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# 5 Experimental sand burial affects seedling survivorship, morphological traits and 6 biomass allocation of *Ulmus pumila var. sabulosa* in Horqin Sandy Land

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22 Abstracts As a native tree species, Ulmus pumila var. sabulosa (Sandy elm) is widely distributed in Horqin Sandy Land. 23 However, seedlings of this species have to withstand various depths of sand burial after emergence because of increasing soil 24 degradation. So an experiment was conducted to evaluate the changes in the survivorship, morphological traits and biomass 25 allocation buried with different burial depths (unburied, and seedlings buried vertically up to 33, 67, 100 or 133% of the 26 initial mean seedling height). The results showed that partial sand burial treatments (i.e., less than 67% burial) did not influence seedling survivorship, which still reached 100%. However, seedling mortality increased as sand burial was equal to 27 28 or greater than 100%. Seedling height and stem diameter increased at least by 6 to 14 % with partial burial in comparison 29 with control treatment. Whilst seeding taproot length, total biomass, and relative growth rates at least enhanced by 10%, 30 15.6%, and 27.6%, respectively, with the partial sand burial treatment. Furthermore, sand burial decreased total leaf area and 31 changed biomass allocation on seedlings, transferring more biomass to aboveground rather than belowground parts. 32 Complete sand burial after seedling emergence inhibited its growth, and even lead to death. Our findings indicated that 33 seedling of sandy elm had a certain resistance to partial sand burial and acclimated to sandy environments. The negative 34 effects of common excessive sand burial after seedling emergence help to understand failures in recruitment of sparse elm





- 35 woodland in this study region.
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- 37 Keywords: sand accretion, seedling, sandy elm, morphological, biomass allocation, Horqin sandy land
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39 Introduction

40 Soil genesis is the pivotal process that determines the evolution of soil system and offer services and resources to humankind (Berendse et al., 2015; Niu et al., 2015). Simultaneously, due to increasing population and consumption, external disturbance 41 such as land use intensification has a profound impact on soil genesis process, especially overgrazing and inappropriate 42 43 cultivation around the world(Brevik et al., 2015; Verheijen et al., 2009; Wang et al., 2016). These excessive human 44 interference changes soil hydrological, geochemical and biological cycles, inducing to serious land degradation primary 45 presented land acidification, salinization and desertification (Bellamy et al., 2005; Foley et al., 2005; Gabarron-Galeote et al., 2013; Smith et al., 2015). Horqin Sandy Land, shaping in the middle period of Pleistocene, was located in the southeast of 46 the Mongolia Plateau, China(Qiu, 1989). Because of climatic changes (rainfall distribution and climate warming and drying) 47 48 and excessive human activities (settlement, overgrazing and gathering), vegetation degradation and land desertification are becoming more obvious in recent 50 years (Cao et al., 2008; Jiang et al., 2003; Zhang et al., 2004). Combine with the effects 49 50 of strong winds from March to June, sand moves fast in the horizontal or vertical space leading to different burial depths, 51 which might range from 0.5cm to 56.0cm (Liu et al., 2014). 52 It is well known that vegetation plays an important role controlling the soil genesis and degradation in the fragile ecosystems

54 always restricted by barren and harsh environments. However, compared with plant production and ecological function for

(eg. estuarine, desert and sandy land)(Berendse et al., 2015; Cerda, 1998; Miao et al., 2014). And their survival and growth is





55	humans, less attention was drawn to the interactions of soil and plants during the long-term evolution and succession
56	processes under relatively stressful and variable conditions(Foley et al., 2011; Zhao et al., 2004; Zhou et al., 2006). In sandy
57	ecosystems, instability of the soil surface is one of the most destructive factors and sparse vegetation coverage and loose soil
58	texture is highly susceptible to sand movements (Liu and Guo, 2005; Yan et al., 2005) Sand movement, the most direct
59	performance caused by land degradation, is regarded as a selective force to determine colonization, distribution and
60	establishment of vegetation (Maun, 1994; Maun and Lapierre, 1986). Plants might suffer from varying degrees of sand burial
61	and evolve different regenerative adaptations in the period of soil seed bank formation, seed germination and following
62	seedling emergence and development(Li et al., 2014; Qian et al., 2016; Tang et al., 2016). And increasing number of
63	researches have involved in this field and studies on the effects of sand burial on seedlings have been widely reported on
64	their survival (Harris and Davy, 1987; Li et al., 2015; Liu et al., 2008; Perumal and Maun, 2006), physiological
65	characteristics (Shi et al., 2004; Wang et al., 2012; Zhao et al., 2015), and reproduction strategies (Liu et al., 2014; Sun et al.,
66	2014b; Zhao et al., 2007). In general, there have a threshold sand burial depth for each plant species to maximize its vigor
67	and the following growth(Maun, 1997). Below the burial level, plant emergence and development have been promoted by
68	sand burial depth (Qu et al., 2012; Yang et al., 2007); however, exceeded that threshold, a deterioration of seedling vigor and
69	growth was occur, and even seedling death (Maun, 1997; Maun and Lapierre, 1986).
70	As a indigenous tree species in this area, Ulmus pumila var. sabulosa (sandy elm) was widely distributed in the leeward
71	slope of fixed and semi-fixed sand dunes and becomes the main proportion of sparse woodlands in Horqin sandy land(Jiang

ret al., 2013; Tang et al., 2014; Tang et al., 2013). Since prehistoric times, it is closely relate to human life, which could





73	provide hardwood for farming tools and furniture, fuel for nomad, fodder because of tender leaves, young fruits and
74	edible bark(Ma, 1989; Schlütz et al., 2008). At same time, sparse elm woodlands, this landscape type not only offers
75	shelter for wildlife and domestic animals and paradise for psammophytes, but also prevent soil from wind erosion and
76	burial in the arid land and semi-arid land, expressing maximum ecological and social function(Yang et al., 2003).
77	However, even though plenty of seeds germinated without dormancy and seedlings emerged after dispersal in the late spring,
78	few of seedlings survived were detected in the following field vegetation surveys in the degraded sparse woodlands. This
79	phenomenon has negative effects on community future structure, and on hampering its recruitment on woodlands
80	ecosystems.
81	Despite realization that the effects of sand burial, much of our comprehension and recognition come from ocular
82	observations at the field rather than from controllable experiments (Maun 1997). Previous studies focused on plant
83	physiological characteristics and population adaptive strategies to burial in coastal marshes and wetlands (Belcher, 1977;
84	Cheplick and Grandstaff, 1997; Maun and Lapierre, 1986; Shi et al., 2004; Sun et al., 2010; Sun et al., 2014a). Few has
85	involved in the effects of sand burial on the establishment and growth of seedlings after their emergence, especially in sandy
86	environments. To date, no research has been conducted on the effects of continual sand accumulation on sandy elm seedlings
87	after emergence. This might partially due to the limited, sparse elm woodland area. So we investigated the effects of
88	experimental sand burial on seedling survivor and growth of sandy elm and provide a theoretical basis for recruitment and
89	vegetation reconstruction on sandy elm woodlands.

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#### 91 Materials and methods

#### 92 Study site

93	The experiment was conducted at the U'lanaodu Desertification Experimental Station of the Institute of Applied Ecology,
94	Chinese Academy of Sciences (43°02'N,119°39'E, 480m a.s.l), where located in western Horqin Sandy Land, China. This
95	site belongs to temperate continental climate. Mean annual temperature and precipitation are 7.3°C and 315mm, respectively.
96	Almost 75% of precipitation occurs during June to September in the growing season (Figure 1). Annual average wind speed
97	is 4.4m/s; the windy season is from March to June (Liu et al., 2012; Miao et al., 2014). The landscape is characterized by
98	sparse woodlands, sand dunes and lowland areas. Dominant soils are sandy, and major plant species include some shrubs
99	(e.g., Salix gordejevii and Caragana microphylla L.), and perennial and annual herbs (e.g., BassiadasyphyllaL., Agriophyllum
100	squarrosum L) (Cao et al., 2011).

#### 101 *Experimental methods*

In mid-May 2015, sandy elm seeds were first collected from multiple, mature individuals and then mixed altogether. After careful selection, uniform and intact seeds were chosen and sowed in plastic pots (45cm diameter, 30cm height). Sandy soil was taken from nearby woodlands, and it was sieved to remove debris and branches. All seeds were covered by sand to a depth of 0.5-1.0cm. In a parallel study, we found that that depth was the most suitable for having the greatest percentage and speed of seedling emergence for sandy elm(Tang et al., 2016). Holes at the bottom of the pots were covered with nylon mesh to prevent soil loss, while allowing drainage of water at the same time. All pots were watered every three days to keep the soil moist. Twenty days after sowing, 8 to 12 seedlings emerged; similar seedlings were left in each pot, and the rest was





109	removed. Mean seedling height (5.4±0.5 cm) was obtained after measuring the height of each seedling in every pot.
110	Afterwards, seedlings were experimentally buried to either 0(T0, no burial, control treatment) or 33% (T33; 1.8cm), 67%
111	(T67; 3.6cm), 100% (T100; 5.4cm) or 133% (T133; 7.2cm) soil depth of the original mean seedling height. With this
112	purpose, sandy soil was added to the pots according to the different burial depths. Each seedling was kept vertical while
113	buried. Six replicates were used per treatment, so there were a total of 30 pots in this experiment. Meanwhile, 15 randomly
114	selected seedlings were harvested to determine the original measurements for growth analysis before sand burial.
115	Surviving seedlings were counted after treatment started of 45 days. They were considered alive in case that fresh phloem
116	occurred in both stem and roots, and green tissue in leaf blades. Immediately after burial, seedling height was measured from
117	the new soil surface level to the seedling apex. Stem diameter was measured close to the burial surface using a vernier
118	caliper. Meantime, 15 randomly selected seedlings were dug out in each treatment; roots were picked up as intact as possible
119	from the sandy soil. Taproot lengths were measured, and total leaf area was obtained using a Portable Area Meter
120	(Li-Cor3000A, Lincoln, Nebraska, USA). Finally, plant organs (leaves, stems and roots) were dried at 80°C and weighed
121	after reaching a constant mass for each seedling in the laboratory.

# 122 Calculations

- 123 The (1) relative height growth rate (RHGR, mm.cm<sup>-1</sup>d<sup>-1</sup>), and (2) relative growth rate of seedlings (RGR, mg.mg<sup>-1</sup>.d<sup>-1</sup>) were 124 calculated according to the following equations (Walck et al., 1999; Zhao et al., 2007):
- 125 RHGR= $\frac{H_2-H_1}{H_1(T_2-T_1)}$  (1);
- 126  $RGR = \frac{\ln M_2 \ln M_1}{T_2 T_1}$  (2);



## 127 where $H_2$ and $H_1$ were seedling heights at the end and initiation (i.e., immediately before sand burial) of the experiment,

- 128 respectively; M<sub>2</sub> or M<sub>1</sub> were the total dry biomass of seedlings either after 45 days from study initiation or just before sand
- burial, respectively; ln was the natural logarithm, and  $T_2$ - $T_1$  was time from sand burial (i.e., 45 days).

#### 130 Statistical analysis

(i) (i)

- 131 All data were tested for normality and homogeneity of variance prior to analysis. Data were log-transformed if necessary
- 132 (Sokal and Rohlf 1995). The effects of experimental sand burial on seedling height, RHGR, plant stem diameter, total leaf
- 133 area, RGR, dry biomass and percentage biomass allocation were evaluated by one-way ANOVA. Whenever F tests were
- significant, Tukey's test was used to compare treatment means at P<0.05. All statistical analysis used SPSS 21.0 (SPSS Inc.,
- 135 Chicago, USA), and drawing was made using Origin Pro 9.0 (Origin Lab Corp, USA).
- 136

#### 137 **Results**

#### 138 Effects of continual sand burial on seedling survival

- 139 The effect of sand burial depth on seedling survival was significant ( $F_{4,235}$ =38.339, P=0.000). During the whole study,
- seedling survival was 100% on the unburied (T0) and partial burial treatments (T33, T67). Simultaneously, seedling survival
- 141 (84.48±8%) was significantly lower in the completely sand burial treatment (T100). No seedling survived after burial depth
- exceeded the mean original height of seedlings (i.e., on T133).
- 143 Changes of morphological seedling traits in response to sand burial
- 144 Seedling height and height growth rate

(i) (c)



# 145 Seedling height was significantly affected by sand burial depths after 45 days of burial ( $F_{3,56}$ =139.978, P=0.000). The highest

#### seedling height of 22.35cm was observed in the T33 treatment, which was significantly greater than that in the T67 treatment

- 147 (Figure 1A; P<0.05). Height of seedlings in the control treatment of 16.28cm was significantly lower than that in the T33 and
- 148 T67 treatments, but higher than in the T100 treatment of 10.66cm (Figure 1A; P<0.05).
- 149 The relative seedling height growth rate (RHGR) was significantly affected ( $F_{3,56}$ = 286.877; P=0.000) by sand burial of 45
- days(Figure 1B). Highest of 0.0574 mm.cm<sup>-1</sup>d<sup>-1</sup> and lowest of 0.0232 mm.cm<sup>-1</sup>d<sup>-1</sup> in relative growth rates for seedling height

151 were shown in the T33 and T100 treatments, respectively (Figure 1C). The pattern of change with burial depth was similar to

- that described for seedling height (Figure 1A); values were greater in the control than 100% covered by sand (Figure 1B;
- 153 P<0.05). Seedling stem diameter, taproot length and total leaf area

154 After 45 days from initial study, stem diameter ( $F_{3.56}$ =26.669, P=0.000), taproot length ( $F_{3.56}$ =30.942, P<0.001) and total leaf 155 area (F<sub>3.56</sub>=35.961, P<0.001) of seedlings were also affected by sand burial (Figure 3 A, B, C). Stem diameter was 20% 156 greater (P<0.05) in the T33 than in the T0 treatment of 1.793mm (Figure 3A). However, diameters of stems were similar in 157 the control and T67 treatments (Figure 3A). The values in the T100 treatment, nevertheless, were 13.4% lower than unburied 158 control of 1.493mm (Figure 3A). While taproot length was lowest in the control treatment of 19.39cm, it was highest in the 159 T67 treatment (Figure 3B; 35.7% higher than in the control; P<0.05). The total leaf area of seedlings was significantly greater in the control of 23.87cm<sup>2</sup> than in the T67 and T100 treatments (Figure 3C; P<0.05). The lowest total leaf area, 160 however, was found in the T100 treatment of 16.89cm<sup>2</sup> (Figure 3C). 161

# 162 Effects of sand burial on biomass growth and relative growth rate



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#### 163 Dry biomass and percentage allocation

164	There were significant differences in the total seedling biomass ( $F_{3,56}$ =129.949, P=0.000) and its component organs after the
165	experiment: leaves ( $F_{3,56}$ =93.965, P=0.000) and roots ( $F_{3,56}$ =50.474, P=0.002). The only exception was for seedling stem
166	biomass ( $F_{3,56}$ =2.017, P=0.122) which was similar in all sand burial treatments (Figure 4A). And seedling organs also
167	showed a similar pattern in their dry biomass. Greatest total biomasses were reached in the T33 and T67 treatments of
168	369.65mg and 372.50mg, respectively (Figure 4A). While total biomass of seedlings was significantly lower in T100
169	treatment of 272.67mg than in those treatments (Figure 4 A). Patterns shown for the biomasses of leaves and roots among
170	treatments were similar to those shown for the total biomass of seedlings (Figure 4A).
171	Significant differences were found in allocation of seedling biomass to leaves ( $F_{3,56}$ =12.841, P=<0.001), stems ( $F_{3,56}$ =27.579,
172	P=0.000) and roots ( $F_{3,56}$ =7.594, P=<0.001). On leaves, percentage biomass allocation of 52.9% and 54.2% was greatest in
173	the T33 and T67 treatments, and lowest in the control and T100 treatments (Figure 3B). Percentage biomass allocation to
174	stems was greatest in the T100 treatment of 24.1% and the value of stems was greater in the control of 20.9% than in the T33
175	and T67 treatments (Figure 4B). Finally, percentage biomass allocation to roots was similar in the control, T33 and T67
176	treatments (Figure 4B); values determined in the T100 treatment for this organ were significantly lower than in the control
177	and T33 treatments (Figure 4B).

# 178 Seeding relative growth rate

The relative growth rate of seedlings was significantly affected by sand burial after experiment (F<sub>3,56</sub>=136.370, P=0.000).
Greatest relative growth rate values of 0.031mg.mg<sup>-1</sup>day<sup>-1</sup> were shown in the T33 and T67 treatments (Figure 5). These





- values were significantly greater than those found in the control (Figure 5). Lowest relative rate of growth was determined
- 182 on seedlings grown in the T100 treatment, just  $0.026 \text{ mg mg}^{-1}$  (Figure 5).
- 183
- 184 Discussion
- 185 Seedling survivorship in response to continual sand burial

186 In Sand land regions, seedlings might be buried to different depths after emergence by the end of the windy season from late 187 spring to early summer(Chen and Maun, 1999). After 45-day-experiment, survivorship remained unchanged when seedlings 188 were either unburied or exposed to partial [i.e., 1.8 (T33) and 3.6 (T67) cm soil depth] sand burial. These results agreed with studies by He et al. (2008), Liu et al. (2008) and Qu et al. (2012), which reported that vigor of Artemisia halodendron, 189 190 Corispermum macrocarpum and Caragana microphylla was either maintained or increased by moderate sand burial in 191 Horqin Sandy Land. Survivorship of these shrubs, however, varied among plant species once their seedlings were covered by 192 sand either equal to or more than 100% of their height. Whilst the values decreased significantly by a mean of 15.6% given completely covered the whole, original seedling height [i.e., 5.4cm soil depth (T100)]. Maun (1981, 1997) and Disraeli 193 194 (1984) indicated that a certain tolerance of sand burial was an effective strategy for determining the survival and subsequent 195 establishment of seedlings in sandy environments. While sand burial exceeded 33% of the original seedling height [i.e., 196 7.2cm soil depth (T133)], there was no seedling survival, only withered and rotted in the soil. Harris and Davy (1987) and 197 Perumal and Maun (2006) believed that plant energy exhaustion and suppression of photosynthesis most likely severely 198 reduced seedling survival under extreme shade, sand burial environments. Most seedlings of the grass Distichlis spicata died





when completely covered by sand in North America (Brown, 1997; Li et al., 2015). While some *Artemisia.squarrosum*seedlings remained still alive even though sand burial depths reached 266% of initial seedling height in the Horqin Sandy
Land (Li et al. 2015). Compared with other species, seedlings of sandy elm showed a certain resistance to partial sand burial,
but complete sand burial significantly increased mortality.

203 Effects of sand burial on seedling morphological traits

Sand burial can alter the biological (e.g., the photosynthetic active radiation) and abiotic (e.g., soil temperature, moisture availability) environment of living plants which influence morphological structures and subsequent growth(Disraeli, 1984; Sun et al., 2014b).Our results demonstrated that various seedling morphological traits (i.e., height; stem diameter; taproot length; total leaf area; dry biomass; partitioning of biomass to shoots and roots; RHGR and RGR ) were greater at the intermediate(i.e., T33 and T67) than at the more extreme (i.e., T100 and T133) sand burial depths. Changes on these traits were determinant in allowing the obtained seedling developments in the different study burial environments.

In our experiment, seedling height of sandy elm was greater in the partial than in the unburied and completely burial treatments, which indicated that partial sand burial stimulated stem elongation. This acceleration could be explained by the fact that the processes of growth and elongation benefited water and nutrient uptake in arid and semi-arid regions (Li et al., 2015). This observation is also consistent with previous research reported by Disraeli (1984) that partial burial stimulated growth of *Ammophila Breviligulata* in coastal dunes of northeastern North America (Disraeli, 1984) and Belcher (1977) that seedling heights of *Rosa rugosa* were higher in the partial than in the unburied and partial continuous sand burial treatments

in desert.

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217	When seedlings re-emerged from the new experimental soil surface after the various sand burial treatments, it was
218	critical that the ability to compensate from the effects of sand burial. Seedling height growth rate was a critical parameter to
219	determine the speed of growth. The greater RHGR of seedlings in the partial (T33 and T67) than in the unburied and
220	completely burying treatments (T100) was an indication that partial burial did contribute to seedling height after a
221	45-day-growth period via accelerating the speed of growth in height. Nevertheless, the greatest seedling growth in height in
222	the T33 treatment came from its greatest RHGR than any other treatments. The same phenomena have been observed by Liu
223	et al. (2008) and Miao et al. (2012) who also found that shallow burial depths could promote the relative growth rates in
224	height of Salix gordejevii, Artemisia wudanica and A. halodendron. However, some species(e.g., A.gmelinii) have decreased
225	their growth rates as a result of sand burial (Liu et al., 2008). These findings confirmed that growth resistance to sand burial
226	might be species-specific.
227	Compared with the unburied treatment, partial burial treatments fostered increments in stem diameter and taproot length. Sun
228	et al. (2014a) also showed that seedling diameter and taproot length of Suaeda salsa were increased by a partial burial
229	treatment in the coastal marches of the Yellow River estuary, China. Caldwell et al. (1998) found that increases in taproot

obtained from deep depths by dicots species could be released at shallower soil depths if soil is drier than plant tissues at
those depths (Caldwell et al. 1998). If this happens, both water and nutrients can be parasitized by shallower-rooted species,
with subsequent implications in nutrient cycling (Cardon et al. 2013). Total leaf area, however, was either similar or lower in
the partial burial than in the unburied treatment. This was in agreement with the results obtained by Liu and Guo (2005) who

length were conducive to a greater nutrient and water uptake from deeper soil depths. Even more, water and nutrients

(i) (ii)



noted that increasing depth of sand burial decreased the total leaf area of *Caragana intermedia*.

236 An appropriate resource allocation is essential for plant establishment and growth (Bazzaz FA, 1997). Also, plants shift 237 resource allocation to minimize external changes (Maun, 1997; Ni et al., 2015). Numerous findings, especially those living 238 in sandy environments, reported that plants could withstand various depths of sand burial by changing biomass allocation. 239 Some species (e.g. Artemisia ordosia, Elymusfarctus) would transfer biomass from underground to leaf and stem organs 240 (Brown, 1997; Li et al., 2010), while others (e.g., Caraganamicrophylla, Nitrariasphaerocarpa) either maintained or 241 increased biomass allocation to roots(He et al., 2008; Sykes and Wilson, 1990). In our experiment, it was somewhat 242 surprising that no difference in the dry biomass of seedling stems was observed among all sand burial treatments even 243 though seedlings showed an increased stem diameter in the T33 sand burial treatment, that was probably due to 244 different-diameter, fresh stems of this species showed different water contents(Zhao et al., 2015). 245 Partial burial treatments determined a greater dry biomass for leaves, roots and the whole seedlings than values shown for 246 these traits in the unburied and completely sand burial treatments. These results were expected as previous studies showed 247 that 67% burial of seedlings of the shrub Caragana intermedia determined a greater biomass allocation to leaves and stems, 248 and a lower one to roots, compared with values in the unburied control(Xu et al., 2013). Meanwhile, there was a trend for an 249 increasing aboveground (leaf + stem), and a decreasing belowground allocation with increasing burial depth. Nearly 50% of 250 the total seedling biomass corresponded to leaves, which suggested that leaves were important for sandy elm, which 251 sufficient leaves could guarantee normal photosynthesis and maintain evapo-transpiration for sandy elm exposed to high 252 temperature environments in the growing season(Dulamsuren et al., 2009).





253	Relative growth rates measure the mean efficiency rate of producing new biomass (Walck et al., 1999). Dalling and Hubbell
254	(2002) found that seedling growth rate instead of biomass was the key to determine the successful seedling establishment. In
255	our experiment, relative growth rates were higher in the partial than in the other treatments, indicating that moderate sand
256	burial was beneficial for rapid growth after seedling sand burial. However, all sandy elm seedling mass relative growth rates
257	were small compared with those of other plant species (e.g., Artemisia wudanica, Solidagoshortii and Solidago. altissima) in
258	the same area. This suggests that sandy elm biomass accumulation was slow during the first growing season (Brown, 1997;
259	Liu et al., 2014).
260	Biomass accumulation and allocation, and the plasticity of various morphological traits, were critical in determining the
261	response, and survivorship and development of sandy elm seedlings in sandy environments. However, this burial study was
262	conducted in a common garden. Under natural, rangeland conditions, some factors (e.g. abrasion of plant tissues by sand
263	grains; gnaw by herbivores and granivores) might reduce or eliminate some of the positive effects of the partial burial
264	treatments (Baker et al., 2009; Dulamsuren et al., 2009). Therefore, more comprehensive studies on physiological and
265	biochemical mechanisms which are involved in sandy elm seedling survivorship and performance under sand burial
266	conditions are necessary in future research.

# 267 Conclusion

Sand burial affected seedling survivorship, morphological traits, and biomass production and allocation of *Ulmus pumila var*.
 *sabulosa*. Seedlings of sandy elm showed a certain resistance to sand burial. Partial sand burial treatment did not influence
 seedling survivorship, but complete sand burial significantly increased mortality. Compared with the unburied treatment,





271	seedling height, absolute and relative height growth rates, taproot length, total biomass and relative growth rates were
272	stimulated because of partial sand burial. At the same time, percentage biomass allocation of seedlings was changed; these
273	shifted more biomass to aboveground organs to sustain photosynthesis and evapo-transpiration in response to the sand burial
274	depth. Complete sand burial after seedling emergence, however, could inhibit their growth, and even result in seedling death;
275	this is why this burial depth should be controlled by making enclosures and increasing vegetation coverage. The observed
276	variation in all parameters indicated that Ulmus pumila var. sabulosa could tolerate partial sand burial, and that it could
277	acclimate to sandy environments.
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279 280 281 282 283	Acknowledgements This study was supported by National Natural Science Foundation of China (31370706) and the U'lanaodu Desertification Experimental Station of the Institute of Applied Ecology, Chinese Academy of Sciences. We thank Yongming Luo ,Xuehua Li, Quanlai Zhou, Hongmei Wang, Meiyu Jia, Ya Liu and Xu Han for assistance during the experiment. Thanks Authony Davy from University of East Anglia for guiding of statistical analysis in the experiment.
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285 286	References
287 288 289	Baker, J. T., McMichael, B., Burke, J. J., Gitz, D. C., Lascano, R. J., and Ephrath, J. E.: Sand Abrasion Injury and Biomass Partitioning in Cotton Seedlings, Agronomy Journal, 101, 1297-1303, 2009. Bazzaz FA, G. J.: Plant resource allocation Academic Press, San Diego, 1997.
290	Belcher, C. R.: Effect of sand cover on the survival and vigor of Rosa rugosa Thunb, Int J Biometeorol, 21, 276-280, 1977.
291 292	Bellamy, P. H., Loveland, P. J., Bradley, R. I., Lark, R. M., and Kirk, G. J. D.: Carbon losses from all soils across England and Wales 1978-2003, Nature, 437, 245-248, 2005.
293	Berendse, F., van Ruijven, J., Jongejans, E., and Keesstra, S.: Loss of Plant Species Diversity Reduces Soil Erosion Resistance,
294	Ecosystems, 18, 881-888, 2015.
295	Brevik, E. C., Cerdà, A., Mataix-Solera, J., Pereg, L., Quinton, J. N., Six, J., and Van Oost, K.: The interdisciplinary nature of
296	SOIL, SOIL, 1, 117-129, 2015.
297	Brown, J. F.: Effects of Experimental Burial on Survival, Growth, and Resource Allocation of Three Species of Dune Plants,
298	Journal of Ecology, 85, 151-158, 1997.





- 299 Cao, C., Jiang, D., Teng, X., Jiang, Y., Liang, W., and Cui, Z.: Soil chemical and microbiological properties along a
- chronosequence of Caragana microphylla Lam. plantations in the Horqin sandy land of Northeast China, Applied Soil
   Ecology, 40, 78-85, 2008.
- 302 Cao, C., Jiang, S., Ying, Z., Zhang, F., and Han, X.: Spatial variability of soil nutrients and microbiological properties after the
- 303 establishment of leguminous shrub Caragana microphylla Lam. plantation on sand dune in the Horqin Sandy Land of
- 304 Northeast China, Ecological Engineering, 37, 1467-1475, 2011.
- Cerda, A.: The influence of aspect and vegetation on seasonal changes in erosion under rainfall simulation on a clay soil in
   Spain, Canadian Journal of Soil Science, 78, 321-330, 1998.
- Chen, H. and Maun, M. A.: Effects of sand burial depth on seed germination and seedling emergence of Cirsium pitcheri,
   Plant Ecology, 140, 53-60, 1999.
- 309 Cheplick, G. P. and Grandstaff, K.: Effects of sand burial on purple sandgrass (Triplasis purpurea): the significance of seed
- 310 heteromorphism, Plant Ecology, 133, 79-89, 1997.
- Disraeli, D. J.: The Effect of Sand Deposits on the Growth and Morphology of Ammophila Breviligulata, Journal of Ecology,
  72, 145-154, 1984.
- 313 Dulamsuren, C., Hauck, M., Nyambayar, S., Bader, M., Osokhjargal, D., Oyungerel, S., and Leuschner, C.: Performance of
- Siberian elm (Ulmus pumila) on steppe slopes of the northern Mongolian mountain taiga: Drought stress and herbivory in
   mature trees, Environmental and Experimental Botany, 66, 18-24, 2009.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K.,
- Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., and
- 318 Snyder, P. K.: Global Consequences of Land Use, Science, 309, 570-574, 2005.
- Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K.,
- 320 West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockstrom, J., Sheehan, J., Siebert, S.,
- Tilman, D., and Zaks, D. P. M.: Solutions for a cultivated planet, Nature, 478, 337-342, 2011.
- 322 Gabarron-Galeote, M. A., Martinez-Murillo, J. F., Quesada, M. A., and Ruiz-Sinoga, J. D.: Seasonal changes in the soil
- 323 hydrological and erosive response depending on aspect, vegetation type and soil water repellency in different
- 324 Mediterranean microenvironments, Solid Earth, 4, 497-509, 2013.
- Harris, D. and Davy, A. J.: Seedling Growth in Elymus farctus after Episodes of Burial with Sand, Annals of botany, 60,
  587-593, 1987.
- He, Y., Halin, Z., Xueyong, Z., and Xinping, L. I. U.: Effects of different sand burial depths on growth and biomass allocation in Caragana microphylla seedlings, Arid Land Geography, 31, 701-706, 2008.
- Jiang, D., Liu, Z., Cao, C., Kou, Z., and Wang, R.: Desertification and Ecological Restoration of Keerqin Sandy Land, China
   Environmental Science Press, Beijing, 2003.
- Jiang, D., Tang, Y., and Busso, C. A.: Effects of vegetation cover on recruitment of Ulmus pumila L. in Horqin Sandy Land,
- northeastern China, Journal of Arid Land, 6, 343-351, 2013.
- Li, J., Qu, H., Zhao, H., Zhou, R., Yun, J., and Pan, C.: Growth and physiological responses of Agriophyllum squarrosum to
- sand burial stress, Journal of Arid Land, 7, 94-100, 2015.
- Li, S.-L., Werger, M. A., Zuidema, P., Yu, F.-H., and Dong, M.: Seedlings of the semi-shrub Artemisia ordosica are resistant to





- moderate wind denudation and sand burial in Mu Us sandland, China, Trees, 24, 515-521, 2010.
- 337 Li, X., Jiang, D., Zhou, Q., and Oshida, T.: Soil seed bank characteristics beneath an age sequence of Caragana microphylla
- shrubs in the Horqin Sandy Land region of northeastern China, Land Degradation & Development, 25, 236-243, 2014.
- Liu, B., Liu, Z., and Guan, D.: Seedling growth variation in response to sand burial in four Artemisia species from different
- habitats in the semi-arid dune field, Trees, 22, 41-47, 2008.
- Liu, B., Liu, Z., Lü, X., Maestre, F. T., and Wang, L.: Sand burial compensates for the negative effects of erosion on the
- dune-building shrub Artemisia wudanica, Plant and Soil, 374, 263-273, 2014.
- Liu, H. and Guo, K.: The impacts of sand burial on seedling development of Caragana intermedia, Acta Ecologica Sinica, 25,
  2550-2555, 2005.
- Liu, Z., Zhu, J., and Deng, X.: Arrival vs. retention of seeds in bare patches in the semi-arid desertified grassland of Inner
   Mongolia, northeastern China, Ecological Engineering, 49, 153-159, 2012.
- 347 Ma, C. G.: A Provenance Test of White Elm (Ulmus-Pumila L) in China, Silvae Genet, 38, 37-44, 1989.
- 348 Maun, M. A.: Adaptations enhancing survival and establishment of seedlings on coastal dune systems, Vegetatio, 111, 59-70,
- 349 1994.
- Maun, M. A.: Adaptations of plants to burial in coastal sand dunes, Canadian Journal of Botany-Revue Canadienne De
   Botanique, 76, 713-738, 1997.
- Maun, M. A. and Lapierre, J.: Effects of Burial by Sand on Seed Germination and Seedling Emergence of Four Dune Species,
   American Journal of Botany, 73, 450-455, 1986.
- 354 Miao, R., Jiang, D., Musa, A., Zhou, Q., Guo, M., and Wang, Y.: Effectiveness of shrub planting and grazing exclusion on
- degraded sandy grassland restoration in Horqin sandy land in Inner Mongolia, Ecological Engineering, 74, 164-173, 2014.
- Ni, J., Luo, D. H., Xia, J., Zhang, Z. H., and Hu, G.: Vegetation in karst terrain of southwestern China allocates more biomass
   to roots, Solid Earth, 6, 799-810, 2015.
- Niu, C. Y., Musa, A., and Liu, Y.: Analysis of soil moisture condition under different land uses in the arid region of Horqin
   sandy land, northern China, Solid Earth, 6, 1157-1167, 2015.
- Perumal, V. J. and Maun, M. A.: Ecophysiological response of dune species to experimental burial under field and controlled
   conditions, Plant Ecology, 184, 89-104, 2006.
- 362 Qian, J., Liu, Z., Hatier, J.-H. B., and Liu, B.: The Vertical Distribution of Soil Seed Bank and Its Restoration Implication in an
- Active Sand Dune of Northeastern Inner Mongolia, China, Land Degradation & Development, 27, 305-315, 2016.
- 364 Qiu, S.: Study on the formation and evolution of Horqin Sandy Land, Scientia Geographica Sinica, 9, 317-328, 1989.
- Qu, H., Zhao, H., Zhou, R., Zuo, X., Luo, Y., Wang, J., and J, O. B.: Effects of sand burial on the survival and physiology of three
   psammophytes of Northern China, African Journal of Biotechnology, 11, 4518-4529, 2012.
- 367 Schlütz, F., Dulamsuren, C., Wieckowska, M., Mühlenberg, M., and Hauck, M.: Late Holocene vegetation history suggests
- natural origin of steppes in the northern Mongolian mountain taiga, Palaeogeography, Palaeoclimatology, Palaeoecology,
   261, 203-217, 2008.
- 370 Shi, L., Zhang, Z. J., Zhang, C. Y., and Zhang, J. Z.: Effects of sand burial on survival, growth, gas exchange and biomass
- allocation of Ulmus pumila seedlings in the Hunshandak Sandland, China, Annals of botany, 94, 553-560, 2004.
- 372 Smith, P., Cotrufo, M. F., Rumpel, C., Paustian, K., Kuikman, P. J., Elliott, J. A., McDowell, R., Griffiths, R. I., Asakawa, S.,





- Bustamante, M., House, J. I., Sobocká, J., Harper, R., Pan, G., West, P. C., Gerber, J. S., Clark, J. M., Adhya, T., Scholes, R. J.,
  and Scholes, M. C.: Biogeochemical cycles and biodiversity as key drivers of ecosystem services provided by soils, SOIL, 1,
  665-685, 2015.
- 376 Sun, Z., Mou, X., Lin, G., Wang, L., Song, H., and Jiang, H.: Effects of sediment burial disturbance on seedling survival and
- growth of Suaeda salsa in the tidal wetland of the Yellow River estuary, Plant and Soil, 337, 457-468, 2010.
- Sun, Z., Song, H., Sun, J., and Sun, W.: Effects of continual burial by sediment on seedling emergence and morphology of
- Suaeda salsa in the coastal marsh of the Yellow River estuary, China, Journal of Environmental Management, 135, 27-35,
  2014a.
- 381 Sun, Z., Song, H., Sun, W., and Sun, J.: Effects of continual burial by sediment on morphological traits and dry mass
- allocation of Suaeda salsa seedlings in the Yellow River estuary: An experimental study, Ecological Engineering, 68, 176-183,
   2014b.
- Sykes, M. T. and Wilson, J. B.: An experimental investigation into the response of New Zealand sand dune species to
   different depths of burial by sand, Acta Botanica Neerlandica, 39, 171-181, 1990.
- Tang, J., Busso, C., Jiang, D., Wang, Y., Wu, D., Musa, A., Miao, R., and Miao, C.: Seed Burial Depth and Soil Water Content
- 387 Affect Seedling Emergence and Growth of Ulmus pumila var. sabulosa in the Horqin Sandy Land, Sustainability, 8, 68, 2016.
- 388Tang, J., Jiang, D., and Wang, Y.: A review on the process of seed-seedling regeneration of Ulmus pumila in sparse forest
- 389 grassland, Chinese Journal of Ecology, 33, 1114-1120, 2014.
- Tang, Y., Jiang, D.-M., and Lü, X.-T.: Effects of Exclosure Management on Elm (Ulmus Pumila) Recruitment in Horqin Sandy
   Land, Northeastern China, Arid Land Research and Management, 28, 109-117, 2013.
- 392 Verheijen, F. G. A., Jones, R. J. A., Rickson, R. J., and Smith, C. J.: Tolerable versus actual soil erosion rates in Europe,
- 393 Earth-Science Reviews, 94, 23-38, 2009.
- Walck, J. L., Baskin, J. M., and Baskin, C. C.: Relative competitive abilities and growth characteristics of a narrowly endemic
   and a geographically widespread Solidago species (Asteraceae), American Journal of Botany, 86, 820-828, 1999.
- Wang, J., Zhou, R., Zhao, H., Zhao, Y., and Hou, Y.: Growth and physiological adaptation of Messerschmidia sibirica to sand
   burial on coastal sandy, Acta Ecologica Sinica, 32, 4291-4299, 2012.
- Wang, K., Deng, L., Ren, Z., Li, J., and Shangguan, Z.: Grazing exclusion significantly improves grassland ecosystem C and N
   pools in a desert steppe of Northwest China, Catena, 137, 441-448, 2016.
- Xu, L., Huber, H., During, H. J., Dong, M., and Anten, N. P. R.: Intraspecific variation of a desert shrub species in phenotypic
   plasticity in response to sand burial, New Phytologist, 199, 991-1000, 2013.
- Yan, Q. L., Liu, Z. M., Zhu, J. J., Luo, Y. M., Wang, H. M., and Jiang, D. M.: Structure, pattern and mechanisms of formation of
  seed banks in sand dune systems in northeastern Inner Mongolia, China, Plant and Soil, 277, 175-184, 2005.
- Yang, H., Zhiping, C AO., Ming, D., Yongzhong, Y. E., and Zhenying, H.: Effects of sand burying on caryopsis germination and
   seedling growth of Bromus inermis Leyss, The Journal of Applied Ecology, 18, 2438-2443, 2007.
- 406 Yang, L., Zhou, G., Wang, G., and Wang, Y.: Effect of human activities on soil environment and plant species diversity of elm
- 407 sparse woods, The Journal of Applied Ecology, 14, 321-325, 2003.
- 408 Zhang, T.-H., Zhao, H.-L., Li, S.-G., Li, F.-R., Shirato, Y., Ohkuro, T., and Taniyama, I.: A comparison of different measures for
- stabilizing moving sand dunes in the Horqin Sandy Land of Inner Mongolia, China, Journal of Arid Environments, 58,





- 410 203-214, 2004.
- 211 Zhao, H., Li, J., Zhou, R., Qu, H., Yun, J., and Pan, C.: Effects of Sand Burial on Growth Properties of Pinus sylvestnis
- 412 var.mongolica, Journal of Desert Research, 35, 60-65, 2015.
- 213 Zhao, T., Ou, Y., Jia, L., and Zheng, H.: Ecosystem services and their valuation of China grassland, Acta Ecologica Sinica, 24,
- 414 1101-1110, 2004.
- Zhao, W. Z., Li, Q. Y., and Fang, H. Y.: Effects of sand burial disturbance on seedling growth of Nitraria sphaerocarpa, Plant
  and Soil, 295, 95-102, 2007.
- 417 Zhou, Z., Sun, O. J., Huang, J., Gao, Y., and Han, X.: Land use affects the relationship between species diversity and
- 418 productivity at the local scale in a semi-arid steppe ecosystem, Functional Ecology, 20, 753-762, 2006.





### 447 Figure legends

- Fig. 1 Dynamics in precipitation and temperature (T) from 1980 to 2014 in U'lanaodu. The solid line shows the average annual precipitation and the dashed line the average precipitation from June to September, during that period. The insert shows the average monthly precipitation (mm) and temperature (°C) during 1980 to 2014.
- 451
- 452 Fig.2 Seedling height and relative growth rate for height (RHGR) of Ulmus pumila var.sabulosa exposed to various sand
- 453 burial treatments during a 45-day- growth period. These treatments included sand burial of seedlings to a depth equivalent to
- 454 33 (T33), 67 (T67) or 100% (T100) of the mean seedling height at the initiation of the study (see the Material and Methods
- 455 Section for further details). Each histogram is the mean  $\pm 1$  S.E. of n=15.
- 456
- 457 Fig.3. Stem diameter, taproot length and total leaf area on seedlings of *Ulmus pumila var.sabulosa* exposed to various sand
  458 burial treatments during a 45-day-growth period. These treatments included sand burial of seedlings to a depth equivalent to
  459 33 (T33), 67 (T67) or 100% (T100) of the mean seedling height at the initiation of the study. Each histogram is the mean ± 1
- 460 S.E. of n=15.
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**Fig.4** Seedling dry biomass and percentage biomass allocation to leaves, stems and roots on seedlings of *Ulmus pumila var.sabulosa* exposed to various sand burial treatments during a 45-day-growth period. These treatments included sand burial of seedlings to a depth equivalent to 33 (T33), 67 (T67) or 100% (T100) of the mean seedling height at the initiation of the study. Each histogram is the mean  $\pm 1$  S.E. of n=15.



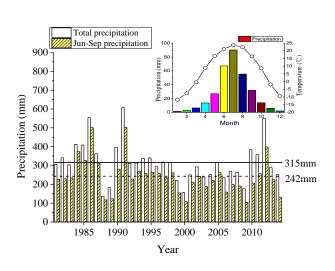


467	Fig.5 Relative growth rates on seedlings of Ulmus pumila var.sabulosa exposed to various sand burial treatments during a
468	45-day-growth period. These treatments included sand burial of seedlings to a depth equivalent to 33 (T33), 67 (T67) or 100%
469	(T100) of the mean seedling height at the initiation of the study. Each histogram is the mean $\pm 1$ S.E. of n=15.
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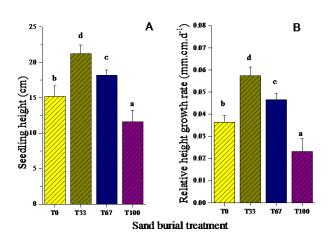


Figure2

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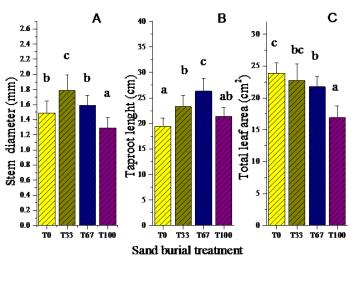


Figure3

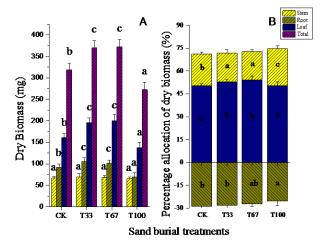
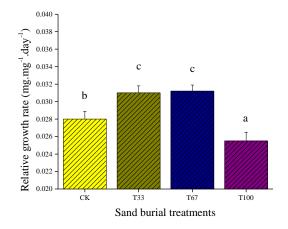


Figure4

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