Reproductive Ecology of Two Common Woody Species, *Juniperus sabina* and *Artemisia santolinifolia*, in Mountain Steppes of Southern Mongolia

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Reproductive ecology of two common woody species - *Juniperus sabina* and *Artemisia santolinifolia* - in mountain steppes of southern Mongolia

K. Ronnenberg

Abstract

The present study describes the reproductive ecology of the prostrate shrub *Juniperus sabina* and the dwarf shrub *Artemisia santolinifolia* in dry mountain steppes of southern Mongolia. Whereas stands of the juniper are located at the drought limit of the genus’ distributional range, the genus *Artemisia* is typical of central Asian drylands. Both species produce large numbers of reproductive organs. For *Juniperus sabina*, however, only 2.5% of the morphologically intact seeds were found to be viable. Correspondingly, neither seedlings nor saplings were found in the field, and recruitment by reseeding happens at most rarely under the present climatic conditions.

Instead, clonal growth is apparently the main mode of reproduction of the juniper. RAPD-fingerprinting demonstrated that patches of *J. sabina* were constituted by a single genet. As mean current growth rates were between 1.8 and 6.8 cm/a, the largest patches found in the study area are estimated to have a minimum age of 769 to 2941 years. Thus, seedling establishment might have taken place under more favorable climatic conditions as they occurred e.g. 1800 yr BP, whereas in dry phases such as today survival is mainly guaranteed by clonal growth.

In contrast to that, more than 90% of the achenes of *Artemisia santolinifolia* were found viable. Achenes are not dormant, however, increasing temperatures positively affected time needed for germination ($32^\circ > 20/10^\circ > 8/4^\circ$ C). Germination is possible in both, light and darkness. The higher the osmotic stress the slower is germination and the fewer achenes remain viable.

Therefore, it can be concluded that *Artemisia santolinifolia* seeds are well adapted to germinate under a wide variety of conditions, allowing the plant to colonize open sites rapidly and enabling it to invade further stands providing open space is available.

Since both species grow in the same habitat, *A. santolinifolia* is a possible candidate for replacing *J. sabina* provided that the climatic conditions are not reversing again so that chances of sexual reproduction for juniper increase.

Keywords  Gobi, mountain steppe, *Juniperus*, *Artemisia*, reproduction, germination, clonal growth

Introduction

In the southern, Gobi part of Mongolia true deserts and desert steppes are the prevailing vegetation types (Günün & Vostokova, 1995; Karamysheva & Khramtsov, 1995). The Gobi can be characterized as a non-equilibrium ecosystem with water as the dominant limiting factor (Stumpp et al., in press; Fernandez-Gimenez, 1999). The mountains of the Gobi Gurvan Saykhan National Park, however, receive considerably more precipitation than the lowlands (Retzer et al., in review; Retzer, 2004), and, not surprisingly support vegetation types very different from the neighboring desert steppes and deserts. Examples are stands of *Juniperus sabina*, which form extreme outposts within the overall species’ range (Meusel et al., 1965). They are restricted to steep and comparatively moist slopes in the Gobi Altay and are considered of special value for nature conservation in the park (Bedunah & Schmidt, 2000). However, seedlings of *Juniperus*...
sabina are currently not found, and there is evidence that Artemisia santolinifolia invades and possibly replaces the juniper scrub (Wesche & Ronnenberg, 2004).

The two species are the dominating woody perennials on the slopes of the easternmost mountains (Züün and Dund Saykhan) of the national park. At some sites both species grow together; other sites are, however, exclusively inhabited by A. santolinifolia. This distributional pattern could either indicate competition with A. santolinifolia being superior and having already replaced J. sabina on some sites, or simply relate to differing niche requirements. Because preliminary data suggest limited sexual reproduction of the juniper this question is of special interest.

Low rates of sexual reproduction of juniper species are also reported from other dry regions of the northern hemisphere (Kosmin & Tezekbaev, 2001). Especially seed viability is often low and the number of parasitized cones is high (Knopf, 1990; Garcia et al., 2000; Yilmaz, 2001). Instead of reseeding, e.g. J. communis grows clonally under adverse conditions (Houle & Babeux, 1994).

Although A. santolinifolia is a very widespread species in central Asia and reaches into eastern Europe (Tutin et al., 1976), its biology is poorly known. There are very few population biological studies on Asian Artemisia species in general. Recent exceptions are studies by Huang and Gutterman, (1998; 2003) on A. sphaerocephala and A. ordosica. Somewhat more detailed information exists on Holarctic or American Artemisia species like A. frigida (Sabo et al., 1979; Wilson, 1982), A. absinthium (Maw et al., 1985; Khasanova & Abramova, 2000), and especially A. tridentata (Hemstrom et al., 2002; Perfors et al., 2003; Wroblewski & Kauffman, 2003).

As a first approach to decide whether A. santolinifolia will eventually replace stands of the juniper the habitat requirements of the two species were analyzed by sampling relevés of the relevant communities followed by analysis of soil parameters and other environmental characteristics. In a second step, the reproduction of the two species was studied with special focus on the germination biology and the extent of vegetative growth.

**Study area**

The study region is situated in the Gobi Gurvan Saykhan National Park (GGS NP) located in southern Mongolia. At some 27,000 km² it is the second largest protected area in Mongolia (Bedunah & Schmidt, 2000) and covers deserts, desert steppes, and mountain steppes. The study was performed in the eastern parts of the park, i.e. in the two easternmost ranges of the Gobi Altay, which are surrounded by desert steppes (43°25’–43°35’N, 103°45’–104°05’E). In this region, J. sabina is restricted to steep slopes at altitudes of 2300–2700 m asl. (Wesche et al., in press), where it occupies south-facing slopes. Artemisia santolinifolia grows in the same sites but occurs also on the upper pediments surrounding the mountains. Soils are generally shallow as scree movement in freeze and thaw cycles is the dominant erosive process.

The climate in the GGS NP is semi-arid and highly continental with a pronounced seasonality. The nearest governmental weather station, Bayandalay (1570 m asl.) reports a mean annual temperature of 4.5 °C (mean temperature in July 20 °C, in January -18 °C; National Meteorological Service of Mongolia). Frosts occur regularly from September to May. Mean annual precipitation at Bayandalay is 110 mm but higher in the mountains; short-term measurements of Retzer and Nadrowski (Retzer et al., in review; Retzer, 2004) suggest that annual means might total to 130 mm at 2300 m asl. Precipitation shows a high inter-annual variability (Stumpp et al., in press). 2001 was a year of drought, while the present study was performed under the more typical weather conditions of 2002.
Species studied

*Juniperus sabina* L. (Cupressaceae) is distributed from the Mediterranean region to east Siberia (Meusel et al., 1965) and belongs to the section Sabina. The subspecies *J. sabina arenaria* in Mongolia is probably the most drought-tolerant of all Asian juniper species (Farjon et al., 2001). Young plants are characterized by needle-like leaves but develop scale-like leaves after ten years (Hegi, 1965). They have a prostrate and creeping growth form, which develops in a centrifugal pattern to form elliptical patches of up to 100 m in diameter. In contrast to Hegi (1965) who describes the species as both monoecious and dioecious, plants were exclusively dioecious in our study region. The small hanging cones are green in the first year turning to dark blue in the second. Ripe cones have the size of a pea, contain 2–6 seeds, and are mainly dispersed by birds. Since the stem apices are very poisonous due to their content of sabinol (C10H15OH), diacetyl (CH3COCOCH3) and sabinen (C10H16), they are not browsed by livestock. Junipers have a sacred status in Buddhist mythology, so Mongolians collect shoots only for ceremonial burning. As the impact of this practice is limited, *J. sabina* is currently not directly threatened by land use in the Gobi Altay.

The genus *Artemisia* is widely distributed in various, mainly semi-arid regions of the northern hemisphere. The number of accepted taxa ranges between 400 and 500, and central Asia is regarded as one of its main centers of speciation (Vallès et al., 2003). *Artemisia santolinifolia* Turcz. ex Bess. is widespread in Central Asia and even into Europe (Tutin et al., 1976). In the south-eastern Gobi Altay it is the most common woody perennial in the montane zone and colonizes disturbed sites (Ronnenberg et al., submitted), where it grows up to 0.2–0.4 m in height. The species is a semi-shrub with three-pinnatisected leaves, which are underneath greyish-lanate (Grubov, 2001). Inflorescences and achenes of *A. santolinifolia* are usually abundantly produced (Ronnenberg & Wesche, 2003) and mature in late September to early October. *Artemisia santolinifolia* is wind-pollinated and achenes are anemochorous. Infestation by parasites is limited, but livestock and even small mammals (Mongolian Pika, *Ochotona pallasi*) feed on it.

Methods

Habitat requirements

We adopted a statistical plot-based approach. Sites for relevés were selected with the help of a GPS using randomly generated UTM-coordinates within the mountain ranges Dund and Züün Saykhan at an altitudinal range of 2300–2800 m, i.e. above the pediment regions. We sampled 145 sites, excluding only those coordinates that fell on bare rock (altogether 15). Relevés were 9 m² in size, chosen as a compromise between comprehensive community data and a spatial resolution that allows assessment of fine-scale patterns. All vascular plant species and estimated species’ cover values were recorded directly in percent, because commonly used cover scales (Londo, 1976) would have been too coarse for the sparse vegetation of the Gobi.

Species were tentatively identified in the field with the help of a standard flora (Grubov, 2001) and identifications were later checked with the collection of our herbarium (HAL) and recent accounts of the flora of Mongolia (Gubanov, 1996; Grubov, 2000 ff). Additional records included several parameters easily assessed in the field plus soil chemical characteristics obtained from mixed top soil samples (-5 cm) taken on the plots.

Soil samples were kept dry until analysis of the fine soil fraction (<2 mm) in the lab of the Institute of Geobotany in Halle. Soil pH and conductivity were analyzed in a water extract (20 g soil, 50 ml water) with standard probes (PH537 & COND315I by WTW, Germany). Carbonate content was initially estimated with 10% HCl; as no reaction was detected we refrained from detailed subsequent measurements with a Scheibler apparatus. Total contents of carbon and nitrogen were analyzed with a CN Analyzer (ELEMENTAR, Germany). Plant available cations
Table 1: Treatments employed in assessing germination of *Artemisia santolinifolia* achenes.

<table>
<thead>
<tr>
<th>Temperature-regime</th>
<th>Treatment</th>
<th>Simulated field conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 32°C</td>
<td>Control</td>
<td>Optimal conditions</td>
</tr>
<tr>
<td>B 20/10°C</td>
<td>Control</td>
<td>Situation in autumn</td>
</tr>
<tr>
<td>C</td>
<td>7 days cold stratification</td>
<td>Situation in spring</td>
</tr>
<tr>
<td>D</td>
<td>-0.5 MPa Mannitol</td>
<td>Osmotic stress</td>
</tr>
<tr>
<td>E</td>
<td>-1 MPa Mannitol</td>
<td>Osmotic stress</td>
</tr>
<tr>
<td>F</td>
<td>Germination in darkness</td>
<td>Disturbed sites</td>
</tr>
<tr>
<td>G 8/4°C</td>
<td>Control</td>
<td>Situation in autumn</td>
</tr>
<tr>
<td>H</td>
<td>7 days cold stratification</td>
<td>Situation in spring</td>
</tr>
</tbody>
</table>

where extracted with NH₄Cl and measured with Atomic Absorption Spectrometry (Ca, Mg) and flame photometry (Na, K) respectively. These measurements were carried out in an acetylene flame using the VARIO AAS by ANALYTIK JENA (Germany). Contents of all elements were corrected to refer to oven-dried soil (105°C).

*Artemisia santolinifolia* – reproduction

All small plants on the study plots and additionally 10 larger plants were dug out to find out whether they are separate individuals or connected by subterranean organs to neighboring *Artemisia* shrubs. Achenes were collected at the peak of dispersal in October 2003 after an extraordinarily moist year in this area. Seeds were stored in cotton bags, and initial dormancy tests were performed immediately after the return to Germany at the end of October. Achenes were put on filter paper and then in Petri-dishes in two different climate chambers at temperatures of 8/4°C and 20/10°C (12h of light/12h of darkness; n=2x50 seeds). As no dormancy could be detected, all further germination experiments were started directly in November 2003.

Table 1 illustrates all tested treatments and also indicates how these might correspond to conditions in the natural environment. Varied factors were: temperature (8/4°C, 20/10°C, 32°C), osmotic stress (-0.5 MPa, -1.0 MPa, in D-Mannitol, cf. Swagel et al., 1997) and light regime (warm white light and darkness). In order to detect the influence of the cold Mongolian winter one batch of achenes was exposed to cold temperatures (1 week, -18°C). If not marked otherwise, germination tests were carried out at temperatures of 20/10°C (12h of light/12h of darkness; n=2x50 seeds). As no dormancy could be detected, all further germination experiments were started directly in November 2003.

For germination tests, ripe cones were collected from randomly selected plants in August 2002, and stored for one month in cotton bags. Germination tests were performed in the laboratory using morphologically intact cones and seeds. Dormancy was tested using both, intact cones and bare seeds which were put on filter paper in Petri-dishes, and incubated in climate chambers.

*Juniperus sabina* – sexual reproduction

For germination tests, ripe cones were collected from randomly selected plants in August 2002, and stored for one month in cotton bags. Germination tests were performed in the laboratory using morphologically intact cones and seeds. Dormancy was tested using both, intact cones and bare seeds which were put on filter paper in Petri-dishes, and incubated in climate chambers.
Table 2: Treatments for *Juniperus sabina* seeds, mean fraction of seeds still viable after treatment, and overall germination.

a) cotton bag, dry

<table>
<thead>
<tr>
<th>conditions</th>
<th>treatment</th>
<th>viability</th>
<th>germination</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 months 18°C</td>
<td>control</td>
<td>0.7%</td>
<td>0</td>
</tr>
<tr>
<td>H₂SO₄ (95–97%)</td>
<td>2.0%</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>100°C</td>
<td>4.0%</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>liquid N₂</td>
<td>4.0%</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>scarified (cut)</td>
<td>2.0%</td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>

b) moist sand

<table>
<thead>
<tr>
<th>conditions</th>
<th>treatment</th>
<th>viability</th>
<th>germination</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 months 18°C</td>
<td>control</td>
<td>6.0%</td>
<td>0</td>
</tr>
<tr>
<td>scarified (cut)</td>
<td>0.7%</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>3 months 18°C/</td>
<td>control</td>
<td>7.3%</td>
<td>0</td>
</tr>
<tr>
<td>scarified (cut)</td>
<td>2.0%</td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

at temperatures of 8/4°C and 20/10°C (12 h of light/12 h of darkness; n = 2 x 50 cones or seeds). As germination of juniper seeds is known to increase after storage (Garcia, 2001), cones were kept in either dry cotton bags or moist sand at different temperatures for various intervals (Table 2).

Additionally, we tried to break dormancy by submerging cones and seeds for 90 min in sulfuric acid, in liquid nitrogen (-96°C, 5 min), or in hot water (10 min). Five batches of seeds were mechanically scarified by cutting a hole (1–2 mm) into the seed coat. All germination tests on these treatments were carried out at temperatures of 20°C/10°C (12 h of light/12 h of darkness; n = 5 x 30 seeds). The experiments were stopped after 120 days and viability of ungerminated seeds was assessed using the Tetrazolium Test (Baskin & Baskin, 2001).

*Juniperus sabina* – vegetative reproduction

We confirmed the known capability to form adventitious roots (Gumbatov, 2001) by exemplarily putting three cuttings of *J. sabina* in water for one week. All shoots rapidly developed roots in this week. Growth rate under field conditions was assessed with two methods. Firstly, we randomly selected six shoots and dug them out as deeply as possible. Age of shoots and calculation of average growth rate was based on counting tree rings since these are quite obvious under the seasonal climate of Mongolia (Jacoby et al., 2000). Secondly, we tagged 108 shoots of 9 randomly selected patches on the 27th of May and measured length increment 75 days later.

In order to check whether patches are formed by one or several individuals, one *Juniperus* patch was dug out fully. Since there was evidence for patch disintegration, clonal growth was subsequently assessed with RAPD-Fingerprinting. The method has been successfully employed for taxonomic studies on Asian junipers before (Adams & Demeke, 1993; Adams, 2000; Hsiang & Huang, 2000), and was also used to map genets in other clonal species (Steinger et al., 1996; Herben et al., 2001).

As our main object was to assess genetic diversity within patches, we randomly collected 10 leaf samples from six widely spaced (> 100 m) juniper patches. Genomic DNA was extracted from 25 mg portions of silica-dried leaf material following the protocol described by Qiagen (2000; DNeasy Plant Mini Kit, p. 15). Amplifications of DNA were performed in reaction volumes of 10 µl containing 0.8 µl DNA (10 ng/µl), 0.6 µl of primer (Roth), 1 µl of each dNTP (Peqlab),
1 µl 10x buffer (Qbiogene), 0.1 µl Taq Polymerase (5U/µl, Qbiogene) and 6.5 µl H2O. PCR was carried out in an Eppendorf Mastercycler Gradient which was programmed for one cycle of 2 min at 94°C followed by 40 cycles of 12 s at 94°C, 45 s at 36°C and 120 s at 72°C with a final cycle of 7 min at 72°C. DNA fragments were separated by electrophoresis in 2% agarose gels with a tris-acetate-EDTA (TAE) buffer system at 150 V for 150 min and stained with ethidium bromide.

DNA bands were then visualized by UV light and documented using a video camera. In order to ensure reproducibility each sample was run in at least two independent RAPD-PCR amplification reactions. Gel pictures were analyzed with the software Cross Checker Version 2.91 (Buntjer, 1999); only bands in the range between 200 and 2000 bp were scored. An initial screening of 100 RAPD primers (ROTH sets A, B, D, J, N) was performed in order to test amplification profiles for polymorphism, readability, and reproducibility. This resulted in the selection of four primers (A18: AGGTGACCGT; D05: TGAGCGGACA, J14: CACCCGGATG, J15: TGTAGCAGGG) for use in the analysis.

Statistical Analysis

For differentiation of plant communities, the multivariate classification by Wesche & Ronnenberg (2004, which is based on the same data), was adopted and resulted in 7 plant communities. In a second step a Canonical Correspondence Analysis was performed in order to assess species-environment relations. Species with less than 2 occurrences were omitted, cover values were log-transformed and rare species were downweighted to account for the unduly influence they have in Correspondence Analysis. Aspect was transformed into ‘northness’, i.e. the cosine of the exposure in degrees, and ‘eastness’, the sinus of the exposure, to allow statistical analysis. We used forward selection to include only those environmental variables that had significant impact on the ordination (p < 0.05, Monte Carlo test with 999 runs, ter Braak & Smilauer, 2002). Stability of the final ordination was assessed with two Monte Carlo tests, one for the first axis, one for all axes together (9999 runs).

RAPD data was converted into a matrix which included presence/absence (1/0) data for all the scorable bands. Statistical analysis were based on Nei & Li (1979) distances among RAPD phenotypes; clustering was done with the UPGMA method (Unweighted Pair Groups Method, Jongman et al., 1995) and calculated with MVSP 3.1 (Kovach, 1995).

Statistical analysis of the germination tests were performed using SPSS 10.0 (SPSS Inc., 1999). Statistically tested parameters included the overall percentage of germinated achenes at the end of the given experiment, and the speed of germination by calculating the Timson Index (Baskin & Baskin, 2001) using the module non-parametric tests. Multifactorial analysis of differences between viability or germination rates were performed with a Kruskal-Wallis (H)-Test followed by reciprocal Mann Whitney U-Tests. The latter were Bonferroni-corrected to account for inflation of type 1 errors (Sokal & Rohlf, 1995).

Results

Habitat requirements

Plots with juniper can be found on the left side of the ordination diagram (figure 1). They are mainly characterized by a high cover of litter and relatively high pH-values. Especially the juniper stands with Lonicera microphylla prefer eastern exposures. The Artemisia santolinifolia scrub community is placed in the central and upper part of the diagram, indicating that A. santolinifolia often occurs on small mammal burrows.

The steppe community with Festuca valesiaca as the most characteristic species is found at high altitudes in northern exposures while Stipa gobica steppes are found in the central and right
Figure 1: CCA of relevé data and environmental data. Species cover values were log-transformed; only species (abbreviated) with a weight $> 6$ are displayed (axis 1: Eigenvalue 0.59 / species environment correlation explained is 41.4%; axis 2: EV 0.38 / 26.7%; axis 3: EV 0.10 / 8.7%, significance of axis 1: $p < 0.001$; of all axes $p < 0.001$).

part of the diagram mediating between Festuca valesiaca steppes and Artemisia santolinifolia scrub. They show a preference for the occurrence of fine scree (stones $< 2$ mm). The two samples with Achnatherum inebrians are placed in the uppermost part of the diagram. They occupy heavily disturbed sites, where annuals like Chenopodium vulvaria are very abundant. The second community concentrating in the upper part of the diagram is the Carex stenophylla (including C. duriuscula and C. stenophylloides cf. Dickoré, 1995) steppe with A. santolinifolia being present most of the time. This community depends on soil disturbance as well but avoids steep slopes.

Although juniper and sagebrush grow together at several sites (figure 2), there are also several spots where A. santolinifolia reaches its highest cover values but juniper is completely absent. So there is some overlap of habitat between the species but also evidence for mutual exclusion. This is supported by the weak albeit significantly negative correlation for the presence of J. sabina and A. santolinifolia ($r = -0.21$, $p < 0.05$).

Artemisia santolinifolia – reproduction

There was no sign for extensive vegetative reproduction or clonal growth of A. santolinifolia. Instead, achenes of A. santolinifolia were not dormant and capable of rapid germination directly after dispersal. Experiments in different climate chambers revealed a high temperature dependency (figure 3). At 32°C, achenes started to germinate after 24 h, whereas in a climate
Figure 2: Mutual exclusion of *Juniperus sabina* and *Artemisia santolinifolia* in the area – given as correlation between cover values of the two species over all sites (Pearson $r = -0.21$, $p < 0.05$).

Figure 3: Germination of *Artemisia santolinifolia* achenes at different temperature-regimes (all treatments were significantly different in Bonferroni-corrected reciprocal U-tests).

Chamber with an alternating temperature regime of 8/4°C the first achenes germinated after 5 days. However, temperature-regimes did not affect viability (figure 4); overall a median of 94% of the achenes were viable. No differences could be detected between germination in darkness and in light (figure 5).

Radicle emergence took longer in Mannitol-solutions than in distilled water (figure 6), and a higher fraction of seeds were not viable after incubation under strong osmotic stress (figure 7). At 20/10°C, the cold-stratified achenes germinated a little slower than the unstratified ones (figure 8). At 8/4°C this difference disappeared.

These data correspond to our field observations. Seedlings of *A. santolinifolia* are regularly found in the field, particularly in moist years such as 2003 and 2004. Furthermore, the species is often found on secondary sites such as old vehicle tracks, which were certainly colonized by successful reseeding.
Figure 4: Viability of *Artemisia santolinifolia* achenes after seeds were incubated at different temperatures (Box & Whisker Plots, Kruskal-Wallis Test, $p > 0.4$).

Figure 5: Course of germination of *Artemisia santolinifolia* achenes in darkness and in warm white light (alternating temperatures of 10/20 °C).

Figure 6: Germination of *Artemisia santolinifolia* achenes in Mannitol-solution (all treatments were significantly different in Bonferroni-corrected U-Tests).
Juniperus sabina – sexual reproduction

Neither seedlings nor saplings could be found in the field. Since young plants up to the age of 10 years usually form needle like leaves (Hegi, 1965), they can be easily identified. However, we had the impression that no individuals in this age class were present. Just three out of 2100 juniper seeds germinated all of which were mechanically scarified and germinated between the 60th and 90th day. The TTC-Tests revealed that only 2.5% of the morphologically intact seeds were viable.

Juniperus sabina – clonal growth

RAPD analysis revealed that bands in five of the six patches were identical within the respective patch (figure 9). Only within patch 5 two samples differ from the neighboring shoots in respect to one band. Consequently, these patches can be regarded as single genets each originating from a single reseeding event.

The six shoots cut in the field had 22–84 year-rings, which resulted in a mean growth rate of
1.7–6.8 cm when divided by the shoot length. The mean growth rate from May 27th to August 11th 2004 was 1.48 cm.

Discussion

The plant communities of the easternmost mountain ranges of the Gobi Gurvan Saykhan National Park differ with respect to their site conditions. As indicated by figure 1, *Juniperus sabina* grows often in eastern exposures, especially so for the *Juniperus sabina*-Lonicera microphylla scrub. Moreover, the juniper patches accumulate litter, and the pH-value of the soil is higher than in the other sites. This can be explained by the vegetation cover which is higher than in all other communities of the area. Due to the high amount of standing biomass transpiration is also greater and consequently more water and cations are transported to the upper soil layers resulting in raised pH-levels there.

*Artemisia santolinifolia* grows on scree slopes in all exposures except those facing strictly northwards. It is also often found on small mammal burrows. This pattern indicates that herbaceous plants are more competitive in suitably moist and little disturbed sites, where they form dense networks of roots. Herbs have their roots concentrated in the uppermost soil layers in the study region (Borisova & Popova, 1985), as it is often the case in arid and semi-arid climates (Dormaar, 1992). Under such conditions, the establishment of seedlings is often hindered. Under soil disturbances, e.g. in moving scree or on burrows, however, *A. santolinifolia* has the advantage that its roots reach deeper into the soil, and are hence less vulnerable to disturbances in the uppermost soil centimeters. In contrast, the grass-dominated *Festuca valesiaca* steppes grow in northern exposures with relatively high levels of moisture and relatively weak soil movement due to freeze-thaw processes. These rock steppes occupy the most favorable sites in the area. Where the community of *A. santolinifolia* and *Carex stenophylla* is found, scree movement is also low, but sites are especially characterized by grazing. This community grows on weakly inclined slopes, which are preferentially grazed by livestock.

*Artemisia santolinifolia* – reproduction

Achenes of the sagebrush are not dormant and more than 90% of them are viable. A lack of dormancy was also reported from *A. ordosica* and *A. sphaerocephala* which occur in the Gobi desert on sand dunes (Huang & Gutterman, 1998, 2003). These species germinate as soon as the water supply is sufficient. In contrast to these two sagebrush species, *A. santolinifolia* achenes
also germinate well in darkness, which is possibly an adaptation to disturbance as the achenes will easily get buried by moving scree or by the burrowing activity of pikas (*Ochotona pallasi*), which are abundant in this altitudinal range (Nadrowski et al., 2002).

Artemisia species from the American continent are known to lack a long-lived soil seed bank and also do not have the ability to resprout (Young & Evans, 1975, 1983; Huang & Gutterman, 2003, Meyer, 2003). This corresponds to the lack of dormancy which was found for *A. santolinifolia* in the present study. Seeds germinated readily if sufficient moisture is available, but seeds not germinated are most likely to survive the following winter. Although there was a significantly negative effect of cold-stratification (figure 8), the time lack of the stratified achenes was only a matter of a few hours and could be a mere artefact of different checking times during the day. For the same study region, Pietsch & Wesche (unpublished) confirmed the presence of an at least transitory soil seed bank, also suggesting that some seeds survive the winter.

*Juniperus sabina* – reproduction

Field observations suggest extremely limited sexual reproduction since no seedling and only one sapling (in 2004) could be found in the area. The lab-studies support this observation. Only three out of 2100 seeds germinated after an incubation period of 60–90 days, all of which were scarified. Considering the low amount and high variability of precipitation such extended periods of sufficiently moist conditions certainly are rare in the natural habitat. Nevertheless, scarification is likely to occur easily in the natural environment as scree slopes are unstable and have regularly moving substrate. Thus, germination might be possible but, with respect to the overall limited precipitation, should be rather erratic under field conditions.

Apart from the germination requirements, the low viability of seeds certainly is another major reason for the lack of sexual reproduction. Inferior diaspores are sometimes caused by low pollen viability and pollen vigor (Arista et al., 2001). Such a trend in juniper species was principally confirmed by Garcia et al. (1999). They found that seed viability of *J. communis* decreases towards dryer habitats. This is also in line with results from Verdu et al. (2004) who reported a seed viability of 50% for a region in Spain with a decent 600 mm of precipitation. Instead, clonal growth is apparently the major mode of reproduction in the study region. RAPD-fingerprinting revealed that patches are most likely constituted by a single clone. This confirms that even in the more favorable conditions provided by the mother plants sexual reproduction still is very rare. Only the results of patch 5 (figure 9) might indicate the establishment of one closely related seedling in such a safe site.

Dry conditions are likely to be one principal factor responsible for the lack of sexual reproduction of *J. sabina*. Being extremely long-lived, populations survive adverse conditions by vegetative growth. Apparently, this is a widespread strategy in Asian drylands, as the majority of the most important grasses of Asian deserts and semi-deserts are long-lived, and several are known to grow clonally (Lavrenko & Karamysheva, 1993; Hilbig, 1995; Liang et al., 2002; Huang et al., 2004). Moreover, the relative importance of clonal herbaceous species increases towards drier steppe types and deserts in Central Asia (Song et al., 2002).

In junipers, Houle and Babeux (1994) assume a negative trade off between the quality of seeds and the capacity of forming adventitious roots in *J. communis*, and Gumbatov (2001) reports a similarly inverse relationship between intensity of vegetative regeneration and the amount of cones produced by several juniper species in Azerbajan. Recently, Bruehlheide (2003) demonstrated that *Populus euphratica* (*P. diversifolia*) in the Taklamakan desert propagates by extensive clonal growth, and data from Qong et al. (2002) suggest that a similar strategy is followed by *Tamarix ramosissima* in the same landscape. Thus the reproductive behavior of *J. sabina* might represent a wide-spread strategy of plants living in the cold deserts of central Asia. This is in line with theoretical considerations on the decreasing importance of sexual regeneration under adverse conditions (Peck et al., 1998).
The maximum diameter of visually discernible patches of *J. sabina* in the study area was 100 m, and if strictly centrifugal growth is assumed, growth measurements suggest a minimum age of 769–2941 years for these large patches. At such time scales, climatic conditions can not be assumed to be constant. For Mongolia, climatic measurements and tree-ring analysis of Jacoby et al. (2000) demonstrate a trend towards higher temperatures in autumn, winter and spring during the last 40 years. In contrast, summer conditions got slightly cooler.

However, recent changes were well within the variance of the last 450 years, so data do not necessarily indicate a major trend. However palaeo-climatic studies from Gunin et al. (1999) showed large-scale climatic variations in Mongolia during the Holocene. According to these data, which are based on pollen-profiles and lake-level analysis, the climate between 8000 and 5000 yr BP, and at about 1800 yr BP was moister than today.

If we except that moisture availability is a limiting factor for sexual reproduction in *J. sabina*, then establishment of the oldest genets might well date back to 1800 yr BP. This is of importance for management considerations, as plant population dynamics might be generally slow in central Asian deserts, making assessment and rapid mediation of human impact exceedingly difficult. Stands appear to be stable at the moment, but stochastic events might still increase the vulnerability of the populations and pose at least some threat to their persistence.

**Conclusion**

The likeliest candidate to replace stands of *J. sabina* in the GGS certainly is the dwarf shrub *A. santolinifolia*, which is relatively unspecific with respect to its habitat preferences, provided that soil disturbance reduces the root competition with the otherwise densely growing hemicryptophytes. Since most of the slopes actually covered by *J. sabina* have moving scree, these sites would generally be suitable for both species. At present, the overlap between communities is limited as indicated by the CCA (figure 1) and the (weakly) negative correlation between the two species.

However, figure 2 suggests that *A. santolinifolia* is usually found in dominance stands of the juniper, whereas the latter is absent from many stands of the *A. santolinifolia* community. Thus, their is a potential of *A. santolinifolia* replacing juniper patches. However, this process appears to be in its infancy but will require continued monitoring in the next decades with junipers ageing and possibly dying.

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