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Effects of altitude on plant-species diversity and productivity in an alpine meadow, Qinghai–Tibetan plateau

Chang Ting Wang[A,B], *Rui Jun Long*[A,C,E], *Qi Ji Wang*[A], *Lu Ming Ding*[A] *and Mei Ping Wang*[D]

[A]Northwest Plateau Institute of Biology, The Chinese Academy of Sciences, Xining 810008, PR China.
[B]Graduate School of the Chinese Academy of Science, Beijing 100039, PR China.
[C]Center for Tibetan Grassland and Yak Studies, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730020, PR China.
[D]Grassland Science College of Gansu Agriculture University, 730070, PR China.
[E]Corresponding author. Email: longruijun@sina.com

Abstract. During the growing seasons of 2002 and 2003, biomass productivity and diversity were examined along an altitudinal transect on the south-western slope of Beishan Mountain, Maqin County (33°43′–35°16′N, 98°48′–100°55′E), Qinghai–Tibetan Plateau. Six altitudes were selected, between 3840 and 4435 m. Soil organic matter, soil available N and P and environmental factors significantly affected plant-species diversity and productivity of the alpine meadows. Aboveground biomass declined significantly with increasing altitude ($P < 0.05$) and it was positively and linearly related to late summer soil-surface temperature. Belowground biomass (0–10-cm depth) was significantly greater at the lowest and highest altitudes than at intermediate locations, associated with water and nutrient availabilities. At each site, the maximum belowground biomass values occurred at the beginning and the end of the growing seasons ($P < 0.05$). Soil organic matter content, and available N and P were negatively and closely related to plant diversity (species richness, Shannon–Wiener diversity index, and Pielou evenness index).

Introduction

In recent years, there has been a rapidly increasing interest in the effects of species richness on community productivity. The relationship between species diversity and ecosystem function, combined with the worldwide loss of species, has become one issue that has attracted considerable attention (Zhang 2000; Zhang and Zhang 2002, 2003). Decreasing primary productivity and changes in the structure of plant communities have been caused by the destruction of biodiversity, unreasonable exploitation and overgrazing of grassland resources in some areas, with consequent impacts on human society. Productivity is one of the important modalities by which to evaluate ecosystem functions (Tilman 1999), so a better knowledge of the association between plant-species diversity and ecosystem functioning would help in understanding whole ecosystems. Many investigations have been carried out by ecologists to identify a model that adequately describes the species richness–productivity relationships (Huston *et al.* 2000). However, because of various ecological contexts (such as the characteristics of the surrounding environment, and spatial and temporal scales of investigation) this work has indicated positive, negative or even non-existent relationships between diversity and productivity. For example, Tilman *et al.* (1996, 1997*a*, 2001) and Naeem *et al.* (1994) found that there was a positive correlation between species diversity and productivity, especially for aboveground biomass. In contrast, Kassen *et al.* (2000) indicated that the maximum species diversity occurred at an intermediate level of productivity. Therefore, the species richness–productivity connection still remains unclear.

The Qinghai–Tibetan plateau is the single largest and the highest plateau in the world, covering an area of nearly 2.5 million km^2, at an altitude of 2000–5000 m, with a cold, semi-humid climate. The available alpine rangelands of the plateau cover ~128.2 million ha, or ~30.7% of China's total area of rangelands. These alpine rangelands consist of mainly alpine meadow (49.3%) and alpine steppe (44.9%) (Zhou 2001). Given the high altitude and extremely harsh environmental conditions, this grazing-land ecosystem is arguably among the least-affected by modern society. The rangeland resources are vital for the livelihoods of the indigenous people through livestock-raising. Because of the high altitude and harsh environment, agricultural cultivation is not possible; continuous year-round extensive grazing, transitory grazing on the vast plain of the central plateau, or seasonal rotation within certain mountain regions are the land-use patterns throughout the Qinghai–Tibetan plateau. Therefore, ruminant (yak and Tibetan sheep) farming is the most important activity in the socio-economic and environmental systems of the plateau (Long 2003).

Since the 1980s, some rangelands on the plateau have suffered persistent overgrazing, leading to adverse impacts on ecosystem function, reflected in losses in both primary productivity and plant-species diversity. However, little information is available on the changes of ecosystem function caused by these variations in plant-species diversity and productivity, or their importance to rangeland management strategies. The aim of this study is to

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investigate the relationship between plant-species diversity and productivity of alpine meadows with variation in altitude during the years 2002 and 2003 and to evaluate their consequences for rangeland management in the region.

Materials and methods

Experimental area

The study was conducted at Maqin County, Guoluo Prefecture, Qinghai Province (33°43′–35°16′N, 98°48′–100°55′E), located in the hinterland of the Qinghai–Tibetan Plateau at an average altitude of over 4000 m. It has a cold climate, with long harsh winters and short cool summers. The annual average precipitation is 542.1 mm, with rainfall of 445.0 mm from May to September. The annual average air temperature is −2.3°C and the annual accumulated temperature above 0°C is 914.3°C days. Sunshine duration during the growing season is 2450.8 h. The soil types ranged from swamp meadow soil at the bottom, through alpine shrub soil to alpine meadow soil at the top (see Table 1). Four vegetation types, i.e. *Kobresia tibetica* swamp meadow, *Stipa aliena* meadow, *Kobresia pygmaea* meadow and *Kobresia capillifolia* meadow, are found at increasing attitudes on the south-western slope of the mountain (Table 2). In all four vegetation types, the main accompanying plant species are *Festuca ovina*, *Poa pratensis*, *Elymus nutans* and *Ptilagrostis dichotoma*.

Experimental design and statistical analysis

This experiment was conducted during the growing seasons of 2002 and 2003. Six plots were established at altitudes of 3840, 3856, 3927, 3988, 4232 and 4435 m of south-western slope of the Beishan Mountain to sample a range of temperature regimes and vegetation types. Five sampling quadrats (50 × 50 cm) were selected from areas of 50 × 50 m and were considered to represent the general characteristics of the alpine meadow at each altitude. From May to September, the aboveground vegetation biomass in each quadrat was measured by clipping at the soil-surface level. The biomass was separated into grasses, sedges, forbs and litter. The samples were weighed after oven-drying at 80°C for 48 h.

The belowground biomass from the areas where the aboveground biomass had just been removed was also measured in three 25 × 25 cm sample areas per 50 × 50 m quadrat. Three soil layers were sampled, including 0–10-, 10–20- and 20–30-cm depths. The total biomass of the 0–30-cm soil layer was described as total belowground biomass. The samples were carefully washed through a 1-mm sieve, and oven-dried at 80°C overnight before weighing.

Two sampling strips of 250 × 25 cm were selected from a sampling area of 50 × 50 m at each altitudinal level for counting the number of plant species and measuring cover, height and aboveground biomass of the whole plant community. Sampling occurred 15–25 August each year. This corresponds approximately with the time of peak aboveground standing crop at each site.

Soil temperatures were determined for the 0–10-, 10–20- and 20–30-cm layers with a HOBO H8 Family Data Loggers Temperature Sensor. Soil moisture content for each layer was also determined by gravimetric sampling and drying (105°C for 48 h).

Organic matter contents of the soil samples were determined by the FAO (1974) method. The contents of total N and total P in the soil samples were measured by methods described by Bremner and Mulvaney (1982) and Olsen and Sommers (1982), respectively. In addition, the methods of Olsen *et al*. (1954) and

Table 1. Geographical and edaphic characteristics of the study sites in the altitude gradient

1–6 indicate altitude sites; SW, south-western aspect; SMS, swamp meadow soil; AMS, alpine meadow soil; ASS, alpine shrub soil

Parameter	Site					
	1	2	3	4	5	6
Latitude, longitude	34°23.618’N, 100°21.740’E	34°24.618’N, 100°21.806’E	34°24.828’N, 100°21.971’N	34°25.347’N, 100°21.850’E	34°26.022’N, 100°22.524’E	34°26.153’N, 100°22.789’E
Altitude (m)	3840	3856	3927	3988	4232	4435
Slope, aspect	5°, SW	5°, SW	35°, SW	35°, SW	50°, SW	55°, SW
Soil type	SMS	ASS	ASS	ASS	ASS	AMS

Table 2. Changes in species number, cover of plant species and communities at six altitude sites

Site	Total species	Dominant species	Dominant cover (%)	Subdominant species	Subdominant cover (%)	Community plant cover (%)
1	35	*K. tibetica*	50–80	Forbs and grasses	10–15	60–95
2	37	*Stipa aliena*	45–65	*Scirpus distigmaticus*	15–20	60–88
3	41	*K. pygmaea*, *K. humilis*	50–60	*Poa annua*, *Gueldenstaedtis diversifolia*, *Ligularia virgaurea*	25–35	60–85
4	39	*K. pygmaea*, *K. humilis*	50–60	*Poa annua*, *Gueldenstaedtis diversifolia*, *Ligularia virgaurea*	25–35	60–85
5	40	*K. pygmaea*, *K. humilis*	50–60	*Poa annua*, *Gueldenstaedtis diversifolia*, *Ligularia virgaurea*	25–35	60–85
6	26	*K. capillifolia*	5–20	Forbs and grasses	5–10	10–35

Buresh *et al*. (1982) were employed to measure soil available P and N, respectively.

The richness index, Shannon–Wiener index and Pielou index were calculated according to the diversity and evenness indices (Ma and Liu 1994), as follows:

$$\text{Richness index : R} = \text{S};$$

Shannon–Wiener index :

$$H' = -\sum_{i=1}^{s} P_i Ln P_i;$$

Pielou index :

$$J = \left(-\sum_{i=1}^{s} P_i L_n P_i\right) / L_n S,$$

where P_i stands for relative importance value of species i (P_i = (relative cover + relative height + relative frequency)/3), S is the species number of the sampling quadrats.

Statistical analysis

The data obtained from the experiments described above were analysed with SPSS version 10.0 (SPSS Incorporated 2000).

Results and discussion

Characteristics of the plant community

Species number, and the cover of dominant and subdominant species and the plant community varied greatly with altitude (Table 2). The *Kobresia tibetica* swamp meadow was found at the lowest altitude (3840 m), where the community structure was simple and the most of vegetation was contributed by perennial meadow species. At the second altitude (3856 m) *Stipa aliena* was dominant and the subdominant species was *Scirpus distigmaticus*. *K. pygmaea* dominated the communities at the third (3927 m), the fourth (3988 m) and the fifth (4233 m) altitudes. *K. capillifolia* meadow was found at the sixth and highest altitude (4435 m). This community structure was relatively simple compared with the others (Table 2).

Seasonal pattern of change in aboveground and belowground biomass at different altitudes

Figure 1 shows a clear variation in aboveground biomass within the growing season and between sites. There was a progressive decrease in biomass in each month with increasing altitude and a delay in the commencement of rapid growth at the higher altitudes. Across all sites, biomass in August was significantly ($P < 0.05$) greater than at other times in the growing season, and between sites it decreased from 368.4 g m^{-2} at 3840-m altitude to 119.6 g m^{-2} at 4435 m (Fig. 1).

Air temperature appeared to be the single most important factor determining the biomass production of the alpine vegetation. For example, the aboveground biomass in August was closely related to August mean temperature (Fig. 2). This association would reflect the patterns of both temperature variation and productivity during the growth season (Fig. 1).

The seasonal course of belowground biomass at each altitude was approximately V-shaped, with greater values ($P < 0.05$) at the start (May) and the end (September) of the growing period (Fig. 3), and values at the lowest altitude that were significantly greater ($P < 0.01$) than those at other sites. *Kobresia tibetica*, the dominant species at the 3840-m site, has a large rhizome and much a more extensive root system than species at the other sites, but belowground biomass at the highest altitude (4435 m) was also greater ($P < 0.05$) than at the four middle levels. Minimum belowground biomass occurred in late June when the plants were growing very actively about 1 month after re-greening

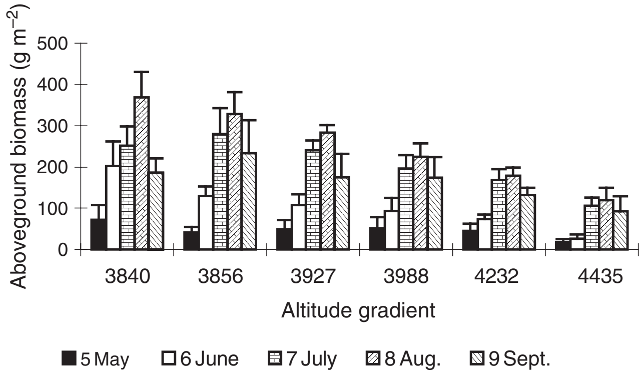

Fig. 1. Seasonal dynamics of the aboveground biomass at six altitudes in an alpine rangeland.

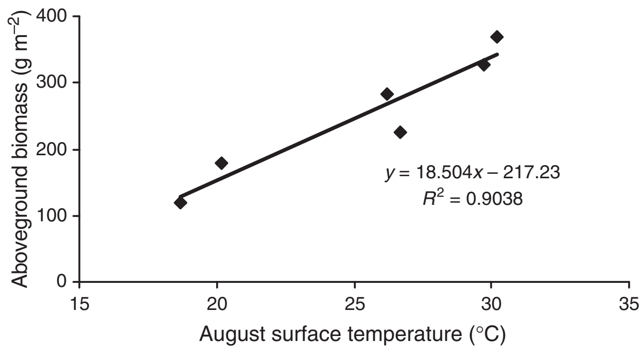

Fig. 2. The relationship between aboveground biomass and the surface temperature in alpine-rangeland sites in August.

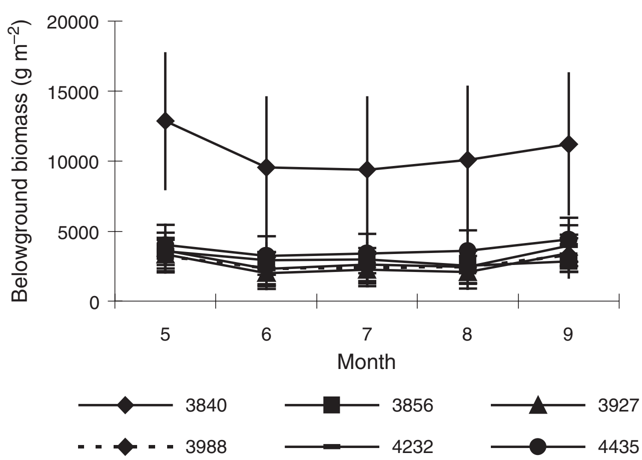

Fig. 3. Seasonal dynamics of the underground biomass at six altitudes in an alpine rangeland.

in spring. This growth would consume reserves stored in the roots and rhizomes in the previous autumn. Precipitation and temperature favoured plant growth in July, so that although plants were flowering (grasses and forbs) or seeding (sedges), some photosynthetic production would be transferred into the belowground parts, leading to some increase in the underground biomass.

Characteristics and diversity of the six communities in the altitudinal gradient

Change in diversity

The trend of the Shannon–Wiener diversity index was similar to that of species richness from the second site (3856 m) to the fifth site (4232 m) (Table 3). However, there was lower richness, evenness and diversity at the lowest- (3840 m) and the highest-altitude (4435 m) sites than at the four other altitudes. Each of the highest and lowest communities had a single dominant species that resulted in reduced evenness and diversity whereas multi-dominant species communities led to higher richness, evenness and diversity at the four middle-altitude sites (Table 2). Species richness showed similar relationships that are the approximately inverse of soil organic matter, moisture and nutrient contents at the six altitudes (Table 3).

Relationship between biomass and diversity

The highest species number, diversity index and evenness index were found in intermediate aboveground-biomass microhabitats (Table 3), although there was no indication of a simple relationship between species richness and aboveground biomass (Fig. 4). Soil organic matter, nutrients and soil moisture contents were greatest at the lowest- (3840 m) and highest-altitude (4435 m) sites (Table 3). The relatively high nutrient availability made a few species so robust that the less vigorous species were excluded. At the sites with lower nutrient availabilities, the growth of all species was restricted and there was space for the survival of the less vigorous species so that competitive exclusion did not occur. Although aboveground biomass decreased with increasing altitude, the highest biomass (aboveground plus belowground biomass) occurred at the lowest- (3840 m) and highest-altitude sites (4435 m), both of which had high soil nutrient concentrations. The ability of a species to utilise resources becomes more important in the presence of high nutrient availabilities, so the plant species that can grow taller and more quickly will become more abundant. In the present situation, tolerance of waterlogged conditions would also be important at the lowest- and highest-altitude sites.

It is important to differentiate between aboveground and belowground biomass when considering the relationships between plant diversity and biomass. A unimodal curve describes the relationship between plant diversity and aboveground biomass (Fig. 4), but there is a close negative linear relationship between the plant-species richness and belowground biomass for all sites except the lowest-altitude site (Fig. 5). This result suggests that belowground biomass has a greater influence on plant diversity than does aboveground biomass. Sampling belowground biomass has been limited and field studies of the relationships between biodiversity and ecosystem function have focused mainly on aboveground productivity or aboveground biomass.

Some authors have indicated that species composition (the consequence of species' biology) controls ecosystem functioning (Huston 1997; Huston *et al*. 2000; Grime 1997; Wardle 1998; Tilman *et al*. 1997*a*; Tilman 1999). Soil moisture content was highest in the *Kobresia tibetica* swamp meadow (the lowest-altitude site); excessive water would lead to decreased spatial heterogeneity in nutrient resources, to decreased spatial complexity in resource ratios and to increased intraspecific and interspecific competition. Competition is a much more important factor in high-biomass habitats (Abrams 1995; Bonser and Reader 1995), and it is possible for a few highly dominant species to inhibit germination or outcompete existing species, causing local extinctions at these microsites (Abrams 1995). He *et al*. (2003) proposed that a plant community could be considered as a unit that comprises many different populations in a given spatial and temporal context, so that when the plant density increases, species richness would decrease proportionally. In this case, the community would be described as having a

Table 3. Environmental parameters, soil characteristics and plant-species diversity indices (mean ± s.d.) at six altitudes on Beishan Mountain

Values indicate means and standard deviations for each site. Radiation indicates radiation at noon on a cloudless day (this is a instantaneous value)

Variable	Attribute	Altitude of the site (m)					
		3840	3856	3927	3988	4232	4435
X_1	Radiation (W m^{-2})	1.33 ± 0.09	1.35 ± 0.11	1.40 ± 0.11	1.50 ± 0.16	1.49 ± 0.11	1.22 ± 0.14
X_2	Reflected radiation (W m^{-2})	0.07 ± 0.01	0.07 ± 0.02	0.07 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.04 ± 0.01
X_3	Soil surface temperature (°C)	30.2 ± 2.40	29.7 ± 1.58	26.2 ± 2.02	26.7 ± 2.88	20.2 ± 0.25	18.7 ± 3.47
X_4	Soil temperature (0–30 cm) (°C)	13.5 ± 3.31	13.0 ± 1.87	13.3 ± 1.44	12.2 ± 2.35	11.6 ± 3.32	7.9 ± 0.00
X_5	Surface moisture (%)	60.0 ± 0.36	45.1 ± 3.85	47.7 ± 2.31	48.6 ± 6.07	54.5 ± 1.09	58.3 ± 2.50
X_6	Soil moisture (0–30 cm) (%)	89.7 ± 13.78	33.6 ± 7.71	24.9 ± 9.12	35.7 ± 7.00	50.0 ± 4.89	80.0 ± 18.36
X_7	Soil organic matter (%)	11.3 ± 0.94	6.4 ± 1.14	4.3 ± 2.41	6.2 ± 1.52	7.7 ± 2.31	16.5 ± 2.13
X_8	Soil total N (%)	0.56 ± 0.06	0.30 ± 0.01	0.18 ± 0.02	0.20 ± 0.02	0.31 ± 0.13	0.76 ± 0.04
X_9	Soil total P (%)	0.10 ± 0.05	0.07 ± 0.004	0.06 ± 0.03	0.06 ± 0.04	0.08 ± 0.07	0.10 ± 0.06
X_{10}	Soil available N (mg kg^{-1})	36.1 ± 8.78	16.9 ± 0.86	15.4 ± 4.68	18.6 ± 3.23	20.7 ± 6.41	44.9 ± 3.06
X_{11}	Soil available P (mg kg^{-1})	4.31 ± 1.12	2.78 ± 1.18	2.12 ± 1.35	2.33 ± 1.79	2.94 ± 1.14	6.09 ± 1.79
X_{12}	Species richness	34.5 ± 0.71	37.0 ± 0.00	41.5 ± 0.71	39.5 ± 0.71	39.5 ± 0.71	26.5 ± 0.71
X_{13}	Shannon–Wiener index	3.1 ± 0.068	3.4 ± 0.001	3.5 ± 0.002	3.4 ± 0.0001	3.3 ± 0.007	2.8 ± 0.003
X_{14}	Pielou index	0.89 ± 0.023	0.93 ± 0.000	0.94 ± 0.004	0.92 ± 0.012	0.91 ± 0.004	0.85 ± 0.007

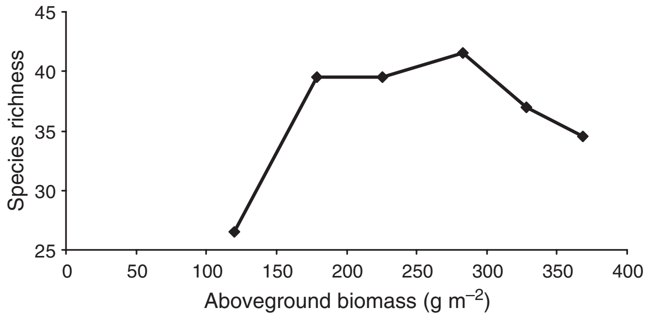

Fig. 4. Relationship between species richness and aboveground biomass in August.

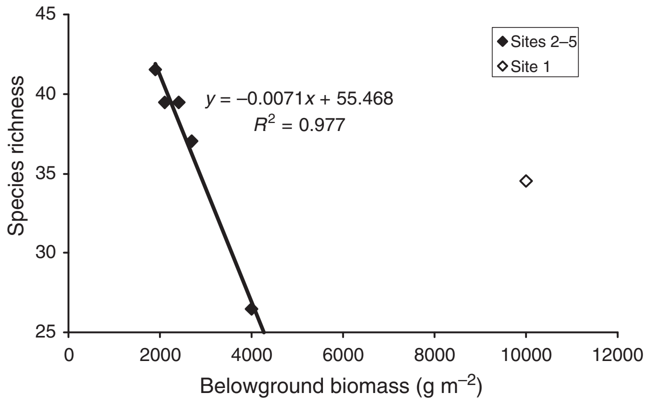

Fig. 5. Relationship between species richness and belowground biomass in August. There is a close negative linear relationship between these variables at the lowest-altitude site, except for the lowest-altitude site indicated with an open symbol.

'weak' competitive ability to utilise resources. Tilman *et al.* (1997*b*) indicated that niche-complementary effects resulted from interspecific differences in resource requirements. Pacala and Tilman (2002) suggested that niche complementarity was a long-term mechanism that maintained species diversity and ecosystem function. With increasing plant density, dominance would increase in a community, probably leading to a single dominant population. It was proposed that diversity would decline in the community, but the evenness and dominance would be enhanced. This explanation could account for the occurrence of *Kobresia tibetica* as a single dominant species at the lowest altitude.

The lowest aboveground biomass production and the second highest belowground biomass occurred at the highest-altitude site (4435 m). The reasons for this could be the following: (1) the air temperatures at the highest altitude were lower than at other sites (Table 3), resulting in a later commencement and an earlier cessation of seasonal growth; or (2) topography may have a greater effect on snowpack accumulation and hence growing-season length, soil water availability and the distribution of plants at the highest-altitude site than at other sites. The features developed on alpine meadow might be a phenomenon of an adaptation to the harsh alpine environment. Although the experimental sites were affected by grazing activity, this may not have been the main perturbation as animals graze on those grasslands only in winter and spring (Long *et al.* 1999).

Soil nutrients at different altitudes

Table 3 shows that soil organic matter, and total and available N and P contents were greater at the lowest and highest altitudes than elsewhere. These were consistent with the distribution of belowground biomass. The vegetation type at the lowest altitude was *Kobresia tibetica* swamp meadow. At this level most small soil pores were filled with water, resulting in restricted aeration and reduced microbial decomposition of soil organic matter. Zhu (1982) also indicated that a lower mineralisation rate in soil organic matter resulted in a higher proportion of soil organic matter being accumulated and preserved. Also, owing to lower temperatures at the most elevated site, slower mineralisation of soil organic matter may have resulted in a higher proportion of soil organic matter being accumulated and preserved.

Relationship between diversity, productivity and environmental factors

Soil organic matter content at the six sites was closely related to soil moisture and temperature (Fig. 6), and soil available N and P increased with increasing soil organic matter content (Figs 7, 8). The extent of change in an environmental gradient is therefore a key factor in the development of the species richness–biomass relationship. Gough *et al.* (2000) found that aboveground net primary productivity increased and plant-species density decreased following addition of N, although considerable variation characterised the magnitude of the response. Significant negative correlations were found between species richness and soil organic matter, soil available N and soil available P in the present study (Figs 9, 10, 11). Similar results were obtained when Shannon–Wiener and Pielou indices were compared with soil available P (Figs 12, 13). It is possible that the soil resources (organic matter, and available N and P) could determine species richness indirectly. Fridley (2002) indicated that community productivity was affected significantly by soil fertility, species diversity and species composition. The positive effect of species diversity on productivity was less in quadrats with lower nutrient availability than in those with higher nutrient availability. In order to further examine the relationship between soil characteristics and diversity index, we followed changes in aboveground biomass of plant communities and environmental factors (presented in Table 3). Stepwise regression analyses of aboveground biomass (Y_a) and Shannon–Wiener index (Y_b) against soil-surface temperature (X_3) and soil organic matter content (X_7) provided the best predictors of variations in the two plant-community characteristics:

$$Y_a = -215.00 + 18.414\,X_3;\ F = 38.283;\ P = 0.05;$$

$$Y_b = 3.742 - 0.057X_7;\ F = 881.063;\ P = 0.001.$$

The contents of carbon, N and P in soil are related not only to temperature and precipitation, but also to soil type, vegetation characteristics, utilisation patterns and human disturbance (Wang *et al.* 2002). Soil nutrient concentrations at the lowest and highest altitudes were greater than at other altitudes. This difference may explain why the total biomass

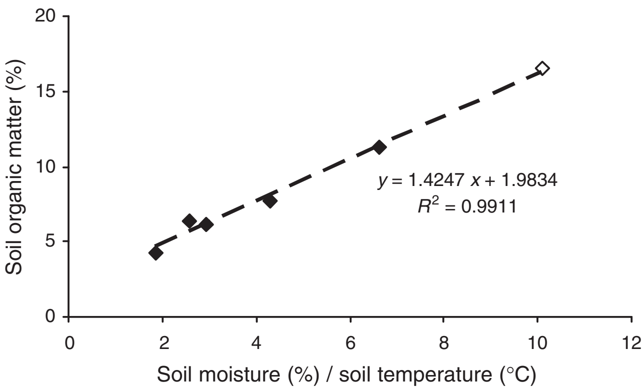

Fig. 6. Relationship between soil organic matter and soil moisture and soil temperature along an altitudinal gradient in alpine rangeland. The value for the lowest-altitude site is indicated with an open symbol.

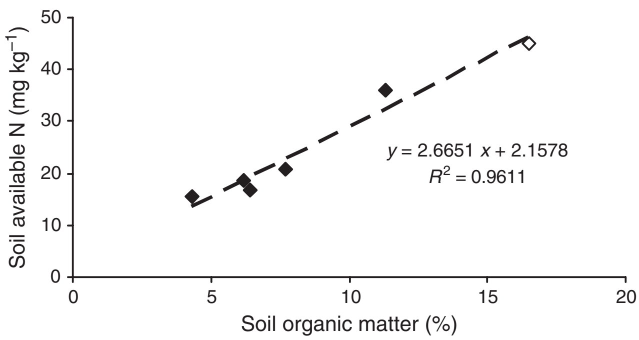

Fig. 7. Relationship between soil N and soil available organic matter along altitudinal gradient in an alpine rangeland. The value for the lowest-altitude site is indicated with an open symbol.

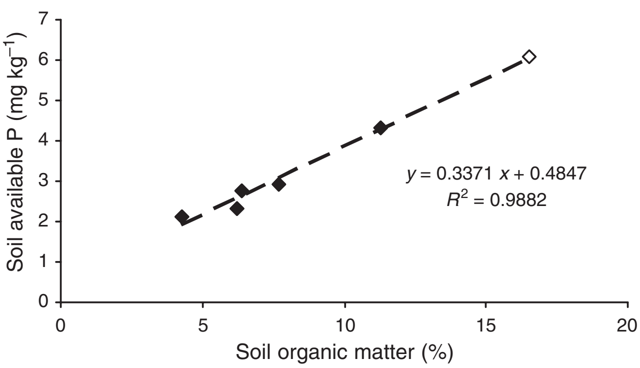

Fig. 8. Relationship between soil available P and soil organic matter along altitudinal gradient in an alpine rangeland. The value for the lowest-altitude site is indicated with an open symbol.

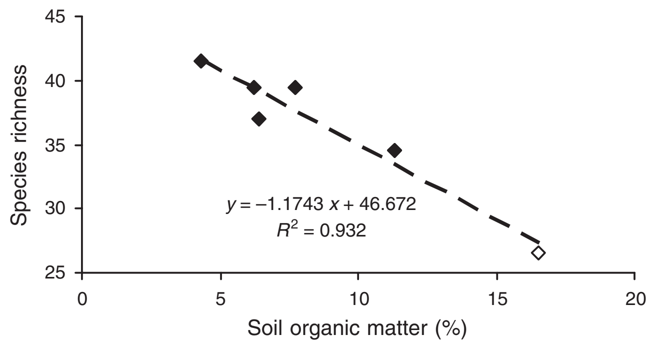

Fig. 9. Relationship between species richness and soil organic matter along an altitudinal gradient in an alpine rangeland. The value for the lowest-altitude site is indicated with an open symbol.

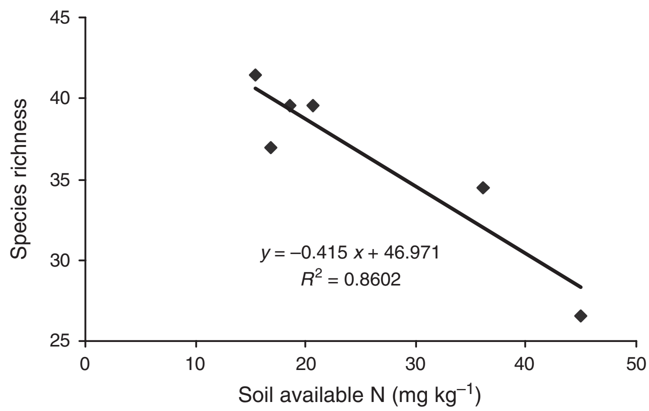

Fig. 10. Relationship between species richness and soil available N along an altitudinal gradient in an alpine rangeland.

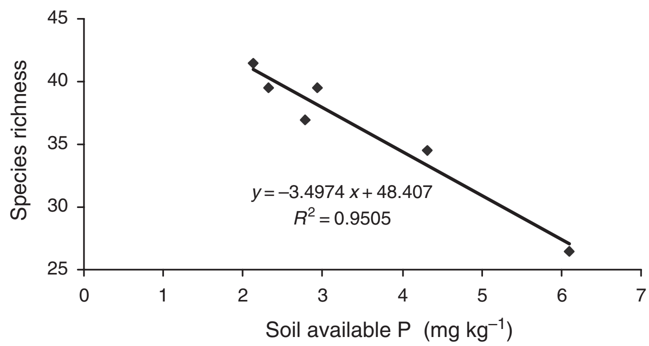

Fig. 11. Relationship between species richness and soil available P along an altitudinal gradient in al alpine rangeland.

(above- plus belowground) increased, while species numbers decreased. The findings of this study are consistent with those of Tilman (1987) who showed that total biomass of a community increased while species diversity was reduced by fertilisation. The two habitats of low diversity were wet, so that the nutritional environment might be expected to be more uniform than in the dry habitats. That might mean a smaller number of niches in the wet than dry habitats, and a greater tendency to dominance by a few species that are able to tolerate low soil aeration. In the alpine meadow, the relationship between species diversity and productivity was influenced by species selection, resource competition and environmental factors i.e. water and temperature.

Conclusion

The six sites, spanning altitudes from 3840 to 4435 m and surface soil water contents from 45 to 60% in August, showed linear correlations between diversity, evenness, species number and soil resources as well as between diversity, evenness, species

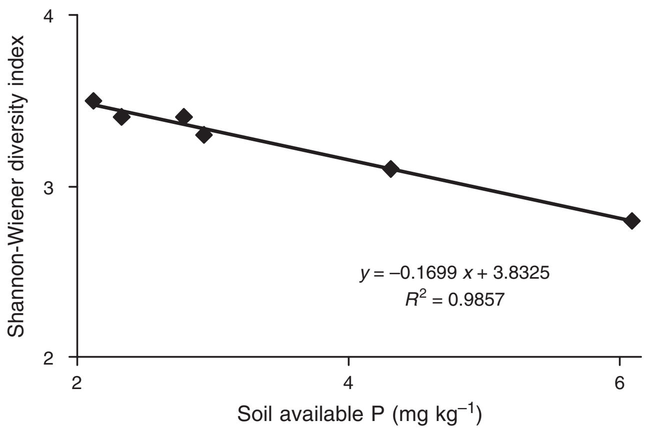

Fig. 12. Relationship between diversity index and soil available P along an altitudinal gradient in an alpine rangeland.

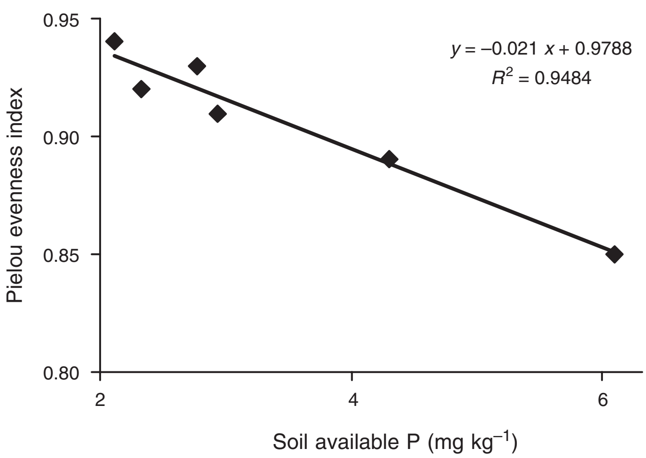

Fig. 13. Relationship between diversity index and soil available P along an altitudinal gradient in alpine rangeland.

number and aboveground biomass. Biodiversity of the Qinghai–Tibetan plateau rangelands is also a result of many factors, particularly of imposed stresses such as year-round grazing. Therefore, further studies should focus on the effects of grazing pressures on the interactions among plant-species diversity, richness, evenness and ecosystem function. These studies should also attempt to clarify the extent to which, in alpine rangelands, species diversity is affected by community productivity, or community productivity is influenced by species diversity. Much work remains to be done to better understand the effect of the soil nutrient content on diversity and ecosystem functions, particularly in regard to the discrepancy between the biodiversity of artificially established vegetation communities and that of natural vegetation communities, which are affected by soil heterogeneity.

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