



1 **The role of sexual versus asexual recruitment of *Artemisia wudanica* in transition**
2 **zone habitats between inter-dune lowlands and active dunes in Inner Mongolia,**
3 **China**

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23

24 **Abstract** *Artemisia wudanica* is an endemic, perennial, pioneering psammophyte
25 species in the sand dune ecosystems of western Horqin Sand Land in northern China.



26 However, no studies have addressed how sexual and asexual reproduction modes of *A.*
27 *wudanica* perform at the transitional zones between active dune inter-dune lowlands
28 and active dunes. In early spring, quadrats were randomly set up in the study area to
29 monitor surviving seedling and/or ramet density and frequency coming from
30 sexual/asexual reproduction of *A. wudanica*. Iron sticks were also inserted near each
31 quadrat to determine wind erosion (WE) intensity. Additionally, soil samples were
32 collected nearby each quadrat to test for soil moisture (SM) and organic matter (OM)
33 contents, and pH, respectively. Surviving seedlings of *A. wudanica* showed an inverse
34 response in comparison with ramets to SM, OM and WE. Soil moisture showed the
35 most positive effect, and WE the negative effect, on surviving, sexual reproduction
36 seedlings. Contrarily, WE had the most positive effect, and SM the negative effect, on
37 asexual reproduction ramets. This suggests that increases in SM and decreases in WE
38 should benefit recruitment of *A. wudanica* seedlings. On the contrary, ramets coming
39 from asexual reproduction showed a different response to environmental factors in
40 transition zone habitats. While SM was not a key constraint for the survival of
41 seedlings, they showed a better, positive response to wind erosion environments.
42 Overall, various study environmental parameters could be improved to foster *A.*
43 *wudanica* invasion and settlement in the plant community through different
44 reproductive modes, thereby promoting vegetation restoration and rehabilitation.

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46

47 **Keywords:** Sexual reproduction, Asexual reproduction, Redundancy analysis, Wind
48 erosion intensity, Soil physicochemical characteristics.

49

50



51 **Introduction**

52 Soil and vegetation are key components in the earth system (Raven et al., 1986;
53 Poelking et al., 2015). In spite of this, abusive exploitation (e.g., overgrazing;
54 intensive agriculture on fragile, coarse-textured soils) of these renewable natural
55 resources has led to a lack of soil cover with vegetation, and subsequent soil and
56 water losses from various types of ecosystems to a world-wide scale (Dregne and
57 Chou, 1992; Fernández and Busso, 1999; Ni et al., 2015). As a result, large surface
58 areas in the world have been transformed into deserts because of their exploitation
59 rather than a sustainable utilization (Dregne and Chou, 1992). Therefore, an
60 appropriate cover of the soil with vegetation is critical to prevent degradation, and
61 desertification, of the renewable natural resources (i.e., soil, vegetation, water
62 resources). This has been the subject of much research, for example, in China where
63 useless desert, sandy areas constitute more than 27%, or 2.5 million square kilometers,
64 of the country (Deming et al., 2014; Liu et al., 2014b).

65 Transition zones in sand dune ecosystems are located between sand dune systems
66 and other ecosystems, different types of sand dunes and dune slacks. Under different
67 environments, and their special background, different types of transition zones show
68 variation in their structure and function (Yan et al., 2007). In recent years, research
69 about transition zones has greatly increased. This has been the result of the need of
70 studies on vegetation recovery to disturbances and diversity conservation. These
71 studies were located between sand dune systems and other ecosystems [i.e.: ocean -
72 sand dune transition zones (Greaver and Sternberg, 2006); swamp - sand dune
73 transition zones (Munoz-Reinoso, 2001); sand dune - shrubby transition zones (Lei,
74 1998), and sand dune - forest transition zones (Sykes and Wilson, 1991; Oyama,
75 1994)]. However, there are few studies about inner sand dune systems (i.e., active



76 sand dune -dune slack transition zones).

77 Each dune slack can be a self-containing, transition zone unit (McLachlan et al.,
78 1996; van der Hagen et al., 2008). This is the result that while small parts of the
79 surface area are subjected to wind erosion, transition zone surfaces are composed by
80 wind erosion zones that formed in recent years. Slack dunes might be isolated among
81 themselves, and the transition zones occur here as small, naturally fragmented
82 systems in the whole dune landscape (Bossuyt et al., 2003). The environment
83 contrasts with that on the adjacent active dunes, and fluctuates throughout the year,
84 maintaining available water in the winter, but being prone to drought stress in summer
85 (Stark et al., 2003). Transition zones between active sand dunes and dune slacks in
86 south-western Horqin Sandy Land are characterized by a vegetation mosaic of
87 psammophyte, limnocyrtophyte-meadow and steppe species (Wang et al., 2015; Yan
88 et al., 2007; Yan, 2007). This is where pioneer species establishment is the initiation
89 of community succession (Allen and Nowak, 2008). Therefore, it is essential to
90 elucidate how pioneer species respond to transition zone habitats at different growth
91 stages. This will allow to gain decision-making guidelines which contribute to plant
92 recovery after disturbance, and control of wind erosion.

93 Because of their ecotone nature, transition zones ecosystems contain gradients in
94 environmental conditions that span a wide range of variation. They frequently
95 intensify or concentrate the flow and processing of materials; nutrient retention may
96 also be related to their spatial pattern of variation (Traut, 2005). The spatial (e.g., area
97 and perimeter) and soil edaphic (e.g., salinity, redox, moisture, texture) characteristics
98 of the transition zones might reflect changes in species richness and distribution
99 (Cantero et al., 1998; Helzer and Jelinski, 1999). Since transition zones might be
100 important for specific species (Morrison, 2001), and are sensitive to climate changes



101 and human activities (Peters, 2002a; Puyravaud et al., 1994; Gehrig-Fasel et al., 2007),
102 they have become a hotspot landscape unit for ecologists. However, for many
103 transition zones, there is little understanding of the key processes that allow dominant
104 species to persist at those zones, and how differences in these processes affect species
105 responses to changes in environmental conditions (Peters, 2000, 2002b).

106 *Artemisia wudanica*, a perennial psammophyte (Liu et al., 2014a), is a an endemic,
107 major pioneering species in sand dune ecosystems of western Horqin Sand Land in
108 northern China (Liu et al., 2007b; Yan and Liu, 2010; Wendurihu et al., 2013). It is
109 typically found only in active dunes, where wind erosion and sand burial are severe
110 and frequent (Liu et al., 2007a; Liu et al., 2014a). This species has unique adaptive
111 and functional traits (Yan and Liu, 2010). It can reproduce through either seedling
112 recruitment (sexual reproduction) or vegetative propagation (asexual reproduction;
113 ramet production) (Eriksson, 1988; Liu et al., 2014a). There are many perennial buds
114 on its rhizomes which may grow out to produce aboveground shoots. *Artemisia*
115 *wudanica* can be found in Wengniute Banner and surrounding areas in the western
116 Horqin Sandy Land, and it grows in either drifting or semi-drifting dunes as a
117 sand-fixing plant species. The distribution area of this species is narrow (Wendurihu,
118 2013), with a recession trend in recent years (Liu et al., 2014a).

119 Liu et al. (2014a) indicated that erosion has negative effects on sexual reproduction
120 of *A. wudanica*. However, whether these negative effects can extend to asexual
121 reproduction is not known in this species. Also, the importance of knowing how
122 various factors affect seedling frequency and abundance of *A. wudanica* was recently
123 emphasized by Yan and Liu (2010). These authors found that the (1) number of
124 pioneer species (e.g., *A. wudanica*) relative to total species number, and (2)
125 abundance of pioneer species relative to total abundance decreased on active and



126 stabilized sand dunes as the surface area increased in wetland areas. Also, soil fine
127 particles, soil organic C, total N and P concentrations, and formation of biological soil
128 crusts increase with the stabilization of sand dunes (Zhang et al., 2004; Su et al.,
129 2005). Creation of these favourable habitats for typical dune wetland (and steppe)
130 species also led to a high plant species richness in inter-dune lowlands (Zhang et al.,
131 2004; Su et al., 2005). However, Yan and Liu (2010) determined the local
132 disappearance of the endemic, pioneer *A. wudanica* from inter-dune wetlands in
133 stabilized dunes. This was because this species did not find suitable habitats in
134 stabilized sand dunes, as a result of its adaptation to unstable substrates in active
135 dunes. These authors reported that the increase in species richness after dune
136 stabilization was at the cost of the loss of endemic, pioneering species.

137 The importance of studying regenerative strategies on plants inhabiting active
138 dunes in the Horqin Steppe, Inner Mongolia, northeastern China, was highlighted by
139 Liu et al. (2014b). They reviewed various morphological, reproductive and/or
140 physiological adaptations in response to sand burial, wind erosion or sand abrasion.
141 These authors reported different regenerative strategies in three typical psammophytes
142 (e.g., *A. wudanica*) of the Horqin Steppe in response to wind erosion. Achenes of the
143 semi-shrub *A. wudanica* produce mucilage after being moistened (Liu et al., 2005)
144 which holds sand to form a sand-binding agglomerate as a mechanism to protect
145 psammophyte diaspores of being removed from the active sand dunes. Plants of this
146 species fall down because of wind erosion and trap blowing sand. Thereafter, the
147 buried, falling plants produce adventitious roots and form a cluster of emergent
148 ramets on the active sand dunes (Liu et al., 2014b).

149 We hypothesized that density coming from asexual reproduction of *A. wudanica* is
150 different from that coming from sexual reproduction in transition zone habitats of



151 sand dune systems in northeastern Inner Mongolia, China. We investigated the
152 density (and frequency) of *A. wudanica* coming from either sexual or asexual
153 reproduction at those habitats in the field. The relationship between sexual/asexual
154 reproduction versus environmental factors was also evaluated in the study species.
155 The importance of our study lies in the need to understand the reproductive strategy of
156 pioneering species (like *A. wudanica*), and is especially relevant if we want to manage
157 and restore natural ecosystems properly.

158

159 **Materials and Methods**

160 **Study area**

161 The study was conducted at the Wulanaodu region (42°29'~43°06'N, 119°39'~
162 120°02'E, approx. 480 m.a.s.l.) in south-western Horqin Sandy Land, Inner Mongolia,
163 China. Climate is semiarid, the mean annual temperature is 6.3°C, and the frost-free
164 period extends over 130 days. The coldest and hottest months are January and July,
165 respectively. The mean annual precipitation is 340.5 mm, 70% of which falls between
166 June and September. Mean annual wind velocity varies between 3.2 and 4.5 m s⁻¹, and
167 is dominantly from the north-west in March - May and the south-west in June -
168 September. The area has been intensively grazed since 1950, and as a result
169 overgrazing is the major force leading to its desertification. Mobile dunes, advancing
170 to a rate of 5-7 m year⁻¹, are widely distributed. In this region, not only sand dune
171 movement, but also wind erosion and sand burial are very frequent (Wang et al.,
172 2015). In these wind-eroded zones, vegetation is composed of only a few pioneering
173 plant species such as *Agriophyllum squarrosum* and *A. wudanica*, with a coverage of
174 less than 15%.

175



176 **Experimental design**

177 In early April 2011, we randomly selected three dune slacks in mobile dunes. Their
178 size was either 2.06 ha or 1.62 ha or 1.10 ha. Height of sand dunes was approximately
179 equal around these study areas. At each of the three transition zones (see Fig. 1) with
180 a vegetation cover of less than 5%, we randomly set up nine 1m×1m quadrats.

181

182 **Wind erosion intensity**

183 Iron sticks (2 mm diameter, 200 cm height) were inserted near each quadrat to
184 monitor wind erosion intensity (WEI) (Liu et al., 2014a). In 2011, aboveground height
185 of the sticks was measured and recorded at 5-day intervals from early April to late
186 May, before and after seedling emergence, respectively. At the end of the experiment,
187 we obtained a measure of the erosion depth on the 27 iron stick following Liu et al.
188 (2014a).

189

190 **Soil physicochemical characteristics**

191 Ten soil samples were taken nearby each quadrat (core diameter 7.0 cm, depth 20 cm)
192 in late May 2011. These samples were first pooled and then subdivided into 0–10 cm
193 and 10–20 cm soil layers. Each soil sample was air-dried and then sieved through a 5
194 mm screen to remove stones, roots and rhizomes. Large aggregates were gently
195 processed by hand during the screening procedure (Zhang et al., 2013). Sample
196 splitting methods were applied to a total of 54 soil samples (1 pooled sample/quadrat
197 x 2 depths/quadrat x 9 quadrats/replicate x 3 replicates). These samples, repeatedly
198 divided into halves by coning and quartering until the desired sample size was
199 achieved, were brought to the laboratory for analyses. They included (1) pH,
200 measured using a potentiometer, and (2) organic matter content, determined using the



201 potassium dichromate heating method (Cao et al., 2011).

202 Also in late May 2011, four soil samples were taken close to each quadrat (core
203 diameter 7.0 cm, depth 30 cm); vegetation and litter were removed from these
204 samples (Karle et al., 2004). Thereafter, these samples were first subdivided into 0–10
205 cm; 10–20 cm, and 20–30 cm soil layers, and immediately taken to the laboratory for
206 SM analysis. Thereafter, a total of 324 soil samples (4 samples/depth/quadrat x 9
207 samples/depth/replicate x 3 sampling depths/sample x 3 replicates) were obtained at
208 the field. Soil moisture content was determined by gravimetry following Brown
209 (1995).

210

211 **Sexual and asexual reproduction**

212 The number of surviving either seedlings (i.e., sexual reproduction) or ramets (i.e.,
213 asexual reproduction) of *A. wudanica* was counted within each of the 27 (1 x 1m)
214 quadrats in late May 2011. Remaining seed coats on surviving seedlings after their
215 emergence facilitated to distinguish their counting. Whenever doubts arised for
216 counting, soil was excavated to distinguish if individuals came from either sexual or
217 asexual reproduction. Frequency and density were determined following
218 Müller-Dombois and Ellenberg (1974), Liu et al. (2007a), and Wu et al. (2015).

219

220 **Data analyses**

221 One-way ANOVA was used to compare density and frequency between the two (i.e.,
222 sexual versus asexual) reproduction modes of *A. wudanica*. The mean number of
223 surviving seedlings per square meter was taken as a measure of plant density (Wu et
224 al., 2015). Data to determine density were transformed to $\sqrt{x+0.5}$ (Soakal and Rholf,
225 1984) previous to analyses because neither seedlings nor ramets survived in many



226 quadrats/replicate (i.e., there were many 0 values); untransformed values are reported
227 in Figures. Multi-way ANOVA analyses were applied using SPSS version 16.0.
228 (SPSS for Windows, Version 16.0, Chicago, Illinois, USA) to determine correlations
229 among WE, pH, OM and SM versus density of either surviving seedlings or ramets of
230 *A. wudanica* at the transition zone habitats in active dune fields. Furthermore,
231 Redundancy Analysis (RDA) using CANOCO software (2012) was used to gain
232 insights of the relationship between the two reproductive modes of *A. wudanica*
233 versus WE, pH, OM, and SM (Liu et al., 2015).

234

235 **Results**

236 **Environmental parameters**

237 From early April to late May, WE reached 4.67 cm (Table 2). In late May, soil
238 moisture content was 13% greater at 20-30 than 0-10 cm soil depth (Table 2). At this
239 time, pH was 2.9% greater at 10-20 than 0-10 cm soil depth (Table 2). Despite WE
240 showed a negative correlation with SM, OM, and PH, these correlations were
241 non-significant ($p > 0.05$; Table 3). Soil moisture content showed positive correlations
242 with OM and pH1 but none of these correlations was significant ($p > 0.05$). Soil
243 organic matter at 10-20 cm and 0-20 cm soil depth was positively correlated ($p < 0.05$)
244 with pH at 10-20 cm soil depth (Table 3).

245

246 **Sexual and asexual reproduction**

247 We found 34 and 18 individuals coming from sexual and asexual reproduction,
248 respectively, in all 27 plots. The mean density coming from sexual reproduction was
249 51% higher ($p < 0.05$) than that coming from asexual, vegetative reproduction (Fig. 2).
250 Frequency was approximately 11% greater for surviving ramets coming from asexual



251 than for surviving seedlings originated from sexual reproduction, but differences were
252 not significant ($p>0.05$; Fig. 2).

253

254 **Relationship between sexual or asexual reproduction and environmental**
255 **conditions**

256 *Sexual reproduction*

257 The first axis of the RDA analysis explained 78.3% of the variation between the
258 production of surviving seedlings and the environmental factors (i.e., WI, SM, OM
259 and pH; Fig 3). The second axis of such analysis, however, only explained 13.7% of
260 such variation. The amount of variability explained by all canonical axes was 92%.
261 Environmental factors showed a significant effect ($p<0.05$) on the density of
262 surviving seedlings.

263 The length and angle of the arrows with respect to the small dashed, vertical lines
264 show the degree to which the environmental factors affected seedling density. In this
265 analysis, it was found a positive correlation between seedling density and SM (0-10
266 cm, 10-20 cm, 20-30 cm, 0-30 cm), OM (0-10 cm, 10-20 cm, 0-20 cm), and pH 1
267 (0-10 cm). At the same time, a negative correlation was observed between seedling
268 density and WE and pH 2 (10-20 cm). Additionally, SM (0-10 cm, 10-20 cm, 20-30
269 cm, 0-30 cm) was the most relevant ($p<0.05$) soil physical property among all study
270 environmental factors to explain seedling density on *A. wudanica*.

271

272 *Asexual reproduction*

273 The first axis explained 73.6% of the variation between ramet density and the study
274 environmental factors (Fig. 4). However, it was more strongly correlated with these
275 biotic and abiotic factors than it was the first axis for sexual reproduction. The second



276 axis explained 18.6% of the variation, and it was partially correlated with ramet
277 density and the environmental factors. The amount of variability explained by all
278 canonical axes was 92.2%. Environmental factors had a significant effect ($p < 0.01$)
279 on ramet density.

280 Wind erosion intensity and pH 1 (0-10 cm) showed positive effects on ramet
281 density (Fig. 5). However, SM (0-10 cm, 10-20 cm, 20-30 cm, 0-30 cm), OM (0-10
282 cm, 10-20 cm, 0-20 cm), and pH 2 (10-20 cm) showed negative effects on such
283 density. Additionally, WE was the most positive ($p < 0.05$), relevant factor for ramet
284 density.

285

286 Discussion

287 It is well known that vegetation recruitment occurs via sexual and asexual
288 reproduction, depending on the species and the environmental conditions in the
289 habitat, and that this recruitment is critical for vegetation regeneration and succession
290 (Wu et al., 2011; Qian et al., 2014). Invasive clonal plants have two reproduction
291 patterns, namely sexual and vegetative propagation (Qi et al., 2014). In Horqin Sand
292 Land most plants can reproduce both sexually and vegetatively, and the balance
293 between these two reproductive modes may vary widely between and within species.
294 Such a balance contributes that *A. wudanica* is a successful endemic and major
295 pioneering species in transition zone habitats of active sand dune fields in the sand
296 dune ecosystems of western Horqin Sand Land in northern China. To date, studies
297 were focused on seeds of *A. wudanica* (Li et al., 2012), and its frequency and
298 abundance within dune slack areas (Yan and Liu, 2010), where sand burial
299 compensates for *A. wudanica* seedling losses (Liu et al., 2014b). Compensation is
300 achieved by the production of adventitious roots and emergent ramets, and



301 modification of the biomass partitioning to above- and below-ground organs in this
302 species on active dunes (Liu et al., 2014a). However, no studies dealt with recruitment
303 of *A. wudanica* in transition zone habitats. In these habitats, seedling and ramet
304 densities of *A. wudanica* showed different relationships with various environmental
305 parameters (WE, SM, OM, pH) (Figs. 3 and 4). Therefore, our hypothesis that density
306 coming from asexual reproduction of *A. wudanica* is different from that coming from
307 sexual reproduction in transition zone habitats was supported.

308 The results that more sexual than asexual reproduction was found in all 27 study
309 plots (Fig. 2) suggest that seeds play an important role in *A. wudanica* preservation in
310 transition-zone habitats. Previous studies suggested, however, that *A. wudanica*
311 population recruitment most often takes place from vegetative reproduction (Li et al.,
312 2012; Liu et al., 2014b). Similarly, Zhao et al. (2013) found that while asexual
313 recruitment made a major contribution to the increase of total offspring number after
314 fire, sexual recruitment contributed little to post-fire recovery in a semiarid perennial
315 steppe of the Loess Plateau of north-western China; lack of sexual recruitment was
316 not related to fire management but to inherent traits of the occurring plant species. Wu
317 et al. (2013) also showed that rapid recovery after fire of an arid steppe on the Loess
318 Plateau was mainly attributed to the removal of litter, which provided better
319 microhabitats for the vegetative, asexual regeneration of perennial species. The higher
320 density on sexual than asexual reproduction (Fig. 2) indicates that surviving seedlings
321 most likely showed an aggregate spatial distribution in the soil. This is because this
322 distribution pattern has been reported to facilitate growth of plant individuals within a
323 patch (Holmgren et al., 1997; Schleicher et al., 2011). Ma et al. (2010) indicated that



324 the delay in seed dispersal, and maintenance of high seed viability, after maturation
325 until the end of the windy season and the start of the next growing season is a
326 mechanism which allows the adaptation of the psammophyte *A. wudanica* to sand
327 mobility. Our results are consistent with the Redundancy Analysis (RDA) in that the
328 density of surviving seedlings showed a maximum, positive correlation with SM at all
329 study layers, and a negative correlation with WE (Fig. 3). Xue et al. (2014) reported
330 that even though plant recovery was limited because of the low density and high
331 mortality of seedlings during early stages after a disturbance, long-term plant
332 development would be benefited to a population scale.

333 Generally, low levels of nutrients in coastal dune soils limit plant growth (Gilbert et
334 al., 2008). Nutrient constraints may play a role in limiting the ability of plants to
335 respond to sand-drift activity (Gilbert et al., 2008). Wu et al. (2013) reported that
336 nutrient availability was indirectly related to seedling recruitment on five *Saussurea*
337 species (Asteraceae) from the Qinghai-Tibetan Plateau in China by influencing their
338 seedling relative growth rate and root/shoot dry mass ratio. Our findings agree with
339 those of Yan and Xu (2012) who showed that soil moisture was the most limiting
340 factor in the course for vegetation invasion in transition zone habitats of semiarid sand
341 dunes. In our study, recruitment from different reproduction modes showed different
342 responses to environmental factors. It is well known that individuals coming from
343 asexual reproduction are nourished by soil resources obtained via their mother plants
344 (Pitelka and Ashmun, 1985; Marshall, 1990; de Kroon and van Groenendael, 1996),
345 and that these plants can absorb more water and nutrients from the soil through their



346 flourishing roots. These studies might help explain why SM and OM depicted a
347 negative effect on surviving ramet density in our study. The ability to get water and
348 nutrients from the soil is rather weak on seedlings with undeveloped roots. This is
349 why we found a positive correlation between the density of surviving seedlings and
350 SM and OM. However, the correlation between the density of those surviving
351 seedlings and WE was negative (Fig. 3). Water and nutrient limitation may play a
352 significant role in limiting the ability of *A. wudanica* sexual reproduction to respond
353 to wind erosion.

354 Soils in the 0-10 and 10-20 cm layers were weakly alkaline ($\text{pH} > 7$), and pH in the
355 10-20 cm layer was slightly higher than that in the 0-10 cm layer ($\text{pH}_2 > \text{pH}_1$) (Table
356 2). It might be that calcareous groundwater and surface water could re-enter most
357 slacks in spring, and this might have led to higher pHs in most slacks (Grootjans et al.,
358 2002). Our results also suggested that while pH1 (the topsoil) showed a positive effect
359 on density resulting from sexual and asexual reproduction, pH2 had a negative effect
360 on the density of both reproduction types (Fig. 3, 4); however, the negative effect on
361 the density of ramets was so weak that it could be considered negligible (Fig. 4). This
362 result would indicate that the density of surviving seedlings will decrease as soil pH
363 increases in the 10-20 cm layer, and alkaline soils are unfavourable for the successful
364 establishment from sexual reproduction. Contrarily, alkaline soils in the 10-20 cm soil
365 layer had little effect on the establishment of asexually-originated individuals.

366

367 **Conclusion**

368 *Artemisia wudanica* showed different responses to environmental parameters between
369 its two study reproduction modes. This partially indicates why *A. wudanica* is a major



370 pioneering sand dune species in the sand dune ecosystems of western Horqin Sand
371 Land in northern China. This species can invade and establish in dune slacks through
372 different reproductive modes with changes in environmental conditions. This study
373 revealed that we could improve the various study environmental parameters to foster
374 *A. wudanica* invasion and settlement through different reproductive modes, thereby
375 promoting vegetation restoration and rehabilitation.

376

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592 **Table legends**

593 Table 1. Abbreviated codes for the species and environmental factors.

594

595 Table 2. Wind erosion intensity and soil physicochemical characteristics for the plots
596 sampled in the transition zone. Values are mean \pm 1 S.E. of $n=27$ for WE, and $n=108$
597 for each SM depth, and $n=27$ for each OM and pH depths.

598

599 Table 3. Pearson correlation coefficients between environmental (i.e., intensity of
600 wind erosion) and soil physicochemical variables (i.e., soil moisture and organic
601 matter contents, and pH) at the study site. Correlations were either non-significant or
602 significant at the 0.01 (**) or 0.05 (*) level.

603

604 **Figure legends**

605 Fig. 1. A sketch map showing the transition zone in inter-dune lowlands of an active
606 sand dune system (modified from Yan et al., 2007).

607

608 Fig. 2. Density [number of surviving either seedlings (sexual reproduction) or ramets
609 (asexual reproduction) per m^2] and frequency (%) coming from either sexual or
610 asexual reproduction in the shrub *A. wudanica*. Histograms are the mean \pm 1 S.E. of
611 $n=27$. Different letters above histograms indicate significant differences at $p<0.05$.

612

613 Fig. 3. Redundancy analysis (RDA) of the relationship between sexual reproduction
614 of *A. wudanica* (i.e., seedling density) at the field and environmental factors. The
615 amount of variability explained by all the canonical axes was 92% ($F=3.520$,



616 $p=0.0100$). Abbreviations for the study variables are given in Table 1.

617

618 Fig. 4. Redundancy analysis (RDA) of the relationship between asexual reproduction
619 of *A. wudanica* (i.e., ramet density) at the field and environmental factors. The
620 amount of variability explained by all the canonical axes was 92.2% ($F=2.864$,
621 $p=0.0080$). Abbreviations for the study variables are given in Table 1.

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Table 1

	Abbreviated code	Life form	Full name
1	<i>Ar.wu.</i>	SS	<i>Artemisia wudanica</i>
2	WE	—	wind erosion intensity (cm)
3	SM 1	—	soil moisture of 0-10 cm layer
4	SM 2	—	soil moisture of 10-20 cm layer
5	SM 3	—	soil moisture of 20-30 cm layer
6	SM 4	—	soil moisture of 0-30 cm layer
7	OM 1	—	organic matter of 0-10 cm layer
8	OM 2	—	organic matter of 10-20 cm layer
9	OM 3	—	organic matter of 0-20 cm layer
10	pH 1	—	pH of 0-10 cm layer
11	pH 2	—	pH of 10-20 cm layer

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Table 2

	WE (cm)	SM1 (%)	SM2 (%)	SM3 (%)	SM4 (%)	OM1 (%)	OM2 (%)	OM3 (%)	pH1	pH2
Mean	4.67±1.00	6.10±1.35	6.48±1.23	7.01±1.64	6.53±1.39	0.016±0.00	0.016±0.00	0.016±0.00	7.32±0.01	7.54±0.06

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Table 3

environmental parameters	WE(cm)	SM1	SM2	SM3	SM4	OM1	OM2	OM3	pH1	pH2
WE(cm)	1	-	-	-	-	-	-	-	-	-
SM1(%)	-0.170	1	-	-	-	-	-	-	-	-
SM2(%)	-0.212	0.969**	1	-	-	-	-	-	-	-
SM3(%)	-0.203	0.962**	0.965**	1	-	-	-	-	-	-
SM4(%)	-0.197	0.988**	0.988**	0.989**	1	-	-	-	-	-
OM1(%)	-0.202	0.164	0.083	0.179	0.147	1	-	-	-	-
OM2(%)	-0.198	0.269	0.190	0.304	0.263	0.888**	1	-	-	-
OM3(%)	-0.206	0.229	0.147	0.256	0.218	0.964**	0.978**	1	-	-
pH1	-0.045	0.293	0.286	0.299	0.297	-0.132	-0.124	-0.131	1	-
pH2	-0.279	-0.026	-0.048	0.015	-0.017	0.334	0.460*	0.416*	-0.063	1

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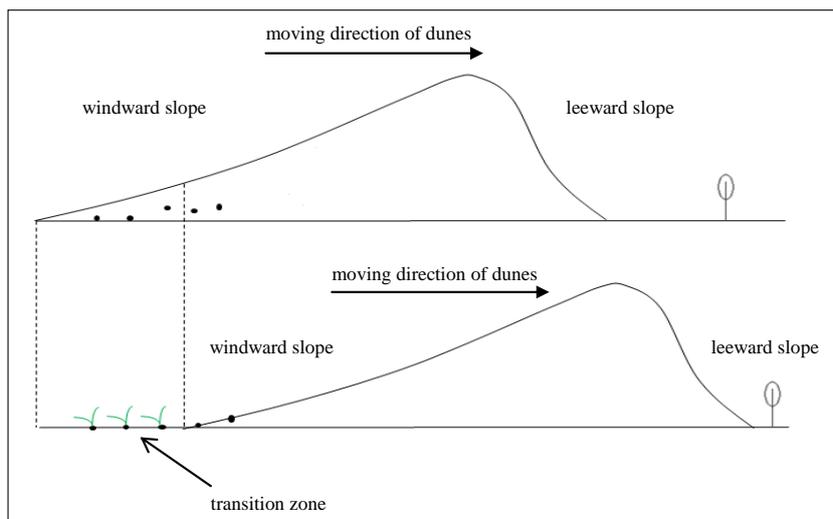
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Fig. 1

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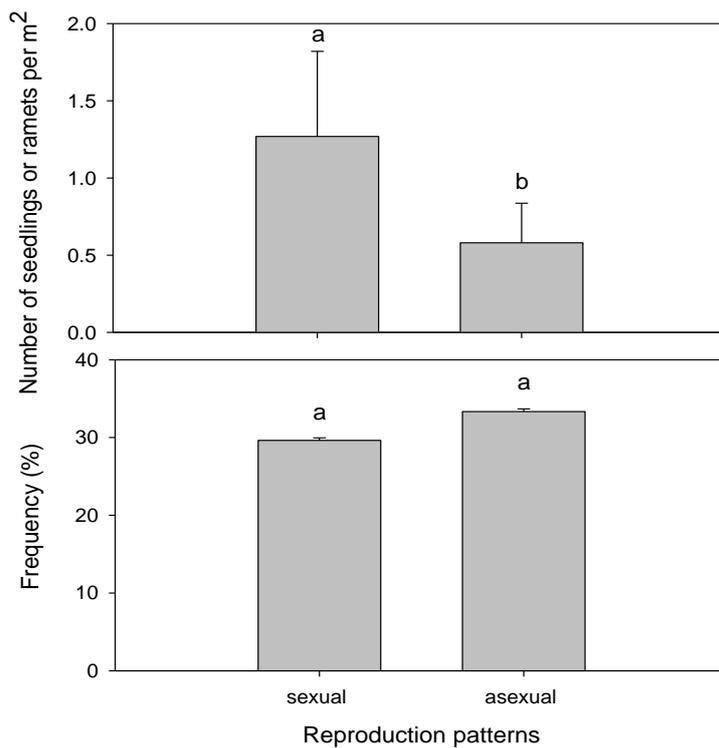
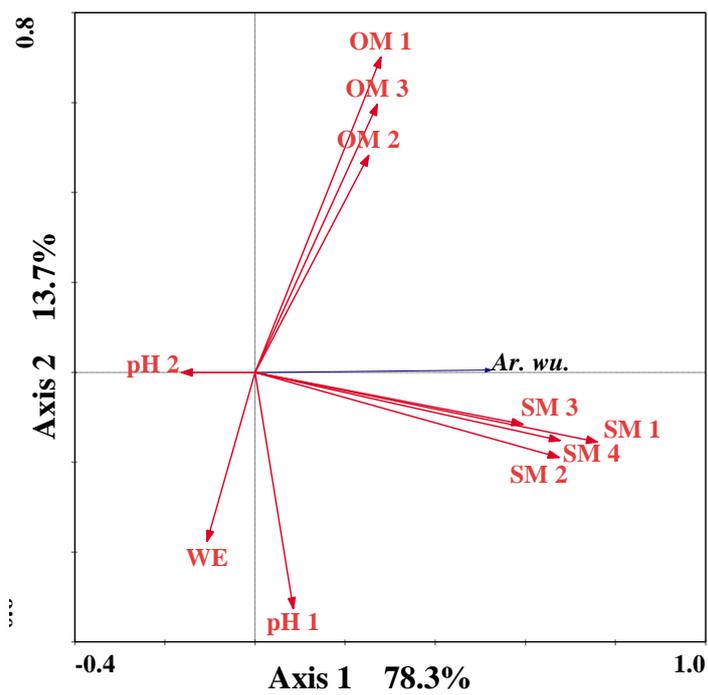


Fig. 2

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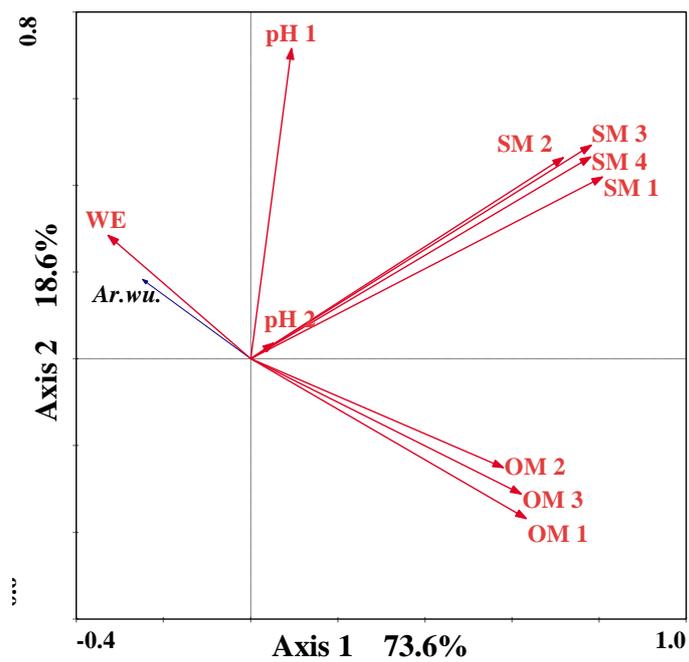


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Fig. 3



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Fig. 4