

# Diversity and Frequency of Clonal Traits Along Natural and Land-Use Gradients in Grasslands of the Swiss Alps

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**Abstract** The frequency of clonal plants in different vegetation types is known to be influenced by environmental and land-use factors. However, the underlying behavior of individual clonal traits or clonal trait diversity has received little attention. Here, we assess for species- and trait-diverse grasslands of the Swiss Alps the relative importance of temperature, soil moisture, land use and species richness on the diversity and frequency of individual compared with all clonal traits. We further analyzed how cover-weighted data alters the relationships found with commonly used presence-absence data. We combined species compositional, land-use and environmental data from 236 28-m<sup>2</sup> grassland plots with clonal trait information for 527 species following the Clonal Growth Organ (CGO) classification. Test results are based on linear models, ANOVAs and ANCOVAs. The grassland sites were 84% dominated by clonal species. Drought-prone grasslands harbored the least clonal species. No increase in clonality was detected with decreasing temperature (= altitude). Mown or pastured grasslands had more clonal species than fallows. Certain sets of traits were correlated. Rhizomatous species especially reacted strongly to climatic and land-use gradients and had highest frequencies in cold, moist and disturbed sites. Clonal diversity was strongly dependent on species richness. Cover-weighted and presence-absence based estimates were largely similar. Overall, our data outlined that common clonal traits react differently to natural and land-use gradients as well as differently to the sum of clonal traits. Also, soil moisture was more decisive than temperature (= altitude) for the presence of clonal species. Lastly, the strong correlation between species-richness and clonal trait diversity needs to be accounted for when interpreting the functional role of clonal traits.

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**Keywords** Altitude · Climatic gradients · CLO-PLA database · Functional traits · Weighted abundance

## Introduction

A general goal of ecology is to understand the frequency and distribution of functional traits across types of vegetation. Clonal traits or clonal growth organs such as rhizomes and stolons are well represented in herbaceous plants and are in many respects advantageous to a plant as well as for site stability (van Groenendael et al. 1996; Körner 2003; Silvertown and Charlesworth 2005). Apart from being an alternative to sexual reproduction, clonality often entails the ability to rapidly colonize open habitats, to pre-emptively occupy space by forming dense patches, to avoid competition by fugitive growth and to forage for resources in a heterogeneous soil matrix (Stöcklin 1992).

The last decades have seen an increased interest in clonal plants within the larger context of studying the functional role of plant traits for biodiversity and ecosystem functioning. This resulted in a series of articles and book chapters on classifying and measuring clonal traits (Klimeš et al. 1997; Cornelissen et al. 2003; Körner 2003; Klimešová and Klimeš 2006, 2007; Kleyer et al. 2008; Klimešová et al. 2008) and on the influence of environmental and land-use factors on the frequency and diversity of clonal traits (Stöcklin 1992; Díaz and Cabido 2001; Rosenfeld 2002; Klimeš 2003; Halassy et al. 2005; Díaz et al. 2007; Klimešová et al. 2008; Evette et al. 2009; Mládek et al. 2011).

In a comprehensive analysis, van Groenendael et al. (1996) have outlined some general trends with regard to site preferences of clonal species at the scale of regional floras. The review revealed that clonal species are more frequently encountered in wet habitats, under nutrient-poor conditions, at lower mean temperatures and, to a lesser extent, at lower light conditions. One common notion therefore is that clonal growth is more prevalent at higher altitudes. However, a decline of clonal species was reported from the upper ranges of the Himalayas and explained by an increase in compromising site factors such as hard substrate texture, slope instabilities and recurrent freeze-thaw-cycles (Klimeš 2003). Related to this, increasing disturbance from grasslands to pioneer grasslands to scree communities decreased the frequency of clonal growth forms in the Swiss Alps (Stöcklin 1992). In this context, Körner (2003) remarked that natural habitat fragmentation and reduced competition, and not temperature as a physiological factor, may explain lower clonal frequencies at high altitudes. However, general trends may be to some degree biased by vegetation type as well as by the definition of what clonal propagation is (Körner 2003).

Other studies that have taken a closer look at individual clonal traits found differential effects of environmental and land-use factors on the frequency of species with a given trait. Halassy et al. (2005) reported from the Italian Apennines that xeric grasslands harbored more plant species with root-derived Clonal Growth Organs (CGOs; *sensu* Klimeš et al. 1997) and limited lateral spread while more CGOs with pronounced lateral spread were found in mesic sites. Evette et al. (2009), however, detected only a weak influence of altitude and duration of snow cover on

the frequency of four selected clonal traits in different plant communities of the subalpine to alpine zone of the Western Alps, i.e., duration of clonal integration, clonal multiplication, spreading rate and bud-bank size. Switching the focus on land use, Díaz et al. (2007) observed in their meta-analysis that grazing favored stoloniferous over tussock architecture and that the latter trend was accentuated in humid systems and in sites with a long grazing history. Lastly, increased site disturbance favored plants with the ability for above- and below-ground resprouting (Klimešová and Klimeš 2003).

One potentially important and little studied aspect is how clonal trait diversity is influenced by environmental or land-use gradients. Clonal diversity, in the conventional sense, refers to the number of genets of a species per unit area (e.g., McLellan et al. 1997) whereas clonal trait diversity refers to clonal trait richness. The above-mentioned literature focused either on changes in frequencies of clonal vs non-clonal species or on changes in frequencies of individuals, groups or subsets of clonal traits. It is likely that clonal trait diversity will react to environmental or anthropogenic stresses and will be further biased by species richness. In this context, the abundance peak of clonal species in the lower alpine belt noted by Körner (2003), which corresponds strikingly well to the hump-backed shape of species diversity in many mountainous regions (Nogués-Bravo et al. 2008), may also translate into highest clonal trait diversities in these mid-domain areas.

An additional point is that most studies with a focus on clonal traits relied on un-weighted presence/absence data and did not take the cover of a species into account (but see Evette et al. 2009). However, cover-weighted trait values have been shown to alter the relationship between reproductive traits, i.e., seed mass and dispersal mechanism, and environmental factors in comparison with un-weighted values (Pakeman et al. 2008). A similar comparative study for clonal traits is currently lacking.

In this study we investigated for the first time the effect of environmental (temperature, soil moisture) and land-use factors (fallow, pasture, meadow) on clonal trait diversity and on all individual CGO types classified by Klimešová et al. (2008), which are found in a single vegetation type (grasslands) and along an altitudinal gradient of 2,500 m thus avoiding a number of biases introduced above. In detail, we ask:

- i) What is the influence and relative importance of species richness, abiotic conditions and land use on the diversity and frequency of clonal types? In this context, we hypothesize that clonal trait diversity is positively related to species-richness, that clonal trait diversity is lowest at extreme cold and/or dry sites, that the frequency of clonal species is highest at low temperatures ( $\approx$  high altitudes), that the frequency of clonal species will increase with increasing site water availability, and that the frequency of clonal species is highest in sites with anthropogenic disturbance (pastures, meadows).
- ii) How do individual types of CGO react in comparison with all CGOs? We hypothesize that individual clonal traits will react individually and independently to changing site conditions (temperature, site water balance, land-use types) and be more accentuated than the sum of traits.
- iii) How does the assessment of CGOs differ between presence/absence and cover-weighted data? We hypothesize that differences are most pronounced for clonal

traits associated with vegetative spread (e.g., rhizomes and stolons), and less so with regeneration (e.g., adventitious buds) or reproduction (e.g., bulbils).

## Material and Methods

### *Site Selection*

We mined data from the Swiss inventory of oligotrophic meadows and pastures (Troockenwiesen und -weiden: TWW; e.g., Eggenberg et al. 2001). The inventory covers >14,000 grasslands and contains vegetation records from standard circular relevés of 28.3 m<sup>2</sup>. We sub-sampled the inventory using a stratified random selection and included only Swiss Alpine sites and 29–30 sites from each of eight plant community types (phytosociological alliances), i.e., *Arrhenatherion*, *Mesobromion*, *Xerobromion*, *Stipo-Poion*, *Nardion strictae*, *Festucion variaae*, *Caricion ferrugineae*, *Seslerion variaae*. Because these communities correlate strongly with natural and land-use gradients (e.g., Ellenberg 1996; Delarze and Gonseth 2008), differences were not tested explicitly.

### *Explanatory Site Factors*

For the resulting 236 sites we extracted 1-km-resolution environmental data from the bioclimatic maps of Switzerland © WSL based on data from stations SMA-Meteo Schweiz (O. Wildi, Swiss Federal Institute WSL, pers. comm.). We used *degree days* and *site water balance* as the biologically most meaningful climate variables. Degree days are the integral of the daily mean temperature curve above the zero line. Degree days are negatively correlated with altitude (in our data set:  $R^2=0.3188$ ,  $P<0.001$ ) but circumvent the prominent *Massenerhebungseffekt* (mass elevation effect) when assessing the indirect effect of an altitudinal gradient. Site water balance is an estimate of the water available to plants during the course of a year. It integrates both climatic (precipitation, evapotranspiration) and soil parameters (physical properties, topographic position) (e.g., Roberts et al. 1993; Guisan et al. 2006). Land use for each site was taken from the TWW inventory and classified into fallow, pasture, or meadow.

To a certain amount the explanatory factors were correlated among each other. Site water balance was negatively correlated to degree days ( $r=-0.64^{***}$ ). Temperature and water availability significantly influenced land use. In this context, fallows were more often found in warm and drought-prone sites than meadows that occurred at the cool end of the gradient where site water balance was rarely negative. Pastures had an intermediate position.

### *Species Pool and Clonal Traits*

The species pool contained 527 species after omitting singular occurrences of trees, tree seedlings and questionable subspecies. For each species we synthesized clonal trait data from the CLO-PLA3 database (Klimešová and Klimeš 2006), literature

sources (Hess et al. 1972; Hegi 1975–2009; Eggenberg and Möhl 2007) or own complementary field work. We followed the clonal growth organ (CGO) classification by Klimešová and Klimeš (2006, 2008) and based our analyses only on CGOs characterized as necessary or additive and recorded at least once as such in the CLO-PLA3 database.

### ***Data Transformation and Weighing of Traits***

The categorical Braun-Blanquet cover-abundance values of the individual vegetation records were transformed to percentage values prior to the analysis, i.e., **r**: 0.1%, **+**: 0.5%, **1**: 2.5%, **2**: 15%, **3**: 37.5%, **4**: 62.5% and **5**: 87.5% (e.g. Dierschke 1994). Based on these values we calculated cover-weighted trait values per plot by summing the cover of all species with a given CGO divided by the total cover of all species (Pakeman et al. 2008).

### ***Statistics***

We used linear regressions as well as *F*-statistics (ANOVA, Tukey Honest Significant Difference test) to test for significant relationships between explanatory (temperature, soil water balance, species richness, land use) and dependent variables (trait frequencies, trait diversity). The multiple regressions were carried out with ANCOVAs including all explanatory variables and their interactions using a stepwise model simplification. All statistics were calculated using R 2.9.0 (R Development Core Team 2009). We used the conventional abbreviations for significance levels, i.e., n.s. – non-significant  $P > 0.05$ ; \* –  $P < 0.05$ ; \*\* –  $P < 0.01$ ; \*\*\* –  $P < 0.001$ .

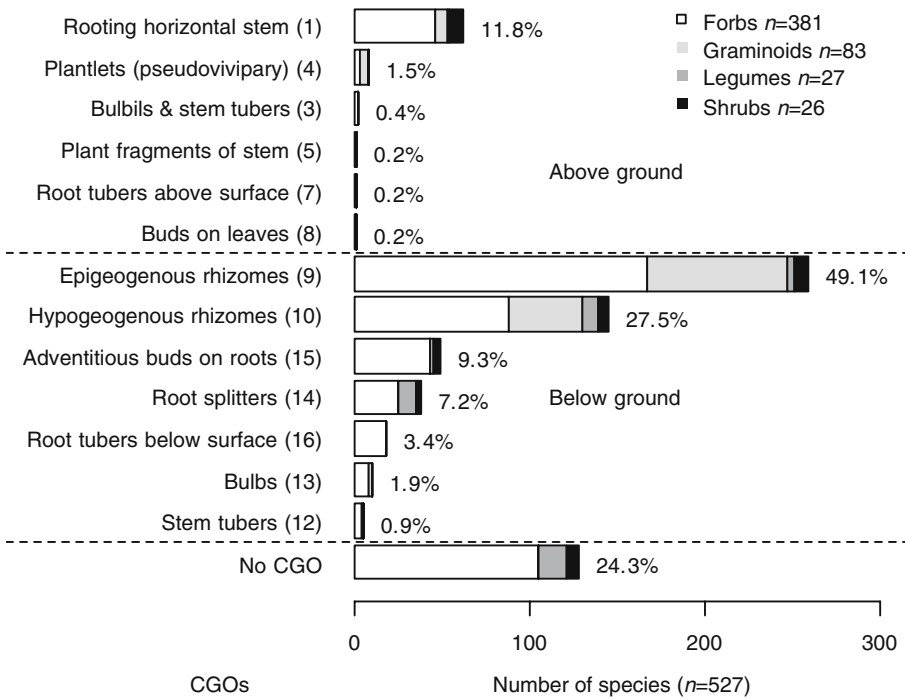
## **Results**

### ***Species Richness and Diversity of Clonal Species***

The species pool consisted of 527 grassland species split disproportionately among the plant functional groups (forbs: 72%, graminoids: 16%, legumes: 7%, shrubs: 5%; Appendix 1a). About 75% of the species were clonal with  $\frac{2}{5}$  of them having more than one CGO. In total, 13 out of 17 CGO types were found in our species pool (Fig. 1). Only four CGO types were absent, two of which related to aquatic plants (turions, budding plants). Most abundant were species with CGOs that occur below-ground. Overall, only five CGO types were present in more than 5% of species and were considered further. The other eight CGO types were rare. Three CGOs were only found in a single species each.

Species richness in a 28-m<sup>2</sup>-relevé ranged from 11 to 59 with an average of 32. A mean of 84% of the species in a relevé were clonal (min: 53%, max: 100%). Clonal species contributed on average 90% to the cover (min: 53%, max: 100%). A mean of 6.4 different CGOs could be found in a relevé (min: 4, max: 9) (Appendix 1b).

CGO diversity within a relevé increased significantly with species richness though showing a considerable amount of scatter ( $R^2=0.30^{***}$ ) (Fig. 2). CGO

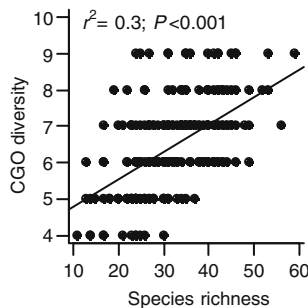


**Fig. 1** Diversity and frequency distribution of Clonal Growth Organs in the species pool split by plant functional groups based on 527 species and 236 vegetation records from Swiss Alpine grasslands. Numbers in brackets refer to CGO numbers as used in the original classification (Klímešová et al. 2008)

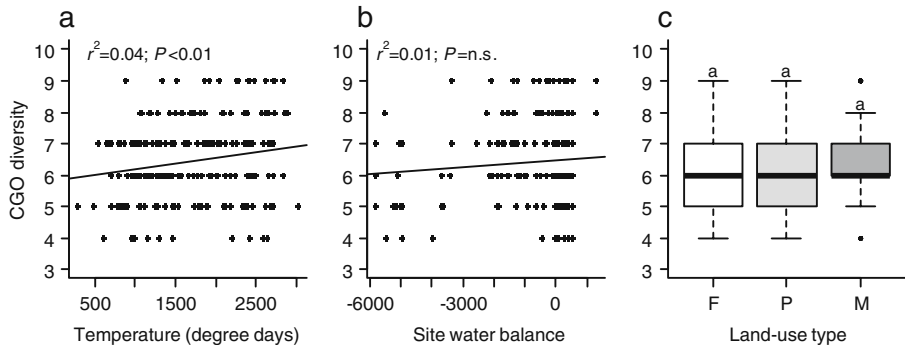
diversity, however, was not or only very little affected by the different gradients (temperature:  $R^2=0.04^{**}$ , Fig. 3a; site water balance:  $R^2=0.01^{n.s.}$ , Fig. 3b; land use: d.f.=2, SS=5.7,  $F=1.81^{n.s.}$ , Fig. 3c).

**Frequency of Clonal Species**

The frequency of clonal species within a relevé did not change along the temperature gradient (Fig. 4a). At the same time, fewer clonal species were found in drought-



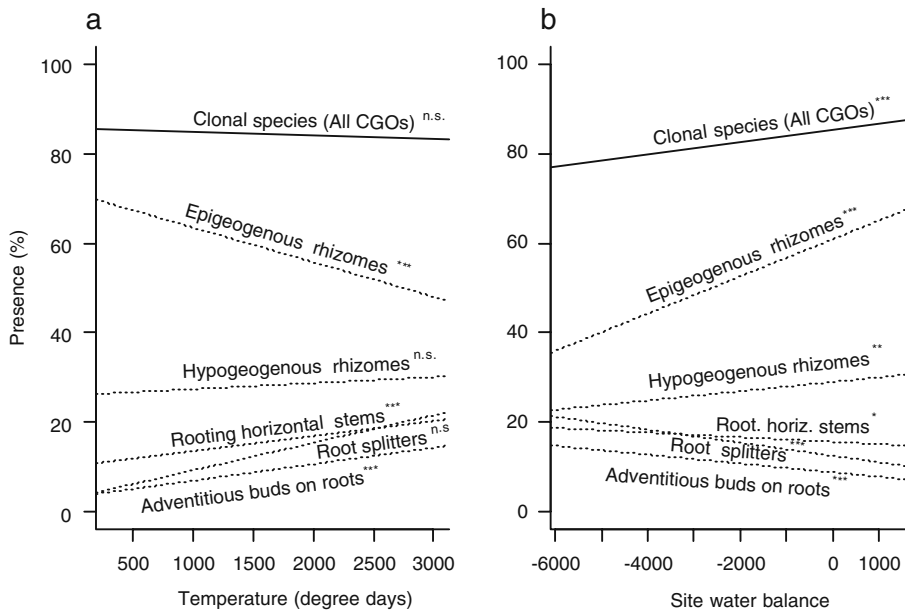
**Fig. 2** Clonal Growth Organ diversity within a given vegetation record in relation to species richness in 236 Swiss Alpine grasslands



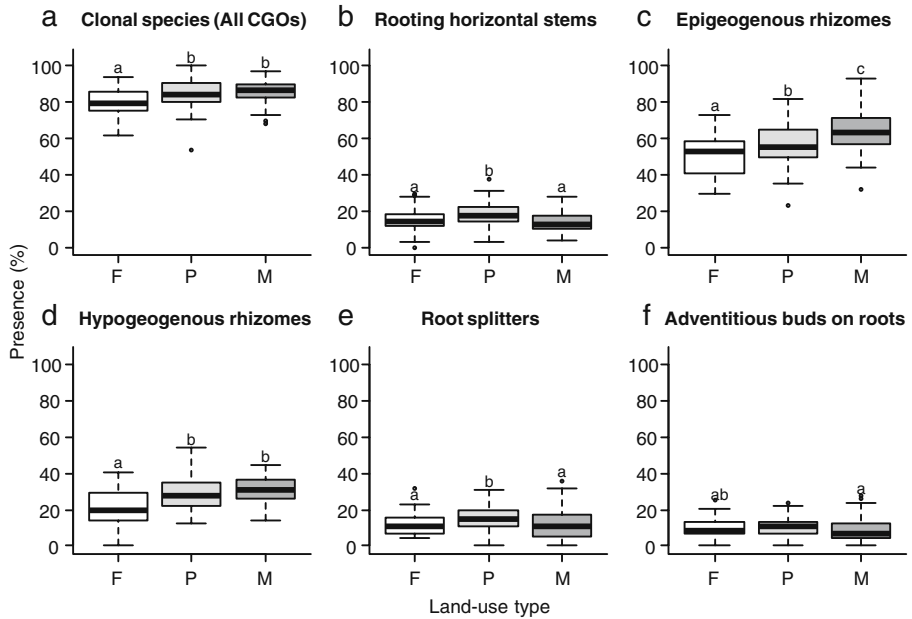
**Fig. 3** Diversity of Clonal Growth Organs (CGO) in a vegetation record in relation to **a** temperature (degree days), **b** moisture (site water balance) and **c** land use. Land-use types: F – fallow, M – meadow, P – pasture. Box plots sharing the same letter were not significantly different at  $P=0.05$  based on Tukey HSD test

prone habitats (Fig. 4b) and in fallows (Fig. 5a) than in sites with an even water balance or in pastures and meadows.

These general relationships represent the cumulative behavior for all clonal species (all CGOs). Looking at individual CGOs there seem to be two groups of traits with largely corresponding behavior, respectively (Figs. 4 and 5). Rhizomatous species tended to decrease in frequency with increasing temperatures or decreasing water availability and were more often found in disturbed habitats than in fallows. At the same time, species with rooting horizontal stems, with splitting roots or with



**Fig. 4** Regression lines of the un-weighted frequency of clonal plants (all CGOs) as well as the five main Clonal Growth Organs (CGOs) in standard relevés **a** along the temperature gradient and **b** along the site moisture gradient. Data points are omitted for clarity. n.s. – non-significant;  $P>0.05$ ; \* –  $P<0.05$ ; \*\* –  $P<0.01$ ; \*\*\* –  $P<0.001$



**Fig. 5** The un-weighted frequency of **a** clonal species in relation to land-use types, and **b–f** of individual Clonal Growth Organs (CGOs) in relation to land-use types. Land-use types: F – fallow, M – meadow, P – pasture. Box plots sharing the same letter were not significantly different at  $P = 0.05$  based on Tukey HSD test

buds on roots showed the opposite trend for temperature and soil water but were only more frequent in pastures.

### Cover-Weighted Trait Frequencies

Results based on cover-weighted trait values (Appendix 2 and 3) were to a large degree similar to presence/absence based data (Figs. 4 and 5). Here, temperature, soil moisture or land-use had no significant effect on the cover of all clonal plants (all CGOs). As with presence/absence data the two groups of clonal traits (rhizomatous vs non-rhizomatous) showed equally concerted and opposing behavior along the temperature and soil moisture gradient but less pronounced for land-use types.

In general, we did not find a complete reversal of a trend when comparing presence/absence data with cover-weighted results. Certain relationships were accentuated, others identical or less pronounced. Also, the different types of clonal traits associated either with vegetative spread (rhizomes and stolons), regeneration (adventitious buds) or reproduction (bulbils) showed no contrasting behavior with regard to cover-weighted values.

### Multifactorial Analysis

We analyzed the effect of all explanatory parameters, i.e., species richness, temperature, soil moisture and land use, on the diversity, frequency and cover of CGOs in separate analyses of covariance (ANCOVA). Unfortunately, multiple regressions did not produce reliable results using either forward (adding terms to the simplest model) or backward



(stepwise removal of non-significant terms from the complete model) selection of parameters or Type I (sequential) and Type III (non-sequential) ANCOVAs. Likely, this is due to the strongly correlated explanatory variables (see Methods; Crawley 2007). Therefore we refrain from presenting and discussing the multifactorial results.

## Discussion

### *Clonal Trait Diversity in Grasslands*

As hypothesized the diversity of clonal traits was strongly dependent on species richness of a given site (Fig. 2). Temperature, soil moisture or land use had little or no direct effect on clonal trait diversity (Fig. 3). It is noteworthy that in our data set, the variability in species-richness was not at all or only at a very low level explained by the investigated site factors, i.e., land use (d.f.=2, SS=416,  $F=2.62^{n.s.}$ ), temperature ( $R^2=0.03^{**}$ ) and site water balance ( $R^2=0.09^{***}$ ). *A priori* we would have expected a positive monotonic or hump-backed relationship between species-richness and temperature because most studies have either found the highest concentration of species at warm lowland sites or in subalpine altitudes (Nogués-Bravo et al. 2008 and references therein). Our data set might be special in this respect because the grassland sites covered are exclusively of high conservation-value due to their species diversity and high frequency of red-listed plants. Nevertheless, we found a slight increase of clonal diversity with temperature giving some support for our hypothesis that more CGOs can be found in less stressful sites.

The strong positive relationship between clonal diversity and species-richness very likely remains true despite that the species recorded in fixed-sized 28-m<sup>2</sup> plots may under-estimate to some extent the diversity of grassland. An argument in support of this is the observation that in our data set rare CGOs tend to be associated with rare species. In detail, the seven CGOs occurring in <5% of the species (Fig. 1) were found in <5% of the grasslands. Notable exceptions were root tubers below ground associated with one abundant orchid species, *Gymnadenia conopsea*, and plantlets found in the forb *Polygonum viviparum* and the grass *Dactylis glomerata* present in 10% and 25% of the sites, respectively. In contrast, half of all species had epigeogenous rhizomes (Fig. 1) that occurred equally frequent in rare (<5% of sites) and increasingly abundant species (>5% of sites).

One of the few studies specifically investigating the association of rare and common traits in rare and common species, respectively, relied on the entire Czech flora (Klimeš and Klimešová 2000). In summary, the latter authors found a similar pattern for root tubers prominent in orchids and species with epigeogenous rhizomes although few other general trends emerged that could be upheld at different spatial scales. Despite that our species pool is only 20% the size of the Czech data set the frequency distribution of individual CGO in our data set (Fig. 1) is very similar to the entire Czech flora (Klimešová and Klimeš 2008: Fig. 2) also with respect to the number of species having more than one CGO (Klimeš and Klimešová 1999) (Appendix 1a).

The relationship between CGOs and certain groups of species is not phylogenetically independent (Klimeš and Klimešová 1999), e.g., root tubers below the surface (GGO 16) are almost exclusively found in orchids (CLO-PLA3 database; Klimešová

and Klimeš 2008). While it would be desirable to correct for this bias, to the best of our knowledge, phylogenetic independent contrasts are not feasible to calculate when the species super tree (species pool) is constantly sub sampled and the subsamples aggregated into site-specific count data (CGO diversity) or frequencies. Phylogenetic constraints, however, are unlikely to change our finding of a strong positive relationship between CGO diversity and species-richness.

### ***Clonal Species Along Natural Gradients***

Our results show a significant increase of clonal species with increasing site water availability (Fig. 4b), which corroborates the findings of van Groenendael et al. (1996). Despite that our site moisture gradient did not include wet or water-logged grasslands, a clear contrast in terms of clonal species frequencies between xeric and mesic sites could be detected. The hard substrate texture that seems to limit clonal species in cold high-altitude environments of the Himalayas (Klimeš 2003) is similarly characteristic of dry sites in the lowlands (Scheffer and Schachtschabel 1998). It is noteworthy that dry and cold sites were hardly ever found in our grasslands. Sites above 1,500 m a.s.l. were for the most part characterized by low evapotranspiration and high precipitation rates (primary data not shown) such that site water balance was rarely negative.

Contrary to our expectation, the frequency of clonal species was not influenced by temperature (Fig. 4a). Neither did the frequency increase at lower temperatures nor was there a peak in the mid-part of the gradient, i.e., the lower alpine belt (Körner 2003). Physiological constraints associated with low temperatures seem not to damage above- or below-ground clonal growth organs in alpine plants (Larcher et al. 2010). Rather, mechanical issues such as hard substrate texture, slope instabilities and local soil movement impede the success of long stolons and rhizomes (Pokarzhevskaya 1995; Klimeš 2003). However, as Körner (2003) emphasized, the choice of vegetation type(s) under study may considerably bias the results of temperature-related clonal frequencies. In our study, we focused exclusively on grasslands that are generally characterized by >75% clonal species (Fig. 1; see also Hartman 1957; Stöcklin 1992; Halassy et al. 2005; Evette et al. 2009). This is in contrast to, for example, pioneer sites and scree communities found in similar (Stöcklin 1992) or higher altitudes (Klimeš 2003) with less clonal species for the above-mentioned reasons. Therefore, a natural temperature-driven disturbance gradient that defines vegetation types to some degree is more likely to influence clonal frequencies than temperature *per se*.

### ***Clonal Traits Along Natural Gradients***

Temperature and especially site moisture exerted a much stronger effect on individual traits than on all traits combined (Fig. 4a,b). Rhizomatous species significantly increased with more favorable site moisture conditions, and epigeogenous species also increased with colder temperature, while the other three CGOs increased in frequency in drought-prone or warmer sites, i.e., rooting horizontal stems, root splitters, and adventitious buds on roots. In cold or dry sites soil development is comparably slow, biomass production is limited and decomposition rates are slow (e.g., Kielland and Chapin 1992; Scheffer and Schachtschabel 1998). In line with Klimeš (1999) who found little vegetative spreading in grasslands of the Bílé

Karpaty Mts., it seems likely that species with epigeogenous rhizomes (vegetative shoots in ultimate proximity to the mother plant) are more common in cold sites because resource investments are small while the chances of survival is high. Nevertheless, arid sites should harbor more species with epigeogenous rhizomes because of their high regrowth potential after drought or herbivory (Milchunas et al. 1988). The discrepancy between Milchunas modeling and our data may be because in our study arid sites had the smallest cover values and potentially less intraspecific competition. These site conditions seem to favor tap-rooted species that are mostly non-clonal (Hartmann 1957; Kutschera and Lichtenegger 1992; Körner 2003).

With respect to the hypogeogenous rhizomes, our results confirm the findings by Halassy et al. (2005), who showed that grasslands with mesic soil moisture conditions harbored higher frequencies of species with laterally spreading CGOs in contrast to xeric sites. Facilitated soil penetration may explain this increase in hypogeogenous rhizomes because moister soils have higher biological activity entailing a softer soil texture and a generally deeper profile (Scheffer and Schachtschabel 1998).

Similarly, the regrowth and regeneration potential in species with adventitious buds on roots may be advantageous in drought-prone and also partly in warmer sites (Fig. 4a,b) as much as species with rooting horizontal stems (stolons) may profit from the open habitats at these sites. For the latter species, successful ramet placing and its persistence in a suitable patch rely on the number and size of favorable patches and their spatio-temporal variability (Oborny and Cain 1997; Piqueras et al. 1999; Kun and Oborny 2003). In this context, aridity and grazing both create open spaces which favor stoloniferous growth.

### ***Clonal Species Along Land-Use Gradients***

The frequency of clonal species was significantly higher in pastures and meadows than in fallows (Fig. 5a). At the same time, individual clonal traits were differently affected by anthropogenic disturbance (Fig. 5b–f). Species with adventitious buds on roots, splitting roots or stolons seemed to have an advantage with soil damage and subsequent microsite creation (trampling), while rhizomatous species tended to be more prominent in meadows lacking below- and close-to-ground disturbance. Interestingly, the CGOs that profited under grazing were identical to those appearing with highest frequencies in drought-prone sites. This corresponds directly to the findings of Milchunas et al. (1988), that aridity and grazing select the same plant attributes. In the context of individual traits, Díaz et al. (2007) noted that all models dealing with plant architecture predicted stoloniferous species to be favored under grazing regimes. Further, according to Díaz et al. (2007) plants with epigeogenous rhizomes (which form a tussock architecture) are not favored in pastures compared to meadows. However, in our data grazing intensity and thus disturbance impact was relatively moderate. Overall, the contrasts between CGOs and land-use types were mostly significant though often not very strong. One aspect that may have blurred strong contrasts relates to the common but coarse land-use classification employed here. Potentially important information was not available, i.e., the duration and intensity of a particular management type. In particular, the temporal aspect of land-use conversion was shown to be important as site contrast increased progressively with time (Fischer and Wipf 2002).

### ***Cover-Weighted Trait Frequencies***

Results based on un-weighted or cover-weighted trait values did not reveal striking differences (Fig. 4a,b, 5a–f, Appendix 2a,b, 3a–f). Despite the potential importance of cover over presence in providing a functional understanding of vegetation (Grime 2006), we did not detect a considerable alteration of the relationship between clonal traits and environmental or land-use factors as Pakeman et al. (2008) did in some of their cases. In our analyses, the identical sets of traits were linked and, as in Pakeman's study, none of the trends were reversed. We acknowledge the importance of cover and might not have found a difference in comparison to un-weighted values because of two potential reasons: *i*) data transformation from categorical Braun-Blanquet cover-abundance to percentage-cover values can increase the variation in cover among sites and thus mask an effect of environmental and land-use gradients; *ii*) we found no significant difference among mean cover values for all CGOs and for individual CGOs across species and vegetation records, which considerably reduces the likelihood of detecting a difference when comparing the two data sets.

### ***Data Limitation***

Our study focused exclusively on clonal plant traits. While we have observed that sets of traits are consistently linked and potentially adaptive to temperature, soil moisture and land use, these traits may also be linked to other traits not considered here. Therefore, clonal traits need not be the primary drivers of the observed patterns.

In addition, the presence and expression of a CGO is not always a fixed characteristic of a plant species. Many studies have shown the plastic response of plants to abiotic factors, e.g., moisture and temperature (Weppler and Stöcklin 2005), nutrients (Piqueras et al. 1999), or biotic factors such as competition (Fischer et al. 2004; Rautiainen et al. 2004) or land-use-related disturbance (Fischer et al. 2008). For our analysis, detailed knowledge about the plastic behavior of CGOs along environmental and land-use gradients was lacking. This last aspect certainly merits detailed investigation especially in terms of adaptability to ongoing climatic perturbations and land-use change.

### **Conclusions**

Overall, our data outlined that consistently linked sets of common clonal traits react differently to natural and land-use gradients as well as differently to the sum of clonal traits. In particular, the presence of rhizomatous *vs* non-rhizomatous species is potentially indicative for site assessments. Also, soil moisture was more decisive than temperature (= altitude) for the presence of clonal species and thus supports the notion that clonality-altitude relationships are strongly biased by vegetation types and mixes thereof. The differences between unweighted and cover-weighted frequencies were small and thus negligible in detecting general trends. Lastly, the strong correlation between species-richness and clonal trait diversity needs to be accounted for when interpreting the functional role of clonal traits.

**Acknowledgement** The authors thank the Swiss Federal Office for the Environment and S. Eggenberg (UNA Bern, CH) for access to and support with the TWW database, O. Wildi (WSL, CH) for provision of bioclimatic parameters and J. Klimešová (Institute of Botany, Třeboň, CZ) for support with clonal trait classification. Further, the authors greatly appreciate the comments by J. Klimešová, D. Prati and two anonymous reviewers on previous versions of the manuscript. Last but not least, the authors kindly acknowledge the financial support of the German Academic Exchange Service (D/07/01321), the Stiftung zur Förderung der Pflanzenkenntnis (Basel, CH) and the logistic facilitation by the Jungfrauabahn AG (Interlaken, CH).

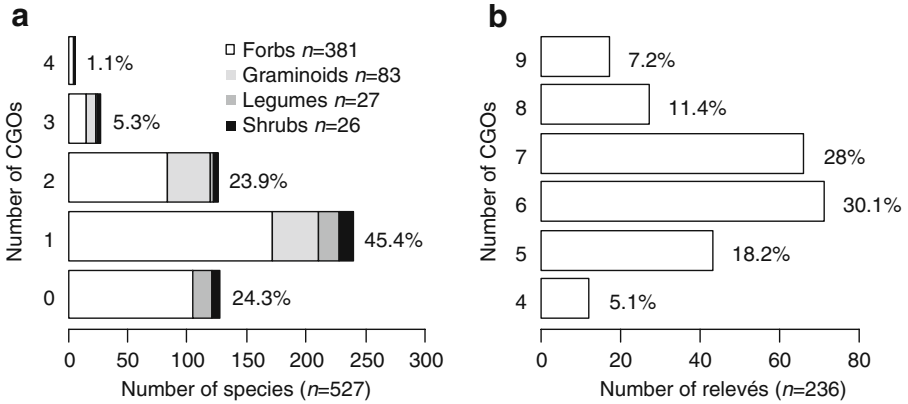
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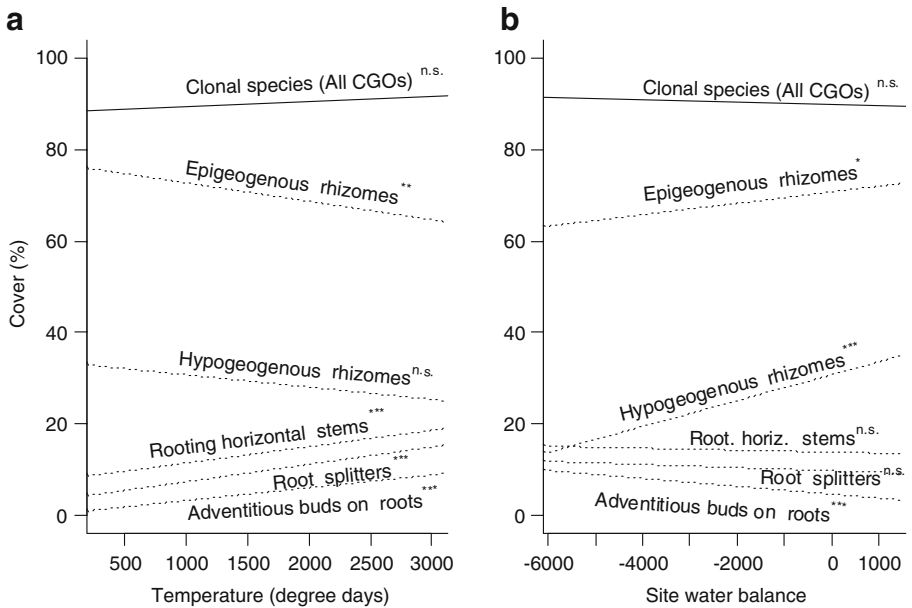
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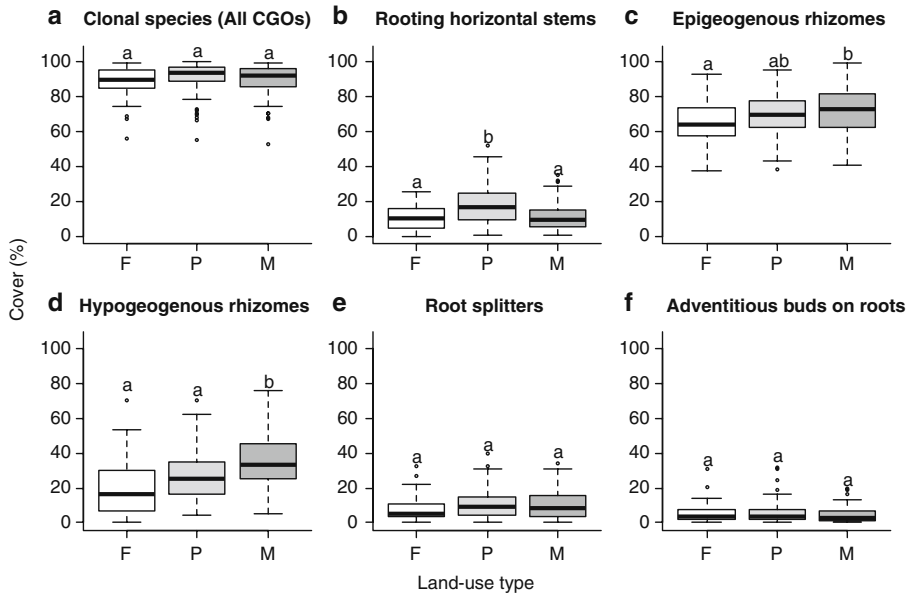
Received: 30 April 2009 / Revised: 21 April 2010 / Accepted: 28 May 2010 /  
 Published online: 8 September 2010



**Appendix 1** Diversity and frequency of Clonal Growth Organs (CGO) in the species pool and 236 grassland plots. **a** Number of CGOs within species split by plant functional groups. **b** Number of CGOs within a single relevés



**Appendix 2** Regression lines of the cover-weighted frequency of clonal plants (all CGOs) as well as the five main Clonal Growth Organs (CGOs) in standard relevés **a** along the temperature gradient and **b** along the site moisture gradient. Data points are omitted for clarity. n.s. – non-significant  $P > 0.05$ ; \* –  $P < 0.05$ ; \*\* –  $P < 0.01$ ; \*\*\* –  $P < 0.001$



**Appendix 3** The cover-weighted frequency of **a** clonal species in relation to land-use types, and **b–f** of individual Clonal Growth Organs (CGOs) in relation to land-use types. Land-use types: F – fallow, M – meadow, P – pasture. Box plots sharing the same letter were not significantly different at  $P=0.05$  based on Tukey HSD test