Microscale patterns of plant species distribution, biomass and leaf tissue quality in calcareous grassland

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Abstract

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This paper contributes to a functional understanding of species richness and species co-existence in highly diverse calcareous grassland on shallow soils. We consider (1) spatial patterns, and (2) functional traits of species within functional groups. The analysis is based on data for 76 species from 48 transects each 80 cm long and 5 cm wide within a 1200 m^2 grassland plot in the foothills of the Jura mountains near Basel. Transects contained 16 contiguous microplots of 5 cm × 5 cm, which permitted tests at different scales. Plant species richness correlated weakly and negatively with biomass at both the 5 cm and 80 cm scale, which is partly explained by the presence of *Bromus erectus,* the dominant grass. Neither species richness or biomass showed any correlation with soil depth. Above-ground plant biomass was slightly higher in the neighbourhood of legumes (where we also found slightly more litter), but neither seedling abundance nor the biomass of *Bromus* appeared to be influenced. Peak season above-ground biomass accounted for 233 gm^{-2} and was composed of graminoids (69%), non-legume forbs (15%), legumes (6%) and mosses (10%). The mean dry mass per tiller (<0.1 g) was slightly higher in forbs than grasses, but there was great overlap. Leaves represented 48% of total above-ground biomass in graminoids, 63% in non-legume forbs and 49% in legumes. Specific leaf area (SLA) showed no significant difference among the three functional groups, and varied around 200 cm^2 g^{-1}. Leaf nitrogen concentration varied around 2% of dry matter in graminoids and non-legume forbs compared to 3% in legumes. We conclude (1) that plant species interactions influence microscale species distribution more than abiotic factors do, and (2) that functional traits of species – except for leaf N-concentration – overlap so widely among the 'functional' groups considered that the predictive value of such grouping attempts appears questionable. The catalogue of species attributes assists in modelling ecosystem consequences of altered species composition.

Key words: Bromus erectus, Trifolium, legumes, functional groups, competition, diversity, dry matter allocation, nitrogen, litter, soil depth

Nomenclature for species follows Binz and Heitz (1990).

Introduction

The prospect of a biodiversity crisis has raised international concern during the last decade. Thus, explaining the causes and ecological values (functions) of biodiversity or species richness, poses a major challenge to biologists (Western 1992). Calcareous grasslands are among the most diverse plant communities in Europe (During and Willems 1984) and are particularly suited for studying patterns, causes and consequences of species diversity.

Although much research has been conducted on grassland diversity, there is still controversy whether there is a causal connection between biomass production and species richness (Abrams 1995). Except for extremely depauperate habitats, there seems to be a trend for species diversity to increase as productivity decreases (e.g. Al-Mufti et al. 1977). No correlation was found by Carson and Pickett (1990) in an old field plant community and even the reverse was reported for artificial assemblages of annual ruderal plants by Naeem et al. (1994). Most of these studies are either comparisons between different vegetation types (e.g. Al-Mufti et al. 1977) or manipulation experiments (e.g. Tilman 1993) and their different results may reflect different soil nutrient levels. The present study considers a natural plant species assemblage on extensively managed, unfertilized calcareous pasture land and the variations of species richness on very small scales (centimeter to meter). This, because processes responsible for the increase or decline of species diversity often operate within those scales (Willems et al. 1993).

The "principle" of Gause explains coexistence by niche differentiation, i.e. two or more competing species cannot coexist in the same niche. This principle has been called into question for explaining species diversity (Armstrong and McGenee 1976a, 1976b; but see Palmer 1994, who defends this principle in a broader context) and a number of studies have been conducted during the last decades (e.g. Grime 1974, Grubb 1977, Mahdi et al. 1989, Huston 1979, van der Maarel and Sykes 1993) to test this hypothesis. There is consensus that unraveling patterns of diversity is a necessary first step towards the understanding of underlying processes. One way of elaborating such patterns is to study correlations between the presence of species or functional groups and environmental parameters, including the biotic micro-environment. In the present paper we tried to do this in a quantitative way. Since functional attributes of species vary, we substantiate our analyses with a suit of plant traits such as tillering, shoot allometry, specific leaf area and leaf nitrogen content and discuss these with respect to the usefulness of plant functional groups.

The study aims at answering the following questions: (1) Is there a relationship between biomass production and biodiversity on very small scales within a community? (2) Are there neighbourhood linkages (between species or functional groups), and (3) is substrate quality (here measured as the depth of the generally rather shallow soil layer) related to biomass production on these small scales? Our objective was further to establish a baseline data set of important plant traits of graminoids, legumes and non-legume forbs of our site and analyse the data for commonness and differences among these functional groups. The data base is designed to assist in estimating ecosystem consequences of changes in biodiversity (Körner 1995a, Leadley and Körner 1996).

Methods

Study site

The study site is located near the village of Nenzlingen on a southwest-facing slope in the northwestern part of Sitzerland (47°27'30"N, 7°34'E, 520 m a.s.l). Mean annual temperature is around

8.5 to 9.0 °C (July mean about 17 °C and annual precipitation is roughly 900 mm (Ogermann et al. 1994). Snow cover usually occurs for less than a month. Soils are of the rendzina type. The A-horizon varies in depth from 2 to 27 cm (mostly around 13 cm) and may become very dry during summer, even during an otherwise wet season (cf. Gigon 1968). The total moisture stored in the top soil may vary spatially between 50 and 115 mm (Leser and Schaub 1995). Due to a strongly loamy texture, shrinkage cracks occur regularly after it has not rained significantly for one to two weeks. The cracks mechanically fragment the top soil. The underlying material is calcareous debris. For many centuries these grasslands, once covered by beech forests, have been grazed by cattle, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Zoller 1947; Schläpfer et al., this issue).

Field and laboratory methods

A 40 m × 30 m area of relatively homogenous grassland (without rocks or gulleys) was selected and divided into 48 grid cells of 5 m × 5 m. Six horizontal rows, each consisting of eight cells, were treated as a downhill sequence of 'blocks'. Within each cell a transect of 5 cm × 80 cm was positioned randomly, half of these transects oriented downslope, the other half parallel to the slope. Each transect was subdivided into 16 microplots of 5 cm × 5 cm. The length of such transects was designed to match the scale of patterns to be tested (Greig-Smith 1961) and measured roughly twice the diameter of the expected pattern. The most obvious pattern on this site is caused by cattle trampling, creating 40 cm wide trails (following contour lines), therefore we chose a length of 80 cm for the transects. In order to detect species-species linkages, the size of the microplots was set at the mean plant size. For each of these 768 microplots soil depth was measured twice by using an iron rod. Pearson's correlation coefficient was used to measure the relative degree of covariation in pairwise species abundance, wherein species biomass on the two scales of 5 cm × 5 cm and 5 cm × 80 cm was taken as a measure of abundance (Ludwig and Reynolds 1988).

At the end of May (1993), the time of seasonal maximum standing biomass, the grass-sward of each microplot was excavated to a depth of 5 cm and taken to the laboratory. There, vegetation was clipped at ground level and separated by species. Tillers or individuals of all species in each of the 768 quadrats were counted. A species was considered 'present' when at least one of its tillers emerged from the ground within the microplot boundaries. For each species, leaves and the remaining live biomass (stem tissue, flowers) were separated, dried at 80 °C and weighed. For the 5 cm × 80 cm scale the values of the 16 microplots of each transect were summed up. For one randomly chosen microplot within each transect (48 in total), litter was analysed (separated into grasses and forbs). For the same microplot seedlings were counted (again separated by grasses and forbs), dried and weighed. Specific leaf area (SLA) was analysed for 5 mature leaves, each collected randomly but from different microtransects for the 36 most common species. Nitrogen concentration (CHN analyzer) was assessed for 27 species from pooled samples taken from all 8×16 microplots within one block (n=6); for each species leaf and non-leaf tissue were analyzed separately. For describing the variation, standard error (s.e.) is used.

Results

Species distribution

A total of 76 phanerogam species (plus a few unidentified, vegetative graminoid and forb species) and several species of mosses and lichens were recorded. On both, the 5 cm × 5 cm and the 5 cm × 80 cm scales, frequency distributions of species richness were approximately normal (insert in Fig. 1). Fig. 1 shows all the species and their importance (frequency) within the 48 transects. High frequency also suggests a homogenous distribution. Grass species and mosses show high frequency, while the distribution of many forbs is relatively inhomogenous, despite a lack of obvious soil heterogeneity.

Pairwise correlations of species biomass for the 30 most common species yielded only 22 significant correlations out of hundreds of possible combinations, which may have occurred
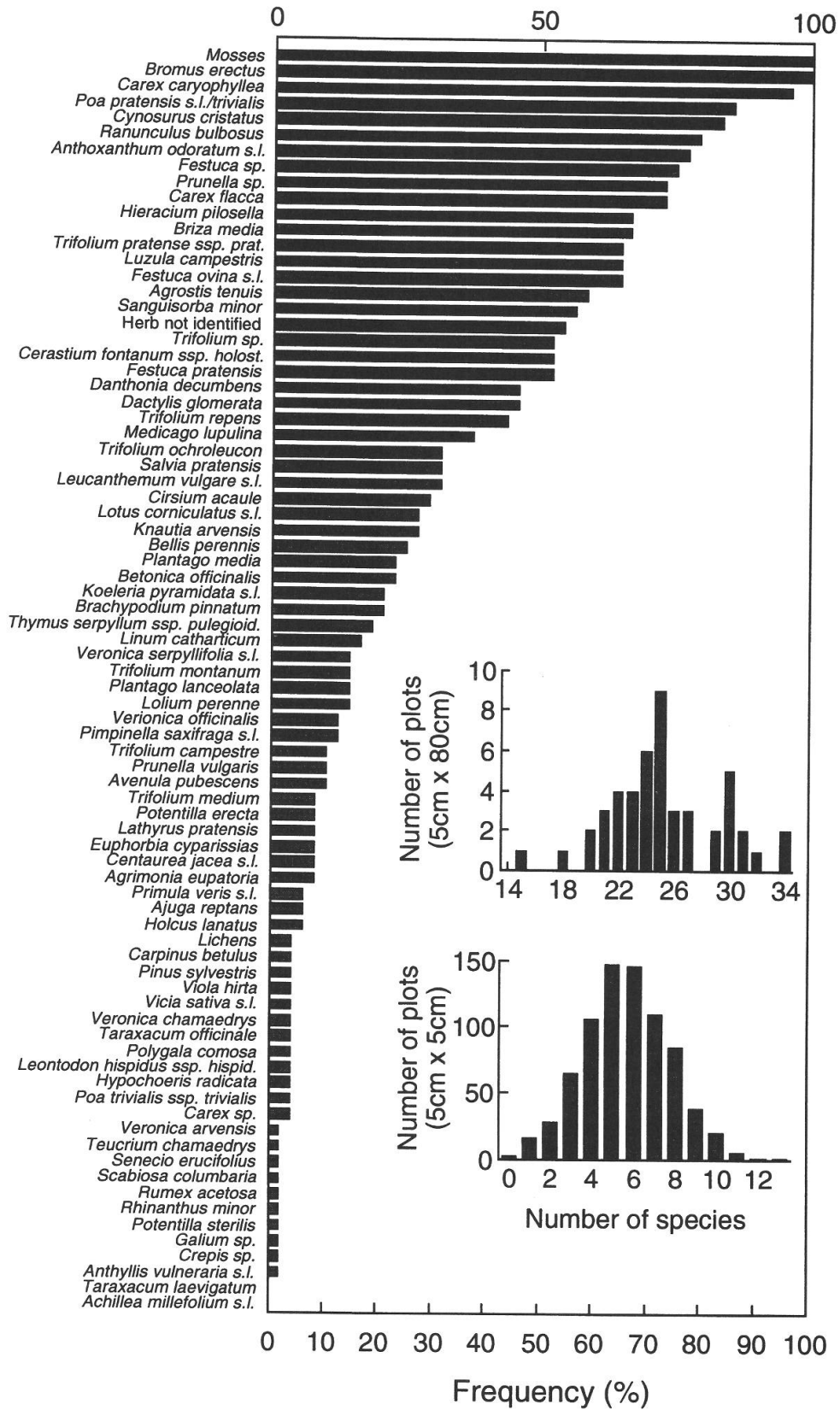
Fig. 1. Frequency of species occurrence, i.e. percentage of 5 cm × 80 cm plots in which a species was found (all 48 plots = 100%). Insert: Frequency distribution of the number of species per plot at the two scales of 5 cm × 80 cm (n = 48) and 5 cm × 5 cm (n = 768).

purely by chance (data not shown). In most cases these correlations were only significant at the 80 cm scale. Species often associated with low canopy density such as *Prunella vulgaris, Anthoxantum odoratum* and *Festuca sp.,* were significantly correlated with moss biomas (explaining 18–26% of the variance). Five species (*Cynosurus cristatus, Dactylis glomerata, Knautia arvensis, Bellis perennis, Salvia pratensis*) correlated positively with the presence of legumes within a common plot (*Trifolium repens, Trifolium ochroleucon, Trifolium pratense, Lotus corniculatus;* explaining 14–37% of the variance). Interestingly, these five non-legume species also showed a leaf nitrogen concentration well above the mean for all non-legume forbs (Tab. 4).

Biomass distribution

At peak season above-ground biomass reached 233±33 g m^{-2} and phytomass was 400 g m^{-2} (Tab. 1). Litter and necromass accounted for 42% of above-ground phytomass. There was no significant difference in biomass between horizontal and vertical transects. Grasses were dominant (almost 70% of the above-ground biomass), *Bromus erectus,* representing 43% of the above-ground biomass, was by far the most dominant. Cryptogams accounted for 10% (lichens alone only 1%). With 6% of the biomass, legumes represented almost one third of the forbs (Tab. 2).

Only a few species accounted for most of the above ground biomass (Tab. 3). At the 5 cm × 80 cm scale the spatial distribution of biomass is near to normal with maxima about two times the mean (Fig. 2). In contrast, microplots show a skewed distribution, with rare

Tab. 1. Plant dry matter pools at peak season (n = 48 plots).

	g m^{-2}±s.e.	%
Above-ground live biomass	232.5±22.6	58.3
Necromass (attached dead) and litter (litter only 76±10)	166.6±19.2	41.7
Total above-ground plant mass including all dead components	399.1±22.6	100.0

Tab. 2. The contribution of plant functional groups to biomass, tiller number and total leaf area per unit land area (LAI) for 48 plots.

plant group	biomass g m^{-2}±s.e.	%	number of tillers per m^2±s.e.	%	LAI m^2 m^{-2}
graminoids	161.0[a]±10.3	69.2	4751±181	81.0	2.32
non-legume dicots	35.3± 3.0	15.2	798± 68	13.6	0.62
legumes	13.8± 2.1	5.9	317± 34	5.4	0.24
cryptogams (largely mosses)	22.4± 3.4	9.7	–	–	(1.0)
total	232.5±22.6	100.0	5866	100.0	3.18[b]

[a] Total attached dead dry mass on graminoids only represents additional 83.2±16.2 g m^{-2}.
[b] LAI pooled for all plots, excluding mosses and less abundant species for which SLA was unknown. Using a common SLA for all the missing phanerogams would add 0.1 LAI. The LAI for mosses would be 1 with SLA = 500 cm^2 g^{-1}, bringing the total to >4.0.
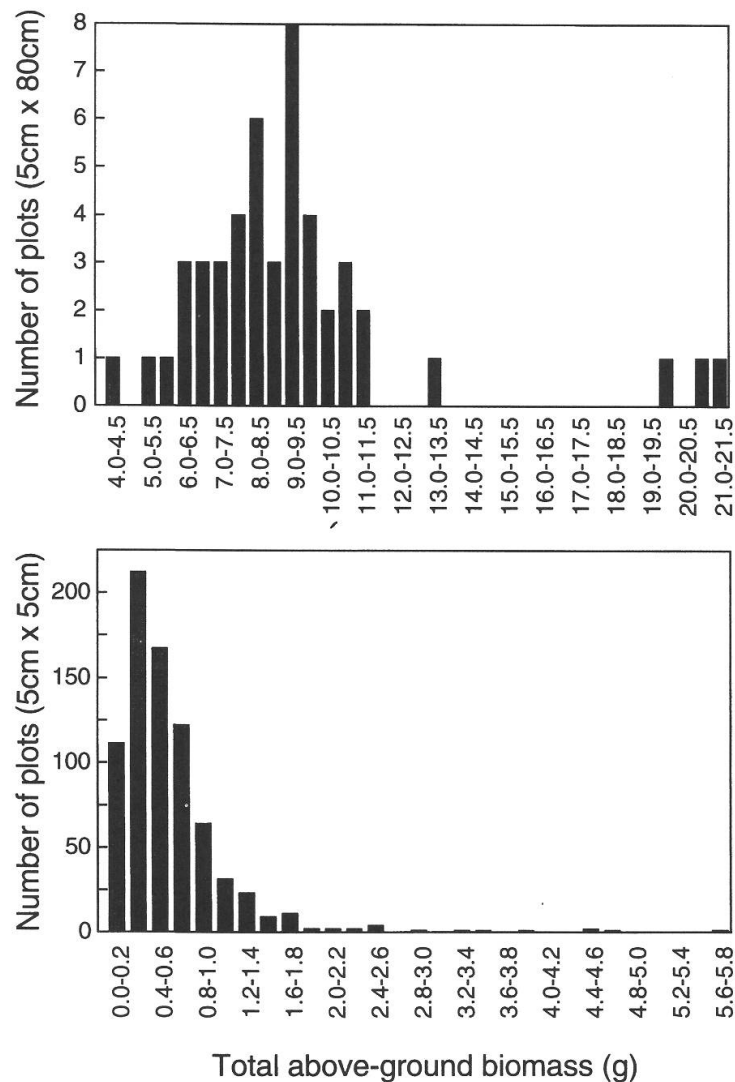
Fig. 2. Frequency distribution of the total above-ground biomass per plot for the two scales of 5 cm × 80 cm (n=48) and 5 cm × 5 cm (n=768).

high biomass extremes exceeding the mean by at least 10-fold, which reflects the greater heterogeneity at this scale. On both scales a very weak, yet statistically significant negative correlation was obtained between biomass and species number (Tab. 5). The fact that only 4% (5 cm scale) or 11% (80 cm scale) of the variation in species number explained the variation in above-ground biomass (or vice versa) reflects a situation similar to the one describe by Moore and Keddy (1989). They found no correlation between the two parameters within a vegetation type. In our case the negative correlation between biomass and species diversity was mainly driven by the presence or absence of *Bromus erectus*. At both scales were biodiversity and above-ground biomass of *Bromus erectus* negatively correlated (Tab. 5). On the 5 cm×5 cm scale this is not surprising, since this area can be occupied completely by one *Bromus* tussock, thus excluding any other species. The 5 cm×80 cm area is definitely much bigger than the mean tussock size but the negative correlation between the abundance of *Bromus erectus* and species diversity was even stronger.

Tab. 3. Above-ground biomass, number of tillers or shoots and leaf traits by species (n = 48 transects of 5 cm × 80 cm). For clarity, numbers were rounded to the nearest digit; if no s.e. is given, the species was found only once. A s.e. of zero indicates that it was smaller than 0.5 of the last digit.

Species	biomass (g m^{-2}±s.e.)	%	number of tillers, shoots per m^2±s.e.	weight per tiller (mg±s.e.)	specific leaf area (cm^2 g^{-1})	leaf area per ground area (m^2 m^{-2})	leaf/ shoot mass ratio
Graminoids							
Bromus erectus	100.58±0.78	43.26	1788±76	55±1	130	1.304±0.127	0.46
Carex caryophyllea	12.62±1.64	5.43	479±55	26±0	205	0.259±0.034	0.68
Festuca ovina	6.07±1.46	2.61	166±41	49±3	80	0.048±0.012	0.51
Festuca pratensis	4.79±1.12	2.06	492±115	15±1	220	0.105±0.025	0.42
Grasses unidentified *	4.47±0.41	1.92	360±29	14±0	–	–	
Cynosurus cristatus	4.25±0.62	1.83	169±26	34±1	223	0.095±0.014	0.34
Briza media	4.09±0.78	1.76	150±30	29±1	210	0.086±0.016	0.53
Dactylis glomerata	3.23±0.84	1.39	65±16	58±2	315	0.102±0.027	0.43
Carex flacca	3.15±0.54	1.35	65±11	53±1	127	0.040±0.007	0.68
Danthonia decumbens	3.11±0.98	1.34	124±36	30±1	183	0.057±0.018	0.45
Poa pratensis	2.86±0.41	1.23	239±33	14±0	252	0.072±0.010	0.55
Festuca sp.	2.20±0.43	0.95	185±35	13±0	–	–	0.51
Anthoxanthum odoratum	1.97±0.41	0.85	120±21	16±0	321	0.063±0.013	0.42
Agrostis tenuis	1.80±0.51	0.77	154±40	12±0	271	0.049±0.014	0.43
Luzula campestris	1.38±0.38	0.59	95±18	13±0	211	0.029±0.008	0.55
Brachypodium pinnatum	1.31±0.78	0.56	48±20	32±2	–	–	0.50
Avenula pubescens	1.02±0.47	0.44	9±4	137±16	–	–	0.18
Koeleria pyramidata	0.63±0.31	0.27	27±12	22±2	142	0.009±0.004	0.56
Lolium perenne	0.57±0.28	0.24	12±6	66±9	–	–	0.38
Holcus lanatus *	0.47±0.33	0.20	3±2	125±31	–	–	0.16
Carex sp. *	0.23±0.05	0.10	2±1	4	–	–	
Poa trivialis ssp. trivialis *	0.14±0.12	0.06	2±1	84±18	–	–	0.02
Non-legume forbs							
Cirsium acaule	6.08±1.68	2.62	12±3	435±22	156	0.095±0.026	1.00
Sanguisorba minor	4.53±1.10	1.95	36±8	120±4	190	0.086±0.021	0.49
Ranunculus bulbosus	2.97±0.85	1.28	113±21	25±1	204	0.060±0.017	0.31
Prunella grandiflora/ vulgaris	2.66±0.48	1.14	139±23	18±0	221	0.053±0.011	0.58
Salvia pratensis	2.48±0.98	1.07	12±3	200±23	256	0.064±0.025	0.51
Hieracium pilosella	2.41±0.61	1.03	73±15	28±1	168	0.040±0.010	0.85
Knautia arvensis	2.07±0.80	0.89	14±5	138±13	270	0.056±0.022	0.67
Plantago media	1.70±0.47	0.73	8±1	205±10	186	0.032±0.009	1.00
Cerastium fontanum ssp. holosteoides	1.68±0.51	0.72	118±34	12±1	167	0.028±0.009	0.35
Betonica officinalis	1.46±0.55	0.63	16±6	122±10	194	0.028±0.011	0.72
Leucanthemum vulgare	1.39±0.57	0.60	29±9	55±6	212	0.029±0.012	0.39
Veronica officinalis	0.67±0.34	0.29	20±10	31±2	209	0.014±0.007	0.68
Agrimonia eupatoria	0.62±0.34	0.27	4±2	146±13	128	0.008±0.004	0.65
Plantago lanceolata	0.52±0.17	0.23	5±2	87±13	157	0.008±0.003	1.00
Primula veris	0.48±0.27	0.21	3±2	119±14	–	–	

Tab. 3. (continued)

Species	biomass (g m^{-2}±s.e.)	%	number of tillers, shoots per m^2±s.e.	weight per tiller (mg±s.e.)	specific leaf area (cm^2 g^{-1})	leaf area per ground area (m^2 m^{-2})	leaf/ shoot mass ratio
Senecio erucifolius	0.16±0.16	0.07	1±1	304	–	–	0.59
Pimpinella saxifraga	0.17±0.11	0.07	6±3	20±3	212	0.004±0.002	0.58
Hypochoeris radicata	0.16±0.11	0.07	2±1	123±56	–	–	0.87
Teucrium chamaedrys	0.15±0.15	0.06	2±2	70	–	–	0.44
Potentilla erecta	0.12±0.07	0.05	5±3	22±6	–	–	0.66
Bellis perennis	0.12±0.05	0.05	11±3	10±1	187	0.002±0.001	0.63
Linum catharticum	0.08±0.04	0.04	8±3	11±1	–	–	0.28
Rumex acetosa *	0.07±0.07	0.03	2±2	45	–	–	0.17
Polygala comosa *	0.07±0.06	0.03	2±2	26±10	–	–	0.46
Crepis sp. *	0.07±0.07	0.03	1±1	136	–	–	–
Veronica chamaedrys *	0.03±0.02	0.01	3±3	15±6	–	–	0.66
Taraxacum officinale *	0.02±0.01	0.01	1±1	14±4	–	–	0.88
Scabiosa columbaria *	0.01±0.01	0.01	1±1	28	–	–	0.79
Leontodon hispidus ssp. hispidus *	0.01±0.01	0.01	1±1	13±8	–	–	0.78
Carpinus betulus *	0.03±0.02	0.01	<1	26±2	–	–	–
Achillea millefolium *	0.02±0.02	0.01	<1	<1	–	–	–
Viola hirta *	<0.01±0.00	<0.01	<1	3±0	–	–	0.62
Veronica arvensis *	<0.01±0.00	<0.01	1±1	8	–	–	0.47
Taraxacum laevigatum *	<0.01±0.00	<0.01	<1	<1	–	–	–
Potentilla sterilis *	<0.01±0.00	<0.01	1±1	9	–	–	0.68
Galium sp. *	<0.01±0.00	<0.01	1±1	1	–	–	–
Legumes							
Trifolium pratense ssp. pratense	5.19±1.07	2.23	127±26	41±0	279	0.145±0.030	0.40
Trifolium repens	2.18±0.60	0.94	48±10	46±2	234	0.051±0.014	0.33
Trifolium medium	1.97±1.30	0.85	12±6	147±20	–	–	0.52
Trifolium montanum	1.73±0.78	0.74	11±5	148±10	187	0.032±0.015	0.41
Trifolium ochroleucon	1.01±0.62	0.43	28±11	18±19	–	–	0.53
Medicago lupulina	0.53±0.19	0.23	33±9	17±1	289	0.015±0.006	0.47
Trifolium campestre	0.32±0.19	0.14	8±4	39±6	–	–	0.38
Anthyllis vulneraria	0.32±0.32	0.14	9±9	36	–	–	0.67
Lotus corniculatus	0.30±0.10	0.13	17±5	19±1	–	–	0.64
Trifolium sp.	0.15±0.03	0.06	20±4	7±0	–	–	0.53
Vicia sativa *	0.06±0.05	0.03	0	60±15	–	–	0.17
Lathyrus pratensis *	0.08±0.06	0.03	6±4	13±2	–	–	0.65
Cryptogams							
Mosses	22.22±3.42	9.56	–	–	–	–	–
Lichens	0.15±0.11	0.06	–	–	–	–	–
Summary							
mean for graminoids	–	–	–	42±6	206±18.8	–	0.48 (±0.03)
mean for forbs without legumes	–	–	–	100±21	192±8.8	–	0.63 (±0.04)
mean for legumes	–	–	–	52±16	247±13.4	–	0.49 (±0.03)
total	232.5±12.0	100	5865±197	–	–	3.184	–

* Species excluded from means (graminoids <0.5 gm^{-2}, forbs <0.08 gm^{-2}; largely small, premature individuals).

Tab. 4. Nitrogen concentrations in live above-ground plant tissues of the 27 most important species. "Remaining biomass" represents the pooled mean for all non-leaf above-ground live tissue (stems, petioles, flowers).

Species	N in leaves (% d.m.)	N in remaining biomass (% d.m.)	total N per species[a] (g m^{-2})
Graminoids			
Agrostis tenuis	2.38±0.34	1.57	0.03
Brachypodium pinnatum	2.29±0.25	1.23	0.02
Carex flacca	2.09±0.09	1.52	0.06
Cynosurus cristatus	2.04±0.18	0.95	0.06
Dactylis glomerata	2.03±0.23	0.86	0.04
Anthoxanthum odoratum	1.99±0.39	1.03	0.03
Dantonia decumbens	1.97±0.22	1.30	0.05
Bromus erectus	1.93±0.10	1.02	1.44
Carex caryophyllea	1.89±0.11	1.61	0.23
Briza media	1.77±0.17	1.12	0.06
Festuca pratensis	1.75±0.21	0.64	0.07
Poa trivialis ssp. *trivialis*	1.72±1.34	1.78	0.00
Festuca ovina	1.62±0.32	1.48	0.07
mean	**1.96±0.30**	**1.24**	**0.17**
other grass species[b]	–	–	0.24
total	–	–	**2.40**
Non-legume forbs			
Sanguisorba minor	2.11±0.19	1.00	0.07
Salvia pratensis	2.03±0.29	1.04	0.04
Knautia arvensis	2.02±0.21	1.00	0.03
Cirsium acaule	1.99±0.34	0.93	0.12
Ranunculus bulbosus	1.97±0.22	1.10	0.04
Prunella sp.	1.71±0.23	0.88	0.03
Hieracium pilosella	1.56±0.16	1.04	0.04
Cerastium fontanum ssp. *holosteoides*	1.43±0.21	0.68	0.02
Plantago media	1.42±0.14	0.79	0.02
mean	**1.80±0.22**	**0.94**	**0.05**
other non-legume forbs[b]	–	–	0.11
total	–	–	**0.52**
Legumes			
Trifolium repens	3.42±0.68	2.27	0.06
Trifolium medium	3.27±0.32	1.82	0.05
Trifolium pratense ssp. *pratense*	3.15±0.29	1.97	0.13
Trifolium montanum	2.80±0.42	1.60	0.04
mean	**3.16±0.41**	**1.92**	**0.07**
other legumes[b]	–	–	0.06
total	–	–	**0.34**
mosses	1.55±0.32	–	0.34
total above-ground biomass N-pool	–	–	3.60

[a] Total N per m^2 of ground area has been calculated using data from Tab. 4.
[b] Calculated from mean nitrogen concentration for the species that were analyzed.

Tab. 5. Correlations between various plant and community traits at the 5 cm×5 cm and 5 cm×80 cm scales (r^2=correlation coefficient).

Type of the corelation			r^2 5 cm	r^2 80 cm
biodiversity	–	total above-ground biomass	0.04*	0.11*
biodiversity	–	above-ground biomass of *Bromus erectus*	0.14*	0.41*
biodiversity	–	soil depth	0.01	0.00
soil depth	–	above-ground biomass	0.00	0.02
litter mass	–	seeding number	0.03	–
litter mass	–	biodiversity	0.00	–
litter mass	–	legume mass	0.45*	–
legume mass	–	total above-ground biomass	0.04*	0.14*
legume mass	–	above-ground biomass of *Bromus erectus*	0.00	0.03

* Statistically significant correlation ($p<0.05$).

Soil depth for all 768 microplots ranged from 2 to 27 cm (mean 13.6±0.4 cm) and did not correlate with species richness or biomass at either scale (Tab. 5), which is consistent with findings of Grime et al. (1987).

No correlation between litter mass and species richness or number of seedlings was observed (Tab. 5). Instead, a significant positive correlation between the amount of litter and the amount of legume biomass occurred at the 5 cm × 5 cm scale and explained 45% of the variation. This seems to be associated with the fact that total biomass production correlated significantly with the neighbourhood of legumes at both scales (explaining 4–14% of the variation at $p<0.05$). Remarkably, *Bromus erectus* does not seem to profit (in terms of biomass) from neighbouring legumes.

Functional plant traits

Individual plants in this grassland community consisted of modules (shoots or tillers) of about 42 mg (graminoids) to 100 mg (forbs) each. On average almost 6000 of these modules were found per square meter (Tab. 3). About half of the individual shoot mass consisted of green leaves, the quality of which varied across functional groups with almost complete overlap. SLA ranged from 80–321 cm^2 g^{-1} in graminoids, from 128–270 cm^2 g^{-1} in non-legume forbs and from 187–289 cm^2 g^{-1} in legumes. *Bromus erectus* and the dominant forb (*Cirsium acaule*) had SLAs which were significantly below functional group specific means, a pattern not seen among legumes. Mean leaf nitrogen concentrations for the 27 most abundant species was 2% in graminoids and non-legume forbs and 3% in legumes (Tab. 4). Non-leaf tissue averaged around 1% in non-legumes compared to almost 2% in legumes. The values for dominant graminoids and non-legume forbs fall midway of the range for the respective functional group.

Seedling abundance

Seedlings were quite rate in this grassland (Tab. 6). Only 33 graminoid seedlings and 133 seedlings of forbs were found per m^2. The number of tillers exceeded the number of seedlings by a factor of 144 in graminoids and by 8 in forbs, hence species spread occurs largely vegetatively and forbs produced more seedlings than graminoids.

Tab. 6. Seedling and tiller (shoot) density (n=48 plots).

Seedling type	number of seedlings per m^2±s.e.	mean number of tillers per m^2±s.e.	n tillers/ n seedlings
graminoids	33±16	4751±181	144
forbs	133±42	1114± 76	8
total	167±43	5865±197	35

Discussion

With a total of more than 76 species within the 48 transects (spread over an area of 1200 m^2) this grassland is extraordinarily species-rich and appears to be very well suited for biodiversity research. With respect to biomass and nitrogen our data indicate great similarity to the grassland north of Zürich studied by Keel (1995) who reported 223 g m^{-2} for a late May cut, containing similar amounts of N. Higher above-ground biomass (330 g m^{-2}) was reported for a site close to ours by Stöcklin and Gisi (1989). This may reflect the season's specific weather situation, the present harvest being conducted at the end of the hot and dry May. However, the 166 g m^{-2} of litter and necromass found, compare well with the 150 g m^{-2} of Stöcklin and Gisi (1989).

We found a weak, but significant negative correlation between the number of species per unit area and biomass, even at the 80 cm scale, which substantially exceeds the size of *Bromus* tussocks. At larger scales of whole communities literature reports are not unanimous with respect to such correlations (see introduction). While Al-Mufti et al. (1977) found such correlations by comparing different vegetation types, other studies did not (Moore and Keddy 1989, Willems et al. 1993).

Many authors have emphasized that small scale processes driving biodiversity are important for vegetation composition and might differ from larger scale processes (e.g. Turkington and Harper 1979, Gigon and Ryser 1986, Carter and O'Connor 1991, Herben et al. 1993, van der Maarel and Sykes 1993). Processes leading to high species richness may be abiotic or biotic. We tested soil depth as a possible abiotic driver on the assumption that depth is an indicator of both moisture supply and nutrient availability at this site. Within our 30 m × 40 m area we found no such effect, which supports the views of Turkington and Harper (1979) who believe that, on large scales, environmental factors determine plant occurrence and diversity, but at small scales direct species-species interactions dominate. This has serious implications for vegetation responses to environmental changes such as atmospheric CO_2-enrichment, currently simulated at this site. Since species are most unlikely to respond identically, species-species interactions and thus, community structure, will be affected in a hardly predictable manner (Körner 1995 a, b).

Litter accumulation has often been suggested to be of great significance for growth and recruitment of plants in dense communities. Tilman (1993) reports that a high amount of litter leads to lower species richness. Similarly, Kienzle (1979) states that germination and establishment of tree seedlings is reduced by a thick layer of litter. In our study, we found no correlation between number of seedlings and amount of litter, suggesting that the density of vegetation, including dead material, is not necessarily unfavourable for seedling establishment in this grassland. This is also in line with the observation by Ryser (1993), who found that the establishment of seedlings is independent of gaps in such calcareous grasslands. Keel

(1985) found both, negative and positive effects of litter on seedling establishment, depending on the amount of litter. Given the periodic drought at this site, litter might have a protective function, improving the seed bed climate, provided enough light reaches the soil surface.

The positive (though weak), correlation of litter mass with biomass of legumes was a surprise. Perhaps it reflects the stimulative effects of legumes on the growth of non-legume neighbours (Turkington and Harper 1979, for additional references see Gigon and Ryser 1986). Stable nitrogen isotope ratios permit to test this hypothesis. [15]N is often more abundant in legumes than non-legumes, because rhizobia do not discriminate against it. We found a slight ^{15}N enrichment (less negative δ15N) in grasses near legumes, suggesting a small N-transfer from legumes to grasses. δ15N for legumes (*Trifolium* spp.) was -1.4 ± 0.3‰, *Bromus erectus* without legume neighbours had -4.1 ± 0.5‰ and *B. erectus* with legumes as neighbours had -3.3 ± 1.1‰ (n = 5; Ch. Körner and R. Siegwolf, unpublished data). However, in the longer term one would expect negative feedbacks on legumes (e. g. mutual shading) which could be a source for patch dynamics.

As mentioned above, the species-species correlations require cautious interpretation, since they may also occur by chance and interactions may involve more than two species (Gigon and Ryser 1986). However, some trends seem to be worth noting. For example, mosses are involved in three of the observed positive correlations. Phanerogam-moss interactions, a well known phenomenon in garden lawns, were also reported to occur in more natural grasslands by van Tooren (1989). He emphasized the negative influence of mosses on seed germination. A dense phanerogam canopy may either suppress mosses (lack of light) or favour mosses (humid microclimate), the first seems to be the case here. Interactions with species like *Cirsium acaule* may reflect the advantage of neighbours which are avoided by cattle (M. Schläpfer, personal communication). Much more intricate interactions may be possible if mycorrhizae are incorporated into the analysis. As part of this multidisciplinary project very specific plant-fungus relationships were discovered (Sanders 1996). The fact that almost all of the significant correlations between species biomass were found for the 5 cm × 80 cm plots and not for the smaller microplots may indicate that direct soil nutrient effects, which usually act on smallest scales, are unlikely to play a major role in these interactions (cf. Leser and Schaub 1995).

The database of functional plant attributes, such as species specific leaf carbon and nitrogen investments, can be used for modelling ecosystem consequences of changing species diversity. For example, the prediction that a doubling of legume biomass would increase the total above-ground biomass nitrogen pool by only 2.5% (while assuming a constant total biomass per unit land area and no further interactions, in a first approximation) could be tested. This multi-species data set also allows us to characterise plant functional groups using species frequency distributions – a more solid basis than simply using means. Species substitution scenarios would suggest that rather massive replacements would be required to, for instance, significantly alter herbage protein content. The observed stimulation of *Carex flacca* to CO_2-enrichment (Leadley and Körner 1996), a species with relatively high nitrogen content, would tend to increase the canopy nitrogen pool and could, thus, mitigate the overall decline in leaf N concentration observed under elevated CO_2 (Körner 1995a).

We conclude that – at the small scales considered here – interspecific interactions among plant species were more important for species distribution than abiotic factors. Among the factors controlling plant species interactions in this grassland, the formation of persistent tussocks (both, shelter and subpression of other species) and symbiotic nitrogen fixation appear to be of particular importance. The data illustrate wide and largely overlapping spectra of functional traits of species within the functional groups tested here and, except for tissue leaf N concentration in legumes, these traits do not suggest that such plant functional groups are adequate substitutes of species for modelling.

Zusammenfassung

Christine Huovinen-Hufschmid und Christian Körner 1997. Kleinräumige Muster der Artenverbreitung, der Biomasse und Spektren der Gewebequalität in einem Kalkmagerrasen.

Diese Arbeit soll zu einem funktionalen Verständnis des Artenreichtums und des Zusammenlebens von Pflanzenarten in einem Kalkmagerrasen beitragen. Wir behandeln (1) räumliche Muster und (2) funktionelle Merkmale innerhalb und zwischen funktionellen Gruppen von Arten. Die Analyse beruht auf Daten für 76 Arten aus 48 Transekten von jeweils $5 \times 80\,cm$ die über eine Fläche von $1200\,m^2$ verteilt waren. Jeder dieser Transekte wurde in 16 zusammenhängende Probeflächen von $5 \times 5\,cm$ aufgeteilt, was eine Auswertung auf unterschiedlichen Skalen ermöglichte. Der ausgewählte Rasen befindet sich auf den Jurahängen bei Basel (Nenzlingen). Sowohl auf der 5 cm wie auf der 80 cm Skala korrelierte die Anzahl an Arten schwach negativ mit der Biomasse pro Grundfläche, was mit der Anwesenheit von *Bromus erectus*, dem dominanten Gras, erklärt wird. Weder die Artenvielfalt noch die Biomasse zeigten irgend eine Korrelation mit der Tiefgründigkeit des relativ geringmächtigen Bodens. Die oberirdische Biomasse, ebenso wie die Menge an Streu, waren in der unmittelbaren Nachbarschaft von Leguminosen etwas erhöht, aber weder die Zahl von Sämlingen noch die Biomasse von *Bromus erectus* schien beeinflußt zu werden. Zum Höhepunkt der Wachstumsperiode erreichte die Gesamtbiomasse $233\,g\,m^{-2}$ und verteilte sich zu 69% auf Gräser und Seggen, zu 15% auf Nicht-Leguminosenkräuter, zu 6% auf Leguminosen und zu 10% auf Moose. Ein einzelner Trieb wog im Durchschnitt für alle Arten weniger als 0,1 g, wobei krautige Pflanzen schwerere Einzeltriebe bildeten als Gräser, aber die Bandbreite ist enorm. Bei Gräsern entfallen 48%, bei Nicht-Leguminosenkräutern 63% und bei Leguminosen 49% der Biomasse auf Blätter, deren spezifische Blattfläche (SLA) um $200\,cm^2\,g^{-1}$ liegt und keinen signifikanten Unterschied zwischen den funktionellen Gruppen erkennen läßt. Nur die mittlere Blattstickstoffgehalt mit 3% für Leguminosen und 2% für die übrigen Arten unterscheidet sich. Wir schließen aus diesen Beobachtungen, daß (1) Art-Art-Interaktionen die Feinverteilung der Arten stärker beeinflussen als abiotische Faktoren, und (2) die untersuchten funktionellen Merkmale der Arten – ausgenommen die Blattstickstoffkonzentration – zwischen den funktionellen Gruppen so weit überlappen, daß solche Gruppierungsversuche für prognostische Modelle einen sehr fragwürdigen Wert haben. Der hier dokumentierte Merkmalskatalog soll die Modellierung von ökosystemaren Konsequenzen einer Änderung der Artenzusammensetzung unterstützen.

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