



Leaf and stem maximum water storage capacity of herbaceous plants in a mountain meadow

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Abstract

Leaf and stem maximum water storage capacities of nine dominant species (three graminoids and six herbs) from a mountain meadow were investigated employing two different methods—submersing of and spraying at phytoelements, respectively. The resulting maximum water storage capacities were in overall good agreement with literature. The submersing method yielded significantly lower values as compared to the spraying method, but, using in situ dew measurements, it could not be conclusively determined which method is to be preferred. Significant correlations between maximum water storage capacity and several morphological parameters could be found both across species and within species, yet these relationships usually possessed relatively little predictive power and were not consistent across species. It is concluded that other plant characteristics than those investigated in the present study are responsible for determining differences between species and that the dependence of the maximum water storage capacities on morphological factors is highly species-specific.

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1. Introduction

Phytoelement wetness plays an important role in the control of plant disease (Campbell and Madden, 1990; Bradley et al., 2003), for plant susceptibility to dry and wet acid deposition (Wesely et al., 1990; Brüggemann and Spindler, 1999), for plant photosynthesis and yield (Brewer and Smith, 1994; Hanba et al., 2004) and is of general biophysical interest due to the fact that phytoelement gas exchange processes

are fundamentally altered with surface wetting (Tanaka, 2001).

One of the key model parameters in this context is the maximum phytoelement water storage capacity, i.e. the amount of water per unit phytoelement area, at which additional water cannot be retained and starts to drip off (Watanabe and Mizutani, 1996; Wilson et al., 1999; Dunkerley, 2000). The maximum phytoelement water storage capacity poses a limit to the wetness duration and thus to the time during which chemical substances in the surface water may react with the cuticle or pathogens may infect the plant, the latter also being the time during which pest management practises, e.g. fungicide applications, need to be

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scheduled (Campbell and Madden, 1990). The maximum phytoelement water storage capacity, together with the plant area index (the amount of plant area per unit ground area) also determines the potential amount of interception evaporation (Watanabe and Mizutani, 1996). Finally, the maximum phytoelement water storage capacity also influences interception/throughfall of precipitation or surplus dew, phytoelements acting as a store for intercepted water, which when filled delivers water to the canopy/soil below (Leuning et al., 1994).

Despite its importance, there are relatively few studies which quantify this parameter: Monson et al. (1992) investigated the water storage capacity of 27 Alpine plant species in the Glacier Lakes area in Wyoming and found maximum water storage capacities to range over four orders of magnitude, the maximum being 50 g m^{-2} . Bradley et al. (2003) compared 18 species of clovers and determined maximum water storage capacities between 130 and 360 g m^{-2} . Watanabe and Mizutani (1996), drawing upon experimental results by Pitman (1989); Kondo et al. (1992), used values of 150 and 200 g m^{-2} for broadleaved and coniferous forests, respectively. Wilson et al. (1999) used a value of 150 g m^{-2} for potato. Values used in current Soil–Vegetation–Atmosphere–Transfer (SVAT) models cover the range of $100\text{--}500 \text{ g m}^{-2}$ (e.g. Sellers et al., 1986; Raupach et al., 1997). This large variability suggests that it is advisable to determine specific maximum phytoelement water storage capacities for the investigated plant species, in particular for mountain ecosystems, whose maximum water storage capacities, according to Monson et al. (1992), seem to be at the very lower end of the spectrum.

The present study was conducted in a mountain meadow in the Eastern Alps, where phytoelement wetness plays a prominent role due to the increase in precipitation with elevation and the frequent occurrence of dewfall during night-time hours (Körner et al., 1989). The objectives of the present study are twofold:

First, the aim is to compare two different methodologies for estimating maximum phytoelement water storage capacity, since it is not in the first place obvious how to measure it (Dunkerley, 2000). In situ estimation, of dew or intercepted precipitation, is hampered by the fact that it is difficult to assess

unambiguously whether the observed amounts indeed represent the maxima or not (Wilson et al., 1999). Artificial wetting usually involves submersing of (Wood et al., 1998) or spraying at phytoelements (Calder et al., 1996; Dunkerley and Booth, 1999; Bradley et al., 2003), the latter generally being perceived as to better mimic the natural wetting process. Probably the most appropriate method in the context of condensation would be the use of so-called dew chambers, closed, humidity controlled systems where air vapor pressure and temperature are manipulated until dew forms on the phytoelements (Burkhardt and Eiden, 1994). In the present study, the submersing and spraying method is used and the observed maximum water storage capacities are compared with maximum amounts of dew observed in the field.

Second, the aim is to investigate the morphological causes for differences in maximum water storage capacity both within and between species. These results will then, in a further step, be used as an input to a SVAT model for simulating dew formation and evaporation of the investigated mountain meadow (Wohlfahrt et al., manuscript in preparation). In contrast to Monson et al. (1992), who investigated a comprehensive suit of plant morphological features, the analysis is restricted to a few simple parameters (e.g. leaf area, width or specific leaf area), which are likely to be routinely available for upscaling in the context of SVAT modeling studies.

2. Material and methods

2.1. Site and investigated species

Investigations were carried out during 2000 and 2001 using plant material collected at a meadow close to the village of Neustift in the Stubai Valley ($47^{\circ}07'N$, $11^{\circ}19'E$). The study site is situated at an elevation of 970 m a.s.l. and receives on an average 850 mm of precipitation per year, the average annual temperature is $6.3^{\circ}C$. The vegetation has been classified as Pastinaco-Arrhenatheretum and is composed by about 20 different species. In the present study, nine of the most dominant (in terms of biomass) graminoids (*Dactylis glomerata*, *Festuca pratensis*, *Poa pratensis*) and forbs (*Achillea millefolium*,

Table 1
Morphological characterisation of leaves and stems of the investigated species

Species	Abbr.	Leaves		Stems
		Morphology	Pubescence	Pubescence
<i>Achillea millefolium</i>	AcMi	Extremely dissected	Sporadic	Yes
<i>Carum carvi</i>	CaCa	Highly dissected	No	No
<i>Dactylis glomerata</i>	DaGl	Graminoid	No	No
<i>Festuca pratensis</i>	FePr	Graminoid	No	— ^a
<i>Poa pratensis</i>	PoPr	Graminoid	No	— ^a
<i>Ranunculus acris</i>	RaAc	5 irregular lobes	Yes	Yes
<i>Taraxacum officinale</i>	TaOf	Longish, serrated	No	No
<i>Trifolium pratense</i>	TrPr	3 elliptic lobes	Yes	Yes
<i>Trifolium repens</i>	TrRe	3 elliptic lobes	No	No

^a Stems not investigated.

Carum carvi, *Ranunculus acris*, *Taraxacum officinale*, *Trifolium pratense*, *Trifolium repens*) were selected. Graminoids and forbs exhibited clearly differing leaf morphologies (Table 1): laminas of the investigated grasses were long, narrow and non-dissected, while those of the herbs were dissected, divided or at least deeply serrated. *Trifolium pratense* and *R. acris* were the only species with significant leaf pubescence. The stems of the investigated species were morphologically far less different, the only major difference being the diameter of *T. officinale* stems (approx. 0.005 m), being about up to five times larger than those of the other species (0.001–0.003 m). The stems were without pubescence, except for *T. pratense*, *R. acris* and *A. millefolium*. In the following, the first two characters of the generic and species names will be used to abbreviate species names (see Table 1) unless otherwise indicated.

2.2. Methods

The maximum water holding capacity was determined as the difference in weight between phytoelements before and after artificial wetting, expressed on a hemi-surface area (HSA) basis. To this end, several turfs were excavated in the field and transported to the laboratory. Leaves and stems (2–3 samples per specimen) were cut (a fixed length of 0.05 m was used for stems) and their fresh ‘dry’ weight determined using a balance (AE-260, Mettler Instrumente AG, Switzerland). Next, phytoelements were wetted either by submersing them in water for

10 s or by spraying water on them until saturation was reached. The slice planes of stems were sealed with wax in order to avoid water ingress into the (often hollow) interior. After allowing all surplus water to drip-off (usually less than ten seconds), phytoelements were re-weighted. The entire procedure typically took less than 1 min, minimizing water loss by transpiration (prior to wetting) and evaporation (after wetting). Immediately after re-weighting, hemi-surface leaf areas were determined using an area meter (CI-203, CID, Inc., USA). The area meter also provided leaf length, maximum width and perimeter, from which the dimensionless aspect and shape factor were calculated. The former is the ratio between leaf length and maximum width, while the latter represents the ratio between hemi-surface area (a) and perimeter (p), corrected so that the shape factor (f) of a circle is equal to unity, i.e. $f=4\pi a/p^2$. Stem hemi-surface areas were calculated from length, upper and lower width, assuming stems to be represented by truncated cones. For determination of the specific leaf/stem areas (SLA, ratio of hemi-surface area to dry weight), dry weights were measured after drying phytoelements at 80 °C for at least 72 h.

In situ dew formation (only for leaves of CaCa, RaAc, TaOf, TrPr, TrRe) was measured on exposed leaves from the upper third of the canopy during the nights of 1st–2nd August 2000 and 23rd–24th August 2001. The same equipment and procedure as described above were used to this end, except that the fresh ‘wet’ weight was determined first and

phytoelements were subsequently carefully dried with a paper cloth before re-weighing.

Differences between average water holding capacities determined by the submersing and spraying method were assessed using a Mann–Whitney U-Test. The degree of linear association between plant morphological traits and the maximum water holding capacity was quantified by means of the Pearson correlation coefficient after log-transforming data.

3. Results and discussion

Average leaf maximum water storage capacities covered a wide range from 44.9 (TrPr) to 414.8 (CaCa), and 13.2 (TrPr) to 314.0 g m^{-2} (CaCa), using the spraying and submersing method, respectively (Fig. 1). Graminoid leaves generally tended to have lower maximum water storage capacities as compared to the investigated forbs, in particular to those with highly dissected/divided leaves (AcMi, CaCa, RaAc). Variability in average stem maximum water storage capacities was much smaller, except for the thick stems of TaOf (spraying method: 453.6 g m^{-2}), ranging from 201.3 (TrPr) to 247.8 (AcMi), and 59.0 (TaOf) to 88.4 g m^{-2} (CaCa), using the spraying and submersing method, respectively (Fig. 2). Our lowest values thus fall into the upper range reported

by Monson et al. (1992) for composite crowns (leaves, stems and reproductive organs) of 27 Alpine plant species, and are several magnitudes larger than the values they obtained for individual leaves and flowers ($<0.1 \text{ g m}^{-2}$). The reason for this discrepancy is particularly surprising, since the species studied by Monson et al. (1992), although there is no actual overlap, originate from very similar habitats (dry and wet meadows). On the other hand, the present study showed, that even closely related species such as TrPr and TrRe may be characterized by distinctively different maximum leaf water storage capacities (Fig. 1), in accordance with the findings of Bradley et al. (2003) for 18 species of clovers. The cause for the observed discrepancy might also be methodological, since Monson et al. (1992) inferred maximum water storage capacities from the water freed from sprayed plants placed in plastic bags by gently tapping them, which is very much likely to underestimate the true amount of surface water. Our experience with in situ dew measurements is that phytoelements need to be carefully dried with a paper cloth in order to collect all surface water. Other literature sources report maximum water storage capacities which fall into the range observed in the present study: 130–360 g m^{-2} (clovers; Bradley et al., 2003); 150 g m^{-2} (potato; Wilson et al., 1999); 150–200 g m^{-2} (broad-leaved and coniferous forest; Pitman, 1989; Kondo

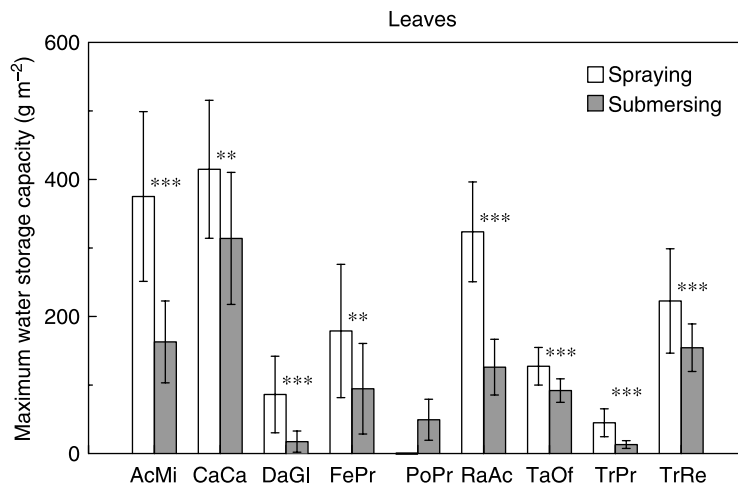


Fig. 1. Average leaf maximum water storage capacities of the investigated species determined using the spraying (open bars) and submersing (grey bars) method. Error bars represent ± 1 standard deviation. Significant differences between the spraying and submersing method were determined using a Mann–Whitney U-Test (** $p < 0.01$, *** $p < 0.001$).

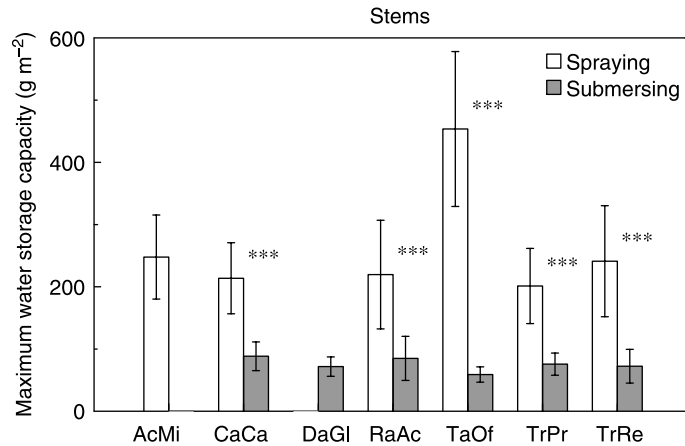


Fig. 2. Average stem maximum water storage capacities of the investigated species determined using the spraying (open bars) and submersing (grey bars) method. Error bars represent ± 1 standard deviation. Significant differences between the spraying and submersing method were determined using a Mann–Whitney U-Test (***) $p < 0.001$.

et al., 1992; cited in Watanabe and Mizutani, 1996). Of notice is the close correspondence between the maximum water storage capacity of TrRe determined by means of the spraying method in this study and by Bradley et al. (2003), 222 and 194 g m^{-2} , respectively.

The maximum water storage capacities obtained using the submersing method were in all cases significantly lower as compared to the spraying method (Figs. 1 and 2), the underestimation ranging from 13 (CaCa leaves) to 76% (TaOf stems). This suggests that spraying is much more effective in wetting phytoelement surfaces, probably due to the formation of coherent droplets (Beysens et al., 1991), which may not be reproduced by submersing phytoelements. Results along this line have been reported by Calder et al. (1996), who showed that wetting rates are higher for drops of smaller size. This finding puts the results of Monson et al. (1992) into a new light, who argued that one to three orders of magnitude lower maximum water storage capacity of individual leaves and flowers, determined by means of the submersing method, as compared to the maximum water storage capacity of composite crowns, which was determined by means of the spraying method, was due to the emergent structural properties at the canopy level. While it is likely true that single-organ values do not necessarily reflect whole-canopy water storage capacities, where water

may be stored, e.g. in axillary shoots, it must be assumed that the magnitude of this effect is exaggerated due to the bias of the submersing method towards lower values.

Maximum in situ dew amounts, reached between 4 and 6 o'clock Central European Time, ranged between 50 and 200 g m^{-2} (Fig. 3), similar to the range of 75–240 g m^{-2} observed by Brewer and Smith (1997) for plants from montane and mountain meadows in the central Rocky mountains, but again higher as compared to the maximum water storage capacities determined by Monson et al. (1992). Maximum dew amounts thus fell within the uncertainty of the maximum water storage capacities determined using the spraying and submersing method in the case of TrPr, and RaAC and TaOf, respectively (Fig. 3). For TrRe and CaCa, maximum dew amounts were clearly below the maximum water storage capacities determined with both methods (Fig. 3). In this comparison, it needs to be noted that the observed maximum dew amounts are likely to underestimate the maximum water holding capacities, as the measured time courses of dew accumulation, except for TrPr, did not exhibit a pronounced saturation (Fig. 3). Maximum dew amounts observed in situ thus provide no clear evidence on whether the spraying or submersing method is to be preferred for determining phytoelement maximum water storage capacities. To this end, further in situ leaf wetness

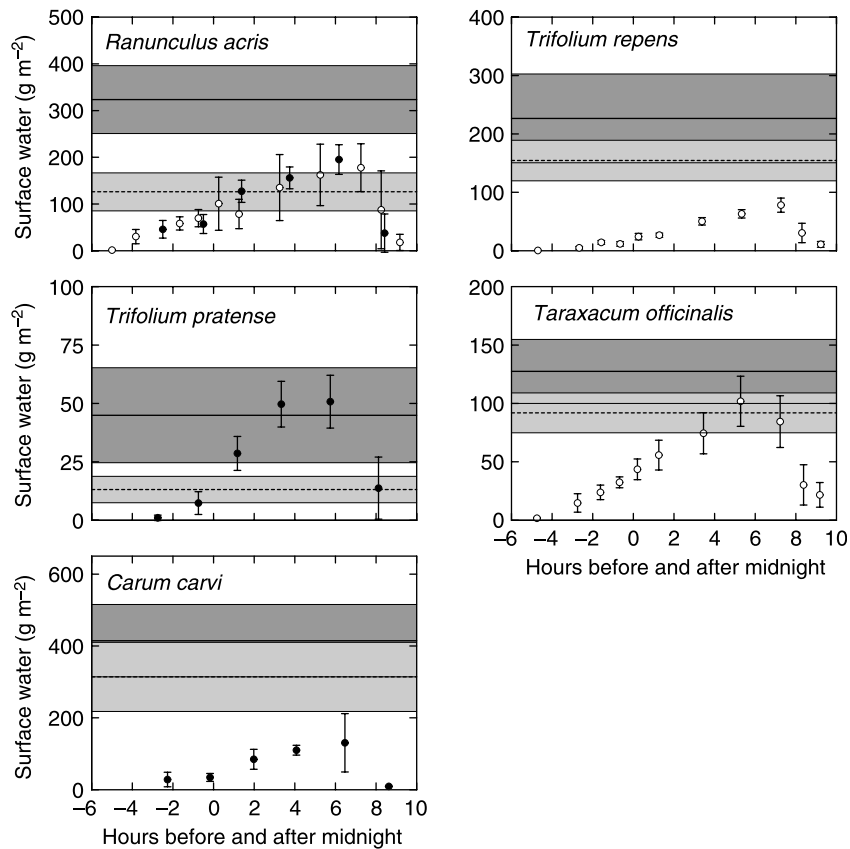


Fig. 3. Time course (Central European Time) of dew formation and drying on the leaves of the investigated species (symbols), as well as the respective maximum water storage capacities (lines and grey areas). Closed symbols refer to 1st–2nd August 2000, open symbols to 23rd–24th August 2001 (error bars represent ± 1 standard deviation). Solid lines and dark grey areas, and dotted lines and light grey areas refer to the average and standard deviation of the spraying and submersing method, respectively (cf. Fig. 1).

measurements, also during rainfall conditions, will be required.

Across all species, as shown in Table 2, the highest degree of linear association between the various morphological parameters and the maximum water storage capacity determined by means of the submersing method was observed for the leaf aspect, the ratio between leaf length and maximum width ($r=0.38$), followed by maximum leaf width ($r=0.30$) and length ($r=0.18$), the latter two though being auto-correlated with the former ($r=-0.66$ and 0.65 , respectively). Correlations with perimeter, hemi-surface area, shape factor and specific leaf area were all not significant. For stems in contrast, hemi-surface area was the most important determinant of how effective surface

water is held ($r=0.22$). At the level of individual species considerable divergence was observed (Table 2): for a few species and organs, significant correlations was observed for almost all independent variables (PoPr leaves, TrPr leaves), while for the rest, significant correlations were found at most for a single independent variable. Specific leaf/stem areas were significantly correlated with the maximum water storage capacities in five organs/species, followed by leaf width and leaf perimeter (three species), and leaf aspect, shape factor and hemi-surface area (two species). Also none of the parameters showed a consistent trend across all species, e.g. phytoelement water storage capacity increased significantly with increasing leaf width in PoPr and TaOf, but decreased in TrPr.

Table 2

Pearson correlation coefficients with the maximum water storage capacity as the dependent variable (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Species ^a	Organ	<i>n</i>	Length	Width _{max}	Perimeter	HSA	Aspect	Shape	SLA
AcMi	Leaves	13	−0.07	−0.15	−0.17	−0.13	−0.62	0.04	0.09
	Stems	— ^b							
CaCa	Leaves	20	−0.13	0.09	−0.02	−0.05	−0.26	−0.16	0.33
	Stems	10		−0.35		−0.43			0.59*
DaGl	Leaves	20	−0.27	−0.22	−0.27	−0.27	−0.17	−0.02	−0.25
	Stems	10		0.22		0.14			−0.35
PoPr	Leaves	21	0.56**	0.48*	0.56**	0.45*	0.44*	−0.56**	0.03
	Stems	— ^b							
RaAc	Leaves	20	0.21	−0.13	0.11	−0.11	0.38*	−0.36	−0.16
	Stems	10		−0.05		−0.08			0.12
TaOf	Leaves	20	0.26	0.50*	0.38*	0.36	−0.25	−0.33	−0.46*
	Stems	10		−0.12		−0.18			0.07
TrPr	Leaves	21	−0.53**	−0.51**	−0.62***	−0.57**	−0.29	0.51**	−0.40*
	Stems	10		0.41		0.49			−0.56*
TrRe	Leaves	21	0.27	0.23	0.32	0.19	−0.11	−0.28	−0.23
	Stems	10		−0.33		−0.19			−0.65*
All species	Leaves	156	−0.18*	0.30***	0.03	0.02	−0.38***	−0.10	0.07
	Stems	60		−0.20		−0.22*			−0.16

^a All species except for FePr, whose morphological parameters were not investigated.^b Stems not investigated.

Two main conclusions may be drawn from this regression analysis. First, the low correlation coefficients suggest that other parameters than those investigated in the present study are responsible for determining maximum water storage capacities across all species and partly within species. This corresponds with the results of Monson et al. (1992), who found leaf pubescence, not investigated in the present study because it is not very likely to be a routinely available plant parameter, to be among the most important properties for leaf water retention. Results along this line have also been reported by Brewer and Smith (1997), who found leaf wettability of montane and mountain plant species to decrease with increasing trichome density. Second, the dependence of the maximum phytoelement water storage capacities on the investigated morphological parameters is highly species-specific, which in turn explains the relatively poor predictive power of the pooled statistics.

4. Summary and conclusion

In the present study, leaf and stem maximum water storage capacities of nine dominant species from a mountain meadow were investigated employing two

different methods—submersing of and spraying at phytoelements, respectively. The resulting maximum water storage capacities were in overall good agreement with literature, except for a closely related study by Monson et al. (1992), whose consistently lower maximum water storage capacities are suggested to be an experimental artifact. The submersing method yielded significantly lower values as compared to the spraying method, but, using in situ dew measurements, it could not be conclusively determined which of both methods is to be preferred. Despite the general notion to consider the spraying method better suited to mimic the natural wetting process, further studies, also during rainfall conditions, are required to corroborate this issue. Significant correlations between maximum water storage capacity and several morphological parameters could be found both across species and within species, yet these relationships usually possessed relatively little predictive power and were not consistent across species. This suggests that other plant characteristics than those investigated in the present study are responsible for determining differences between species and that the dependence of the maximum water storage capacity on morphological factors is highly species-specific.

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