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Status and Dynamics of the *Kobresia pygmaea* Ecosystem on the Tibetan Plateau

This paper provides information about the distribution, structure, and ecology of the world's largest alpine ecosystem, the *Kobresia pygmaea* pastures in the southeastern Tibetan plateau. The environmental importance of these Cyperaceae mats derives from the extremely firm turf, which protects large surfaces against erosion, including the headwaters of the Huang He, Yangtze, Mekong, Salween, and Brahmaputra. The emphasis of the present article is on the climate-driven evolution and recent dynamics of these mats under the grazing impact of small mammals and livestock. Considering pedological analyses, radiocarbon datings, and results from exclosure experiments, we hypothesize that the majority of *K. pygmaea* mats are human-induced and replace forests, scrub, and taller grasslands. At present, the carrying capacity is increasingly exceeded, and reinforced settlement of nomads threatens this ecosystem especially in its drier part, where small mammals become strong competitors with livestock and the removal of the turf is irreversible. Examples of rehabilitation measures are given.

INTRODUCTION

Environmental changes in the Tibetan highlands are of undisputed significance for the global climate (1, 2). In a regional scale any destructive impacts on the vegetation cover of the highlands may furthermore put one-quarter of the world's population living in the surrounding lowlands at risk (3) because the upper catchments of the Huang He, Yangtze, Salween, Mekong, and partly of the Brahmaputra are largely situated in a pastoral ecosystem formed of mats of *Kobresia pygmaea* (Cyperaceae). These pastures are widely supposed to be natural (4, 5, 6). The intention of the present descriptive paper is to present a holistic introduction to the world's largest alpine formation and to raise awareness of the complexity of human-dependent and climate-driven plant-animal interactions. The focus is on questions of the evolution and dynamics of this ecosystem under human's impact.

Plant names follow *Flora Xizangica* (7) and *Flora Qinghaiica* (8).

STRUCTURE AND ENVIRONMENT OF *K. PYGMAEA* MATS

Distribution, Climate, and Weather

Alpine Cyperaceae mats of *K. pygmaea* dominate the southeastern humid Tibetan highlands and the high alpine pastures of the southern and eastern declivity (Fig. 1). In the more arid northwest of the highlands, open short grass steppe with cushions ("Alpine Steppe") prevail.

The *K. pygmaea* ecosystem is the only larger vegetation unit of the Tibetan plateau that forms a closed vegetation cover of Cyperaceae turf. The mats consist of *K. pygmaea,* the smallest of the High Asian Cyperaceae, mostly growing not more than 2 cm tall but dominating mats with up to 90% cover or more

(Table 1). It is thus justified to speak simply of *K. pygmaea* mats. The lowest *K. pygmaea* mats are found on sunny slopes of the montane belt down to 3000 m in the northeast and 4000 m in the eastern and southern declivity. The highest outposts have been found on the north slope of Mt. Everest at 5960 m (9). The area of *K. pygmaea* communities includes surfaces derived from *K. pygmaea* turf, which may largely be colonized by Cyanophyceae, lichens, and cushion plants at present, only with remains of *K. pygmaea* covering often less than 5% of the turf. Including all of these degradation stages, the total area comprises ca. 450 000 km^2.

The hygric range of *Kobresia* pastures as mapped in Figure 1 is difficult to assess, not only because of a lack of data, but to a greater extent because of uncertainties about the vegetation dynamics affecting *K. pygmaea* pastures. This area may receive between more than 1000 mm y^{-1} precipitation in the east and less than 200 mm y^{-1} in western Tibet. The climatic data of Amdo and Nagqu may represent the core area of *K. pygmaea* mats, with summer precipitation ranging between 400 mm y^{-1} in the intramontane basins and probably 800 mm y^{-1} at higher elevations.

Although summer precipitation prevails, heavy snowfall may occur between December and March. This causes catastrophic losses of livestock and small mammals (10), whereas wild ungulates are obviously better adapted (11). However, long-lasting snow cover is not an important ecological factor, at least so far as can be deduced from the absence of snow-cover–dependent plant communities (e.g., snow beds). In summer, drizzling rainfall with wind originates from advective disturbances, which may last for several days; at altitudes above 5000 m slush is common. During fair weather conditions thunderstorms with hail occur regularly in the afternoon, leaving patches of the slopes covered by hail, which melts the following day.

Between November and March the turf remains frozen. Night frosts are regular in spring (March to May) and autumn (September to November). *Kobresia* pastures above 4700 m, however, experience night frosts throughout the whole growing season. Needle-ice solifluction is thus common if the silty soils are moist. Mean monthly temperatures between November and February are below −10°, and mean minimum temperatures in January can be lower than −30°C, especially in areas of cold air pooling in intramontane basins.

Air temperatures during summer attain values between 15°C and 18°C in the 10-cm layer above the surface. The turf cover itself has a strongly insulating effect, and it is quite probable that winter temperatures below a closed turf cover do not drop far below 0°C.

Vegetation Structure and Floristic Composition

The structure of the *K. pygmaea* mats includes pure and completely closed Cyperaceae mats as well as cushion-dominated communities (*Arenaria bryophylla, Arenaria kansuensis, Androsace tapete, Leontopodium nanum*) or almost barren turfs colonized by different lichen life forms between decaying remains of flowering plants. In the core area, cover of *K. pygmaea* is 90% to 98%, resulting in a carpet with only 8 to 10
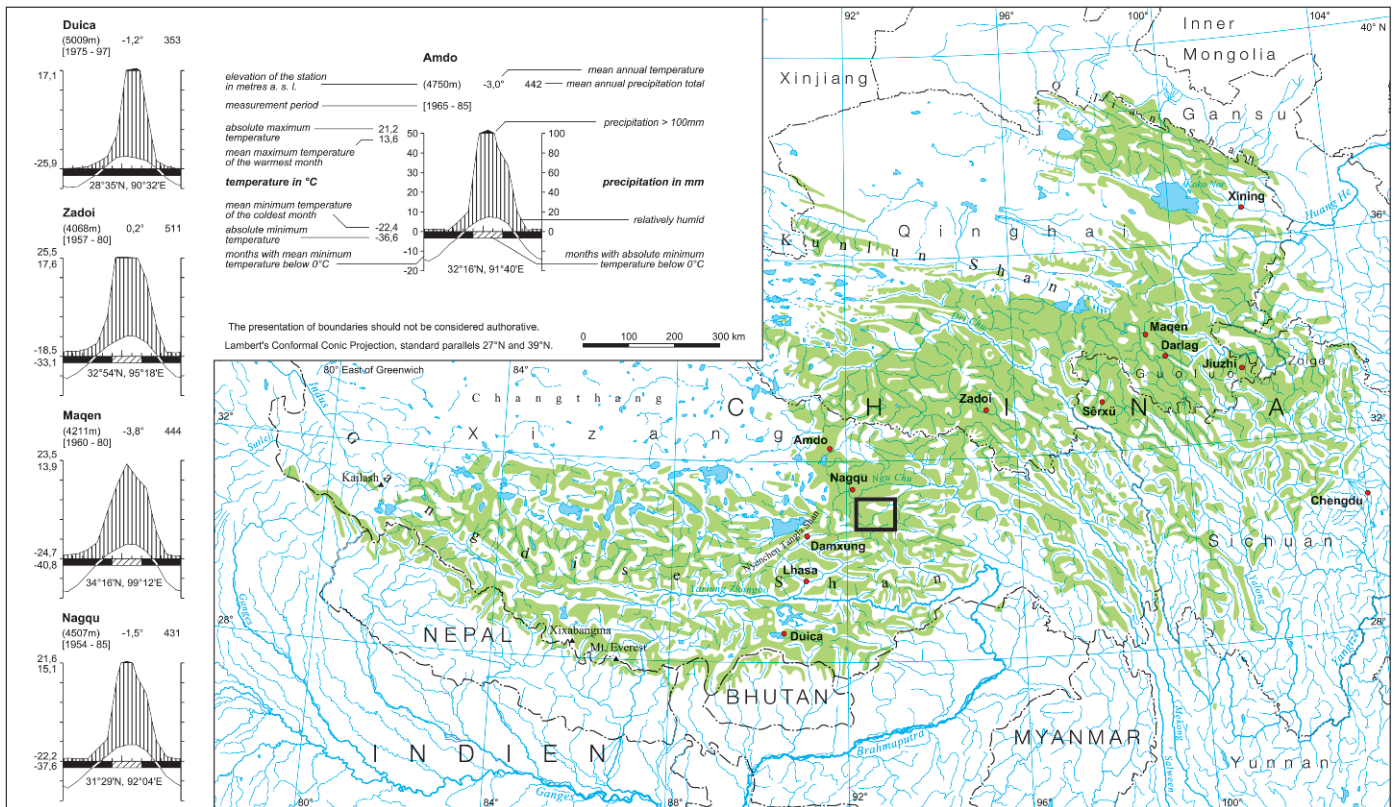
Figure 1. Distribution of the *Kobresia pygmaea* pastures (shaded) in the Tibetan highlands and the Himalayas (from references 12, 56–61, changed; own inventories 1976–2007). The total cover is ca. 450 000 km². Climatic diagrams from the *Kobresia* pasture area after data of the Meteorological Administration of China, as cited (39). The area of the records is marked with a black frame.

additional, mostly tiny annual or biennial rosette species; mosses (mostly Pottiaceae) cover no more than 5%, and lichens are nearly absent. These typus records of the *K. pygmaea* association refer to sites east of Nagqu, between 30°48′ to 31°08′N and 92°18′ to 92°35′E (see Fig. 1) in altitudes between 4600 and 5100 m (Table 1).

Today less than one-quarter of the turf-covered domain has closed *K. pygmaea* mats as represented by Table 1. In the remaining parts, most *K. pygmaea* communities have a complex structure and are richer in species, in consequence of processes changing the Cyperaceae mats into ecotonal mosaics including species of alpine steppes or gelifluction-adapted communities. The most widespread pattern is created by polygonal cracks: the turf cliffs and the space between the sods are colonized by rosettes and cushions favored here by higher humidity, wind-shelter of the depression, and possibly nutrient accumulation between the exposed turfs. The fragmentation process by polygonal cracks is probably an initiation stage for the development of turf exfoliation cliffs.

Polygonal cracks have been explained by heavy frost (12), which may well be true, but if sites from all over the highlands are compared, the following findings suggest desiccation:

– In neighboring sites turf layers on wet sites are homogenous, whereas turfs along streams which recently dried out show polygonal cracks.
– If low temperatures are exclusively responsible for causing the cracks, sunny as well as shady slopes should be affected and there should be an obvious gradient with increasing altitude. This was not the case: turfs at lower altitude and on sunny slopes were separated by wider cracks than turfs at their upper limit and on shady slopes.

A second destructive process is gelifluction, taking place in the course of cooler periods with an increased number of frost events. This affects first the highest turfs of the ecotone between Cyperaceae mats and the free gelifluction belt (13). The turf is either overridden by screes, or frost heaves break up the turf. This depression of altitudinal belts can be correlated with a depression in temperature of 0.6–1.2° during the period of 1951–1980 (14). If the turf is exposed on cliffs because of the destructive chafing habits of yaks or solifluction, the cliffs usually are only colonized by pottiaceous mosses and crustose lichens. The margins of the turf are strongly exposed to desiccation and cooling effects of wind. In addition, cliffs are exposed to deflation and/or corrasion: in the rainshadow of the Main Himalayan range southerly föhn winds destroy the turf along strictly south-facing cliffs, leaving behind open sands that successively become closed stone pavements (13). In western Tibet active cliffs (devoid of mosses, lichens, and Cyanophy-

In undisturbed level sites *Kobresia pygmaea* covers 98% of a closed golf-course–like sedge mat, only 2 cm high. 31°00′N/92°32′E, 4810 m. September 1995. (Photo: G. Miehe)

Table 1. Vegetation records from the *Kobresia pygmaea* core area. Cover degree is given as a percentage. Plus sign indicates <1% cover, r = only 1 record. Plot size 10 × 10 m.

	Record number											Frequency Species (cover) with only one record*
	1	2	3	4	5	6	7	8	9	10	11	
Number of flowering species	9	11	20	15	26	14	18	18	16	22	11	
Kobresia pygmaea	90	75	80	90	70	96	95	95	90	93	98	100
Potentilla saundersiana	·	+	3	3	+	4	2	+	1	1	+	91
Cortiella caespitosa	·	·	·	+	+	+	+	+	+	+	+	73
Aster flaccidus	·	·	r	2	+	·	r	1	1	+	+	73
Primula walshii	·	+	+	+	+	·	+	+	+	+	·	73
Saussurea leontodontoides	·	+	+	2	+	·	+	2	+	1	·	73
Potentilla bifurca s.l.	+	2	·	·	·	·	·	·	·	·	+	27
Androsace tapete	+	4	3	·	8	·	+	+	1	+	·	73
Astragalus strictus	·	+	+	+	·	+	+	+	·	·	·	55
Kobresia vidua	·	3	+	·	+	·	+	+	·	·	·	46
Kobresia royleana	+	+	+	+	+	·	+	+	·	·	·	64
Thalictrum alpinum	+	·	·	·	+	·	+	+	·	·	·	36
Potentilla fruticosa v. *Pumila*	2	·	·	·	·	3	·	·	·	·	·	18
Gentiana sp. indet.	·	+	+	+	2	·	·	·	·	·	·	36
Pedicularis muscoides	·	+	+	+	·	·	·	·	·	·	·	27
Poa attenuata	·	·	+	+	·	·	·	·	·	·	·	18
Taraxacum sp. indet.	·	·	+	+	·	·	·	·	r	·	·	27
Anaphalis xylorhiza	·	·	·	·	+	·	·	·	+	·	·	18
Arenaria bryophylla	·	·	·	·	10	r	·	·	·	·	·	18
Trisetum spicatum	·	·	·	·	+	+	·	·	·	·	·	18
Oreosolen wattii	·	·	+	+	+	+	·	·	·	+	·	46
Saussurea graminea	·	·	+	·	8	+	·	+	·	+	·	46
Ranunculus brotherusii	·	·	+	·	·	·	·	+	·	·	+	27
Sibbaldianthe adpressa	·	·	·	+	·	·	·	·	+	+	+	46
Phlomis rotata	·	·	·	+	·	·	·	+	·	+	·	27
Kobresia humilis	·	·	·	·	·	·	+	+	·	1	·	27
Oxytropis pauciflora	·	·	·	·	·	·	+	·	+	+	·	27
Gentiana pseudoaquatica	·	·	·	·	·	+	+	·	+	+	·	36
Veronica ciliata	·	·	·	·	·	·	+	+	+	·	1	36
Pedicularis roylei	·	·	·	·	·	+	+	+	+	·	·	36
Leontopodium nanum	·	·	·	·	·	+	·	+	·	+	·	27
Festuca forrestii	·	·	·	·	·	+	·	·	·	1	+	27
Kobresia capillifolia	·	·	·	·	·	+	·	·	·	+	+	27
Potentilla exigua	·	·	·	·	·	·	·	·	+	·	1	18
Microcaryum pygmaeum	·	·	·	·	·	·	·	·	+	+	·	18
Musci	·	·	1	3	+	·	·	·	·	·	·	27
Lichenes	·	·	1	·	1	·	·	·	·	·	·	18

Location of record number: 1) Level pasture, herb layer 85%, 0.1–3 cm tall. Loess covered gravel terrace. 4700 m asl, 31°08′N/92°18′E. 2) 5°S-exposed pasture, herb layer 90%, 0.2–2 cm tall. Loess covered ground moraine. 4930 m asl, 30°45′N/92°52′E. 3) 2°S-exposed pasture, herb layer 85%, 0.1–2 cm tall. Loess covered ground moraine. 4810 m asl, 31°00′N/92°32′E. 4) 1°S-exposed pasture, herb layer 95%, 0.1–2 cm tall. Loess covered ground moraine. 4770 m asl, 30°48′N/92°35′E. 5) 1°S-exposed pasture, herb layer 90%, 0.1–3 cm tall. Ground moraine. 5100 m asl, 31°02′N/92°28′E. 6) Level pasture, herb layer 98%, 0.1–2 cm tall. Gravel of terrace. 4620 m asl, 31°07′N/92°15′E. 7) Level pasture, herb layer 100%, 0.1–2 cm tall. Sand and gravel of terrace. 4750 m asl, 30°48′N/92°35′E. 8) 3°S-exposed pasture, herb layer 97%, 0.1–3 cm tall. Loess covered gravel terrace. 4750 m asl, 30°48′N/92°35′E. 9) 2°S-exposed pasture, herb layer 95%, 0.1–2 cm tall. Loess covered pediment. 4770 m asl, 30°48′N/92°35′E. 10) 6°S-exposed pasture, herb layer 98%, 0.1–2 cm tall. Loess covered gravel terrace. 4750 m asl, 30°48′N/92°35′E. 11) 2°S-exposed pasture, herb layer 100%, 0.1–2 cm tall. Loess covered gravel terrace. 4750 m asl, 30°48′N/92°35′E. * 1) *Gentiana* cf. *lawrencei* var. *farreri*: 2; *Stipa roohmooiana*: 1; *Carex melanantha*: +; 3) *Hippolytia kennedyi*: +; *Oxytropis humifusca*: +; 5) *Anemone imbricata*: +; *Comastoma* sp. indet.: +; *Lagotis brevituba*: +; *Oxytropis reniformis*: 2; *Pedicularis nana*: +; *Rheum pumilum*: +; *Saxifraga sinomontana*: +; *Stipa concinna*: 1; 6) *Kobresia pusilla*: 6; 7) *Carex przewalskii*: +; *Gentiana micantiformis*: +; 10) Brassicaeae 04-55-13: +; *Festuca tibetica*: +; *Stipa regeliana*: +.

Polygons of ca. 1 m in diameter have cracked the *Kobresia* turf. The depressions are colonized with moisture-demanding disturbance indicator plants. Soil-dwelling small mammals (*Ochotona curzoniae*) dug their burrows in the polygon junctions and profit from the insulating turf. 29°00′N/91°04′E, 4740 m. September 2002. (Photo: G. Miehe)

On slopes turf cliffs have developed after solifluction separated the polygon-cracked turf cover. Chafing by livestock, turf exfoliation (needle ice plus deflation), and *Ochotona curzoniae* promote the expansion of open soil. The open soil in front of the cliff is colonized by endemic disturbance indicator pioneer plants. 32°43′N/91°52′E, 5120 m. August 1993. (Photo: G. Miehe)

Isolated *Kobresia* turf bears witness to the change from a once closed sedge turf to an open scree slope. Trampling, chafing, and turf exfoliation corrode the turf cliffs uphill while solifluction-moved scree overruns the turf from above. 28°50′N/90°24′E, 4520 m. September 1998. (Photo: G. Miehe)

Figure 2. Livestock numbers 1952–1998 in selected counties of the eastern Tibetan highlands. After (21), changed.

ceae) face west, being corraded by winter winds from this direction. Cliffs not exposed to corrasion are abandoned by *K. pygmaea* and successively colonized by plant species from the surrounding communities of alpine steppe such as *Stipa purpurea, Incarvillea younghusbandii, Saussurea graminea, A. tapete,* and *Carex montis-everestii.* If the turf cover is completely removed, the open sandy or silty substrate is colonized by cushions of high alpine or steppe origin, unpalatable tall forbs (*Aconitum flavum, A. gymnandrum, Rheum* spp., and quite often by *Urtica hyperborea*), or rosettes spreading from wastelands or open soils (*Oreosolen wattii, Microcaryum pygmaeum, Microula tibetica, Eritrichium microcarpum, Lasiocaryum densiflorum, Lancea tibetica, Lagotis brachystachya, Potentilla bifurca, Microgynoecium tibeticum, Przewalskia tangutica, Pomatosace filicula,* and *Persicaria glacialis*). These pioneer communities have a high percentage of endemic monotypic genera. Toward the arid western periphery of the *K. pygmaea* ecosystem, the turfs are often covered merely by a few remaining isolated *K. pygmaea* tufts, carpets of crustose lichens, and tiny rosettes of *Artemisia minor* and *Anaphalis xylorhiza.*

Plant-Animal Interactions

All ecosystems of the Tibetan highlands are influenced by herbivores. Even the highest plant communities rising up to 6000 m are under considerable competitive grazing pressure from Tibetan snowcock (*Tetraogallus tibetanus*), pika (*Ochotona curzoniae*), blue sheep (*Pseudois nayaur*), argali (*Ovis ammon*), and yak (*Phoepagus grunniens*).

Larger wild herbivores for the most part have become extinct during the last 50 y. At the same time, grazing pressure from livestock has increased (Fig. 2). Nothing is known about the impact of small mammals in the past. Issues of plant-animal interactions or even coevolution have so far not been raised in Tibet. A striking feature, however, is that the *K. pygmaea* ecosystem consists largely of species that are beyond the grazing reach of larger herbivores. The common flat hemispherical cushions of *A. tapete* or *A. bryophylla* or *Arenaria polytrichoides* are in any case not suitable for grazing, and nearly all rosette plants are beyond the reach of goats, sheep, yaks, or wild ungulates. Among the grasses and sedges known from the area (7, 8) only four minute species have their main aboveground phytomass beyond the grazing reach of livestock and game (*K. pygmaea, Kobresia yadongensis, Carex sagaensis, Carex tangulashanensis*). Two of them are even hardly known, *C. sagaensis* is found in Cyperaceae swamps and only *K. pygmaea* gains
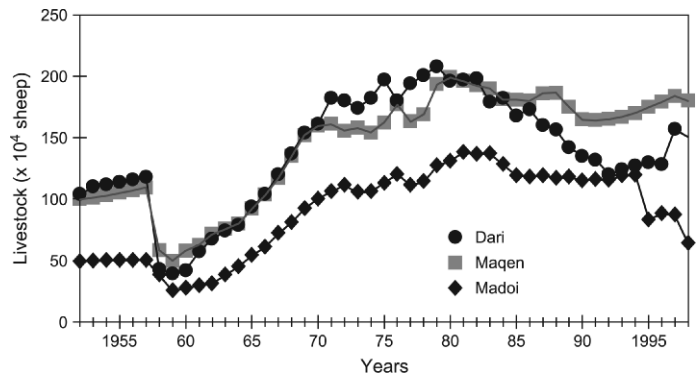
predominance. There have been so far no experimental studies of the causes of the dominance of this single species. However, its growth form makes it an extremely tough competitor under harsh conditions. Even under frequent grazing *K. pygmaea* is able to fruit at dwarf heights of only 1 to 2 cm. Germination experiments showed low vitality (15). It produces dense mats that expand radially by means of lateral vegetative shoots, independent of the generative rate of reproduction. It can be assumed that clonal growth is important. The turf produced by the plant creates a unique microhabitat extremely resistant to mechanical impact and capable of impeding the colonization of most taller growing competitors.

Small mammals are favored under such circumstances because they are able to harvest the aboveground phytomass of *K. pygmaea* completely.

In this context, a serious problem for pastoralism in Tibet is the abundance of pika and zokors (*Myospalax baileyi*). Ground-dwelling pikas seem to be connected with the alpine Cyperaceae mats including the ecotones to the alpine steppe and upper montane pastures. Zokors are most abundant in degraded shrubby pastures with *Potentilla fruticosa* in eastern Tibet. Investigations on the impact of pika and zokors were carried out in the *Kobresia humilis* pastures between Qilian Shan and Koko Nor (16, 17), in the Zoige Basin (33–34°N, 102–103°E, cited in [18]), and in the proper alpine belt of the highlands (19). Figures from the Zoige basin reveal the importance of small mammals: 60 000 hectares, or ca. 10% of all pastures, are infested by pika. In Serxu County ca. 30% of the pastures have very high pika density: 4500 burrows ha⁻¹ were counted with 450 individuals. The loss of fodder plants is estimated to be 50% of the annual forage. In Zoige County this corresponds to 76 000 to 90 000 tons y⁻¹, which is the fodder equivalent for 21 280 sheep (after data cited in reference 18). Similar data are reported from Dari County, where 20% of the pastures have been destroyed by pikas and zokors (21). The central question of whether pikas and zokors are true competitors with livestock on the plateau was intensively studied only in the pastures of Qinghai (Haibei Alpine Meadow Research Station, 37°37′N/101°19′E) (17, 20, 21). Here, pikas do not compete with yaks and sheep for Cyperaceae as long as the grazing pressure is low, enabling the animals to graze selectively. In this case, pikas tend to prefer forbs, including a number of grazing weeds avoided by livestock. Pikas are only forced to consume *K. humilis* when their populations attain very high densities. Controlled stocking rate experiments in the Haibei station revealed that pika increase with the intensity of livestock grazing. However, the increased number of plants with tuberous roots, bulbs, or rhizomes, i.e., an increased subsurface phytomass, attracts subsoil herbivores like zokors. Their creation of soil heaps weakens the remaining plant cover and

gives way to deflation. *K. pygmaea* is very sparsely present here and has not been recorded as contributing to the pika's diet. Thus, the environmental background of these studies is not comparable to the truly alpine *K. pygmaea* pastures, where pikas are forced to feed on this sedge, too. Smith and Foggin (22) generalize these studies for the whole plateau, saying that pikas contribute positively to ecosystem-level dynamics because they control livestock grazing weeds and do not compete with livestock for forage when general grazing intensity is moderate. However, this has yet to be proved. Field evidence clearly shows that pika densities are highest in degraded *K. pygmaea* pastures where the turf is already fragmented. It is moreover evident that pika prefer to dig holes at the junctions of polygonal cracks or at turf cliffs, thus taking advantage of the destruction of the turf cover. It thus seems evident that high pika densities accelerate the removal of the turf layer. Pika, therefore, can be considered a key species of the plateau in the sense that they are landscape engineers in a pastoral ecosystem.

EVOLUTION AND DYNAMICS OF THE *K. PYGMAEA* ECOSYSTEM

Considerations on the Holocene Evolution

The dominating plants in the Tibetan pastures are endemic to the highlands, but the age of the uplift is still a matter of controversy (23–25). In any case, it can be assumed that the alpine flora of Tibet did not develop before Tibet had been uplifted into alpine altitudes.

The present competition of the plant communities and their distribution in the highlands doubtlessly reflects the environmental history of the Holocene, although it is still unknown when the *K. pygmaea* turf developed. It should be considered that a major constraint in the evolution of the present vegetation cover is the extreme environmental changes the present surfaces were exposed to. In the last glacial maximum (ca. 20 000 y BP), wide areas of the highlands were covered by glaciers (26), and shortly after the onset of climatic conditions more favorable for plant life, larger parts of the less elevated habitats were flooded, leaving only small migration routes between the lakes.

Pedological Features and First Datings of the Turf

From the core area of *K. pygmaea* mats around Nagqu (4200–4800 m), recent pedological and paleobotanical data on turfs are available (27). The turf occurs in all relief positions (tops, slopes, depressions) and expositions and covers different substrates (mainly loess) as well as soil types. Structurally, it consists of felty fine root remains. Further components are amorphous humus and minerogenic matter. The turf is not comparable with ordinary organic layers on top of mineral soils, which are called O horizons. Thus a new designation was created for this horizon (Afe = suffix fe from felty [28]).

Most of the profiles recorded were classified as Cambisols. A Humic Cambisol with an idealized succession of Afe/Ah/Bw/C horizons is the prevailing soil type. Pedological analyses yielded the following selected parameters on turfs: thickness = 12.3 ± 3.4 cm (n = 13), amount of roots = 10.1 ± 2.9 roots cm^2 (n = 13), loss-on-ignition = 13.6 ± 5.3% (n = 13), organic carbon = 6.0 ± 2.7% (n = 7), C:N ratio = 14.0 ± 1.7 (n = 7), pH = 5.6 ± 0.5 (n = 7), and CaCO$_3$ = 0.0% (n = 13).

In the Afe horizon, both organic matter content and quantity of roots show a decreasing gradient with depth. According to granulometric and mineralogical parameters, turf and underlying soil horizons are not stratified. Micromorphological analyses, on the one hand, show a large quantity of roots and fungal remains (mycorrhiza). On the other hand, there are no

traces of faunal elements except of small oligochaete worms and protozoa. Microscopic root counts reveal a clear decrease of roots with increasing depth. The macrofossil spectra are dominated by radicels (max. 54.4%), which most probably originate from Cyperaceae. Further fractions comprise woody roots, which originate from perennials or dwarf shrubs (max. 29.7%), and leaf sheaths originating from Cyperaceae (max. 15.6%). The amount of main macrofossil fractions is clearly depth dependent, showing declining percentages with increasing depth. Pollen spectra from the turf are dominated by high percentages of Cyperaceae. Distinctly smaller quantities are contributed by grasses, herbs, and perennials. Arboreal pollen (<2%), from, e.g., *Betula, Alnus*, and *Pinus,* is restricted to areas close to the surface and originates from long-distance transport. Remarkably, there is a large quantity of burned particles. Their paleoecological implications require further investigation.

For *K. pygmaea* turfs, pedological, micromorphological, and paleobotanical evidence suggests that the preexisting soil surface was widely (quasi-) stable and root matter from *K. pygmaea* was gradually deposited downward ("penetration model"). Thus the turf is a matter of simple transformation of a preexisting soil and substrate. Consequently, the turf should be pedologically referred to as a horizon, not a layer. In terms of humus forms it can be classified as Rhizomull (29).

Although climate fluctuations on the Tibetan plateau are increasingly well known (26, 30, 31, 32), it is so far not possible to correlate any humid periods of the highlands with the evolution of the *K. pygmaea* mats. From their present core area with 400 to 800 mm y^{-1}, it seems plausible to conclude that large parts of the highlands currently covered by *K. pygmaea*–derived turf once had a more humid climate. The key problem for the understanding of the vegetation dynamics and environmental history of the highlands is obtaining reliable ^{14}C datings of the turf. Datings in relationship to *K. pygmaea* turfs available so far can be differentiated with respect to their mode (material dated, method, predating/direct dating) and reliability. Direct AMS-^{14}C-datings on macroremains and pollen concentrations give evidence for a subrecent to recent age of *K. pygmaea* turfs. This data set includes both datings from the Nagqu area (−597 ± 50 y to −1.827 ± 41 y BP) (33) and from southern Tibet (321 ± 54 y to −82 ± 57 y BP) (33). The second type are AMS ^{14}C direct datings on bulk-soil matter from the lowermost part of turfs from the Nagqu area yielding Late Holocene ages (1882 ± 50 y to 395 ± 53 y BP). A third source for turf dating are predatings using buried soils and charcoals below turf horizons. The buried soil horizons were found at depths of 15 to 54 cm yielding ages of 4370 ± 125 y to 1580 ± 70 y BP (34). Predatings of turfs from Reting (30°18′N/91°31′E), by contrast, gave ages of 1197 ± 45 y and 243 ± 55 y BP (28). In both cases, the datings represent Late Holocene maximum ages for the turfs. Remarkably, there is no buried turf known from Tibet so far potentially allowing postdating. To sum up, most of the radiocarbon datings available argue for a (very) Late Holocene to recent age of *Kobresia* turfs.

Assessment of Human Impact

Human impact is still a matter of debate since when humans are present in the highlands (35). Thus we cannot exclude that any climate-driven environmental changes in the pastures of the Tibetan highlands occurred during the presence of humans. Since humans tend to modify their environment according to their needs, we can assume that human impacts and climate-driven effects are superposing each other. Yak breeding probably dates back 8000 y (36), and the conversion from forest to pastures using fire is shown by pollen analyses plus charcoal evidence to date back 7000 to 9000 y (6, 37, 38). Since

the first radiocarbon dates of *K. pygmaea* turf on the Tibetan plateau suggest a far younger age, it can be concluded either that there is no connection between the development of animal husbandry and the formation of the mats or that the mats arose only when grazing became intense at some later point. The maximum ages of turfs dated so far, which correspond with the massive expansion of permanent settlements during the growth of the Tibetan empire since the 7th century AD, tend to support the latter hypothesis. At the time all larger settlements were situated in the montane belt. It is from this belt that most indications of the influence of livestock grazing on the formation of *K. pygmaea* mats have been gathered so far:

– In the more humid part of the distribution area of *K. pygmaea,* in the Inner Himalayas of Bhutan and Nepal, *K. pygmaea* obviously replaces taller grasslands and scrub at sites where the intensity of grazing and trampling is higher than in the surroundings.
– Experiments in the Haibei Alpine Meadow Research Station revealed that the relatively tall *K. humilis–Festuca* grassland is replaced by *K. pygmaea* and rosette plants following increased grazing pressure from livestock (21).
– The reverse development is being monitored on exclosure plots in southern Tibet (Reting, 30°18′N/91°31′E, 539 mm y^{-1}) (39, 40). Here, grazing exclosures were set up between 4350 and 4600 m on *K. pygmaea* pastures in 1997. Within 10 y, the cover of *K. pygmaea* was reduced to one-third of its former cover on the lower plot, and forbs and graminoids of meadow steppes became dominant. On the upper plot *K. pygmaea* is still spreading on formerly open substrates. Even at this locality, however, meadow-steppe plants are gaining in dominance.

These studies document two different transformation stages of the natural vegetation in moderately dry forest climates: *i)* forests are replaced by tall meadow-steppe–like pastures under moderate grazing pressure and *ii)* tall plants are removed by selective grazing and trampling with increased grazing intensity, giving *K. pygmaea* a competitive advantage.

No quantitative data are available from the alpine belt, where *K. pygmaea* is supposed to have its natural distribution. However, there are observations from paths in the Himalayas between Bhutan and West Nepal, where *K. pygmaea* replaces taller vegetation of the less disturbed surroundings. The other way round, fencing of alpine pastures in Qinghai (33°45′N/ 95°46′E, 4340 m) showed that grasses overgrow *K. pygmaea* as soon as grazing is seasonally excluded (37).

These observations indicate that even in the alpine belt, the dominance of *K. pygmaea* might be due to human impact. It is probable that *K. pygmaea* is naturally dominant in only a limited number of habitat types. The only habitat in which it seems to be naturally dominant is at the upper limit of alpine mats, where *K. pygmaea* is dominant on fine-grained substrates. Other natural habitats are extremely shallow soil overlying solid rock (e.g., loess-covered boulders), which are unsuitable for taller plants or seepage areas, where *K. pygmaea* is a pioneer on silty substrates.

The wide zonal distribution of *K. pygmaea* thus seems to be largely favored by grazing.

Recent Degradation Processes of *K. pygmaea* Pastures

Environmental studies show that the rangeland policy of the last 50 y has had a serious impact on the status of the *K. pygmaea* pastures (41, 42). Especially in the last 30 y, rangeland policy has resulted in an increase in livestock numbers in all parts of the highlands (20, 43–48). Thus livestock numbers reached their peak in the early 1980s (Fig. 2) and decreased

afterward due to overgrazing, leading to a lower carrying capacity and to drastic losses of livestock following heavy winter snowfalls. Similarly, in the area of Damxung of southern Tibet, human population and livestock numbers tripled within the last 40 y (49) with similar degradation effects.

Since 1990 administrative attempts have been launched to increase the number of sedentary concentrated settlements. Winter villages have been built in all parts of the highlands (50). This has caused heavy degradation and erosion in the vicinity of these places. Figures regarding changes in migratory distances and mobility in general are not yet available, but it is to be feared that the experiences of environmental damage caused by sedentarization policies that have been made in other countries will also be repeated in China. Thus, the positive trend to wealth and better living conditions is going to be threatened by an opposite trend of decreasing carrying capacity of the rangelands. This is caused by local overuse and—at least regionally— by climatic deterioration. In Qinghai Province veterinary data collected during the past 30 y clearly demonstrate that the degradation of pastures has already resulted in a measurable decline in productivity and livestock health (cited by reference 20).

Shortage of fuel is common in the whole highlands. In the *Kobresia* pastures yak droppings are used for fuel since unknown times (51), and even *K. pygmaea* turf is removed for fuel purposes. Large-scale removal of turf bricks was observed along the main roads; these bricks are later sold in Lhasa (49). Another rather destructive impact originates in the need to build walls for exclosures in order to protect grazing reserves or any other durable parts of settlements, roads, or railway dams, which again gives access to turf exfoliation along the human-made cliffs. In larger parts of the *K. pygmaea* domain, the removal of the turf seems to be irreversible. The open loess subsoil is easily eroded, leaving behind gullies that are mostly devoid of plants as a result of their steep slopes. The stony subsoil is much more vulnerable to trampling and erosion than the original *Kobresia* turf, and the pioneer vegetation establishing here is much less productive.

Generally, it can be stated that the more sensitive the environment is (i.e., the closer the site to the drought limit of *K. pygmaea*), the lower the threshold grazing intensity leading to degradation of the mats or irreversible destruction of the turf.

Fairly stable ecological conditions were only encountered at the eastern margin of the Tibetan highlands. At two localities (east of Nagqu and south of Madoi), which are possibly representative for a larger area we found *K. pygmaea* recolonizing silty soils where the turf had been removed for construction or other purposes.

Rehabilitation Trials

In southern Qinghai more than 30% of the pastures are classified as seriously degraded. In the worst degradation stages the *Kobresia* turf cover is completely removed and open humic silt ("black beach") (52, 53) is prone to deflation. Thus a two-pronged management approach is required. This would entail first of all the rehabilitation of the "black beach" and second the conservation of the remaining turfs that protect wide water catchments against erosion. Reseeding indigenous grasses on fenced "black beach" sites yielded a hay meadow with seven times higher productivity than open pastures after 3 y. (Table 2). However, while this may be an effective measure to improve winter fodder supply, is not applicable for the whole pastoral system, which is based on free range management. If open pastures are fenced, tall grasses overgrow the *K. pygmaea* mats and cushions and have a 1.75 times greater dry matter productivity (Table 2). If such pastures are managed with

Table 2. Three years of rehabilitation experiments in four different grassland types of southern Qinghai. Data from experimental plots of the Northwest Institute Plateau Biology, Xining, Chinese Academy of Sciences, in Guoluo prefecture (34°21′N/100°29′E, 3980 m above sea level).

	Artificial grasslands	Improved pastures[1]	Fenced pastures	Open pastures
Total productivity fresh (kg ha^{-1})	33 000 ± 500	13 050 ± 450	7890 ± 660	4500 ± 790
Total productivity dry (kg ha^{-1})	10 995 ± 487	4350 ± 378	4350 ± 415	1500 ± 100
Times of increase in productivity	7.33	2.9	1.75	1.00
Ratio of palatable herbage	100%	80%	40%	20%
Yield of fresh palatable herbage (kg ha^{-1})	33 000 ± 500	10 440 ± 390	3150 ± 227	900 ± 67
Yield of dry palatable herbage (kg ha^{-1})	10 995 ± 487	3480 ± 270	1050 ± 95	300 ± 40
Times of increase in yield of palatable herbage compared with open pasture	36.65	11.60	3.50	1.00
Carrying capacity (sheep ha^{-1} y^{-1})	15.00 ± 2.24	4.80 ± 1.32	1.50 ± 0.30	0.45 ± 0.41
Times of increase in carrying capacity compared with open pasture	33.33	10.67	3.33	1.00

[1] Pastures were improved by artificially adding grass seeds in the natural pastures.

controlled stocking rates, valuable taller fodder plants recover and grazing weeds disappear along with zokors and pika (20, 21). If grass seeds are artificially added, the ratio of palatable herbage is doubled compared with fenced pastures without additional reseeding.

It remains unresolved whether the ongoing privatization of pastures is a sustainable approach from the standpoint of the protection of *Kobresia* turfs. Since the mobility of the herders is now reduced, it must be feared that a quasisedentary livestock economy will not be in a position to cope with climate-driven year-to-year changes of carrying capacity. The improvement of traditional seminomadic rotation systems seems to be more promising from the ecological point of view.

SUMMARY AND CONCLUSIONS

The world's largest alpine plant formation in the southeastern Tibetan highlands consists of a golf-course–like carpet of the endemic Cyperaceae *K. pygmaea* associated with flat cushions and rosette plants, covering an area of about 450 000 km^2. The sedge forms dense clones that can spread vegetatively. The dense turf that is formed by the leaf bases and roots of *Kobresia* is both extremely resilient in the face of mechanical impacts such as trampling or erosion and successfully impedes the colonization of most competitors. The main above-surface phytomass of *K. pygmaea* is beyond the grazing reach of livestock. Consequently, if *K. pygmaea* dominates this ecosystem but the environmental conditions allow the growth of taller plants that would shade out *K. pygmaea* when becoming dominant, we may conclude that this golf-course formation is largely the result of grazing. This hypothesis is supported by succession experiments on grazing exclosures in Xizang and Qinghai and by observations in the Inner Himalayas.

Whether or not the grazing intensity of wild herbivores was ever high enough to produce such a widespread *K. pygmaea* landscape is unknown. First datings of *K. pygmaea* turf point to a late Holocene age. Most dates are in accordance with the expansion of settlement and animal husbandry since the rise of the Tibetan empire. It is hypothesized that the *K. pygmaea* formation is largely a synanthropic pseudoclimax that replaced former plant communities not dominated by Cyperaceae. It is probable that their natural dominance is restricted to the upper limit of alpine mats.

With the help of grazing and trampling, *K. pygmaea* became the winner in the Tibetan pastures down to deep in the forest belt. Pollen analyses (6, 33, 37), ^{14}C-dated charcoal (38), and investigations on fragmented forests surrounded by "alpine" pastures (54) support our view that the *K. pygmaea*–pastures of the Tibetan highlands replace at least partly forests.

The turf built up by the sedge created a very peculiar, tough and resilient ecosystem that is valued as first rate pasture by Tibetan herders (55). It was able to persist even in climatic zones that today have become too dry for the recolonization of *K. pygmaea*. These relicts of more humid periods at the western distribution limit of *K. pygmaea* are threatened by drought, erosion, and strong grazing pressure. Especially in such degraded *K. pygmaea* ecosystems, small mammals are detrimental, since they can harvest the remaining aboveground biomass of *K. pygmaea* completely. Once the *K. pygmaea* turf is removed by erosion or humans, it is irreversibly lost in this drier zone, and the underlying shallow loess layer is easily blown or washed away. A less valuable steppe pasture or cushion formation tends to become established on the stony subsoils that are exposed as a result.

The felty durable cover of *K. pygmaea* protects the upper catchments of the large rivers of Southeast Asia from the risk of higher sediment load and floods. Increased livestock numbers and removal of the turf for construction purposes and fuel consumption lead to serious loss of pastures and decreased carrying capacity. The new rangeland policy since 1990, including settlement of nomads and privatization of pastures with fencing, has led to accelerated loss of pasture land. Restoration measures including artificial reseeding lead to productive hay meadows but require a high labor input. Such measures are thus of only rather local importance for the improvement of winter fodder reserves. Where *K. pygmaea* is still present, a temporary reduction or exclusion of grazing will favor its regeneration at least in the more humid areas, as long as the sedge is not overgrown by taller forbs.

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