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Responses of Photosynthesis and Water Use to Drought in Two Desert Annuals, *Agriophyllum squarrosum* and *Bassia dasyphylla*

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Agriophyllum squarrosum (L.) Moq. is the most common pioneer plant of shifting sand dunes in northern China. As shifting sand dunes are largely fixed by vegetation, this species is found to be excluded from sand dunes which have already become semi-fixed. The purpose of this study was to compare the responses of photosynthesis and water use to drought in *A. squarrosum* and another desert annual, *Bassia dasyphylla* Kuntze, which frequently occurs in semi-fixed sand dunes, and to examine whether soil water availability is responsible for the exclusion of *A. squarrosum* from semi-fixed sand dunes. Seeds of both species were collected from the Shapotou desert area of northern China in September 1990, and grown in a greenhouse. Rates of photosynthesis and transpiration under different leaf water potentials were then measured in controlled environmental conditions. A field survey was conducted at the seed collection sites in August 1992, to measure soil moisture in shifting and semi-fixed sand dunes. Under the given conditions, increases in water stress led to a decline of net photosynthesis in both species. A marked decline in net photosynthesis occurred in *A. squarrosum* as the leaf water potential fell to less than −0.6 MPa, whereas the photosynthetic rate of *B. dasyphylla* decreased gradually as the leaf water potential decreased from −1.2 to −4.8MPa. In other words, *A. squarrosum* appeared to be more sensitive to drought than *B. dasyphylla*. In addition, a higher water use efficiency in *B. dasyphylla* during moderate water deficiency showed that this species was able to use water more economically than *A. squarrosum* under water stress. These findings, and the evidence that water availability in semi-fixed sand dunes is much lower than in shifting sand dunes, suggest that soil water availability may be the key factor determining the exclusion of *A. squarrosum* from semi-fixed sand dunes in the Shapotou area.

Key Words: *Agriophyllum squarrosum*, *Bassia dasyphylla*, Leaf water potential, Photosynthesis, Soil moisture

1. Introduction

Agriophyllum squarrosum (Chenopodiaceae) is a pioneer species in shifting sand dunes of northern China (LIU *et al.*, 1985). Shifting sand dunes represent an unique habitat where an extremely unstable surface and drought conditions prevail (ZHU *et al.*, 1988). The subsequent phases of succession do not progress under these conditions, although *A. squarrosum*, an annual herb, can grow at some sites which are relatively stable in shifting sand dunes, and will become the core of ecological succession if these conditions are relieved (NEMOTO and LU, 1992). However, when shifting sand dunes become largely fixed by plants, and reach a semi-fixed situation, *A. squarrosum* should be excluded (SHEN, 1986). Numerous studies have demonstrated that soil water availability becomes increasingly limited as shifting sand dunes are fixed progressively by vegetation, particularly

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when the sand dunes are independent of ground water (ZHANG and XU, 1985; ZHU *et al.*, 1988; CHEN, W., 1991; CHEN, H., 1992; QIU *et al.*, 1995). This suggests that the exclusion of *A. squarrosum* from semi-fixed sand dunes might be due to the low soil water availability in the dunes (ZHAO, 1991). Only limited information supporting this suggestion is available in relation to the growth of *A. squarrosum* in shifting sand dunes of Inner Mongolia (KOBASHI *et al.*, 1988; NEMOTO and LU, 1992), *e.g.* NEMOTO and LU (1992) have reported that the plant size of *A. squarrosum* is smaller at sites with a lower water content. However, there is still a lack of data on photosynthetic traits to clarify whether this species is drought-sensitive. Indeed, there are some contradictory findings with regard to the characteristics of *A. squarrosum*: it has been reported to be a xerophyte because of its xerothermic structure (LIU, 1982), but also a mesophyte according to its plant water relations (ZHAO and HUANG, 1981; LIU *et al.*, 1987), and has even been regarded as a desert ephemeral (LU, 1980).

LARCHER (1995) has pointed out that the responses of plant species to water deficiency are largely reflected in their features, and that mesophytes and xerophytes can be distinguished precisely according to their photosynthetic response patterns to drought. It has been demonstrated that economical water use by reduction of water loss may postpone the dehydration of plants that are suffering from water deficiency, thus helping to maintain photosynthetic activity during moderate water stress (SCHULZE, 1986). In this study, therefore, we investigated the photosynthesis and water use of *A. squarrosum* in response to drought in controlled environmental conditions, and compared the results with the performance of another annual herb, *Bassia dasyphylla*. This species is suitable for comparison because it usually occurs in semi-fixed sand dunes and belongs to the same family as *A. squarrosum* (LIU *et al.*, 1985). The soil moisture of shifting and semi-fixed sand dunes was also measured at the seed collection sites of the two species. The purpose of this study was to compare the responses of photosynthesis and water use to drought in these two desert annuals, and to clarify their photosynthetic traits and examine whether soil water availability is responsible for the exclusion of *A. squarrosum* from semi-fixed sand dunes.

2. Materials and Methods

1) General description of seed collection sites

The seed collection sites were situated in the Shapotou desert area (1,250-1,500m a.s.l.) in the extreme southeastern part of the Tengger Desert in northern China (Fig. 1). This area has a typical arid continental temperate climate with a mean annual air temperature of 9.7℃ and an annual mean precipitation of 186mm, 80% of the precipitation falling between May and September (LIU *et al.*, 1987). Most of the area is covered by huge shifting sand dunes, 5-20m high, and the ground water level is extremely deep (more than 80m). The dominant wind direction in the area is northwest, and the shifting sand dunes move slowly southeast at a rate of 0.5-2.0m a year (ZHAO, 1991). Shifting sand dunes with sparse vegetation are the natural landscape in this area (Fig. 2; QIU *et al.*, 1995). Only a few species appear on the shifting dunes at some sites with a total coverage of 1-2%. These include *A. squarrosum* (herb), *Corispermum mongolicum* Iljin (herb), *Artemisia*

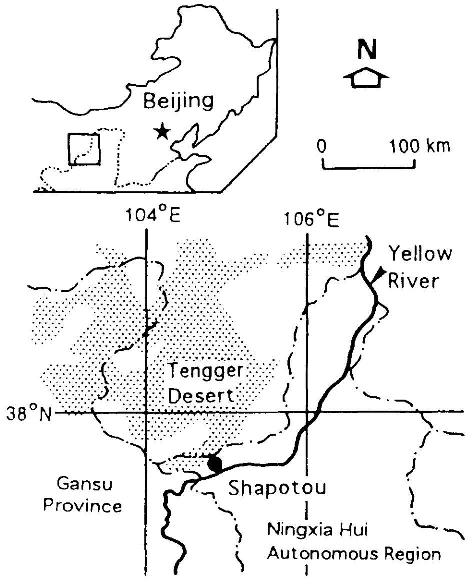


Fig. 1. Location of Shapotou, the seed collection site, with an inset map showing its situation in northern China.

sphaerocephala Krasch. (semi-shrub) and *Hedysarum scoparium* Fisch. et Mey. (shrub)*etc.*

In order to protect railways in this area from the drifting sand, an artificial vegetation system, with and without irrigation, has been established along the right-of-way since 1956 (Fig. 3). As a result, the landscape has changed from shifting sand dunes to semi-fixed and fixed sand dunes in a 500-m-wide non-irrigated artificial vegetation belt (Fig. 3, Fig. 4; QIU *et al.*, 1995). The present vegetation of the semi-fixed sand dunes is dominated by the planted semi-shrub *Artemisia ordosica* Kraschen. and the planted shrubs *Caragana korshinskii* Kom. and *Hedysarum scoparium*, with naturally established annual herbs such as *Bassia dasyphylla*, *Corispermum* spp. and *Salsola ruthenica* Iljin, the total coverage reaching 30% or so (SHEN, 1986; QIU *et al.*, 1995).

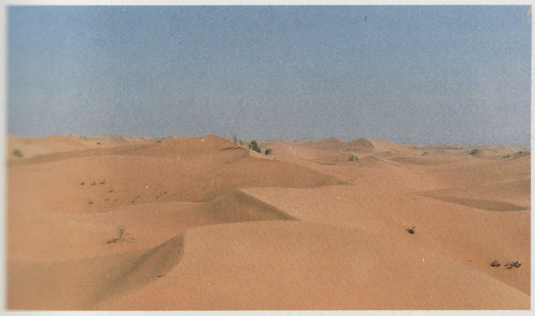


Fig. 2. The natural landscape of shifting sand dunes in the Shapotou area (outside the non-irrigated artificial vegetation belt).

The plants growing at the bottom of sand dunes are *Agriophyllum squarrosum*.

Fig. 4. The landscape of semi-fixed sand dunes in the non-irrigated artificial vegetation belt in the Shapotou area.

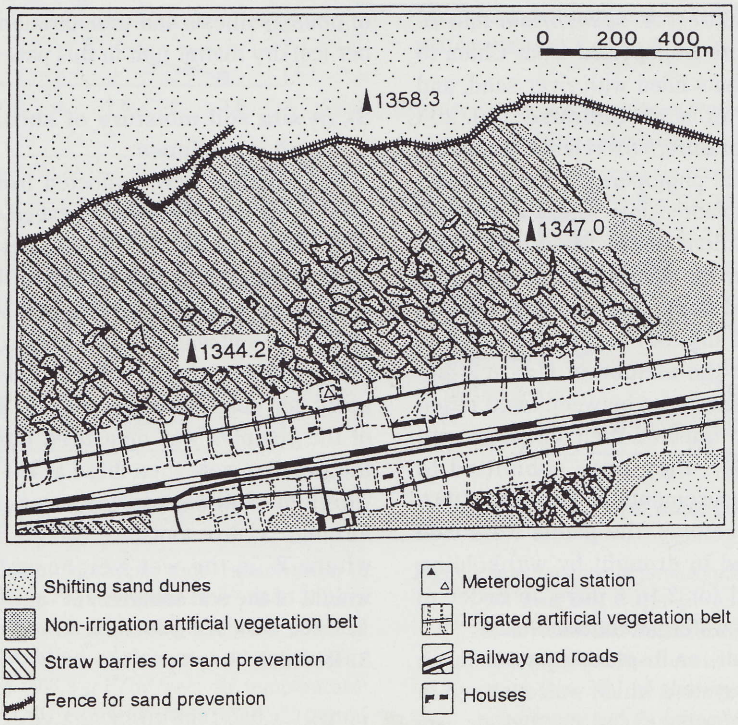


Fig. 3. A sketch map of the artificial vegetation system for prevention railways from drifting sand in the Shapotou area (following LIU *et al.*, 1984)

As one of the native species growing on the shifting sand dunes, *A. squarrosum* was selected for sand fixation when the artificial vegetation system was first instituted in the Shapotou area (ZHAO, 1991). However, *A. squarrosum* was found to be unable to grow well and produce seeds by itself when the sand dunes were largely fixed in the non-irrigated artificial vegetation belt (SHEN, 1986). In contrast, *B. dasyphylla*, which became naturally established in the non-irrigated artificial vegetation belt, is becoming increasingly important to the present vegetation of semi-fixed dunes (ZHAO, 1991; QIU *et al.*, 1995).

A. squarrosum seeds were collected from sites at the bottom of shifting dunes outside the non-irrigated artificial vegetation belt in September 1990. *B. dasyphylla* seeds were gathered at the same time from semi-fixed sand dunes in the non-irrigated artificial vegetation belt (Fig. 3). It should be pointed out that the terms "shifting sand dunes" and "semi-fixed sand dunes" in this paper refer in particular to the areas in which seeds were collected.

2) Plant material and gas exchange analysis

After legal formalities, *A. squarrosum* and *B. dasyphylla* seeds were transported from China to Japan, sown in the bats filled with river sand, and then maintained in a greenhouse (30/20℃ day/night air temperature, 60% relative humidity, 16-hour supplemental photoperiod). Each 60-day-old plant was transplanted into a plastic pot (15-cm diameter and 25cm deep) filled with river sand, and grown in the same greenhouse. The plants were watered daily, and nutrient solution (Hyponex 1000-fold diluted) was applied once a week (according to the method of NATORI *et al.*, 1992). When the plants were between eight to ten weeks old, and had finished their initial growth (NATORI *et al.*, 1994), they were submitted to photosynthetic measurements in February 1992. Before the measurements, the plants were well watered, or exposed to drought by withholding water from the soil for 2 to 6 days, in order to induce different leaf water potentials.

For measurement, each plant was set in an open gas exchange system which was enclosed in a 4.0m^2 phytotron chamber, and normal air was passed through the assimilation chamber (49 × 49 × 95cm^3) at a constant flow rate (38 l/min). The photosynthetic rate was calculated from the change in CO_2 concentration measured with an infrared gas analyzer (ZALDE 152-1, Fuji Electric Co. Ltd., Japan). The plant was placed on an electric balance which was enclosed in the assimilation chamber, and the pot was sealed by two plastic bags to prevent release of CO_2 and H_2O from the soil surface. An NEC computer was used to record readings of the balance at one-minute intervals, and the transpiration rate was calculated from the weight loss of the plant. The water use efficiency of photosynthesis (WUE_{Ph}) was expressed by the ratio of net photosynthesis to transpiration, as defined by LARCHER (1995). The measurements were conducted under constant irradiance (368.5 μ E/m^2/sec) and relatively constant ambient conditions (air temperature: 30℃ air CO_2 concentration: 340 ± 10ppm; relative humidity: 50 ± 10%). Immediately after measurement of photosynthesis, the leaf water potential of the plant was measured with a Dew Point Microvoltmeter (HR-22T, WESCOR, USA). The leaves of the plant were then cut, dried at 80℃ for 48hrs, and weighed. Because the leaves of *B. dasyphylla* are succulent and needle-shaped, rates of photosynthesis and transpiration are expressed per leaf dry matter unit in this paper.

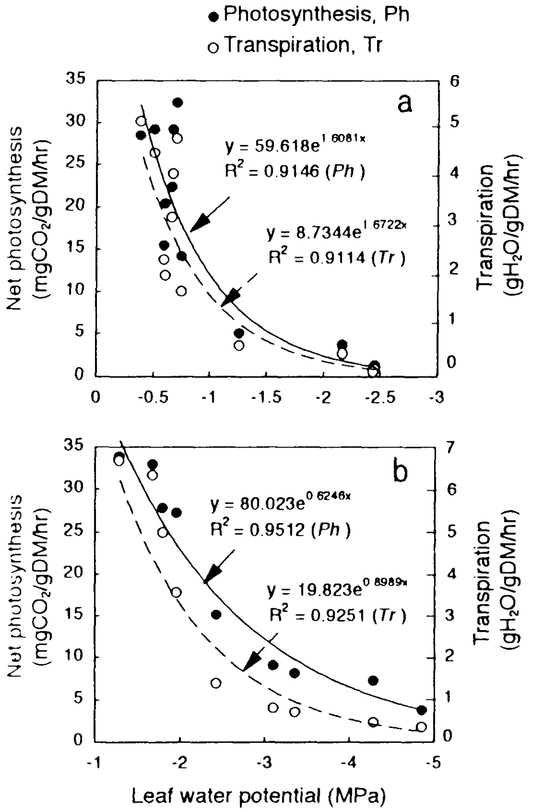
3) *In situ* soil moisture of shifting and semi-fixed sand dunes

Soil samples were collected from shifting and semi-fixed sand dunes at the seed collection sites of *A. squarrosum* and *B. dasyphylla* on Aug. 4, 1992. Because the root system of both species is distributed mainly at a depth of 0-50cm (LIU *et al.*, 1991), the soil was sampled every 5 or 10cm from the ground surface to 60cm deep at each site using soil core samplers (100cc). The wet weight of the samples was measured immediately, and the samples were then dried at 104℃ for 12hrs and weighed. Soil moisture was calculated by the formula: relative moisture (%) = (W − D)/D × 100%, where W is the wet weight and D is the dry weight of the soil sample.

3. Results

1) Responses of photosynthesis and water use to drought

In well-watered plants, the leaf water potential was -0.57 ± 0.03 MPa in *A. squarrosum* and -1.68 ± 0.06 MPa in *B. dasyphylla* (Fig. 5). Rates of photosynthesis in both species maximized in these well-watered plants, which was 29.78 ± 0.37mgCO_2/gDM/hr for *A. squarrosum* and 30.44 ± 0.74mgCO_2/gDM/hr for *B. dasyphylla*. Fig. 5 shows that increases in water stress led to a decline in rates of photosynthesis and transpiration in both species, although the sensitivity of their photosynthetic capacity to water stress differed. A marked decline in net photosynthesis occurred in *A. squarrosum* as the leaf water potential fell to below -0.6MPa, while in *B. dasyphylla* the photosynthetic rate gradually decreased as the leaf water potential declined



5. Rates of photosynthesis and transpiration in *Agriophyllum squarrosum* (a) and *Bassia dasyphylla* (b) with decreasing leaf water potential under controlled environmental conditions (irradiance: 368.5 μ E/m^2/sec; air temperature: 30℃; air CO_2 concentration: 340 ± 10ppm; relative humidity: 50 ± 10 %). All equations are highly significant ($P < 0.001$).

from -1.2 to -4.8 MPa. When the leaf water potential decreased to -2.0MPa, the photosynthetic rate of *A. squarrosum* was only 10% of maximum, whereas that of *B. dasyphylla* was still 80% of maximum.

The relationships of photosynthesis, transpiration and leaf water potential in the two species are re-illustrated in Fig. 6, which shows the values in Fig. 5 as percentages (see Discussion for the threshold and null point of photosynthetic capacity). Fig. 6 shows more clearly that the range of leaf water potential between 100% and near 0% of photosynthetic capacity differed in these two species, which was much wider in *B. dasyphylla* (-1.3 to -4.9MPa) than in *A. squarrosum* (-0.5 to -2.4MPa). It also indicated that a greater reduction of water loss in *B. dasyphylla* than in *A. squarrosum* during moderate water stress, *e.g.* when the photosynthesis of both species decreased to 44% of maximal, the transpiration of *B. dasyphylla* decreased to 21% of its maximum, whereas that of *A. squarrosum* was still 33% of its maximum.

WUE_{Ph} of well-watered plants of the two species was 6.0mgCO_2/gH_2O or so, and both species showed a similar pattern of WUE_{Ph} response to water stress, *i.e.* an increase in WUE_{Ph} at the

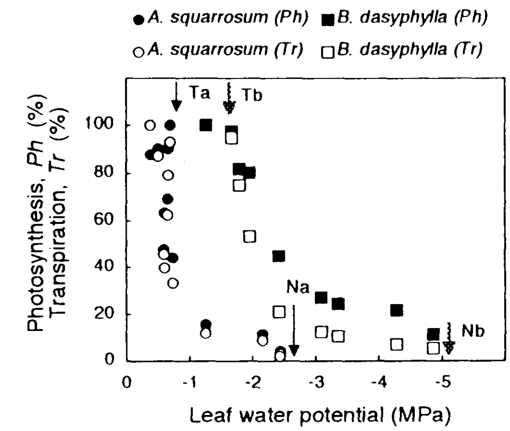


Fig. 6. Relationships of photosynthesis (%), transpiration (%) and leaf water potential in *Agriophyllum squarrosum* and *Bassia dasyphylla*.

Arrows show the threshold (Ta, Tb) and the null point (Na, Nb) of photosynthetic capacity in *A. squarrosum* and *B. dasyphylla* respectively.

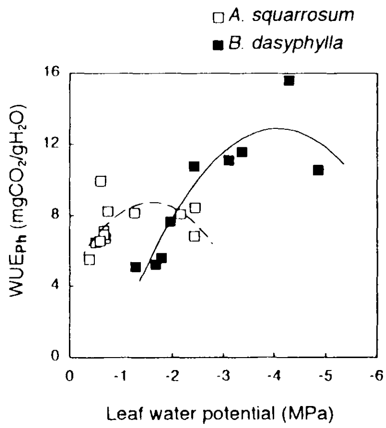


Fig. 7. Relationship between WUE_{Ph} (water use efficiency of photosynthesis) and leaf water potential in *Agriophyllum squarrosum* and *Bassia dasyphylla*.

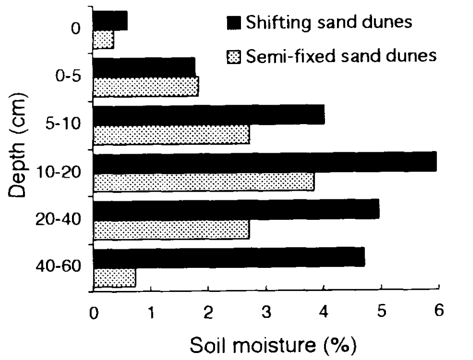


Fig. 8. Soil moisture (%) of shifting and semi-fixed sand dunes in the Shapotou area.

Aug. 4, 1992; there was a 10-mm of rainfall on the two days before sampling.

beginning of water deficit, and then a sharp decline when severe water stress occurred (Fig. 7). During moderate water deficiency, *A. squarrosum* showed a lower WUE_{Ph}, ranging between 6.7 and 9.9 $mgCO_2/gH_2O$, whereas *B. dasyphylla* exhibited a higher WUE_{Ph} which ranged between 7.6 and 15.6 $mgCO_2/gH_2O$.

2) Soil moisture of shifting and semi-fixed sand dunes *in situ*

Figure 8 shows the soil moisture of shifting and semi-fixed sand dunes at the seed collection sites. Because of a 10-mm rainfall on the two days before sampling, the soil moisture of the shifting sand dune was relatively high, reaching 6% in the layer 10-20cm deep. The water content of the semi-fixed dune was much lower than that of the shifting one in almost all layers, especially at 40-60cm depth.

4. Discussion

1) Responses of photosynthesis and water-use to drought in the two desert annuals

When grown under favorable conditions and well watered, *A. squarrosum* and *B. dasyphylla* exhibited similar maximum photosynthetic rates (Fig. 5). A decline in net photosynthesis occurred in both species when they were subjected to water stress, however, *A. squarrosum*, the most common pioneer plant of shifting sand dunes, appeared to be more sensitive to water stress than *B. dasyphylla*, which occurs frequently on semi-fixed sand dunes (Figs. 5, 6). LARCHER (1995) demonstrated that the curve of net photosynthesis vs. leaf water potential shows two critical points, one being the threshold between full photosynthetic capacity (100% of maximal) and reduced capacity (<100% of maximal), the other the null point for gas exchange (near 0% of maximal), and inferred that the sensitivity of photosynthetic capacity to drought is reflected by the position of the threshold and the null point. That is, the more sensitive a species is to drought, the earlier the null point is reached, *e.g.* the leaf water potential between the two critical points ranges between −0.5 and −2.5MPa in mesophytes, and between −1.6 and −7.0MPa or so in xerophytes (LARCHER, 1995). In this study, the leaf water potential between the two points ranged from −0.73 to −2.4MPa in *A. squarrosum*, and from −1.3 to −4.9MPa in *B. dasyphylla* (Fig. 6). Accordingly, *B. dasyphylla* exhibited the features of xerophytes, whereas *A. squarrosum* behaved like a mesophyte. These results on the features of *A. squarrosum* agree with the findings of LIU *et al.* (1987) and ZHAO and HUANG (1981), and show clearly that *A. squarrosum* is a mesophyte rather than a xerophyte, according to its photosynthetic response to drought under our experimental conditions (Figs. 5, 6).

The two species exhibited similar values of WUE_{Ph} when well watered, and both showed an increase in WUE_{Ph} at the beginning of water deficit, followed by a sharp decline when the water stress became severe (Fig. 7). However, *B. dasyphylla* exhibited a higher WUE_{Ph} during moderate water deficiency, *i.e.* it was able to use water more economically than *A. squarrosum* under water stress (Fig. 7). LARCHER (1995) pointed out that this increase of WUE_{Ph} at the beginning of water deficit occurs when the stomata are partially open and when the exchange processes of both CO_2 and H_2O are already slightly limited. The higher WUE_{Ph} in *B. dasyphylla* than in *A. squarrosum* during moderate water stress, may be explained in part by a greater reduction of water loss in the former than in the latter (Fig. 6). A preliminary study on the diurnal course of transpiration in both species has also shown that *B. dasyphylla* tends to reduce transpiration to a great extent when under drought stress (Mo *et al.*, 1994). For xerophytes like *B. dasyphylla*, a greater WUE_{Ph} during water deficiency may contribute to its survival in drought habitats (this will be discussed later). Nevertheless, the above results show clearly that *A. squarrosum* is not drought-resistant and behaves likes a mesophyte, requiring sufficient water for its growth, whereas *B. dasyphylla* tends to tolerate more severe water deficiency like a xerophyte, either through the sensitivity of its photosynthesis to drought, or through its water use efficiency during drought stress (Figs. 6, 7).

2) Soil water availability at the growing sites of the two desert annuals

The drought-sensitive *A. squarrosum* usually occurs as a pioneer species on shifting sand dunes, and is excluded from dunes which have become semi-fixed, whereas the drought-resistant species *B. dasyphylla* is frequent on semi-fixed sand dunes. The results of our field survey indicated that the soil water content is much lower in semi-fixed than in shifting sand dunes at the seed collection sites of the two species (Fig. 8). This suggests that soil water availability may be the key factor responsible for the absence of *A. squarrosum* on semi-fixed sand dunes.

To show more clearly that the water status of semi-fixed sand dunes is poorer than that of shifting dunes, we summarize the soil moisture data from the Shapotou Desert Research Station (SDRS) in Fig. 9 (samples taken every 10cm from the ground surface to 60cm deep at 15-day intervals). Rainfall is the only source of water supply for plant growth in the Shapotou desert area because of the extremely deep ground water level (QIU *et al.*, 1995). The soil moisture depends on the frequency and intensity of rainfall in this area. However, even in this very dry year of 1991 there was a relatively stable water content of 2-3% in shifting sand dunes, whereas the soil moisture

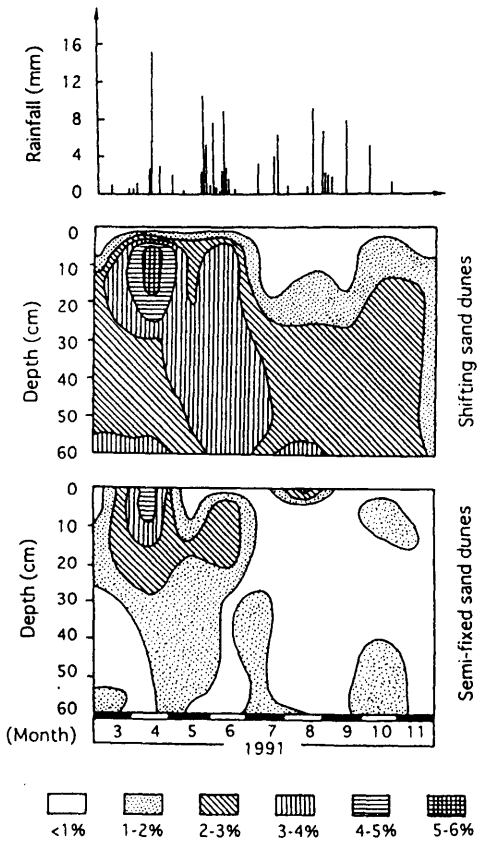


Fig. 9. Soil moisture (%) of shifting and semi-fixed sand dunes in the Shapotou area and its relation to daily rainfall.

1991 was an extremely arid year with annual rainfall of only 125mm; data from the Shapotou Desert Research Station, Lanzhou Institute of Desert Research, Chinese Academy of Sciences.

content of semi-fixed sand dunes was often below 1% (Fig. 9). These results of the field surveys in the Shapotou area (Figs. 8, 9) are consistent with the finding that soil water availability becomes increasingly limited as shifting sand dunes are fixed progressively by vegetation (CHEN, W., 1991; CHEN, H., 1992; QIU *et al.*, 1995). The same phenomena occurs in the Horqin sandy land of eastern Mongolia when the shifting sand dunes are fixed by plants naturally (ZHANG and XU, 1985; ZHU *et al.*, 1988). CHEN, H. (1992) has proposed that this lower water availability of vegetated sand dunes may be explained by (1) greater evapotranspiration because of the higher vegetation coverage, and (2) limited rainfall replenishment to the soil due to rapid evaporation and slow infiltration, which results from the soil surface features and relatively dense plant root systems.

It has been found that *A. squarrosum* has developed lateral roots but *B. dasyphylla* has developed vertical roots from the field surveys in Shapotou desert area by LIU *et al.* (1991) and QIU *et al.* (1995), *e.g.* the lateral root length of *A. squarrosum* is more than 3 times of the vertical root depth, while in *B. dasyphylla* is lower than 1 (calculated from QIU *et al.*, 1995). LIU *et al.* (1991) suggested that this developed lateral root system of *A. squarrosum* may contribute to water uptake from shifting sand dunes, especially in which the dunes are independent of ground water. Many studies have reported that the root weight ratio (root/total) of *A. squarrosum* is small but the top-root (T/R) ration is large, and pointed out this is a characteristic of species growing on unstable sand dunes (KOBASHI *et al.*, 1988; NEMOTO and LU, 1992; OHKURO *et al.*, 1994; NATORI *et al.*, 1994). Although it is still incompletely clarified the meaning of this characteristic for *A. squarrosum*, OHKURO *et al.* (1994) suggested that the root system of *A. squarrosum* is well adapted to shifting sand dunes, and contributes to its rapid growth and reproduction after germination. Finally, it should be pointed out that psammophytes are usually regarded to be drought-resistant because they can survive in severe habitat of sand dunes or sandy lands where drought and poor nutrient conditions prevail, and sometimes even combine with unstable surface condition. However, a psammophyte like *A. squarrosum* (LIU *et al.*, 1991), it is found to be drought-sensitive as a mesophyte rather than a xerophyte, based on its photosynthetic response to drought under our experimental conditions (Figs. 5, 6). On the other hand, the water availability of shifting sand dunes, the growing habitat of *A. squarrosum*, is found to be relatively higher than that of semi-fixed sand dunes where vegetation coverage is greater (Figs. 8, 9). These findings suggest that to clarify the characteristics of a species, must consider carefully both plant itself (including morphological features and physiological reponses) and the habitat conditions.

5. Conclusion

In conclusion, *A. squarrosum* is the most common pioneer plant of shifting sand dunes in northern China. However, when the shifting sand dunes are largely fixed by vegetation, this species becomes excluded. In this study, the clear finding that *A. squarrosum* is more sensitive to drought than *B. dasyphylla*, which frequently occurs on semi-fixed sand dunes (Figs. 5, 6), and the evidence that the soil water content is much lower in semi-fixed than in shifting dunes (Figs. 8, 9), strongly suggest that the exclusion of *A. squarrosum* from semi-fixed dunes is mainly due to the low water availability there. The survival of *B. dasyphylla* on semi-fixed sand dunes in the Shapotou area is obviously due to its ability to maintain its photosynthetic capacity and use water economically during drought (Figs. 5, 7, 9). *A. squarrosum* is sensitive to drought like a mesophyte (Figs. 5, 6) and as a result, is excluded from semi-fixed sand dunes. However, it can grow on shifting dunes where the soil water content is relatively higher and stable (moisture content of at least 2-3%) throughout the growing seasons (Figs. 8, 9).

Plants differ in the ways in which they survive drought (TURNER, 1986) and desert plants vary widely in their capacity to maintain photosynthetic activity under water stress (EHLERINGER, 1994). There are species which can escape drought by timing their growth and reproduction to occur in the brief period when sufficient water is available, LARCHER (1995) has referred to such plants as "drought-escaping xerophytes". A desert plant like *A. squarrosum* is drought-sensitive

(Figs. 5, 6), but it can escape drought by selecting its growth sites, and can survive in desert regions. On the other hand, *A. squarrosum* is able to germinate between spring and summer whenever the conditions are suitable, and then grows rapidly after germination, almost all stands producing seeds (Shi, 1991; Nemoto and Lu, 1992; Ohkuro *et al.*, 1994). Overall, shifting sand dunes still represent an unique habitat where the extremely unstable surface is a common stress for plants growing on them (Nemoto and Lu, 1992). Natori *et al.* (1994) inferred that the growth of *A. squarrosum* on shifting sand dunes, may be mainly determined by other factors such as unstable surface rather than water availability of sand dunes. Clearly, further studies are needed for fully understanding the survival strategies of *A. squarrosum* on shifting sand dunes, especially seed production and dispersal, seed storage during dry seasons, seed longevity, germination and initial growth on the unstable surface.

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References

Chen, H. (1992): The characteristics of biological crust and its environmental significance in Shapotou region. *Chinese Arid Zone Res.*, **9**-1: 31-38. (in Chinese with English summary)

Chen, W. (1991): Water balance in the revegetated area along the railway in Shapotou area. *In* SDRS eds., *Studies on Drifting Sand Control in the Shapotou Area of Tengger Desert (II)*, Ningxia People Press, Yinchuan, China, 66-75. (in Chinese with English summary)

Ehleringer, J.R. (1994): Variation in gas exchange characteristics among desert plants. *In* Schulze, E.-D. and Caldwell, M.M.eds., *Ecophysiology of Photosynthesis*, Springer-Verlag, Berlin, Heidelberg, New York, 361-392.

Larcher, W. (1995): *Physiological Plant Ecology (3rd ed.)*. Springer-Verlag, New York, Berlin, Heidelberg, 388pp.

Liu, J. (1982): The xeromorphic structure of different typical plants in deserts of China. *Acta Phytoecological et Geobatanica Sinica*, **6**-4: 314-319. (in Chinese)

Liu, J. *et al.* (1984): *Map of the Shapotou Artificial Vegetation System for Prevention Railways from Drifting Sand.* Ningxia Press. (in Chinese)

Liu, J., Pu, J. and Liu, X. (1987): Comparative studies on water relations and xeromorphic structure of some plant species in the middle part of the desert zone in China. *Acta Botanica Sinica*, **29**-6: 314-319. (in Chinese)

Liu, Y., Yang, X., Tao, Y. and Zhang, G. (1985): *Flora in Desertis Reipublicae Populorum Sinarum, Vol. 1.* Academy Press, Beijing, China. (in Chinese)

Liu, Y., Li, Y. and Yang, H. (1991): Root systems of psammophytes. *In* SDRS (Shapotou Desert Research Station, Lanzhou Institute of Desert Research, Chinese Academy of Sciences)eds., *Studies on Drifting Sand Control in the Shapotou Area of Tengger Desert (II)*, Ningxia People Press, Yinchuan, China, 185-209. (in Chinese with English summary)

Lu, Z. (1980): Studies on water status in the green organs of xerophytes. *Chinese Bull. Plant Physiol.*, **4**: 23-27. (in Chinese)

Kobashi, S., Yoshikawa, K. and Masuda, T. (1988): Growth of Shami (*Agriophyllum squarrosum*) on sand dune at the Mu Us desert in Inner Mongolia. *Bull. Revegetation Res.*, **10**: 167-199. (in Japanese with English summary)

Mo, W., Natori, T., Omasa, K. and Jiang, S. (1994): Comparative studies on drought resistance of *Agriophyllum squarrosum* and *Bassia dasyphylla* in controlled environment. *In* Ichikuni, M. ed. *Proceedings of the Japan-China International Symposium on the Study of the Mechanism of Desertification*, Toyo Publishing & Printing Co., Ltd., Tokyo, 493-499.

Natori, T., Mo, W., Li, X., Omasa, K. and Jiang, S. (1992): The culture of Chinese desert plants in a greenhouse. *Acta Horticulturae*, **319**: 453-458.

Natori, T., Tobe, K., Mo, W., Li, X., Jiang, X. and Omasa, K. (1994): Growth of several desert plants under favorably controlled conditions. *In* Ichikuni, M. ed. *Proceedings of the Japan-China International Symposium on the Study of the Mechanism of Desertification*, Toyo Publishing & Printing Co., Ltd., Tokyo, 451-454.

Nemoto, M. and Lu, X. (1992): Ecological characteristics of *Agriophyllum squarrosum*, a pioneer annual on sand dunes in eastern Inner Mongolia, China. *Ecol. Res.*, **7**:

183-186.

Ohkuro, T., Nemoto, M., Lu, X., Xu, B. and Liu, X. (1994): Ecological characteristics of three native species, grown in semi-arid grassland in eastern Inner Mongolia, China. *In* Ichikuni, M. ed., *Proceedings of the Japan-China International Symposium on the Study of the Mechanism of Desertification*, Toyo Publishing & Printing Co., Ltd., Tokyo, 440-445.

Qiu, G.Y., Yano, T., Momii, K. and Shi, Q.H. (1995): The succession of planted communities in Tengeri Desert in relation to root distribution and soil water status. *J. Arid Land Studies*, 4: 81-89.

Schulze, E.-D. (1986): Carbon dioxide and water vapor exchange in response to drought in atmosphere and in the soil. *Ann. Rev. Plant Physiol.*, **37**: 247-274.

Shen, W. (1986): The status of Artemisia ordosica in vegetation succession at Shapotou area. *Chinese J. Desert Res.*, **6**-4: 13-22. (in Chinese)

Shi, Q. (1991): The plant phenophase in Shapotou area. *In* SDRS (Shapotou Desert Research Station, Lanzhou Institute of Desert Research, Chinese Academy of Sciences) ed., *Studies on Drifting Sand Control in the Shapotou Area of Tengger Desert (II)*, Ningxia People Press, Yinchuan, China, 425-435. (in Chinese with English summary)

Turner, N.C. (1986): Adaptation to water deficits: a changing perspective. *Aust. J. Plant Physiol.*, **13**: 175-190.

Zhang, J. and Xu, B. (1985): Moisture condition in different dunes in southern Horqin steppe. *Chinese J. Desert Res.*, **5**-3: 33-39. (in Chinese)

Zhao, C. and Huang, Z. (1981): A preliminary study of xeromorphism of some important xerophytes growing in Tengger Desert. *Acta Botanica Sinica*, **23**-4: 278-283. (in Chinese)

Zhao, X. (1991): Problems of revegetation on sand dunes in Shapotou area. *In* SDRS (Shapotou Desert Research Station, Lanzhou Institute of Desert Research, Chinese Academy of Sciences) ed., *Studies on Drifting Sand Control in the Shapotou Area of Tengger Desert (II)*, Ningxia People Press, Yinchuan, China, 27-57. (in Chinese with English summary)

Zhu, Z., Zou, B., Di, X., Wand, K., Zhang, J., Chen, G., Wen, Z., Shao, L. and Xu, B. (1988): *Desertification and Rehabilitation: Case Study in Horqin Sandy Land.* Lanzhou Institute of Desert Research, Chinese Academy of Sciences, Lanzhou, China, **2**-16, 60-63.