Population Ecology of *Stipa* Species in Mongolian Drylands

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1 Summary

The ecology of *Stipa* species (*S. krylovii, S. gobica* and *S. glareosa*), which are widespread and often dominant in the dry Central Asian steppes, was investigated in southern and central Mongolia. For comparison, some co-dominant taxa were also taken into account.

The Mongolian steppes host numerous herds of domestic and wild herbivores and herewith provide the means of livelihood for the majority of nomadic Mongolians. Biomass productivity is known to be water-limited in the dry steppes, but grazing leads to nutrient withdrawal and may thus indirectly constrain plant growth. In a fertilization and irrigation study, we found that nutrients accumulate in the soil. Biomass and number of inflorescences increased dramatically in all species groups after fertilization but irrigation showed little impact. The contents of nutrients in plant tissue were higher on fertilized plots. All studied species benefited from fertilization, although the magnitude of responses varied among species-groups. The effect of irrigation on biomass production was very limited. Nutrient depletion is an indirect effect of over-grazing, but can eventually lead to severe rangeland degradation.

Effects on the community level do not necessary reflect effects on the population level and data on population ecology were extremely rare. Thus, we also tested the effect of fertilization and water-surplus on seed viability of *S. krylovii*. The number of viable seeds per area was vastly increased by fertilization. Seed viability was negatively correlated to precipitation along a large-scale gradient. Experimental irrigation increased the number of seeds per inflorescence but reduced the percentage of viable seeds. These results were entirely unexpected and contradict ecological theory, which predicts that reproduction in a dryland is mainly limited by moisture availability. In dry years, *S. krylovii* pollinates cleistogamous, however in wetter conditions partly chasmogamous. In a study on pollen characteristics, we found that pollen longevity is very short under ambient conditions. Thus, reduced pollen vigour may explain lower seed viability under chasmogamous pollination and cleistogamy, due to higher resilience to abiotic stress, increases pollination efficiency and herewith seed viability.

Seed germination of the three *Stipa* species differed slightly. The earlier flowering species, *S. gobica* and *S. gobica* germinated to 100% without pre-treatment. *Stipa krylovii*'s germination rate was increased after cold-stratification, and even more so in the more mesic central Mongolian sample regions. Germination was, however, near zero until extraordinarily heavy rains triggered seedling emergence. The study showed the importance of in-situ studies and highlighted the disproportionably large effects of extreme rainfall events.

To put results into perspective we also analysed five co-dominant species. All five species germinated best at warm temperatures and low osmotic pressure. The dicots *Arenaria meyeri*, *Artemisia frigida* and *Art. santolinifolia* showed almost instantaneous germination, whereas *Allium polyrrhizum* and *Agropyron cristatum* were more similar to the *Stipa* species.

Our studies show the importance of preserving the *Stipa* steppes. Sexual reproduction is rarely possible, which would impede natural expansion into degraded areas or artificial restoration measures. Thus, soil nutrient depletion must be stopped to prevent further steppe degradation.

1.1 Zusammenfassung

Die Ökologie der *Stipa*-Arten (*S. krylovii, S. gobica* und *S. glareosa*), welche in den Zentralasiatischen Steppen weit verbreitet und oft auch dominant sind, wurde im Süden und der Zentralmongolei untersucht. Zum Vergleich wurden auch einige kodominante Arten in die Untersuchungen einbezogen.

Die Mongolischen Steppen beherbergen große Herden domestizierter und wilder Herbivoren und bieten damit der Mehrheit an nomadisch lebenden Mongolen ihr Auskommen. Die Biomasse- und damit Futterproduktivität ist bekanntermaßen wasserlimitiert in den trockenen Steppen, aber Beweidung führt auch zu Nährstoffentzug und kann so das Pflanzenwachstum behindern. In einer Bewässerungs- und Düngungsstudie akkumulierten die Nährstoffe im Boden. Nach Düngung war sowohl die Biomasse als auch die Anzahl an Infloreszenzen drastisch erhöht bei allen Arten(-Gruppen) während Bewässerung keinen Effekt hatte. Die Nährstoffkonzentration im Pflanzengewebe war höher auf gedüngten Flächen. Somit konnten alle Arten von Düngung profitieren; das Ausmaß war jedoch von Art zu Art verschieden. Die beweidungsbedingte Nährstoffverarmung ist ein versteckt verlaufender Prozess, der jedoch mittelfristig zu ernsthafter Degradation des Weidelandes führen kann.

Ein Prozess, der auf der Ebene der Pflanzengesellschaften läuft, muss nicht zwangsläufig Prozesse auf Artebene widerspiegeln. So haben wir auch die Effekte von Düngung und Wasserzugabe auf die Samenproduktion von *S. krylovii* getestet. Durch Düngung wurde die Anzahl lebensfähiger Samen stark erhöht. In einer großräumigen Transektstudie war die Samenlebensfähigkeit negativ mit den jährlichen Niederschlagssummen korreliert. Experimentelle Bewässerung erhöhte die Anzahl an Samen pro Infloreszenz, reduzierte aber den Prozentsatz an lebensfähigen Samen. Dieses Ergebnis war unerwartet und widerspricht gängiger, ökologischer Theorie, die besagt, dass Reproduktion in Trockengebieten durch Wasserverfügbarkeit limitiert wird. In trockenen Jahren blüht *S. krylovii* kleistogam, bei höherer Wasserverfügbarkeit jedoch teilweise chasmogam. Eigene Untersuchungen ergaben, dass die Pollenlebensfähigkeit in den sie umgebenen Bedingungen sehr kurz ist. Möglicherweise ist daher herabgesetzte Pollenvitalität für die reduzierte Samenlebensfähigkeit bei chasmogamer Bestäubung verantwortlich und Kleistogamie erhöht, durch geringere Anfälligkeit auf abiotischen Stress, die Bestäubungseffizienz und damit auch die Lebensfähigkeit der Samen.

Die Samenkeimung der drei *Stipa*-Arten unterscheidet sich etwas. Die früher blühenden Arten *S. gobica* und *S. glareosa* keimen zu 100% ohne Vorbehandlung. Die Keimrate von *S. krylovii* konnte durch Kaltstratifikation erhöht werden. Dies war in den etwas feuchteren Sammelregionen in der Zentralmongolei noch stärker ausgeprägt. Bei einem Aussaatexperiment keimten in Jahren mit normalem Niederschlag gar keine Samen *in situ*, und erst ein außerordentlich starkes Niederschlagsereignis hatte Keimung zur Folge. Die Studie zeigt wie wichtig *in-situ* Untersuchungen sind, und dass Starkregen-Ereignisse große Bedeutung für die Vegetation im Untersuchungsgebiet haben.

Da andere Arten ein anderes Keimverhalten zeigen könnten, untersuchten wir auch fünf andere kodominante Arten. Alle fünf Arten keimten am besten bei warmen Temperaturen und geringem osmotischen Druck. Die Dikotyledonen *Arenaria meyeri*, *Artemisia frigida* und *Art. santolinifolia* zeigten

fast unmittelbare Keimung, während *Allium polyrrhizum* und *Agropyron cristatum* sich ähnlicher zu den *Stipa*-Arten verhielten.

Unsere Untersuchungen zeigen wie wichtig die Erhaltung der *Stipa*-Steppen ist. Die natürliche Zurückgewinnung einmal degradierter Flächen, oder eine künstliche Renaturierung würde durch die niedrige sexuelle Reproduktionsrate massiv erschwert. Die Verarmung an Bodennährstoffen muss daher gestoppt werden um eine weitergehende Degradation zu verhindern.

2 Introduction

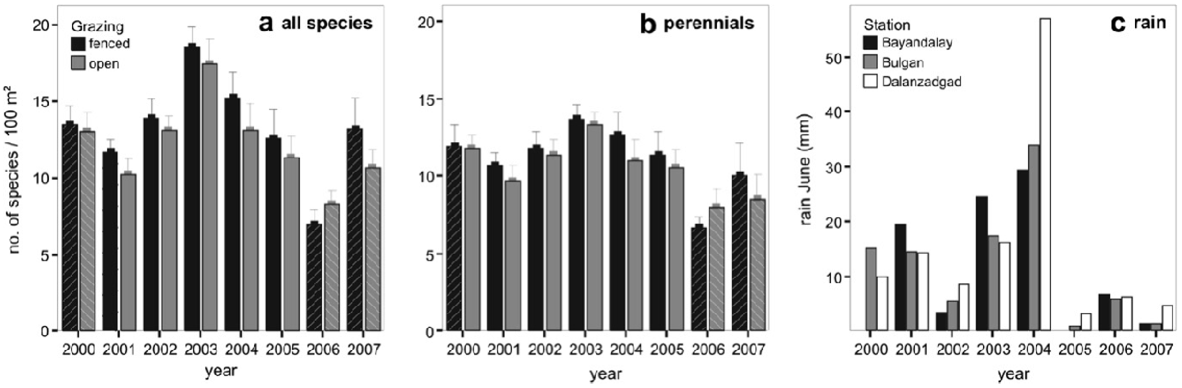
Grasslands cover some 30% of the terrestrial surface and their potential as carbon sinks has raised the attention of science (White *et al.* 2000). Human land management and utilization has altered or even destroyed most temperate grasslands and only a disproportionably small area is currently protected worldwide (Henwood 1998, Hoekstra *et al.* 2005). Central Asia still hosts one of the most extensive grassland regions of the world. In Northern China, grassland degradation continues despite attempts to stop desertification (Akiyama & Kawamura 2007). In these overgrazed areas, grassland degradation has led to a net loss in soil organic carbon (Xie *et al.* 2007), which is relevant for global carbon cycles. In comparison to the vast majority of Chinese rangelands, ecosystem stability is higher in the few remaining undisturbed mature steppes of Inner Mongolia (Bai *et al.* 2004). Outer Mongolian steppes are also relatively intact and cover about 1.3 Mio. km^2 and are still subject to traditional nomadism (Sneath 1998, Fernandez 2006). Here we find unique circumstances that give valuable research opportunities and allow for a new understanding of grassland dynamics.

In southern Mongolia, *Stipa* species dominate many vegetation communities (Wesche *et al.* 2005a), however, they are reportedly more sensitive to over-grazing than other steppe species (Fernandez-Gimenez & Allen-Diaz 1999, van Staalduinen & Anten 2005). The *S. krylovii* steppes are increasingly degraded in northern China (Zhan *et al.* 2007). Thus, in order to preserve the typical steppe communities, it seemed crucial to gain more knowledge about typical *Stipa* species. The main focuses of this thesis are the three *Stipa* species *S. krylovii*, *S. gobica* and *S. glareosa*. However, it seemed advisable to also study co-dominant species such as *Agropyron cristatum*, *Allium polyrrhizum*, *Arenaria meyeri*, *Artemisia frigida* and *Art. santolinifolia*.

In drylands, biomass productivity is highly dependent on notoriously unpredictable rainfalls (Ellis & Swift 1988, Illius & Connor 1999). The coefficient of variation of mean annual precipitation is one important indicator for assessing whether an ecosystem is prone to degradation. A CV of more than 30-33% is said to be within the non-equilibrium (NEQ) zone (Boone & Wang 2007). Following this NEQ paradigm, human influence through livestock keeping should be limited. The theory describes how herbivore pressure is driven by climatic stochasticity and herbivore numbers cannot recover to damaging numbers due to recurrent droughts and fodder scarcity. Mongolia, especially its southern regions, is largely situated within the NEQ zone and this is reflected in traditional, highly nomadic and flexible land use. The NEQ theory has some limitations if livestock herds are managed (Briske *et al.* 2003), which makes it possible to keep livestock numbers above the carrying capacity.

Pastoral nomadism is still the dominant life-strategy of society in rural Mongolia; however, there have been considerable changes along with new political and economic circumstances (Fernandez-Gimenez 1999, Bedunah & Schmidt 2004). Millennia of grazing by wild and domestic herbivores have resulted in a species set entirely adapted to grazing which should reduce sensitivity to grazing effects (Milchunas & Lauenroth 1993, Cingolani *et al.* 2005).

With well below 200mm precipitation annually, southern Mongolia is very dry and, especially in years of drought plant growth, is very sparse. The main study site was within the Gobi Gurvan Saykhan National Park. The national park hosts a wide variety of habitats ranging from extrazonal, high altitude woodlands, to true deserts in the depressions (Wesche *et al.* 2005a) but also offers widespread plains dominated by *Stipa* steppes. With the exception of the highest mountain peaks, the national park is situated well within the NEQ zone with a coefficient of variation of 35-45% (von Wehrden & Wesche 2007). The notion of limited susceptibility to over-grazing was supported in an 8 year fencing experiment, which we conducted in the Gobi Gurvan Saykhan National Park. Variation in species richness was most apparent between years; which is most likely explained by annual precipitation. The difference between fenced and non-fenced plots was less prominent and especially so if annual species were excluded from the analysis (Fig. 2.1). Thus, in the sense of biodiversity loss, no serious sign of degradation was found in the experiment (Wesche *et al.* 2010).



2.1 Fig. 2.2: Vascular plant species richness inside (‘fenced’) and outside (‘open’) exclosures for the years 2000-2005. a) Data for all growth forms; b) perennials only (bars indicate mean plus 1 standard error, hatching indicates data not used for statistical tests). c) June precipitation at Bayandalay and Dalanzadgad for the same period. (Wesche *et al.* 2010)

However, signs of nutrient depletion have been reported from diverse investigations (Su *et al.* 2004, Yong-Zhong *et al.* 2005, Su *et al.* 2006, Pei *et al.* 2008). Moreover, human impact has led to soil erosion (Starkel 1998) and a massive problem with dust storms over Northern China caused by overgrazing and wind erosion in the Gobi (Natsagdorj *et al.* 2003, Wang *et al.* 2004).

Nutrient cycling is just as well determined by the factors flora, fauna, soil and climate. Human activities will also play an increasingly important role. But before human impact was exerted in such intensities, large herds of wild herbivores and more locally, small mammals will have already been part of the nutrient cycle. Burrow-dwelling pikas (*Ochotona pallasi*), cause a patchiness of nutrient distribution, with nutrient rich soils around the burrows (Wesche *et al.* 2007), whereas livestock and here mainly sheep, goats and horses, lead to the translocation of nutrients at a slightly larger scale towards wells and semi-permanent settlements (Fernandez-Gimenez 2000, Fernandez-Gimenez & Allen-Diaz 2001, Stumpp *et al.* 2005, Fernandez 2006). The impact of large wild herbivores has been less intensively studied, but their migrations are usually extensive and flexible (Reading *et al.* 1999b, Ito *et al.* 2006, Kaczensky *et al.* 2008), and they will thus presumably distribute nutrients more evenly.

The question arises, whether the influence of domestic herbivores exceeds the natural impact wild herbivores had in prehistoric times. This is not easily answered however, even at similar stocking densities, C sequestration was found to be lower on sites that were browsed by livestock in comparison to wild herbivores as a consequence of different fodder preferences in the west Himalayan region (Bagchi & Ritchie 2010). Moreover, grazing increased nutrient limitation in otherwise primarily water limited plants (Bagchi & Ritchie 2011). Livestock is transported towards the cities to feed the population and – perhaps more importantly - faeces are still the main source of fuel in rural Mongolia. Nitrogen deposition due to industrial burning of fossil fuels and increasing traffic (Galloway et al., 2004) is likely to be limited in the remote areas of southern Mongolia and is unlikely to mitigate the loss. Overall, human activities, i.e. mainly livestock grazing, is thus likely to abstract more nutrients than artificially introduce them into the ecosystem.

Previously nutrient limitation of plant production in Central Asia was found on irrigated plots (Slemnev *et al.* 2004) and in the somewhat wetter northern China (Xiao *et al.* 2007, Lü & Han 2009). One study described co-limitation of water and N (Gong *et al.* 2011). Moreover, it was found that plant regrowth after grazing was not specifically related to N fertilization and water addition, but only to grazing intensity (Fanselow *et al.* 2011). In a previous study, we could also prove that NPK fertilization increased biomass production dramatically in *Agropyron cristatum* and *Allium*-species (Wesche & Ronnenberg 2010). In that earlier study the effect of water addition was not tested and thus, we could not evaluate the relative effect of water and nutrient limitation. A new study was therefore necessary. Moreover, in that earlier study, we had not distinguished between *S. gobica* and *S. krylovii,* which, due to their different ecological preferences, could be suspected of showing divergent reactions. In Chapter 4 of the present thesis, we therefore study the effect of fertilization and irrigation on *Stipa gobica* and *S. krylovii* and other dominant species-(groups) on plant productivity, number of inflorescences and plant tissue nutrient contents. Moreover, we examined the effectiveness of fertilization by testing whether nutrients accumulate in the soil, or are leached due to irrigation.

One of the most important characteristics of this environment is its variability (von Wehrden & Wesche 2007) and species will need strategies to cope with it. The question of the importance of water vs. nutrient availability is just as crucial with respect to sexual reproduction as it is in terms of productivity. Often the reproductive functions are more sensitive to stress situations than mere vegetative persistence of perennial plants (Obeso 2002, Wesche *et al.* 2005b). Perennial species don’t have to rely on sexual reproduction each year. Sexual reproduction was indeed found to occur with low frequency in the

Mongolian steppes (Lavrenko & Karamysheva 1993). In a widely distributed species like *S. krylovii*, one may expect to find differences between provenances. Even within species, the strategy might change between years. However, there are few examples of species changing their dominant reproduction strategy between regions of more mesic vs. extreme environments. Hence, one of the overarching questions of this thesis is to compare reproduction between regions of dry mountain steppes to the more mesic meadow steppes of *S. krylovii*. Moreover, genetic or maternal and direct environmental effects may constrain seed quality (Broadhurst *et al.* 2008). Thus in chapter 5 we also combine a large-scale study with a comparison of three different seed provenances, a 5 year study on the effect of precipitation on seed viability and an irrigation and fertilization study on seed mass, seed viability and on the number of seeds of *S. krylovii*.

Pollen characteristics can influence seed quality in wind pollinated species (Arista *et al.* 2001). Pollination of wind-pollinated species (anemophily), which is the predominant pollination mechanism in Poaceae, is less well studied than for example pollination through insects (entomophily, Friedman & Barrett 2009). Besides wind-pollination (chasmogamy - pollination in open flowers), *Stipa* species are also known for cleistogamous pollination (selfing within enclosed flowers; e.g. Ponomarev 1961). The ratio of cleistogamous to chasmogamous inflorescences in *S. leucotricha* is environmentally controlled through soil water content (e.g. Dyksterhuis 1945, Brown 1952). However, in other grasses such as *Danthonia spicata,* next to the environmental control a hereditable aspect was also found (Clay 1982).

The ratio of cleistogamous and chasmogamous pollination in *S. krylovii* was unknown just as whether the mechanism of cleistogamy vs. chasmogamy was indeed regulated by water availability. Pollen-ovule ratios can give an indication of the mating system (Cruden 1977, Cruden & Millerward 1981, Cruden 2000). Thus, we determined pollen-ovule ratios and pollen viability in the wettest and driest study sites and pollen rain density in the driest site.

In drylands, sexual reproduction is often confined to very favourable years, and persistence by means of clonal growth becomes the overwhelmingly dominant strategy in many plant species (Wesche *et al.* 2005b, Vonlanthen *et al.* 2010). This is in line with other case studies and global reviews that show how clonal growth becomes more important in extreme environments (Eriksson 1996, Peck *et al.* 1998, Garcia & Zamora 2003). On the northeast China transect it was found, that the ratio of species with a predominantly clonal reproduction strategy increases with aridity (Ni 2003). In chapter 6, we thus mapped 1m^2 plots and took DNA samples for a RAPD study on the clonal diversity of *S. krylovii* within our three study regions.

Irrespective of potential clonal growth capacity, seed germination (the term “seed” is used as a simplification for diaspores of all phylogenetic groups mentioned here, including the caryopses of the grasses) is one of the major bottlenecks for sexual reproduction. Adaptations to the habitat and environment are crucial to guarantee survival at a given site. Our initial study testing 26 species from the Gobi Gurvan Saykhan region found that most perennial plant species showed no indication of seed dormancy and seed viability is also very high (Fig. 2.2). In this study, the three *Stipa* species showed some peculiarities; seed viability of *S. gobica* was very low in general and frost treatment damaged seeds of *S. krylovii* and *S. glareosa* (Wesche *et al.* 2006). Thus, it seemed advisable to investigate germination characteristics of these species in more detail.

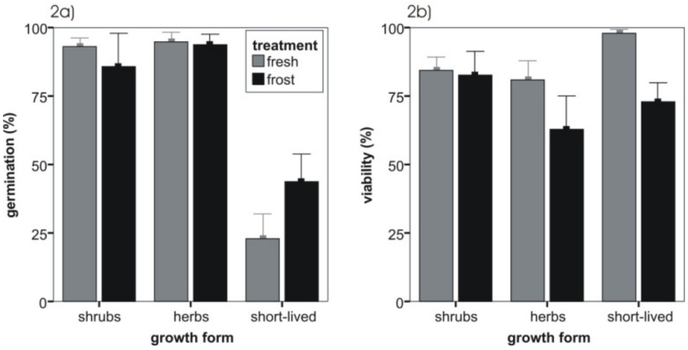


Fig. 2.2: Summary of germination characteristics for three major groups of growth forms. Columns give mean values; error bars indicate one standard error. Fig. 2.1 a) germination of fresh and frost-treated seeds, Fig. 2.1 b) viability of fresh and frost-treated seeds (Wesche *et al.* 2006).

In Chapter 7, we again investigate differences between seed provenances of *S. krylovii*, but focus on seed germination. In a second approach, we compare the germination of the three *Stipa* species (*S. gobica*, *S. gobica* and *S. krylovii*). The entire data set thus covers an ecological amplitude from the desert steppes (*S. glareosa*) to two provenances of *S. krylovii* in the comparably mesic meadow steppes in Central Mongolia. Specifically, we tested temperature requirements and the effect of cold stratification. We asked whether seed dormancy plays a role in any of the species/ provenances and whether that is related to the origin of seeds. Since seeds of the *Stipa* species were known to be sensitive to frost treatment (see above), we also examined seed survival in the soil over one winter, and germination in the field.

In chapter 8, we examine germination requirements of five other dominant and widely distributed species of the dry steppes in Mongolia. In that chapter, we provide more in-depth data on germination including effects of different temperatures and light versus darkness and osmotic pressure. Thus, we screened the general germination requirements of co-dominant species of the typical dry *S. krylovii* steppes in southern Mongolia, and adjacent areas. Sexual reproduction is for most species a very rare event, and if steppes undergo further degradation, the threat is to get to Chinese conditions where the natural bunchgrass vegetation was successively replaced by first rhizomatous grasses, then sandy vegetation and eventually annual plant communities (Huang *et al.* 2007). In northern China, artificial reseeding measures of mostly annuals were already tested to overcome the consequences of desertification (Tobe *et al.* 2001, Zeng *et al.* 2003, Tobe *et al.* 2005). In southern Mongolia, the situation is not as severe yet and perennial species still dominate the zonal vegetation (Wesche *et al.* 2005a).

Thus, here we tested dominant perennial species. Ultimately, chapters 7 and 8 both provide baseline data for potential steppe restoration measures, which we hope will never become necessary.

1.2 Outline of the present thesis

The present thesis comprises four published articles and one chapter of baseline data that has not yet been published but seemed crucial to complete the overall picture of results. Data were derived from altogether 4 stays in Mongolia and subsequent lab-work.

Whereas the chapters and papers deal with specialized aspects, the entire thesis answers three overarching questions: The general "reproduction strategy" of the *Stipa* species, their "plasticity in response to environmental conditions" and the importance of "water vs. nutrient limitation". The thesis also gave room to introduce the study area and species in more detail. The articles were inserted without changes in the wording and only the numbering of chapters, figures and tables was changed to achieve a more consistent layout. In a final chapter, the "Synthesis" the results are discussed under the aspect of the three main study questions. This is followed by a chapter discussing the limits of the results and possible further studies emerging from our results and moreover implications for nature conversation. We bundled references of all chapters at the end of the thesis, thereby also using the opportunity to update references to the status of current availability. We placed the appendices of the chapters 4 and 5 at the end of the respective chapter.

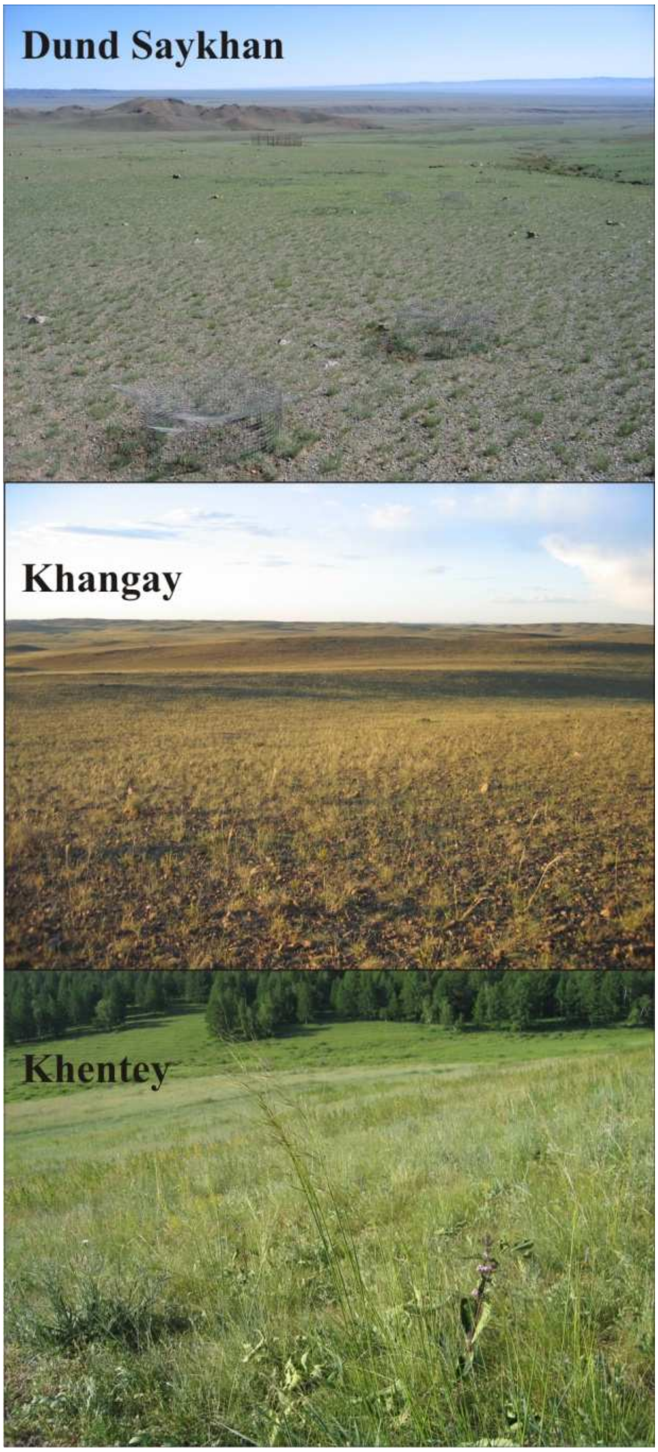
The following aspects of the overarching questions were answered in the chapters and published articles:

- *Reproduction strategy:* Which survival strategy do the *Stipa* species follow? How do they pollinate (chapter 6), germinate (chapter 7), how important is clonal growth (chapter 6), is the reproduction strategy similar to other dominant species in the study area (chapter 8)?
- *Plasticity in response to environmental conditions*: Does *S. krylovii* change its reproduction strategy between the dry southern populations towards the more mesic steppes in central Mongolia? A gradient of increasing water availability is examined in a large-scale study in chapters 5, 6 and 7.
- *Water vs. nutrient limitation*: Which effect does water or nutrient addition have on productivity (chapter 4) and reproduction (chapter 5) of the two *Stipa* species (*S. gobica* and *S. krylovii*) and other co-dominant species?

3 Study region and study species

3.1 General site description

We chose three study sites spread over approximately 600 km from southern Mongolia (Dund Saykhan) to the central regions east of the Khangay (“Khangay” site) to a site 70km north of Ulaanbaatar (here referred to as the “Khentey” site). The main study site is situated in the Gobi Gurvan Saykhan National Park in southern Mongolia. The park was founded in 1993 in order to guarantee long-term sustainable use; protection of rare wildlife, (endemic) plant species, and special landscape features as well as the undisturbed development of the ecosystems (Reading *et al.* 1999a). However, livestock grazing is intense and livestock densities outnumber wild herbivores by a factor of 60 on the pediments and 6 in the mountain ranges (Retzer *et al.* 2006). Hunting is prohibited, but as large herbivores, such as gazelle and Khulan (wild ass) are seen as competitors, herders poach them and, especially in winter, the meat is a popular supplement to their diet. Hence, numbers are below the potential maximum under natural conditions and continue to shrink. The impact of domestic herbivores on the vegetation is undoubtedly considerable.



3.1: Photos of the three study sites (note that the picture of the Khangay was taken one year after the survey was conveyed)

Small mammals on the other hand, such as pikas (*Ochotona pallasi*), are abundant, especially in the upper pediment zone and the mountains in the east and wetter parts of the park. The amount of biomass consumed by pikas is substantial at about 50% of aboveground standing crop (Wesche *et al.* 2007), Moreover, their habits of hoarding fodder and faeces also lead to nutrient accumulation on burrow soils, which enhances the productivity of the vegetation above the burrows (Wesche *et al.* 2007).

In the moister Khangay in central Mongolia, signs of grazing by goats, sheep and horses were also abundant and the nearest pastoral families lived at a distance of about 1km from the sampling sites there. Small mammal burrows were widespread, however seemed mostly deserted. This and the general shape of the burrows suggested that the vole species *Microtus brandtii* (Brandt's vole) dominates in this area. Brandt's vole population dynamics is characterised by regular outbreaks with detrimental effects on the vegetation and almost complete breakdowns. They are considered a pest species and the frequency of outbreaks is positively related to grazing intensity (Zhang *et al.* 2003).

The Khentey site was mainly grazed by cattle and horses. Marmot burrows were abundant; but here too most of them seemed deserted. The endangered species *Marmota sibirica* is regarded as favourable for vegetation development, and its burrows are also used by other endangered species such as the corsac fox *vulpes corsac* (Murdoch *et al.* 2009). However, the meat is considered a delicacy and thus Mongolians still shoot them and drive populations to near extinction.

3.2 Climate

The climate of Mongolia is highly continental with high interannual temperature extremes. In winter, a very stable anticyclone system brings extremely low temperatures of often below -40 °C. During the summer months, temperatures are relatively high and are characterised by alternating cyclone and anticyclone systems. In spring, the transition between the two contrasting weather systems brings strong winds, which cause severe dust storms over the Gobi desert (Haase 1983, Weischet & Endlicher 2000).

Precipitation is dominated by two phenomena: Especially in eastern Mongolia, offshoots of the East-Asian monsoon bring episodic rainfalls, whereas in the west disturbances caused by the west-wind drift dominate the weather system (Weischet & Endlicher 2000). In the central part of Mongolia including the Gobi Gurvan Saykhan National Park, the eastern weather system dominates; however, episodic rains from the west might still occur. Nevertheless the south is characterized by low overall sums of precipitation; which are concentrated within the short growing period (von Wehrden *et al.* 2010). Thus, totals of rain per month of growing season are not exceedingly low and provide sufficient water to enable sparse but continuous plant growth throughout most years.

Climate change scenarios predict increasing precipitation (Christensen *et al.* 2007). Potential positive effects, may, however, be overridden by concordantly predicted rising temperatures and could lead to water balances becoming more arid overall.

The mountain ranges are favoured with regard to precipitation and thus more productive than the surrounding semi-deserts. In the uppermost mountain ranges we can even find shrub lands and birch woods (Hilbig 1995, Wesche & Ronnenberg 2004, von Wehrden *et al.* 2009a). Our main experimental site at the footzone of the Dund Saykhan study site, on the upper pediments was clearly situated within the non-equilibrium zone with a CV of 35-45% (von Wehrden & Wesche 2007).

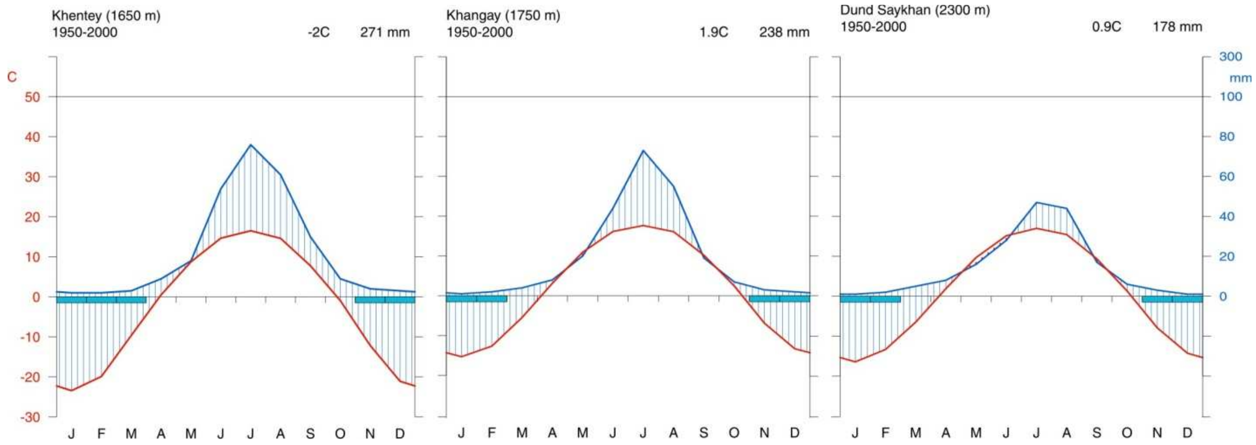


Fig. 3.2: Walther-Lieth diagrams of the three study sites. Data from the interpolated climate model by Hijmans *et al.* (2005). This is based on measurements at national climate stations in Mongolia (length of observation period 1950-2000). The figure shows the name and altitude of the study sites (first line), mean annual temperature and precipitation sums (second line right side) and most importantly, it shows mean temperature (red curve) and mean precipitation sums (blue curve) for the months (Jan-Dec). Diagram created with the R software (R Version 2.9.1. 2009, climatol package).

Dund Saykhan: Own rain measurements over four years suggest a mean of 127 mm precipitation (range 28-211mm), whereas a climate model predicts 180mm with 160mm falling during the vegetation period (April-September, Hijmans *et al.* 2005). Mean annual temperatures are with a mean of 0.9 just slightly above freezing (Fig. 3.2).

Khangay: Annual precipitation is predicted to lay at 240 mm with 210 mm falling between April and September. Annual mean temperatures lay at 1.9°C (Fig. 3.2).

Khentey: Precipitation totals 270 mm of which 250 are concentrated within the 6 warmest months. The Khentey study site, with a mean annual temperature of -2°C, is the coldest of the three sites, although temperature differences are small overall (Fig. 3.2).

3.3 Geology & soils

Parent rock material is diverse with mostly metamorphic origins. Quaternary processes formed the present landscapes; after the retreat of the glaciers (Lehmkuhl *et al.* 2004, Yang *et al.* 2004) the climate became successively drier in mid Holocene (Gunin *et al.* 1999). The dry climate and partial overgrazing resulted in the deflation of most plains and pediments, leaving gravelly deserts and steppes behind (Yang *et al.* 2004).

The main study site is in the upper pediments region of the Dund Saykhan in the Gobi Gurvan Saykhan National Park, with gently sloping pediments intersected by erosion gullies.

In the northern, more mesic regions of Mongolia, pedogenesis has formed Chernosems as typical continental steppes soils, whereas soils in southern latitudes are mostly shallow Kastanosems or even Burosems.

For details on soil conditions see chapter 3.6.

3.4 Flora & Vegetation

Mongolia is part of the Holarctic floral Kingdom and all three study regions are classified as part of the West and Central Asian desert region (Meusel *et al.* 1965). According to the climatic differences described above, this is divided into a western and eastern subregion. The majority of higher plant species in southern Mongolia have an eastern Eurasiatic distribution centre (Jäger 2005). In central and northern Mongolia, eastern Asian elements dominate and many of these are still represented at higher altitudes on the mountain peaks of southern Mongolia. In the basins and lowlands of central Mongolia, we find, however, a number of Central Asian endemics.

Not only the current flora but also the vegetation types are of evolutionary old age. At the end of the Eocene a grassy vegetation began to develop in continental Eurasia and by the Oligocene today’s grassland vegetation types appeared (Numata 1979, Bredenkamp *et al.* 2002). An intense process of co-evolution of grassland plants and animals occurred (Mack & Thompson 1982, Carroll 1988). General herbivore sizes increased due to the availability of large amounts of forage plants in the open grasslands. Today’s vegetation has thus been subject to grazing by wild herbivores over millennia and virtually all plant species are drought and grazing resistant.

The different study sites represent various vegetation belts within Mongolia. According to Wallis de Vries *et al.* (1996) our Khentey study site lays in the transition zone of forest steppe zone to steppe zone. In the mountains and hills there, differences in topography trigger a differentiation of the vegetation in forest on the north-facing slopes and higher areas, and steppes on the south-slopes and in valleys. Due to logging and presumable burning activities in this region, the forest has further retreated and the steppes, especially meadow steppes, have expanded.

The Khangay study site is situated at the boundary between steppe zone and semi-desert, where grasses dominate the vegetation. The *Stipa* steppe (Cymbario-Stipetum krylovii; Hilbig 1995) is a characteristic community of this region.

The Dund Saykhan study site is situated in the semi-desert zone, where the vegetation becomes considerably sparser. Two main types of vegetation can be distinguished; the *Stipa-Allium* semi-desert and the shrub semi-desert (Yunatov 1950). They occupy rocky, stony-gritty and sandy sites. The zonal vegetation is dominated by *Artemisia* spec., *Allium* spec. and various Poaceae (von Wehrden *et al.* 2009a). Dwarf-shrubs are more dominant on disturbed sites including semi-permanent water courses, steep slopes and small mammal burrows (Wesche *et al.* 2005a). In contrast to the severely degraded steppes of northern China, annuals are negligible in their relative contribution to biomass and flora. However, they are important on disturbed sites and may reach higher abundances in moister years (Wesche *et al.* 2010).

All studied *Stipa* communities belong to the class of the Agropyretea cristati (Hilbig, 1995); however, along with the gradient of increasing water availability, vegetation communities differ. *Stipa* species are important constituents of many plant communities in the Gobi Gurvan Saykhan National Park and follow in their occurrence a moisture gradient from very dry semi-deserts, which are dominated by *S. glareosa*, to the upper slightly moister pediments which are occupied by *S. gobica*, to the uppermost pediments and mountainous slopes were *S. gobica* is successively replaced by *S. krylovii* (Wesche *et al.* 2005a, von Wehrden *et al.* 2009b); the latter then becomes increasingly dominant in the moister steppes of central and northern Mongolia.

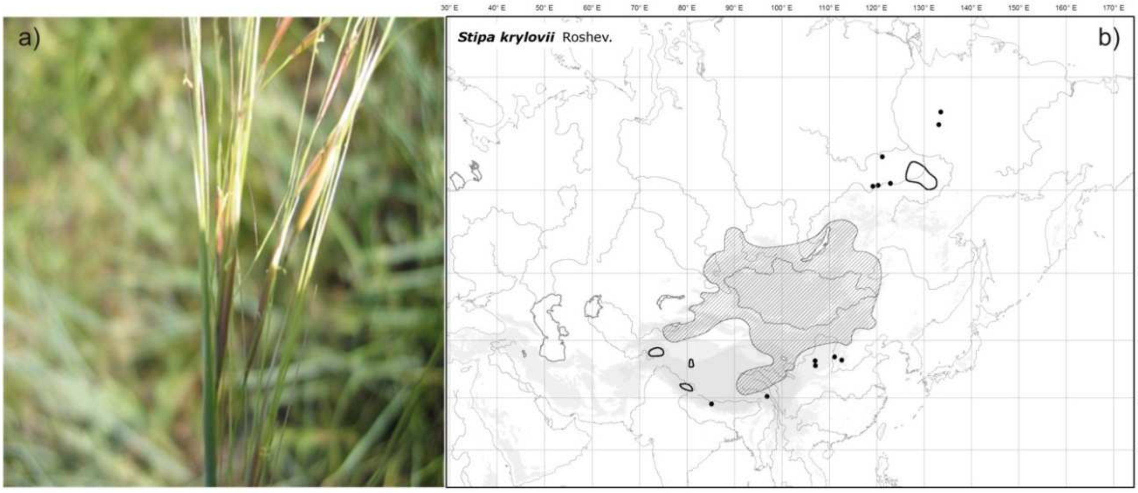
Most studies were undertaken in the association of the Hedysaro pumili-Stipetum krylovii –typicum with the diagnostic species: *Stipa krylovii*, *Artemisia frigida*, *Agropyron cristatum*, *Arenaria meyeri*, *Astragalus multicaulis*, *Bupleurum bicaule*, *Oxytropis pumila*. Seeds for the broader screening were also collected in the Hedysaro pumili-Stipetum krylovii, *Festuca valesiaca* sub-community. *Stipa glareosa* does not occur at altitudes where the *F. valesiaca* community is common, and seeds were collected from several communities of the Stipetea – Allion polyrrhizi (von Wehrden *et al.* 2009b).

3.5 Study species

Stipa species are important vegetation constituents throughout temperate grasslands, including Central Asia (Lavrenko & Karamysheva 1993). They are important by virtue of their sheer dominance and can be regarded as key species for vast areas of Mongolia and adjacent areas. Moreover, the high fodder value (Jigjidsuren & Johnson 2003) makes them important rangeland species.

Stipa species are known to be capable of both cleistogamous and allogamous pollination. The pollination strategy is related to water availability and seed germinability was found to be lower in allogamously flowering plants in *S. leucotricha* from North America (Dyksterhuis 1945, Brown 1952). The Russian literature finds the same relation and goes more into detail on the phenology of *Stipa* species. They find that most species open for pollination at night, and that each species has a distinctive requirement of air humidity to open for pollination (Ponomarev 1954, Ponomarev 1961, Bespalova

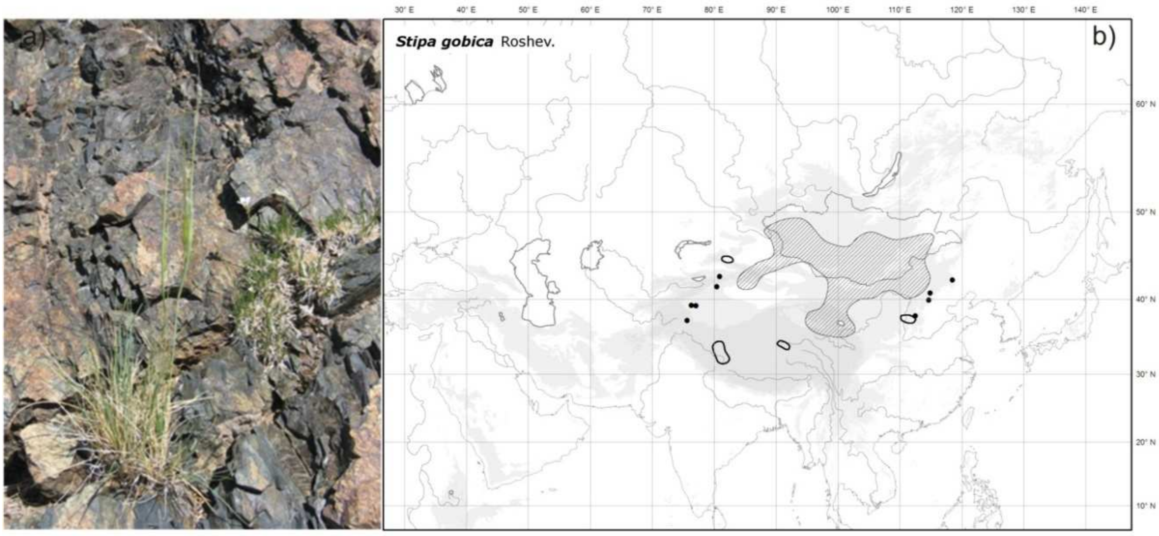
1962, Ponomarev 1966). Germination rates are usually low, but dispersal and germination at safe sites is enhanced by the hygroscopic awn (e.g. Fowler 1986, Hensen 1997, Boeken *et al.* 2004, Schöning *et al.* 2004). In Central Asia, some research on *Stipa* species has focussed on molecular aspects and demonstrate that populations are more strongly differentiated than most wind-pollinated species, and this effect is stronger in drier sites (Shan *et al.* 2006, Wang *et al.*2006, Zhao *et al.* 2006). Moreover, growth parameters and steppe degradation of *Stipa* steppes in northern China and the effect of overgrazing were studied (Xie & Wittig 2003, 2004, Xie & Wittig 2007, Zhan *et al.* 2007). *Stipa krylovii* is known to have high compensatory growth after grazing, however, *Leymus chinensis* capacity is stronger and thus replaces *S. krylovii* in severely overgrazed areas (van Staalduinen & Anten 2005).



3.3: a) Chasmogamously flowering inflorescence of *S. krylovii* and b) distribution map (draft by Jan Treiber)

Among the three main focus species of the present thesis, *Stipa krylovii* Roshev. (*Stipa* section— Leiostipa, Poaceae) is most widely distributed in Mongolia, China, Kazakhstan and Russia (Fig. 3.3). In Mongolia (Gubanov 1996, Wu & Raven 2006) it inhabits a wide macroclimatic gradient from the central Mongolian meadow steppes to the southern dry mountain steppes. Its phenology is highly dependent on rainfall (Yuan *et al.* 2007). In an average year, flowers pollinate in July and seeds mature in August, with southern populations starting their reproductive cycle earlier than the northern populations. Moreover, individuals in northern, moister populations grow higher and more vigorously. *Stipa krylovii* inhabits the widest ecological amplitude of the three study species and was thus examined in more detail than the other two species.

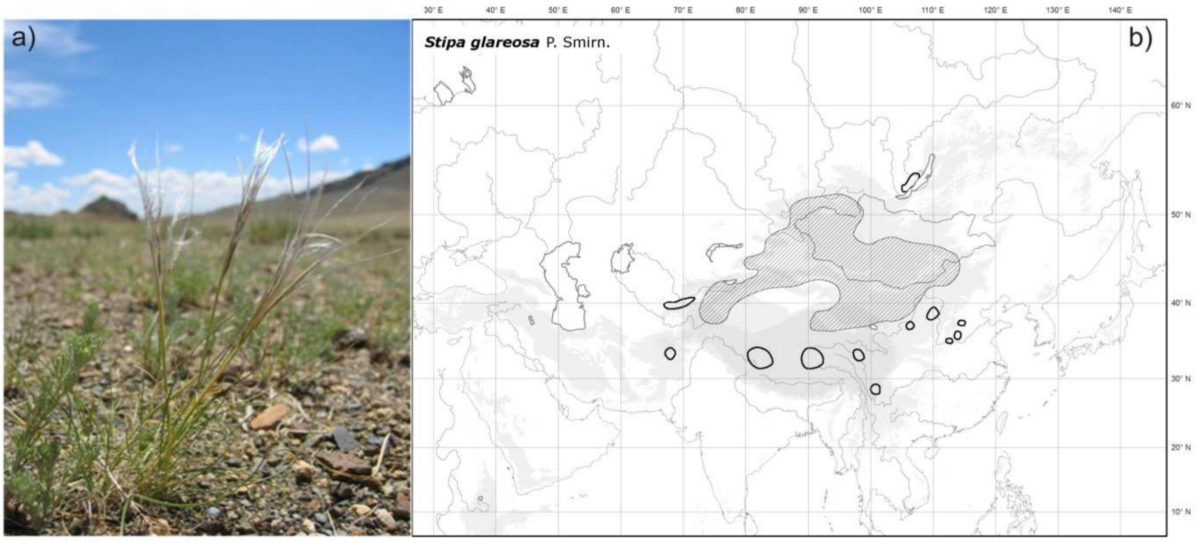
The distribution range of *S. gobica* Roshev. (section— *Stipa*) is restricted to the dry mountain steppes and semi-deserts of southern Mongolia and northern China with a few outliers in the Tibetan plateau and the Himalayas (Wu & Raven 2006, Fig. 3.4). Flowering usually takes place in June; seed dispersal in July or August. It is typical for the upper pediments but also for rocky habitats in the higher mountain areas (Wesche & Ronnenberg 2004).



3.4: a) *Stipa gobica* tussock in the Dund Saykhan mountain range on a crack in the rocks, and b) distribution map (draft by Jan Treiber).

Stipa glareosa P. Smirn. (section—*Stipa*) occupies the driest sites of the three species. Its distribution range includes Middle Asia with Kazakhstan, Afghanistan, Kyrgyzstan, but also Siberia, Mongolia and China (Wu & Raven 2006, see Fig 3.5). Flowering and seed dispersal are usually completed by the end of June.

At dry sites, populations of all three species, but especially *S. gobica* and *S. glareosa*, form relatively low inflorescences, attaining 25–35 cm in height. All studied feather grasses are typical bunchgrasses (caespitose hemicryptophytes).



3.5: *Stipa glareosa* in a typical dry steppe site (left) and distribution map (right; draft by Jan Treiber).

For comparison we also studied a selection of other species which were, besides *S. krylovii* and *S. gobica,* some of the most common species on the upper pediments of the main study area (Wesche *et al.* 2005a):

Agropyron cristatum (Poaceae) is the most abundant grass species in the Dund Saykhan.

Allium polyrrhizum (Liliaceae) is - especially in dry years - the most dominant species in the main study site because it is the first species to benefit from even a slight drizzle. Due to secondary compounds, it is less commonly eaten by livestock and small mammals.

Arenaria meyeri (Caryophyllaceae) is a little cushion forming species, which can be very prominent on the pediments.

Artemisia frigida (Asteraceae) is the most common dicot in the study area.

Artemisia santolinifolia (Asteraceae) is a dwarf shrub and very common on disturbed sites such as small mammal burrows and steeper, scree slopes.

3.6 Comparison of vegetation and soil characteristics in the three sites of the large-scale study

This section is not intended as a comprehensive site description, but since the study sites were mainly selected for their macroclimatic conditions on a gradient of increasing water availability, we had to gather some basic soil data in order to detect potentially underlying causes for differences of the three sites. Moreover, competition, or plant-plant interaction in general, can alter plant performance. Thus, we compare here the vegetation and give some general site characteristics of the three areas.

First impressions of the physiognomy i.e. productivity and species set made the Khangay and the Dund Saykhan site seem fairly similar, whereas the Khentey site seemed different with more luxuriant plant growth, and *S. krylovii* having many inflorescences (compare photos Fig. 3.1). However, according to precipitation means, the Khangay and Khentey site are more similar and the Dund Saykhan is by far the driest site (confer Fig. 3.2). Thus, other environmental variables should explain the differences. With equal precipitation sums, water availability can still vary depending on soil types and soil water capacity. Soil nutrients can also be limiting be it because they are not available to plants, or because there are low concentrations in the soil. Thus, we compared the field capacity of 10 soil samples from each region and the plant available fraction of the following macronutrients: K, Mg. and P and total N and total organic C, see below (for details of soil analytics, see chapter 4 - method section).

In 2005, we surveyed 25 randomised plots in each of the three study sites distributed over an area of approximately 50 ha situated in the regionally typical *Stipa* steppes. On these 1m^2-plots, we recorded cover of all vascular plant species, measured the height of plants situated on a 100 point grid and took soil samples (mixed soil samples of at least three locations in the plot). Moreover, we counted the number of *S. krylovii* inflorescences in the plot and noted whether they were potentially chasmogamous or unquestionably cleistogamous. The category chasmogamous includes all inflorescences, of which at least some flowers were protruding from the leaf-sheaths. Thus, it represents an overestimation of chasmogamy on the level of the single flower, and allows for an unknown proportion of seeds that were still produced after cleistogamous pollination.

Vegetation cover in general as well as of *S. krylovii* in specific was highest in the Khentey study site (Fig. 3.1). Mean vegetation height in Khentey was 12±0.8cm (SE) and 6±0.4cm and 4.3±0.2cm for Khangay and Dund Saykhan respectively. The maximum height shows the difference in physiognomy even clearer (47±3.3cm, 16±1.6cm and 9±0.7cm for Khentey, Khangay and Dund Saykhan respectively). These, and the following differences were statistically significant at $p < 0.001$ (ANOVAs of rank transformed data).

In the Khentey study site, mean vegetation cover was 55±1.6% and *S. krylovii* had a mean cover of 2.4±0.3%. It had on average 11 inflorescences per m^2, of which about 50% flowered chasmogamously. This number results in 110,000 inflorescences and potentially 55,000 chasmogamous inflorescences per ha.

In Khangay, mean vegetation cover was 14.1±1.4% and the cover of *S. krylovii* was on average 0.9±0.3%. Altogether, we found 5 *Stipa* inflorescences on our randomly chosen $1m^2$ plots of which 4 were clearly cleistogamous and 1 potentially chasmogamous. Thus, our density estimation of potentially chasmogamous flowers results in at most, 2000 per ha (compared to 8000 cleistogamous florets).

In Dund Saykhan, mean vegetation cover was 12.8±0.8%, the cover of *S. krylovii* was 0.8±0.2. On the randomly chosen plots, there was not a single *Stipa* inflorescence. Thus, the density of *Stipa* inflorescences was well below 400 per ha, of which only a negligible proportion flowered chasmogamously.

Tab. 3.1: Mean Bray-Curtis dissimilarities (cover weighted) between relevés of the three study regions.

	Khentey	**Khangay**	**Dund Saykhan**
Khentey	**0.61**		
Khangay	0.97	**0.78**	
Dund Saykhan	0.97	0.87	**0.43**

Within study sites themselves, the Dund Saykhan has the the most homogenous vegetation as indicated by the mean Bray-Curtis dissimilarity between samples of 0.43. For comparison, the Khentey has a value of 0.61 and the Khangay of 0.78. Whereas the vegetation of the Khentey is very different from the two other sites, Dund Saykhan and Khangay still have a few more species in common and thus a lower Bray-Curtis index (Tab. 3.1).

Besides *S. krylovii*, the most common species in the Dund Saykhan are *Agropyron cristatum*, *Allium polyrrhizum* and *S. gobica.* In Khangay, the most common species are *Carex stenophylla*, *Chenopodium* *acuminatum* and *Salsola pestifera*. In Khentey, *Potentilla acaulis* dominates with 25% mean cover followed by *Carex stenophylla* and *Leymus chinensis*.

Annuals as indicators of disturbance were very abundant in the Khangay site with 42±7% of the total cover. In contrast, they were almost exclusively confined to small mammal burrows and only made up 5±2% and less than 1% of the total cover in the Khentey and Dund Saykhan site, respectively. The following year, annuals were also less prominent in Khangay (personal observations). The high abundance of annuals could be a sign of strong early rainfalls in that season, or possibly the consequence of a recent outbreak of the Brandts vole, and the associated disturbance (Zhang *et al.* 2003).

Soils in Dund Saykhan and Khangay are degraded chestnut soils with a field capacity of 17±1 and 17±0.5% respectively. Soils in the Khentey study site are chernozems with a field capacity of 42±2. The difference between the Khentey and the other two sites is statistically significant (ANOVA $p<0.001$).

The higher biomass productivity in Khentey is also reflected by the higher cover of litter and higher organic carbon content in the soil (ANOVA of rank transformed data $p<0.001$; Fig. 3.6). The Khentey had the widest CN-ratio but also the highest percentages in C and N (ANOVA of rank transformed data $p<0.001$). A content of about 5% of organic carbon can roughly be translated into 10 percent of organic matter, which are present as humic complexes, which is typical of Chernozem soils (Schachtschabel *et al.* 1992). The humic soil also explains the relatively high field capacity. In all three habitats, the CN ratio is very narrow (Fig. 3.6). The Dund Saykhan had the narrowest CN-ratio, but had slightly higher percentages in C and N than the Khangay. Whereas in the Khentey the ratio of about 10 is typical of black soils, the even narrower ratio in the other two sites must be an indication that N is available in inorganic compounds. The number of visible roots on the surface of a 10*10 cm² spade cut did not significantly differ between the three regions. This corresponds to a superficial impression on root densities as gained from the presence of visible roots on spade cuts, however the spade cuts in the stony soils of Khangay and Dund Saykhan were harder to count than in the smooth soils of the Khentey and thus perhaps not entirely comparable.

Available P was highest in Khangay and lowest in Dund Saykhan (19±3mg/kg, 17±3, 16±2mg/kg soil, for the regions Khentey, Khangay and Dund Saykhan), however these differences were not significant ($p>0.5$, Fig. 3.6). Magnesium was highest in the Khentey region and lowest in the Khangay, with all three regions differing significantly (ANOVA $p<0.001$, Tukey-test $p< 0.05$). Potassium is significantly higher in Khangay than in Dund Saykhan (ANOVA $p=0.004$). However, the contents of these bases were in general very high and unlikely to be limiting.

The higher biomass productivity and species richness in Khentey in comparison to the Khangay is most likely explained by the more favourable soils, while the precipitation means seem to be less important for the difference in plant growth. Otherwise, the Khangay should allow for similarly high productivity as the Khentey.

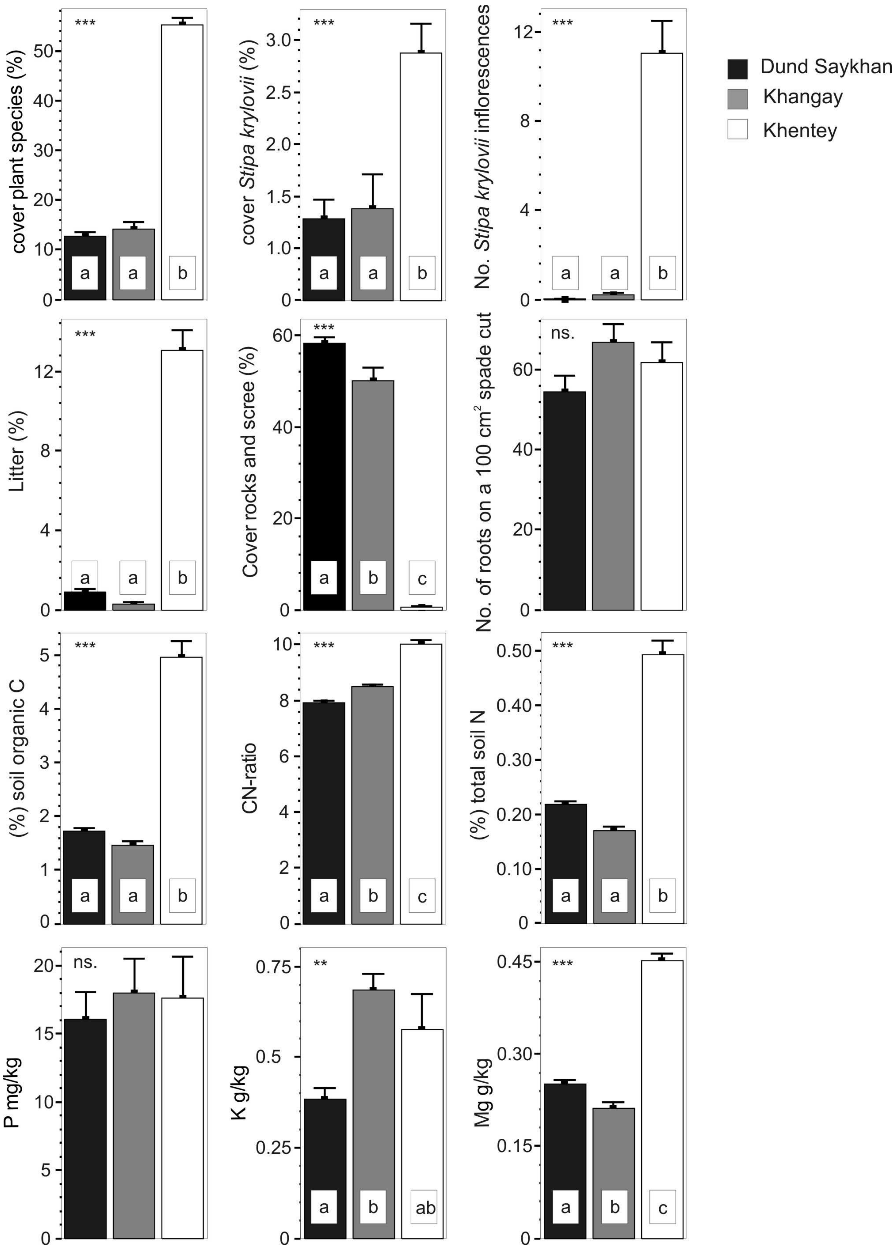


Fig. 3.6: Site and soil characteristics in the three study regions (mean+SE). Statistical differences of the main effect (ANOVA of rank transformed data) are indicated by ** = $p<0.01$; *** = $p<0.001$; ns. = $p>0.05$. Lower case letters highlighted by white boxes indicate statistical differences between groups (tuckey test) at $p<0.05$.

Stipa krylovii should also find the most favourable conditions in the Khentey, which is supported by the high cover, the density of inflorescences and the shoot height. Aboveground competition is highest in Khentey; however, aboveground competition is mostly relevant for light gain (Hautier *et al.* 2009). This should be less of a problem in the still relatively sparse vegetation stands of most Mongolian grasslands. Belowground competition is the competition for resources, such as nutrients and water, which should be more relevant for our study sites as evidenced by the almost closed root layers. In terms of number of roots, we found, however, no difference between study sites (Fig. 3.6).

4 Effects of fertilization and irrigation on productivity, plant nutrient contents and soil nutrients in southern Mongolia

(Ronnenberg & Wesche 2011: Plant & Soil 340. 239-251)

Abstract

Aims: The study attempts to evaluate the effect of fertilization and irrigation on steppe productivity in dry southern Mongolian desert-steppes.

Methods: We conducted an irrigation- and NPK fertilization experiment, irrigating at levels of +100 mm and fertilizers at amounts equivalent to 20 gN $(m^2\ year)^{-1}$ in a factorial design. We tested the effects on soil nutrients and biomass production. Nutrients in plant tissue were analysed for *Stipa krylovii* and *S. gobica*, and for mixed sub-samples of total above- and belowground biomass.

Results: Available P and K and total K increased in the soil after fertilization while irrigation reduced total N. Biomass yield almost tripled and inflorescence numbers increased by factors of 4-8 due to fertilization while irrigation alone had very restricted effects and only increased biomass of *Agropyron cristatum*. Nutrient content of biomass was elevated on fertilized plots.

Conclusions: Results indicate that steppe productivity is severely restricted by nutrient availability even under ambient precipitation levels, raising the question whether nutrient withdrawal caused by current land use practices has detrimental effects on pasture productivity. The anticipated beneficial effect of increasing water availability however could not be confirmed. Whether there is an improvement in productivity due to increasing rainfall, as predicted by some climate change models, will depend on the distribution and intensity of rain events.

Keywords
Biomass, dryland, nutrient limitation, primary productivity, Steppe, water availability

5 Contrasting effects of precipitation and fertilization on seed viability and production of *Stipa krylovii* in Mongolia

(Ronnenberg, Hensen & Wesche 2011: Basic and Applied Ecology 12: 141-151)

Abstract

In drylands, primary production is predominantly limited by water availability; however, there is evidence for co-limitation by nutrients. We tested whether improved water and nutrient availability facilitate reproduction of dominant steppe species, and studied the effects of increased moisture and fertilization on seed production of the steppe grass *Stipa krylovii*.

Effects of water availability on seed production and seed viability were investigated in a large-scale study on three sites with decreasing precipitation in Mongolia, over three to five consecutive years. In dry southern Mongolia, we additionally conducted an *in-situ* irrigation and fertilization experiment to clarify the role of environmentally induced effects on seed production.

Seed viability of *S. krylovii* was negatively correlated with annual precipitation over five years at the driest study site. The relation between annual precipitation and seed viability in the large-scale study was not as clear, however, in the two moister regions there was a trend of lower seed viability. Experimental irrigation also significantly decreased seed viability and seed mass. Seed production per hectare was not affected by irrigation, while fertilization resulted in a more than five fold increase in both seed weight and number of viable seeds. The underlying mechanisms for these unexpected results were not investigated. However, a switch from cleistogamous pollination under dry conditions to less effective cross pollination in moist years may be an explanation. Our data indicate that plant reproduction may show complex and unexpected reactions, and that nutrient limitation must be considered in global change scenarios even for dry regions.

Zusammenfassung

In Trockengebieten ist die Primärproduktion vor allem durch Wasserverfügbarkeit limitiert, es gibt jedoch auch Hinweise auf eine Ko-Limitierung durch Nährstoffe. Wir haben getestet, ob sich Wasser- und Nährstoffverfügbarkeit auf die Reproduktion eines dominanten Steppengrases auswirken. Dazu untersuchten wir die Auswirkung unterschiedlicher Bewässerung und Düngung auf die Samen-produktion und –qualität der Federgrasart *Stipa krylovii*.

Den Effekt der Wasserverfügbarkeit testeten wir in einem großräumigen Vergleich abnehmender Niederschläge in der Mongolei; die Messungen liefen über drei bis fünf aufeinanderfolgende Jahre. Darüber hinaus führten wir in der südlichen Mongolei, im trockensten der drei Untersuchungsgebiete, ein *in-situ* Experiment mit Beregnung und Düngung durch, um die Rolle von umweltinduzierten Effekten auf die Samenproduktion zu analysieren.

Die Samenlebensfähigkeit im trockensten Untersuchungsgebiet korrelierte signifikant negativ mit dem jährlichen Niederschlag. Das Verhältnis zwischen jährlichem Niederschlag und Samenlebensfähigkeit in der großräumigen Studie verhielt sich weniger eindeutig; die Lebensfähigkeit in den feuchteren Regionen war jedoch tendenziell niedriger. Experimentelle Bewässerung reduzierte sowohl die Samenlebensfähigkeit als auch das Samengewicht. Die Gesamtproduktion von Samen pro Hektar wurde durch die Bewässerung nicht beeinflusst; Düngung hingegen führte zu einer mehr als fünffachen Zunahme von Gesamt-Samengewicht und Anzahl lebensfähiger Samen.

Die Ursachen für diese unerwarteten Ergebnisse wurden von uns nicht untersucht, jedoch könnte ein Wechsel von kleistogamer Bestäubung bei trockenen Bedingungen zu weniger effektiver Fremdbestäubung in feuchteren Jahren unsere Ergebnisse erklären. Unsere Daten zeigen, dass die Reproduktion von Pflanzen komplexe und unerwartete Reaktionen auf den Klimawandel zeigen könnte, und dass Nährstoffmangel in entsprechenden Zukunftszenarien selbst für sehr trockene Gebiete einbezogen werden sollte.

Keywords:

Central Asia; drylands; irrigation; nitrogen deposition; nutrient limitation; Poaceae; reproduction; seed ecology; steppes; water availability

6 Baseline data on *Stipa krylovii*: Plasticity in pollination traits and vegetative persistence

6.1 Introduction

One of our aims was to assess potential plasticity in reproduction responses to different levels of water availability. *Stipa krylovii* was the most suitable species, because it inhabits the widest hygric gradient. In this chapter, we summarise data on pollination characteristics and the importance of clonal growth that were gathered in a large-scale study. Sexual reproduction is known to be rare in that species, but it can occur in exceptionally favourable conditions, even in dry southern Mongolia (Lavrenko & Karamysheva 1993, Chapter 7). However, sexual reproduction will only add to the genetic diversity of a population if seeds are produced as consequence of outcrossing pollination. Mere cleistogamous pollination, as well as predominantly clonal growth will result in genetic impoverishment, even in a common and widespread species (Honnay & Jacquemyn 2007).

Based on an analysis of genetic diversity (Wang *et al.* 2006) predict a partly selfing and partly out-crossing breeding system for *S. krylovii*. Similar results were obtained for *Stipa* species in Europe (Hensen *et al.* 2010, Durka *et al.* in prep., Wagner *et al.* in press). *Stipa* species are known for facultative cleistogamy (Campbell *et al.* 1983); however, the importance of cleistogamy for *S. krylovii* in specific was unknown. Moreover, since the extent of cleistogamy depends on soil moisture in *S. leucotricha* (Brown 1952), we asked whether the pollination strategy might vary between wetter and dryer study sites.

The pollen/ ovule ratio is considered an indicator of the flowering strategy. In general, mainly outcrossing species tend to have higher pollen/ ovule ratios than selfing or even cleistogamous species (Cruden 1977, Cruden & Millerward 1981). We thus determined p/o ratios for *S. krylovii*. Successful pollination depends on exchange of fertile pollen, and is thus influenced by pollen viability and longevity. We measured pollen viability under ambient conditions, with the aim of getting an estimate of their survival rates. Moreover, the density of flowering individuals in a given stand will play a role in determining the likelihood of cross-pollination in wind pollinated species (Cruden 2000). The vegetation records from the three study sites (chapter 3.6) give us a crude estimate of the population density and thus of the chances for chasmogamous pollination. We found a vast difference between the density of potential pollen donors (chapter 3.6). However, the category “potentially chasmogamous” includes all inflorescences, where at least one floret had emerged from the leaf sheaths. Many of the lower florets may still remain closed, and we thus only obtained an optimistic estimate of the potential for xeno-gamous pollination.

Vegetative persistence is the main alternative to sexual reproduction. In drylands, as well as in high altitudes, the proportion of species with mainly clonal reproduction increases (Eriksson 1996, 2000, Song *et al.* 2002, Chen *et al.* 2004). In harsh environments, there are many examples of very large and old clones, which persist in those unfavourable climatic conditions and lack sexual reproduction (Steinger *et al.* 1996, Vonlanthen *et al.* 2010). The relative importance of sexual reproduction may also depend on altitude as was shown for *Poa alpina* and *Carex curvula* (Steinger *et al.* 1996, Stöcklin *et al.* 2009). Since *S. krylovii* grows at both high altitudes and in dry steppes, we wanted to see if clonal growth is an important persistence strategy. We also tested whether the importance of clonal growth increased towards the driest site, the Dund Saykhan.

6.2 Methods

Pollination

In July 2004 in Dund Saykhan, we tagged 11 inflorescences (of 5 tussocks) and observed the progress of pollination every morning until no further flower opened for pollination. All five tussocks were situated in favourable sites and were bigger and more vigorous than average.

To quantify the pollen-ovule ratio we took a quarter of an anther and suspended the pollen grains in a solution of aniline blue in lactophenol, then counted the number of pollen grains in 1µl of the solution using an Abbe Zeiss cell. After including the dilution factor we multiplied the resulting number by four (for the quarter of the anther) and by three (for the three anthers) to estimate the number of pollen per floret. Because Poaceae flowers have only one ovule this is equal to the pollen/ ovule ratio. We compared the pollen/ ovule ratios between the two regions Dund Saykhan and Khentey (n=10 each). Moreover, since the lower flowers in an inflorescence basically never open for pollination while at least in Khentey some of the uppermost flowers of the inflorescence usually open, we also compared upper and lower flowers in the same inflorescence (n=10 each).

Pollen viability was determined using the DAB technique (Sigma FastTM 3,3´-diaminobenzidine tablets; Sigma D-9167) outlined by Dafni (2003) which indicates the presence of peroxidases (Dafni & Firmage 2000, Dafni 2003). A control of non-viable pollen was prepared by killing pollen in 70% ethanol and subsequent heating. We randomly selected 5 fields of view on a microscope slide per sample to count control and treatment pollen at x40 magnification.

At the peak of the flowering period in late July 2006, we originally established 160 pollen traps fixed to the cages of the irrigation * fertilization study (chapter 4 and 5). In the setup of the traps, we followed the recommendations by Amots Dafni as described in Dafni (1992). On each of the straps, there were 3 sticky surface areas 0.4 cm^2 in size. Traps were exposed for one night and straps were collected the following morning. The original plan was to identify the pollen in the camp immediately after the collection; however, the light conditions of our microscope were not sufficient to safely identify the systematic groups. Thus, we carefully wrapped the samples and transported them to Germany, where they were sent to Frank Schlütz (Göttingen / Berlin), who was so kind to identify the pollen groups found on 8 sticky surface areas. Since the reliability of pollen numbers could have suffered during transport, we decided against counting pollen grains from more than those 8 samples.

Clonal growth

In 2004, we mapped the clonal diversity in the three study regions on 3 randomly chosen $1m^2$ plots each; all three plots were situated within the same population at distances of 10-100m from each other. We took 2-4 samples from different shoots per tussock in order to check whether they can be considered as one genetically identical individual. In some rare occasions when plant tissue was too scarce, we took only one sample per tussock. A total of 378 samples were analysed.

Tissues were stored in Silica-Gel directly after sampling. Genomic DNA was extracted from 25 mg of dried leaves with a standard kit (Wizard® Genomic DNA Purification Kit, Promega). 100 primers were screened for readability and reproducibility (Random Primer Kits, Roth). This resulted in the selection of eight primers (A03: AGTCAGTTAC; A18: AGGTGACCGT; D02: GGACCCAACC; D07: TTGGCACGGG; N07: CAGCCCAGAG; N09: TGCCGGCTTG; N16: AAGCGACCTG; N18: GGTGAGGTCA). DNA was amplified in 10 µl reaction volumes containing 8 ng DNA, 0.6 µmol/L primer (Roth), 0.2 mmol/L of each dNTP (Peqlab), 0.5 units Taq Polymerase (Qbiogene), 1 µl buffer 10 x (Qbiogene) and 6.5 µl H_2O. PCR was carried out in a thermocycler (Flexigene 384, Techne) that allowed for the simultaneous processing of all samples. The thermocycler was programmed for one cycle of 2 min at 94 ºC followed by 36 cycles of 12 sec at 94 ºC, 45 sec at 36 ºC and 120 sec at 72 ºC with a final cycle of 7 min at 72 ºC. DNA fragments were separated by electrophoresis in 2 % agarose gels with a Tris-acetate- EDTA (TAE) buffer system at 150 V for 150 min (equalling 10 cm distance) and stained with ethidium bromide. DNA bands were then visualised by UV light and documented using a digital camera. As a check of reproducibility every tenth sample was run in at least two independent cycles. Only bands in the range between 240 and 1500 bp were scored. This resulted in 75 variable bands.

RAPD data were scored into a 0/1 matrix and used to calculate Sörensen dissimilarities among samples. We performed an outlier analysis in the program PcOrd 5.0 (McCune & Mefford 1999), and excluded 4 samples, which differed by more than 2 standard deviations from the mean dissimilarity among all samples. Soerensen dissimilarites were square-root transformed for the Principal Coordinate Analysis (PCoA), as these have metric properties (Legendre & Legendre 1998). For the PCoA the program CANOCO (ter Braak & Smilauer 2002) was used. To quantify the distribution of genetic variation at different hierarchical levels (i.e. within plot, among plots, among regions) we calculated an analysis of molecular variance (AMOVA). We also calculated an AMOVA with only 2 hierarchical levels including the three $1m^2$ plots as one population and compared that for the regions. For all AMOVAs, we only used one sample per tussock, data were treated as binary diploid. The AMOVA was calculated using the Excel Add-in GENALEX (Peakall & Smouse 2006). We refrain from giving Φst values, as the $1m^2$-plots cannot be considered a representative sample of populations. Instead, we give H_e as indication of gene diversity within regions.

6.3 Results & Discussion

Pollination

Chasmogamous pollination took place over the course of three nights (16th-18th of July) within our observation period. Most inflorescences remained fully closed for pollination and were thus presumably cleistogamous (Tab. 6.1). In three inflorescences, 3-7 flowers emerged from leaf-sheaths but never opened for pollination. Only three inflorescences opened completely for pollination resulting in a total of 9 flowers. The anthers were mostly shed before the stigma fully matured, however in most flowers there seemed to be some overlap, and we thus cannot entirely rule out autogamy. Only in one flower, pollination and stigma receptivity were clearly separated by one night.

The uppermost flower pollinates first with the next following in the strict sequence of 1-n. However, here too we observed some overlap. During the second night there were four flowers in one inflorenscence which shed pollen while the four stigmas were also receptive. Thus, without resolving the question conclusively, our impression is that even in open flowers, both autogamous (fertilization within a floret) and geitonogamous pollination (fertilization within one genet) might be relatively common.

Tab. 6.1: number of flowers per inflorescence/ tussock that were chasmogamous, cleistogamous outside of the leaf-sheaths or cleistogamous inside the leaf-sheaths. Numbers refer to the uppermost flower as 1 to the lowest as n (total number of flowers/ seeds could not be counted because tussocks were eaten by sheep and goat before we could collect them after seed maturation).

Tussock	Inflorescence	chasmogamous	cleistogamous, outside of leaf-sheaths	cleistogamous, inside leaf-sheaths
1	1	1-2	3-7	8-n
	2	1-6	7-9	10-n
	3	0	1-4	5-n
	4	0	0	1-n
2	1	0	1-7	8-n
	2	0	0	1-n
	3	0	0	1-n
3	1	1	2-6	7-n
	2	0	1-3	4-n
4	1	0	0	1-n
5	1	0	0	1-n

The pollen/ ovule ratio was more than twice as high in Dund Saykhan as in Khentey (23500 ±5000 vs. 12800 ±2000 respectively; $p<0.001$, ANOVA of rank transformed data, Fig. 6.1), but in both regions the ratio falls into the group of strictly outcrossing species (pollen/ ovule ratio of >10000, Cruden 1977). The difference between the two regions could have environmental causes. In less favourable conditions the distance between putative mates increases, which is reportedly the most important factor affecting pollen number in wind pollinated species (Cruden 2000). In Khentey there was no difference in p/o ratios between the upper and the lower flowers of an inflorescence (paired t-test = $p>0.9$).

Stipa species are facultatively cleistogamous, but they seem to be more adapted to an outcrossing breeding system. This is surprising, at least with respect to the normally dry Dund Saykhan. *Stipa krylovii* plants there invest resources in the production of pollen grains, which are never dispersed, and these resources could ideally be used for seed production. However, in favourable years when chasmogamous pollination is possible, they need all the pollen to facilitate cross-pollination. Rainfall is unpredictable and a dry early season could be followed by wet conditions for pollination, thus they have to be opportunistic and be prepared for chasmogamous and hopefully xenogamous pollination.

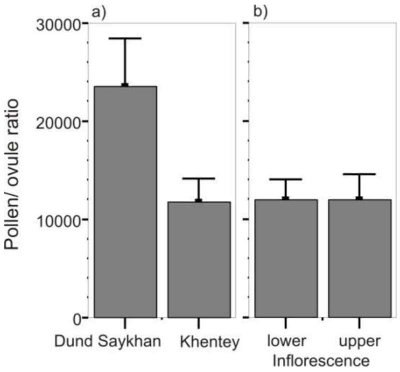


Fig. 6.1: Pollen ovule ratio in a) the regions Khentey and Dund Saykhan and b) comparison of the upper (potentially chasmogamous) and the lower (cleistogamous) part of the inflorescence in Khentey.

Pollen viability analysed directly after opening of the pollen tube was always high at >70% relatively. There was no significant difference between the regions Dund Saykhan and Khentey (t-test of arcsin transformed data $p>0.5$, confer Fig. 6.2c). In Dund Saykhan, pollen viability differed somewhat between the years of 2005 and 2006 (ANOVA of arcsin transformed data $p=0.009$, confer Fig. 6.2b). However, pollen viability decreased dramatically when pollen was exposed to ambient conditions (Fig. 6.2a).

The rapidly declining pollen viability under hot and dry conditions explains very well why most *Stipa* species should pollinate during the night or in the early morning hours when air humidity conditions are relatively high. This was also thoroughly documented by Ponomarev (1954, 1961, 1966). For *S. krylovii*, we could also only observe chasmogamous flowering during the night and early morning hours (see above). However, we tested viability only during daytime, when radiation was very high and air humidity very low, and either of these could have damaged the pollen. Thus, we have no measurements of pollen longevity during colder, more humid conditions. However, at least for daytime conditions, it seems unlikely that viable pollen can be transported over large distances as reported for e.g. marihuana pollen (Cabezudo *et al.* 1997) and thus is unlikely to contribute to gene flow.

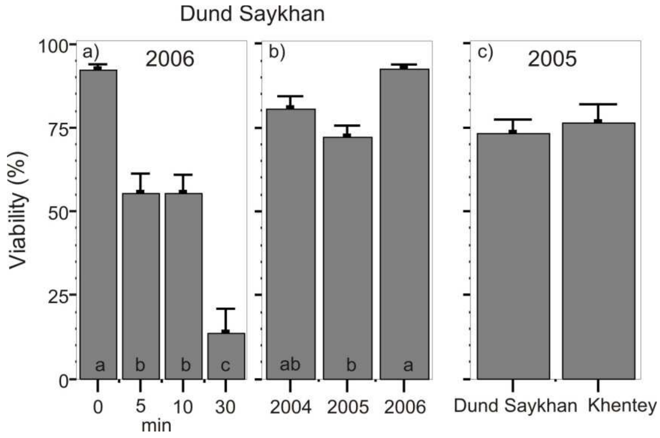


Fig. 6.2: Pollen viability a) after 0, 5, 10 and 30 minutes of exposure to ambient light, temperature and humidity conditions on a hot and sunny day in July 2006; b) in three different years in Dund Saykhan and c) in the regions Dund Saykhan and Khentey in 2005. Small letters at the bottom of the bars indicate statistical differences at $p<0.05$.

Morphologically, *Stipa* pollen can not be differentiated from other Poaceae. A median of zero and a maximum of up to 2 Poaceae pollen grains were found on the pollen traps, which were exposed overnight. Other species groups were represented more frequently. There was a median of 5 and 11 for pollen grains of the genera *Artemisia* and *Allium* respectively, and 9 of the family of Chenopodiaceae. Given that other grasses (especially *Agropyron cristatum*) are also common, it seems unlikely that huge numbers of *Stipa* pollens were shed during the time of trap exposure. We should clearly not over-interpret these data, as the number of samples was rather low and pollen was only counted months after collection after long transportation. However, as a preliminary result they support the notion that pollen rain density was low in Poaceae, and thus also in *Stipa* spp. during that night. Taken together, obstacles for out-crossing seem rather strong, and in populations with few genets, autogamous or geitonogamous pollination could be the consequence of chasmogamous pollination (Zhang & Zhang 2007). Thus, cleistogamous pollination may be the safer strategy to produce seeds.

Preconditions for the reproduction of *S. krylovii* differ widely between the regions. The cover and density of *Stipa* is much higher in the northern population and also the number of chasmogamously flowering individuals is higher. Thus, we assume that despite the lower p/o ratios the pollen density is also higher than in the southern population. The chance of cross-pollination seems rather low in the southern population in most years and the climate seems to be the most important factor determining the flowering strategy.

Clonal growth

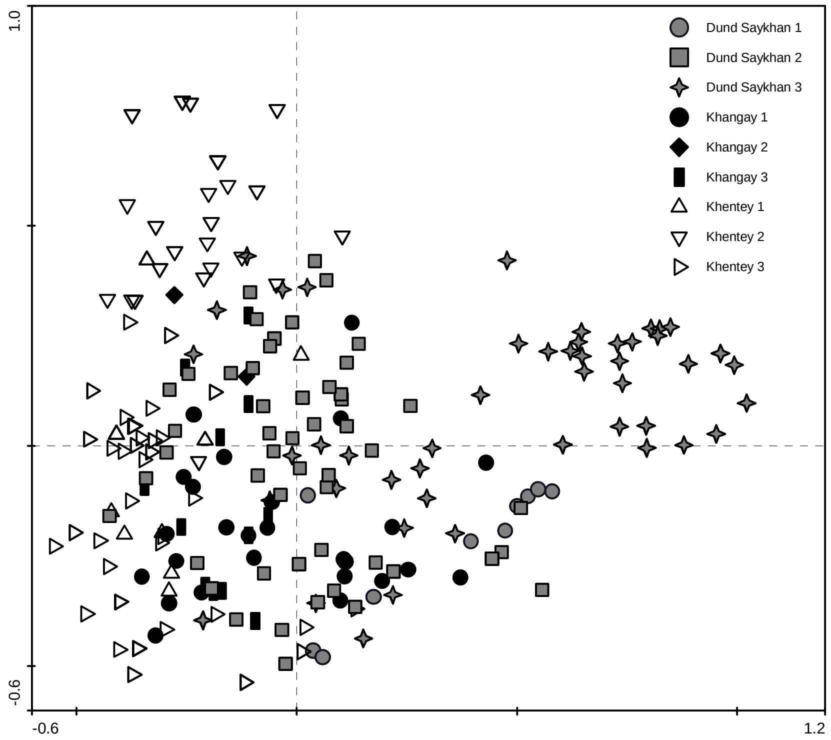


Fig. 6.3 Principal coordinate analysis of RAPD data for nine m^2 plots in three regions of *S. krylovii* (based on square-root transformed Bray-Curtis dissimilarity; Eigenvalues axis 1 = 0.13; axis 2 = 0.10; axis 3 = 0.09).

The ordination of the RAPD data indicated relatively weak genetic differentiation between plots and even regions; although samples within most plots clustered together, there were clear overlaps between plots and even regions (Fig. 6.3). In fact, the rather low eigenvalues of 0.13, 0.1 and 0.09 for the axis 1,2 and 3 point to the lack of any simple spatial structure. Along the first axis, some of the variation between regions is captured, with the samples from the Khentey dominating on the right side and the samples from the Dund Saykhan being more concentrated on the left side of the ordination diagram. The difference between plots within a region is explained with variations on the slightly less important 2nd axis (e.g. the difference between Dund Saykhan 1 vs. 3 and Khentey 2 vs.3). The least variation was displayed among the plots from the Khangay, with samples mostly clustering in the centre of the diagram. However, most importantly, there is abundant variation within plots i.e. clonal diversity. The expectation of *S. krylovii* mainly growing clonally must clearly be rejected.

Accordingly, the AMOVA partitioned most genetic variation within plots (72%), 21% among plots and only 7% of the variation among regions. In the second AMOVA, comparing the $3m^2$ plots as population with the regions, we found 84% variation within populations and 16% among regions. This is very similar to the findings of an AFLP analysis of the core populations in Kazakhstan of the related *S. capillata* with 85 within populations and 15 among regions (Wagner *et al.* in press). H_e values were at 0.132, 0.096 and 0.119 for the regions Dund Saykhan, Khangay and Khentey respectively.

In a RAPD study comparing *S. krylovii* populations in drier and more mesic areas in northern China, similar numbers were found, with 7.5% of variation among regions, while values within populations were lower at 56% (Wang *et al.* 2006). In the same study, the genetic variability as indicated by two diversity indices (Shannon, Nei's) was found to be lower compared to allogamous, wind-pollinated species. The authors, assuming that *S. krylovii* was an outcrossing species, argue that habitat fragmentation has lead to relatively high Φst values and low gene diversity, indicating high differentiation between populations and regions. They found a positive correlation between annual precipitation means and genetic diversity and a negative correlation to summer mean temperatures. However, comparing their data on genetic variability to other species with a mixed pollination strategy of selfing and outcrossing, revealed that values are well within the normal range (Nybom & Bartish, 2000; Nybom, 2004). On the contrary, in our opinion the observed tendencies confirm that cleistogamous pollination is more common in dryer areas, which is represented by the lower Φst, H and Nei's values. Similarly, *Stipa capillata* was found to have relatively low genetic variation both in core and edge populations of its distribution range, as a consequence of a partly selfing reproduction strategy (Wagner *et al.* in press). Indeed, populations with very low genetic variability have been found for several *Stipa* species at their distribution edge (Hensen *et al.* 2010, Durka *et al.* in prep.).

The finding of high clonal diversity is also graphically supported in Fig. (6.4). Here we show a sketch of mapped m2-plots from each of the three regions. In Khentey (c), we found two pairs of neighbouring tussocks with identical bands which might be considered as clones. In Khangay (b) we found none and in Dund Saykhan (a) 1 pair of genetically identical tussocks. Moreover, there was one pair of neighbouring tussocks that only differed by one band. None of the tussocks that were spatially further apart were identical; instead, they were clearly genetically distinct in their pattern of bands. All samples run in two independent cycles showed the same band patterns, and we consider the methodology as largely reproducible and the results as plausible. However, there was some variation within tussocks. Two samples of a given tussock varied by one band (1 tussock in Khentey 2 in Khangay and 6 in Dund Saykhan) or more than one (1 in Khentey and 2 in Dund Saykhan). The tussocks that differ by more than 1 band could represent mistakes in the methodology. That could be either at the stage of mapping, or at a later stage and either be two different individuals, or just polluted samples. Tussocks that differ by 1 band could either indicate methodological artifacts, genetic differences between shoots due to mutations during mitosis, or simply two very near relatives due to possibly cleistogamous reproduction. All clones (ramets) with the exact same band structure grew in the immediate vicinity of each other, and most likely originated from the same tussock that was split by some kind of disturbance. Belowground they were mostly still connected by old leaf sheaths and roots. As physiological approaches (e.g. isotopes) were not available, it was, however, impossible to identify whether there were still living roots that connected the entire genet. Overall, clonal reproduction is insignificant in all three regions (Tab. 6.2), but the frequency of tussocks with genetic variability (Fig. 6.4) possibly due to somatic mutations suggests that genets could be relatively old (Salomonson 1996, Loxdale & Lushai 2003).

We found unequivocal evidence for sexual reproduction in the Khentey region only. Here we found one sapling that seemed to have germinated earlier in the season. Several times we found small tussocks with 2-5 shoots in all three regions, but more frequently in the southern regions. Nevertheless, these seemed to be older tussocks, because we could find remnants of a bigger network of roots when we dug specimens up.

Overall, the results clearly indicate that sexual regeneration via reseeding is an important survival strategy in *S. krylovii*, which was thus pursued in the following chapters.

Tab. 6.2: Comparison between the three regions (all three m²-plots) of the number of tussocks and clones, and tussocks with differing band structure .

	No. of tussocks	Clones		Clones 1 differing band		Tussocks (1 differing band)		Tussocks (>1 differing bands)		Distinct tussocks	
		absolute	%	absolute	%	absolute	%	absolute	%	absolute	%
Dund Saykhan	**85**	**3**	3.5	**2**	2.4	**8**	9.4	**7**	8.2	**65**	76.5
Khangay	**27**	**1**	3.7	**0**	0	**4**	14.8	**4**	14.8	**18**	66.7
Khentey	**59**	**4**	6.8	**1**	1.7	**2**	3.4	**8**	13.6	**44**	74.6

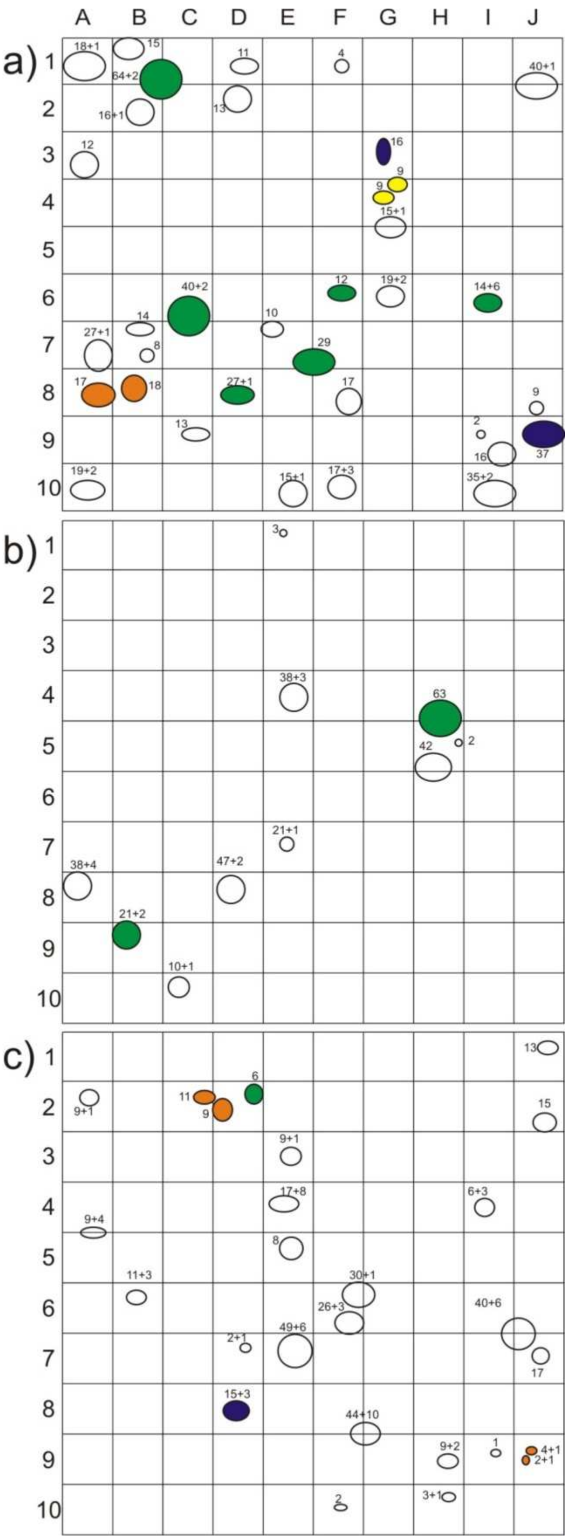


Fig. 6.4: One example m2 plot for each of the three regions a-Dund Saykhan, b-Khangay, c-Khentey. All blank tussocks are genetically distinct from other tussocks in the plot and identical within. Orange: two genetically identical, neighbouring tussocks. Yellow: two neighbouring tussocks that differ by only 1 band. Green: varies by one band between samples of same tussock. Blue: varies by >1 band between samples of the same tussock.

7 Germination ecology of Central Asian *Stipa* spp: differences among species, seed provenances, and the importance of field studies

Katrin Ronnenberg, Karsten Wesche, Isabell Hensen (Plant Ecology 2008: 196, 269-280)

Keywords: dormancy, Mongolia, restoration, seed viability, steppe, stratification

Abstract

Stipa-species are wide-spread in Central Asia, but sexual reproduction in the dry steppes is rare. To facilitate conservation and restoration of these important rangelands, we studied germination characteristics of three common Mongolian *Stipa*-species under field- and lab conditions.

Seeds of *Stipa krylovii*, *S. gobica* and *S. glareosa* were sown at the study site in Southern Mongolia over two consecutive years during which period tests were carried out to ascertain whether competition or herbivory are the main constraints of seedling establishment. In addition, we tested germination and seed viability in the laboratory under two different temperature regimes (20/10°C and 8/4°C), as well as the effect of cold-stratification. The lab experiments also included *S. krylovii* seeds originating from three climatically different provenances.

None of the three *Stipa*-species seedlings emerged during the first two years of the field study. However, after an unusually intense rain event in the third year, 3% of *S. krylovii*, 0.6% of *S. glareosa* and 0.1% of *S. gobica* seeds germinated in the study plots. The factors ‘sowing-year’ and ‘vegetation’ significantly affected seedling emergence, whereas grazing had no effect at all. Under laboratory conditions a high percentage of viable seeds of *S. gobica* and *S. glareosa* germinated at both incubation temperatures, and cold-stratification had no effect on germination or viability. Germination of *S. krylovii* seeds required warmer temperatures and cold-stratification had a positive effect. Such evidence for dormancy was more pronounced in seeds from the moister, northern provenances.

Germination of *Stipa*-species in the field is rare and only possible under exceptionally moist conditions. Conservation should thus concentrate on steppe conservation rather than on restoration. Where artificial reseeding is necessary, differences among species and also among different seed provenances should be taken into account.

8 Seed germination of five mountain steppe species of Central Asia

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(Journal of Arid Environments 2007: 71(4) 404-410)

Abstract

This paper presents data on the germination traits of five perennials (*Allium polyrrhizum*, *Agropyron cristatum*, *Arenaria meyeri*, *Artemisia frigida* and *Artemisia santolinifolia*) widespread in the mountain steppes of southern Mongolia. Germination and seed viability were assessed at three alternate temperatures (8/4°C; 20/10°C; 32/20°C), three levels of osmotic stress (deionised water; -0.5MPa, -1MPa Mannitol solution), and under conditions of alternate light/darkness versus complete darkness. The results of a factorial ANOVA with treatments and species as main effects showed that all five species germinated best at higher temperatures, with only *Agropyron cristatum* showing some seed mortality. Osmotic stress reduced seed viability and total germination in all five species. Darkness had no influence on viability, but positively affected seed germination of *Allium polyrrhizum* and *Agropyron cristatum*. We therefore conclude that, in the field, germination of all five species is mainly controlled by ambient temperatures and water availability, both of which drop towards the end of summer when dispersal takes place and effectively delay seedling recruitment until the next vegetation period.

Keywords: *Agropyron, Allium, Arenaria, Artemisia,* restoration, seed viability

9 Synthesis

Reproductive strategy

The *Stipa* steppes in southern and central Mongolia are dominated by perennial herbaceous plant species and generally generation cycles are slow. In the Dund Saykhan, germination of the *Stipa* species and other grass species is only possible after extreme events of heavy rainfall, which occur every few years (Lavrenko & Karamysheva 1993, Ronnenberg *et al.* 2008). In the more mesic north, we found evidence of recent establishment, as we found 1 sapling of *S. krylovii* within our three 1m^2 plots. Clonal growth is of minor importance in all three study sites (chapter 6). At the studied sites, *Stipa* species thus seem to rely mainly on persistence through long-lived tussocks, similar to the long-term vegetative persistence of *Populus euphratica* (Vonlanthen *et al.* 2010) and *Juniperus sabina*, (Wesche *et al.* 2005b). However, we cannot say whether tussocks can survive over similar time spans (several hundreds to thousands of years) as has been described for juniper patches in the southern Mongolian mountains, or *Carex curvula* in the alps (Steinger *et al.* 1996). Measuring longevity of clonal herbaceous plants in general is complicated, and *Stipa* spp. are no exception (de Witte & Stöcklin 2010).

The importance of cleistogamous pollination is still not entirely understood. It seems very common in the study species if not even dominating, thus recombination and genetic exchange should be limited. However, the results of the AMOVA and the H_e values do not indicate an exceedingly low genetic variation within populations (or 1m^2-plots respectively, chapter 6). A possible explanation could be that successful establishment takes place in years that are wetter than usual, which are also the years when chasmogamous pollination is more common (see however further down, chapter 9.1). Moreover, epizoochoric long distance dispersal of *S. krylovii* seems very effective (Bläß *et al.* 2010) and thus, with the given land use practices (long-range migrations of herds), some exchange via seeds rather than pollen should be guaranteed and counteract genetic impoverishment.

Pollination of *S. krylovii* is a mixed strategy of cleistogamous and chasmogamous pollination as found in many *Stipa* species (Hensen et al., 2010). It is an opportunistic strategy in the sense that plants produce many pollen grains to provide sufficient pollen to enable xenogamous pollination if climatic conditions are sufficiently humid for the flowers to open. Since pollen dies very rapidly under hot and dry conditions, this mating system can be considered an adaptation to drylands, resulting in predominantly cleistogamous pollination in the dry south (chapter 6).

Also, germination of all analysed species follows an opportunistic strategy and at least some germination is possible as soon as soil moisture and temperature conditions meet their minimum requirements. This stands in contrast to annual species in the study area, which usually show some kind of dormancy (Wesche *et al.* 2006). There are, however, some differences in germination characteristics of the analysed species. Whereas the late flowering species *Artemisia frigida*, *Art. santolinifolia* and

Arenaria meyeri germinate almost instantaneously under favourable conditions (chapter 8), the grasses *Agropyron cristatum* and *S. krylovii* need over two weeks of favourable conditions until a substantial proportion of the seeds will germinate (compare chapters 7 and 8). *Stipa glareosa* and *S. gobica*, which are typical of the dry semi-deserts, also germinate after only a few days and are probably among the few species that can germinate the same year as they mature (chapter 7).

Environmental plasticity

There is no doubt that *S. krylovii* is more productive in the more mesic northern steppes, both in the sense of biomass, as well as seed production. Aboveground competition in the moister sites is stronger; however, soil conditions are better and aboveground competition should not be relevant in the still relatively sparse stands at any of the three sites (chapter 3.4). Even in the southern steppes, we have found serious nutrient limitation; thus, we can conclude that the northern Khentey region benefits from better soil conditions as well as from higher precipitation.

A question arising from the fact that seed viability was lower in the northern regions (chapter 5) is whether populations are actually at disadvantage. Our random approach of counting number of inflorescences per m^2 (as in our vegetation study, chapter 3.6) should theoretically be suitable to extrapolate numbers (Zimmerman & Harville 1991). However, as we did not find a single inflorescence in our Dund Saykhan plots, we have to calculate with maximum estimates for the Dund Saykhan. Another limitation is that viable/ non-viable seeds might not be evenly distributed within the inflorescence. For logistical reasons however, we could only collect the mature seeds when we travelled to the study sites. Nevertheless, we think extrapolating these numbers is helpful to putting the negative water effect into perspective.

We therefore multiplied the number of inflorescences per hectare (chapter 3.6) by the number of seeds per inflorescences and the mean percentage of viable seeds (chapter 5) in each region. In the Khentey region, this results in about 1.7 million viable seeds per hectare, which stands in contrast to 18000 in Khangay and less than 5000 in the Dund Saykhan. Since we also know that germination and establishment are highly dependent on strong rainfall events (chapter 7), the Khentey region has a considerable advantage over the other two regions, which was supported by the small sapling we found (chapter 6).

Concerning seed germination, we find specific adaptations to the slightly wetter climate with higher rates of seed dormancy to defer germination to the following year, and avoid exposure of the vulnerable sapling to extreme winter conditions. Similarly, seeds of *S. krylovii* from different provenances in China show adaptations to osmotic pressures, with the drier populations being more tolerant than the more mesic provenances (Jia & Gao 2009). This pattern can also be found in other dryland regions e.g. *Stipa* species from Jordan showed more effective germination patterns in the drier, than in the more mesic populations (Hamasha & Hensen 2009).

Moreover, the fraction of chasmogamously flowering inflorescences is higher in the north. However, in neither study site clonal growth seems to play a major role. Whereas the share of clonal plants increases with decreasing precipitation (Song et al., 2002), we did not find a strategy change within a species on a climatic gradient of about 100mm rise in precipitation.

Water vs. nutrient limitation

The third of our main questions remains only partly resolved (see also chapter 9.1). While we could unequivocally prove that fertilization increases biomass productivity and seed production, our results regarding the effect of irrigation on steppe productivity remain surprising. Soil water content was the most important factor controlling CO_2 exchange in northern Chinese *S. krylovii* steppes (Wang *et al.* 2008), which is a factor explaining plant growth, and we also found a relationship between precipitation and biomass production in other studies (Wesche *et al.* 2010). In dry steppes the timing and intensity of rainfall is often more decisive than the precipitation sums (Knapp *et al.* 2008, Heisler-White *et al.* 2009). In accordance, we also assume that larger irrigation pulses and possibly an earlier start to the irrigation treatment in the season would have increased biomass productivity in the irrigated plots.

If irrigation does not explain biomass productivity we could assume that plants are able to access the groundwater table to counteract water scarcity, as was found for e.g. *S. grandis* in northern China (Yang *et al.* 2011). However, the *S. grandis* steppes receive naturally more precipitation and the groundwater table is higher than in either of our study sites. In the somewhat drier steppes in northern China, the root system of several grass species such as *Agropyron cristatum*, *Leymus chinensis*, and *Bromus inermis* is mostly distributed within the uppermost 10 cm (Ao *et al.* 2009), which is according to our own observations also true for the *Stipa* species.

In the studies directly included in this thesis, we did not test the effect of either fertilization or irrigation on species composition. In a prior study, however, we found that although fertilization changed cover and relative contribution of specific species, it did not change plant community composition (Wesche & Ronnenberg 2010). It is, however, likely that plant - plant interactions and competition confounds the results. We could observe a positive effect of irrigation on *Agropyron cristatum*. In this respect, irrigation did shift the species composition while fertilization mainly affected steppe productivity as a whole.

Nevertheless, we could observe an effect of water addition on sexual reproduction. Thus, the water did not evaporate without any effect on the plants. The mechanism of the *Stipa* flower to open is controlled by cell turgor. Because we usually applied irrigation in the evening (to avoid burning of the plants), cell turgor increased over night, when *Stipa* species usually pollinate (chapter 6). However, photosynthesis does not occur overnight and due to winds and morning sunshine, water might have evaporated before substantial plant growth occurred. This scenario is entirely speculative, however, would explain why we find differences in reproductive traits, but hardly any in plant growth.

9.1 The way forward – options for further studies emerging from our results

Not surprisingly, our studies on cleistogamy still left a bundle of questions unanswered. The originally planned pollination studies did not work, as all inflorescences in the setup pollinated while hidden in the leaf-sheaths making any manipulation of pollination impossible. This extent of cleistogamy was somewhat unexpected and thus experiments were initially not specifically designed to clarify this phenomenon. According to our field observations, most seeds in all three study areas, but especially in the Dund Saykhan, are produced after cleistogamous pollination. The results on high genetic diversity seem to contradict this finding (see above), if most plants originated from cleistogamous seeds, genetic diversity should be lower as was found in other *Stipa* species (Hensen *et al.* 2010, Durka *et al.* in prep.). The assumption, that in wet years, most seeds are produced after chasmogamous pollination and thus, the seeds that establish in those wet years contribute to gene flow and genetic diversity is the most likely explanation. To quantify the ratio of cleistogamously produced plants in a population calls for a typical microsatellite study, which provides evidence on actual relationships of plants in a population and gene flow (Ouborg *et al.* 1999). The fact that seed viability was higher in dry years, with presumably mostly cleistogamous inflorescences is, however, a slight contradiction and more importantly, seeds from the more mesic regions showed stronger levels of seed dormancy. We assumed that this was a mechanism to prevent establishment in the autumn, directly after seed maturation and thereby risking the death of relatively weak saplings over the winter (chapter 7).

Other approaches, as conducting simply more detailed observations, as described by the Russian authors (Ponomarev 1954, Ponomarev 1961, Bespalova 1962, Ponomarev 1966), could help to better understand the mechanisms of cleistogamy vs. chasmogamy, and the effect of water availability on the reproduction of *Stipa* species. However, they should be made in a wetter study site as the Dund Saykhan; otherwise, it is too much a question of chance to observe chasmogamous pollination. Further research would require more elaborate and costly experimental setups. One way could be to add more populations and install full climate stations to the large-scale study. This would enable us to calculate an ANCOVA with precipitation data as co-variable. The other option would be a greenhouse experiment with full climatic control. In such a setup, one important improvement to our field experiment should be different irrigation pulses and frequencies. Data from the dry steppes in the US indicate that fewer, larger pulses will have a positive effect on steppe productivity (Knapp *et al.* 2008, Heisler-White *et al.* 2009). The advantage of a greenhouse experiment would be that flowering modes could be more easily observed.

However, it lacks realistic conditions such as the strong winds that disperse pollen over wide distances, and results are only partly transferable to the natural environment, as *S. krylovii* was found less resilient in the greenhouse than in the field (van Staalduinen 2005).

In the fertilization experiment, a straightforward question is the main limiting factor: is plant growth and reproduction mainly limited by N or by P? To answer this question, an additional fertilization experiment should be designed with reciprocal application of at least the two nutrients (N and P). Generalisations on that question for the entire Gobi cannot be expected though, as P availability strongly depends on Calcium carbonate and P concentrations in the bedrock (Neff *et al.* 2006). Whereas indications of P limitation, as indicated by the high N:P ratios, were pronounced in our study, water and N were found to be co-limiting in the slightly wetter *S. grandis* steppe of the Xilin province in Inner Mongolia, China (Gong *et al.* 2011). Although N addition primarily increased Net Ecosystem Exchange (NEE) by 60%, the effect lost its strength over the years, because the higher growing *S. krylovii* became more dominant and overshadowed the lower canopy species *Artemisia frigida* (Niu *et al.* 2010). Thus, a general shift in species composition was observed. Phosphorus addition, however, had no effect.

9.2 Implications for nature conservation

Implications for nature conservation resulting from this thesis are complex. Steppe degradation in the sense of nutrient depletion is observable; however, this is an indirect process not observable to the herders. Direct degradation in the sense of a change in vegetation communities was not observed (Wesche *et al.* 2010). We currently find a trend of decreasing camel stocks but increasing numbers of goats (Chimed-Orchir 1998, Vallentine 2001); which may give reason for concern, as goats with their limited daily movements will aggravate the tendency of nutrient accumulation in restricted areas. They will thereby also aggravate impoverishment of soils in the main steppe matrix (Fernandez-Gimenez & Allen-Diaz 2001, Stumpp *et al.* 2005).

Although the climatic conditions are somewhat wetter, the Chinese steppes may serve as an indication of what the Mongolian steppes might face in the future; which are as a consequence of higher grazing pressure more severely degraded (Zhang *et al.* 2005). Restoration is difficult in degraded rangelands. Here historic management as agricultural use or animal husbandry was the most important factor impeding the restoration potential (Xu *et al.* 2010). In comparison to that, the steppes of the Gobi Gurvan Saykhan are still relatively intact and should be preserved as evinced by national park status.

However, I feel reluctant to suggest specific measures for the management of the national park. Although a restriction of stocking densities (especially of goats) seems desirable, first socioeconomic measures would need to take effect before any determined ecologic suggestion were realistic. The people of the Gobi need new prospects to earn their livelihoods that go beyond production of cashmere wool. Failing that, a deterioration of the grazing grounds is likely and consequently a breakdown of social and ecologic stability in the Gobi must be considered as the principle threat in the future. A comprehensive approach to nature conservation should therefore involve social and educational aspects, and some efforts have been made to reach that goal (Ykhanbai *et al.* 2004). On the scientific side, we still cannot evaluate natural resilience of the steppes (Mori 2011) and the boundary between sustainable stocking density, especially of goats and overgrazing, is still not fully known. Clearly, more studies specifically designed on the effect of goats, rather than livestock in general, are needed.

To the local or regional threats, the industrialised world adds another global risk which is climate change. The effect of climate change is difficult to predict. Most climate change scenarios assume warmer temperatures and an increase of precipitation for the Gobi. If we consider the difference of the three regions, we find despite a decrease in seed viability in general, a higher probability of sexual regeneration in the wetter regions; thus, overall a positive effect. However, we have different soils in the Khentey region and the development of healthy chernozems takes millennia (Pesochina 2008). Thus, we may only expect marginal increments in biomass and seeds in Dund Saykhan in the near future; seed quality, however, might decrease. Overall, we have gained crucial insights into the ecology of the *Stipa* species; to develop practical suggestions, however, would require more data to confirm and specify our results.

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11 Erklärung über den persönlichen Anteil an den Publikationen

Die folgende Auflistung gibt einen Überblick über meinen persönlichen Anteil an den hier zusammengestellten Publikationen mit Co-Autorenschaft:

EFFECTS OF FERTILIZATION AND IRRIGATION ON PRODUCTIVITY, PLANT NUTRIENT CONTENTS AND SOIL NUTRIENTS IN SOUTHERN MONGOLIA

Datenerhebung: Felderhebung: 90%, Im Gelände halfen Christine Bläß, Badrakh Turmandakh, und Philipp Boockhoff
Chemische Analysen: 50%, als Hiwis halfen Friedemann Haß und Jan Treiber
Datenanalyse: 100%
Schriftliche Umsetzung: 80% (Korrekturen durch Karsten Wesche)

CONTRASTING EFFECTS OF PRECIPITATION AND FERTILIZATION ON SEED-VIABILITY AND PRODUCTION OF *STIPA KRYLOVII* IN MONGOLIA

Datenerhebung: 100%
Datenanalyse: 100%
Schriftliche Umsetzung: 80% (Korrekturen durch Isabell Hensen und Karsten Wesche)

GERMINATION ECOLOGY OF CENTRAL ASIAN *STIPA* SPP: DIFFERENCES AMONG SPECIES, SEED PROVENANCES, AND THE IMPORTANCE OF FIELD STUDIES

Datenerhebung: Aussaat der Etablierungsversuche zu 50% durch Denny Walther, Keimungsversuche im Labor zu 10% von Sebastian Ploch betreut, alles weitere in Eigenarbeit.
Datenanalyse: 100%
Schriftliche Umsetzung: 80% (Korrekturen durch Isabell Hensen und Karsten Wesche)

SEED GERMINATION OF FIVE MOUNTAIN STEPPE SPECIES OF CENTRAL ASIA

Datenerhebung: Keimungsversuche 20%; 80% durch Matthias Pietsch
Datenanalyse: 100%
Schriftliche Umsetzung: 80% (Korrekturen durch Isabell Hensen und Karsten Wesche)

Halle (Saale), den

Unterschrift:

12 Curriculum Vitae

- 18.10.1977, born in Hannover, Germany
- 1984-1997: attended the “Freie Waldorfschule Hannover-Bothfeld”
  Abitur (1.9)
- 1997-2004 studied biology at the Martin-Luther-University Halle-Wittenberg
  Diplom (1.4), specialisations: Botany, Zoology, Soil Science, Nature Conservation. Master Thesis: “Reproductive biology of *Juniperus sabina* and *Artemisia santolinifolia* in the dry mountain steppes of southern Mongolia”
- 2004-present: PhD student at the same institution
- 2007-2009: Freelance surveyor for the RPS-group in Glasgow, UK
  Surveys mainly for the NWSS (Native Woodland Survey of Scotland) but also Phase I and NVC surveys of Up- and Lowland Scotland
- 2009-present: “Elternzeit” after the birth of son Milan in October 2009

13 Publications of the author

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15 Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit nicht bereits zu einem früheren Zeitpunkt der Naturwissenschaftlichen Falkultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Im Übrigen erkläre ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

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