

Leaf water relations for 23 angiosperm species from steppe grasslands and associated habitats in Hungary

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Abstract: Pressure-volume (p-V) analysis, instantaneous transpiration rate and relevant leaf structural information were used to compare leaf water relations for 23 angiosperm species from semiarid temperate loess-, sand- and saline steppe grasslands and several associated habitats representing a water availability gradient. For the species studied, the most marked differences occurred between grasses and dicots. Grasses in our survey possessed low (highly negative) osmotic potential both at water saturation and at turgor loss, moderate transpiration rate, relatively high leaf dry matter proportion (DMP) and - except for the sclerophyllous *Festuca* species - high specific leaf area (SLA, area per unit dry mass). In contrast, dicots had lower bulk tissue elasticity, higher (less negative) osmotic potentials, intense transpiration, and lower SLA and DMP than grasses. Therefore, grasses mainly invest in osmotic potential to extract water from drying soil, while dicots rely on relatively inelastic tissue that decreases water potential by a rapid drop of turgor with turgor loss occurring at relatively high water content. Habitat effects were significant for osmotic parameters only. Osmotic potential at full turgor and at turgor loss decreased in the following order: loess grassland > sand grassland \cong saline grassland > loess wall. Life form influenced leaf structure only, since annuals possessed markedly higher SLA and lower DMP than perennials. Comparison of habitat specialist species within the same genus revealed that certain congeners (*Achillea* and *Aster* spp.) do not differ significantly in leaf water relations, thus they might rely on similar water supply in the three steppes. Other congeners (*Festuca*, *Kochia* and *Plantago* spp.) differed considerably, thus for these plants leaf function and structure must be different to ensure survival under the contrasting water regime. For the two generalist grasses (*Cynodon dactylon* and *Dactylis glomerata*) habitat-specific populations showed a tendency of increasing capacity for water extraction from soil (more negative water potential) with increasing habitat dryness, although differences were significant only between the extremes of the water availability gradient.

Abbreviations: E - potential transpiration rate, DMP - leaf dry matter proportion, ⁰RWC - relative water content at turgor loss, SLA - specific leaf area, ϵ_i - bulk modulus of elasticity, Ψ_p - turgor potential, Ψ_w - water potential, Ψ_π - osmotic potential, ¹⁰⁰ Ψ_π - osmotic potential at full turgor, ⁰ Ψ_π - osmotic potential at turgor loss, $\Delta\Psi_\pi$ - the amplitude of osmotic response (¹⁰⁰ Ψ_π - ⁰ Ψ_π).

Introduction

Under the semiarid temperate climate of the Hungarian Plain, natural steppe habitats experience various degrees of temporary water shortage depending on local conditions. Soil properties, particularly parent material, texture and ionic composition appear to be an important determinant, since water deficit increases in the direction of loess-, sand- and saline steppe grasslands (Fekete et al. 1997). These communities possess their own characteristic flora (Soó 1964, Varga 1998, Zólyomi and Fekete 1994), where often the same genus is represented by dif-

ferent species in different steppe vegetation. Several species, however, seem to be of wider ecological tolerance since they appear in more than one type of these habitats. Among other plant traits (dispersal, life history, ionic tolerance, etc.) water relations certainly play an important role in making species capable of inhabiting one or the other type of these habitats. To test this assumption we compared leaf water relations for congeneric or closely related plant species occurring in only one of the above three grassland types or certain associated steppe habitats ('specialists'), and also for two grass species growing in all three habitats ('generalists'). For this purpose, the

Table 1. The list of species studied.

Class	Life form	Loess grassland, loess wall semidesert (LWD), or ruderal weed (W)	Sand grassland	Saline grassland, summer-dry pool (SDP), or ruderal weed (W)
Dicots	Annuals	<i>Kochia scoparia</i> (W)	<i>Plantago indica</i>	<i>Camphorosma annua</i> (SDP) <i>Atriplex tatarica</i> (W)
	Perennials	<i>Achillea pannonica</i>	<i>Achillea ochroleuca</i>	<i>Achillea asplenifolia</i>
		<i>Aster amellus</i>		<i>Aster tripolium</i>
		<i>Plantago stepposa</i>		<i>Plantago maritima</i> <i>Limonium gmelini</i>
		<i>Salvia pratensis</i>	<i>Potentilla arenaria</i>	
		<i>Taraxacum serotinum</i>		
		<i>Kochia prostrata</i> (LWD)		
Grasses	Annuals	<i>Hordeum murinum</i> (W)	<i>Secale sylvestre</i>	
	Perennials	<i>Festuca valesiaca</i>	<i>Festuca vaginata</i>	<i>Festuca pseudovina</i>
		<i>Cynodon dactylon</i> (LWD)	<i>Cynodon dactylon</i>	<i>Cynodon dactylon</i>
		<i>Dactylis glomerata</i>	<i>Dactylis glomerata</i>	<i>Dactylis glomerata</i>

standard procedure of pressure-volume (p-V) analysis was used. This method has been successively applied to explore differences in leaf water relations between sympatric species (e.g., LoGullo and Salleo 1988, Muller 1991, Nobel and Jordan 1983), genotypes (e.g., Rascio et al. 1988), or seasons with different water regime (e.g., Bowman and Roberts 1985ab, Grammatikopoulos 1999, Knapp 1984, Pavlik 1984, Prior and Eamus 1999, Tyree et al. 1978, Wan et al. 1993). However, we are not aware of a study that compares similar vegetation types along a water availability gradient involving a number of species. Using different techniques, Kvet and Rychnovská (1965) explored leaf water relations for a number of Central European steppe plants. In addition to interspecific and between-site comparisons, we were also curious whether rough taxonomic affiliation (dicot or grass) and life form (annual or perennial) have measurable influence on leaf water relations and associated structural characteristics.

Materials and methods

Plants were collected on the Great Hungarian Plain in their original steppe habitat from June to August 1997. Sampling mainly focused on three natural steppe grassland associations characteristic of the region: *Salvio-Festucetum rupicola* (on loess), *Festucetum vaginatae danubiale* (on sand), and *Achilleo-Festucetum pseudovinae* (on saline soil). Few species were collected from other phytocoenoses commonly associated with these grasslands, i.e., *Agropyro-Kochietum prostratae* (loess-wall semidesert), *Camphorosmetum annuae* (halophyte

vegetation in summer-dry saline pools), and ruderal weed associations. Altogether 23 plant species were studied: 16 dicot and 7 grass species, 18 of these were perennial (H) and 5 annual (Th). Each species was from one habitat only except the two generalist grasses (*Cynodon dactylon* and *Dactylis glomerata*), which were collected from all three types of steppe. The species studied are listed in Table 1.

Water relations parameters

In the field, the most recent fully expanded leaves were cut from several shoots per population and were transferred to laboratory in closed chambers with the leaf base immersed in water. Before measurement, at least 12 hours were allowed for leaves to reach full turgor. Then, pressure-volume (p-V) analysis was performed by repeatedly measuring water potential (Ψ) and mass (m, for relative water content determination) on leaf samples slowly losing their water content in the hygrometer sample chamber which was repeatedly opened up for weighing. Water potential was measured hygrometrically by using a Wescor HR-33T psychrometer/hygrometer connected to eight C52-SF sample chambers (Wescor Inc., Logan, Utah). At least four hours were allowed between consecutive measurements thus leaf samples could equilibrate with chamber air. Mass was measured with 0.1 mg accuracy by using a Kern 410 electronic analytical balance (Kern Inc., Japan). For each species, three replicate p-V analyses were conducted. A logarithmic regression was fitted to each $1/\Psi$ vs. (100-RWC) data set (type II trans-

Table 2. Leaf water relations and leaf structural parameters for the species groups studied. Abbreviations: $^{100}\Psi_{\pi}$: osmotic potential at full turgor; $^0\Psi_{\pi}$: osmotic potential at turgor loss; $\Delta\Psi_{\pi}$: the amplitude of osmotic response ($^{100}\Psi_{\pi}-^0\Psi_{\pi}$); ^0RWC : relative water content at turgor loss; ϵ_i : bulk modulus of elasticity; E: potential transpiration rate; SLA: specific leaf area; DMP: leaf dry matter proportion. For more details see text. For each grouping, values in a column followed by the same letter are not significantly different (ANOVA with LSD test).

Species group	$^{100}\Psi_{\pi}$ (MPa)	$^0\Psi_{\pi}$ (MPa)	$\Delta\Psi_{\pi}$ (MPa)	^0RWC (%)	ϵ_i (MPa)	E ($\text{g m}^{-2} \text{min}^{-1}$)	SLA ($\text{m}^2 \text{kg}^{-1}$)	DMP (%)
Grasses	-1.58 ^a	-2.93 ^a	1.35 ^a	73.2 ^a	7.96 ^a	2.64 ^a	18.8 ^a	27.0 ^a
Dicots	-1.12 ^b	-1.91 ^b	0.79 ^b	78.5 ^b	11.11 ^b	4.85 ^b	15.7 ^b	17.6 ^b
Loess grassland	-1.00 ^a	-1.70 ^a	0.70 ^a	75.6 ^a	8.55 ^a	4.35 ^a	19.1 ^a	21.5 ^a
Sand grassland	-1.40 ^b	-2.75 ^b	1.35 ^b	74.7 ^a	9.23 ^a	4.07 ^a	17.2 ^a	23.0 ^a
Saline grassland	-1.35 ^b	-2.48 ^b	1.12 ^{ab}	77.5 ^a	11.50 ^a	3.54 ^a	15.1 ^a	19.2 ^a
Loess wall	-2.12 ^c	-2.97 ^b	0.86 ^{ab}	80.2 ^a	10.11 ^a	3.56 ^a	15.1 ^a	26.2 ^a
Annuals	-1.33 ^a	-2.25 ^a	0.92 ^a	73.6 ^a	9.50 ^a	3.51 ^a	26.9 ^a	12.6 ^a
Perennials	-1.30 ^a	-2.35 ^a	1.05 ^a	77.1 ^a	9.92 ^a	4.07 ^a	14.1 ^b	24.0 ^b

formation, Tyree and Richter 1981) and the following parameters were calculated according to Koide et al. (1989):

- $^{100}\Psi_{\pi}$: osmotic potential at full turgor,
- $^0\Psi_{\pi}$: osmotic potential at turgor loss,
- $\Delta\Psi_{\pi}$: the amplitude of osmotic response ($^{100}\Psi_{\pi}-^0\Psi_{\pi}$), mostly determined by tissue elastic properties (i.e., low for rigid leaf tissue, Cheung et al. 1975),
- ^0RWC : relative water content at turgor loss,
- ϵ_i : bulk modulus of elasticity calculated as the change of turgor with unit change in RWC ($\epsilon_i = d\Psi/d\text{RWC}$, Pavlik 1984) during the initial fast turgor loss, thus $\epsilon_i = [-(b/a)x^{-(b-1)}+c/(cx+d)^2]*100$, where $x = 100-\text{RWC}$ at the fastest loss of turgor, near to full turgidity, (ax^b) is the equation of a curve, $cx+d$ is the equation of a line).

Since the estimation of apoplastic water content (R_a) is not reliable in this way (Kubiske and Abrams 1990, Tyree and Richter 1981), we did not use this parameter. Although effort was made to remove all surface water from leaves after water saturation, for several species (e.g., *Festuca* spp. with inrolled leaves) this was not successful. This resulted in an initial plateau on the curve when RWC declined with no associated change in leaf water potential. Curves were corrected for this effect in the following way:

$$\text{original RWC} = [(m_a - m_d)/(m_i - m_d)] * 100$$

$$\text{corrected RWC} = [(m_a - m_d)/(m_i - m_p + 0.0001 - m_d)] * 100$$

where m_i = mass at full turgor, m_p = mass at the end of the plateau (until Ψ does not change), m_a = actual mass, and m_d = dry mass.

In addition to p-V analysis parameters, several related variables were determined for each species. A measure of potential transpiration rate (E) was obtained by determining the rate of water loss from fully turgid cut leaves (or leaf pieces) in a growth chamber (at $120 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density and $23-25^\circ\text{C}$ air temperature). To characterize leaf structure, the specific leaf area (SLA, area per unit leaf dry mass) and the percentage proportion of dry matter in the water saturated leaf mass (DMP) were calculated. Specific leaf area has two components: leaf thickness and bulk tissue density. Although these parameters were not determined directly, leaf dry matter proportion measured in our study is closely related to tissue density and is independent of leaf thickness (Ninemets 1999, Wilson et al. 1999). Leaf area was determined to $\pm 0.1 \text{ cm}^2$ by using a LI-COR 3100 Area Meter (LICOR Inc., Nebraska).

For each variable, analysis of variance (ANOVA) with subsequent least significant difference (LSD) tests were used for statistical evaluation by using the Statistica 4.5 package (StatSoft Inc. 1993). Differences were considered significant at $p < 0.05$ probability level. Additionally, multivariate statistical analysis of the full dataset was completed by the Centered Principal Components Analysis routine of the SYN-TAX 5.0 program package (Podani 1993).

Results and discussion

The most marked differences in the species studied were between grasses and dicots. Osmotic potential at full turgor ($^{100}\Psi_{\pi}$) and at turgor loss ($^0\Psi_{\pi}$) was lower (more negative), while the amplitude of osmotic change in grasses was twice that in dicots (Table 2). Furthermore, grasses had more elastic leaf tissue (lower bulk elastic modulus, ϵ_i), lower transpiration rate (E), and higher specific leaf area (SLA) and leaf dry matter proportion (DMP) than dicots. These findings suggest that the osmotic component is more important in generating water potential gradients from leaf to soil in grasses, while the relatively inelastic cell walls of dicots allow this gradient to be achieved by a more rapid loss of turgor near full turgidity. This is clearly seen on the Höfler-diagrams presented for a representative species of dicots and grasses (Fig. 1). The grass *Cynodon dactylon* has lower osmotic and water potentials at a given RWC value and maintains turgor to a RWC lower than that in the dicot *Achillea pannonica*, which exhibits a more rapid drop in turgor. We assume that these patterns are at least partly associated with the differences in root system morphology and thus in the source of available water for the plant. The fibrous root system of steppe grasses primarily exploits the top-most soil layers (Jackson et al. 1996) where water is less readily available, and hence these plants develop a greater water potential gradient. In contrast, the taproot system of

dicots may rely on the more readily available water that is stored deeper in the soil, and these plants can cope with temporary stress by steepening the water potential gradient by turgor loss alone. This strategy is less expensive than investment into osmotic substrates. Knapp and Medina (1999) came to a similar conclusion when compared rooting depth and dry season leaf water potential for dominant C_4 grasses and subordinate C_3 dicots in the tall-grass prairie. Owing to their root system morphology grasses may be capable of more efficient use of small rainfall events rewetting soil layers near surface than dicots (Sala and Lauenroth 1982). As far as the osmotic versus elastic component is concerned, Nilsen (1983) argued that although the rapid drop of water potential with water loss in rigid tissues generates a high leaf-to-soil water potential gradient, turgor becomes lost at moderate water deficits and growth stops. Instead, in seasonally dry environments - like our steppe grasslands - relatively elastic cell walls coupled with the ability to increase solute concentration in the cytoplasm (i.e., osmotic component) are the two attributes drought tolerant species should exhibit. In our study, the higher importance of the osmotic component in grasses (compared to dicots), their more elastic leaf tissue and reliance on drier soil strata supports this reasoning. Knapp (1984) experienced a similar relationship between drought tolerance and the osmotic vs. elastic components of leaf water potential when compared

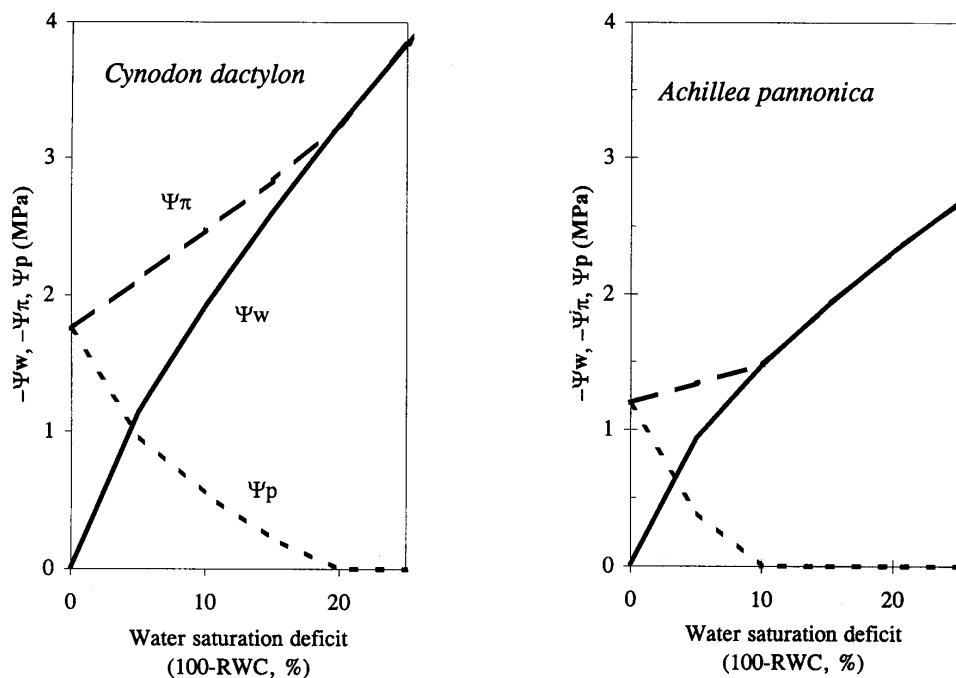
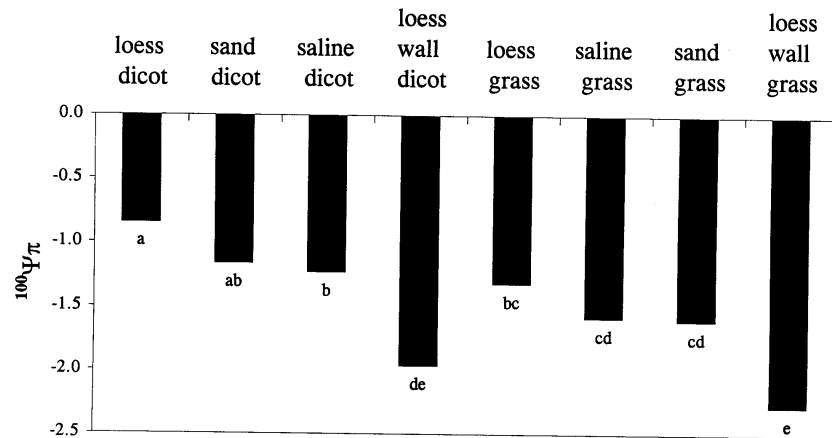


Figure 1. Höfler diagrams for a dicot (*Achillea pannonica*) and a grass (*Cynodon dactylon*) species as examples of their own groups. Abbreviations: Ψ_w : water potential; Ψ_{π} : osmotic potential; Ψ_p : turgor potential.

Table 3. Leaf water relations and leaf structural parameters for the species studied. Mean values \pm SE. Abbreviations: $^{100}\Psi_{\pi}$: osmotic potential at full turgor; $^0\Psi_{\pi}$: osmotic potential at turgor loss; $\Delta\Psi_{\pi}$: the amplitude of osmotic response ($^{100}\Psi_{\pi} - ^0\Psi_{\pi}$); $^0\Psi_{\pi}$: relative water content at turgor loss; ε : bulk modulus of elasticity; E: potential transpiration rate; SLA: specific leaf area; DMP: leaf dry matter proportion. Habitat classes are steppe grasslands on loess, sand or saline soil, loess wall, semidesert and ruderal weed association.

Species	Habitat	$^{100}\Psi_{\pi}$ (MPa)	$^0\Psi_{\pi}$ (MPa)	$\Delta\Psi_{\pi}$ (MPa)	$^0\Psi_{\pi}$ (%)	ε_i (MPa)	E (g m ⁻² min ⁻¹)	SLA (m ² kg ⁻¹)	DMP (%)
Dicots									
<i>Achillea pannonica</i>	loess	-1,06 \pm 0,17	-2,03 \pm 0,22	0,96 \pm 0,12	71,9 \pm 5,9	18,54 \pm 3,01	7,79 \pm 0,91	11,4 \pm 0,5	22,7 \pm 1,0
<i>Achillea ochroleuca</i>	sand	-1,08 \pm 0,01	-2,35 \pm 0,53	1,28 \pm 0,52	76,0 \pm 5,0	7,61 \pm 0,45	8,38 \pm 0,42	14,2 \pm 0,6	20,0 \pm 0,8
<i>Achillea asplenifolia</i>	saline	-1,10 \pm 0,15	-2,08 \pm 0,65	0,98 \pm 0,50	72,7 \pm 8,5	7,12 \pm 0,68	6,18 \pm 0,16	9,6 \pm 0,8	20,5 \pm 0,4
<i>Plantago indica</i>	sand	-0,78 \pm 0,02	-2,20 \pm 0,18	1,42 \pm 0,20	71,7 \pm 0,5	5,33 \pm 0,66	8,39 \pm 2,37	17,4 \pm 2,2	9,7 \pm 1,5
<i>Plantago maritima</i>	saline	-0,76 \pm 0,13	-2,58 \pm 0,17	1,80 \pm 0,04	76,3 \pm 0,6	10,38 \pm 2,43	4,95 \pm 0,89	10,0 \pm 1,3	9,6 \pm 0,1
<i>Plantago stepposa</i>	loess	-0,69 \pm 0,19	-1,00 \pm 0,27	0,31 \pm 0,07	94,6 \pm 0,8	18,63 \pm 6,24	4,89 \pm 0,50	10,2 \pm 0,2	19,4 \pm 0,6
<i>Aster tripolium</i>	saline	-0,71 \pm 0,04	-1,10 \pm 0,07	0,39 \pm 0,04	85,8 \pm 0,3	5,75 \pm 0,10	2,24 \pm 0,23	16,4 \pm 0,1	12,7 \pm 1,0
<i>Aster amellus</i>	loess	-0,92 \pm 0,07	-1,17 \pm 0,06	0,25 \pm 0,07	72,1 \pm 1,8	9,34 \pm 0,46	6,30 \pm 0,40	15,1 \pm 1,0	18,4 \pm 1,8
<i>Kochia scoparia</i>	weed	-1,26 \pm 0,02	-1,79 \pm 0,28	0,53 \pm 0,29	60,5 \pm 1,0	7,32 \pm 0,86	2,60 \pm 0,62	35,9 \pm 2,2	14,4 \pm 0,4
<i>Kochia prostrata</i>	loess wall	-1,96 \pm 0,26	-2,57 \pm 0,14	0,61 \pm 0,16	85,4 \pm 2,3	9,28 \pm 1,41	5,32 \pm 0,78	11,7 \pm 1,6	19,9 \pm 2,6
<i>Salvia pratensis</i>	loess	-0,57 \pm 0,06	-1,15 \pm 0,20	0,64 \pm 0,18	76,9 \pm 2,7	3,60 \pm 1,24	3,72 \pm 0,34	22,5 \pm 0,3	20,7 \pm 0,6
<i>Taraxacum serotinum</i>	loess	-0,61 \pm 0,02	-0,85 \pm 0,02	0,24 \pm 0,00	87,1 \pm 0,7	5,17 \pm 0,36	4,07 \pm 0,62	12,8 \pm 0,6	17,7 \pm 1,7
<i>Potentilla arenaria</i>	sand	-1,62 \pm 0,15	-2,25 \pm 0,11	0,63 \pm 0,14	80,4 \pm 2,5	11,27 \pm 2,61	3,81 \pm 0,32	10,3 \pm 0,7	34,3 \pm 0,7
<i>Limonium gmelini</i>	saline	-1,72 \pm 0,18	-3,57 \pm 0,70	1,85 \pm 0,68	73,6 \pm 6,6	26,78 \pm 7,00	2,54 \pm 0,11	5,8 \pm 1,0	21,2 \pm 2,3
<i>Atriplex tatarica</i>	saline	-1,12 \pm 0,08	-1,48 \pm 0,06	0,36 \pm 0,04	84,2 \pm 1,1	18,50 \pm 1,51	4,30 \pm 0,23	25,8 \pm 0,7	10,8 \pm 1,5
<i>Camphorosma annua</i>	saline	-1,96 \pm 0,15	-2,40 \pm 0,22	0,43 \pm 0,07	87,0 \pm 1,9	13,17 \pm 2,21	2,08 \pm 0,25	22,7 \pm 1,9	9,7 \pm 1,0
Grasses									
<i>Festuca vaginata</i>	sand	-1,17 \pm 0,13	-1,68 \pm 0,15	0,51 \pm 0,03	89,3 \pm 1,2	14,80 \pm 0,32	1,59 \pm 0,29	4,5 \pm 0,2	40,0 \pm 0,7
<i>Festuca valesiaca</i>	loess	-1,07 \pm 0,10	-1,71 \pm 0,16	0,64 \pm 0,06	78,3 \pm 1,1	3,59 \pm 0,50	5,60 \pm 1,73	7,8 \pm 0,6	40,2 \pm 1,1
<i>Festuca pseudovina</i>	saline	-1,70 \pm 0,06	-3,40 \pm 0,31	1,70 \pm 0,25	65,0 \pm 1,7	4,64 \pm 0,17	3,89 \pm 0,78	8,8 \pm 0,5	38,5 \pm 1,2
<i>Dactylis glomerata</i>	sand	-1,70 \pm 0,36	-4,13 \pm 1,28	2,42 \pm 0,94	67,4 \pm 7,7	8,80 \pm 1,94	1,76 \pm 0,13	25,8 \pm 1,2	16,6 \pm 3,9
<i>Dactylis glomerata</i>	loess	-1,34 \pm 0,22	-2,79 \pm 0,58	1,45 \pm 0,80	70,1 \pm 6,2	4,14 \pm 1,94	2,04 \pm 0,19	22,6 \pm 1,9	23,0 \pm 1,7
<i>Dactylis glomerata</i>	saline	-1,79 \pm 0,04	-2,28 \pm 0,03	0,55 \pm 0,06	82,9 \pm 0,4	12,06 \pm 2,03	1,63 \pm 0,20	18,7 \pm 1,3	24,3 \pm 1,7
<i>Cynodon dactylon</i>	sand	-2,14 \pm 0,19	-3,84 \pm 0,85	1,70 \pm 0,71	69,3 \pm 8,0	10,78 \pm 3,30	2,98 \pm 0,60	22,6 \pm 2,8	26,4 \pm 3,4
<i>Cynodon dactylon</i>	saline	-1,31 \pm 0,11	-3,34 \pm 0,79	2,03 \pm 0,85	70,1 \pm 5,3	5,07 \pm 0,88	4,04 \pm 0,58	17,7 \pm 3,1	25,2 \pm 2,7
<i>Cynodon dactylon</i>	loess wall	-2,27 \pm 0,12	-3,37 \pm 0,19	1,10 \pm 0,22	74,9 \pm 4,6	10,94 \pm 2,80	1,80 \pm 0,11	18,6 \pm 0,6	32,4 \pm 0,9
<i>Hordeum murinum</i>	weed	-1,53 \pm 0,04	-2,82 \pm 0,46	1,29 \pm 0,48	69,3 \pm 2,4	6,67 \pm 1,90	2,14 \pm 0,17	33,8 \pm 2,1	16,8 \pm 0,8
<i>Secale sylvestre</i>	sand	-1,31 \pm 0,18	-2,82 \pm 0,69	1,51 \pm 0,58	68,8 \pm 7,6	6,03 \pm 0,37	1,57 \pm 0,05	25,8 \pm 1,1	14,0 \pm 2,7

Figure 2. Osmotic potential at full turgor ($^{100}\Psi_{\pi}$) for dicots and grasses in the four steppe habitats. Columns with the same letter are not significantly different.



three tallgrass prairie grass species. The relatively elastic walls of grasses allow the maintenance of positive turgor and hence growth at lower water content values (RWC at turgor loss is 73.2% and 78.5% for grasses and dicots, respectively, Table 2). However, the low osmotic potential means that the grasses must be tolerant to relatively high concentrations of osmotic substances in their cells, while dicots are less constrained in this respect. The grasses have thin leaves (high SLA) of relatively high density (high DMP), while the thicker and less dense leaves of dicots are built of less carbon (since density reflects the volume of apoplast (i.e., cell wall and support tissue) made of polysaccharides, Niinemets 1999). Note that these between-group differences hold true only for the set of species studied and are not representative of either grasses or dicots in general. In other studies, xerophytic grasses were found to possess relatively rigid leaf tissue, low SLA and low water potentials (Kalapos 1994, Loik and Harte 1997, Maxwell and Redmann 1978). As a group, the studied dicots were much more heterogeneous for the parameters studied than the grasses, most probably due to their greater variety of growth forms, ranging from xerophyllous to leaf succulent species. Among grasses, the three *Festuca* species had a more markedly different leaf structure than the other species, with cylindrical scleromorphic leaves that had the lowest SLA and the highest DMP (Table 3).

Habitat effects were less marked, significant differences appeared in osmotic parameters only. Osmotic potential at full turgor and at turgor loss decreased in the following order: loess grassland > sand grassland \cong saline grassland > loess wall (Table 2), and this pattern was consistent within subgroups of species (i.e., among grasses and dicots, Fig. 2). The osmotic amplitude was the smallest in loess grassland, and the greatest in sand grassland.

Saline grassland and loess wall semidesert plants tended to have less elastic tissue (higher ϵ_l), lower transpiration rate (E) and SLA than loess and sand grassland species. The highest dry matter investment in building leaf tissue (DMP) occurred in loess wall species, the lowest in saline grasslands, while sand and loess grasslands were comparable intermediates, although the difference is not significant statistically. Thus, in accordance with habitat water regime, plants from the least dry loess grassland need the least steep water potential gradient to extract water from soil (high osmotic potential values), use water less sparingly (high E) and possess the most 'mesic-like' leaf structure (relatively large surface, elastic tissue). The loess wall semidesert represents the dry end of the gradient, where leaf osmotic potentials ($^{100}\Psi_{\pi}$ and $^0\Psi_{\pi}$) are indeed the lowest, leaf dry matter proportion is the highest, while in other parameters it does not differ from the also relatively dry saline steppe. The two leaf structural parameters, SLA and DMP change in a different way among habitats, as it was already found for woody (Niinemets 1999) and herbaceous (Wilson et al. 1999) plants. For example, the equally low leaf area per unit dry mass (i.e., SLA) of loess wall and saline grassland plants is caused by different structure, i.e., by high tissue density in the xeric leaves of loess wall species, while by relatively high leaf thickness in the low-density succulent leaves of saline grassland species (Table 2).

Life form influenced leaf structure, but had no measurable effect on water relations. Annuals had much higher SLA and lower DMP than perennials (Table 2). This is because the shorter-lived foliage of annual species is thinner and cheaper in terms of invested dry matter than that of the longer-lived leaves of perennials. Differences in structural parameters between annuals and perennials were more marked than between grasses and dicots.

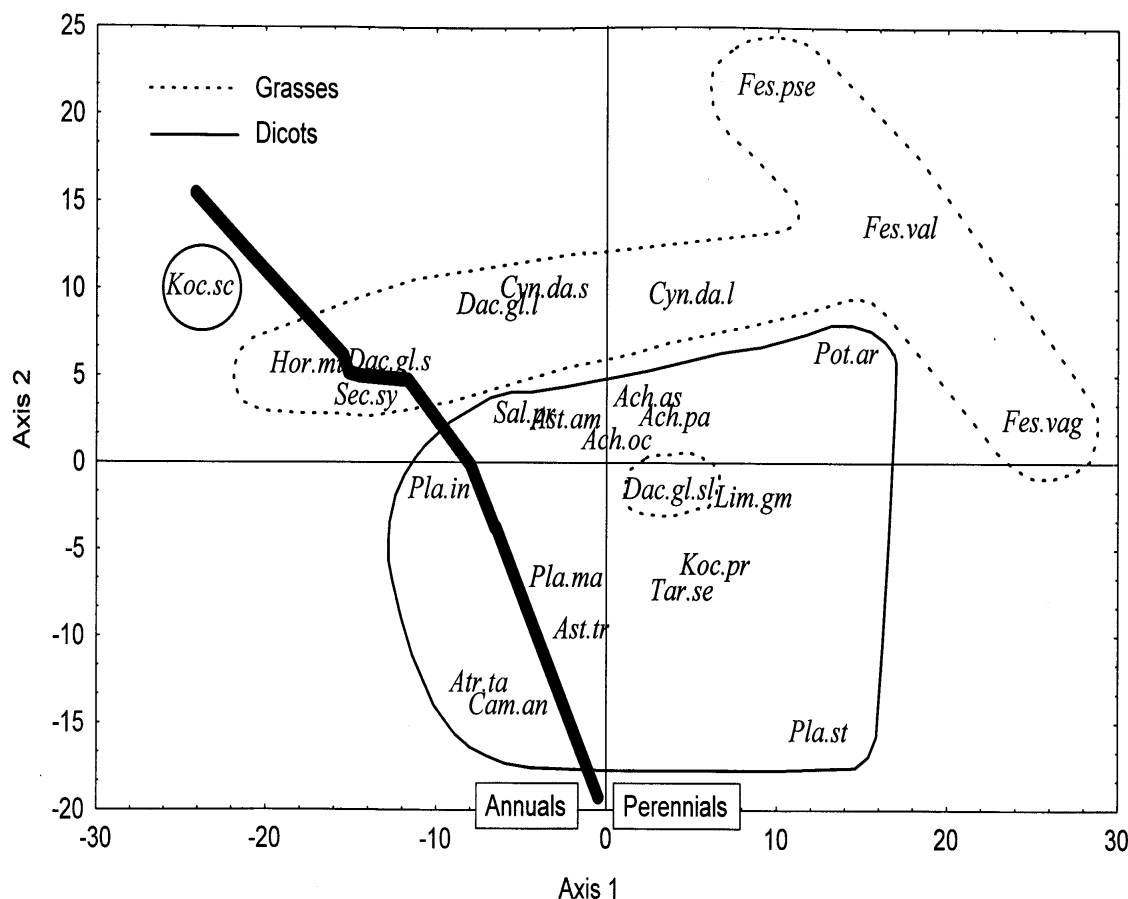


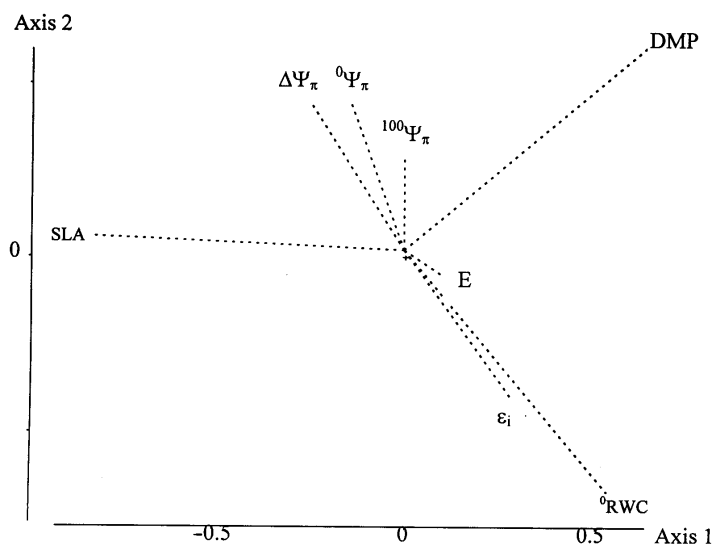
Figure 3. Ordination diagram of the species studied (Centered PCA). Species are coded with the first three letters of the genus name plus the first two or three characters of the species name (e.g., *Fes.vag* = *Festuca vaginata*). For the two habitat generalist grasses (*Cynodon dactylon* and *Dactylis glomerata*) abbreviation for habitat type follows the species code, where .l = loess, .s = sand, and .sl = saline steppe. The thick diagonal line separates annuals and perennials. For species names see Table 1.

The multivariate analysis of all studied parameters resulted in a fair segregation of grasses and dicots in the ordination space (with only one outlier for each group, Fig. 3). This segregation mainly comes from the osmotic vs. turgor component dominance dichotomy discussed earlier, since mainly the pV-analysis parameters are responsible for that. The contribution of original parameters to principal components was such that the first PCA axis was associated almost exclusively with structural variables (SLA, DMP, 0RWC , ϵ_i), while the second axis was mainly associated with pV-analysis parameters ($^0\Psi\pi$, $^{100}\Psi\pi$), although certain structural variables also had some contribution (Fig. 4). In a similar study, Bannister (1986) also found leaf structural variables and pV-analysis parameters to influence different PCA ordination axes. The segregation of *Kochia scoparia* and saline grassland *Dactylis glomerata* from their own groups is mostly caused by an outlier 0RWC value. Furthermore, annuals and perennials fully segregate along the first PCA axis,

which is predominantly associated with the structural parameter, SLA. However, neither grasses nor dicots form a compact group, and dicots display the greatest heterogeneity. Among grasses, sclerophyllous *Festuca* species with high-density terete leaves segregate sharply from flat-leaved species, but themselves are also quite different. The sand-dweller *Festuca vaginata* with highly rigid leaf tissue differs markedly from *F. pseudovina* from the salt affected grassland which has a high osmotic component, while *F. valesiaca* from loess grassland is intermediate between the two (Fig. 3, Table 3). For the complete data set, the three steppe types do not segregate in the ordination space (figure not shown).

Data for each species are given in Table 3. For habitat specialist species within the same genus, it appears that difference in leaf water relations is not significant statistically for certain congeners (*Achillea* and *Aster*, although the two *Aster* species are placed quite apart in the ordination space, Fig. 3). The absence of significant differences

Figure 4. Correlations of the original variables with the first two principal components in centered PCA. For abbreviations, see Table 2.



suggests that these congeners might rely on similar water supply in the three steppe grasslands. In contrast, the *Festuca*, *Kochia* and *Plantago* species from habitats with dissimilar water regimes differed significantly, thus leaf function and associated structure in these congeners must be different to ensure survival in their own habitat. For the two generalist grasses (*Cynodon dactylon* and *Dactylis glomerata*), habitat-specific populations showed a tendency of increasing capacity for water extraction from soil (more negative water potential) with increasing habitat dryness, although differences were significant only between the two extremes of the water availability gradient (Table 3).

Conclusions

It appears that in the studied steppe habitats no generalization can be made on how leaf water relations change with water availability. Several specialist congeners and two generalist grasses showed a capacity for generating greater soil-to-plant water potential gradient with increasing habitat dryness, which in turn enables them to take up water from less easily available source. However, for other habitat specialists no substantial differences were observed in leaf water relations. These plants might occupy microsites with similar water regime, and/or other habitat or plant properties have more profound influence on their ecological distribution than water relations do. For the whole species set, life form (annual or perennial) and rough taxonomic affiliation (dicot or grass) have a more profound influence on leaf water relations and/or associated structural properties than habitat type.

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