RELATIONSHIP BETWEEN PLANT SPECIES RICHNESS AND BIOMASS IN AN ARID SUB-ALPINE GRASSLAND OF THE CENTRAL HIMALAYAS, NEPAL

Khem Raj Bhattarai[1], **Ole R. Vetaas**[2] **& John A. Grytnes**[1]

1) Department of Botany, University of Bergen, Allégaten 41, 5007 Bergen, Norway; Corresponding author: fax +47 55 589 667, e-mail khem.bhattarai@bot.uib.no
2) Centre for Development Studies, University of Bergen, Nygaardsgaten 5, 5015 Bergen, Norway

Abstract: The hump-shaped relationship between plant species richness and biomass is commonly observed at fine scale for herbaceous vegetation in temperate climates. This relationship predicts that herbaceous species richness is highest at an intermediate level of biomass that corresponds to moderate competition or disturbance. However, this relationship has not previously been investigated in high arid sub-alpine mountain grasslands. We tested the humped-back prediction in the arid Trans-Himalayan mountain grassland with a seasonal grazing system. The study area is located in the bottom of a U-shaped valley, in the Manang district (3500 m a.s.l.). We sampled two hundred plots (1m $\times$ 1m) in two different types of pastures: common pasture and old field, which both have similar grazing practices. There was a significant unimodal relationship between species richness and biomass only in the common pasture, and when the two sites were analyzed together. The species turnover is estimated by DCA in standard deviation unit. The turnover was lower in the old field than in the common pasture. The unimodal relationship between plant species richness and biomass did not disappear after accounting for unknown environmental gradients expressed as DCA (detrended correspondence analysis) axes and spatial variables. The species richness is highest at 120 ± 40 g/m^2. The results indicate that a hump-shaped relationship is also found in arid Trans-Himalayan grasslands.

Keywords: Generalized linear model, Gradient length, Grazing, Hump pattern, Species composition

Nomenclature: HARA et al. (1978, 1982), HARA & WILLIAMS (1979), PRESS et al. (2000)

INTRODUCTION

The relationship between species richness and biomass or productivity has been a central focus in community ecology (e.g. GRIME 1973, 1979, 1997, ROSENZWEIG 1992, 1995, HUSTON 1994, ABRAMS 1995, JOHNSON et al. 1996, GRACE 1999, WAIDE et al. 1999, MITTELEBACH et al. 2000, FOX 2003, CORNWELL & GRUBB 2003, VENTERINK et al. 2003). This relationship has been investigated since the mid-1960s (CONNELL & ORIAS 1964, MACARTHUR & PIANKA 1966), but the causal mechanisms have been in dispute for almost as long (see VALENTINE 1976, ELSETH & BAUMGARDNER 1981, OKSANEN 1996, BROCQUE & BUCKNEY 2003). The relationship between herbaceous biomass and richness often has a hump-shape with a peak in species richness at a low to intermediate level of biomass (GRIME 1979, 1997). At a very low level of biomass, richness is primarily limited by the inability of a species to survive the abiotic conditions. In this range, an increase in biomass reflects a decrease in the harshness of the environment. Above some point roughly corresponding to the peak species richness, the abiotic environment is presumably amenable to most species.

At higher levels of biomass the decline in species richness is believed to be due to competitive exclusion (GRIME 1973, HUSTON 1994, GOUGH et al. 1994). ROSENZWEIG (1995) emphasized that it is the decline at high biomass level that is the unsolved puzzle, whereas the positive correlation between richness and biomass is inevitable, and some authors classify it as a sampling artefact, i.e., more biomass, more individuals, higher probability for more species (MAY 1975, cf. OBA et al. 2001). The decline of species richness at high biomass is the crucial question for its application in conservation and management of grassland (VAN DER MAAREL 1997, OBA et al. 2001).

Several studies have indicated that the relationship may differ when a range of different habitats are analyzed together, i.e., high beta diversity, compared to when only one vegetation type is analyzed (MOORE & KEDDY 1989, GUO & BERRY 1998, VIRTANEN et al. 2000, GROSS et al. 2000, OBA et al. 2001). From literature survey, MITTLEBACH et al. (2000) reported that at smaller spatial scales hump-shaped relationships are dominant both for within-community type and for across-community type, but percentage of the occurrence of hump-shaped curves is higher at the latter condition. WAIDE et al. (1999) reported that unimodal relationships are three times more common than the positive relationship at the between-communities scale.

Most of the studies, where biomass has been related to species richness, have been done in temperate grasslands (e.g. WALKER & PEET 1983, DURING & WILLEMS 1984, SHMIDA & ELLNER 1984, WILLEMS et al. 1993, KLIMEŠ 1995, WAIDE et al. 1999 and reference therein, RYDIN & BARBER 2001) and wetlands (e.g. WHEELER & GILLER 1982, WILSON & KEDDY 1989, WHEELER & SHAW 1991, GOUGH et al. 1994, GRACE & JUTILA 1999). Not many studies have been undertaken in the alpine region or in arid and semi-arid areas (but see GRYTNES 2000, WILSON et al. 2000, OBA et al. 2001). However, no study has, to the best of our knowledge, evaluated the relationship between biomass and species richness in dry and high mountain grasslands. In dry regions competition is assumed to be weak (GUO & BERRY 1998), and in such relatively unproductive areas, external factors such as moisture or other environmental factors are thought to be much more important than internal interactions (DARWIN 1859, NOY-MEIR 1973, GRIME 1979, VETAAS 1993). This study's aim is to test the prediction deduced from the hump-shaped model in arid mountain grassland. Specifically this study addresses the following issues: (1) to quantify the relationship between species richness and biomass in arid sub-alpine grasslands in the Himalayas, (2) to evaluate the importance of compositional gradient length on this relationship, and (3) to evaluate the strength of the unimodal relationship after accounting for unknown environmental gradients expressed as ordination scores and spatial variables (i.e., distances among the plots).

MATERIALS AND METHODS

Study area

The study area is located in the Manang district, within the Annapurna Conservation Area, in north-central Nepal, latitude 28º 40′ N and longitude 84º 01′ E (Fig. 1). It is situated at 3500 m a.s.l. in the Trans-Himalayan region between the Himalayan range and the Tibetan Plateau. The grasslands are found on fluvio-glacial deposits in the bottom of a U-shaped valley extending from north-west to south-east, along the Marsyandi River. The area is north
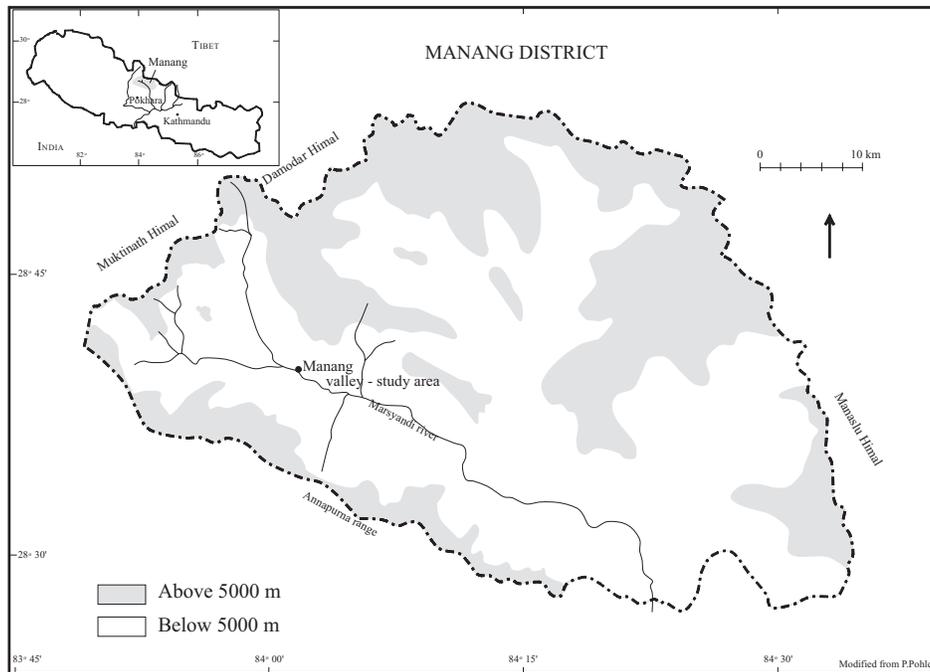
Fig. 1. Map showing the location of the study area in Manang, central Nepal.

of the massive Annapurna range with a maximum elevation above 7000 m a.s.l. Thus the area receives little of the monsoon rain that comes from the south-east. The mean annual precipitation during the year is ca. 400 mm (ANONYMOUS 1995). The mean maximum/minimum temperatures were recorded (Jomsom, nearest comparable station) as 7.9 °C / -1.75 °C in winter and 22.6 °C / 14.15 °C in summer during 1995 (ANONYMOUS 1999). Snow is common during winter.

There is decreasing moisture from east to west in the upper Manang valley, and the south-facing slopes are significantly drier than those facing north. This is reflected in the vegetation and forest formation. At 3000 m a.s.l. there are forests of *Picea smithiana*, *Quercus* spp., and *Tsuga dumosa*. At higher elevations (above 3000 m a.s.l.), there is *Pinus wallichiana* and *Betula utilis* forest on the north-facing slopes, and *Juniperus indica* and *Rosa* spp. shrubs on dry south-facing slopes (MIEHE 1982). The valley bottom is in an intermediate situation, and *Pinus wallichiana* forest is the mature vegetation where grazing and forest cutting is restricted. Above the timberline (4000–4300 m a.s.l.) there is a harsh continental climate, which allows only steppe vegetation similar to that of the Tibetan plateau (MIEHE 1982).

The dominant land-use is agriculture with domestic animals such as yak, horse, mule, sheep, and goats grazing the alpine pastures above the timberline (4300 m a.s.l.) during the summer. In the winter these animals are brought down to graze the grasslands of the lower slopes and valley floor.

Field sampling

The sampling was done during September and October 2000, prior to the domestic cattle's return from the high alpine summer pasture. We sampled two hundred plots (1m × 1m) in two grasslands sites (here referred to as sites I and II), ca. 1 km apart. Site I is a common pasture, which has been used for grazing for more than a century. Site II is an old field or fallow land, which has been abandoned for the last 15 years, and used to cultivate wheat, barley, potato, and buckwheat in the past. Two different sites were chosen with the criterion that they should be as homogeneous as possible. Thus, both sites have a similar physiognomic type of vegetation and are mostly dominated by species of *Artemisia* and grasses (*Stipa* sp., *Piptatherum aequiglumis*, *Pennisetum* sp.) but in site I species like *Rumex nepalensis*, *Lotus corniculatus*, *Taraxacum* spp., which grow in more productive areas, were more common. All these species are palatable to cattle. The moisture condition in site I increases from one end of the transect to the other, but site II is more uniform. Site I and site II are located ca. 200 m and ca. 250 m respectively away from river. The river is deep so there is no probability of flooding over the areas. The domestic animals are in mountain pasture during the summer months (May to September), but they are brought down to the study area for grazing during the winter season (October to April). Both study sites have experienced the same grazing practice for the last 15 years. The stratified random sampling procedure was used in both sites. Sampling followed a subjectively chosen transect line (ca. 300 m in 120° Eastern direction). The central plots were made along the transect line. The first plot was placed at the start of the transect line and the distance to the next plot (here called x-distance), was chosen randomly between 1 and 10 m. From each of these central plots two plots were placed on each side (i.e., north and south) of the transect line. Distances were randomly chosen between 1 to 20 m, called the y-distance. If a plot hit a large stone or woody shrub, the location was moved 1m further on. Thus the position of all the plots is known. The variable species richness may exhibit distance decay (TOBLER 1969), which means that species richness in two nearby plots is on average more similar than species richness in more distant plots. We used the spatial variables (x-distance and y-distance) to account for any potential spatial trends, i.e., spatial autocorrelation (LEGENDRE 1993), in the regression analyses.

The species richness is defined as the total number of species occurring within one square metre, which is a common plot size in these type of analyses (e.g. GRIME 1973, AL-MUFTI et al. 1977, MARAÑÓN & GARCÍA 1997, OBA et al. 2001, and references therein). All the vascular plant species rooted inside the 1 m^2 plots were recorded, and standing, above-ground biomass was clipped at ca. 0.5 cm above-ground level and harvested. The harvested biomass from all plots was dried in a sunny and windy place in the field. Dry weight was taken 10 days after harvesting and continued until a constant weight was obtained (e.g. WHEELER & SHAW 1991).

Numerical analysis

We used generalized linear models (GLM; MCCULLAGH & NELDER 1989, DOBSON 1990, HASTIE & PREGIBON 1993), which were performed separately for the two sites as well as for them combined to elucidate the relationship between species richness and biomass.

We used species richness as the response variable and biomass as the explanatory variable (MOORE & KEDDY 1989, GOUGH et al. 1994, GUO & BERRY 1998, GRYTNES 2000, OBA et al. 2001). A preliminary analysis indicated a severely skewed distribution towards low biomass, thus a logarithmic transformation of biomass was made. The response variable, species richness, is discrete data (counts) and a Poisson distribution of error was assumed (MCCULLAGH & NELDER 1989), and a logarithmic link was used in the GLM. These assumptions were evaluated by comparing the residuals of the analysis with the residuals from models by using an identity link function (assuming normal distributions of error) (HASTIE & PREGIBON 1993). The Poisson models seemed reasonable when examining the residuals with diagnostic plots. Unimodality was evaluated by testing the significance of the model including a second order polynomial term against a linear model. The explanatory variable was tested until the third order polynomial. The adequacy of the fitted models was confirmed by plotting standardized residuals against fitted values, and by the normal probability plots of the fitted values (CRAWLEY 1993). An *F*-test was used, as most of the deviance was underdispersed (HASTIE & PREGIBON 1993).

Detrended correspondence analysis (DCA; HILL & GAUCH 1980), with detrending by segments and non-linear rescaling was used to: (i) describe the difference in species composition between the sites, (ii) estimate the compositional gradient length in SD-units (HILL 1973, LEPŠ & ŠMILAUER 2003) (i.e., beta diversity) at each site and both sites combined, and (iii) derive the DCA plot scores, which were subsequently used to account for unknown environmental gradients (e.g. OBA et al. 2001). We used presence-absence data for calculation. Preliminary analyses detected some outliers in site I, which caused a very long gradient (SD = 5.7). These were excluded (GAUCH 1980), and the gradient length was decreased to 3.3 SD-units. The area is arid and one may expect that biomass and species richness are influenced by an environmental gradient in the grassland. To check for this, we used a DCA plot score as a covariable to evaluate whether the relationship between biomass and species richness was statistically significant after accounting for any environmental gradients captured by DCA axis I. DCA is the most accessible and widely applied indirect ordination method in vegetation science (e.g. VAN DER MAAREL et al. 1985, ØKLAND & EILERTSEN 1996, EJRNÆS 2000, EXNER et al. 2002, LEPŠ & ŠMILAUER 2003). It is popular for providing an effective approximation of the underlying environmental gradients in a data set and results are less influenced by rare species (TER BRAAK & PRENTICE 1986, TER BRAAK 1995). The first DCA axis addition to log biomass and (log biomass)^2 was related to species richness to account for the effect of underlying environment gradients; which is assumed to be a moisture gradient (see below). The regression with spatial variables (i.e., x-distance and y-distance) was done to check the dependency between the observations of the response variables that can be described by spatial autocorrelation (LEGENDRE 1993). To check this we used a generalized additive model (GAM; HASTIE & TIBSHIRANI 1990), with the species richness as the response variable, and the two spatial variables as the explanatory variables. The GAM is a flexible method where both linear and smoothing methods, as well as a mixture of the two, can be applied. A smoothing spline function in the framework of the GAM was used. No priori shape of the relationship between the species richness and the spatial variables was assumed. Therefore nine different models for each spatial variable (x-distance and

Table 1. Summary of DCA results, correlation coefficient (*r*) between biomass, species richness and ordination axes. n.s. – non-significant.

Ordination axis	I	II
Site I. Common pasture		
Eigenvalue	0.56	0.35
Length of gradient	3.31	2.71
Cumulative % variance	9.10	14.6
Biomass (*r*)	0.50	0.41
Species richness (*r*)	-0.58	-0.27
Site II. Old field		
Eigenvalue	0.23	0.15
Length of gradient	2.92	2.08
Cumulative % variance	8.80	14.70
Biomass (*r*)	-0.35	n.s.
Species richness (*r*)	0.23	n.s.
Combined I & II		
Eigenvalue	0.59	0.311
Length of gradient	4.12	2.94
Cumulative % variance	8.0	12.20
Biomass (*r*)	n.s.	-0.19
Species richness (*r*)	-0.24	0.26

y-distance) were made including the null model that there was no relation to the geographical or spatial variable. The nine models were set up in GAM with a smoothing spline, where the first model used one degree of freedom, the second model used two degrees of freedom, and so on. These nine models were then simultaneously tested with Mallow's C_p, a variant of cross validation test (HASTIE & TIBSHIRANI 1990), and models with the lowest C_p value were selected for each spatial variable. The addition of the log biomass and (log biomass)^2 was tested after accounting for each spatial model to account for the effect of spatial variables. Even though this procedure will not completely remove the effect of spatial autocorrelation, it can reduce the effect of autocorrelation on the relationship between the species richness and biomass.

There may be several differences between the two sites, so there may be some confounding factors that may influence the species richness biomass relationship when the sites are combined. To account for these factors we made dummy variables, taking only the values 0 for site I and 1 for site II, which were used as co-variables, to check whether the species richness biomass relationship would still be significant after accounting the site effects. The difference in mean species richness between the two grasslands was tested by a student *t*-test. We used S-Plus (version 4.5) and CANOCO for Windows ver. 4 for regressions and ordination, respectively.

RESULTS

Species composition

The summary of DCA results is presented in Table 1. The variation of species composition in the total data was large (SD = 4.12), whereas the gradient length was shorter in the two sub-sets (SD = 3.3 and 2.9 for site I and site II respectively). Figure 2 shows that the two sites are fairly well separated and that each site represents a lower beta-diversity than the two sub-sets combined (Table 1). When sites I and II are combined, the first DCA axis separates the two sites. The eigenvalue of the first DCA axis was larger than 0.50, which indicates a good dispersion of species along the axis. The variance explained by the first DCA axes are statistically significant in all analyses (Table 3), but it explained only 8% to 9% of the species data. The low percentage of the variance explained by the axes is probably due to the larger number of species and the many zero values, but the significance of variances explained by axes is much more important than amount of variance explained. Site I is characterized by
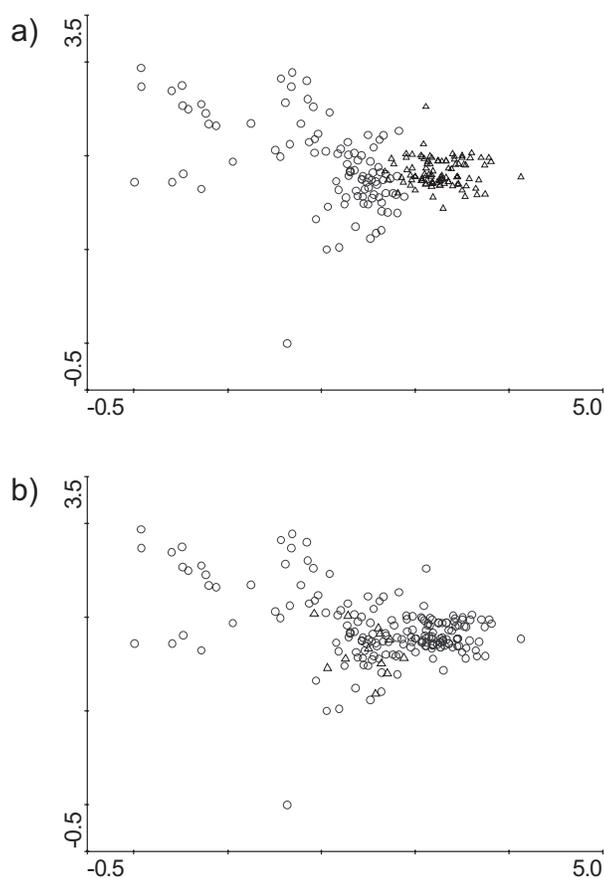
a)

b)

Fig. 2. (a) DCA diagram (horizontal axis-1 and vertical axis-2) with samples, two different symbols representing the two different grassland sites: (O) indicates site I, and (Δ) indicates site II. (b) DCA diagram with plots (O), where plots with high biomass (Δ) are dispersed in the central part of the diagram.

more moisture-loving species, such as *Juncus royleana* var. *himalaica*, *Kobresia* sp. and *Kobresia pseuduncinoides* found towards the negative end of DCA-axis one. Species with an affinity to arid habitats, such as *Artemisia sieversiana*, *Piptatherum aequiglumis* and *Stipa* sp. are found towards the positive end of axis one and are more common on site II. Species that occurred in the intermediate position, include *Poa pagophylla*, *Cynoglossum wallichii*, and *Sonchus wightianus*. Thus this axis probably reflects a gradient of moisture. The ecological meaning of the second DCA axis is also to some extent interpretable. Species that grow in nitrogen-enriched habitats, such as *Rumex nepalensis* and *Taraxacum* sp. have high scores, and species like *Aster indamellus* and *Saussurea stracheyana* that grow in marginal habitats have low scores. This indicates that the second DCA-axis may reflect soil nitrogen conditions. A similar moisture gradient was interpreted when only site I was included in the analysis. Only the first DCA-axis is used in the regression analysis, because the eigenvalue of axis one (> 0.50) is considerably larger than the subsequent axes.

Relationship between species richness and biomass

We recorded 83 herbaceous species at site I and 40 at site II (old field), but mean species richness is higher at site II (11.2 species/m^2) than site I (10.3 species/m^2). This difference is statistically significant ($t = -2.44$, d.f. =198, $P < 0.05$), although the difference is less than one species (0.9 species/m^2). Although both sites are located in same elevation and surrounded by similar geo-morphological features there are only 25 species that are common to both sites.

Table 2. Summary statistics of generalized linear model (GLM). Number of herbaceous species per square metre are regressed against a linear and quadratic term of log-biomass in two different sites (I, II and combined). d.f. – degrees of freedom.

Sites	Variables	d.f.	Explained deviance	Residual deviance	F-value	P-value
Site I	null	97		85.12		
	log biomass)	96	4.7	80.42	5.85	0.017
	(log biomass) ^{2}	95	7.13	73.29	9.72	0.002
Site II	null	99		26.98		
	log biomass	98	0.01	26.98	0.31	0.85
	(log biomass) ^{2}	97	0.09	26.88	0.35	0.55
Combined I & II	null	198		114.93		
	log biomass	196	5.14	109.79	9.33	0.002
	(log biomass) ^{2}	195	6.56	103.22	13.06	0.0003

The difference in species richness between plots is higher at site I (range: 3–18 species/m^2) than at site II (range: 6–15 species/m^2). The range of biomass is also higher at site I (range: 50–1020 g/m^2) than site II (range: 30–290 g/m^2). Species richness and biomass are both significantly correlated with the first DCA-axes at both sites (Table 1). Species richness is correlated with the first DCA-axis when the two sites are combined, but biomass is not (Table 1).

The response in species richness to biomass was different in the two sites (i.e., grasslands) (Table 2, Fig. 3). A statistically significant unimodal relationship was found at site I, but there was no significant relationship between biomass and species richness at site II. The unimodal relationship between species richness and biomass was also significant when the sites were combined. Maximum species richness was found in the biomass interval between ca. 115–160 g/m^2 at site I, and ca. 80–140 g/m^2 when the two sites were combined (Figs. 3a and 3c).

There was a significant relationship between x-distance and species richness, shown by GAM (with 8 d.f.) with F-value as 5.4 (P < 0.001), but y-distance was not significant (Table 3). In the combined sites, we did not use the spatial variable due to their different locations (about one km distance) and used only the first DCA axis and site factors, both of which significantly explained the species richness.

The unimodal or hump-shaped relationship between species richness and biomass was also significant after accounting for the unknown environmental gradient expressed as the first DCA-axis and spatial variables (Table 3). This indicates that the unimodal relationship between species richness and biomass is not confounded with the environmental gradients represented by the first DCA-axis and spatial variables. In the combined site, the hump shape did not disappear after taking the first DCA axis and site factors into account. The hump-shaped pattern was still significant when four plots with high biomass (> 700 gm) were excluded from the same analysis. This indicates that the hump-shaped pattern is not dependent on a few high biomass-yielding plots.
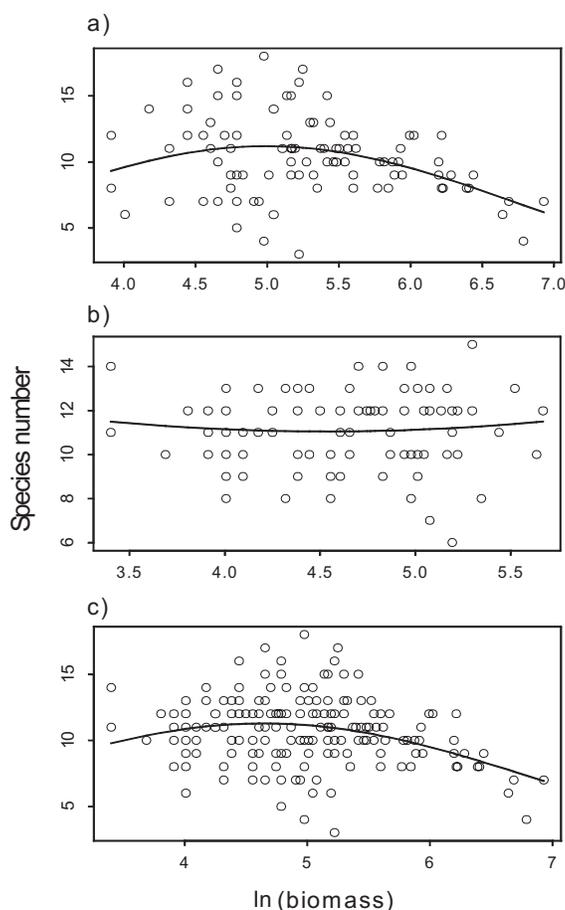
a)

b)

Species number

c)

ln (biomass)

Fig. 3. The relationship between herbaceous species richness and biomass in an arid high sub-alpine grassland: (a) a significant relationship at site I (common pasture), (b) a non-significant relationship at site II (old field), and (c) a significant relationship when sites I and II are combined. The fitted lines in (a) and (c) are based on a second order polynomial regression with generalized linear models.

DISCUSSION

Species richness and hump pattern

The unimodal or hump-shaped relationship between species richness and biomass is tested with data from arid sub-alpine grasslands. The result agrees with earlier studies (e.g. GRIME 1973,1979, AL-MUFTI et al.1977, GROSS et al. 2000). However, there was no relationship between species richness and biomass at site II (old field). This site is in the process of succession and has short range in biomass, it also has the shortest gradient length (SD = 2.9, Table 1). The compositional gradients are relatively longer at site I (SD = 3.3) and at the two sites combined (SD = 4.1) where the hump model was observed. Although the beta diversity was not very different, this may indicate that the hump-backed model depends on the magnitude of species turnover between the plots. This is consistent with the findings of GUO & BERRY (1998) and GOUGH et al. (1994), GROSS et al. (2000) who argue that the humped pattern is a result of the floristic heterogeneity, and will only be detected when sampling covers total gradient of different microhabitats (MOORE & KEDDY 1989). Many studies have suggested that a unimodal relationship is most common between vegetation types rather than within a single vegetation type (RICKLEFS & SCHLUTER 1993, MOORE & KEDDY 1989, WAIDE et al.1999, VIRTANEN et al. 2000, MITTLEBACH et al. 2000). On the contrary, GRYTNES (2000) reported the unimodal relationship between species richness and biomass at a fine scale (within a vegetation type).

A short floristic gradient may also mean a short biomass gradient, as in this study. It is therefore possible that the lack of a statistically significant relationship at site II is due to the short biomass gradient, which only captures a part of the humped relationship (cf. GRACE

Table 3. Summary of regression statistics after accounting for DCA axis1and spatial variables in site I, and DCA axis and site factors in the combined sites (site I and site II). Polynomial regression is used within GAM for spatial variables but restricted to GLM for the DCA model. Each model is described by the explanatory variables used, where (p, x) is polynomial regression with x degrees of freedom used, and (s, x) is GAM smoothing spline with x degrees of freedom. The test refers to which models are tested against each other. d.f. = degrees of freedom, logbiom = log biomass, n.s. – non-significant.

Models no.	Models	Test	d.f.	Residual deviance	Explained deviance	F-value	P-value
	Site I						
	(a) Accounting for DCA axis						
0	Null		97	85.12			
1	DCA1	1 vs. 0	96	58.15	26.99	46.84	$P < 0.001$
2	+logbiom (p,1)	2 vs.1	95	57.42	0.71	1.23	n.s.
3	+logbiom (p,2)	3 vs.1	94	50.81	7.34	7.19	$P < 0.012$
	(b) Accounting for space						
0	Null		97	85.12			
1	xdis (s,8)	1 vs. 0	88	58.07	27.05	5.40	$P < 0.001$
2	+logbiom (p,1)	2 vs.1	87	57.82	0.24	0.39	n.s.
3	+logbiom (p,2)	3 vs.1	86	49.68	8.39	7.73	$P < 0.001$
	(c) Accounting for both a & b						
0	Null		97	85.12			
1	xdis (s,8)+DCA1	1 vs. 0	87	51.24	33.87	6.7	$P < 0.001$
2	+xdis (s,8)+DCA1+logbiom(p,1)	2 vs.1	86	51.13	0.11	0.2	n.s.
3	+xdis (s,8)+DCA1+logbiom (p,2)	3 vs.1	85	44.61	6.64	6.75	$P < 0.019$
	Combined sites						
	Accounting for DCA axis						
0	Null		197	114.93			
1	DCA1	1 vs. 0	196	108.61	6.32	12.23	$P < 0.001$
2	+logbiom(p,1)	2 vs.1	195	100.77	7.83	16.17	$P < 0.001$
3	+logbiom (p,2)	3 vs.1	194	96.13	4.64	13.53	$P < 0.001$
	Accounting for site factors						
0	Null		197	114.93			
1	Site factor	1 vs. 0	196	112.12	2.82	5.06	$P < 0.025$
2	+logbiom(p,1)	1 vs. 2	195	109.42	2.71	4.98	$P < 0.026$
3	+logbiom(p,2)	2 vs. 3	194	102.85	6.57	12.96	$P < 0.001$

1999). GUO & BERRY (1998) reached a similar conclusion when they reported that the unimodal relationship exists only when a large range of biomass is sampled. However, GRYTNES (2000) reported a unimodal relationship in a very small range of biomass, and a linear relationship in a larger range of biomass, but the plot size was only 0.04 m^2.

Mechanisms underlying the hump-shaped pattern in the species richness-biomass relationship have been much debated. GRIME (1973) suggests that species richness in herbaceous vegetation is controlled by antagonistic forces of inter-specific competition and disturbance (stress). In stable, productive habitats, competitively dominant species are able to

monopolize space, excluding inferior competitors from the community. Biomass is high but species richness is low in such environments. In an environment with high disturbance (low productivity), only a few species persist, and standing crop (biomass) is also low. The highest species richness occurs at the intermediate level of biomass with moderate disturbance or productivity (GRIME 1973, 1979). There are few plots that contain low species numbers even at intermediate levels of biomass and this may be the reason the observed relationship is a sort of "filled" hump-shape (VENTERINK et al. 2003).

Robustness of the humped pattern

The present results show that the unimodal pattern did not disappear after accounting for unknown environmental gradients that are expressed as ordination axis and that explain a significant fraction of the variation (ca. 6.5%–27%, Table 3), indicating the importance of environments. Although it is assumed that arid ecosystems are driven more by external factors, such as moisture, than internal interactions (NOY-MEIR 1973, DEANGELIS & WATERHOUSE 1987, ELLIS & SWIFT 1988, FERNANDEZ-GIMENEZ & ALLEN-DIAZ 1999, FYNN & O'CONNOR 2000, OBA et al. 2000, 2001), these results may indicate that other factors, such as competitive exclusion may also be important in explaining the decrease of species at high biomass (cf. MARAÑÓN & GARCÍA 1997). In plots where biomass is high, only a few dominant species will monopolize the available resources (GRIME 1973, 1979). In this study the plots with high biomass are often dominated by *Artemisia* spp. and tuft forming grasses, such as *Stipa* sp. and *Piptatherum aequiglomis*. These species grow taller (ca. 0.2–0.5 m) and denser than other small stature species such as *Lotus corniculatus* L., *Medigo sativa* L., *Gentianella* sp. that cannot compete for resources.

The importance of environmental factors has been emphasized in wetlands, where only a few large species can tolerate extreme environmental conditions (GARCÍA et al. 1993, GOUGH et al. 1994, GRACE et al. 2000). However, the plots with very high biomass ($n = 12$) in the present study appear rather dispersed in the central part of the ordination diagram (Fig. 2). This suggests that these plots do not have extreme environmental conditions that could have excluded many species in the local flora.

The hump-shaped relationship between species richness and biomass (site I) did not disappear after accounting for spatial variables (Table 3). Only the x-distance variable is related to species richness. The hump was still significant after accounting for the first DCA-axis scores and the spatial variables. This shows that the spatial variables (x- and y-distances) and the unknown underlying gradient do not confound the biomass-species richness relationship.

Maximum species richness and low biomass level

We found maximum species richness at relatively low biomass (120 ± 40 g/m^2). This is much lower than the model developed by GRIME (1973), which predicts maximum species richness of between 350 and 500 g/m^2. The difference in overall productivity in an arid sub-alpine grassland (3500 m a.s.l.) compared to temperate grassland may account for this discrepancy. Productivity in arid regions is generally limited by moisture. Low moisture conditions may constrain nutrient supply (particularly nitrogen) in soil, which limits the

primary production (LUDWIG et al. 1989). From a literature survey, WAIDE et al. (1999) observed very low productivity in dry ecosystems compared to other terrestrial biomes. In the arid region, below-ground productivity is relatively higher than above-ground productivity (LUDWIG et al. 1989). This indicates that root competition brings a decrease in species richness at high biomass. However, from this data set it may not be possible to distinguish between above-ground and below-ground competition in determining the hump-shaped relationship. Ephemeral species frequently occur in arid regions, which generally have very low biomass. We have observed the occurrence of several annual herbaceous species (e.g. *Chenopodium album* and *Polygonum* sp.), growing in minute forms among the most dominant species (e.g. *Piptatherum aequiglumis*, *Stipa capensis*, *Artemisia caruifolia*). Having small stature due to low productivity, being sometimes less than 1 cm high, they contribute to species richness but their contribution to biomass is negligible. The documented optimum level, however, is also much lower than that found in arid grasslands (OBA et al. 2001), where maximum species richness was at a similar interval to that of Grime's model (GRIME 1973).

The presented hump-back relationship was assessed by accounting for unknown environmental gradients, pure spatial variables, site effects and the removal of four high biomass plots. All these analyses indicated the significance of the relationship. In conclusion, this study presents evidence for a unimodal relationship between species richness and biomass in arid sub-alpine grasslands of the central Himalayas. Although the environmental factors are considered much more important in an arid ecosystem, the importance of internal interaction should also not be overlooked in the biomass-species relationship. However, this still needs to be verified in further studies.

REFERENCES

ABRAMS P.A. (1995): Resource productivity-consumer species diversity: simple models of competition in spatially heterogeneous environments. *Ecology* 69: 1418–1433.

AL-MUFTI M.M., SYDES C.L., FURNESS S.B., GRIME J.P. & BAND S.R. (1977): A quantitative analysis of shoot penology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759–791.

ANONYMOUS (1995): *Iso-climatic map of mean annual precipitation.* ICIMOD/MENRIS, Kathamndu, Nepal.

ANONYMOUS (1999): *Climatological records of Nepal 1995–1996.* Department of Hydrology and Metrology, Kathmandu, Nepal.

BROCQUE A.F.L. & BUCKNEY R.T. (2003): Species richness-environment relationships within coastal sclerophyll and mesophyll vegetation in Ku-ring-gai Chase National Park. New South Wales, Australia. *Austral. Ecol.* 28: 404–412.

COLLINS S.L., GLENN S.M. & BRIGGS J.M. (2003): Effect of local and regional process on plant species richness in tallgrass prairie. *Oikos* 99: 571–579.

CONNELL J.H. & ORIAS S.E. (1964): The ecological regulation of species diversity. *Amer. Naturalist* 98: 399–411.

CORNWELL W.K. & GRUBB P.J. (2003): Regional and local patterns in plant species richness with respect to resource availability. *Oikos* 100: 417–428.

CRAWLEY M.J. (1993): *GLIM for ecologists*. Blackwell Scientific Publications, Oxford.

CURRIE D.J. (1991): Energy and large-scale pattern of animal- and plant- species richness. *Amer. Naturalist* 13: 27–49.

DARWIN C. (1859): *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. Murray, London.

DEANGELIS D.L. & WATERHOUSE J.C. (1987): Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57: 1–21.

DOBSON A.J. (1990): *An introduction to generalized linear models*. Chapman & Hall, London.

DURING H.J. & WILLEMS J. H. (1984): Diversity model applied to chalk grassland. *Vegetatio* 57: 103–114.

EJRNÆS R. (2000): Can we trust gradient extracted by Detrended Correspondence Analysis? *J. Veg. Sci.* 11: 565–572.

ELSETH G.D. & BAUMGARDNER K.D. (1981): *Population biology*. Van Nostrand, New York.

ELLIS J.E. & SWIFT D.M. (1988): Stability of African pastoral ecosystem: alternate and implications for development paradigms. *J. Range Managem.* 41: 450–459.

EXNER A.,WILLNER W. & GRABHERR G. (2002): *Picea abies* and *Abies alba* forests of the Austrian Alps: Numerical classification and ordination. *Folia Geobot.* 37: 383–402.

FERNANDEZ-GIMENEZ M.E. & ALLEN-DIAZ B. (1999): Testing a non-equilibrium model of range vegetation dynamics in Mongolia. *J. Appl. Ecol.* 6: 871–885.

FOX J.W. (2003): The long-term relationship between plant diversity and total plant biomass depends on the mechanism maintaining diversity. *Oikos* 102: 630–640.

FYNN R.W.S. & O'CONNOR T.G. (2000): Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savana, South Africa. *J. Appl. Ecol.* 37: 491–507.

GARCÍA L.V., MARAÑÓN T., MORENO A. & CLEMENTS L. (1993): Above-ground biomass and species richness in a mediterranean salt marsh. *J. Veg. Sci.* 4: 417–424.

GAUCH H.G. (1980): Rapid initial clustering of large data sets. *Vegetatio* 42: 103–111.

GOUGH L., GRACE J.B. & TAYLOR K.L. (1994): The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* 70: 271–279.

GRACE J.B. (1999): The factors controlling species richness in herbaceous plant communities: an assessment. *Perspectives Pl. Ecol., Evol. Syst.* 2: 1–28.

GRACE J.B. & JUTILA H. (1999): The relationship between species richness and community biomass in grazed and ungrazed coastal meadows. *Oikos* 85: 398–408.

GRACE J.B., LARRY A. & CHARLES A. (2000): Factors associated with plant species richness in a coastal tall-grass prairie. *J. Veg. Sci.* 11: 443–452.

GRIME J.P. (1973): Control of species richness in herbaceous vegetation. *J. Environm. Managem.* 1: 151–167.

GRIME J.P. (1979): *Plant strategies and vegetation process*. John Wiley & Sons, Chichester.

GRIME J.P. (1997): The humped-back model: a response to Oksanen. *J. Ecol.* 85: 97–98.

GROSS K.L., WILLIG M.R., GOUGH L., INOUYE R. & COX S.B. (2000): Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* 89: 417–427.

GRYTNES J.A. (2000): Fine-scale vascular plant species richness in different alpine vegetation types: relationship with biomass and cover. *J. Veg. Sci.* 11: 87–92.

GUO Q. & BERRY W.L. (1998): Species richness and biomass: dissection of the humped- shaped relationship. *Ecology* 79: 2555–2559.

HARA H., CHATER A.O. & WILLIAMS H.J. (1982): *An enumeration of flowering plants of Nepal III*. British Museum Natural History, London.

HARA H., STEARN W.T. & WILLIAMS H.J. (1978): *An enumeration of flowering plants of Nepal I*. British Museum Natural History, London.

HARA H. & WILLIAMS H.J. (1979): *An enumeration of flowering plants of Nepal II*. British Museum Natural History, London.

HASTIE T.J. & TIBSHIRANI R.J. (1990): *Generalized additive models*. Chapman & Hall, London.

HASTIE T.J. & PREGIBON D. (1993): Generalised linear models. In: CHAMBERS J.M. & HASTIE T.J. (eds.), *Statistical models*, Chapman & Hall, London, pp.195–247.

HILL M.O. (1973): Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61: 237–249.

HILL M.O. & GAUCH H.G. Jr (1980): Detrended correspondance analysis: An improved ordination technique. *Vegetatio* 42: 47–58.

HUSTON M.A. (1994): *Biological diversity. The coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.

JOHNSON K.H., VOGT K.A., CLARK O.J., SCHMITZ & VOGT D.J. (1996): Biodiversity and productivity and stability of ecosystem. *Trends Ecol. Evol.* 11: 372–377.

KLIMEŠ L. (1995): Small-scale distribution of species richness in a grassland (Bílé Karpaty Mts., Czech Republic). *Folia Geobot Phytotax.* 30: 499–510.

LEGENDRE P. (1993): Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.

LEPŠ J. & ŠMILAUER P. (2003): *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.

LUDWIG J.A.,WHITEFORD W.G. & CORNELIUS J.M. (1989): Effects of water, nitrogen and sulfur amendments on cover, density and size of Chihuahuan Desert ephemerals. *J. Arid Environm.* 16: 35–42.

MACARTHUR R.H. & PIANKA E.R. (1966): On the optimal use of patchy environment. *Amer. Naturalist* 100: 603–609.

MARAÑÓN T. & GARCÍA L.V. (1997): The relationship between diversity and productivity in plant communities: factors and artefacts. *J. Ecol.* 85: 95–96.

MAY R.M. (1975): Patterns of species abundance and diversity. In: CODY M. & DIMOND J.M. (eds.), *Ecology and evolution of communities*, Belknap Press, Haward University, Cambridge, pp. 81–120.

MCCULLAGH P. & NELDER J.A. (1989): *Generalized linear models.* Ed. 2. Chapman & Hall, London.

MIEHE G. (1982): Vegetationsgeographische Untersuchungen im Dhaulgiri in Annapurna-Himalaya. *Diss. Bot.* 66: i–xi, 1–224.

MITTLEBACH G.G., STEINER C.F., SCHEINER S.M., GROSS K.L., REYNOLDS H.L., WAIDE R.B., WILLIG M.R., DODSON S.I. & GOUGH L. (2000): What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.

MOORE D.R.J. & KEDDY P.A. (1989): The relationship between species richness and standing crop in wetlands: the importance of scale. *Vegetatio* 79: 99–106.

NOY-MEIR I. (1973): Desert ecosystems: environment and producers. *Annual Rev. Ecol. Syst.* 4: 25–51.

OBA G., STENSETH N.C. & LUSIGI W. J. (2000): New perspectives on sustainable grazing management in arid zones of sub-Saharan Africa. *Bioscience* 50: 35–51.

OBA G., VETAAS O.R. & STENSETH N.C. (2001): Relationship between biomass and plant species richness in arid zone grazing lands. *J. Appl. Ecol.* 38: 836–845.

ØKLAND R.H. & EILERTSEN O. (1996): Dynamics of understory vegetation in an old-growth boreal coniferous forest, 1988–1993. *J. Veg. Sci.* 7: 747–767.

OKSANEN J. (1996): Is the humped relationship between species richness and biomass an artefact due to plot size? *J. Ecol.* 84: 293–295.

POHLE P. (1990) *Useful plants of Manang district: a contribution to the ethnobotany of the Nepal-Himalaya*. Franz Steiner Verlag Wiesbaden GMBH, Stuttgart.

PRESS J.R., SHRESTHA K.K. & SUTTON D.A. (2000): *Annotated checklist of the flowering plants of Nepal*. The Natural History Museum, London.

RICKLEFS R.E. & SCHLUTER D. (1993): *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.

ROSENZWEIG M.L. (1992): Species diversity gradients. We know more and less than we thought. *J. Mamm.* 73: 715–730.

ROSENZWEIG M.L. (1995): *Species diversity in space and time*. University Press, Cambridge.

RYDIN H. & BARBER K.E. (2001): Long-term and fine-scale coexistence of closely related species. *Folia Geobot.* 36: 53–61.

SHMIDA A. & ELLNER S. (1984): The coexistence of plant species with similar niches. *Vegetatio* 58: 29–55.

TAYLOR D.R., AARSSEN L.W. & LOEHLE C. (1990): On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239–250.

TER BRAAK C.J.F. (1995): Ordination. In: JONGMAN R.H.G., TER BRAAK C.J.F. & VAN TONGEREN O.F.R. (eds.), *Data analysis in community and landscape ecology*, Cambridge University Press, Cambridge, pp. 91–173.

TER BRAAK C.J.F. & PRENTICE I.C. (1986): A theory of Gradient analysis. *Advances Ecol. Res.* 18: 271–317.

TOBLER W.R. (1969): Geographical filters and their inverse. *Geo. Anal.* 1: 234–253.

VALENTINE J.W. (1976): Genetic strategies of adaptation. In: AYALA F.J. (ed.), *Molecular evolution*, Sinauer, Sunderland, pp.78–94.

VAN DER MAAREL E. (1997): *Biodiversity: from babel to biosphere management*. Opulus Press, Uppsala.

VAN DER MAAREL E., VAN DROP P. & RIJNTJES J. (1985): Vegetation succession on the dunes near Oostvoorne, The Netherlands, a comparison of the vegetation in 1959 and 1980. *Vegetatio* 58:137–187.

VENTERINK H.O., WASSEN M.J., VERKROOST A.W.M. & DE RUITER P.C. (2003): Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* 84: 2191–2199.

VETAAS O.R. (1993): Spatial and temporal vegetation changes along a moisture gradient in north-eastern Sudan. *Biotropica* 25: 164–175.

VIRTANEN R., MUOTKA T. & SAKSA M. (2000): Species richness-standing crop relationship in stream bryophyte communities: pattern across multiple scales. *J. Ecol.* 89: 14–20.

WAIDE R.B., WILLIG M.R., STEINER C.F., MITTELBACH G., GOUGH L., DODSON S. I., JUDAY G.P. & PARMENTER R. (1999): The relationship between productivity and species richness. *Annual Rev. Ecol. Syst.* 30: 257–300.

WALKER J. & PEET R.K. (1983): Composition and species diversity of pine-waregrass savannah of the Green Swamp, North Carolina. *Vegetatio* 55: 163–179.

WHEELER B.D. & GILLER K.E. (1982): Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above ground plant material. *J. Ecol.* 70: 179–200.

WHEELER B.D. & SHAW S.C. (1991): Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *J. Ecol.* 79: 285–302.

WHITTAKER R.J., WILLIS K.J. & FIELD R. (2001): Scale and species richness: towards a general, hierachical theory of species diversity. *J. Biogeogr.* 28: 453–470.

WILLEMS J.H., PEET R.K. & BIK L. (1993): Change in chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4: 203–212.

WILSON S.D. & KEDDY P.A. (1989): Species richness survivorship and biomass accumulation along an environmental gradient. *Oikos* 53: 375–380.

WILSON J.B., STEEL J.B., NEWMAN J.E. & KING MCG.W. (2000): Quantitative aspects of community structure examined in a semi-arid grassland. *J. Ecol.* 88: 749–756.