Postprint: Photosynthetic Characteristics of Leymus mollis on Different Coastal Slope Aspects in Relation to Wind Speed Heterogeneity

Authors: Ma Huilei, Zhang Tingfeng, Zhou Ruilian, Zhang Yue

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Abstract

Under natural conditions, measurements and analyses were conducted on environmental factors of different slope aspects on coastal sand dunes, as well as plant height, leaf chlorophyll content, soil water content, and diurnal variation characteristics of photosynthesis in Leymus mollis during calm wind days in summer and autumn and strong wind days in autumn, aiming to elucidate the physiological regulatory mechanisms of Leymus mollis in response to different wind speed environments. The results showed significant environmental heterogeneity among different slope aspects, with Leymus mollis exhibiting strong morphological plasticity. On coastal windward slopes, wind speed was high, temperature was low, and humidity was high, with Leymus mollis plants being short-statured and having higher chlorophyll content; on leeward slopes, temperature was high, soil was dry, and air circulation was poor, with Leymus mollis plants being tall and having low chlorophyll content. During calm wind days in summer and autumn, the photosynthetic "midday depression" phenomenon occurred in leaf Pn of Leymus mollis on both windward and leeward slopes, but the daily average Gs, Tr, and Pn of Leymus mollis on windward slopes were significantly higher than those on leeward slopes; whereas during strong wind days in autumn, the photosynthetic "midday depression" phenomenon in leaf Pn of Leymus mollis disappeared on both slopes, and the daily average Pn, Tr, and Gs of Leymus mollis on leeward slopes were significantly higher than those on windward slopes. Compared with the same slope aspect, during strong wind days in autumn, the daily average Pn, Tr, and Gs of Leymus mollis on windward slopes were significantly lower than those during calm wind days in autumn, while the daily average leaf Pn, Tr, and Gs of Leymus mollis on leeward slopes increased by 126%, 66.3%, and 134%, respectively, compared with calm wind days. Strong sea wind caused temperature reduction on windward slopes, leaf swaying in Leymus mollis, and decreased stomatal conductance, leading to reduced Pn, whereas strong sea wind accelerated air circulation, reduced temperature, and increased stomatal conductance on leeward slopes, with the disappearance of "midday depression" resulting in increased Pn. The adaptation of Leymus mollis on different slope aspects to different sea wind speeds exhibited obvious photosynthetic physiological plasticity, which plays an important role in Leymus mollis adapting to different wind forces, improving its photosynthetic rate, and increasing material accumulation. Moreover, the morphological and photosynthetic physiological plasticity of Leymus mollis may be important physiological regulatory mechanisms for its survival, growth, and population expansion under different sea wind intensities, and this characteristic has important application value in future wind-resistant and salt-resistant breeding of crops, forage grasses, and trees.

Full Text

Preamble

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The Relationship Between Photosynthetic Characteristics of *Leymus mollis* Leaves and Wind Speed Heterogeneity on Different Coastal Dune Slopes

MA Huilei, ZHANG Tingfeng, ZHOU Ruilian*, ZHANG Yue
School of Life Sciences, Ludong University, Yantai 264025, China

Corresponding author. E-mail: zhour726@163.com

Abstract

Under natural conditions, we measured and analyzed environmental factors, plant height, leaf chlorophyll content, soil water content, and diurnal photosynthetic characteristics of *Leymus mollis* on different slopes of coastal dunes during calm days in summer and autumn, as well as during windy days in autumn. The objective was to elucidate the physiological regulation mechanisms by which *L. mollis* responds to varying wind speed environments. The windward slopes of coastal dunes experience strong winds and exhibit high morphological plasticity, with *L. mollis* plants being relatively short and having low chlorophyll content. During calm days in both summer and autumn, photosynthetic rates on windward slopes were significantly higher than those on leeward slopes. However, during autumn windy days, the daily average net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) of *L. mollis* on windward slopes were markedly lower than during autumn calm days, while on leeward slopes, Pn increased by 126%, Gs by 66.3%, and Tr by 134%

compared to calm days. The midday depression of photosynthesis disappeared on leeward slopes during windy days. Strong sea wind caused temperature reduction on windward slopes, leading to decreased stomatal conductance and reduced Pn. On leeward slopes, wind accelerated air flow, increased stomatal opening, and eliminated midday depression, thereby enhancing Pn. *L. mollis* demonstrated significant photosynthetic physiological plasticity in adapting to different sea wind speeds, which plays a crucial role in improving photosynthetic rates and increasing biomass accumulation. This morphological and photosynthetic plasticity may represent an important physiological regulation mechanism for survival and population expansion under varying sea wind intensities, with significant potential applications for future wind-resistance breeding in crops, forage grasses, and trees.

Keywords: sea wind; environmental heterogeneity; physiological plasticity; adaptation

Introduction

Environmental heterogeneity is a fundamental attribute of biological habitats, and plants possess the capacity to alter their morphology, physiology, and behavior to maximize adaptability in heterogeneous environments—a phenomenon known as phenotypic plasticity. This plasticity represents a potential strategy for plants to adapt to heterogeneous environments, maintain species survival, and expand ecological niches. Phenotypic plasticity encompasses both morphological and physiological plasticity.

Studies on morphological plasticity have revealed that plants can modify structural characteristics such as branching patterns and branch biomass to enhance competitiveness within communities. For instance, *Zygophyllum xanthoxylum* adjusts resource allocation by reducing flower size and increasing flower number when soil water content decreases. Under drought conditions, *Ziziphus jujuba* var. *spinosa* exhibits reduced leaf area, length, and petiole length, while specific leaf area increases, demonstrating strong variation in aboveground morphological traits along aridity gradients. *Kobresia humilis* adapts to drought by reducing tiller number, whereas *Kobresia pygmaea* increases tiller number and root length. In response to varying light conditions, *Potentilla anserina* increases maternal plant height, leaf length, and total leaf area as light intensity decreases. Under shading treatments, *Buchloe dactyloides* shows significant reductions in main vein diameter, vascular bundle sheath cell number, leaf thickness, and mesophyll cell thickness on both adaxial and abaxial sides. Liana seedlings also increase plant height and reduce leaf size and specific leaf area to enhance light availability.

Under wind stress, *Salsola arbuscula* reduces plant height, increases leaf number, and enlarges stem diameter in the wind direction to minimize wind resistance. Maize seedlings exhibit decreased plant height, stem diameter growth, and aboveground biomass under long-term strong winds to reduce mechanical damage. These examples illustrate how plants allocate energy and materials to modify morphology and adapt to environmental changes.

Research on physiological plasticity has focused heavily on photosynthetic responses to environmental change, as photosynthesis is fundamental to autotrophic plants and a key determinant of survival and competitive success across different regions. Many studies demonstrate that photosynthetically active leaves are highly sensitive to environmental changes, with maximum photosynthesis occurring only under optimal conditions. Cotton seedlings under low temperature stress reduce net photosynthetic rate and adjust stomatal conductance to maintain higher photosynthetic capacity and enhance cold resistance. Maize adapts to warming conditions (18°C) by increasing net photosynthetic and transpiration rates while reducing dark respiration. Studies have shown that *Phyllostachys aurea* exhibits a bimodal Pn diurnal curve under controlled temperature and humidity conditions, but this pattern becomes less pronounced in open conditions. *Haloxylon ammodendron* shows a non-typical bimodal Pn curve in arid environments but a unimodal pattern after rainfall. Under sustained strong winds, *Pinus sylvestris* var. *mongolica* seedlings exhibit increased dormancy.

Previous research on plant adaptation to stress and its relationship with photosynthetic physiology has primarily used seedlings, crops, and inland desert plants, with experimental methods often involving artificial environmental simulation and potted plants. Few studies have investigated the seasonal photosynthetic characteristics of perennial plants growing naturally in heterogeneous environments and their relationship with microenvironmental conditions.

Leymus mollis (Trin.) Hara is a dominant species in coastal zones that plays an irreplaceable role in sand fixation and microenvironmental improvement. Due to its extensive root system, it serves as an important soil and water conservation species. *L. mollis* can robustly grow under highly heterogeneous coastal dune conditions, forming monospecific populations near the high tide line on windward slopes while coexisting with other plants on leeward slopes. Strong sea winds and resulting sand burial are critical ecological factors that prevent many plants from establishing in nearshore areas, leading to low species diversity and fragile ecosystems. How *L. mollis* adapts to sea winds, whether photosynthetic physiological characteristics differ between windward and leeward slopes, whether coastal dune environmental heterogeneity induces photosynthetic physiological plasticity, and the relationship between phenotypic plasticity and environmental heterogeneity remain poorly understood. This study investigates the relationship between external phenotypes and photosynthetic rates of *L. mollis* in different ecological zones (windward and leeward slopes) by measuring plant height, chlorophyll content, and photosynthetic physiological parameters during calm summer days, calm autumn days, and windy autumn days. This research will enrich theories on plant resistance to wind and sand, clarify the relationship between photosynthetic physiological plasticity of *L. mollis* on different slopes and wind speed heterogeneity, reveal physiological mechanisms of wind resistance, and provide theoretical foundations for coastal ecological restoration, species introduction, and development of wind-resistant genes.

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1. Study Site Overview

The study was conducted at Xibozi coastal sandy land in Yantai, located in central Shandong Peninsula (119°34 -121°57 E, 36°16 -38°23 N). The region has a temperate monsoon climate with an average annual precipitation of 651.9 mm, concentrated in summer. The average annual temperature is 11.8°C, with inland summer temperatures reaching 24.6°C. Average wind speeds range from 3–4 m/s inland to 4–6 m/s in coastal areas. The soil is primarily aeolian sandy soil. The natural community at Xibozi is dominated by *Carex kobomugi*, *Messerschmidia sibirica*, *Calystegia soldanella*, and *Leymus mollis*.

A parallel sand dune was selected approximately 10 m, 30 m, 50 m, and 70 m from the high tide line. The dune front consists of mobile sand, the middle is fixed sand, and the backside is also fixed sand. At each distance, ten *L. mollis* plants with consistent growth were marked. The second fully expanded mature leaf from the top of each plant was marked for continuous photosynthetic measurements.

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2. Methods

2.1 Environmental Measurements

Environmental temperature, humidity, and wind speed were measured using an AR836 anemometer and a TES-1360 hygrometer. Soil water content was determined by the oven-drying method.

2.2 Chlorophyll Content Measurement

On each measurement day, leaves adjacent to the marked plants were collected with scissors, quickly fixed in liquid nitrogen, and stored in an ultra-low temperature freezer for chlorophyll analysis. Chlorophyll content was determined spectrophotometrically. A known amount of liquid nitrogen-fixed leaf tissue was ground in 80% acetone, filtered through gauze, and absorbance was measured at 665 nm, 649 nm, and 470 nm wavelengths.

2.3 Photosynthetic Parameter Measurements

Photosynthetic measurements were conducted on calm summer days (July 21, 27, August 3, 9, 16) and calm autumn days, as well as windy autumn days. To avoid cloud interference, supplementary lighting was used during measurements. Diurnal photosynthetic measurements were performed at 8:00, 10:00, 12:00, 14:00, and 16:00. A portable photosynthesis system (TPS-1, USA) was used for in situ measurement of gas exchange in marked mature, healthy leaves. Parameters measured included leaf net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs).

2.4 Data Processing

Data were processed using Microsoft Office Excel 2003 and presented as means ± standard deviation (SD) from more than three replicates. Statistical analysis was performed using SPSS 13 software with one-way ANOVA and least significant difference (LSD) tests to compare differences between data groups.

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3. Results

3.1 Microenvironmental Variation Across Ecological Zones

Environmental conditions varied significantly across different coastal ecological zones and seasons (Table 1). During calm summer days, wind speed was highest at the windward slope near the high tide line (10 m), gradually decreasing with distance. Temperature increased with distance from the high tide line, reaching a maximum at 70 m (41.1°C), which was 9.3% higher than at the windward slope. Humidity decreased with distance, with a difference of 35.7% between windward and leeward slopes. During calm autumn days, average wind speed and humidity increased while temperature decreased compared to summer. The trends were similar to summer, but differences in temperature, humidity, and wind speed between windward and leeward slopes increased to 6.2°C, 14.4%, and 1.80 m/s, respectively.

During windy autumn days, average wind speed increased while temperature and humidity decreased compared to calm autumn days. The environmental trends remained similar, but at the windward slope (10 m), temperature dropped to 18.4°C and wind speed peaked at 7.04 m/s, which was 5.14 m/s higher than at the leeward slope. These results demonstrate strong temporal and spatial heterogeneity in microenvironmental conditions across seasons and between windy and calm days.

3.2 Plant Height, Chlorophyll Content, and Soil Water Content

Plant height of *L. mollis* varied significantly across ecological zones, reflecting environmental heterogeneity. Plants on windward slopes were shorter, with height gradually increasing with distance from the high tide line. Plants at 70 m were 40.1%, 20.7%, and 18.6% taller than those at 10 m, 30 m, and 50 m, respectively. Leeward slope plants were significantly taller than windward slope plants, showing stronger growth performance.

Chlorophyll content also varied across zones, decreasing with distance from the high tide line. Chlorophyll a, chlorophyll b, and carotenoid contents at 30 m, 50 m, and 70 m were 29%, 48%, and 56% lower, respectively, than at 10 m. The chlorophyll a/b ratio and carotenoid content also declined with distance (10 m: 1.97 > 30 m: 1.85 > 50 m: 1.74 > 70 m: 1.68). Soil water content was highest near the high tide line on windward slopes due to seawater influence, decreasing with distance. Soil water content at 10 m was significantly higher than at other positions (36.1% and 72.6% higher than at 30 m and 50 m, respectively).

[Figure 1: see original paper]

3.3 Daily Average Net Photosynthetic Rate Under Calm and Windy Conditions

The diurnal photosynthetic patterns of *L. mollis* varied across ecological zones and wind conditions (Figures 2-4). During calm days in both summer and autumn, all zones showed midday depression of photosynthesis, with Pn peaking at 12:00. Autumn Pn was slightly higher than summer Pn. During calm summer days, Pn decreased with distance from the high tide line, with windward slope Pn being significantly higher than leeward slope (23.8%, 31.8%, 125%, and 388% higher at 10 m, 30 m, 50 m, and 70 m, respectively). Similar patterns were observed during calm autumn days.

During windy autumn days, the diurnal photosynthetic pattern changed dramatically. Midday depression disappeared, and Pn peaked between 10:00–12:00. Pn was highest on leeward slopes and lowest on windward slopes, with leeward slope Pn being 34.8% and 7.4% higher than windward slope at 10 m and 30 m, respectively. Compared to calm days, windy conditions reduced Pn by 16.8% and 15.8% at 10 m and 30 m on windward slopes, but increased Pn by 3.2%, 11.1%, 155%, and 995% at 10 m, 30 m, 50 m, and 70 m on leeward slopes. Overall, strong sea wind inhibited photosynthesis on windward slopes but enhanced it on leeward slopes, particularly near the high tide line where Pn increased by 13.3% compared to calm autumn days.

[Figure 2: see original paper]

3.4 Daily Average Transpiration Rate Under Calm and Windy Conditions

Diurnal transpiration rates (Tr) showed midday depression at 12:00 during calm summer days, particularly at 10 m and 30 m on windward slopes. Daily average Tr on windward slopes was 45.5%, 118%, and 90.9% higher than on leeward slopes at 10 m, 30 m, and 50 m, respectively. During windy autumn days, Tr on windward slopes fluctuated slightly but not significantly, while leeward slopes showed significant midday depression. Leeward slope daily average Tr was 83% and 48.8% higher than windward slope at 10 m and 30 m, respectively. Compared to calm days, windy conditions reduced Tr on windward slopes by 37.5%, 50.0%, and 47.6% at 10 m, 30 m, and 50 m, but increased Tr on leeward slopes by 10%, 14.3%, and 10%, respectively.

[Figure 3: see original paper]

3.5 Daily Average Stomatal Conductance Under Calm and Windy Conditions

Diurnal stomatal conductance (Gs) showed a bimodal pattern during calm days, with midday depression at 12:00. Daily average Gs was highest near the high tide line on windward slopes and decreased with distance. During calm summer days, Gs on windward slopes was 48.9% higher than on leeward slopes at 10 m and 30 m. During calm autumn days, Gs increased compared to summer at all positions, with windward slope Gs being 111%, 50.0%, 80.5%, and 125% higher than leeward slope at 10 m, 30 m, 50 m, and 70 m, respectively.

During windy autumn days, midday Gs depression occurred only near the high tide line on windward slopes. Leeward slope daily average Gs was 22.7%, 3.6%, and 33.1% higher than windward slope at 10 m, 30 m, and 50 m, respectively. Compared to calm days, windy conditions reduced Gs on windward slopes by 10%, 26.6%, and 17.2% at 10 m, 30 m, and 50 m, but increased Gs on leeward slopes by 134%.

[Figure 4: see original paper]

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4. Discussion

4.1 Environmental Heterogeneity and Morphological Plasticity

Coastal dune environments exhibit strong heterogeneity between windward and leeward slopes, with topography being the dominant factor. During summer, autumn, and different wind conditions, significant differences in temperature and humidity were observed between slopes. During windy autumn days, windward slopes had 27.8% higher humidity and 5-6°C lower temperature than leeward slopes. Wind is another critical ecological factor influencing plant growth and architecture.

Our results show that leeward slope *L. mollis* plants were significantly taller than those on windward slopes. Previous studies indicate that plants growing in strong wind environments tend to be dwarfed. Under natural strong winds, *Zygophyllum xanthoxylum* and *Salsola arbuscula* showed reduced plant height and leaf length. Maize seedlings exhibited decreased height, stem diameter, and biomass under long-term wind stress. Wind-exposed *L. mollis* on windward slopes near the high tide line transfer non-structural carbohydrates underground earlier in winter, store more carbohydrates in buds, and accumulate more cellulose in leaves for freeze and wind resistance. Plants can reduce wind resistance and mechanical damage by decreasing the force-bearing area of branches and leaves and allocating energy efficiently. Windward slope *L. mollis* controls growth rate to form a low stature, reducing wind resistance and mechanical damage, while leeward slope plants grow rapidly under high temperatures to form a slender, tall morphology. This controlled morphogenesis may be an important adaptation to wind speed heterogeneity, with morphological plasticity playing a crucial role in adapting to coastal heterogeneity.

4.2 Environmental Heterogeneity and Pigment Composition Plasticity

Plant morphological structure construction requires photosynthetic energy support, and chlorophyll is a crucial pigment in photosynthesis. Carotenoids participate in dissipating excess light energy in photosynthetic apparatus, protecting plants from photoinhibition. Our results show significant differences in chlorophyll and carotenoid contents between slopes, with windward slope leaves having much higher chlorophyll content than leeward slopes. At 10 m, chlorophyll a, chlorophyll b, and carotenoids were 56.7%, 33.7%, and 117% higher on windward slopes, respectively.

Many environmental factors affect chlorophyll synthesis. High temperatures can destroy chloroplast structure in ryegrass, significantly reducing chlorophyll content. Water deficit also dramatically decreases chlorophyll content in maize seedlings. We found that high soil water content on windward slopes, combined with more reflected UV light from the sea surface, favored chlorophyll synthesis, resulting in higher content. In contrast, high temperature and water deficit on leeward slopes were unfavorable for chlorophyll synthesis, leading to lower content. However, leeward slope *L. mollis* could capture light more efficiently by reducing the chlorophyll a/b ratio to enhance photosynthetic capacity. Sea wind indirectly affects leaf chlorophyll and carotenoid contents by influencing temperature, humidity, and soil moisture on different slopes.

4.3 Wind Speed Heterogeneity and Photosynthetic Plasticity

Photosynthesis is the primary energy source for plant growth, and energy production depends on photosynthetic rate. During autumn, daily average Pn and Gs on windward slopes were higher than in summer, likely due to cooler autumn temperatures (26.9–33.1°C) being more suitable for photosynthesis than high summer temperatures (38.2–41.1°C). During calm days in both seasons, windward slope Pn and Gs were higher than leeward slopes. However, during windy autumn days, windward slope Pn and Gs decreased compared to calm days, while leeward slope Pn and Gs increased.

Calm days significantly enhanced photosynthesis on windward slopes, but since windy days outnumber calm days annually in coastal zones, windy conditions favor leeward slope photosynthesis, resulting in greater biomass accumulation and taller plants on leeward slopes. Gentle breeze on windward slopes (44.2–57.9% humidity) promotes stomatal opening, and high soil water content maintains high Gs and Tr, increasing Pn. Wind accelerates air flow and promotes intercellular gas exchange, raising photosynthetic and transpiration rates. On leeward slopes, blocked wind and drought conditions cause stomatal closure, reducing Gs, Tr, and Pn.

Strong sea wind on windward slopes significantly reduces temperature (to 18.4°C) and causes substantial leaf swaying, promoting partial stomatal closure, reducing Gs and gas exchange, and accelerating cuticular transpiration, leading to water loss. *L. mollis* regulates stomatal aperture to reduce water loss, further decreasing Gs and causing declines in Pn and Tr. On leeward slopes, although wind speed is reduced, it is sufficient to sway plants and accelerate air flow, lowering temperature (to 23.8°C) to an optimal range for photosynthesis, increasing stomatal opening, enhancing CO absorption, and raising Pn. The synergistic effects of topography and sea wind on temperature and air flow are the dominant ecological factors causing photosynthetic differences between slopes.

During windy days, leeward slope *L. mollis* showed no midday depression, with Pn increasing by 35.4% compared to windward slopes. Previous studies have shown that *Haloxylon ammodendron* exhibits non-typical bimodal Pn curves in desert environments but unimodal patterns after rainfall. Sustained strong wind reduces ambient temperature and alters diurnal photosynthetic patterns, eliminating midday depression. This demonstrates that *L. mollis* can regulate stomatal conductance under different wind conditions to optimize resource utilization and enhance photosynthesis and biomass accumulation, representing a key physiological adaptation to wind speed heterogeneity.

Long-term adaptation to wind heterogeneity has induced morphological and photosynthetic metabolic plasticity in *L. mollis* across different ecological zones. Windward slope plants are shorter with high chlorophyll content, showing increased stomatal conductance and Pn during calm days but reduced conductance and Pn during windy days due to leaf swaying and low temperature. Leeward slope plants are taller with low chlorophyll content, showing low Pn during calm days due to poor air flow and drought, but increased Pn during windy days due to enhanced air flow and optimal temperatures. Since windy days are more frequent than calm days in coastal zones, leeward slope plants accumulate more biomass. This morphological and photosynthetic plasticity is a crucial physiological regulation mechanism for survival and population expansion under varying sea wind intensities, with important applications for wind-resistance breeding in crops, forage grasses, and trees.

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