *T. hirsuta* and *R. raetam* could be also observed in the wadi systems in the Central Negev Highlands (Fig. 4). Pre-dawn water potentials of *T. hirsuta* were significant lower ($\psi_{pd} = -2.41 \pm 0.08$ MPa) in the rocky parts, where infiltration is limited, than in the terraced wadi parts ($\psi_{pd} = -1.27 \pm 0.25$ MPa). In the upstream parts beyond the terraces ψ_{pd} decreased again to -1.47 MPa (Fig. 4). However, this difference was not significant between plants of both parts of the wadi. At the adjacent slopes only one *T. hirsuta* shrub occurred and water potential was here -1.88 MPa.

In the wadi El Miyit in southern Morocco pre-dawn water potentials of the phanerophytes were higher at the downstream parts of the main wadi (W1) than in the smaller wadi systems (SW1–3). The mean pre-dawn water potential of *A. tortilis* was -0.65 ± 0.19 MPa, of *R. raetam* -0.78 ± 0.22 MPa and of *Z. lotus* -0.75 ± 0.11 MPa (Fig. 5). The pre-dawn water potential, especially of *R. raetam*, decreased further with higher altitude reaching an average ψ_{pd} of -1.22 MPa at the higher parts of the wadi. The soils of this habitat contained a high proportion of rocky material (section W3).

The water potential measured in all investigated species was used as the basis for the definition of water potential classes (Fig. 6). Decreased plant water availability was related with the decrease of the pre-dawn water. Therefore, plant water potential of each individual was combined with its spatial distribution in order to classify soil water accessibility spatially within the watershed.

A classified spatial model of the water accessibility is presented in Fig. 7. For phanerogames the main wadi ($\psi_{pd} > -0.58$ MPa) is optimal in terms of water supply and therefore the highest tree density could be found in this areas. At the slopes and the parts of the watershed at higher altitude the water availability is lower and dominated by *Retama raetam*.

4 Discussion

The presented results of the pre-dawn water potential showed spatial and temporal differences in all investigated sites. Vegetation pattern and water potential reflect the water availability. Topographic depressions, such as wadis have higher infiltration rates and tend to store soil moisture due to sand deposits. Whereas, the adjacent Hamada and the steep rocky slopes as well as topographic convexities show low infiltration and high runoff coefficients. Therefore, overland flow occurs

mainly on shallow rocky soils. In the wadi El Miyit the highest density of *Acacia* trees can be found in the downstream parts of the watershed. As impressively shown by our results water potential of plants closely reflects soil water availability. This finding was true for all species and irrespective of the habitat studied. Hence, it proves that plant water potential can be related to vegetation pattern and biomass. A close relation between plant water status and vegetation cover were also found by on regional scale in Mediterranean drylands (Vertovec et al., 2001).

In our study, small-scale spatial differences in the predawn water potential were observed in *R. raetam*. Plants growing at the margin in a higher altitude in general had lower water potentials than plants standing in the riverbed. Investigations on *Welwitschia mirabilis* in the Namib deserts (von Willert, 1994) showed that plants growing at the edge of the wadi had a lower pre-dawn water potential ($\psi_{pd} = -5$ MPa) and a lower leaf growth rate ($0.2 \text{ mm} \cdot \text{d}^{-1}$) than plants located in middle of the river ($\psi_{pd} = -3.3$ MPa, leaf growth = $0.34 \text{ mm} \cdot \text{d}^{-1}$). In this case, the water potential reflects the small-scale differences in hydrological

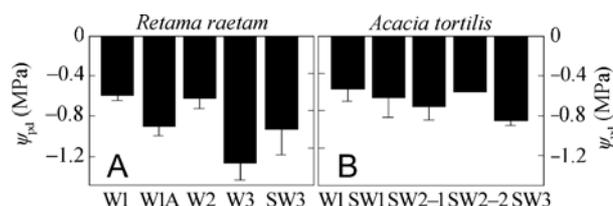


Fig. 5 Mean pre-dawn water potential (ψ_{pd}) of *T. hirsuta* and *R. raetam* in Sede Boqer. Main wadi: W1, W2, at the edge of the wadi W1A; site wadi: SW1–SW3 in El Miyit (Marocco).

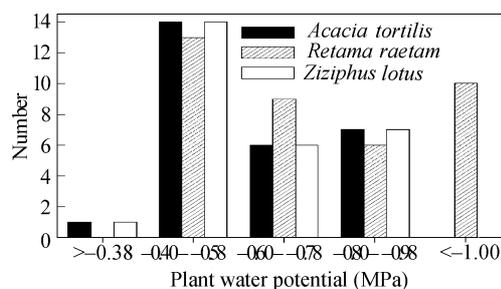


Fig. 6 Pre-dawn water potential (ψ_{pd}) of *R. raetam* and *A. tortilis* ssp. *raddiana* in different wadi areas

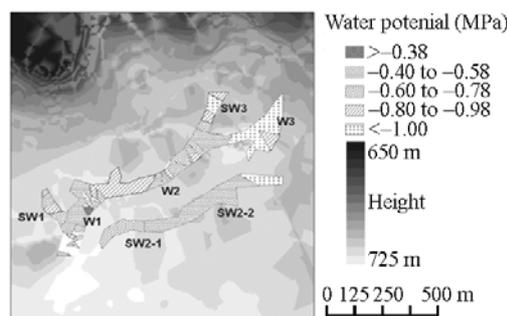


Fig. 7 Classes of pre-dawn water potential of investigated species in the wadi El Miyit

conditions.

Long-term investigation in the Central Negev Highlands showed that runoff from the upper to the lower hillslope the water amount increased by 200–300 mm by an average annual rainfall of 97 mm (Yair, 1983, 2001; Yair and Shahack, 1987). The upper part of the wadi system has stone terraces as it is used for runoff agriculture in the Negev since pre-historical times (Evenari et al., 1982; Yair, 1983). In this part of the wadi the infiltration is increased and water availability is higher than in the neighbouring rocky parts and slopes, where infiltration is limited and runoff occurs. After the rainy seasons the water potential of *Thymelaea hirsuta* and *Retama raetam* plants growing on the slopes and in the wadi are similar (Tenbergen, 1991; Veste and Breckle 1996a). However, the water potential data indicate that the spatial differences are more pronounced during the dry seasons. Both habitats differ in the soil water storage and soil volume.

The presented data just reflect the area-related water availability and not the three-dimensional water distribution in the soil. In the sand dunes of Nizzana water can infiltrate in sand layers deeper than 3 m (Yair et al., 1997). Furthermore, lateral water flows are observed at depths between 1.20 and 3.30 m (Yair et al., 1997). After a two-day rainstorm that yielded 42 mm of precipitation the direct infiltration into the dune was limited to the upper soil layers (up to 0.6 m). During summer time the upper sand layers are completely dry and water is only available in deeper layers. Detailed information about the rooting depths of the investigated shrubs in the sand dunes is still missing. The tap root systems of *Cornulaca monacantha* and *Anabasis articulata* were excavated in the sand dunes to a depth of 2.5 m (Veste and Breckle, 1996b; 2000). The rooting depth of *Thymelaea hirsuta* is more than 3.5 m in wadis (Evenari et al., 1982) and of *Retama raetam* may exceed 10 m (Zohary and Fahn, 1952). For *Acacia tortilis* from the northern Negev water uptake from 12 m depth was found by Adar et al. (1995). All species mentioned above develop an additional surface root system (“T-root system”) enabling them to use the water from both layers. However, the ratio of the water collecting efficiency of both rooting systems is unclear. *Banksia* tree species in Mediterranean sand dunes in Australia is developing a T-root system. The deep root system of *Banksia* species reaches 8–9 m (Groom, 2004). Investigations showed in this case a rapid switch in water uptake from upper soil to groundwater and deeper soil water sources with the onset of the dry summer period (Dawson and Pate, 1996; Zencich et al., 2002). In the winter rainy season the shallow root system collected high amounts of water from the upper soils. In summer months pre-dawn water potential was lower for dune crest plants as compared to plants in the interdunes, due to the larger distance (up to 30 m) to the groundwater sources. From the relatively high shoot water potential

maintained during the dry season Zencich et al. (2002) concluded that subsurface water storage within the Australian dunes is a sufficient water source for the trees. These findings from the Australian dunes support our results from the water potential measurements and the soil water investigations that water sources within deeper layers of the dune play an important source for the dune plants (Yair et al., 1997; Rummel and Felix-Henningsen, 2004; Yair, 2005). Hydraulic lift can also contribute to the soil water heterogeneity. Several phreatophytes from very different deserts (e.g. *Artemisia tridentata*, *Banksia prionotes*) absorb water with their deep reaching root system and release it from the root into the dry upper soil layer at night and take it up again at daytime (Caldwell et al., 1998; Burgess et al., 2000).

Still controversial is the question if the pre-dawn water potential is in equilibrium with the soil water potential. Studies by Donovan et al. (1999, 2001) with the cold-desert shrubs *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* showed that pre-dawn plant water potential was significantly lower than soil water potential. This discrepancy is consistent with the accumulation of salts and other organic solutes in the leaves of halophytes and xerohalophytes. Accumulation of inorganic and organic solutes results in lowering the osmotic potential. In xerohalophytes accumulation mainly of NaCl is a common feature and the ions pattern is genetically fixed (Breckle, 1990; Albert et al., 2000). Even on non-saline soils such plants accumulate high amounts of salts. Therefore, it is not surprising that in (xero-) halophytes the water potential is drastically lower than the soil water potential. The Chenopodiaceae *Anabasis articulata* and *Cornulaca monacantha* growing in the sand dunes of the Negev showed lower water potential than the shrubs investigated in this study (Veste and Breckle, 1995, 2000). However, also in *Anabasis articulata* spatial differences in ψ_{pd} could be observed. At the end of the rainy season shrubs growing on the fine-grain soils in the interdunes showed lower water potential ($\psi_{pd} = -2.53$ MPa) than those growing on sandy soils ($\psi_{pd} = -1.62$ MPa). This difference in water potential clearly reflects differences in water availability between both soil types. At the end of the dry season pre-dawn water potential dropped to -4.2 MPa on the playa and -3.88 MPa on sandy soils.

Another factor potentially leading to plant-soil disequilibrium is nighttime transpirational loss. Its contribution was approx. 0.1 MPa in *Chrysothamnus* and approx. 0.6 MPa in *Sarcobatus* (Donovan et al. 1999). In our study the contribution of nighttime transpiration cannot be fully excluded, but gas exchange measurements of *Artemisia monosperma* and *Thymelaea hirsuta* showed a minimal transpiration rate during the night (Veste and Breckle, 1996a).

In fact the aims of the investigations are the relative temporal and spatial differences rather than the exact

measurement of the soil water potential of the wettest soil. In a split root experiments with walnut trees Améglio et al. (1999) showed that the pre-dawn water potential equilibrated to the wet soil conditions. It is not reflecting a mean water status of the soil. An important role for the recovery of leaf water potential after sunset is also the soil hydraulic conductivity. In *Retama raetam* and *Thymelaea hirsuta* leaf water potential regained its pre-dawn values within less than 1 h after sunset. When soils dry, the soil hydraulic conductivity declines and water uptake is limited by a reduced water flow rates at the soil-root interface (Kutilek and Nielsen, 1994; Schmidhalter, 1997). Tomato plants under different irrigation regimes showed no significant differences in their pre-dawn water potential when irrigation amount was reduced by 40%. In the well-watered plants the water potential recovered shortly after sunset, whereas in the plants with reduced irrigation the recovery times increased by nearly one hour (Veste, unpublished). One reason for this time lag is the different water flow rates in the soil due to changes in the hydraulic conductivity of drying soils.

5 Conclusions

We are aware that the pre-dawn water potential does not exactly reflect the water potential of the wettest soil. However, it is a good estimation of a mean nearest root zone soil water potential. Therefore, the pre-dawn water potential shows spatial differences in plant water availability in xeric ecosystems. Measuring water potential has the advantage that the needed instrument is very easy to use. In contrast, other methods to determine soil water content and soil water potential are often at their physical limits in dry soils. Thermocouples psychrometers and especially tensiometers are direct methods but they are working only at moderate or high soil water potential and salinity further limits their application. Even TDR systems have limits due to the low water content of the sandy soils (e.g. Rummel and Felix-Henningsen, 2004). In addition, instrumental investigations in most cases cover only the upper soil layers and not the entire rooting soil volume.

To summarize, the leaf water potential can be used as a diagnostic tool to measure and to map changes in water availability in drylands on different scales. Linking spatial pattern of the water potential with a spatial model of vegetation pattern (Littmann and Veste, 2005) will help optimize shelterbelt design and rehabilitation measures in arid and semi-arid regions in the future.

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