

Vegetation effects on the water balance of mountain grasslands depend on climatic conditions

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ABSTRACT

Mountain regions are key for humanity's water supply, and their water yield depends on climatic, soil and vegetation effects. Here we explore the effects of vegetation composition and structure on the water balance of high elevation grasslands with different climatic conditions across the Alps. Using a total of 220 deep seepage collectors with intact soil-vegetation monoliths in different types of mountain grasslands in the Austrian, French and Swiss Alps, we solved the water balance equation for evapotranspiration (ET) and related the results to biomass, the abundance of certain plant functional types and structural and functional vegetation properties. While daily mean ET during the growing season was similar at all sites, ET to precipitation ratios were significantly higher and ET to potential ET ratios significantly lower at the drier French sites than at the more humid Swiss and Austrian site. Large variability of ET, seepage and soil moisture within all sites pointed at a high influence of vegetation on the water balance. While ET increased significantly with biomass at all sites, the influence of other vegetation properties was site specific. At the more humid, subalpine Austrian site the effects of vegetation on ET were stronger and more diverse than at the higher elevation Swiss site and the drier French sites, where climatic drivers dominated ET. The potential to influence ET and water yield of mountain areas by manipulating the plant canopy with systematic land management is therefore higher in regions with good growing conditions than in areas with harsh climate. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS evapotranspiration; biodiversity; canopy structure; vegetation composition; functional diversity

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INTRODUCTION

Mountains are a major source of water for public use, irrigation and hydropower all over the world (Messerli and Ives, 1997; Viviroli *et al.*, 2003; Viviroli and Weingartner, 2004). At the same time mountain regions are particularly vulnerable to land use and climate change (de Vries, 2010) with potentially negative influences on catchment water yield (IPCC, 2007). As transpiration largely dominates over evaporation in terrestrial ET (Jasechko *et al.*, 2013) the very nature of the plant cover has major effects on the water balance (Asbjørnsen *et al.*, 2011). Thus, changes in vegetation such as an increase of biomass and the dominance of tall tussock-grasses and dwarf shrubs due to the abandonment of traditional land management (Tasser and Tappeiner, 2002; Quétier *et al.*, 2007) will affect the water

balance of mountain regions (Körner, 2003; Inauen *et al.*, 2013). Understanding the interrelation of climatic and biotic controls of the water balance will improve predictions of future water yield and facilitate distinctive management to protect water resources.

The partitioning of precipitation water into evapotranspiration (ET) and seepage/runoff is controlled by water availability and atmospheric demand (Budyko, 1958; Zhang *et al.*, 2001): in humid conditions precipitation exceeds potential ET (PET), actual ET approaches PET and runoff as well as percolation is closely related to precipitation (Everson, 2001). In contrary, PET exceeds precipitation in dry condition; therefore, actual ET equals precipitation, and runoff/percolation declines to zero (Gu *et al.*, 2008). ET is the water balance component most directly driven by climatic conditions and modified by vegetation properties (Monteith, 1965; for mountains see van den Bergh *et al.*, 2013). Four meteorological variables are considered the main drivers of ET: (1) global radiation as the source of energy, (2) vapour pressure deficit (VPD), which describes the atmospheric demand, (3) wind speed

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which influences the boundary layer between the vegetation and the atmosphere and (4) soil water content or more precisely water availability to plants (Kelliher *et al.*, 1993). Global radiation and VPD have been described as the main drivers of ET when enough water is available (Obriest *et al.*, 2003; Olchev *et al.*, 2008; Wieser *et al.*, 2008) while soil water content is the main control in dry conditions (Baldocchi *et al.*, 2004; Chen *et al.*, 2008; Wilske *et al.*, 2010).

Plant cover influences ET and other water balance components through three main mechanisms (Eviner and Chapin, 2003; Donohue *et al.*, 2007): (1) leaf area, biomass or canopy height directly affect the both water and energy fluxes related to all three components of ET (Couturier, 1973; Rutter, 1975; Campbell and Murray, 1990). At low values of leaf area, transpiration increases proportionally with increasing leaf area, while soil evaporation decreases (Schulze *et al.*, 1994). Above a leaf area index of 3–5 aerodynamic resistance and air humidity exert a limiting effect on transpiration and ET becomes less responsive to changes in leaf area (Larcher, 2003). Leaf area also plays an important role for rainfall interception, particularly in regions with frequent rainfall. Plant litter and necromass, which are not actively transpiring, increase interception (Gross *et al.*, 2007) and decrease soil evaporation (Evans and Young, 1970; Suding and Goldberg, 2001). (2) Physiological properties such as leaf diffusive conductance influence ET (Donohue *et al.*, 2007). The rate of photosynthesis is correlated with the rate of transpiration (Wong *et al.*, 1979), through stomatal control which in turn depends on water supply and ambient humidity (Ponce Campos *et al.*, 2013; Salvucci and Gentine, 2013). (3) Rooting depth and rooting density control the amount of soil water extraction for transpiration (Gordon and Rice, 1993). Deep-rooted species can explore additional water sources even during dry periods (Nippert and Knapp, 2007a, 2007b), while evaporation from the soil surface rapidly diminishes after precipitation (Ritchie, 1972). Changes in rooting depth can considerably alter the effective water availability in an ecosystem (Donohue *et al.*, 2007).

So far the influence of climatic conditions and land use on the water balance and in particular on ET has been studied comparatively well at the ecosystem level with micrometeorological methods (Tappeiner and Cernusca, 1998; Baldocchi *et al.*, 2004; Hammerle *et al.*, 2007; Harding and Lloyd, 2008) or with analytical models (Arora, 2002; Donohue *et al.*, 2007). Apart from the well-established relationship between ET and biomass, the influence of vegetation composition and structure on the water balance in natural mountain grasslands and their interrelation with growing conditions is less known. Existing studies on this topic focus on the influence of one specific vegetation property (e.g. species diversity or

rooting depth) and are usually conducted in artificially composed, experimental grasslands (Spehn *et al.*, 2000; Van Peer *et al.*, 2004; De Boeck *et al.*, 2006).

In this study we compare the influence of easily measurable vegetation properties on the water balance of natural mountain grasslands. Comparing three regions with different climate in the subalpine and alpine belt across the Alps shows which plant properties are relevant for ET at specific conditions and should therefore be accounted for in hydrological models or could be manipulated via land management to optimize water yield. Measuring the water balance of soil monoliths in deep seepage collectors (DSCs) also closes a gap between physiological measurements at the leaf/plant scale and micrometeorological studies at the landscape level. Combining water balance with meteorological measurements and comprehensive data on vegetation properties at multiple sites enabled us to test the following hypothesis: (1) in addition to biomass and leaf area, plant structural and functional composition exert strong influence on ET, and (2) these vegetation influences on the water balance depend on climatic conditions (especially water availability) and become more pronounced under drier conditions.

STUDY AREAS AND METHODS

Site description

The three study areas were located in the subalpine and alpine belt along a W to E transect from the Western French Alps to the Swiss and the Austrian Central Alps (Table I): In the French study area in the vicinity of the Lautaret pass in the Central French Alps (département Hautes-Alpes) the two experimental sites 'Les Cours' and 'Le Jardin' were situated at different elevations. The Swiss study area was located at the Furka Pass, which is connecting the Cantons of Uri and the Valais. The Austrian study area 'Kaserstattalm' was situated above the village of Neustift (Stubai Valley, North Tyrol). In each study area, mesocosms were extracted from three to four locations with different vegetation types. Most mesocosms were combined in one respectively two (in the French study area) main experimental sites per study area to ensure equal climatic conditions. A smaller number was installed at their excavation site to control for possible transplantation effects (Table I).

There were two main differences in climatic conditions between the study areas: precipitation was considerably lower at the French than at the Swiss and Austrian study area, especially during the growing period. Second, in accordance with site elevation the mean air temperature during the growing season was lowest at the Swiss site followed by the higher French, the Austrian and the lower French site (Table I).

Table I. Location, vegetation and soil characteristics of the study areas and description of vegetation/land use types from which deep seepage collector (DSC) were extracted. In France DSCs were placed in two experimental gardens (main garden with eight DSCs and control at the extraction site with four DSCs of each type) at each altitude. At the Swiss site DSCs were placed at three main gardens (two close to each other but with different time of snow melt in spring). At the Austrian site DSCs were placed in one main garden (in an abandoned grassland) with some as controls at the meadow and pasture.

	France—Lautaret			Switzerland—Furka (CH)			Austria—Stubai (AUT)														
	Low site—Le Cours (FRA low)	High site—Le Jardin (FRA high)		Altitude	Position	Aspect	N° DSCs	Altitude	Position	Aspect	N° DSCs										
Experimental gardens	Les Cours ^a	1810 45° 02' 42" N 6° 20' 36" E	S	24	Le Jardin ^a	2120 45° 02' 15" N 6° 24' 00" E	S	16	SEwind ^a	2436 46° 34' 39" N 8° 25' 18" E	SE	38	Meadow ^b	1870 47° 07' 44" N 11° 18' 20" E	E-SE	10					
	Terrace ^b	1810 45° 02' 25" N 6° 21' 43" E	S	12	Meadow ^b	2000 45° 02' 15" N 6° 24' 00" E	S	8	SEwet ^a	2436 46° 34' 39" N 8° 25' 18" E	SE	16	Pasture ^b	1950 47° 07' 44" N 11° 18' 20" E	S-SE	10					
Sampling dates	15. 5/9. 7/25. 7/12. 8/10. 9/15. 10.													2000 47° 07' 30" N 11° 17' 24" E	S-SE	66					
MAT/MP08	4.5 °C/956 mm	20. 6/9. 7/25. 7/12. 8/10. 9/15. 10. 2 °C/943 mm												22. 5/16. 7/30. 7/6. 8/11. 9/6. 11. 3 °C/1100 mm							
T08/P08	21.5.2008–15.10.2008	9.7.2008–15.10.2008												29.5.2008–6.11.2008							
Soil type	11.3 °C/503 mm	9.8 °C/322 mm												10.5 °C/887 mm							
Infiltration rate	Cambisol	Cambisol												Dystic cambisol							
Photosociological associations in the study area	4445 ± 181 mm h ⁻¹	6850 ± 108 mm h ⁻¹												1027 ± 108 mm h ⁻¹							
	Tristo flavescenti-Polygonion bistortae mixed with Festucum spadicea (Fertilized meadows), Onobrychido-vicifoliae-Brometum (Unfertilized meadows and Abandoned grassland)	Onobrychido-vicifoliae-Brometum/ Centaureo-Festucetum paniculatae (Meadow), Centaureo-Festucetum paniculatae (abandoned grasslands)												Festuco-agrostietum (Meadow and pastures), Nardetum strictae (Abandoned grassland)							
Peak biomass	278.6 ± 7.4 g m ⁻²	302.3 ± 11.5 g m ⁻²												Empetro-Vaccinietum gaultherioides, Caricetum sempervirentis (abandoned grasslands)							
Canopy height	17.0 ± 0.8 cm	19.6 ± 1.2 cm												23.4 ± 0.8 cm							
Necromass	17.0 ± 1.7 %	22.0 ± 2.2 %												3.6 ± 0.4 %							
Vegetation-/management types transplanted into DSCs (N° of DSCs)	Mown and fertilized meadow dominated by <i>Festuca laevigata</i> , <i>Dactylis glomerata</i> and <i>Onobrychis montana</i> (12), mown meadow dominated by <i>Bromus erectus</i> , <i>Briza media</i> , <i>F. laevigata</i> and <i>O. montana</i> (12), abandoned grassland dominated by <i>B. erectus</i> , <i>F. laevigata</i> and <i>Sesleria caerulea</i> (12)	Mown meadow dominated by <i>B. erectus</i> , <i>Carex sempervirens</i> , <i>F. laevigata</i> , <i>F. paniculata</i> , <i>Thymus serpyllum</i> and <i>Trifolium alpestre</i> (12), abandoned meadow dominated by <i>F. paniculata</i> and <i>F. nigrescens</i> (12)												Nutrient-poor meadow dominated by <i>Leontodon hispidus</i> , <i>Agrostis capillaris</i> and <i>Plantago lanceolata</i> (15), nutrient-rich meadow dominated by <i>Alchemilla vulgaris</i> , <i>A. capillaris</i> and <i>Ranunculus acris</i> (15), nutrient-poor pasture dominated by <i>A. vulgaris</i> , <i>N. stricta</i> , <i>Festuca alpina</i> (15), nutrient-rich pasture dominated by <i>A. vulgaris</i> , <i>L. hispidus</i> and <i>R. acris</i> (15) nutrient-rich abandoned grassland dominated by <i>Luzula sylvatica</i> , <i>Geranium sylvaticum</i> and <i>Potentilla aurea</i> (10), nutrient-poor abandoned grassland dominated by <i>N. stricta</i> , <i>Carex sempervirens</i> and <i>Potentilla erecta</i> (6), shrub-rich abandoned grassland dominated by <i>Vaccinium gaultherioides</i> , <i>V. myrtillus</i> and <i>Geum montanum</i> (10)							

^a Main experimental garden.

^b Additional DSCs at excavation site.

Sampling dates: Start of the measuring period plus the five sampling dates in 2008 used for further analysis. MAT: mean annual precipitation. (Quétier *et al.*, 2009; Hefel and Stöcklin, 2010; Leitinger *et al.*, 2010). MP08: measuring period in 2008. 08: mean air temperature during measuring period in 2008. P08: sum of precipitation during measuring period in 2008. Infiltration rate, peak biomass, canopy height, necromass: mean value of study area ± standard error of mean. Canopy height and necromass (% of plant cover) measured at peak biomass.

Vegetation at the French study area was dominated by grasses which accounted for 50 to 80% of plant cover. At the Austrian study area the forb fraction was higher in meadows than in pastures and dwarf shrubs such as *Vaccinium uliginosum* occurred only in fallows. The alpine vegetation at the Swiss study area was composed of short stature communities dominated by graminoids such as *Nardus stricta* or *Carex curvula*, plus turfs dominated by small forbs or prostrate dwarf shrubs like *Loisleuria procumbens*, *Salix herbacea* and *Vaccinium uliginosum*. Biomass and canopy height were similar at the French and Austrian study area but were considerably lower at the higher situated Swiss study area (Table I). Live plant cover at peak biomass was lowest, while the proportion of necromass was highest at the French study area. Species numbers and diversity at plot level were lowest at the French and highest at the Austrian study area.

To describe soil hydraulic properties, infiltration rates were estimated for each mesocosm in 2009 by using the mesocosm as single ring infiltrometers and measuring the infiltration time of 2 l of water. Overall, we found high but very site-specific values. By far the highest rates were measured at the French sites and were 25 to 40 times higher than the lowest ones at the Swiss site (Table I). Infiltration rates at the Austrian site were in-between these extremes and on average four times higher in mesocosms from the abandoned site than from pastures and meadows.

Linking water balance and vegetation using a mesocosm approach

By measuring precipitation, seepage and soil water content and by preventing surface and lateral soil water flow, ET could be calculated as the residual of the ecosystem water balance. To measure seepage and soil moisture and to be able to correlate the water balance with vegetation properties, intact monoliths of 25 cm diameter and 28 cm depth were extracted manually, fit in open top cylinders of stainless steel (DSCs, height: 40 cm) with a steel sieve and a filter pad 10 cm above the bottom, and buried in the soil. Seepage water was collected in the extra space at the bottom of the monoliths. The remaining 2 cm of the steel cylinder stayed above the soil surface to prevent lateral fluxes of surface water. From measured precipitation, seepage and soil moisture ET could be calculated as the residual of ecosystem water balance:

$$ET = P - (DS + \Delta B)$$

where *ET* was evapotranspiration, *P* precipitation, *DS* seepage and ΔB the difference of soil water content between the actual and the previous sampling point.

By channeling precipitation, infiltration and seepage through a defined section of vegetation and soil and by solving the water balance equation for this section we were

able to attribute results to specific types of vegetation. While the restricted monolith volume might constrain deep water access of the vegetation, it is known that in alpine grasslands approximately 75% of all roots are confined to the top 10 cm, and given the high volume of micropores in alpine soils, the 280-mm-deep profile holds nearly 140 mm of plant available water, which makes a severe restriction of plant water supply unlikely on such high elevation sites (Körner, 2003). Yet, we had planned to add water to the DSCs during prolonged drought periods to avoid aggravated water shortage, the impact of which was not an issue to be explored here. In 2008, the year of our inter-site comparison, no such periods occurred, even at the drier French sites. Further, it is known that monoliths resting on a drainage layer may show less rapid seepage than an intact soil profile ('hanging capillaries' issue, (Flury *et al.*, 1999)). However, such effects do not affect ET signals, as long as enough water is available in the soil profile.

The monoliths placed in the DSCs were selected to represent the vegetation and management types at the study areas, while differences in abundance of species and plant functional types within each type were accounted for. In total, 86 DSCs were installed at the Austrian study area, 70 at the Swiss study area and 60 at the French study area (details in Table I). At the French study area 12 DSCs of each management type (i.e. fertilized hay meadow, non-fertilized hay meadow and abandoned grassland at the lower site, non-fertilized hay meadow and abandoned at the higher site) were installed. At the Austrian study area monoliths were extracted from two to three different variants of each management type (a total of 30 each from meadows and pastures and 26 from fallows). At the Swiss study area 7 common vegetation types were represented by 8 DSCs each, 7 rarer types with 2 DSCs each, totaling 70 DSCs.

Water balance and meteorological measurements

Precipitation was measured with tipping bucket rain gauges at 2-m height. Seepage water was pumped from the DSCs using portable vacuum systems (VK-lite, UMS, Munich, Germany), and its volume was determined in 2-week intervals or at least 1 day after major precipitation events. Volumetric soil water content was measured in the main rooting horizon in each DSC. To calculate ET the change of soil moisture between two sampling occasions (ΔB) was calculated, and water content (θ) values in m^3m^{-3} were converted to mm by relating actual values to field capacity (θ_{FD}) and multiplying the difference with soil depth (*z*).

$$\Delta B = [(\theta_i - \theta_{FD}) - (\theta_{i-1} - \theta_{FD})] \cdot z$$

According to the definition by the Soil Science Glossary Terms Committee (2008), θ_{FD} was determined for each DSC as the average water content during the second and

third day after the first sampling after snow melt, when soil in the DSCs were completely saturated. While measuring soil moisture only at rooting depth might slightly overestimate soil moisture dynamics, ΔB diminishes over longer time periods compared to ET and DS, and this overestimation of ΔB becomes negligible.

Meteorological measurements included solar radiation, wind speed, air temperature and humidity at 2-m height. Water VPD and PET were calculated according to Allen (1998). Meteorological variables were measured with a Hobo weather station (ONSET, Bourne, MA, USA) at the French sites, with a Wireless Vantage Pro2 Plus™ climate station (Davis Instruments, Hayward, CA, USA) at the Swiss site and with a climate station by Campbell Scientific (Logan, UT, USA) at the Austrian site. Soil moisture was measured with ECH2O EC-10 Sensors (Decagon, Pullman, WA, USA) at all sites.

Assessment of vegetation properties

The plant species composition and the abundance of plant functional types (graminoids, forbs, legumes, dwarf shrubs, cryptogams) in each DSC were assessed at peak season at each site. To quantify species diversity, species number, Shannon-Index and evenness were calculated for each DSC. Canopy height as well as total plant cover and cover by necromass were estimated three to five times during the growing season and interpolated linearly to get values at all seepage sampling occasions. In order to determine plant biomass, half of the DSCs were clipped at peak season at 2-cm height. Biomass during the growing season was estimated by calculating a biomass-to-canopy height ratio at peak biomass for each site and applying it at all time steps (Lavorel *et al.*, 2011). To estimate the structural and functional diversity of each DSC, averaged values of plant size, leaf type, area, length, and width, root density, depth and horizontal distribution and Ellenberg indicator values were collected for each species from literature (Lauber *et al.*, 1998; Sitte *et al.*, 2002; Senghas and Seibold, 2003; Spehn *et al.*, 2005; Shane *et al.*, 2006; Quétier *et al.*, 2007; Ellenberg and Leuschner, 2010; Pohl *et al.*, 2011). For each of these properties a weighted mean value was calculated for each DSC by multiplying the functional parameter value for each species with its relative contribution to plant cover (Garnier and Navas, 2011).

Data structure and analysis

In this study we used water balance and vegetation data for the 2008 growing period when 216 DSCs operated concurrently at four sites in three study areas (Stubai/Austria, Furka/Switzerland and the lower and higher site at Lautaret/France). The number of sampling dates varied between sites due to different weather conditions and season lengths. Seepage and soil moisture as well as

estimated biomass and canopy height were specific for each DSC unit and date, whereas precipitation and other climatic variables were measured at just one location for each site/experimental garden. All vegetation properties except biomass and canopy height were measured for each DSC at peak biomass. Because of multicollinearity (tolerance <0.2) climatic variables were summarized into PET calculated according to Allen *et al.* (1998). For the same reason, the 30 vegetation properties assessed at peak season (plant cover, abundance of plant functional groups, plant size-, leaf- and root-properties derived from species data, Ellenberg-indicator values) were condensed to seven factors using principal component analysis. Four individual DSCs from the Swiss site and one from the high French site were excluded from further analysis because of strongly deviating vegetation characteristics (DSCs with bare ground covered with lichens only at the Swiss site and extremely high leaf area at the high French site). Five more Swiss DSCs were excluded because of erroneous seepage measurements in autumn.

When using linear regression in order to explain daily ET by climatic and vegetation variables, the residuals revealed major correlation, both serial and spatial, of the model, indicating a violation of the independence assumption (Figure 1). Spatial correlations of the residuals were possibly caused by small scale, within-site spatial patterns of meteorological parameters, micro-topography- or surrounding-vegetation-effects. Temporal correlations could be attributed to insufficient representation of the seasonal development of the vegetation. Therefore, a spatial panel model was used to account for spatial and temporal correlations (Millo and Piras, 2012). The spatial panel model required the same number of time intervals at each site; therefore, five common time periods were formed (early growing season, main growing season, peak season until clipping, peak season after clipping to late summer, autumn) using common sampling dates (see Table I). The spatial panel model was defined as:

$$y_{it} = x'_{it} b + \varepsilon_{it} ,$$

with $i = 1, \dots, n$ is the number of DSCs, $t = 1, \dots, T$ is the number of time periods, ε_{it} the residuals, b the vector of coefficients, x_{it} the independent variables for observation unit i at time t and y_{it} the value of the dependent variable of observation unit i at time t . The stochastic noise ε_{it} still displays spatial and temporal patterns which is modeled as

$$\varepsilon_t = \rho W \varepsilon_t + v_t \text{ and } v_t = \rho v_{(t-1)} + e_t,$$

where ρ is the spatial correlation parameter, W the inverse distance matrix, v_t part of the noise explained by temporal patterns, ψ the temporal correlation parameter and e_t is the remainder noise fulfilling the independence assumption. The distance matrix W is computed as row-normalized

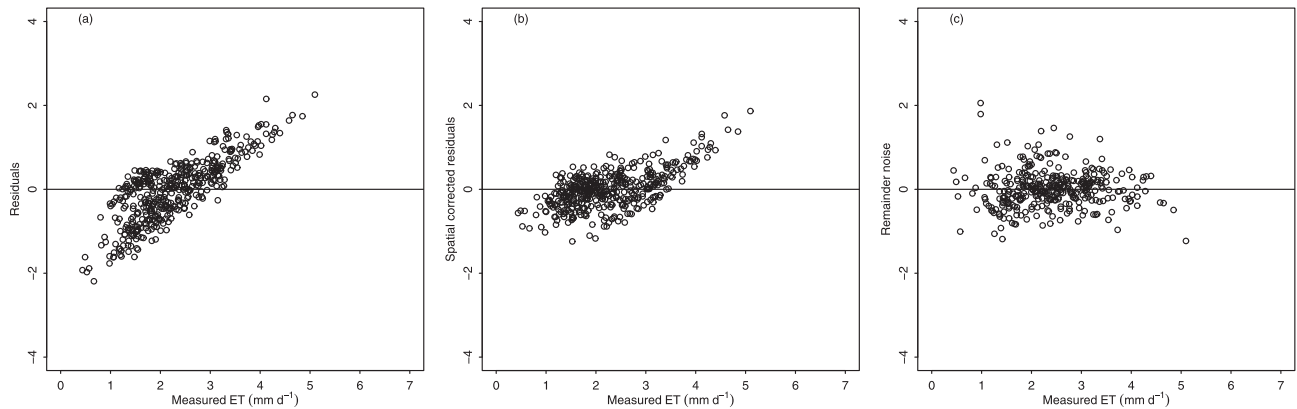


Figure 1. Correction of autocorrelation by using a spatial panel model. Plots of evapotranspiration estimated from water balance measurements (measured ET) versus the residuals of a linear regression (a), a spatially corrected regression (b) and a spatial panel model (c) used to predict ET from climate and vegetation properties for the Austrian sites (the other sites show similar patterns). The residual plot for linear regression (a) indicates autocorrelation which is reduced if spatial correlation of the residuals is accounted for (b) and disappears completely if temporal correlation is included (c).

inverse distance between a DSC, and each other DSC of the same study area, inverse distance between sites is zero. Using this model delivered uncorrelated, homoscedastic, randomly distributed residuals; therefore, significance levels regarding tests and confidence intervals of independent variables should be correct.

To evaluate the relative importance of the variables for our study sites we report both the drop in the Akaike information criterion (AIC, Akaike, 1973) and the so-called Akaike weights (Akaike, 1979). According to the given ratio of sample size to model parameters the finite sample correction for the Akaike value (AIC_c) is used (Burnham and Anderson, 2002):

$$AIC_c = -2LL + 2K + \frac{2K(K+1)}{(n-K-1)},$$

where LL is the minimized likelihood value, K is the number of parameters and n is the sample size. How much statistical importance should be attached to a specific difference in the AIC values between the best model and the next best model is assessed by using Akaike weights:

$$w_i(AIC) = \frac{\exp(-0.5\Delta_i(AIC))}{\sum_{m=1}^M (-0.5\Delta_m(AIC))},$$

where $\Delta_i(AIC) = AIC_i - \min(AIC)$ is the difference of the AIC_c value of the considered model i and the lowest AIC_c value, and M is the number of models. Weight $w_i(AIC)$ can be interpreted as the probability that model i is the best model (in the AIC sense), i.e. that it minimizes the Kullback–Leibler discrepancy given the data and the set of candidate models (e.g. (Burnham and Anderson, 2002).

SPSS/PASW statistics version 18 was used for principal component analysis, RStudio version 0.97.248/R version 2.15.0 for further analysis (Millo and Piras, 2012; R Development Core Team, 2012).

RESULTS

Water balance and climatic drivers

Precipitation totals and aridity index (P/PET, UNEP, 1997) during the growing season characterized the French study area as far drier than the Austrian and Swiss sites (Table II).

Table II. Mean and standard deviation (s.d.) of the components of DSC–water balance. Daily precipitation (P), deep seepage (DS), change of soil moisture during measured periods (ΔB) and evapotranspiration (ET) as well as ET/P and actual to potential evapotranspiration (ET/PET) ratios, and aridity index (P/PET) for the whole growing season at each site. For ET/P and ET/PET ratios maximum (max) and minimum (min) values for each site are also shown.

Site	P (mm d ⁻¹)		DS (mm d ⁻¹)		ΔB (mm d ⁻¹)		ET (mm d ⁻¹)		ET/P (-)				ET/PET (-)				P/PET (-)
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	
FRA low	3.29	0.00	1.17	0.22	0.08	0.03	2.19	0.22	0.67	0.07	0.77	0.52	0.70	0.07	0.81	0.55	1.05
FRA high	2.75	0.00	0.77	0.22	0.09	0.04	2.07	0.24	0.75	0.09	0.89	0.53	0.67	0.08	0.80	0.47	0.89
CH	6.13	0.53	3.59	0.48	-0.01	0.04	2.53	0.40	0.41	0.06	0.49	0.28	1.04	0.19	1.28	0.64	2.50
AUT	5.17	0.21	3.04	0.39	0.02	0.03	2.15	0.32	0.42	0.07	0.56	0.28	0.93	0.14	1.26	0.62	2.22

No general temporal trend of precipitation throughout the growing season was found across sites (Figure 2a). Seepage followed the course of precipitation quite closely (evidencing small influence of ΔB on the five test period's water balance) and reflected the differences in precipitation between the sites, though with high variability within sites

(Figure 2b). At all sites soil water contents gradually decreased during the early growing season from saturation at snowmelt, with no clear trends thereafter, but passing through field capacity several times during the season and showing again high variability within sites (Figure 2c). Soil moisture changes accounted for up to 70% of ET during

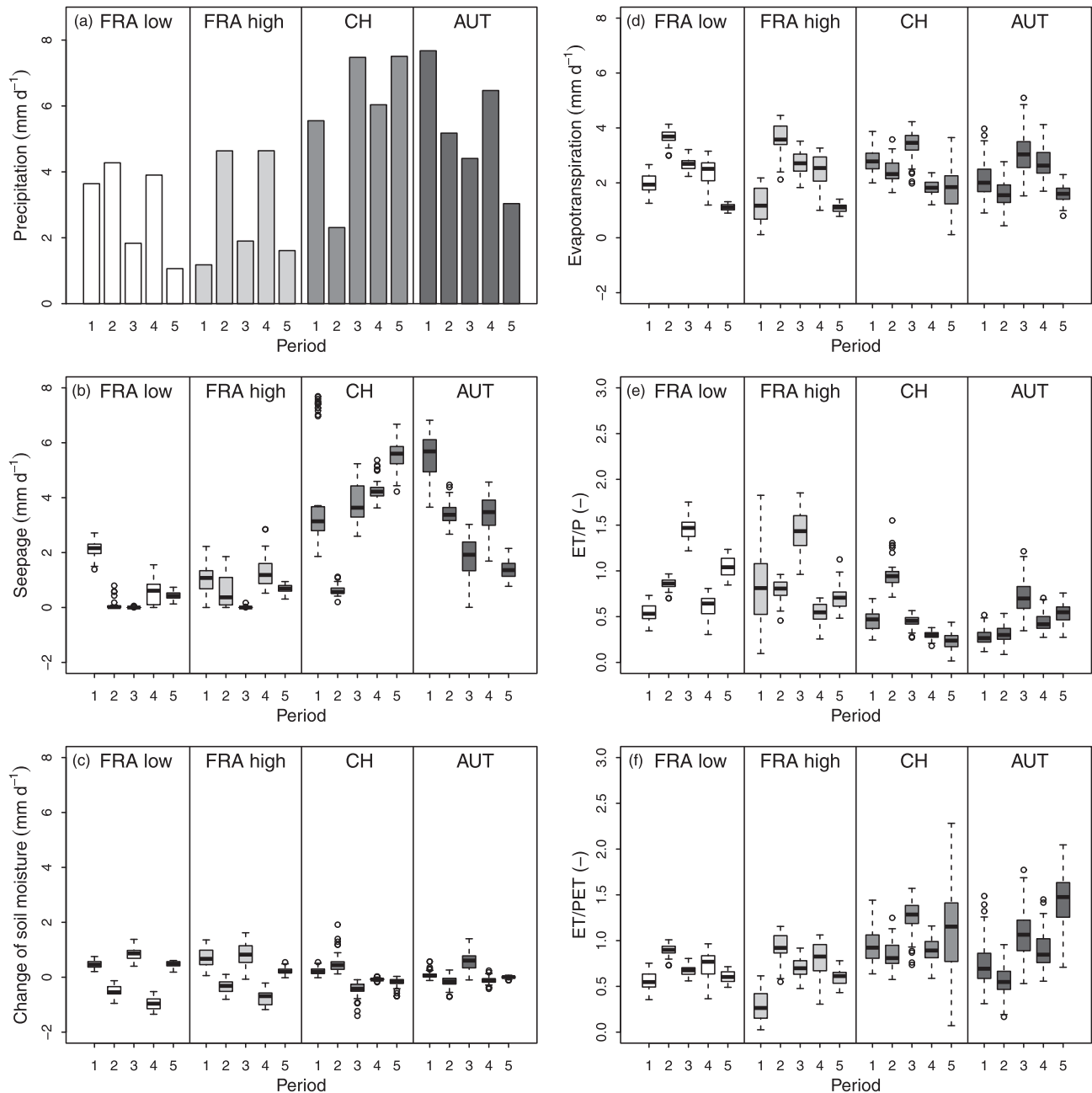


Figure 2. Seasonal course of water balance components for the sites in France (FRA low and FRA high), Switzerland (CH) and Austria (AUT). Mean daily precipitation (a) illustrates the difference between the dry French and the more humid Swiss and Austrian sites. Seepage (b) and soil moisture changes (c) presented as soil moisture deficit, i.e. positive values mean that the soil gets drier and vice versa, followed the course of precipitation with large variability within sites. Evapotranspiration (d) was generally lowest at the start and at the end of the measuring period. Generally, higher ET/P and lower ET/PET ratios indicate drier conditions at the French sites. (Periods: 1 early growing season, 2 main growth period, 3 peak biomass, 4 peak biomass after clipping, 5 autumn. (b)–(f) the 25th and 75th percentiles define the boxes, lines are 1.5 times the length of the box, points are outliers, n according to Table I).

dry periods at the French sites but, as expected played a negligible role at maximum 4% of ET for the whole growing season. Resulting from high intra-site variation of seepage and soil moisture, calculated ET was also found to be highly variable within sites. In contrast to precipitation and soil moisture, ET showed seasonal trends with highest values during the main growing period and at peak biomass and lower ones early and late in the season (Figure 2d). The sum and variability of ET calculated for the five test periods agreed well with ET calculated from the growing season sums of precipitation minus seepage, further indicating the diminishing importance of soil moisture in long-term observations. Relating ET to precipitation (P) and PET revealed major differences between sites (Figure 2e, f). For the whole growing season, average ET/P was clearly lower and ET/PET clearly higher at the more humid Austrian and Swiss sites than at the dry French sites (Table II). However, the large variability of ET within sites also caused a large amplitude of ET/P and ET/PET values and even some overlap between study areas.

VPD decreased with site elevation from the lower French to the Swiss site (Figure 3a). Differences in VPD between the French and the Austrian sites were mainly related to lower air humidity in France, while the ones between the two French sites and the low values at the Swiss site were related to different air temperatures (air temperature and humidity not shown). Due to the long measuring periods, global radiation

was more a general indicator of different cloudiness between sites, and its daily sum reflected the changing day length during the progression of the season (Figure 3b). Wind speed was moderate overall but was slightly higher at the Swiss site (Figure 3c). Summarizing all climatic drivers, calculated PET was slightly higher at the French sites than at the Swiss and the Austrian site (Figure 3d).

Vegetation

Average peak biomass was by far lowest at the alpine Swiss site and did not differ significantly between the lower elevation French and Austrian sites; intra-site variability was lowest at the two French sites (Figure 4a). The seven plant characteristics which were derived with principal component analysis out of 30 plant properties (Table III) showed the following pattern (Figure 4b–h): Component one represented green plant cover as well as Ellenberg-light (L), continentality (K) and humidity (F)-values with high values at the Austrian and (with some outliers) at the Swiss site, and lower ones at the French sites (Figure 4b). The second component coded for the abundance of forbs with soft leaves like *Leontodon helveticus*, *Ligusticum mutellina* and *Potentilla aurea* at the Swiss and *Alchemilla vulgaris*, *Leontodon hispius* and *Ranunculus acris* at the Austrian site. At the grass-dominated French sites it was primarily negatively correlated with the abundance of hard-leaved grasses

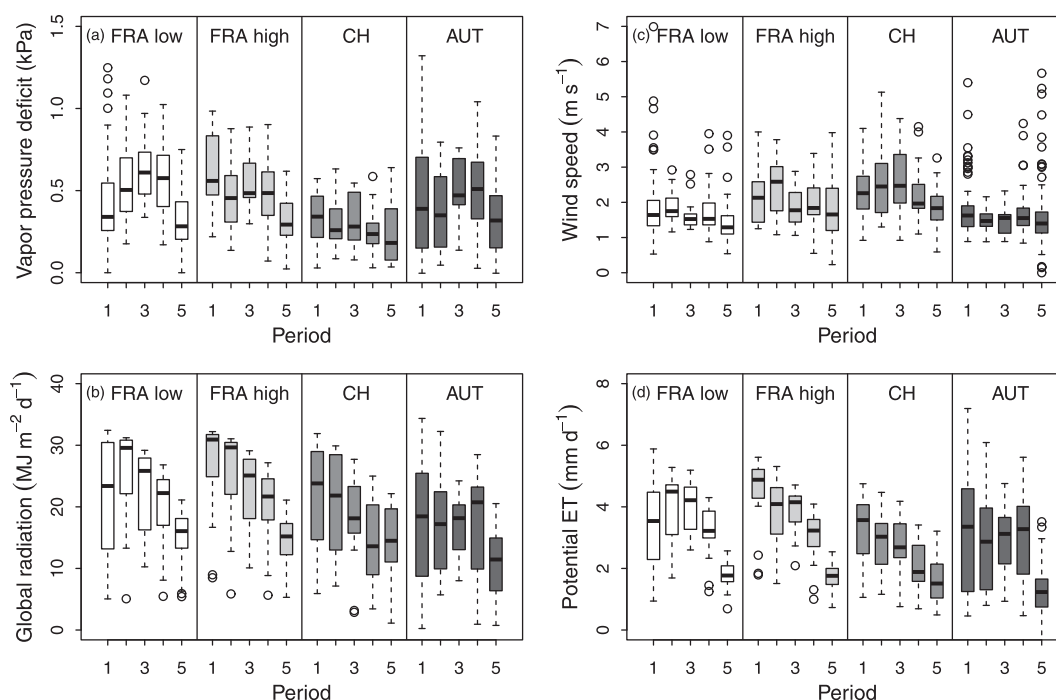


Figure 3. Seasonal course of climatic driving forces for the sites in France (FRA low and FRA high), Switzerland (CH) and Austria (AUT). Daily means of potential evapotranspiration (d) decrease towards the end of the growing season, mainly due to a decrease of global radiation (b) and vapour pressure deficit (a). Wind speed increased with site elevation (c). (Periods: 1 early growing season, 2 main growth period, 3 peak biomass, 4 peak biomass after clipping, 5 autumn. The 25th and 75th percentiles define the boxes, lines are 1.5 times the length of the box, points are outliers, *n* according to Table I).

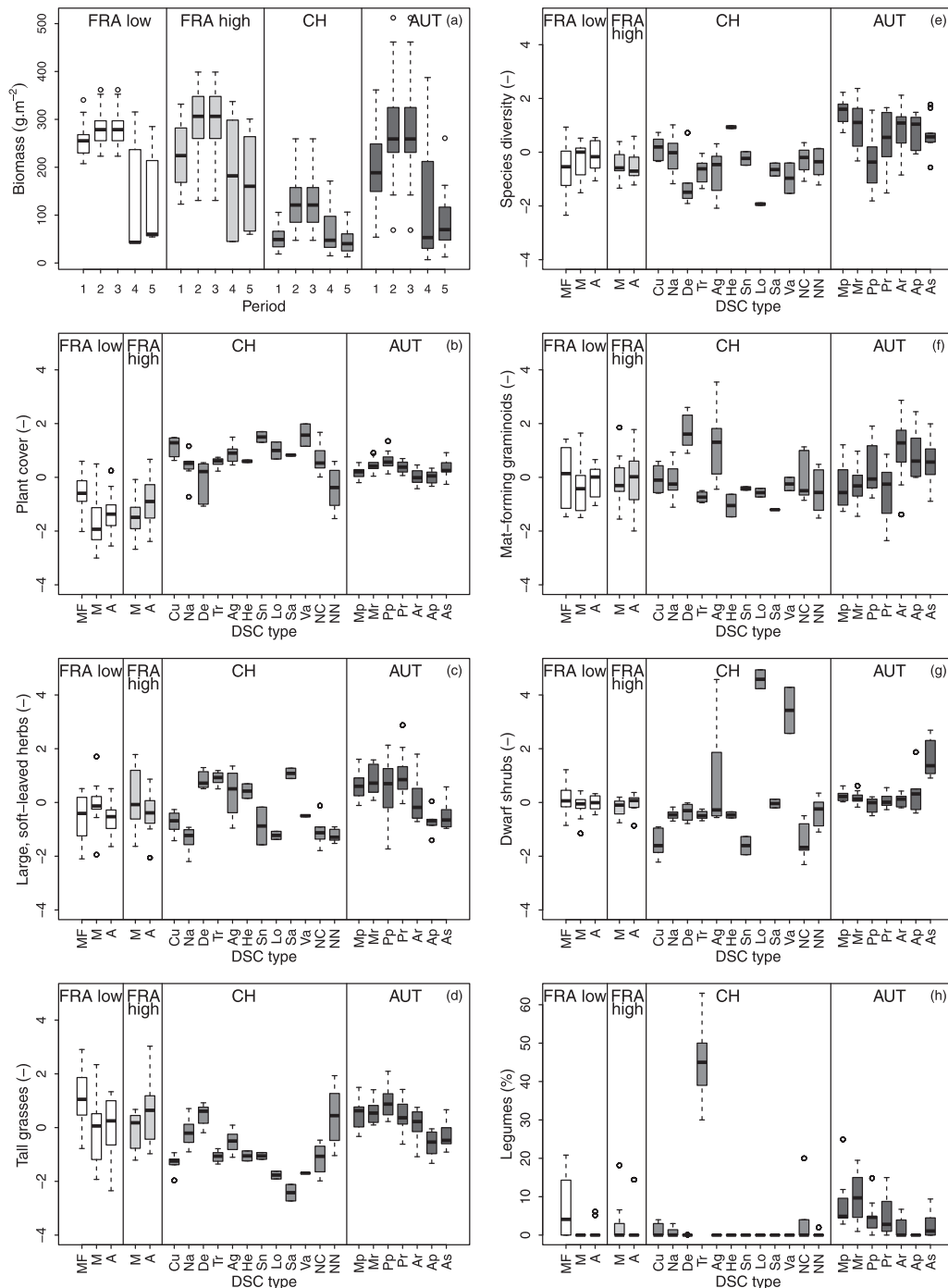


Figure 4. Development of green biomass during the season at each site (a) and distribution of vegetation properties among DSC-types (aggregated by principal component analysis, b-h). Biomass was measured for half of the DSCs at peak vegetation and calculated for the other time periods (periods: 1 early growing season, 2 main growth period, 3 peak biomass, 4 peak biomass after clipping, 5 autumn). Large variation in biomass in periods 4 and 5 was caused by clipping half of the DSCs. All other vegetation properties were derived from the abundance of species and functional groups at peak biomass. As the abundance of dwarf shrubs was correlated negatively to the component 6 (see Table II) negative component values in figure (g) correspond to a high abundance. As component 7 was coding for the abundance of legumes only, the abundance values were plotted in figure (h) and used for further analysis. (DSC types: French sites: MF...mown and fertilized meadow, M...mown meadow, A... abandoned grassland; Swiss site: Cu... *Carex curvula*-dominated, Na...*Nardus stricta*-dominated, De...*Deschampsia flexuosa*-dominated, Tr...*Trifolium alpinum*-dominated, Ag...*Agrostis schraderiana*-dominated, He...herb-rich vegetation, Sn...snow bed vegetation, Lo...*Loiseleuria procumbens*-dominated, Sa...*Salix herbacea*-dominated, Va...*Vaccinium uliginosum*-dominated, NC...*Carex curvula*-dominated-north slope, NN...*Nardus stricta*-dominated-north slope; Austrian site: Mp... Nutrient-poor meadow, Mr...Nutrient-rich meadow, Pp...Nutrient-poor pasture, Pr...Nutrient-rich pasture, Ar...Nutrient-rich abandoned grassland, Ap...Nutrient-poor abandoned grassland, As...Shrub-rich abandoned grassland; the 25th and 75th percentiles define the boxes, lines are 1.5 times the length of the box, points are outliers, *n* according to Table I).

Table III. Aggregation of vegetation properties. 31 correlated structural and functional vegetation properties were aggregated to seven vegetation characteristics using principal component analysis. Together these seven characteristics explained 80.5 % of the variance within the 31 plant properties. The factor loading indicates the correlation of each vegetation property with the component (only parameters with a factor loading >0.4 or <-0.4 appear in the table). Factor values for factor six were multiplied with -1 for further analysis to facilitate interpretation as this factor is mainly correlated negatively with the abundance of dwarf shrubs. As factor seven is only loading for one variable, the abundance of legumes, this variable was directly used in further analysis.

Rotated component matrix	Aggregated vegetation characteristics						
	1	2	3	4	5	6	7
Interpretation	Plant cover	Abundance of soft-leaved forbs	Abundance of tall grasses	Species diversity	Abundance of mat-forming graminoids	Abundance of dwarf shrubs	Abundance of legumes
% of explained variance (total: 80.5 %)	21.66	16.14	14.93	12.62	5.82	4.94	4.35
Plant cover (green plant material)	0.926						
Ellenberg indicator L (light)	0.918						
Ellenberg indicator K (continentality)	0.886						
Ellenberg indicator F (humidity)	0.813						
Average horizontal root distribution	0.779						
Cover of necromass	-0.748						
Average root density	0.670		0.572				
Abundance of species with hard leaves		-0.814					
Abundance of broad-leaf grasses (width >2 mm)		-0.766					
Average leaf width		0.735					
Average leaf size (ln-transf.)		0.729					
Abundance of species with soft leaves	0.500	0.726					
Ellenberg indicator N (nutrients)	0.421	0.651		0.459			
Abundance of forbs	0.454	0.535					
Average leaf length			0.833				
Ellenberg indicator T (temperature)			0.791				
Average root depth			0.780				
Abundance of poaceas			0.721				
Average plant size		0.469	0.706				
Ellenberg indicator R (pH-value)		0.425	0.655				
Abundance of cryptogams			-0.445				
Effective species number				0.879			
Shannon index				0.864			
Evenness				0.789			
Species number	0.478			0.693			
Abundance of narrow-leaf grasses (width <2 mm)					0.776		
Abundance of juncaceas					0.583		
Abundance of dwarf shrubs						-0.836	
Abundance of cyperacea						0.519	
Abundance of legumes							-0.889

Extraction method: Principal component analysis.

Eigen value of extracted factors >1 .

Orthogonal rotation method: Varimax with Kaiser normalization.

KMO and Bartlett's test.

Kaiser-Meyer-Olkin measure of sampling adequacy: 0.609.

Bartlett's test of sphericity: approx. Chi-square = 11 120.124; df = 435; Sig. <0.0011 .

Festuca laevigata, *F. nigresens*, *Carex sempervirens* and *Sesleria caerulea*. The highest and lowest values were found at the Austrian site (DSCs from managed grasslands) and the French sites, respectively. The highest variability was observed at the Swiss site, where the range of different vegetation types was highest (Figure 4c). Component three was driven by plant size which correlated with leaf length and rooting depth and was tied to the abundance of tall grasses like *Festuca paniculata* and *Bromus erectus* at both French sites, *Deschampsia cespitosa* at the Swiss site, and *Dactylis glomerata*, *Anthoxanthum odoratum* and *Festuca rubra* at the Austrian site. Values of component three were generally lower at the Swiss site but highly variable between vegetation types, and higher at the Austrian and French sites where they decreased from DSCs extracted from managed to those from abandoned grasslands (Figure 4d). The fourth component summarized four plant diversity parameters (Figure 4e). The fifth component coded for the abundance of narrow-leaved, mat forming graminoids (such as *Nardus stricta*, *Carex curvula* and *Festuca laevigata*) and showed hardly any differences between sites but high variance within them (Figure 4f). The sixth and seventh components coded for the abundance of dwarf shrubs and legumes, respectively, with no general trends between sites but high values for specific DSC-types (Figures 4g and 4h).

Climate and vegetation effects on ET

Generally, abiotic variables such as precipitation, soil moisture and evaporative demand of the atmosphere had significant and strong effects on ET (Tables IV–VI). ET increased significantly with soil moisture at all sites, with precipitation at the higher French and the Swiss site, and with PET at the lower French and the Swiss site.

Biomass was the most consistent biotic variable with a significant influence on ET and standardized regression coefficients (beta-values) comparable to abiotic variables at all sites. The significance of other vegetation characteristics was highly site specific with mostly lower beta-values (Table IV). With a significant influence on ET at two sites each, the abundance of tall grasses and of legumes (even though with very low beta values) were the most consistently influential plant characteristics, followed by species diversity and the abundance of soft leaved forbs as well as of dwarf shrubs. Plant cover and the abundance of mat-forming graminoids had no significant influence on ET at any study area.

The fraction of variance explained by the models also differed between sites (Table IV): At the French sites three and four significant independent variables explained more than 75% of the variation of ET, and at the Swiss site six significant variables explained 68%. On the other hand, the model for the Austrian site reached only an adjusted R^2 of 0.24 with five significant independent variables. Splitting

biomass by periods and putting these five new variables separately in the model to account for vegetation development during the growing season increased R^2 especially for the Austrian site but to a smaller extent at all other sites (Table V). While including the spatial and temporal correlation parameters of the spatial panel model increased the adjusted R^2 of all models, this effect was strongest at the Austrian study area (Tables IV and V).

DISCUSSION

Assessing the water balance of intact monoliths at four sites in three study areas across the Alps provided evidence that ET in subalpine and alpine grasslands is influenced not only by climatic drivers, aboveground biomass and leaf area but also by the structural and functional composition of the vegetation. This influence was found to be site specific; it was highest at the more humid subalpine Austrian study area. At the other sites, vegetation composition played a less significant role in explaining the variability of ET which was largely determined by climatic drivers and soil moisture.

Water balance

Daily mean ET for the growing season, calculated from the water balance for each of the five census periods, was very similar between the four sites with the highest mean ET at the Swiss sites and no significant difference between the other study areas (Table III). In earlier works, daily mean ET has been found to be constant with elevation in mountain grasslands (Körner *et al.*, 1989; Wieser *et al.*, 2008). This phenomenon had been explained by more pronounced microclimate effects at high elevation (canopy warming over air temperature) and by more pronounced stomatal reduction of transpiration at low (<1000 m) elevation in response to VPD and/or soil moisture deficits. Elevational gradients in wind speed may add to that pattern (de Jong's 2005 data for 2000- to 2500-m elevation in Switzerland), although, aerodynamic boundary layer commonly counteracts such action of wind in mountains. Van den Bergh *et al.* (2013) found no wind effects between 1500 and 2440 m but illustrated that conventional ET models (the Penman–Monteith approach) systematically overestimate ET at high elevation, and so do evaporimeters, underlining the significance of vegetation on ET.

A clear difference in the water balance between the more humid Austrian and Swiss sites and the drier French sites became obvious once actual ET was related to precipitation (ET/P) and PET (ET/PET). Mean ET/P ratios for the whole growing season of 0.67 and 0.75 at the lower and higher French sites, respectively, as well as 0.41 at the Swiss site and 0.42 at the Austrian site corresponded well with values from various grassland sites at different elevation in the

Table IV. Model results relating ET to meteorological, soil and vegetation variables for site-specific spatial panel models: Environmental variables (meteorological variables were summarized to potential evaporation due to multicollinearity) are important at all sites; the influence of vegetation properties was strongest at the more humid, subalpine Austrian site. (Regression coefficient (estimate), standardized regression coefficient (beta), significance levels of independent variables (p), spatial (rho) and temporal (psi) correlation parameter, and explained variance (R^2)).

	FRA low (France)			FRA high (France)			CH (Switzerland)			AUT (Austria)		
	$N=180$ (36 DSCsx5)			$N=115$ (23 DSCsx5)			$N=305$ (61 DSCsx5)			$N=430$ (86 DSCsx5)		
	Estimate	Beta	p	Estimate	Beta	p	Estimate	beta	p	Estimate	beta	p
(Intercept)	-0.695		0.108	-0.827		0.145	-1.505		0.003	0.866		0.124
Precipitation	0.151	0.213	0.181	0.558	0.763	<0.001	0.244	0.656	<0.001	-0.130	-0.250	0.401
Mean soil moisture deficit	0.011	0.145	<0.001	0.046	0.311	<0.001	0.041	0.320	<0.001	0.019	0.126	<0.001
Potential evapotranspiration	0.679	0.617	<0.001	0.184	0.150	0.169	0.877	0.635	<0.001	0.551	0.500	0.101
Infiltration rate	-0.019	-0.038	0.088	-0.004	-0.011	0.818	0.086	0.030	0.388	0.024	0.047	0.282
Biomass	7.4E-04	0.081	0.007	0.001	0.109	0.040	0.002	0.153	<0.001	0.002	0.312	<0.001
Plant cover	-0.087	-0.088	0.087	-0.007	-0.005	0.944	0.071	0.064	0.101	0.019	0.008	0.862
Soft-leaved forbs	0.046	0.040	0.118	-0.022	-0.019	0.736	-0.019	-0.025	0.532	0.132	0.141	0.001
Tall grass	0.075	0.103	0.043	0.017	0.015	0.817	0.058	0.068	0.052	0.175	0.138	0.001
Species diversity	0.002	0.001	0.960	-0.278	-0.116	0.078	0.097	0.100	0.008	0.041	0.046	0.255
Mat-forming graminoids	-0.010	-0.009	0.725	0.158	0.131	0.056	-1.3E-04	0.000	0.996	-0.030	-0.037	0.367
Dwarf shrubs	0.117	0.057	0.018	0.264	0.078	0.140	0.033	0.067	0.062	0.098	0.072	0.069
Abundance of legumes	0.004	0.024	0.349	-0.007	-0.031	0.508	0.006	0.115	0.001	-0.016	-0.103	0.004
R^2 -ind.var-only	0.756			0.753			0.684			0.240		
R^2 -incl. $\rho + \psi$	0.891			0.891			0.802			0.782		
Spatial and temporal correlation parameters												
ψ (temporal)	-0.175		0.028	-0.019		0.867	-0.010		0.905	0.167		<0.001
ρ (spatial)	0.793		<0.001	0.657		<0.001	0.694		<0.001	0.867		<0.001

Table V. Model results relating ET to meteorological, soil and vegetation variables for site-specific spatial panel models with period-specific biomass: Entering the biomass in the model separately for each period allows a stronger representation of vegetation dynamics during the season. R^2 increases especially at the Austrian site, beta-values indicate that the influence of biomass is stronger during the main growth period and peak biomass than at the start and end of the season. (Regression coefficient (estimate), standardized regression coefficient (beta), significance levels of independent variables (p), spatial (rho) and temporal (psi) correlation parameter and explained variance (R^2)).

	FRA low (France)				FRA high (France)				CH (Switzerland)				AUT (Austria)			
	$N = 180$ (36 DSCsx5)				$N = 115$ (23 DSCsx5)				$N = 305$ (61 DSCsx5)				$N = 430$ (86 DSCsx5)			
	Estimate	beta	P		Estimate	Beta	P		Estimate	Beta	p		Estimate	Beta	p	
(Intercept)	-0.366		0.296		-0.062		0.890		-1.650		0.002	**	0.659		0.095	
Precipitation	0.028	0.040	0.787		0.334	0.457	<0.001	***	0.259	0.696	<0.001	***	-0.040	-0.078	0.737	
Mean soil moisture deficit	0.011	0.146	<0.001	***	0.056	0.382	<0.001	***	0.040	0.308	<0.001	***	0.017	0.115	<0.001	***
Potential evapotranspiration	0.695	0.633	<0.001	***	0.052	0.042	0.708		0.906	0.655	<0.001	***	0.463	0.420	0.066	
Infiltration rate	-0.020	-0.039	0.102		-0.005	-0.013	0.814		0.121	0.043	0.231		0.024	0.048	0.283	
Biomass P 1 (early growing season)	-7.3E-04	-0.084	0.167		-5.7E-04	-0.046	0.715		-5.4E-04	-0.016	0.784		0.002	0.158	0.018	*
Biomass P 2 (main growth period)	0.003	0.403	<0.001	***	0.005	0.525	<0.001	***	0.003	0.213	<0.001	***	4.3E-04	0.060	0.425	
Biomass P 3 (peak biomass)	-1.8E-04	-0.022	0.859		0.002	0.225	0.010	**	0.003	0.186	0.002	**	0.004	0.492	<0.001	***
Biomass P 4 (peak biomass after clipping)	7.6E-04	0.064	0.061		0.001	0.091	0.081		2.8E-04	0.013	0.771		0.003	0.236	<0.001	***
Biomass P 5 (autumn)	4.7E-04	0.037	0.333		3.1E-04	0.021	0.742		0.003	0.073	0.143		0.003	0.154	0.002	**
Plant cover	-0.065	-0.067	0.216		0.044	0.032	0.731		0.072	0.065	0.087		0.015	0.006	0.894	
Soft-leaved forbs	0.038	0.034	0.216		-0.042	-0.036	0.504		-0.020	-0.027	0.487		0.133	0.141	0.002	**
Tall grass	0.056	0.077	0.150		0.005	0.004	0.957		0.061	0.072	0.041	*	0.179	0.142	0.001	**
Species diversity	0.007	0.006	0.837		-0.288	-0.120	0.123		0.104	0.107	0.005	**	0.038	0.043	0.291	
Mat-forming graminoids	-0.013	-0.013	0.655		0.077	0.064	0.345		-0.001	-0.002	0.952		-0.031	-0.039	0.347	
Dwarf shrubs	0.103	0.050	0.056		-0.011	-0.003	0.953		0.033	0.069	0.054		0.104	0.077	0.058	
Abundance of legumes	0.004	0.025	0.373		-0.007	-0.029	0.599		0.006	0.114	0.001	**	-0.017	-0.106	0.003	**
R^2 -ind.var.only	0.891				0.870				0.724				0.525			
R^2 -incl. $\rho + \psi$	0.889				0.907				0.797				0.788			
Spatial and temporal correlation parameters																
ψ (temporal)	-0.067		0.420		0.181		0.093		-0.018		0.810		0.184		<0.001	***
ρ (spatial)	0.563	<0.001	***		-0.356		0.196		0.626		<0.001	***	0.795		<0.001	***

Table VI. Importance of variables measured by the drop of the fit criterion AIC (with finite sample correction, delta AIC) and the Akaike weight $w(AIC)$: the combination of lowest delta AIC/highest $w(AIC)$ for the mode excluding the vegetation structure variables indicates a low importance of these variables at the two French sites; they should even be left off to get the best mode according to AIC. Climatic variables (precipitation and VPD) are most important at both French as well as at the Swiss site. The influence of biomass is relatively lowest at the Swiss site. On the other hand, biomass and structural and functional vegetation properties are more important than climatic variables and soil moisture at the Austrian site.

Models (differing in variables used)	FRA low		FRA high		CH		AUT	
	delta AIC	$w(AIC)$	delta AIC	$w(AIC)$	delta AIC	$w(AIC)$	delta AIC	$w(AIC)$
All variables	11.90	0.003	15.28	4.81E-04	0	0.598	0	0.993
Excluding climatic variables	45.91	1.07E-10	63.47	1.65E-14	58.30	1.31E-13	14.84	5.94E-04
Excluding soil moisture	29.17	4.61E-07	42.61	5.58E-10	35.59	1.12E-08	10.21	0.006
Excluding biomass	29.56	3.79E-07	32.30	9.69E-08	6.77	0.020	59.75	1.06E-13
Excluding vegetation structure	0	0.997	0	0.9995	0.90	0.382	16.15	3.09E-04

Austrian Alps collected by Wieser *et al.* (2008). They found annual ET/P-values to decrease from 0.7 to 0.1 as precipitation increased with elevation. Sites at the same elevation showed higher ET/P-values in the drier inner Alpine region than in the more humid Northern and Southern Limestone Alps. In comparison, Everson (2001) found ET/P ratios of 0.44 and 0.56 in wet years and 0.64 and 0.69 in dry years in a montane grassland in South Africa he considered not to be restricted by soil moisture. In dry conditions, Gu *et al.* (2008) found an ET/P ratio of 0.6 at a meadow on the Qinghai-Tibetan Plateau they characterized as water limited.

The ratio of actual ET to PET (ET/PET) is an often-used indicator for the relation between the evaporative demand of the atmosphere (PET) and the actual water lost to the atmosphere (ET, Yao, 1974; Specht, 1981; Churkina *et al.*, 1999). Mean ET/PET ratios of 1.04 and 0.93 at the Swiss and the Austrian study areas, respectively, indicate sufficient water supply (Parton *et al.*, 1981; Specht, 1981). On the other hand, ET/PET values of 0.70 and 0.67 and growing season deficits of ET–PET values of 143 mm and 120 mm at the lower and higher French sites, respectively, indicate seasonally limited water availability.

A unique feature of our study is the comparison of various different grassland types at each study area with a large number of samples, which revealed high intra-site variability of ET, seepage and soil moisture leading to overlapping ET/P and ET/PET ratios for single DSCs between our drier and more humid study areas despite the significant difference between the site means. As the DSCs were grouped in common experimental gardens at each site, the within-site variation of climatic conditions should be minimized. While infiltration rate, which was used as an integrated measure of soil hydraulic properties, did not have a significant influence on ET at any site in our analysis, small-scale heterogeneity of soils could contribute to the large variation in seepage and ET. Still the large intra-site variability of ET/P and ET/PET is an indicator for a high influence of vegetation on the water balance.

Soil moisture, climate and vegetation effects on ET

The general increase of ET with higher soil moisture deficit at all sites is surprising especially for the drier French sites (Tables IV and V). Apparently, for the five analysed time periods, the positive effect of warm weather conditions on ET which led to larger plant water uptake and drier soils is larger than the limitation of ET due to limited water availability at the end of dry periods. For the French sites, periodic water limitations are nevertheless likely considering relatively high ET/P and low ET/PET for the full growing season and single periods (Table II, Figure 2).

The positive correlation between ET and atmospheric evaporative demand (PET) at the Swiss and the lower French site is consistent with climatological theory (Monteith, 1975) and was confirmed for mountain grasslands (Wieser *et al.*, 2008). At the other two sites the lack of such a significant correlation was probably caused by a combination of high PET and low ET during the spring period. The positive correlation of precipitation with ET at the higher French site is an indicator of water limitation. At the lower French site such correlation was again prevented by a combination of high precipitation and low ET during spring. Due to generally high precipitation, the significantly positive influence of precipitation on ET at the Swiss site is probably not connected to water limitations but to high rates of evaporation from the soil surface and from intercepted water after rainfalls.

In accordance to the literature (Monteith, 1965; Larcher, 2003; De Boeck *et al.*, 2006; Hammerle *et al.*, 2008) ET increased with biomass, which was used as a proxy for leaf area, at all sites. The higher increase of ET with biomass at the more humid Swiss and Austrian sites is another indicator that the French sites periodically experienced dry conditions, where ET was most likely limited by low soil moisture during periods with high biomass. The presence of soft-leaved forbs in DSCs was positively correlated with ET only at the Austrian site, where the abundance of forbs was highest. Compared with graminoids, forbs were found

to have a higher leaf conductance, a lower sensitivity to VPDs (Körner and Mayr, 1981), a slightly higher specific leaf area and a higher leaf nitrogen concentration (Bahn *et al.*, 1999), all of which are correlated positively with canopy conductance (Kelliher *et al.*, 1993; Schulze *et al.*, 1994). The significantly positive correlation of ET with the abundance of tall grasses at the lower French and the Austrian site can be explained by the increase of surface roughness and aerodynamic conductance of the plant canopy with plant height and density (Kelliher *et al.*, 1993).

Species diversity had a significant influence on ET only at the Swiss site, where a large variety of alpine vegetation types differed especially in evenness. In the literature, higher species diversity was positively correlated with ET and stronger depletion of soil moisture in studies on artificially composed grasslands by De Boeck *et al.* (2006), Van Peer *et al.* (2004) and Verheyen *et al.* (2008). On the other hand neither Stocker *et al.* (1999) nor Spehn *et al.* (2000) found an effect of species diversity on water balance. Our last three vegetation characteristics were mainly tied to the abundance of three functional and morphological groups: mat-forming graminoids (and to a lesser extend graminoids in general), dwarf shrubs and legumes. In mountain ecosystems, daily sums of stomatal conductance were found to decrease from forbs to grasses and dwarf shrubs (Körner *et al.*, 1979; Körner and Mayr, 1981) leading to larger surface resistance and consequently lower transpiration rates (Oke, 1987). In our study, ET was not influenced by the abundance of mat-forming and narrow-leafed graminoids. The reason for the small, but significantly positive influence of the sixth vegetation component (abundance of dwarf shrubs) on ET at the lower French site cannot be attributed to dwarf shrubs as they hardly contributed to biomass at either French site. Instead, ET is influenced by the occurrence of *Carex*-species which was correlated to dwarf-shrub abundance in the principal component analysis (Table III). The abundance of legumes was correlated with ET at the Swiss and Austrian site, but in opposite direction. Again, we presume coincidental effects, influenced by site conditions and not directly attributed to legumes as such. At the Swiss site, legumes were represented by *Trifolium alpinum*, which was highly abundant in one vegetation type with high ET-rates relative to its low biomass. At the same time, *T. alpinum* was absent in the three vegetation types with the lowest ET-rates (*Loisleuria procumbens*-dominated, *Salix herbacea*-dominated and snow-bed vegetation dominated by mosses and small forbs like *Soldanella pusilla*, *Gnaphalium supinum* and *Alchemilla pentaphyllea*). On the other hand, legumes (mostly *Trifolium pratense* and *T. repens*) played a subordinate role in all vegetation types in the Austrian site, but just like ET, their abundance declined from DSCs extracted from meadows to those from abandoned grassland.

Even though the model adjustment (without spatial and temporal correlation coefficients) was by far the lowest at the sub-alpine Austrian site, the following reasons suggest that the influence of plant cover was nevertheless highest there: (1) the highest number of vegetation characteristics with a significant influence on ET, (2) the large standardized regression coefficients (beta) of biomass and other vegetation characteristics compared to the beta values of abiotic variables (Table IV) and (3) the high delta AIC values for models without biomass or vegetation characteristics (Table VI). Additionally, the strong increase of R^2 when biomass was incorporated period-specifically in the model, which indicates the importance of vegetation development during the growing season for the water balance at the Austrian site (Table V). On the other hand, at the alpine Swiss site the influence of harsh climatic conditions on water balance dominates over vegetation properties. A recent study by van den Bergh *et al.* (2013) which included lower elevation sites at 1490 m and 1960 m a.s.l. in the Swiss study area showed that the influence of biomass on ET was higher at these lower elevation sites than at the highest one. At the same time the influence of vegetation on the water balance is also small at the French sites where water supply was seasonally restricted. Overall, our results indicate that the highest potential to influence ET and water yield in mountain grasslands is in subalpine areas with sufficient water supply. In this areas reducing the biomass by mowing or grazing will lead to the largest decrease of ET and a higher water yield (see Inauen *et al.* (2013) for an estimation of economic gains). On the other hand, intensification measures like fertilization which lead to a higher, lush vegetation with a higher abundance of forbs might increase ET during the early growing season before mowing reduces biomass. When plant growth is limited by cold or dry climatic conditions the influence of vegetation on the water balance is smaller, and therefore the potential to influence water yield through land use is smaller.

For a more detailed causal understanding of the influence of vegetation on the water balance, a better understanding of the influence of rooting depth and the temporal spacing of rainfall events relative to water storage capacity would be important. Vegetation clearly modifies the action of the physical drivers of ET. In conclusion, our results support our first hypothesis that ET in subalpine and alpine grasslands is influenced not only by aboveground biomass and leaf area but also by the structural and functional composition of the vegetation. In contrast to our second hypothesis, the influence of vegetation composition and structure was highest at the more humid, subalpine Austrian site and lower at the humid but high elevation Swiss site and the drier French sites. The significant variability of ET we observed in DSCs within sites, and the ability to explain this variation by characteristics of the

vegetation, illustrates a significant influence of land cover on ET that goes beyond LAI. Hydrological models working on the catchment scale or beyond could be improved by accounting for the species- or functional-type-composition, rather than just biomass or LAI.

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REFERENCES

- Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In *Proceedings of the Second International Symposium on Information Theory*, Petrov BN, Caski F (eds). Akademiai Kiado: Budapest; 267–281.
- Akaike H. 1979. A Bayesian extension of the minimum AIC procedure of autoregressive model fitting. *Biometrika* **66**: 273–242.
- Allen RG, Pereira LS, Raes D, Smit M. 1998. *Crop evapotranspiration - Guidelines for computing crop water requirements*. FAO - Food and Agriculture Organization of the United Nations: Rome.
- Arora V. 2002. Modeling vegetation as a dynamic component in soil-vegetation-atmosphere transfer schemes and hydrological models. *Reviews of Geophysics* **40**: 1006–1006. DOI: 10.1029/2001RG000103
- Asbjornsen H, Goldsmith GR, Alvarado-Barrientos MS, Rebel K, Van Osch FP, Rietkerk M, Chen J, Gotsch S, Tobon C, Geissert DR, Gomez-Tagle A, Vache K, Dawson TE. 2011. Ecohydrological advances and applications in plant-water relations research: a review. *Journal of Plant Ecology* **4**: 3–22. DOI: 10.1093/jpe/rtr005
- Bahn M, Wohlfahrt G, Haubner E. 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. In *Land-Use Changes in European Mountain Ecosystems. ECOMONT- Concept and Results*, Cernusca A TU, Bayfield N (ed). Blackwell, Wissenschaft: Berlin; 247–255.
- Baldocchi DD, Xu L, Kiang N. 2004. How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland. *Agricultural and Forest Meteorology* **123**: 13–39.
- Budyko MI. 1958. *The heat balance of the earth's surface*. U.S. Dept. of Commerce: Washington.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodal inference: A practical information-theoretic approach*. Springer Verlag: New York.
- Campbell DI, Murray DL. 1990. Water balance of snow tussock grassland in New Zealand. *Journal of Hydrology* **118**: 229–245. DOI: 10.1016/0022-1694(90)90260-5
- Chen HS, Shao MG, Li YY. 2008. The characteristics of soil water cycle and water balance on steep grassland under natural and simulated rainfall conditions in the Loess Plateau of China. *Journal of Hydrology* **360**: 242–251. DOI: 10.1016/j.jhydrol.2008.07.037
- Churkina G, et al. 1999. Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. *Global Change Biology* **5**: 46–55.
- Couturier DE, Ripley EA. 1973. Rainfall interception in mixed grass prairie. *Canadian Journal of Plant Science* **53**: 659–663.
- De Boeck HJ, et al. 2006. How do climate warming and plant species richness affect water use in experimental grasslands? *Plant and Soil* **288**: 249–261. DOI: 10.1007/s11104-006-9112-5
- de Vries A. 2010. European territories confronted with climate change: Awaiting the events or timely preparation? *Futures* **42**: 825–832. DOI: 10.1016/j.futures.2010.04.014
- Donohue RJ, Roderick ML, McVicar TR. 2007. On the importance of including vegetation dynamics in Budyko's hydrological model. *Hydrology and Earth System Sciences* **11**: 983–995. DOI: 10.5194/hess-11-983-2007
- Ellenberg H, Leuschner C. 2010. *Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht*, 6th edn. UTB: Stuttgart.
- Evans RA, Young JA. 1970. Plant Litter and Establishment of Alien Annual Weed Species in Rangeland Communities. *Weed Science* **18**: 697–703.
- Everson CS. 2001. The water balance of a first order catchment in the montane grasslands of South Africa. *Journal of Hydrology* **241**: 110–123.
- Eviner VT, Chapin FSI. 2003. FUNCTIONAL MATRIX: A Conceptual Framework for Predicting Multiple Plant Effects on Ecosystem Processes. *Annual Review of Ecology, Evolution, and Systematics* **34**: 455–485. DOI: 10.1146/annurev.ecolsys.34.011802.132342
- Fitschen J, Schmeil O. 2003. *Flora von Deutschland und angrenzender Länder*, 92 edn. Quelle + Meyer.
- Flury M, Yates MV, Jury WA. 1999. Numerical Analysis of the Effect of the Lower Boundary Condition on Solute Transport in Lysimeters. *Soil Science Society of America Journal* **63**: 1493–1499.
- Garnier E, Navas M-L. 2011. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. *A review. Agronomy for Sustainable Development* **32**: 365–399. DOI: 10.1007/s13593-011-0036-y
- Gordon DR, Rice KJ. 1993. Competitive Effects of Grassland Annuals on Soil Water and Blue Oak (*Quercus Douglasii*) Seedlings. *Ecology* **74**: 68–82. DOI: 10.2307/1939502
- Gross N, Suding KN, Lavorel S, Roumet C. 2007. Complementarity as a mechanism of coexistence between functional groups of grasses. *Journal of Ecology* **95**: 1296–1305. DOI: 10.1111/j.1365-2745.2007.01303.x
- Gu S, et al. 2008. Characterizing evapotranspiration over a meadow ecosystem on the Qinghai-Tibetan Plateau. *Journal of Geophysical Research* **113**: D08118. DOI: 10.1029/2007jd009173
- Hammerle A, et al. 2007. Eddy covariance measurements of carbon dioxide, latent and sensible energy fluxes above a meadow on a mountain slope. *Boundary-Layer Meteorology* **122**: 397–416. DOI: 10.1007/s10546-006-9109-x
- Hammerle A, Haslwanter A, Tappeiner U, Cernusca A, Wohlfahrt G. 2008. Leaf area controls on energy partitioning of a temperate mountain grassland. *Biogeosciences* **5**: 421–431. DOI: 10.5194/bg-5-421-2008
- Harding RJ, Lloyd CR. 2008. Evaporation and energy balance of a wet grassland at Tadham Moor on the Somerset Levels. *Hydrological Processes* **22**: 2346–2357. DOI: 10.1002/Hyp.6829
- Hefel C, Stöcklin J. 2010. Flora der Furka. *Bauhinia* **22**: 33–59.
- Inauen N, Körner C, Hiltbrunner E. 2013. Hydrological consequences of declining land use and elevated CO₂ in alpine grassland. *Journal of Ecology* **101**: 86–96. DOI: 10.1111/1365-2745.12029

- IPCC. 2007. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jasechko S, Sharp ZD, Gibson JJ, Birks SJ, Yi Y, Fawcett PJ. 2013. Terrestrial water fluxes dominated by transpiration. *Nature* **496**: 347–350.
- Kelliher FM, Leuning R, Schulze ED. 1993. Evaporation and canopy characteristics of coniferous forests and grasslands. *Oecologia* **95**: 153–163.
- Körner C. 2003. *Alpine Plant Life*, 2nd edn. Springer: Heidelberg.
- Körner C, Mayr R. 1981. Stomatal behaviour in alpine plant communities between 600 and 2600 meters above sea level. In *Plants and Their Atmospheric Environments*, Grace J, Ford ED, Jarvis PG (ed). Blackwell Scientific Publishers: Oxford; 205–218.
- Körner C, Scheel J, Bauer H. 1979. Maximum leaf diffusive conductance in vascular plants. *Photosynthetica* **13**: 45–82.
- Körner C, Wieser G, Cernusca A. 1989. Der Wasserhaushalt waldfreier Gebiete in den österreichischen Alpen zwischen 600 und 2600 m höhe. In *Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern*, Cernusca A (ed). Wagner: Innsbruck; 119–153.
- Larcher W. 2003. *Physiological plant ecology*, 4th edn. Springer-Verlag: Berlin.
- Lauber K, Michel A, Wagner G. 1998. *Flora Helvetica*. Paul Haupt: Bern.
- Lavorel S, *et al.* 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* **99**: 135–147. DOI: 10.1111/j.1365-2745.2010.01753.x
- Leitinger G, Tasser E, Newsely C, Obojes N, Tappeiner U. 2010. Seasonal dynamics of surface runoff in mountain grassland ecosystems differing in land use. *Journal of Hydrology* **385**: 95–104. DOI: 10.1016/j.jhydrol.2010.02.006
- Messerli B, Ives JD (eds). 1997. *Mountains of the world. A global priority*. Parthenon Pub.: New York, 495 pp.
- Millo G, Piras G. 2012. splm: Spatial Panel Data Models in R. *Journal of Statistical Software* **47**: 1–38.
- Monteith JL. 1965. Evaporation and environment. *Symp. Soc. Exp. Biol.* **19**: 205–234.
- Monteith JL. 1975. *Vegetation and the Atmosphere, Volume 1 Principles*. Academic Press: London - New York - San Francisco.
- Nippert JB, Knapp AK. 2007a. Linking water uptake with rooting patterns in grassland species. *Oecologia* **153**: 261–272. DOI: 10.1007/s00442-007-0745-8
- Nippert JB, Knapp AK. 2007b. Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos* **116**: 1017–1029. DOI: 10.1111/j.2007.0030-1299.15630.x
- Obrist D, Verburg PSJ, Young MH, Coleman JS, Schorran DE, Arnone JA. 2003. Quantifying the effects of phenology on ecosystem evapotranspiration in planted grassland mesocosms using EcoCELL technology. *Agricultural and Forest Meteorology* **118**: 173–183. DOI: 10.1016/s0168-1923(03)00111-4
- Oke TR. 1987. *Boundary Layer Climates*. Methuen: London: 435.
- Olchev A, *et al.* 2008. Effects of land-use changes on evapotranspiration of tropical rain forest margin area in Central Sulawesi (Indonesia): Modelling study with a regional SVAT model. *Ecological Modelling* **212**: 131–137. DOI: 10.1016/j.ecolmodel.2007.10.022
- Parton WJ, Lauenroth WK, Smith FM. 1981. Water loss from a shortgrass steppe. *Agricultural Meteorology* **24**: 97–109. DOI: 10.1016/0002-1571(81)90036-4
- Pohl M, Stroude R, Buttler A, Rixen C. 2011. Functional traits and root morphology of alpine plants. *Annals of Botany* **108**: 537–545. DOI: 10.1093/aob/mcr169
- Ponce Campos GE, *et al.* 2013. Ecosystem resilience despite large-scale altered hydroclimatic conditions. *Nature* **494**: 349–352.
- Quétiér F, Rivoal F, Marty P, Chazal J, Thuiller W, Lavorel S. 2009. Social representations of an alpine grassland landscape and socio-political discourses on rural development. *Regional Environmental Change* **10**: 119–130. DOI: 10.1007/s10113-009-0099-3
- Quétiér F, Thébaud A, Lavorel S. 2007. Plant Traits in a State and Transition Framework as Markers of Ecosystem Response to Land-Use Change. *Ecological Monographs* **77**: 33–52.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna, Austria.
- Ritchie JT. 1972. Model for predicting evaporation from a row crop with incomplete cover. *Water Resources Research* **8**: 1204–1213.
- Rutter AJ. 1975. The hydrological cycle in vegetation. In *Vegetation and the Atmosphere. Vol. 1. Principles*, vol. 1, Monteith JL (ed). Academic Press: London; 111–154.
- Salvucci GD, Gentile P. 2013. Emergent relation between surface vapor conductance and relative humidity profiles yields evaporation rates from weather data. *Proceedings of the National Academy of Sciences* **110**: 6287–6291. DOI: 10.1073/pnas.1215844110
- Schulze DEK, Francis M, Körner C, Lloyd J. 1994. RELATIONSHIPS AMONG MAXIMUM STOMATAL CONDUCTANCE, ECOSYSTEM SURFACE CONDUCTANCE, CARBON ASSIMILATION RATE, AND PLANT NITROGEN NUTRITION: A Global Ecology Scaling Exercise. *Annual Review of Ecology and Systematics* **25**: 629–660.
- Shane MW, Cawthray GR, Cramer MD, Kuo J, Lambers H. 2006. Specialized 'dauciform' roots of Cyperaceae are structurally distinct, but functionally analogous with 'cluster' roots. *Plant, Cell & Environment* **29**: 1989–1999. DOI: 10.1111/j.1365-3040.2006.01574.x
- Sitte P, Weiler EW, Kadereit JW, Bresinsky A, Körner C. 2002. *Strasburger. Lehrbuch der Botanik für Hochschulen*, 35th edn. Spektrum Akademischer, Verlag: Heidelberg.
- Soil Science Glossary Terms Committee. 2008. Glossary of soil science terms 2008. Ed. Soil Science Society of America edn
- Specht RL. 1981. Growth indices — Their rôle in understanding the growth, structure and distribution of Australian vegetation. *Oecologia* **50**: 347–356. DOI: 10.1007/BF00344975
- Spehn EM, *et al.* 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs* **75**: 37–63.
- Spehn EM, Joshi J, Schmid B, Alphei J, Körner C. 2000. Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. *Plant and Soil* **224**: 217–230.
- Stocker R, Körner C, Schmid B, Niklaus PA, Leadley PW. 1999. A field study of the effects of elevated CO₂ and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* **5**: 95–105.
- Suding KN, Goldberg D. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* **82**: 2133–2149. DOI: 10.1890/0012-9658(2001)082[2133:DDACHM]2.0.CO;2
- Tappeiner U, Cernusca A. 1998. Effects of land-use changes in the Alps on exchange processes (CO₂, H₂O) in grassland ecosystems. In *Proceedings of the HeadWater '98 Conference* April 1998, IAHS Publ: Meran/Merano, Italy **248**: 131–138.
- Tasser E, Tappeiner U. 2002. Impact of land use changes on mountain vegetation. *Applied Vegetation Science* **5**: 173–184.
- UNEP. 1997. *World Atlas of Desertification*, 2nd edn. Edward Arnold: London, Baltimore.
- van den Bergh T, Inauen N, Hiltbrunner E, Körner C. 2013. Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps. *Journal of Hydrology* **500**: 75–83. DOI: 10.1016/j.jhydrol.2013.07.013
- Van Peer L, Nijs I, Reheul D, De Cauwer B. 2004. Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. *Functional Ecology* **18**: 769–778.
- Verheyen K, *et al.* 2008. Can complementarity in water use help to explain diversity-productivity relationships in experimental grassland plots? *Oecologia* **156**: 351–361. DOI: 10.1007/s00442-008-0998-x
- Viviroli D, Weingartner R. 2004. The hydrological significance of mountains: from regional to global scale. *Hydrology and Earth System Sciences* **8**: 1017–1030.
- Viviroli D, Weingartner R, Messerli B. 2003. Assessing the Hydrological Significance of the World's Mountains. *Mountain Research and Development* **23**: 32–40.
- Wieser G, Hammerle A, Wohlfahrt G. 2008. The water balance of grassland ecosystems in the Austrian Alps. *Arctic Antarctic and Alpine Research* **40**: 439–445. Doi: 10.1657/1523-0430(07-039)[Wieser]2.0.Co;2

- Wilske B, *et al.* 2010. Evapotranspiration (ET) and regulating mechanisms in two semiarid *Artemisia*-dominated shrub steppes at opposite sides of the globe. *Journal of Arid Environments* **74**: 1461–1470. DOI: 10.1016/j.jaridenv.2010.05.013
- Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**: 424–426.
- Yao AYM. 1974. Agricultural potential estimated from the ratio of actual to potential evapotranspiration. *Agricultural Meteorology* **13**: 405–417. DOI: 10.1016/0002-1571(74)90081-8
- Zhang L, Dawes WR, Walker GR. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research* **37**: 701–708. DOI: 10.1029/2000WR900325