Life-forms and clonality of vascular plants along an altitudinal gradient in E Ladakh (NW Himalayas)*

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Abstract

Altitudinal distribution of life-forms of vascular plants was studied in E Ladakh (W Himalayas, NW India) along one of the world's most prominent altitudinal gradients, ranging from 4180 to 6000 m a.s.l., in an area of 10,227 km². Among 404 species recorded in total, hemicryptophytes prevailed strongly (251 species, 62.1%), followed by therophytes with 90 species (22.3%). Chamaephytes comprised 22 species (5.4%) and geophytes 17 species (4.2%). Phanerophytes (14 species, 3.5%) and hydrophytes (7 species, 1.7%) were rare. The life-form spectrum reflects prevailing desert-steppe and steppe vegetation in the study area. A Monte Carlo test was used to obtain expected ranges in life-form diversity and abundance of individual life-forms along the altitudinal gradient. The number of actually present life-forms recorded from 50 m altitudinal steps was usually within the range expected from that null model, rarely lower than expected. The number of species belonging to chamaephytes, geophytes, hydrophytes and phanerophytes along the altitudinal gradient fall within the range predicted by the null model. Therophytes were under-represented in most altitudinal segments above 4900 m a.s.l. Nevertheless, many therophytes reach remarkably high altitudes in Ladakh as compared to other regions of Central Asia and the W Himalayas. Complementary to this pattern, hemicryptophytes were over-represented in most altitudinal steps from 4900 to 5600 m a.s.l. Relative abundance of geophytes and chamaephytes between 4150 and 5800 m a.s.l. was remarkably constant. Clonal plants comprised 26.7% of the total species number. About 30% of plant species were clonal from the lowest altitudes up to 5000 m a.s.l., from where the proportion of clonal plants gradually declined down to zero at the highest altitudes. Different factors are likely to be responsible for the relatively low proportion of clonal plants and their decline at higher altitudes. At the highest altitudes clonal plants with persisting inter-connections between widely spaced ramets are damaged by virtue of repeated freezing and thawing of the soil, breaking their integrated systems. In large screes at intermediate altitudes most types of clonal plants are injured by their mobility and at the lower altitudes tough soil texture prevents horizontal growth in the below-ground. Therefore, diversity of clonal plant types is small in prevailing habitats of the study area and most clonal plants are restricted to small patches of wetlands at intermediate and lower altitudes.

Die Höhenverbreitung der Lebensformen von Gefäßpflanzen wurde in O-Ladakh (W Himalaya, NW Indien) entlang eines in der Welt hervorragenden Höhengradienten untersucht, der von 4180 bis 6000 m über NN reicht und ein Areal von 10.277 km² umfasst. Bei den 404 Arten, die insgesamt

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erfasst wurden, herrschten Hemikryptophyten stark vor (251 Arten, 62,1%), gefolgt von Therophyten mit 90 Arten (22.3%). Chamaephyten stellten 22 Arten (5,4%) und Geophyten 17 Arten (4,2%). Phanerophyten (14 Arten, 3,5%) und Hydrophyten (7 Arten, 1,7%) waren selten. Das Spektrum der Lebensformen spiegelt die vorherrschende Wüstensteppen- und Steppenvegetation im Untersuchungsgebiet wider. Ein Monte-Carlo-Test wurde verwendet, um die erwartete Variationsbreite der Lebensform-Diversität und die Abundanz der individuellen Lebensformen entlang des Höhengradienten zu ermitteln. Die Anzahl tatsächlich vorhandener Lebensformen, die in 50 m Höhenschritten aufgenommen wurden, befand sich gewöhnlich innerhalb der Variationsbreite, die aufgrund des Null-Modells erwartet wurde, und war selten geringer als erwartet. Entlang des Höhengradienten befand sich die Anzahl der Arten, die zu den Chamaephyten, Geophyten, Hydrophyten und Phanerophyten gehören, innerhalb der Variationsbreite, die durch das Null-Modell vorhergesagt wurde. Therophyten waren in den meisten Höhenstufen über 4900 m über NN unterrepräsentiert. Dennoch erreichten im Vergleich zu anderen Regionen in Zentralasien und dem W-Himalaya viele Therophyten bemerkenswert große Höhen in Ladakh. In Ergänzung zu diesem Muster waren die Hemikryptophyten in den meisten Höhenstufen zwischen 4900 und 5600 m über NN überrepräsentiert. Die relative Abundanz der Geophyten und Chamaephyten zwischen 4180 und 5800 m über NN war bemerkenswert konstant. Klonale Pflanzen stellten 26,7% der Gesamtartenzahl. Um 30% der Pflanzenarten waren von der geringsten Höhe bis zu 5000 m über NN klonal, von da an nahm der Anteil klonaler Pflanzen graduell bis auf null in den größten Höhen ab. Verschiedene Faktoren sind wahrscheinlich für den relativ geringen Anteil klonaler Pflanzen und ihre Abnahme in höheren Lagen verantwortlich. In den höchsten Lagen werden klonale Pflanzen mit persistenten Verbindungen zwischen weit auseinanderliegenden Rameten durch die Wirkung wiederholten Frierens und Tauens des Bodens beschädigt, so dass ihre verbundenen Systeme zerbrechen. In großen Schotterfeldern mittlerer Höhen werden die meisten Typen klonaler Pflanzen durch deren Beweglichkeit beschädigt und in den tieferen Lagen verhindert die zähe Struktur des Bodens das horizontale Wachstum im Untergrund. Deshalb ist die Diversität klonaler Pflanzentypen in den vorherrschenden Habitaten des Untersuchungsgebietes gering und die meisten klonalen Pflanzen sind auf kleine Bereiche in Feuchtgebieten der mittleren und tieferen Lagen beschränkt.

Key words: altitude – biogeography – clonal plants – diversity – Himalayas – India – Ladakh – lifeforms – null models – Rupshu – vascular plants

Introduction

The concept of vascular plant life-forms, which dates back to von Humboldt (1806), was originally developed for a non-taxonomical comparison of vegetation types in different regions of the Earth. The system of life-forms as morphological-ecological categories, became soon complicated and difficult to use (Drude 1886, Warming 1909). Raunkiaer (1910) developed a simple life-form system, which was strictly based on the height of hibernating buds in relation to the soil surface, and which became widely accepted and applied in comparative vegetation studies. This approach is particularly useful in environments with pronounced climatic seasonality, especially where winter frost and summer drought strongly affect seasonal plant growth and development. Although Raunkiaer's system was often refined (e.g. Braun-Blanquet 1928, Ellenberg & Müller-Dombois 1967, Müller-Dombois & Ellenberg 1974, Barkman 1988), basic categories (phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes) were generally maintained.

It has been repeatedly shown that life-form spectra (proportion of species belonging to individual life-forms) can be predicted for particular climate properties, for any continent, biogeographic region and altitude (Raunkiaer 1910, Sarmiento & Monasterio 1983). Conversely, the life-form spectrum gives basic climatic information (Meher-Homji 1981, Campbell & Werger 1988, Komárková & McKendrick 1988, Cody 1989, Danin & Orshan 1990). Therefore, Raunkiaer life-forms are useful categories with a great predictive power, potentially applicable in any environment colonized by plants but particularly useful in regions with seasonal climate. Many basic elements of life history of plants are strongly affected or even largely determined by the life form. Also, species pools from which plants co-existing in individual habitats are selected, are to some extent determined by life forms.

One of the basic gradients along which life-form changes is altitude (e.g. Tareen & Qadir 1993, Berg

1998, Mark et al. 2000, Pavón et al. 2000, Mark et al. 2001). Diversity of life-forms usually decreases with increasing altitude and one or two life-forms remain at extreme altitudes (Dickoré & Nüsser 2000, Pavón et al. 2000). Correlations between relative life-form abundance and environmental variables have sometimes been calculated in order to identify factors responsible for changes of the life-form spectra along altitudinal gradients (Montana & Valientebanuet 1998, Pavón et al. 2000). However, altitude itself represents a complex combination of related climatic variables closely correlated with numerous other environmental properties (soil texture, nutrients, substrate stability, etc.; Stevens 1992, Auerbach & Shmida 1993, Ramsay & Oxley 1997). Therefore, it is usually impossible to separate individual variables and to identify those directly responsible for variation in life-form spectrum (Montana & Valientebanuet 1998). Moreover, all analyses of this type suffer from a lack of independent data points because the presence of a species at any given altitudinal interval is not independent from its occurrence at neighboring altitudinal steps. The significance of correlations between percentage of life-forms and environmental variables was accordingly over-estimated in numerous surveys (e.g., Kessler 2000, Pavón et al. 2000).

In response to severe environments, plants either develop adaptations that enable protection of renewing buds (as reflected by Raunkiaer life-forms) and/or spread the risk of bud mortality by multiplying buds through clonal growth. Therefore, clonality is an important feature of plants, and is particularly widespread in harsh environments such as high latitudes. In temperate Europe about 70% of vascular plant species are clonal. Towards the north, the percentage of clonal plants may be as high as more than 90% in tundra wetlands (Klimeš et al. 1997). However, the scarce data from the true Arctic indicate that the relative abundance of clonal plants declines again towards the latitudinal extremes of vascular plant distribution (Aleksandrova 1983). Unfortunately, there is very little data from corresponding altitudinal gradients that include extreme altitudes. It is therefore not clear to which extent the latitudinal pattern of clonal plant distribution is mirrored by the altitudinal gradient.

In this paper I examine participation of individual life-forms and life-form diversity in the inner W Himalayas, along one of the world's most prominent altitudinal gradients with altitude ranging from 4180 to 6000 m a.s.l. There, I conducted intense field research from 1998 to 2000. In analysing altitudinal trends, I compared observed data with predictions from Monte Carlo simulations. In this way, the effect of species richness on observed altitudinal trends was removed. Further, I examined altitudinal trends in clonality.

The following questions were addressed: (a) Which life-forms of vascular plants occur in the area? (b) How are they distributed along the altitudinal gradient? (c) Can the altitudinal trends in participation of individual life-forms and in life-form diversity be explained by species richness patterns? (d) How does plant clonality change along the altitudinal gradient?

Materials and methods

Study area

The study area covers 10,227 km² (including 207 km² of lakes) in Ladakh, Jammu and Kashmir State, India (Fig. 1). The shape of the area is approximately rectangular, slightly prolonged in the northwest-southeast direction (32°26′–33°36′N, and 77°18′–78°30′E). The study area encompasses the south-westernmost extension of the high level Tibetan Plateau including several basins without external drainage, and its rim towards the high mountain ranges of the Inner Himalaya, respectively parts of the regions "Leh" (Upper Indus Valley), "Zanskar" and "Rupshu" as defined by Dickoré (1995). Altitude in the study area ranges from 4180 m at the bottom of the Indus Valley to 6622 m a.s.l. at Chhamser Kangri peak (Kapadia 1999). Vascular plants were found up to 5970 m a.s.l.

There is no climatic station located in the study area. However, data from a broader region (Dickoré 1995, Hartmann 1997, 1999, Miehe et al. 2001) show that the study area is generally arid. It is rarely affected by monsoonal precipitation, which usually fails to cross the high crest of the main Himalayan range (Bhattacharyya 1989). High summer temperatures at the lower altitudes result in evaporation values being much higher than precipitation. The available climatic data indicate an aridity gradient from southwest to northeast. Along the arid valley stations of the Indus valley precipitation decreases from 115 mm at Leh (3514 m, N34°09′ E77°34′, about 75 km NW of the study area) to 54 mm at Gar in SW Tibet (4232 m, N32°07′ E80°04′, c. 160 km SE of the study area). No pronounced seasonality in precipitation has been recorded in Leh, in Gar maximum precipitation occurs in summer. Few climatological data are available for higher altitudes of Ladakh, except for a single-year measurements in Aksai Chin at 4900 m a.s.l. (about 280 km NNE of the studied area, now under Chinese administration) where there mean annual temperature is –8.2 °C, mean monthly temperature rises above 0 °C from June to August only, and precipitation is as low as 19 mm per year (Miehe et al. 2001). Temperatures are expected to be similarly low at corresponding alti-
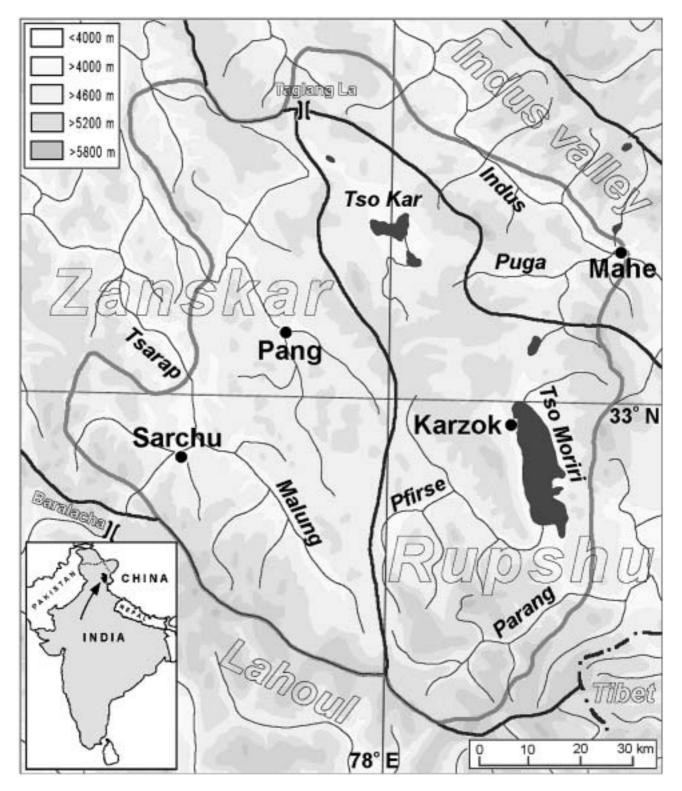
Fig. 1. Map of E Ladakh, NW India. The study area is delimited by a gray line. Black lines denote borders of geographical sub-areas according to Dickoré (1995).

tudes within the study area (Brazel & Marcus 1991), precipitation is likely somewhat higher here.

There is a variety of substrates ranging from siliceous rocks of the Tso Morari Complex to calcareous or saline sediments. Low precipitation determines vegetation in the largest fraction of the study area. Accordingly, small areas at the relatively lowest altitudes of the Indus Valley are occupied by desert and semi-desert. Steppe vegetation prevails in the whole studied area and extends up to about 5300 m. It is dominated by several species of *Stipa* and *Artemisia*, other frequent species include *Oxytropis microphilla*, *Tanacetum fruticulosum* and *Alyssum canescens*. Plant cover ranges between 10 and 40% in steppe. Higher up, a narrow belt of alpine grasslands occurs where *Kobresia pygmaea*, *Carex pseudo-foetida* and *Carex sagaensis* usually dominate. Above about 5300 to 5700 m, a sparse subnival vegetation is developed, characterized by *Astragalus confertus*, *Thylacospermum cespitosum* and *Potentilla pamirica*. Vascular plants occur regularly up to 5900 m, locally up to nearly 6000 m a.s.l. Detailed surveys of vegetation of various regions of Ladakh focused on semi-deserts, steppes and alpine grasslands have been published by Hartmann (1983, 1984, 1987, 1990, 1995, 1997, 1999). Little attention has been paid to wetlands, which occupy relatively large areas of flat and broad valley bottoms in the whole area and are dominated by *Carex orbicularis*, *Carex microglochin*, *Eleocharis quinqueflora* and *Juncus thomsonii*. These habitats are often saline, as indicated by the presence of *Puccinellia himalaica*, *Blysmus compressus* and *Triglochin palustre*. Snow-field patches with some characteristic plants, such as *Pegaeophyton scapiflorum* and *Saxifraga nanella*, are found near the snow line. Synanthropic vegetation includes plant assemblages developed on eutrophicated ground by stables of domestic animals and near villages up to 5400 m a.s.l. Weedy assemblages grow in arable fields up to 4700 m a.s.l.

There are few and very small permanent settlements on the plains situated at about 4550 m a.s.l. and large mountainous areas are uninhabited (Negi 1995). Barley and less often oat is cultivated on a small scale up to 4700 m a.s.l. Steppe and alpine turf vegetation is grazed by sheep, goats and yaks up to 5600 m a.s.l. Synanthropic vegetation types include plant assemblages developed in villages and by stables of domestic stock up to 5400 m a.s.l., and weed communities occur in arable fields up to 4700 m a.s.l. The grazing effect of wild ungulates seems to be negligible due to the low densities of most species (Fox et al. 1991, Mallon 1991). During recent decades the area is characterised by continuous overgrazing due to high numbers of domestic sheep, goats and yaks (Jina 1995, Holzner & Kriechbaum 1998).

Data sampling and analysis

I collected field data on three expeditions lasting four to five weeks each, in 1998, 1999 and 2000. Altogether I recorded the vascular flora of 411 localities, each approximately 1 ha in size. The localities were non-randomly distributed, which is mainly due to part of the study area being devoid of vascular plants (very unstable slopes, glaciers, lakes, highest altitudes). However, I attempted to cover all altitudes and habitats in all parts of the delimited area. As my aim was to record as many species of vascular plants as possible most localities included various habitats and vegetation types. Plant abundances were not recorded. Depending on habitat diversity, accessibility, species richness and altitude, plants in individual localities were searched for about 30 minutes to one day. Total number of records was 10,322. Altitude of all localities was estimated with an altimeter (Thommen TX, Revue Thommen®, Waldenburg, Switzerland).

Representatives of all recorded herbaceous plant species were dug out and their below-ground organs were examined and classified within the life-form system. Life-forms were defined according to Raunkiaer (1910), based on the position of the renewing buds in relation to the soil surface.

Trends in life-form distribution along the altitudinal gradient were tested using a Monte Carlo simulation. The species number recorded in a particular altitudinal interval was randomly selected from a species pool which was defined as the set of species recorded in the whole study area. Subsequently, the number of species with individual life-forms represented in the selection was counted. For the number of life-forms at individual altitudinal steps the same procedure was used but the number of different life-forms represented in the selection was counted. An estimate of variation was obtained by repeating this procedure 10,000 times. The observed values were compared against the calculated distribution, and the significance of difference was assessed at the 5, 1 and 0.1% levels.

Clonal plants were defined as plants that multiply vegetatively on a regular basis, consisting of potentially independent ramets or spreading by vegetatively originated propagules. Non-clonal plants included (1) annual and perennial species with a main (tap) root of the primary root system and without adventitious roots and buds, (2) pleiocorm plants with short below-ground branches bearing very few or no roots; these are unable to survive when detached from the rest of the plant, (3) root-splitters that multiply vegetatively only when very old (senile), and spread over very limited distance, and (4) apomicts lacking other modes of vegetative multiplication.

Regression analyses were performed using SYSTAT for Windows, version 7.0, programs for the Monte Carlo simulations were written in Delphi.

Results

Altogether 404 species of vascular plants were recorded in the study area. Altitudinal distribution of species numbers was hump-shaped and positively skewed (Fig. 2). Maximum species number (>200 species) was found between 4500 and 4750 m a.s.l., respectively along the bottom of the high-altitude plains.

Six different Raunkiaer life-forms were distinguished among the total vascular flora. Hemicryptophytes with 251 species prevailed (62.1%), followed by therophytes with 90 species (22.3%). Chamaephytes were represented by 22 species (5.4%) and geophytes by 17 species (4.2%). The two rarest life-forms were phanerophytes with 14 species (3.5%) and hydrophytes with 7 (1.7%) species. All six plant life-forms occured at most altitudinal steps between 4200 and 4900 m a.s.l. (Fig. 3). Above this altitude their number gradually declined. Hemicryptophytes only, represented by four species, were recorded at the highest altitudes above 5900 m a.s.l.

The life-form that ceased at the lowest altitude were the phanerophytes. Only two species were found above 5050 m a.s.l.: *Lonicera spinosa* up to 5065 m a.s.l. and *Dasiphora parvifolia* up to 5060 m a.s.l. *Ranunculus trichophyllus* was the only hydrophyte recorded above 5000 m a.s.l. (up to 5140 m). The four remaining life-forms ascended to much higher altitudes. Two therophytes (annuals), *Actinocarya acaulis* and *Hedinia tibetica* were found up to 5650 m a.s.l. *Pegaeophyton scapiflorum*, a root-sprouting geophyte, was recorded up to 5800 m a.s.l., and *Thylacospermum caespitosum*, a cushion chamaephyte, up to 5900 m a.s.l. Hemicryptophytes reached the highest altitudes, among them *Poa attenuata* and *Waldheimia tridactylites* (to 5900 m), *Christolea pumila* and *Saus-*

surea gnaphalodes (to 5940 m) and by *Alyssum klimesii* (5970 m a.s.l.).

The number of life-forms recorded at individual altitudinal steps was usually within the range expected from the null model (Fig. 3), except for five steps (4500–4550 m, 5150–5200 m, 5250–5300 m, 5300–5350 m, and 5800–5850 m a.s.l.), where it was lower than expected. Low life-form diversity between 5150 and 5350 m a.s.l. was due to a lack of phanerophytes and hydrophytes which reached maximum altitudes at 5065 and 5140 m a.s.l., respectively. The remaining deficits at the lower and the very high levels (4500–4550 m, 5800–5850 m) were likely caused by inadequate collecting.

The species numbers of chamaephytes, geophytes, hydrophytes and phanerophytes along the altitudinal gradient fell within the range predicted by the null model. This means that the low number of species belonging to these four life-forms at higher altitudes and their absence in the subnival belt can be explained by the low number of species recorded at high altitudes. In the case of hydrophytes and phanerophytes two departures from the null model were observed at the higher altitudes. However, the broad range of expected values indicates that due to the low total number of species there is also a low power of the Monte Carlo simulations, which may be responsible for this failure to reject the null hypothesis (Fig. 4). The simulations demonstrate that chamaephytes and geophytes are poorly represented or missing at the highest altitudes due to their overall poor representation, and not owing to their inability to adapt to the harsh environmental conditions. Therophytes are under-represented at two lower altitudinal steps (4200–4250, 4400–4450 m a.s.l.) where plant recording was possibly less complete, and in
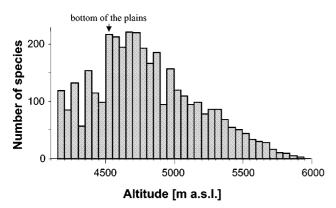

Fig. 2. Altitudinal distribution of 404 species of vascular plants recorded in the study area (E Ladakh).
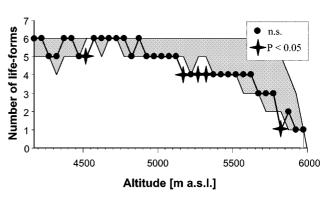

Fig. 3. Number of life-forms along the altitudinal gradient in E Ladakh. Shaded area denotes the range of values predicted by a null model in which species recorded at particular altitudinal steps were randomly assigned to the life-forms.

most altitudinal steps above 4900 m a.s.l. Contrary to this pattern, hemicryptophytes are over-represented in most altitudinal steps above 4900 m a.s.l., up to 5600 m a.s.l.

The proportion of geophytes and chamaephytes between 4150 and 5800 m a.s.l. is remarkably constant (Fig. 5). Therophytes represent about 20% of the species from 4150 to 4800 m a.s.l., and decline gradually above. In contrast, hemicryptophytes, dominating the life-form spectrum throughout the altitudinal gradient, comprise about 65% between 4150 and 4900 m a.s.l., with a gradual increase up to 100% at the highest altitudes (Fig. 5).

Clonal plants account for 26.7% of the total. From 4150 to 5000 m a.s.l. about 30% of the vascular plant species are clonal, and above the proportion declines gradually to zero at the highest altitudes (Fig. 6).

Discussion

Total species numbers

The total of 404 species recorded in the studied area is certainly not final. More thorough field investigations and refined taxonomy would probably add more species, although published records very probably add much redundance due to prolific and poorly understood taxonomy. Since species were recorded in numerous localities, it is possible to use the $Chao_2$ formula (Chao 1987, corrected in Colwell 1997) for estimation of the true species numbers in the whole area:

$$S_{Chao2} = S_{obs} + Q_1^2/(2*(Q_2+1)) - Q_1*Q_2/(2*(Q_2+1)^2),$$

where S_{obs} is total number of species observed in all samples pooled and Q_j is number of species that occur
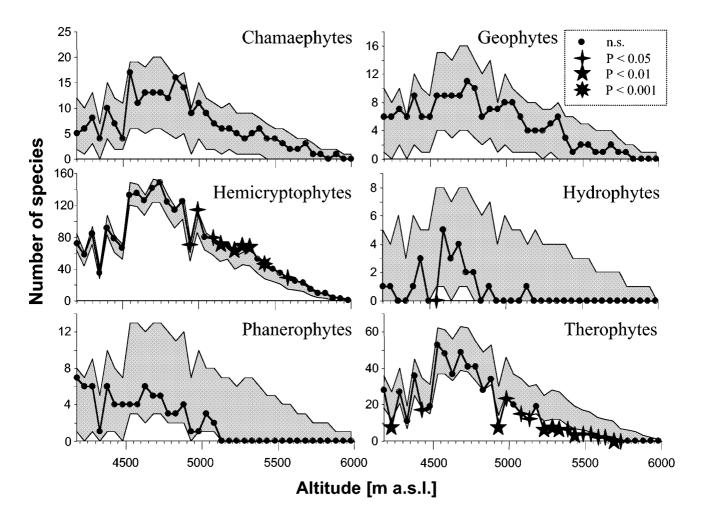

Fig. 4. Number of species belonging to individual life-forms along the altitudinal gradient in E Ladakh. Shaded area denotes the range of values predicted by a null model in which species recorded at particular altitudinal steps were assigned to the life-forms randomly. Different symbols were used to indicate the significance of departures from the null model.
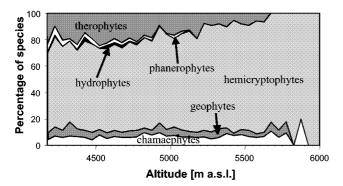
Fig. 5. Changes in life-form spectra along the altitudinal gradient in E Ladakh.
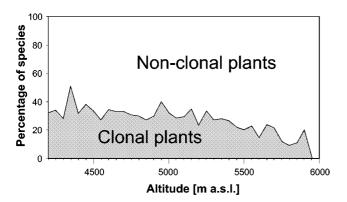

Fig. 6. Changes in proportions of clonal and non-clonal plants along the altitudinal gradient in E Ladakh. 100% corresponds to the total number of species of vascular plants recorded at particular altitudinal steps.

in exactly j samples (Q_1 is the frequency of uniques, i.e. species recorded in one locality only, Q_2 the frequency of duplicates, species recorded in two localities). The $Chao_2$ formula estimates 452 species, i.e. about 10% species potentially to be added. Both the total and true species numbers are considerably lower than the estimate by Barthlott et al. (1996) who gave 1000–1500 species per 10,000 km² for the respective section of NW India. The presented data suggest that the species-poor area of western Tibet which, according to Barthlott et al. (1996), reaches the border between NW India and Tibet, extends in fact more to the west and covers the whole of Ladakh, including the study area. In contrast, the 452 species obtained by the $Chao_2$ formula fall within the range of 200–500 species estimated by Dickoré & Miehe (2002) for the majority of the study area. A similar discrepancy between Barthlott's estimates and reality were reported for the Karakorum by Dickoré & Miehe (2002) who found up to about 1500 species per 10,000 km², whereas Barthlott's et al. (1996) estimate was 2000–3000 species.

Life-forms and vegetation types

The vegetation of Ladakh as a whole is often referred to by local authorities as desert (Negi 1995) or cold desert (Chowdhery & Rao 1990). Proportion of life-forms in local floras serves as a reliable indicator of habitat type (Danin & Orshan 1990), vegetation type (Hartmann 1995, 1999, Ramsay & Oxley 1997, Mark et al. 2000) and biomes (Pavón et al. 2000) in various regions. Life-form spectra in the study area are markedly different from those reported from typical deserts in India (Sharma & Rajpal 1991) and other parts of the world (Shmida & Burgess 1988, Tareen & Qadir 1993). Therophytes, attaining usually about 30 to 55% of species in (semi-) deserts (Sharma & Rajpal 1991), are represented by 22% of species in the studied area. Moreover, many of these are limited to extra-zonal vegetation and to rare habitats (weeds of arable land, nitrophilous plants that grow in villages and in areas where domestic animals concentrate over nights, river banks). In the large cold high-altitude plains and on gentle slopes covered by relatively sparse but homogeneous vegetation of E Ladakh, therophytes are rare, attaining < 5% of species and having low abundances (Hartmann 1995, 1999). Hemicryptophytes prevail markedly in these habitats, and reach 62%. According to Hartmann (1995), nearly 50% of all species are hemicryptophytes in the main plant communities of E Ladakh. Such high representation of hemicryptophytes is considered characteristic for various types of grasslands and steppes (Raunkiaer 1910), but not for (semi-)deserts. High proportions of turf grasses (several species of *Stipa, Elymus* etc.) and *Artemisia* species also indicate affinities to steppes vegetation rather than to true deserts (see also Schweinfurth 1957).

Distribution of true (semi-)deserts and cold deserts is rather restricted in the studied area (Hartmann 1995, 1997, 1999). Hartmann (1995, 1997, 1999) who paid considerable attention to altitudinal zonation of vegetation in Ladakh, distinguished several vegetation types, from a subalpine desert at the lowest altitudes, through subalpine desert-steppe, alpine steppe, up to open grasslands of the upper alpine zone. In agreement with his treatments, I suggest that (semi-) deserts such as the ones characterised by *Arnebia guttata, Bassia dasyphylla, Erodium tibetanum,* and *Halogeton glomeratus,* are limited in the study area to the lowest altitudes of the Indus river valley. Higher up, where turf grasses predominate steppe is the main vegetation type, reaching E of the Tso Morari lake up to 5300(–5500) m a.s.l. Frigid (semi-)deserts are locally distributed at higher altitudes, mainly along a narrow strip between Parang La (32°30′N, 78°00′E) and Marang La (33°09′N, 77°34′E). Rarely they occur

above the belt of steppes in localities with nutrient-poor soils developed on granite rocks where plants are strongly limited by water supply.

Life-form diversity

Diversity of life-forms in the study area decreases gradually above 4900 m a.s.l. Phanerophytes and hydrophytes cease first, below 5150 m, therophytes decline gradually, geophytes and chamaephytes keep a low but constant share up to 5800 m a.s.l., and hemicryptophytes reach absolute dominance at the highest altitudes. Similar orders of cessation of individual life-forms and prevalence of hemicryptophytes at the highest altitudes have been reported from other mountains in Central Asia, such as Hindukush (Agakhanyantz & Breckle 1995) and Nanga Parbat (Dickoré & Nüsser 2000). However, in the study area particular changes in the life-form spectrum take place at extremely high altitudes. For example, in the Hindukush therophytes do not occur above 5000–5200 m a.s.l. while they reach 5650 m a.s.l. in Ladakh. In the comparatively wetter area of Nanga Parbat a single therophyte, *Gentiana marginata*, has been found above 4300 m a.s.l. Another three species (*Draba altaica, Stellaria irrigua, Cerastium pusillum*) treated as therophytes by Dickoré & Nüsser (2000), were recorded at even higher altitudes, but according to my experience from the study area as well as to literature (e.g. Wu & Raven 1994) these species are hemicryptophytes rather than therophytes. The relatively high proportion of therophytes distinguishes the studied area from most alpine floras world-wide, where, according to Raunkiaer (1910) and Körner (1999), therophytes become increasingly rare with increasing altitude and commonly do not represent more than 2% of the total alpine flora. In arid regions a different pattern has been observed, with therophytes (and also chamaephytes) increasing in dominance and/or abundance along the altitudinal gradient (Cain & Castro 1959, Pavón et al. 2000).

The detailed plant census of the Nanga Parbat region Dickoré & Nüsser (2000) allowed an analysis of altitudinal distribution of species shared with E Ladakh. In the study area altitudinal maxima of perennials are on average by 1175 m higher than in Nanga Parbat (based on 134 species shared for which altitudinal data were available from both regions). This corresponds to the shift of vegetation belts to higher altitudes in dry mountains (Hermes 1955, Körner 1999). However, for different life-forms maximum altitude differences between the two regions diverge strongly ($F_{5, 128} = 6.17$, $P < 0.00005$; one-way ANOVA). Chamaephytes (1030 m), geophytes (1087 m) and hemicryptophytes (1093 m) extend on average around 1000 m higher in the study area than on Nanga Parbat. For therophytes the divergence is much larger, 1592 m on average. The finding that in E Ladakh many therophytes are unexpectedly successful at very high altitudes fits well into the high number of therophytes reported from Tibet (Wang 1988, Zhang Jingwei 1988) to which by its geography the study area belongs. Explanation of this pattern is probably complex and includes both ecological and evolutionary factors.

Diversity of life-forms is usually correlated with climatic heterogeneity (Cowling et al. 1994) and decreases with increasing altitude (Montana & Valiente-banuet 1998, Pavón et al. 2000). This is usually interpreted as a result of deteriorating conditions (Raunkiaer 1910). However, due to the decreasing species numbers at higher altitudes the same trend can be expected from random data. In my data the observed number of life-forms was rarely lower than the range predicted by the null model which included total number of species recorded at individual altitudinal intervals. The two deficiencies observed between 5150 and 5350 m a.s.l. were apparently caused by the cessation of phanerophytes and hydrophytes below these altitudes. While phanerophytes occur rarely above 5000 m elsewhere in the world (Hermes 1955, Körner 1998), hydrophytes have been observed well above this altitude. Hydrophytes are mainly limited by the presence of permanent bodies of stagnant or slowly running, seasonally liquid water, which can be found in Tibet at even higher altitudes. While on Nanga Parbat hydrophytes have not been found above 3500 m (Dickoré & Nüsser 2000), they ascend to at least 5140 m in Ladakh, and in W and Central Tibet aquatic habitats are colonised by vascular hydrophytes up to 5300 m a.s.l. (Schmid 1932, Dickoré 1995). In the study area there are numerous small glacial lakes east of the Tso Moriri at altitudes between 5700 and 6000 m a.s.l. However, no vascular plants occur there.

The percentages of geophytes and chamaephytes are remarkably stable along the altitudinal gradient and the number of species belonging to them corresponded to the expected numbers along the whole altitudinal gradient. This contrasts with the pattern reported from Nanga Parbat (Dickoré & Nüsser 2000), where chamaephytes decrease from a maximum at comparatively very low altitudes (1200–1400 m a.s.l.) to 3000–3400 m a.s.l., with a slight increase again towards higher altitudes. The percentage of geophytes in the Nanga Parbat region was reportedly the highest between 2600 and 4200 m a.s.l., with a decrease towards both, the higher and lower altitudes. In the Hindukush chamaephytes are represented by 10 to 17% of the total species number (Agakhanyantz & Breckle 1995), i.e. about two times more than in Ladakh, with no trend of relative abundance along the altitudinal

gradient observed. Geophytes are poorly represented in life-form spectra from the Hindukush, between 4 and 10%, and this proportion is also independent of altitude, similar as in E Ladakh. The percentage of hemicryptophytes in Hindukush increases from 61% at 4000–4500 m a.s.l. to 70% above 5400 m a.s.l., also similar to my records from E Ladakh. Taxonomic and phytogeographical constraints of the respective areas, as well as different approaches and data sources may account for some of the inter-area variation.

Clonality

Clonal plants are generally abundant in wet, cold and nutrient-poor conditions (Klimeš et al. 1997). Towards extreme climatic conditions (i.e., the Arctic and high altitudes) their proportion usually increases (Klimeš et al. 1997). The percentage of clonal plants is relatively low in the study area, with the highest values reached at low and middle altitudes. Upwards from about 5000 m a.s.l. the share of clonal species declines gradually. This result contrasts with patterns reported earlier (reviewed in Klimeš et al. 1997). The discrepancy between results reported by individual authors was possibly partly caused by the definition of clonal plants. In this paper I use a rather narrow delimitation of clonality. This may have reduced absolute numbers. Nevertheless, the decrease of clonal plants towards higher altitudes requires another explanation. Among clonal plants of Ladakh, tuft grasses with limited clonal spreading prevail (12.1% of species), followed by plants with hypogeogenous (initiated below-ground) rhizomes (7.4%). All other growth forms are represented by less than 2% of species. Plants with long rhizomes or stolons are very rare in the studied area, and almost confined to wet extrazonal habitats along streams. In contrast, non-clonal plants are represented by 28.5% of species in the studied area and play a significant role in zonal semi-desert and steppe vegetation. Non-clonal plants are basically represented by two types, i.e. species with a main (tap) root of the primary root system and without adventitious roots and buds, and pleiocorm plants with short below-ground branches. The poor representation of clonal plants with widely spaced ramets and long-persisting connections between these is probably due to two main reasons. Slope instability at high altitudes due to periglacial phenomena such as solifluction, disturbs whole plants and ramet-connections. In addition, the extremely hard substrate texture of most level areas, whether due to accumulative sedimentation or deflation, is difficult to penetrate. *Carex moorcroftii*, with extremely tough, long, deep-underground rhizomes is one of the few exceptions, and characteristic of sand accumulations (Dickoré 1995). Accordingly, compact growth-forms without or with very limited clonal growth and spreading prevail in the study area, increasingly so with altitude towards the highest altitudes where there substrate instability is becoming a most severe constraint for plant growth. Similar trends of decreasing clonality in vascular plants can be expected also at extreme latitudes of the Arctic (Aleksandrova 1983).

Conclusion

1. The life-form spectrum with dominating hemicryptophytes (62.1%), followed by therophytes (22.3%), chamaephytes (5.4%) and geophytes (4.2%), indicates prevailing desert-steppe and steppe vegetation in the study area.

2. At higher altitudes the abundance of therophytes was lower than expected from a null model, based on random selection of observed number of species from the species pool. On the contrary, hemicryptophytes were more abundant than expected at those altitudes. The number of species belonging to chamaephytes, geophytes, hydrophytes and phanerophytes along the altitudinal gradient fall within the range predicted by the null model, indicating that these life-forms are not significantly favoured at any altitudinal step.

3. Out of 404 species of vascular plants recorded in the study area clonal plants comprised 26.7% of species. From 4180 to 5000 m a.s.l. about 30% of plant species were clonal and above this altitude they gradually diminished. Substrate instability at the middle and high altitudes and tough soil texture preventing horizontal growth in the below-ground at the lower altitudes are probably main factors responsible for the relatively low participation of clonal plants in the study area.

References

Agakhanyantz O, Breckle SW (1995) Origin and evolution of the mountain flora in Middle Asia and neighboring mountain regions. Ecological Studies 113: 63–80.

Aleksandrova VD (1983) Vegetation of polar deserts of the USSR. Leningrad, Nauka [in Russian].

Auerbach M, Shmida A (1993) Vegetation change along an altitudinal gradient on Mt Hermon, Israel – no evidence for discrete communities. Journal of Ecology 81: 25–33.

Barkman JJ (1988) New systems of plant growth forms and phenological plant types. In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic Publishing bv, The Hague, pp 9–44.

Barthlott W, Lauer W, Placke A (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. Erdkunde 50: 317–327.

Berg AL (1998) Plant communities and life forms of the superparamo of the "Sierra Nevada de Merida" National Park, Venezuela. Phytocoenologia 28: 157–203.

Bhattacharyya A (1989) Vegetation and climate during the last 30 000 years in Ladakh. Palaeogeography, Palaeoclimatology & Palaeoecology 73: 25–38.

Braun-Blanquet J (1928) Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verlag, Berlin.

Brazel AJ, Marcus MG (1991) July temperatures in Kashmir and Ladakh, India: comparisons of observations and general circulation model simulations. Mountain Research and Development 11: 75–86.

Cain SA, Castro MO (1959) Manual of vegetation analysis. Harper Brothers, New York.

Campbell BM, Werger MJA (1988) Plant form in mountains of the Cape, South Africa. Journal of Ecology 76: 637–653.

Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43: 783–791.

Chowdhery HJ, Rao RR (1990) Plant life in the Himalayan cold deserts: some adaptive strategies. Bulletin of Botanical Survey of India 32: 43–56.

Cody ML (1989) Growth-form diversity and community structure in desert plants. Journal of Arid Environments 17: 199–209.

Colwell RK (1997) EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Cowling RM, Esler KJ, Midgley GF, Honing MA (1994) Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. Journal of Arid Environments 27: 141–158.

Danin A, Orshan G (1990) The distribution of Raunkiaer life forms in Israel in relation to the environment. Journal of Vegetation Science 1: 41–48.

Dickoré WB (1995) Systematische Revision und chorologische Analyse der Monocotyledoneae des Karakorum (Zentralasien, West-Tibet). Flora Karakorumensis I. Angiospermae, Monocotyledoneae. Stapfia 39. Botanische Arbeitsgemeinschaft am ÖO Landesmuseum, Linz.

Dickoré WB, Miehe G (2002) Cold spots in the highest mountains of the world – Diversity patterns and gradients in the flora of the Karakorum. In: Körner C, Spehn, E (eds) Mountain Biodiversity: A Global Assessment. Parthenon Publishers, Lancaster, pp 129–147.

Dickoré WB, Nüsser M (2000) Flora of Nanga Parbat (NW Himalaya, Pakistan): An annotated inventory of vascular plants with remarks on vegetation dynamics. Englera 19. Botanic Garden and Botanical Museum Berlin-Dahlem & Freie Universität Berlin, Berlin-Dahlem.

Drude O (1886) Deutschlands Pflanzengeographie. Handbuch der Deutschen Landes- und Volkskunde 4: 1–502.

Ellenberg H, Müller-Dombois D (1967) A key to Raunkiaer plant life forms with revised subdivisions Berichte des Geobotanisches Institut ETH Stiftung Rübel, Zürich 37: 56–73.

Fox JL, Nurbu C, Chundawat RS (1991) The mountain ungulates of Ladakh, India. Biological Conservation 58: 167–190.

Hartmann H (1983) Pflanzengesellschaften entlang der Kashmirroute in Ladakh. Jahrbuch des Vereins zum Schutz der Bergwelt 48: 131–173.

Hartmann H (1984) Neue und wenig bekannte Blütenpflanzen aus Ladakh mit einem Nachtrag zur Flora des Karakorum. Candollea 39: 507–537.

Hartmann H (1987) Pflanzengesellschaften trockener Standorte aus der subalpinen und alpinen Stufe im südlichen und östlichen Ladakh. Candollea 42: 277–326.

Hartmann H (1990) Pflanzengesellschaften aus der alpinen Stufe des westlichen, südlichen und östlichen Ladakh mit besonderer Berücksichtigung der rasenbildenden Gesellschaften. Candollea 45: 525–574.

Hartmann H (1995) Beitrag zur Kenntnis der subalpinen Wüsten-Vegetation im Einzugsgebiet des Indus von Ladakh (Indien). Candollea 50: 367–410.

Hartmann H (1997) Zur Flora und Vegetation der Halbwüsten, Steppen und Rasengesellschaften im südöstlichen Ladakh (Indien). Jahrbuch des Vereins zum Schutz der Bergwelt 62: 129–188.

Hartmann H (1999) Studien zur Flora und Vegetation im östlichen Transhimalaya von Ladakh (Indien). Candollea 45: 171–230.

Hermes K (1955) Die Lage der oberen Waldgrenze in den Gebirgen der Erde und ihr Abstand zur Schneegrenze. Kölner geographische Arbeiten, Heft 5. Geographisches Institut, University of Köln.

Holzner W, Kriechbaum M (1998) Man's impact on the vegetation and landscape in the Inner Himalaya and Tibet. In: Elvin M, Ts'ui-Jung L (eds) Sediments of time. Environment and society in Chinese history. Cambridge University Press, Cambridge, pp 53–106.

Jina PS (1995) High pasturelands of Ladakh Himalaya. Indus Publishing Company, New Delhi.

Kapadia H (1999) Across peaks & passes in Ladakh, Zanskar & East Karakoram. Indus Publishing Company, New Delhi.

Kessler M (2000) Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. Plant Ecology 149: 181–193.

Klimeš L, Klimešová J, Hendriks R, van Groenendael J (1997) Clonal plant architectures: a comparative analysis of form and function. In: de Kroon H, van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys Publishers, Leiden, pp 1–29.

Komárková V, McKendrick JD (1988) Patterns in vascular plant growth forms in arctic communities und environ-

ment at Atkasook, Alaska. In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic Publishing bv, The Hague, pp 45–70.

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115: 445–459.

Körner C (1999) Alpine plant life. Springer, Berlin.

Mallon DP (1991) Status and conservation of large mammals in Ladakh. Biological Conservation 56: 101–119.

Mark AF, Dickinson KJM, Hofstede RGM (2000) Alpine vegetation, plant distribution, life forms, and environments in a perhumid New Zealand region: oceanic and tropical high mountain affinities. Arctic, Antarctic, and Alpine Research 32: 240–254.

Mark AF, Dickinson KJM, Allen J, Smith R, West CJ (2001) Vegetation patterns, plant distribution and life forms across the alpine zone in southern Tierra del Fuego, Argentina. Australian Ecology 26: 423–440.

Meher-Homji VM (1981) Environmental implications of life-form spectra from India. Journal of Economic and Taxonomic Botany 2: 23–30.

Miehe G, Winiger M, Böhner J, Zhang Yili (2001) The climatic diagram map of High Asia. Purpose and concepts. Erdkunde 55: 94–97.

Montana C, Valientebanuet A (1998) Floristic and life-form diversity along an altitudinal gradient in an intertropical semiarid Mexican region. Southwestern Naturalist 43: 25–39.

Müller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Negi SS (1995) Cold deserts of India. Indus Publishing Company, New Delhi.

Pavón NP, Hernandez-Trejo H, Rico-Gray V (2000) Distribution of plant life forms along an altitudinal gradient in the semi-arid valley of Zapotitlan, Mexico. Journal of Vegetation Science 11: 39–42.

Ramsay PM, Oxley ERB (1997) The growth form composition of plant communities in the Ecuadorian paramos. Plant Ecology 131: 173–192.

Raunkiaer C (1910) Statistik der Lebensformen als Grundlage für die biologische Pflanzengeographie. Beihefte zum Botanischen Centralblatt 27: 171–206.

Sarmiento G, Monasterio M (1983) Life form and phenology. In: Bourlièrre F (ed) Tropical savannas. Elsevier, Amsterdam, pp 79–108.

Schmid E (1932) Pteridophyta, Gymnospermae, Angiospermae. In: Bosshard W (ed) Botanische Ergebnisse der Deutschen Zentralasien-Expedition 1927–1928. Feddes Repertorium 31: 27–75.

Schweinfurth U (1957) Die horizontale und vertikale Verbreitung der Vegetation im Himalaya. Bonner Geographische Abhandlungen 20: 1–373.

Sharma M, Rajpal K (1991) Life-forms and biological spectrum of the flora of the Punjab state, India. Bulletin of Botanical Survey of India 33: 276–280.

Shmida A, Burgess TL (1988) Plant growth-form strategies and vegetation types in arid environments. In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA (eds) Plant form and vegetation structure. SPB Academic Publishing bv, The Hague, pp 211–241.

Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. American Naturalist 140: 893–911.

Tareen RB, Qadir SA (1993) Life form and leaf size spectra of the plant-communities of diverse areas ranging from Harnai, Sinjawi to Duki regions of Pakistan. Pakistan Journal of Botany 25: 83–92.

von Humboldt A (1806) Ideen zur einer Physiognomik der Gewächse. Cotta, Stuttgart.

Wang J-T (1988) The steppes and deserts of the Xizang Plateau (Tibet). Vegetatio 75: 135–142.

Warming E (1909) Oecology of plants: an introduction to the study of plant-communities. Oxford University Press, Oxford.

Wu Z, Raven PH (1994) (eds) Flora of China. Science Press, Bejing & Missouri Botanical Garden Press, St. Louis.

Zhang Jingwei (1988) Vegetation of Xizang. The series of the Scientific Expeditions to the Quinghai-Xizang Plateau, Beijing.