
This is the **accepted version** of the journal article:

Tariq, Akash; Tariq, Akash; Sardans i Galobart, Jordi; [et al.]. «Alhagi sparsifolia : an ideal phreatophyte for combating desertification and land degradation». Science of The Total Environment, Vol. 844 (October 2022), art. 157228. DOI 10.1016/j.scitotenv.2022.157228

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1 ***Alhagi sparsifolia*: an ideal phreatophyte for combating desertification and land degradation**

2
3 **Akash Tariq, Abd Ullah, Jordi Sardans, Fanjiang Zen, Corina Graciano, Xiangyi Li, Weiqi Wang,**
4 **Zeeshan Ahmed, Sikandar Ali, Zhihao Zhang, Yanju Gao, Josep Peñuelas**

5
6 **Abstract**

7 The upcoming launch of the post-2020 biodiversity framework entails elucidating the future priorities and strategies
8 for conserving biodiversity on a regional and global scale. Desertification has caused significant environmental and
9 socio-economic problems in many arid and semiarid areas of the world. Phreatophytes increase nutrient levels and
10 water reserves in the ground below them and are essential resources for other plants and animals. Factors that can
11 enhance or reduce the island effect of phreatophytes are worthy of research since they can contribute to the survival
12 and growth of this group of plants. Furthermore, these plants substantially impact the whole environment and boast
13 necessary evolutionary adaptations for sustaining islands of life in the arid landscape to prevent complete
14 desertification. *Alhagi sparsifolia* is a semi-shrub legume and a typical desert phreatophyte. The main objective of
15 this review is to disseminate research-based knowledge and improve awareness of this important plant species and
16 provide a framework that could effectively improve regional socio-ecological environments, particularly in
17 controlling desertification, thereby enhancing human welfare. First, we synthesized knowledge of the physiological
18 acclimation of this species, above all in terms of water and nutrient use, the impact of salinity, and its response to
19 different light environments and temperatures. Then, we analyzed the socio-ecological services
20 that *A. sparsifolia* offers, highlighted the anthropogenic threats to its habitats, and strategies for its sustainable
21 utilization and management. We conclude that more knowledge of how *A. sparsifolia* interacts with groundwater
22 will contribute significantly to elucidating the possible effects of climate change and human activities on the
23 sustainable use of groundwater. Protected areas must be set up, and key knowledge shared to combat desertification
24 and improve people's welfare as a means of guaranteeing sustainable development. An integrative socio-ecological
25 approach must be adapted to improve understanding of this valuable phreatophyte's importance and sustainable use
26 and fulfill Sustainable Development Goals (SDGs).

27 **Key words:** *Alhagi sparsifolia*, desertification, abiotic stresses, environmental adaptation, Conservation
28
29

30 **1. Introduction**

31 Drylands have enormous scientific and socio-economic values. Drylands, of which almost 15% are salt-affected
32 (Acosta-Motos et al., 2017), cover 41% of the Earth's surface and are inhabited by 38% of the world's population
33 (Maestre et al., 2012). Specifically, arid and semiarid (herein, arid lands) landscapes occupy 25.8% of the Earth's
34 land surface and are home to 18.5% of its population. Arid regions contain unique biological and cultural diversity
35 and have been sustaining the livelihoods of dependent communities for generations. However, the global awareness
36 of the great value and the efforts required to protect and manage arid regions remained frustratingly low (Yao et al.,
37 2020; Spinoni et al., 2021). Extensive agriculture, unsustainable use, improper management, biodiversity loss, and
38 global climate change are causing irrecoverable damage to arid lands (Sala et al., 2000; Feng and Fu, 2017). Such
39 damages could have far-reaching consequences on valuable plant species having a variety of socio-economic and
40 ecological values (reduction of soil erosion, desertification, land degradation, and reclamation of saline soils),
41 ground-water resources conservation and use-efficiency, ecosystem productivity, and ultimately the communities'
42 dependant on these systems. Therefore, understanding the importance of arid lands, threats to their productivity, and
43 their sustainable management is essential to fulfilling global biodiversity conservation targets since the ecosystems
44 they harbor are particularly vulnerable to climate change and unsustainable anthropogenic activities (Lian et al.,
45 2021).

46
47 Desertification has caused major environmental and socio-economic problems in many arid and semiarid
48 areas of the world (Ibáñez et al., 2007). It can provoke soil and nutrient degradation and severely reduce potential
49 land productivity leading to the degradation of ecosystem functioning and services. In the final analysis, the
50 economic development of these regions thus is also under threat. Phreatophytes grow in semiarid and arid regions
51 and satisfy their water and nutrient requirements by using extensive root systems to access groundwater (Gao et al.,
52 2022) and playing important ecological functions. For example, *Prosopis juliflora* is a widespread hyper-
53 accumulating phreatophytic perennial tree/shrub, and a representative species of Sonaran Desert. *P. juliflora* is very
54 important and effective in controlling erosion and desertification, reclamation of salinized soils, and dune
55 stabilization (Choge et al., 2022), and hence demand a call of thorough studies on its management practices. Its pods
56 and leaves are used as animal fodder, its wood as fuel, railroad sleeper and charcoal, and its fruit is used as a food in
57 the form of beverages, syrup, and flour (Shackleton et al., 2014). Similarly, *Ziziphus lotus* is a dominant deep-rooted
58 facultative or partial phreatophytic shrub of arid and semi-arid Mediterranean habitats. Its anisohydric stomatal

59 regulation enables it to obtain water from lower soil horizons and from groundwater table (Torres-Garcia et al.,
60 2021). It is considered as an ecosystem engineer that plays a crucial role in improving semi-arid ecosystem
61 productivity by mitigating desertification under global climate change, but despite its importance the habitat of *Z.*
62 *lotus* is severely fragmented, and the conservation status is poor (Constantinou et al., 2021). Another example,
63 *Tamarix ramosissima* is a drought-tolerant typical phreatophyte and is widely distributed native species in Asia
64 (Gries et al. 2005). As a halophyte with high resistance to drought, wind erosion, and sand burial, *T. ramosissima*
65 has been widely used in desertification control in China (Zhang and Zhang 2012). In addition, *Karelinia caspia* is an
66 ecologically important deep-rooted phreatophyte occurring across the desert ecosystems of Russia, Central Asia, and
67 northwest China (Xu et al., 2018). It exhibits both drought and salt tolerance, which allows it to play a role in
68 reducing wind erosion and desertification (Vonlanthen et al., 2011; Tariq et al., 2022). Similarly, many other
69 phreatophytes in arid and semi-arid regions play an important role in reducing soil erosion, controlling
70 desertification and land degradation, and also sustaining livelihood, but very fewer efforts have been paid to the
71 threats they are facing and their management and conservation issues.

72

73 The present review aims to present and gather the utmost information on one of the best representative
74 phreatophytes *Alhagi sparsifolia* (camelthorns), which belongs to Fabaceae and serve as an ecological engineer in
75 mitigating desertification in Central and Eastern Asia (GBIF, 2021). In China, it is mainly found in the Xinjiang
76 Autonomous Region, Inner Mongolia, Gansu, and Qinghai provinces (Flora of China Editorial Committee, 1998)
77 (Fig. 1). It is a semi-shrub legume and typical desert phreatophyte, about 25–40-cm tall, and with a deep root system
78 (20m long) (Thomas et al., 2008) (Fig. 2). As a model, it can help decipher the mechanisms plants in arid
79 environments use to adapt to drought, temperature, and salinity. For example, the Taklamakan desert in Xinjiang
80 province is one of the most arid regions globally, where the annual precipitation is less than 50mm. The survival and
81 establishment of *A. sparsifolia* in such a harsh environment result from evolutionary adaptations (Gong et al., 2012;
82 Schenk, 2005). Water availability is a key factor driving growth and establishment of *A. sparsifolia* in arid
83 environments. In deserts where water occurs in form of short pulses in limited amount, *A. sparsifolia* rely on access
84 to water in deep soil layers. *A. sparsifolia* can be established through vegetative reproduction via root suckers and
85 seedlings recruitment via seeds, however; regardless of propagation method its root must grow faster to reach the
86 groundwater to guarantee successful establishment due to low soil water content in the upper layers of desert soils

87 (Vonlanthen et al., 2010; Zhang et al., 2012; Padilla et al., 2007). Successful establishment of *A. sparsifolia* is a rare
88 event, which is reflected in low seedling densities and low survival rates (Vonlanthen et al., 2011; Vonlanthen et al.,
89 2010). Gui et al. (2013) stated that different irrigation treatments affected *A. sparsifolia* seedling growth. However,
90 compared to the aboveground growth traits, there were generally more pronounced variations in root growth and
91 morphology traits, including relative growth rate (RGR), root biomass allocation and R:S. Thus, *A. sparsifolia*
92 adjusted its root structure to adapt to the variations in soil water content (SWC), however, root growth suffered
93 seriously at low SWC levels as compared to the irrigation treatments. Therefore, water availability is one of main
94 driving factors of *A. sparsifolia* establishment and management in arid environments. Better water supply is crucial
95 to guarantee successive seed germination, seedlings development and survival until the root system reaches the
96 groundwater table. An irrigation of $>0.1 \text{ m}^3/\text{m}^2$ should be provided during the first year (Gui et al., 2013). Although
97 *A. sparsifolia* has higher RGR compared to many other species, its root still requires long time to reach a deeper
98 groundwater table. The frequency, time and amount of irrigation should depend more on the variations in SWC, and
99 more water should be provided when gravimetric SWC $<8\%$ or soil metric potential is lower than plant water
100 potential. In addition, literature review also revealed that nutrients concentration, salinity, light and resource
101 competition are also the main ecological factors driving and affecting the normal growth and reproduction of *A.*
102 *sparsifolia* (Zeng et al., 2002; Huang et al., 2021).

103
104 *A. sparsifolia* plays a crucial role in sand fixation, vegetation restoration, preventing desertification and soil
105 erosion, and guaranteeing ecosystem services in desert ecosystems (Gao et al., 2022). With the increasing degree of
106 irrational exploitation of natural resources, desertified land in the Taklamakan Desert is expanding (Li et al., 2015).
107 In the process of desertification in arid and semi-arid areas, wind and sand control measures based on desert plants
108 are more economical and practical. The wind and sand control by plants are mainly the result of the joint action of
109 the aboveground and underground part (Ma et al., 2012), where the aboveground part plays a key role. Differences
110 in structural characteristics and biomass allocation patterns of aboveground parts can cause different wind and sand
111 fixation effects (Tong et al., 2018). *A. sparsifolia* has a well-developed root system and relatively coarse and hard
112 stalks, and when the airflow passes through, the branches swing little with the airflow, and the wind-sand flow
113 encounters a larger amount of settlement and accumulation. In the desert transition zone, the cover of *A. sparsifolia*
114 is about 30% (Li and Zhang, 2002), the wind speed, the corresponding surface sand flux and the wind erosion rate

115 on the surface are significantly reduced (Wang et al., 2011), this is because the vegetation cover gradually increases,
116 so that the fine particles in the wind and sand flow gradually settle on the surface. Therefore, the higher the
117 vegetation cover, the lower the wind speed, and the more the fine-grained matter in the sand material is accumulated.
118 Thus, with the protection of *A. sparsifolia*, it can effectively prevent wind and sand and reduce the speed of the wind
119 and sand migration (Feng et al., 2016). In addition, the sparse-leaved *A. sparsifolia* is densely distributed in the
120 aboveground parts of the branches, which have more vital spatial occupancy ability, and the area of wind protection
121 on the surface is large, so the plant has a higher capacity to block sand (Han et al., 2013).

122
123 The strength of the sand interception capacity of individual plants and communities can be measured by the
124 volume of accumulated sand deposited around the plants (Tang et al., 2011), which is affected by various factors
125 such as the aboveground morphological structure and density of plants. In a study of the morphological parameters
126 of sand piles in *A. sparsifolia* bushes, it was found that the volume of sand piles increased exponentially with the
127 increase of plant height and increased linearly with the rise of crown width area (Han et al., 2013). Based on the
128 relationship between measured sand transport and wind energy, Wang et al. (2011) inferred that without the
129 protection of the surface by the sparse-leaved *A. sparsifolia*, the annual single-width sand transport from the oasis
130 front to within the oasis could reach $170.24 \text{ t} \cdot \text{km}^{-1} \cdot \text{a}^{-1}$, which shows that the sparse-leaved *A. sparsifolia* has an
131 excellent effect on the wind damping, sand fixation, and soil erosion.

132
133 Most phreatophytes are considered species of little economic value; however, aside from its ecological
134 importance, *A. sparsifolia* also provides various socio-economic services. For instance, due to its high protein
135 content, it is regarded as an essential source of forage for livestock (Li et al., 2021) and is used in traditional
136 medicine for treating human ailments such as colds, diarrhea, joint pains, and stomach-, head- and toothache (Wei et
137 al., 2021). Despite its significant ecological and socio-economic importance, anthropogenic activities such as
138 unsustainable harvesting, overexploitation for agriculture expansions, and over-grazing are posing serious threats
139 to *A. sparsifolia* populations. Moreover, the amount of available information on most phreatophyte species is scarce.
140 Notwithstanding their abundance as species, very little attention has ever been paid to this valuable group of
141 plants. To the best of our knowledge, no published review has ever attempted to either document information
142 regarding the ecological, physio-biochemical, and growth responses in *A. sparsifolia* to environmental stresses or

143 design an effective and practical framework for its sustainable utilization and conservation. Besides *A. sparsifolia*
144 and other phreatophytes also demand more attention, especially under anthropogenic and future climate change
145 threats. They are the end-product of plant evolution in arid environments, and their functionality, ecology, and
146 general minimal biotic and abiotic requirements for survival thus warrant far more attention. Further study will
147 provide more tools for their management and the prevention of total desertification in several areas of our planet.

148

149 This review provides concrete and baseline information for understanding the response mechanisms of this
150 valuable plant species to environmental changes and identifying scientific gaps in the knowledge that could be
151 critical for the design of future studies. The main objective of this review is thus to disseminate research-based
152 knowledge and improve awareness of the role of *A. sparsifolia*, which we hope will improve regional socio-
153 ecological environments and, above all, halt desertification and fulfillment of Sustainable Development Goals
154 (SDGs) to ensure greater human welfare.

155

156 **2. *Alhagi sparsifolia* responses to drought and nutrients availability**

157 *Alhagi sparsifolia* dominates hyper-arid desert ecosystems where groundwater resources (i.e., water and nutrients)
158 determine species' survival. It has a web-like root system with dichotomously branched architecture (Zeng et al.,
159 2013a). Of the first five branch orders of its fine roots, the first two are ephemeral and have a primary anatomical
160 structure, with high nitrogen (N) concentration, high respiration rate, and a very short life span (1–4 months). By
161 comparison, the final two branch orders are perennial, with thicker roots with no or a collapsed cortex, distinct
162 secondary growth, low N concentration, and a low respiration rate — but with a much longer life span (Liu et al.,
163 2016). Based on several years of experiments and observations, it is suggested that the root systems of mature *A.*
164 *sparsifolia* could reach 7–16 m of soil depth to exploit the groundwater in the natural environment (Thomas et al.,
165 2000; Arndt et al., 2004a; Zeng et al., 2013b). The root systems of one-year-old *A. sparsifolia* could reach 2.8 m of
166 soil depth to utilize the soil water under controlled conditions (Zeng et al., 2013b). *A. sparsifolia* seedlings mainly
167 adapted to drought by increasing the vertical root length and growth rate. It was also observed in this study that
168 vertical roots growth was greatly susceptible to soil water content, it grew fastest when soil moisture was low within
169 the range of 3%–9%, but root growth rates showed a slow downward trend when the soil moisture content rise and
170 was between 13% and 20%. The vertical roots stopped growing when soil moisture content exceeded 30%, point at

171 which soil moisture became the limiting factor on root growth. Root morphological plasticity is an essential strategy
172 for improving the uptake of soil moisture and adapting to arid environments. When the groundwater table was
173 shallow, horizontal roots quickly expanded and tillering increased to compete for other resources than water,
174 whereas when the groundwater table was deeper, vertical roots developed quickly to exploit space in the deeper soil
175 layers (Zheng et al., 2013b).

176
177 To survive in harsh environmental conditions, *A. sparsifolia* utilizes different strategies to combat salt and
178 drought stress and, for instance, increases its root biomass to reach groundwater resources, enhances its vertical root
179 growth, has a narrow leaf-area ratio to reduce transpiration, and accumulates excess Na⁺ ions (to improve osmolarity
180 and lower water potential) in its roots (Zeng et al., 2008; Zhang et al., 2020). Controlled experiments suggest that *A.*
181 *sparsifolia* possesses strong ecological plasticity in its morpho-physiological characteristics and can withstand
182 drought stress in progressive stages. For example, it can alter shoot and root biomass partitioning, water-use
183 efficiency, photosynthetic pigments, light-saturated photosynthetic rate, and concentrations and distribution of C and
184 N (Gui, 2013; Zeng et al., 2013a; Zeng et al., 2013b; Zeng et al., 2016). These findings demonstrate that *A.*
185 *sparsifolia* distributes more metabolism products to the roots (i.e., deep roots), absorbing more groundwater,
186 decreasing the number of shoots, and limiting water loss through transpiration (Fig 3).

187
188 Groundwater is also a major source of nutrients, as shown by the high concentrations of NO₃⁻ and PO₃⁻ in
189 the xylem sap of *A. sparsifolia* indicating the existence of nutrient supply from groundwater (Arndt et al., 2004b;
190 Thomas, 2014; Zeng et al., 2006). Therefore, the roots approaching the deep water table are more sensitive to soil
191 nutrients than the aboveground parts, which have stable nutrient stoichiometry regardless of the soil fertility. The
192 impact of groundwater and its depth on *A. sparsifolia* growth and nutrient accumulation have been extensively
193 studied in natural hyper-arid desert ecosystems (Gui et al., 2013; Li et al., 2015a; Zeng et al., 2020; Zhang et al.,
194 2018a; Zhang et al., 2018b; Zhou et al., 2018; Li et al., 2021; Li et al., 2021). Researchers suggest that variation in
195 groundwater depths significantly impacts biomass, growth rate, cover, foliar phosphorus (P) content, and the
196 nutrient resorption strategies of *A. sparsifolia*. Besides their dependency on groundwater resources, soil properties
197 and nutrient concentrations are also crucial for the growth of phreatophytes.

198

199 *A. sparsifolia* acclimates to low-P availability in soil by increasing their foliar-P allocation proportion to
200 nucleic acid-P while decreasing P allocation to structural-P. It indicates that *A. sparsifolia* requires higher foliar-P to
201 synthesize enzymes and proteins. Moreover, foliar-P fractions positively correlate with soil labile-P, moderately
202 labile-P, and soil electrical conductivity (Gao et al., 2022). Furthermore, soil nutrients also significantly impact the
203 C:N:P stoichiometry of different organs (above- and below-ground) in *A. sparsifolia* (Zhang, 2018; Yin et al., 2021;
204 Zhang et al., 2021). *A. sparsifolia* plants in nutrient-poor soils display greater sensitivity to environmental changes.
205 Zhang et al. (2021b) suggested that nutrient input (N) and water addition can alleviate drought-associated damage
206 in *A. sparsifolia* seedlings by improving nutrient uptake and biomass allocation to roots and by affecting microbial
207 communities' abundances and functions (Zhang et al., 2020; Zhang et al., 2021). Soil nutrient concentrations drive
208 rhizospheric microbial communities, and, for instance, simulated N deposition has no impact on bacterial
209 communities but does alter fungal communities in the soil beneath *A. sparsifolia* plants. This indicates that
210 rhizobacteria are more resistant to N and water input than fungal communities (Li et al., 2021). These findings imply
211 that *A. sparsifolia* adapts various strategies for surviving in harsh environments (Fig. 3) and is greatly dependent on
212 groundwater and soil resources (depending on its maturity stage and stress level).

213

214

215

216 **3. Impact of salinity on *A. sparsifolia***

217 Most of the world's arid and semiarid regions are facing salinity problems that affect plant productivity by hindering
218 water and nutrient uptake. Saline soils and saline groundwater in the Taklamakan desert decrease the soil water
219 potential (ψ) and so make it difficult for plant roots to absorb water, restrict water uptake and photosynthesis, and
220 influence pH and nutrient availability and absorption (Munns, 2002; Shao et al., 2019; Perri et al., 2020; Wang et al.,
221 2020). Under moderately salt-dominated groundwater, *A. sparsifolia* shows no salt-related stress or nutrient
222 imbalance; however, in young *A. sparsifolia* seedlings, photosynthetic gas-exchange traits decrease at high salinity
223 levels but can withstand moderate salt stress (Arndt et al., 2004; Zeng et al., 2008). In *A. sparsifolia*, two kinds of
224 salt ion allocation patterns occur –root > stem > leaf and branch > stem > root > leaf – in field and controlled
225 environments, respectively (Jin et al., 1996). This implies that mature stands of *A. sparsifolia* accumulate salt ions in
226 roots or stems rather than in leaves, which helps them withstand and adapt to saline soil in hyper-arid deserts. The
227 extensive root systems of *A. sparsifolia* may allow excessive salts to be diluted with the growth of new shoots

228 (Zhang et al., 2017). Increased salt ion concentrations in the roots and shoots of *A. sparsifolia* indicate how this plant
229 improves its cellular osmolarity and reduces its water potential. Moreover, its root system excludes Na^+ to maintain
230 low foliar salt concentrations, representing a high degree of ion selectivity (Arndt et al., 2004). Salinity affects
231 biomass allocation patterns in *A. sparsifolia* plants, which invest more in roots and increase the root-to-shoot ratio
232 (Zeng et al., 2008). In addition, soil nutrients also impact the growth and salt tolerance of *A. sparsifolia* in salinized
233 soil. For instance, total K^+ determines the uptake of salt ions (Na^+) and alleviates the toxic accumulation of
234 Na^+ . Despite being a leguminous phreatophyte, saline groundwater has no significant impact on the biological
235 nitrogen fixation (BNF) of *A. sparsifolia* in riparian zones; when growing in low saline sand dunes, it uses
236 groundwater N. Salt treatment also has no significant effect on the nodulation capacity of *A. sparsifolia*, a fact that
237 highlights its BNF tolerance to salt stress (Li et al., 2021). Thus, the relationship of BNF and salt tolerance in this
238 species illustrates the adaptability of desert legumes to changing environments and its strategies for thriving in a
239 saline environment consisting of either building symbiotic relationships with Rhizobium or using readily available N
240 under low salt stress conditions.

241

242 **4. Responses in *A. sparsifolia* to different light intensities**

243 Light plays a vital role in developing the photosynthetic apparatus and thus in the process of photosynthesis
244 and plant growth. The leaves of plants growing in high light conditions generally exhibit greater photosynthetic
245 capacity – as shown by their high ribulose biphosphate carboxylase/oxygenase and electron carrier concentrations –
246 than plants growing in low-light conditions (Jiang et al., 2011). However, high irradiance can also lead to
247 photoinhibition and reduce the photosynthetic efficiency of plants. *A. sparsifolia* is regarded as a sun plant because it
248 thrives under high irradiance in the Taklamakan desert. It can also grow under the canopies of tree species inside
249 oases, which reveals its ability to thrive in shaded conditions. Low-light conditions have been reported to hamper the
250 growth of *A. sparsifolia* by increasing the proportion of biomass allocated to leaves and reducing the proportion of
251 biomass in assimilative branches (Li et al., 2014) and by decreasing leaf photosynthetic efficiency (Li et al., 2015).
252 These findings indicate that xerophytes appear to undergo light acclimation similar to the light acclimatization
253 commonly observed in mesophytic plants. The assimilative branches and leaves of *A. sparsifolia* respond differently
254 under low-light conditions. *A. sparsifolia* in low light invests more energy in its leaves to increase its efficiency of
255 capturing light resources. For instance, low-light conditions (related to high soil water content) cause assimilative

256 branches to disappear. In contrast, high light conditions (where soil water content is lower) cause assimilative
257 branches to increase to prevent evaporation and maintain water balance. Therefore, *A. sparsifolia* may have evolved
258 assimilative branches as an adaptation for survival in arid environments (Li et al., 2014; Li et al., 2015). The
259 fluorescence kinetics of chlorophyll is one of the principal methods for investigating the function and reaction of
260 photosystem II (PSII) under changing environmental and growth conditions (Zhang et al., 2010; Lazár, 2015).
261 Accordingly, chlorophyll fluorescence can be used to measure electron-transfer efficiency from the donor side of
262 PSII to the acceptor side of the intersystem chain (Strasser et al., 2010). Li et al. (2016) investigated the chlorophyll
263 fluorescence emission of *A. sparsifolia* seedlings grown under high (HL) and low (LL) light conditions and reported
264 that the fluorescence intensity in the leaves of the LL-grown plants was significantly greater than in the HL-grown
265 plants. Shade conditions inhibit the donor side of PSII, whereas high light conditions diminish the acceptor side of
266 PSII. Under ambient conditions, PSII activity is severely affected; conversely, plants growing in the shade suffer
267 less environmental stress and experience greater energy transport at midday. PSII activity is enhanced under shaded
268 conditions while blocked energy transfers between PSII and PSI. Consequently, plants have a lower photosynthetic
269 capacity in the shade than under full sun, resulting in lower biomass (Fig. 3). Further, the PSII activity of mature and
270 immature *A. sparsifolia* leaves has been reported to be enhanced at less than 50% of full light conditions. Moreover,
271 both immature and mature leaves exhibit a decline in electron transport activity on the acceptor side of PSII after
272 being kept in the shade for an extended period. Consequently, immature leaves have been found to be more
273 susceptible to inhibition following exposure to high natural light than mature leaves (Li et al., 2015).

274

275 **5. Impact of temperature on *A. sparsifolia***

276 Climate change scenarios predict that our planet is likely to continue to warm during the current century
277 and, based on climatic model simulations, the Earth's average temperature could be 1.1–5.4°C warmer in 2100 than
278 it is today (Friedlingstein et al., 2010). Temperature is another crucial abiotic stress factor that affects plant growth
279 and distribution. When temperatures exceed acceptable levels for plant growth, the structure and function of
280 photosynthetic proteins are destroyed, resulting in decreased photosynthetic efficiency (Allakhverdiev et al., 2008;
281 Crafts-Brandner and Salvucci, 2002). Photosystem II (PSII) consists of several stress-sensitive proteins, so the
282 thermostability of PSII is weak (Čajánek et al., 1998). Elevated temperatures, for example, reduce the electron
283 transport on the acceptor side of PSII and the activity of the oxygen-evolving complex (OEC) (Chen et al., 2008).

284 PSII in the leaves of *A. sparsifolia* is irreversibly damaged under heat stress of over 43°C for 15 minutes but is
285 unaffected at temperatures below 42°C (Xue et al., 2012). However, the maintenance of heat of over 43°C for 40
286 min and 60 min limits or severely damages PSII activity, respectively (Li et al., 2014). Rubisco activity first
287 increases at 34°C and then declines with the increase of temperature due to the excessive generation of ROS. Even
288 though *A. sparsifolia* has the potential to develop a strong stress-resistance mechanism (i.e., PSII activity at high
289 temperatures) to adapt to extremely arid desert environments, high temperatures in summer at noon can cause a
290 significant decline in cell vitality, in particular, due to damage to photosynthetic proteins (Xue et al.,
291 2012). Moreover, Li et al. (2014) suggest that assimilative branches are more effectively adapted to high
292 temperatures than leaves and have better light efficiency, light transfer, and electron transport at 52°C. Thus,
293 assimilative branches of *A. sparsifolia* are more tolerant to high temperatures than the leaves, suggesting that
294 assimilative branches may be better adapted to severe conditions (Fig. 3).

295 **6. Socio-ecological services of *Alhagi sparsifolia***

296 A total of seven species belong to the genus *Alhagi* worldwide, of which three are found in China (Jin et al.,
297 2014). *A. sparsifolia* has a variety of ethnomedicinal uses, and the sugary exudation from its aerial parts is used as
298 an important Ethnomedicine (known as Tarangabin) for treating gastrointestinal problems. Its leaves are used to
299 treat swelling and joint pain, its flowers to detoxify the body, and its seeds to treat toothache and dysentery. The
300 whole plant is used to treat fever and enteritis (Yuan et al., 2012) and is included in the *Pharmaceutical Standards of*
301 *the Ministry of Health of the People's Republic of China* (Uyghur Medicines) (Chinese Pharmacopoeia Commission,
302 1998). To date, 178 chemical constituents, including flavonoids, alkaloids, and phenolic acids, as well as 19
303 polysaccharide fragments, have been identified in *A. sparsifolia*. Modern pharmacological studies reveal that
304 isolated components and crude extracts are hepato-protective and have anti-cancer, antioxidant, anti-neuro-
305 inflammatory, and andreno-protective properties (Wei et al., 2021). Moreover, this plant contains large amounts of
306 crude fat and digestible proteins, minerals, and oils that increase during flowering and make it a very nutritious
307 forage grass in desert systems (Wang et al., 2019). *A. sparsifolia* is used as a fodder crop in Central Asia and
308 Northwest China (Muhammad et al., 2014) and is an important resource for local livestock husbandry. Natural
309 stands of *A. sparsifolia* are used as pasture throughout the year and are grazed by sheep, goats, cattle, and camels.
310 Local farmers also use it as a source of fuel and are one of the primary sources of fuel in the villages of southern
311 Xinjiang (Li et al., 2021). *A. sparsifolia* is a crucial component of local agricultural systems (Siebert *et al.*, 2004),

312 especially on the southern rim of the Taklamakan desert. Besides its socio-economic value, *A. sparsifolia* also play a
313 significant ecological role in arid and semiarid regions. Desertification is an important environmental and socio-
314 economic issue in the modern world and threatens the development, livelihood, and survival of mankind. China has
315 to face up the threat of severe desertification, a matter that has attracted much attention in recent decades (Zhang &
316 Huisingh, 2018). Northwest China, which has arid and semiarid regions, accounts for approximately 38% of Chinese
317 territory. *A. sparsifolia* has a key role to play here by providing shelterbelts to combat sand drifts, reduce soil
318 erosion, stabilize sand dunes, improve soil fertility on the southern fringe of the Taklamakan desert, and promote the
319 sustainability of oases (Zeng et al., 2002b; Thomas et al., 2008; Vonlanthen et al., 2011). The environmental and
320 ecological importance of deep-rooted legumes in drylands is attracting great attention due to the threat of soil
321 degradation and global climate change. In addition, *A. sparsifolia* may also be helpful in the prevention of
322 salinization due to its tolerant BNF to salinity and its ability to reduce the water table of shallow aquifers that may
323 be highly saline (Li et al., 2021). Deep-rooted desert legumes can grow in N-poor soils and play a crucial role in
324 bioremediating areas affected by salinization as they can improve soil structure and productivity (Dovrat and
325 Sheffer, 2019). Therefore, *A. sparsifolia* is an invaluable desert plant species and very important in the re-vegetation
326 and restoration of degraded desert landscapes.

327

328

329 **7. Environmental and anthropogenic threats**

330 Climate change is a global phenomenon altering the distribution and abundance of plant species worldwide
331 (Feeley et al., 2020). Spatiotemporal changes in temperature and precipitation affect the growth of plants, habitat
332 conditions, and soil moisture content, thereby inducing changes in the spatial patterns of vegetation distribution
333 (Guan et al., 2020; Zhao et al., 2020). As mentioned above, various studies have explored how *A.*
334 *sparsifolia* responds to changing climatic variables. Results suggest that rises in temperature and drought will affect
335 its photosynthetic capacity, the biomass of its aerial parts, nutrient concentrations, and growth and provoke
336 metabolic impairments (Li et al., 2013; Xu et al., 2012; Zeng et al., 2016). Ecological plasticity of *A. sparsifolia* is
337 up to certain levels of stress (drought, salinity, temperature, light, etc), however, progressive high level of stress can
338 affect its growth and survival. Therefore, climate change is already having an impact and will continue to have grave

339 effects on the growth and survival of *A. sparsifolia* especially at the seedlings stage when the roots are still
340 dependent on soil water and nutrient resources.

341
342 The results of model simulations reveal that under climate change scenarios RCP 2.6 and RCP 8.5, the
343 suitable habitats and abundance of *A. sparsifolia* will tend to decrease (Yang et al., 2017). This survey, also
344 suggested that annual precipitation, temperature annual range, mean temperature of the coldest quarter, precipitation
345 of the coldest quarter, annual mean temperature, precipitation of the wettest month, mean temperature of the wettest
346 quarter were the seven climatic factors influencing present to future the geographic distribution of *A. sparsifolia*
347 under current climate. The future distribution of *A. sparsifolia* for from 2015 to 2070 under two climate change
348 scenarios (RCP2.6 and RCP 8.5) has also been projected to lose 8.71×10^4 km² and 5.08×10^4 km², as documented in
349 the Fifth Assessment Report of Intergovernmental Panel on Climate Change (IPCC). *A. sparsifolia* offers many
350 services to local people and, over and beyond the impact of climate change, anthropogenic activities will also affect
351 its growth and distribution patterns. Population growth, overgrazing, burning, overcutting, farmland expansion,
352 over-exploitation of groundwater, salinization, urbanization, and industrialization are the main anthropogenic
353 activities responsible for the transformation of plant communities and natural habitat loss in arid and semiarid
354 regions (Bedair et al., 2021). As the primary source of fodder for livestock around oases (Thomas et al., 2000), *A.*
355 *sparsifolia* is extensively harvested and overgrazed, which constitutes a further severe threat to this species (Gries et
356 al., 2005; Bruelheide et al., 2010). Increased population and economic growth lead to the cutting and clearing of
357 large areas of natural vegetation – including *A. sparsifolia* – in desert ecotones to increase the amount of agricultural
358 land. The controlled burning of vegetation is also practiced to clear land for cultivation. Li et al. (2012), in an
359 experiment to determine the impact of human activities on *A. sparsifolia* regeneration in desert ecotones, show that
360 burning in spring leads to lower *A. sparsifolia* height (31%) and less biomass than if it is cut in the fall. Moreover,
361 the decrease in biomass resulting from spring burning was higher than after spring cutting. Burning and cutting in
362 spring destroys the stems and buds of *A. sparsifolia* and causes stunted plant growth. Conversely, cutting in the fall
363 results in greater production that could help sustainable development in desert ecotones. Zhou et al. (2020)
364 investigated the impact of different types of land-use and distances from farmland on the growth and community
365 structure of dominant vegetation species (including *A. sparsifolia*) in the desert ecotone in the southern Taklamakan
366 desert. Their results indicate that, although the type of land-use affects some of the growth indices in *A. sparsifolia*,

367 the distance from the farmland has few significant effects. This suggests that land-use heterogeneity can alter
368 vegetation growth and plant community structure. The overexploitation of groundwater resources for irrigation can
369 lead to a fall in groundwater levels that, in turn, cause significant alterations in plant structure, species composition,
370 and diversity. As a consequence of falls in groundwater level, certain herbaceous plant species including
371 *A. sparsifolia* have become extinct in the region (lower reaches of the Tarim basin) (Liu and Chen, 2002; Chen et
372 al., 2006). The risk of overexploitation of groundwater resources is more serious in semiarid regions due to the
373 projected increase in the intensity and frequency of droughts; an expanding population with higher standards of
374 living and agriculture expansion will intensify the demand for groundwater even further (Richard et al., 2012).
375 Therefore, it is essential that the vegetation cover of *A. sparsifolia* be managed in light of current anthropogenic
376 disturbances and predicted future climate change as a way of promoting its sustainable utilization. In Fig. 3, we
377 summarized the relationships between *A. sparsifolia* and its environment. On the one hand, the leaves of the plant
378 feed the cattle, so the greater the leaf biomass, the greater the animal fattening. The presence of neighboring plants
379 will reduce the availability of light, which could decrease the photosynthetic activity, and ultimately the leaf
380 biomass will be lower. Roots have a beneficial effect on microorganisms and soil fauna since they are a source of
381 photoassimilates and increase the availability of some nutrients. If the predicted climatic changes occur, they will
382 have different effects on biomass partitioning. N deposition will increase leaf biomass and reduce shallow root
383 biomass. An increase in temperature and decrease in precipitation will proportionally increase branch biomass and
384 reduce leaf biomass. Finally, overexploitation of groundwater and its consequent deepening will stimulate the plant
385 to produce more deep roots. Groundwater, in case of reduced precipitation, will be even more relevant for water and
386 nutrient supply, but if salinization occurs, the total plant biomass will be reduced.

387 **Sustainable utilization and management proposal**

388 The sustainable utilization and management goal of *A. sparsifolia* and other phreatophytes require a practical socio-
389 ecological approach (Fig. 4). The survival and reproduction of *A. sparsifolia* and other deep-rooted phreatophytes
390 depend on groundwater sources, and therefore keeping the groundwater level to a suitable depth is the most
391 important question. There is a direct need to make comprehensive water management plans to determine the
392 rationale distribution of available water resources. Statutory regulations should be issued to ensure the control and
393 enforcement of plans. Thus, special attention should be paid to water conservation (preventing excessive
394 groundwater pumping, applying artificial recharge, improving irrigation efficiency, and promoting water rights and

395 price mechanisms). Therefore, it is crucial to utilize all kinds of water-conservation techniques to combat the water
396 wastage problem. Moreover, to provide the farmers with sufficient fuel from other resources, promotion of
397 environment-friendly alternative energy sources like solar and wind energies is needed. This could effectively
398 decrease the over-exploitation of natural vegetation, including *A. sparsifolia*, and would support restoration and
399 future rational use of this vegetation. Advanced scientific knowledge of the ecology of *A. sparsifolia* and other
400 phreatophytes is also an essential step toward sustainable management and conservation. The government should
401 provide more funds to the researchers in Central and East Asian countries to extend the scope and duration of their
402 scientific investigations. Researchers should be focusing on attention-demanding aspects (especially molecular,
403 exact distribution, and abundance) of *A. sparsifolia* and other important phreatophytes to provide sound knowledge
404 that could be helpful for their proper management. This could also help prioritize specific areas where the *A.*
405 *sparsifolia* population is facing severe reduction and therefore require urgent attention to be protected and
406 sustainably managed in natural reserves. In addition, there is a dire need to estimate the quantity of biomass
407 harvested by the local population and consumed by domestic animals annually to make sure that it must not exceed
408 the growth of *A. sparsifolia* and other phreatophytes. A balance between demand and supply would help to avoid
409 overexploitation. One of the main hindrances is also that the government laws and regulations concerning
410 conservation and sustainable utilization are in effect but not adequately observed. Therefore, the local population
411 should be sufficiently informed about these laws, and the farmers should be urged to monitor the regulations on
412 vegetation conservation. Moreover, the rapid growth in population, especially in the arid regions of developing
413 countries, poses a particular strain on the fragile environment, increases water shortage, and accelerates the
414 destruction of the natural vegetation, resulting in desertification. Therefore, capacity building of the local population
415 is direly needed to make them fully aware of the consequences of vegetation destruction and the advantages of its
416 conservation and the sustainable utilization. The local people should be encouraged to utilize their traditional
417 knowledge to promote the sustainable cultivation of *A. sparsifolia* and other representative phreatophytes. Poverty is
418 another factor that requires attention because local people living in arid and semi-arid regions are economically not
419 stable and are often compelled and dependent on natural resources. Therefore, alleviating poverty in these harsh
420 regions could support the efforts for rational use of vegetation. The application of these initiatives and strategies is
421 imperative to promote sustainable utilization and management of important phreatophytes that could strengthen
422 global efforts to combat desertification, land degradation, and livelihood improvement.

423

424

425

426 **Conclusions**

427 *Alhagi sparsifolia* is a typical phreatophyte of arid land that employs various mechanisms for coping with abiotic
428 stresses. It also provides indispensable socio-ecological services including protection against desertification and
429 reducing salinization, and in general helps to improve people's overall welfare. The adaptation of *A. sparsifolia* to
430 harsh environmental conditions is based on its deep and extensive root system that it uses to tap groundwater
431 resources. However, several studies have suggested that extreme drought, temperature, and other environmental
432 stresses can affect its growth and metabolism, especially during its initial growth stages, and so pose serious threats
433 to its survival since roots are dependent on soil resources and properties. Population growth, overgrazing, burning,
434 overcutting, farmland expansion, urbanization, and industrialization are the main threats to its abundance and
435 habitats. All these factors have led to an overexploitation of groundwater resources and severely threaten the
436 existence of natural stands of *A. sparsifolia*. While most studies have focused on its physio-biochemical and
437 morphological responses to environmental stresses, literature is very scarce on its molecular mechanisms. Similarly,
438 very little is known about its exact distribution in Central Asia, which is key information for its
439 conservation. Despite offering various socio-ecological services, little attention has been paid to its management,
440 conservation, and sustainable use. Local people must be educated to understand the importance of arid-land plant
441 species and their role in ecosystem and biodiversity protection. Establishing an integrative socio-ecological
442 approach for improving knowledge of the importance and functions of key plant species in arid lands is crucial for
443 protecting ecosystems and promoting sustainable livelihoods. In addition, it is also vital to explore the variety of
444 interactions operating between groundwater, climate change, and human activities in order to improve management
445 of aquifers and sustain groundwater usage. Finally, there is an urgent need to establish nature reserves and shared
446 databases for this and other vital plant species that play critical roles in combating desertification, improving
447 livelihoods, and fulfilling Sustainable Development Goals (SDGs).

448

449 **Acknowledgement**

450 This work was supported by the Key Program of Joint Funds of the National Natural Science Foundation of China
451 and the Government of Xinjiang Uygur Autonomous Region of China (Nos. U1903102), and the National Natural
452 Science Foundation of China (No. 41977050); President's International Fellowship Initiative-Postdoctoral
453 Researchers, Chinese Academy of Sciences (2020PB0002). JP and JS were funded by the Spanish Government
454 Grants PID2019-110521GB-I00 and PID2020-115770RB-I00, the Catalan government grant SGR2017-1005 and
455 the Fundación Ramón Areces grant CIVP20A6621.

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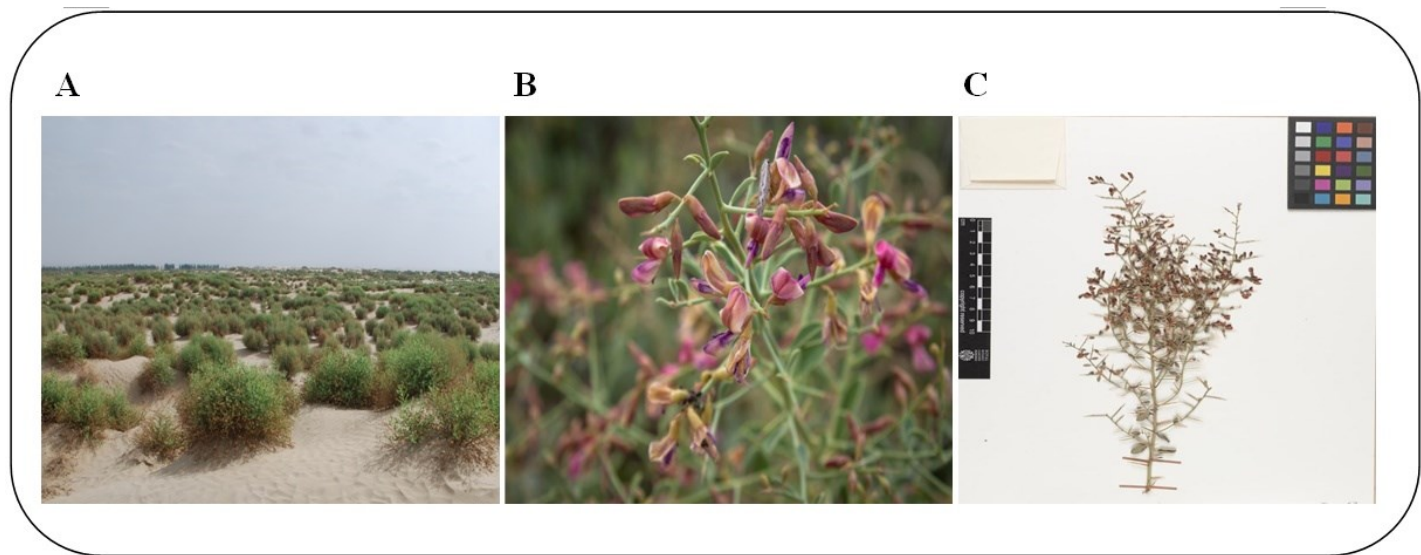
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695 **Figure 1:** Spatial distribution of *Alhagi sparsifolia* in different countries. This map is designed based on the spatial
696 data available in the species database (<https://www.gbif.org/>). The database lacks information from some regions, so
697 the distribution could be wider.

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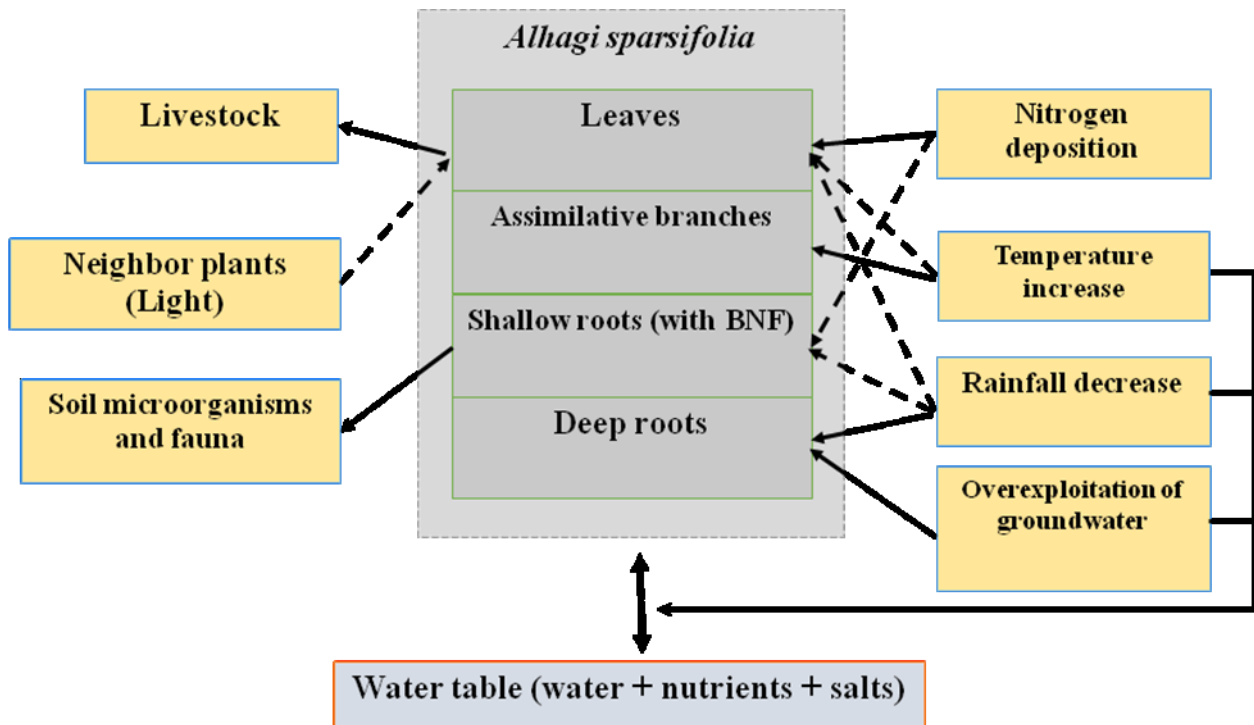
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702 **Figure 2:** Habitat (A), flowers (B), and a specimen (C) of *Alhagi sparsifolia*: (B) source:
703 <https://www.inaturalist.org/photos/43301374>, (C) source: <http://data.rbge.org.uk/herb/E00364493>

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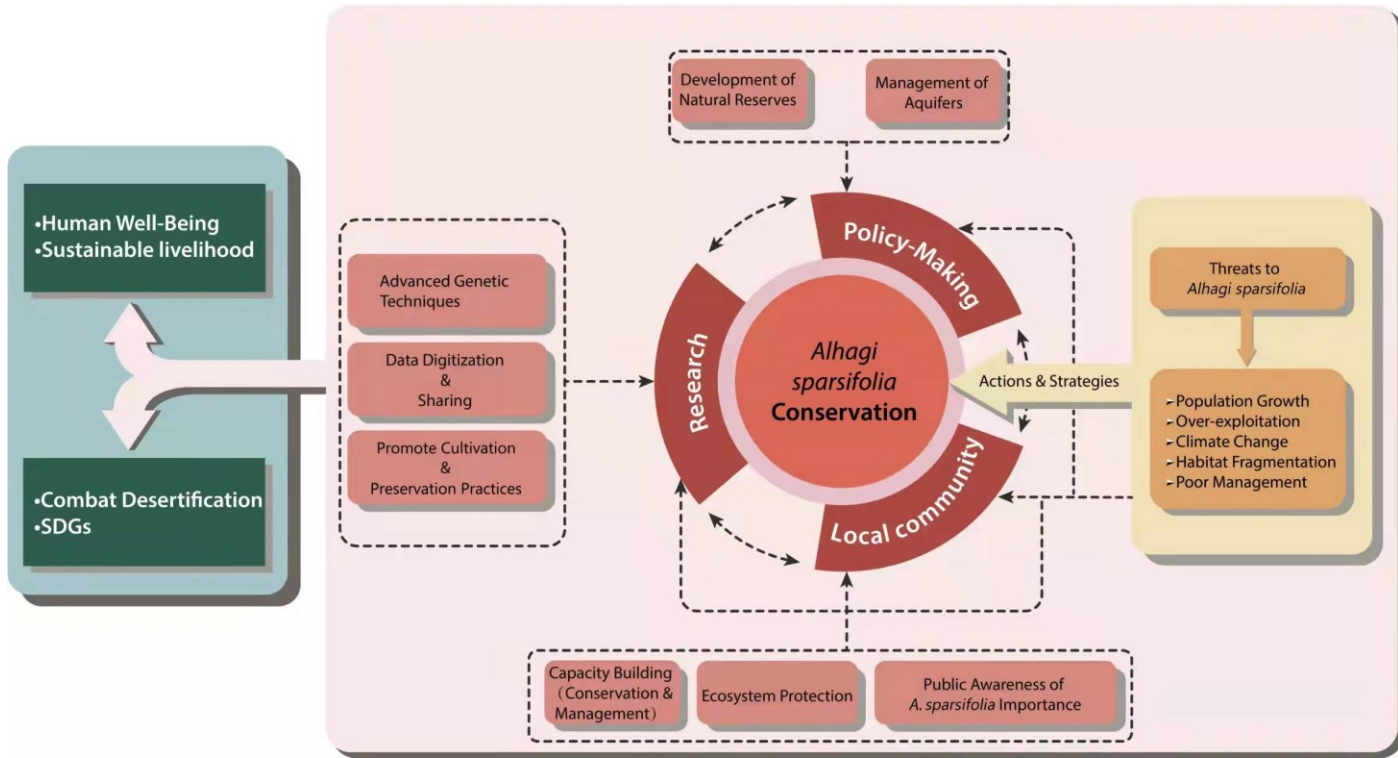
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Figure 3: A conceptual and logical flow diagram based on the existing research-based knowledge and literature review about the impact of environmental changes (nitrogen deposition, increase in temperature, decrease in rainfall, and overexploitation of groundwater) in *A. sparsifolia* biomass partitioning and its relationship with livestock, other plants, and soil biota. The grey rectangle represents the plant, divided in organs. On the left, we included organisms related with each *A. sparsifolia* plant. On the right, we included predicted environmental changes. Solid arrows indicate positive relationships (a increases b), while dashed arrows indicate negative relationships (a decreases b).

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719 **Figure 4:** Threats to the conservation of *Alhagi sparsifolia*, and future strategies for its management and sustainable
720 use. This conceptual framework accentuates an integrated socio-ecological approach involving policymakers, researchers, and
721 local communities for sustainable management and promoting conservation practices of *A. sparsifolia* and could also apply to
722 other deep-rooted phreatophytes in different countries. Policymakers should properly govern and regulate policies associated
723 with the management and conservation of *A. sparsifolia*, such as the development of nature reserves and the management of
724 aquifers. Researchers should play an essential role with policymakers by promoting advanced germplasm, data digitization,
725 sharing, and promoting the cultivation and preservation practices of *A. sparsifolia* and other phreatophytes. Local communities
726 should follow and observe policies and regulations regarding sustainable utilization and management and be aware of the
727 consequences of overexploitation of natural resources in these fragile ecosystems. Eventually, joint efforts of these three
728 stakeholders will help combat desertification and land degradation and sustain human well-being.

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