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Vegetation Growth and Physiological Adaptation of Pioneer Plants on Mobile Sand Dunes

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Abstract: The Hunshandake Sandy Land is one of the largest sandy areas in China and the closest source of sand dust to the Beijing and Tianjing areas. Sand fixation by vegetation is considered the most efficient strategy for sand control and sustainable development, so clarifying the vegetation coverage and plant adaptation characteristics in the Hunshandake Sandy Land is helpful in guiding restoration and improving local sustainability. Here, we investigated the vegetation growth on the mobile sand dunes in the Hunshandake Sandy Land and specified the photosynthesis and stomatal characteristics of the pioneer plants for sand fixation. The vegetation survey showed that the windward slopes of the mobile sand dunes had far lower plant coverage (6.3%) and plant biodiversity (two species m^{-2}) than the leeward ones (41.0% and eight species m^{-2}, respectively). *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. were the only two sand-fixing pioneer plants that grew on both the windward and leeward slopes of the mobile sand dunes and had higher plant heights, greater abundance, and more biomass than other plants. Physiological measurements revealed that *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. also had higher photosynthetic rates, transpiration rates, and water use efficiency. In addition, the stomata density (151–197 number mm^{-2}), length (18–29 μm), and area index (13–19%) of these two pioneer species were smaller than those of the common grassland species in Inner Mongolia, suggesting that they were better adapted to the dry habitat of the mobile sand dunes. These findings not only help in understanding the adaptive strategies of pioneer plants on mobile sand dunes, but also provide practical guidance for sand dune restoration and the sustainable development of local areas. Pioneer sand-fixing plant species that are well adapted to sand dunes can be used for sowing or aerial seeding in sand fixation during ecosystem restoration.

Keywords: sand dunes; pioneer plants; vegetation; photosynthetic rate; stomata

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1. Introduction

The Hunshandake Sandy Land is the northern sand barrier of China and is a major source of wind and sand in the vicinity of the Beijing–Tianjin–Hebei region [1]. It is the closest sandy area to Beijing, with a linear distance of less than 200 km. Located in the transition zone from the typical grassland area to the dryland agricultural area in Northern China, with a fragile ecological environment, it seriously threatens the local sustainability and natural environment of Beijing and its surroundings.

Vegetation plays a key role in controlling desertification. Sand fixation by vegetation is considered to be the most cost-effective and long-lasting of the many sand control measures [2,3]. Sand-fixing plants can not only act as windbreakers and sand traps, but also improve the soil and restore the ecological environment of sandy land. In a sandy environment, vegetation can effectively reduce the wind speed and mitigate soil wind erosion,

thereby reducing the loss of fine particles and nutrients in the surface soil [4,5]. Plants on mobile dunes, especially pioneer sand-fixing plants, play effective roles in blocking surface wind erosion and sand movement, and their role in reducing wind and fixing sand is crucial in improving the surface structure and environment in sandy areas [6–8]. For this reason, pioneer plants growing on sand dunes with severe soil erosion and water shortage are also called "polar pioneers" due to their extreme persistence and vitality [9,10]. These sandy fixing plants are widespread and play key roles in the vegetation ecology of the Hunshandake Sandy Land. Research on the growth characteristics of pioneer plants can provide a theoretical basis for active restoration in sandy areas.

The adaptation strategies of pioneer plants on sandy soils have been extensively studied by previous researchers, especially regarding their physiological traits, such as the photosynthetic rate, transpiration rate, and water utilization rate [11–13]. For example, the transpiration rate and net photosynthetic rate of sandy cypress have been reported to increase linearly with the soil water content in desert ecosystems [14,15]. However, the physiological adaptation mechanisms vary widely among different plants living in sandy soils [16,17]. A pioneer sand-fixing C_3 species, *Hedysarum fruticosum* var. *Mongolicum*, displays C_4 metabolic characteristics, which account for its greater efficiency in photosynthesis and water use, allowing *H. fruticosum* to colonize sand dunes with high temperatures, intense light, and water stress [16]. By comparing the sand fixation capacity of three typical shrubs in the Hunshandake Sandy Land, Dong et al. (2020) clarified that the small-leaved mallow had a better conservation function and a better wind and sand fixation role in the degraded ecosystem [18]. Although the above-mentioned previous studies have conducted some research on plants on fixed dunes in the Hunshandake Sandy Land, no comparative study has been conducted on the plant growth and vegetation composition on mobile dunes, especially comparing the differences in plant growth between windward and leeward slopes, where the wind erosion, soil conditions, and light conditions are different. This provides an opportunity to study pioneer plant growth in different habitats [19,20]. Compared with fixed sand dunes, the restoration of mobile sand dunes is more important and crucial for the sustainable development of the local area. Studying the growth of plants on different slopes of mobile sand dunes can help to more comprehensively restore mobile sand dunes.

Plants can evolve some unique traits to adapt to arid environments, and the leaf stomatal characteristics are some of the most important adaptive traits. Stomata are tiny pores on the surfaces of leaves, formed by two guard cells. They regulate the exchange of water vapor and carbon dioxide between the leaf's interior and the atmosphere, thereby optimizing the efficiency of water use in the leaf [21,22]. The stomatal morphology is diversified with environmental adaptation [23] and has therefore been widely used to understand the plasticity and evolutionary responses to climate change [24,25]. Compared with those in humid environments, species adapted to arid conditions typically have a higher stomatal density, which helps to increase the gas exchange rates during favorable wet periods [26]. In addition, a high ratio of the stomatal length to the guard cell length is beneficial for plants to resist drought [27]. However, few studies have focused on the stomatal characteristics of pioneer plants on mobile sand dunes.

In this study, we investigated plant growth at different slope orientations on mobile dunes in terms of coverage, height, and biomass by comparing the plant species composition and vegetation characteristics on windward and leeward slopes. In particular, two widespread, dominant pioneer plants on mobile dunes, *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq., were studied by examining their photosynthetic rates, transpiration rates, water use efficiency, and stomatal characteristics. These two species have deep and fibrous root systems and can rapidly colonize sandy areas. However, their physiological adaptation has not yet been elucidated. The scientific questions considered in this study are as follows: (1) How do the species composition and vegetation growth differ between the windward and leeward sides of mobile sand dunes? (2) What physiological adaptation traits have pioneer sand-fixing species adopted to adapt to the sandy

environment? The objective of this study is to provide experimental data and a theoretical basis for the restoration of mobile sand dunes and the sustainable management of sandy areas.

2. Materials and Methods

2.1. Experimental Location

The field experiment was carried out at the Hunshandake Sandland Ecological Research Station (42°51′51.05″ N; 116°23′58.66″ E), Institute of Botany, Chinese Academy of Sciences, in August 2022–2024. The Hunsandake Sandy Land is one of the four sandy lands in northern China, located at the southern end of the Xilingol Grassland in Central Inner Mongolia. The area belongs to the inland semi-dry zone, with cold winters, dry and hot summers, rain and heat in the same season, and gusty winds in spring. The annual rainfall amounts to 200–350 mm, and the annual evaporation amounts to 2000–2700 mm. The average annual temperature is 1.7 °C, with a maximum of 36.6 °C in July and a minimum of −24 °C in January. The frost-free period is 100–110 d. Throughout the year, winds with a force of 8 or higher occur 60–80 times, and the average annual wind speed is 4–5 m s^{-1}. The Hunshandake Sandy Land's landscape consists of mobile dunes, semi-fixed dunes, fixed dunes, and grasslands, with mobile dunes accounting for more than 27.91% of the landscape.

2.2. Vegetation Survey

This experiment was conducted during the peak biomass period in August 2022. The typical mobile sand dunes near the Hunshandake Sandland Ecological Research Station in Xilingol League, Inner Mongolia, were selected as the study area. The dunes are oriented in the north–south direction, with windward slopes in the west and leeward slopes in the east. Six 1 m × 1 m sample plots were randomly selected on both the windward and leeward slopes of the mobile dune, and the abundance, cover, and height of different plant species were measured in each sample plot. In total, six replicates were obtained for the vegetation survey. Specifically, a 1 m × 1 m frame was placed over the canopy of each plot, and the frame was further divided into 100 grids (10 cm × 10 cm) to improve the accuracy of the visual inspection. All herbaceous species and their number of individuals, coverage, and height in each grid were recorded. For each surveyed plot, the plant height (unit: cm) was measured as the maximum height of each species in each grid, and the final species height was the average across all 100 grids. The coverage (unit: %) of species in each survey plot was calculated by summing the coverage of all 100 grids. Furthermore, we calculated the relative abundance of the species (unit: %) according to the following equation:

$$\text{Relative abundance of species} = n_i / \sum n_i$$

where n_i is the abundance of individual species i, and Σn_i is the abundance of all species.

For the biodiversity index, we calculated the Shannon–Weiner index using the equation of $H = -\Sigma(P_i)(\log_2 P_i)$, where Pi is the proportion of individual species i, representing the relative density of plant species. P_i was calculated as $P_i = n_i/\mathrm{N}$, where n_i is the number of individual species i, and N is the total number of species.

2.3. Soil Moisture Measurement

Within each of the vegetation sample plots, 0–10 cm and 10–20 cm soil samples were taken with an Earth auger and placed in aluminum boxes, the lids of which were marked. Twenty-four soil samples (six samples from the windward slopes and six samples from the leeward slopes, with two soil depths for each sample plot) were weighed to determine the wet weight. The total number of replicates for the soil moisture measurements was therefore also six. The dry weight was determined after the samples were dried in an oven at 65 °C for 48 h. The water content of the soil samples was calculated from the wet and dry weights of the soil samples in each aluminum box.

2.4. Plant Photosynthesis, Transpiration, and Water Use Efficiency

Based on the plant coverage and vegetation survey, we selected two common pioneer species (*Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq.) in each plot to measure their photosynthesis on both the windward and leeward slopes of the mobile sand dunes during the peak biomass period in 2022. Thus, the total number of replicates for the photosynthesis measurements of each species was also six. Leaf gas exchange was measured using a CIRAS-3 photosynthesis system (PP Systems, Amesbury, MA, USA). The leaf cuvette had a 2.5 cm^2 window, and light was provided by red, green, and blue light-emitting diodes, set at 38% red, 37% green, and 25% blue, to simulate sunlight. Each leaf was randomly selected, ensuring that it was mature, fully exposed to the sun, and free of disease or insect pests. More than three individuals of each species were measured in each plot and averaged to represent the photosynthetic rate of the species within each plot. Measurements were taken between 9:00 and 12:00. The temperature was 31.3–34.9 °C, the relative humidity was 53.1–66.6%, and the photosynthetic active radiation amounted to 2008.0–2247.0 μmol $m^{-2}s^{-1}$. During the measurement, the length and width of the leaves were measured using a small ruler, and then the leaves were clamped in a leaf chamber so that they faced the direction of sunlight, and the data were stored in the photosynthesis instrument after the indicators had stabilized. The water use efficiency (WUE) of individual leaves was calculated as the rate of photosynthesis divided by the rate of transpiration.

2.5. Biomass Measurement

After measuring the vegetation cover and photosynthesis, we collected all plants in each sample plot, including both the above-ground and below-ground parts of the plant, by digging up their roots to a depth of 50 cm. This gave a total of six replicates for the biomass measurements. We then placed them in plastic bags and took them to the laboratory. In the laboratory, the plants in each sample plot were classified into different species and their above-ground and underground parts were separated. The roots were carefully washed by hand. Finally, all samples were oven-dried at 65 °C for 48 h until they reached a constant weight and were weighed. The biomass of all species and each specific species per quadrant was averaged over the six biological replicates.

2.6. Stomatal Microscopy Imaging

To further investigate the drought tolerance mechanisms of pioneer plants based on their stomatal characteristics, we collected the functional leaves of *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. from the mobile sand dunes and measured their stomatal characteristics in August 2024. We randomly collected one functional leaf from each of the two dominant species in each of the six sample plots, with a total of six leaves from each species; then, we placed them in a freezer and brought them back to the laboratory for experimentation. This gave a total of six replicates for the stomata measurements for each species. We used the nail polish imprint method to create the film. The specific method involved evenly applying a layer of nail polish to the underside of the leaves, about two-thirds from the tips of the leaves; allowing it to dry naturally at room temperature; attaching the imprints to the lower epidermises of the leaves with transparent tape; and then attaching them to the glass slides to produce temporary slides. The AOSVI L208PS-HK830 microscopy imaging system (Shenzhen, China) was used for photography and measurement.

The following were the specific measurement and calculation methods used for the porosity indicators.

(1) Stomatal density (SD): We randomly selected nine microscopic visual fields with sizes of about 0.1 mm^2 for each sample, measured the field area, and counted the number of stomata in the field. We converted this value into the number of stomata per unit area, which is the SD (cells mm^{-2}).
(2) Stomatal length (SL): Nine fields with sizes of approximately 0.1 mm^2 were randomly selected from each sample, and five stomata were randomly selected from each field.

The length of the stomata and the length (μm) of the two guard cells shaping the stomata were measured.

(3) Stomatal area index (SPI): The total stomatal area per unit area was calculated as follows: SPI (%) = $SL^2 \times SD \times 10^{-4}$.

These methods and calculations have been widely used in previous studies [24,26].

2.7. Statistic Analysis

We first calculated the means and standard deviations of different variables based on their replicates. An analysis of variance (ANOVA) was then used to compare the statistical differences in the vegetation characteristics between the different slopes, as well as the photosynthetic variables between the two pioneer species and between different slopes. The results for all tests were considered significant if the corresponding *p*-values were <0.05. All analyses were performed using the SPSS software (v 4.0.3, R Development Core Team, Vienna, Austria, 2019), and all figures were generated using Sigmaplot 12. All values are presented as the mean ± SE.

3. Results

3.1. Soil Properties

The soil moisture content of the mobile sand dune at 0–10 cm and 10–20 cm was very low, with a value of 1.3–4.7%. Significant differences were found between the different soil layers and slopes (both $p < 0.05$). The soil moisture was significantly lower on the windward than leeward slopes and was significantly lower at a depth of 0–10 cm than at 10–20 cm (all $p < 0.05$, Figure 1).

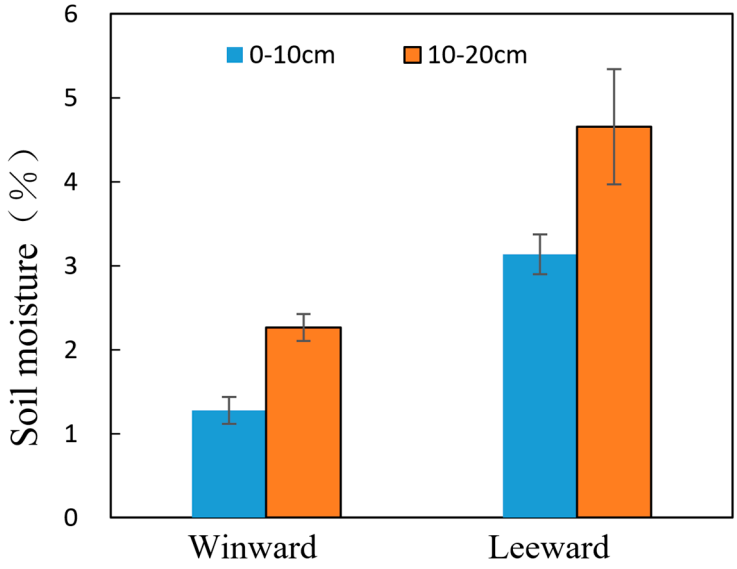


Figure 1. Soil moisture content of different soil layers on the windward and leeward slopes of the mobile sand dunes.

3.2. Species Composition and Community Structure

The plant species composition of the vegetation varied between the windward and leeward slopes of the mobile sand dunes. The dominant plants on the windward slope were *Elymus sibiricus* L., *Agriophyllum squarrosum* (L.) Moq., *Salsola collina* Pall., and *Artemisia ordosica* Krasch., while those on the leeward slope, apart from these four plants, were *Bromus inermis* Leyss., *Cleistogenes squarrosa* (Trin.) Keng., *Bassia dasyphylla* (Fisch. et Mey.) Freitag and G. Kadereit, and *Polygonum sibiricum* (Laxm.) Tzvelev (Figure 2a). The total vegetation coverage was 6.26% on the windward slope and 41.01% on the leeward slope (Figure 2a). As a pioneer plant in the Hunshandake Sandy Land, *Elymus sibiricus* L. had average coverage of 26.25% on the leeward slope, which was significantly higher than that (2.68%) on

the windward slope and much higher than the coverage of other plants on the leeward slope (Figure 2a). The coverage of another pioneer plant, *Agriophyllum squarrosum* (L.) Moq., did not differ significantly between the slopes (2.13% on the windward slope vs. 2.83% on the leeward slope, $p = 0.36$). The abundance of *Elymus sibiricus* L. was obviously the highest on both the windward and leeward slopes (Figure 2b), while the abundance of *Agriophyllum squarrosum* (L.) Moq. on the windward slope was second only to that of *Elymus sibiricus* L. The coverage and abundance of *Bromus inermis* Leyss., *Bassia dasyphylla* (Fisch. et Mey.) Freitag and G. Kadereit, and *Polygonum sibiricum* (Laxm.) Tzvelev, grown only on the leeward slope, were very low. On average, the plant height was significantly higher on the leeward slope than on the windward slope ($p < 0.05$, Figure 2c). These differences in species composition and growth between the windward and leeward slopes are important for restoration practices, which suggests that different species should be selected for restoration on different slopes of the dunes.

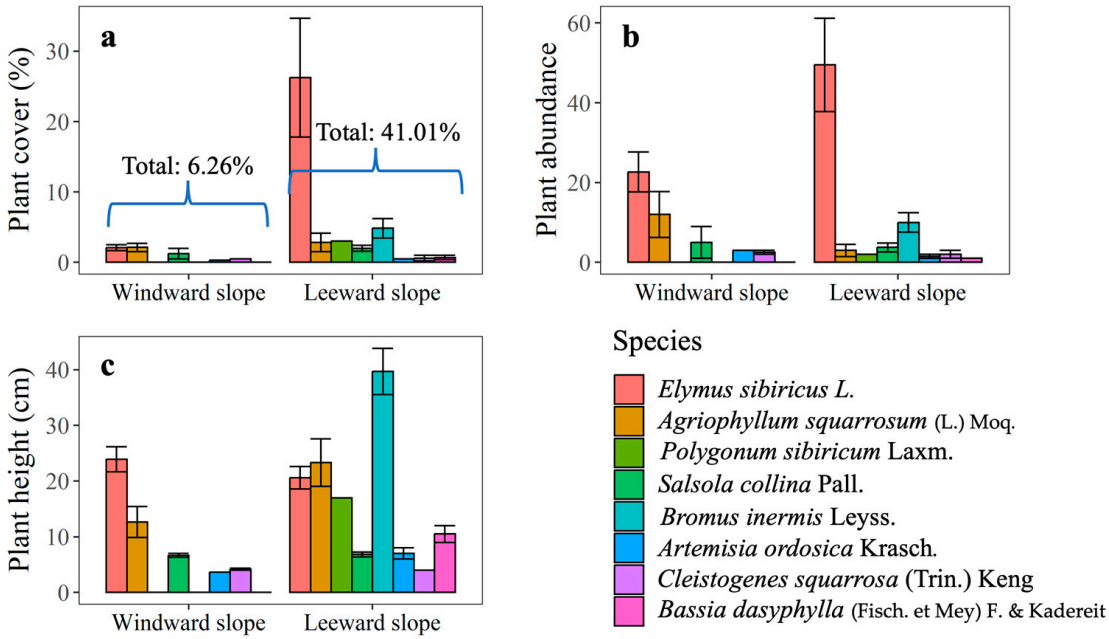


Figure 2. Plant species composition and characteristics, including plant cover (**a**), abundance (**b**) and height (**c**) on windward and leeward slopes of sand dunes.

The above-ground biomass of each plant species was lower on the windward slope than on the leeward slope ($p < 0.05$). For example, the above-ground biomass of *Elymus sibiricus* was 15.75 g m^{-2} on the windward slope, but 33.91 g m^{-2} on the leeward slope. The root biomass difference between the slopes was similar to that of the above-ground biomass, with higher values on average on the leeward slope than on the windward slope ($p < 0.05$). Among them, the root biomass of *Elymus sibiricus* L. was 8.14 g m^{-2} on the windward slope and 49.85 g m^{-2} on the leeward slope (Figure 3b).

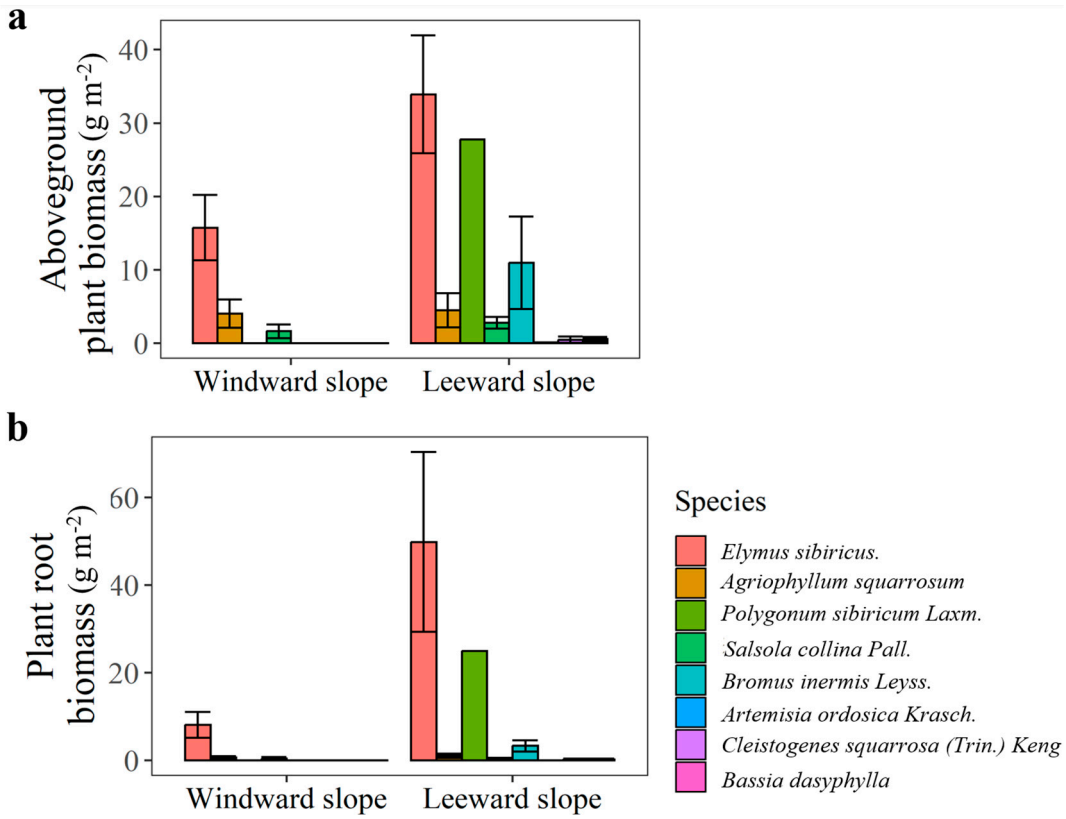


Figure 3. Aboveground biomass (**a**) and root biomass (**b**) of each plant species on the windward and leeward slopes of the sand dunes.

3.3. Vegetation Biomass and Biodiversity

The plant diversity index was higher on the leeward slope than on the windward slope ($p < 0.05$, Figure 4a). The above-ground community biomass was 50.37 g m^{-2} on the leeward slope, which was significantly higher than that on the windward slope (19.28 g m^{-2}) ($p < 0.05$, Figure 4b). The below-ground biomass was 8.48 g m^{-2} on the windward slope, which was also significantly higher than that on the leeward slope (57.15 g m^{-2}) ($p < 0.05$, Figure 4c).

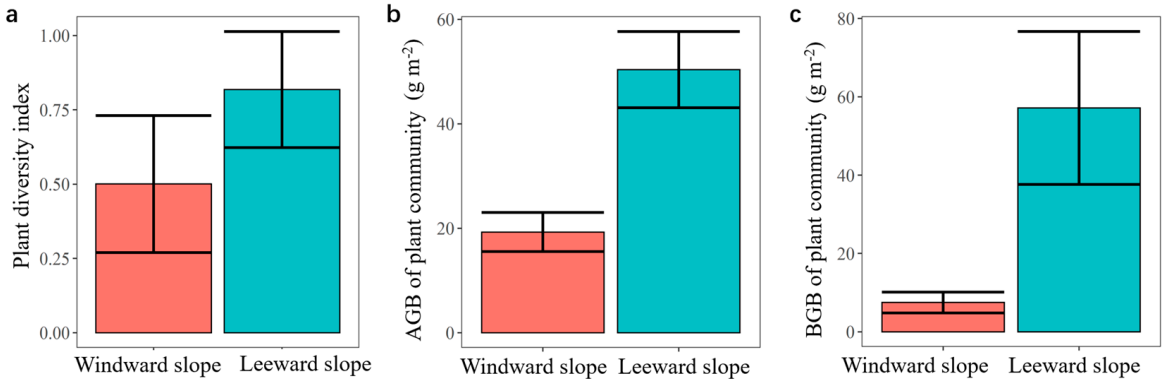


Figure 4. Community diversity index (**a**) and above-ground biomass (AGB, (**b**)) and below-ground (BGB, (**c**)) biomass on the windward and leeward slopes of the sand dunes.

3.4. Photosynthetic Rate, Transpiration Rate, and Water Use Efficiency

As *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. were the two dominant pioneer plants with the highest coverage and abundance on the mobile dune, their photosynthetic characteristics were investigated. The photosynthetic rate of *Elymus sibiricus* L.

was 18.26 μmol $m^{-2}s^{-1}$ on the windward slope and 21.93 μmol $m^{-2}s^{-1}$ on the leeward slope, with no significant difference between them (p = 0.26, Figure 5a). The photosynthetic rate of *Agriophyllum squarrosum* (L.) Moq. was 36.36 μmol $m^{-2}s^{-1}$ on the windward slope and 34.21 μmol $m^{-2}s^{-1}$ on the leeward slope, with no significant difference between them either (p = 0.53). The transpiration rates of *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. (Figure 5b) were 12.37 mmolH_2O $m^{-2}s^{-1}$ and 16.20 mmolH_2O $m^{-2}s^{-1}$, respectively, on the windward slope, again with no significant difference between the windward and leeward slopes (p = 0.66 and 0.15, respectively, for the two species). The water use efficiencies of *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. (Figure 5c) were 1.52 μmolCO_2 mmol$^{-1}H_2O$ and 2.26 μmolCO_2 mmol$^{-1}H_2O$, respectively, on the windward slopes, which were both similar to those on the leeward slopes (p = 0.19 and 0.75, respectively, for the two species).

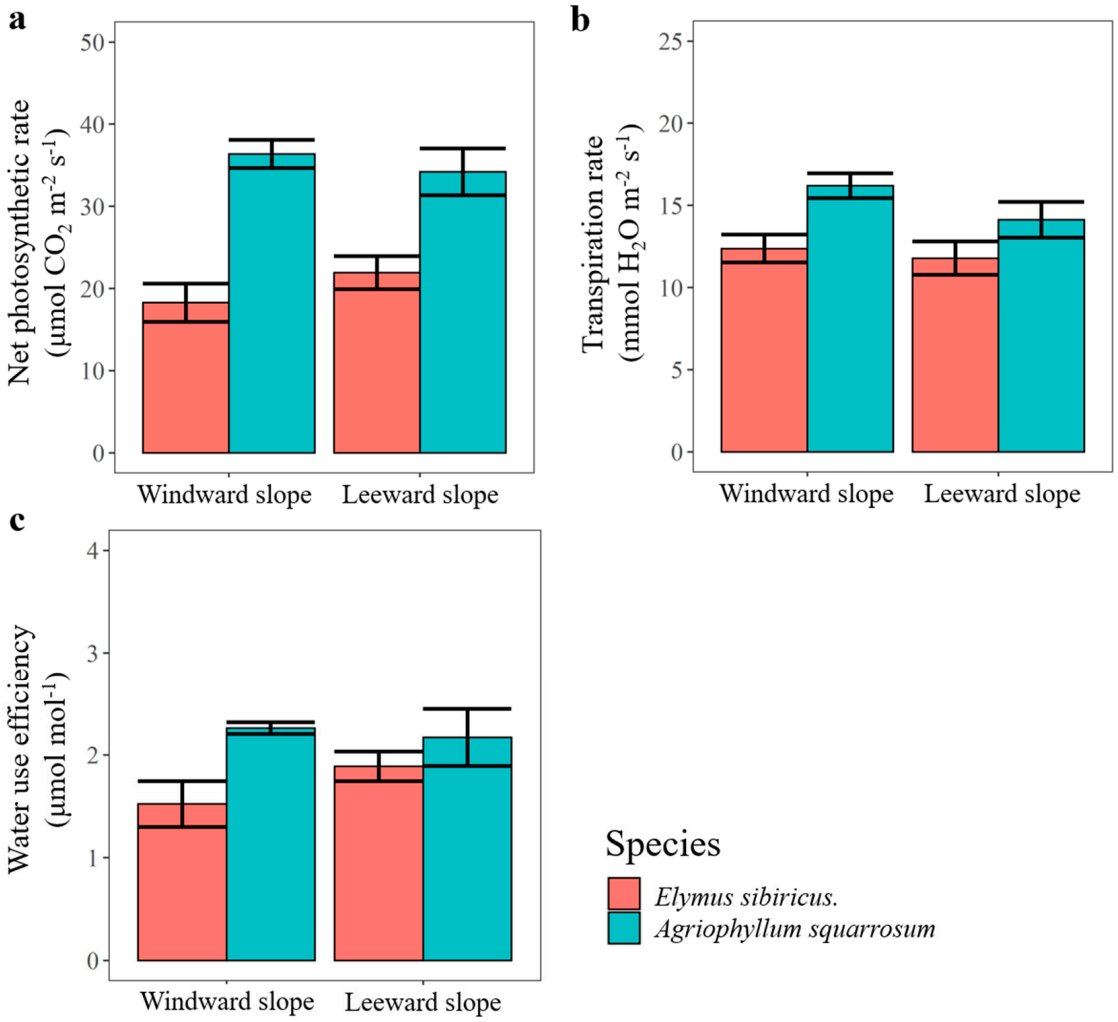
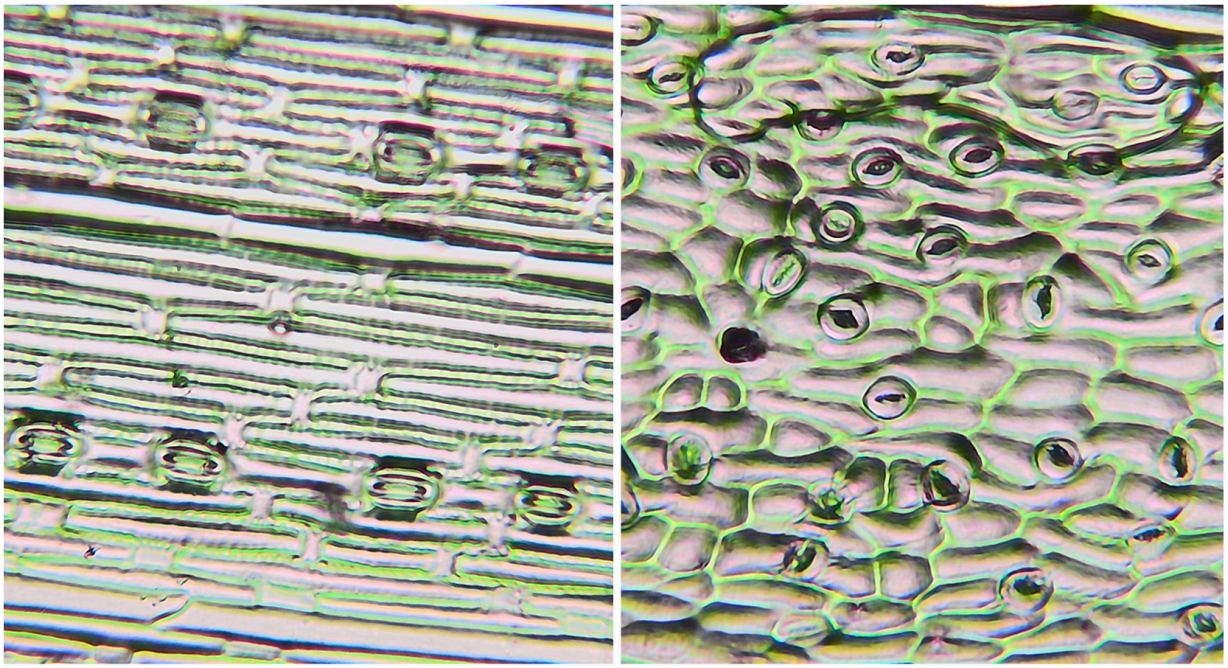


Figure 5. Photosynthetic rates (**a**), transpiration rates (**b**), and water use efficiency (**c**) characteristics of two pioneer plants, *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq., on the windward and leeward slopes, reflecting the physiological adaptation of these two species to the mobile sand dunes.

3.5. Stomatal Characteristics of Two Pioneer Plants

Since no significant difference was found in the photosynthesis and transpiration rates of the two pioneer plants between the leeward slope and the windward slope, we measured the stomatal characteristics of their leaves on the windward slope. The stomatal apparatus of *Elymus sibiricus* L. was dumbbell-shaped, the guard cells outside were of the dumbbell type, and the stomata were distributed in bands (Figure 6a). The stomatal apparatus of *Agriophyllum squarrosum* (L.) Moq. was kidney-shaped, and the guard cells

outside were of the kidney type, with a scattered distribution (Figure 6b). The stomatal density (the number of pores per unit area), stomatal length, and stomatal area index (the total stomatal area per unit area) between the leaves of *Agriophyllum squarrosu* (L.) Moq. and *Elymus sibiricus* L. were also significantly different (Table 1). The stomatal density, stomatal length, and stomatal area index of *Elymus sibiricus* L. were 152.24 ·mm^{-2}, 29.93 µm, and 13.18%, respectively, while their counterparts in *Agriophyllum squarrosu* (L.) Moq. were 197.12 mm^{-2}, 18.21 µm, and 19.31%, respectively (Table 1). Compared with typical grassland plants, the stomatal density, length, and index of the two pioneer plants were smaller.



(**a**) (**b**)

Figure 6. Stomatal shape and distribution of the upper epidermis of the leaves of *Elymus sibiricus* L. ((**a**), dumbbell type) and *Agriophyllum squarrosum* (L.) Moq. ((**b**), kidney type) on the windward slope, which reflect the stomatal adaptation of these two species to the mobile sand dunes.

Table 1. The stomatal characteristics on the upper surfaces of the leaves of the pioneer plants *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. in the mobile sand dunes and their comparison with those of grassland plants.

Stomatal Index	*Elymus sibiricus*	Grassland Plant (Dumbbell Type)	*Agriophyllum squarrosum*	Grassland Plant (Kidney Type)
Stomatal density (number/mm^2)	151.24 ± 35.6	248.9	197.12 ± 43.52	206.0
Stomatal length (µm)	29.93 ± 7.85	33.4	18.21 ± 4.37	23.7
Stomatal area index (%)	13.18 ± 4.12	24.2	19.31 ± 2.12	10.0

The data on the stomata in grassland plants were taken from Wang et al., 2018 [28].

4. Discussion

This study not only compared the plant diversity and species composition, biomass, and photosynthetic traits on the windward and leeward sides of mobile dunes, but also compared the growth and stomatal traits of two pioneer plants. The photosynthetic and stomatal characteristics of the two pioneer plants indicated their physiological adaptation to the arid environment of the mobile sand dunes.

Due to wind erosion, sand burial, strong solar radiation, and extreme drought, the microenvironmental conditions in mobile sand dunes are harsh. The soil water content of the mobile dunes in the Hunshandake Sandy Land was very low (Figure 1), similar to that of other sandy areas like the Mu Us Sandy Land (2–4%) [29]. However, the pioneer plants can still grow well and have high photosynthetic rates (Figure 5), indicating that they can overcome the harsh environment and have unique adaptability to drought [15]. One reason for this adaptability is that the roots of these sandy plants are very long, generally 40–60 cm, and can reach up to 2 m, allowing the plants to absorb water from deep soil [30,31]. In addition, the pioneer plants on the sand dunes can quickly take advantage of the rainy season's rainfall for rapid growth and biomass production [32,33].

We found that the vegetation differed largely between the windward and leeward slopes. The higher wind speed on the windward slope causes more severe wind erosion and sand erosion and thus has more adverse effects on plant growth [34,35], which are characterized by a lower plant growth rate, less vegetation coverage, lower abundance, and less biomass than those on the leeward slope (Figure 2). Based on the plant height and above-ground biomass indicators, the pioneer plants *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. are better adapted to the harsh environment on the windward slopes of the sand dunes than other plants, such as *Salsola collina* Pall., *Bromus inermis* Leyss., *Bassia dasyphylla* (Fisch. et Mey.) Freitag and G. Kadereit, and *Polygonum sibiricum* (Laxm.) Tzvelev. Therefore, when propagating pioneer plants for ecological restoration on windward sand dunes, *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. are the best choices. Besides the two pioneer plants mentioned above, *Bromus inermis* Leyss. and *Polygonum sibiricum* (Laxm.) Tzvelev also showed strong adaptation, with advantages in terms of plant coverage, height, and biomass on the leeward slope. Therefore, compared with the windward slope, more plant species can be used for ecological restoration on the leeward slope to enhance the biodiversity of the ecosystem and to improve the effectiveness of ecological restoration.

Both *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. have high photosynthetic rates and water use efficiencies, indicating their high physiological adaptability. Pioneer species typically have enhanced light-capturing mechanisms that allow them to maximize their photosynthesis even under high solar radiation [36,37]. High water use efficiency allows plants to fix carbon dioxide during wet periods, minimizing water loss through transpiration while maintaining a steady rate of photosynthesis [38]. These physiological properties allow them to grow relatively rapidly and occupy habitats quickly (Figure 5) [39,40]. The relatively rapid growth of pioneer sand-fixing plants helps them to thrive in challenging sandy environments [6], which is critical for the early colonization of sandy areas because faster growth leads to quicker root development, allowing plants to anchor loose sand and reduce erosion more effectively [37]. This provides the basis for the ecological restoration of sandy areas. We also found that, although the photosynthetic rate per unit leaf area of *Elymus sibiricus* L. was lower than that of *Agriophyllum squarrosum* (L.) Moq. (Figure 5), the former had higher abundance, a wider distribution, a larger leaf area per leaf, and more leaves than the latter, so the biomass of *Elymus sibiricus* L. was greater than that of *Agriophyllum squarrosum* (L.) Moq. Therefore, when using artificial aids to promote the fixation of sand dunes, the first priority can be given to the aerial seeding of *Elymus sibiricus* L. seeds, followed by *Agriophyllum squarrosum* (L.) Moq.

The stomatal characteristics of these two pioneer plants have also evolved to adapt to the drought environment. To date, relatively few studies have compared the stomatal characteristics of the dumbbell and kidney types for pioneer sand-fixing species [41]. A few studies have shown that dumbbell-type stomata open and close faster and can respond quickly to transient changes in the external environment, giving plants an advantage in responding to short-term changes in the environment [42–44]. Conversely, the kidney-type stomatal apparatus is slower in stomatal opening and closing and, therefore, cannot respond quickly to transient changes in the external environment [21,28]. This may explain the observed phenomenon in which the abundance, coverage, and biomass of *Elymus sibiricus* L. with dumbbell-type stomata were much higher than those of *Agriophyllum squarrosum* (L.)

Moq. with kidney-type stomata. In addition, we found that the stomatal density and stomatal area index were lower in *Elymus sibiricus* L., which may explain why the photosynthetic rate and transpiration rate of *Agriophyllum squarrosum* (L.) Moq. were higher than those of *Elymus sibiricus* L. By comparing these two species with the averages of grassland plants, we sought to understand why these two species could survive well on a mobile sand dune while other species could not. Notably, both the stomatal density and area index of the two plants were lower than the averages of the plants in Inner Mongolian grasslands [28], indicating that these two sand-fixed pioneer plants can adapt to arid environments by reducing water loss. These findings provide direct evidence for the high physiological adaptability of these two species to sand dunes, suggesting that they should be selected as target species for sand dune restoration.

This study has important implications for ecological restoration practices in arid regions around the world. First, since pioneer sand-fixing species play a critical role in ecological restoration in sandy areas [6,45], we should select appropriate pioneer sand-fixing plant species that have high photosynthetic rates and water use efficiencies and are well adapted to harsh conditions, such as *Agriophyllum squarrosum* (L.) Moq. and *Elymus sibiricus* L. in the Hunshandake Sandy Land. Second, after selecting appropriate species, we can use sowing or aerial seeding to create more opportunities for these species to grow in the mobile sand dunes [46,47]. According to our study, a mix of species can be used to promote biodiversity and resilience on the leeward slopes, where more species can grow well, compared with those on the windward slopes (Figure 2). Sowing or aerial seeding can be conducted at the beginning of the rainy season or during periods of increased humidity to maximize the chances of germination [48]. According to our study, pioneer plants have a high rate of photosynthesis and growth once they germinate on sand dunes. Therefore, ensuring early germination is critical. Third, maintaining plant coverage by reducing grazing in the sandy area is crucial to improving the ability of pioneer sand-fixing species to colonize and modify harsh landscapes, as these areas are always grazed [35,49]. Greater plant coverage helps to build a foundation for more complex ecosystems, promoting biodiversity and accelerating the overall process of habitat recovery. This makes them invaluable for restoration efforts aimed at combating desertification and promoting the sustainability of sandy areas.

5. Conclusions

The main contribution of this study is that we not only compared the plant diversity and species composition, coverage, and abundance between the windward and leeward slopes of the mobile dunes, but also revealed the physiological characteristics of two sand fixation pioneers. By examining vegetation growth, we found that the vegetation on the leeward slope had a higher plant height, coverage, and biomass; more plant species; and better growth advantages than those on the windward slope. Among them, *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. had the best coverage, plant heights, and biomass compared with other plants on the shifting dunes, indicating that these two pioneer plants had better adaptability. Their stomatal characteristics also exhibited adaptability to drought, thus ensuring strong photosynthesis and growth abilities in the harsh environment of the shifting sand dunes. Therefore, for sand dune restoration and the sustainable development of local areas, we suggest that *Elymus sibiricus* L. and *Agriophyllum squarrosum* (L.) Moq. should be preferentially selected for sowing or aerial seeding to fix the mobile sand dunes in the Hunshandake Sandy Land.

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