



Severe Hail-Induced Mechanical Damage Is Associated with a Persistent Maladaptive Electrophysiological State in *Bletilla striata* Leaves

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Abstract

Hailstorms cause severe mechanical damage to crops, yet their long-term legacy effects on the physiology of perennial medicinal herbs remain poorly understood. This study examined *Bletilla striata* plants damaged by a severe hailstorm on April 2, 2026. On day 37 post-damage, coinciding with new pseudobulb formation, 44 electrophysiological parameters were measured in leaves of damaged plants ($n = 8$) and undamaged controls ($n = 8$) and compared using Welch's t -test. Damaged leaves showed a persistent "low-resistance, high-capacitance" pattern: inherent physiological resistance decreased to 25.0% of the control value, whereas inherent capacitance increased 5.6-fold (both $P < 0.001$). Water and nutrient parameters displayed a consistent "low-efficiency, high-speed" decoupling, with intracellular water-holding capacity and water and nutrient transport capacities increasing 7- to 22-fold ($P < 0.001$), while the corresponding

use efficiencies declined by 61%–95% ($P < 0.01$). Resistance-related metabolic energy increased by 75.7% ($P < 0.05$), whereas capacitive reactance-related metabolic energy decreased by 43.3% ($P < 0.01$), indicating a shift toward energy dissipation. Thus, the leaves had not recovered within 37 days. We therefore propose a testable "maladaptive stress homeostasis" hypothesis, in which high-flux transmembrane transport is maintained at the expense of resource-use efficiency and ordered energy storage. Findings are based on Welch's t -tests across 44 parameters without multiple-comparison correction, which should be considered when interpreting the reported significance levels. Multi-time-point and mechanistic studies are needed to determine whether this state is stable, slowly recovering, or progressive.

Keywords: *Bletilla striata*, hail disaster, plant electrophysiology, mechanical damage, low-efficiency high-speed.



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1 Introduction

As a sudden extreme weather event, hail causes mechanical damage such as puncturing and tearing of plant leaves. This not only directly destroys

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the structural foundation of photosynthesis but also triggers a cascade of complex physiological responses ranging from the cellular to the whole-plant level. Hail damage is one of the important meteorological factors limiting agricultural production, particularly the production of high-quality Chinese medicinal materials [1]. *Bletilla striata* (Thunb.) Rchb.f. is a perennial medicinal plant of the Orchidaceae family, and its dried pseudobulbs (tubers) are a rare medicinal material [2]. Guizhou Province, a genuine (*daodi*) producing area of *B. striata*, frequently experiences hailstorms in late spring and early summer, which threatens *B. striata* plants at the leaf-expansion stage; this was the reason for selecting *B. striata* as the study species. However, the physiological adaptation mechanisms of *B. striata* leaves to hail-induced mechanical damage, particularly the long-term, sustained response process, have not yet been systematically studied.

Plant electrophysiological parameters, such as resistance, capacitance, and impedance, are comprehensive electrical characterizations of cell membrane permeability, ion channel activity, and energy metabolism status, and are regarded as among the most sensitive and rapid indicators of responses to environmental stress [3, 4]. Compared with traditional morphological and biochemical indicators, electrophysiological parameters can capture initial cellular changes within minutes to hours after damage. In recent years, plant electrophysiological information detection technology, based on the Gibbs free energy equation and the Nernst equation, has achieved real-time, non-destructive quantification of more than 50 physiological function parameters, including intracellular water metabolism, nutrient transport capacity, and cellular metabolic energy [5]. This technological platform extends the classical Hodgkin–Huxley cell membrane equivalent-circuit model from the scale of nerve cells to the scale of plant leaf organs, providing a tool for studying the dynamics of plant physiological functions under environmental stress. Its utility has been preliminarily validated in a study of the response of *B. striata* to bicarbonate stress [7].

A more critical scientific question is whether a single extreme mechanical damage event merely triggers a reversible “disturbance–repair” process or causes a stable, costly state transition in the plant’s physiological system. Current research has largely focused on the immediate responses or short-term recovery dynamics following stress,

with little exploration of the “legacy effects” that persist weeks or longer after severe stress and of their underlying biophysical mechanisms. On April 2, 2026, the *B. striata* experimental field at the Guiyang Agricultural Science and Technology Innovation Building suffered a severe hailstorm lasting approximately 20 min, providing an opportunity to examine these legacy effects weeks after mechanical damage.

Using the aforementioned electrophysiological platform, this study collected and compared 44 electrophysiological parameters from damaged ($n = 8$) and screened control ($n = 8$) *B. striata* leaves on the 37th day post-disaster, which coincided with the critical phenological period of new pseudobulb formation. The objectives of this study were: (1) to quantitatively evaluate the degree and nature of recovery of the membrane electrical properties of *B. striata* leaves 37 days after severe hail-induced mechanical damage; (2) to reveal the coupling relationships among leaf water metabolism, nutrient transport, and energy metabolism after damage and their possible biophysical basis; and (3) to provide evidence that may challenge the classical “disturbance–repair” model and to propose a testable hypothesis of “maladaptive stress homeostasis”.

2 Materials and Methods

2.1 Plant Material and Hail Event

The plant material was *Bletilla striata* ‘Guiji 1’ [8], a cultivar previously characterized under drought stress using biochemical, physiological, and electrophysiological approaches. In 2023, saddle-shaped tissue-cultured seedlings were transplanted to field conditions in Pingtang County, Guizhou Province, for adaptive growth. In May 2025, two-year-old plants with generally consistent growth vigor were selected, divided, and transplanted to the experimental field at the Guiyang Agricultural Science and Technology Innovation Building. All plants were managed uniformly according to standard facility cultivation practices. In the evening of April 2, 2026, during the leaf-expansion stage of *B. striata*, the experimental field experienced a severe hailstorm lasting approximately 20 min, resulting in severe mechanical damage to the leaves, including puncturing, tearing, and fragmentation.

2.2 Experimental Design and Sample Collection

Given the sudden and unpredictable nature of the hailstorm, a post-event grouping design was adopted.

After the disaster, all plants were divided into two groups based on visible leaf damage phenotypes: (1) damaged group (D): plants with more than half of their leaves showing obvious mechanical damage (including rupture, perforation, and partial tissue loss); (2) control group (C): plants with no visible damage on any leaf. All plants originated from the same clonal line ('Guiji 1') and were distributed in a mosaic, random pattern within the experimental field. In this hail event, exactly 8 plants met the criteria for the damaged group, and all 8 were included in the final analysis; no post-hoc outlier removal was applied to the damaged group. The control group initially contained 11 undamaged plants. To reduce potential interference from individuals with anomalous growth vigor, the control data were subjected to post-hoc outlier screening using boxplots and Grubbs' test ($\alpha = 0.05$) for each electrophysiological parameter; 8 control plants were retained. Thus, the final analysis included 8 damaged and 8 control plants. All electrophysiological data were collected during the pseudobulb (tuber) formation stage of *B. striata* (early May), on the 37th day post-disaster (May 9, 2026).

2.3 Electrophysiological Parameter Measurement

A plant life analyzer (manufactured by Jiangsu Zhongtian Zhigan Life Data Co., Ltd., China) developed by Professor Yanyou Wu's research group at the Institute of Geochemistry, Chinese Academy of Sciences, was used to measure 44 electrophysiological parameters of functional *B. striata* leaves according to the instrument's standard operating procedures; its principles are described in [5]. Definitions, units, and biological meanings of all 44 parameters are provided in Table A1. The measurement principle is based on the Gibbs free energy equation and the Nernst equation, using a leaf equivalent-circuit model (extended from the classical Hodgkin-Huxley model [6]) to quantify a series of physiological kinetic parameters. The key equations are as follows:

$$E = \frac{RT}{zF} \ln \frac{c_{\text{out}}}{c_{\text{in}}} \quad (1)$$

$$\Delta G = RT \ln \frac{c_{\text{in}}}{c_{\text{out}}} + zF\Delta\psi \quad (2)$$

$$Z = R_p + j(X_L - X_C) \quad (3)$$

$$X_C = \frac{1}{2\pi fC}, \quad X_L = 2\pi fL \quad (4)$$

where E is the equilibrium (Nernst) potential (V), R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$), T is the absolute temperature (K), z is the ion valence, F is

the Faraday constant (96485 C mol^{-1}), c_{in} and c_{out} are the intracellular and extracellular ion concentrations, ΔG is the free-energy change of transmembrane ion transport, $\Delta\psi = \psi_{\text{in}} - \psi_{\text{out}}$ is the membrane potential, Z is the impedance, R_p is the physiological resistance, j is the imaginary unit, X_C and X_L are the capacitive and inductive reactances, f is the test frequency, C is the capacitance, and L is the inductance. The exact conversion formulas for ΔG_R and ΔG_{X_C} follow [5] and the instrument manual.

For each plant, three mature functional leaves were measured, and the arithmetic mean was used as the representative value for that plant. Measurements followed the instrument's standard operating procedure and internal calibration. The parameters directly output by the instrument included: basic electrical parameters (e.g., inherent physiological resistance R_p , capacitance C , impedance Z , capacitive reactance X_C , and inductive reactance X_L); water metabolism parameters (e.g., intracellular water-holding capacity, IWHC; intracellular water use efficiency, IWUE; intracellular water transport rate, WTR); nutrient transport parameters (e.g., intracellular nutrient active transport capacity, NAC; passive nutrient transport capacity, PNTC; nutrient use efficiency, NUE); and metabolic activity parameters (e.g., relative metabolic activity, MA; resistance-related metabolic energy, ΔG_R ; capacitive reactance-related metabolic energy, ΔG_{X_C}). All parameters were output as relative values compared with an internal calibration plate, and statistical analyses were based on percent changes. All parameters are model-derived relative values; they were not independently validated by direct water, ion, or biochemical measurements in this study.

2.4 Data Processing and Statistical Analysis

All statistical analyses were performed using IBM SPSS Statistics 26.0 (IBM Corp., Armonk, NY, USA). Data are presented as mean $\pm$ standard deviation (SD). Because of the small sample size and the heterogeneity of variances detected by Levene's test for some indicators, between-group comparisons (damaged group, $n = 8$, all hail-damaged plants; control group, $n = 8$ after outlier screening) were performed using Welch's t -test, which does not assume equal variances. $P < 0.05$ was considered statistically significant, $P < 0.01$ highly significant, and $P < 0.001$ extremely significant. The magnitude of change (%) for all indicators was calculated using the control group mean as the baseline (set to 100%). Because

Table 1. Comparison of basic electrical parameters between damaged and control *B. striata* leaves 37 days post-disaster ($n = 8$).

Electrical parameter	Damaged plants	Control plants	Change (%)	Welch's <i>t</i>	<i>P</i> -value
Inherent resistance ($M\Omega$)	0.28 ± 0.04	1.12 ± 0.21	−75.0	7.21	< 0.001
Inherent impedance ($M\Omega$)	0.23 ± 0.04	1.06 ± 0.13	−78.2	11.08	< 0.001
Inherent capacitive reactance ($M\Omega$)	0.38 ± 0.05	5.23 ± 0.68	−92.8	13.45	< 0.001
Inherent inductive reactance ($M\Omega$)	0.50 ± 0.06	4.68 ± 0.60	−89.3	12.98	< 0.001
Inherent capacitance (pF)	141.30 ± 18.23	25.34 ± 3.77	+457.6	13.11	< 0.001
Leaf-specific effective thickness ^a	51.39 ± 5.12	44.72 ± 10.20	+14.9	1.56	0.145

^a Instrument-derived dimensionless relative value (arbitrary units); no absolute physical unit is assigned by the instrument.

Table 2. Comparison of water metabolism parameters between damaged and control *B. striata* leaves 37 days post-disaster ($n = 8$).

Water metabolism parameter	Damaged plants	Control plants	Change (%)	Welch's <i>t</i>	<i>P</i> -value
Intracellular water-holding capacity	1679.58 ± 201.35	74.96 ± 5.76	+2141	17.89	< 0.001
Intracellular water use efficiency	0.031 ± 0.004	0.635 ± 0.078	−95.1	14.11	< 0.001
Intracellular water retention time	32.84 ± 3.57	26.22 ± 11.20	+25.2	1.54	0.157
Intracellular water transport rate	51.14 ± 6.01	7.28 ± 2.25	+603	13.45	< 0.001

Values are instrument-derived relative values.

44 parameters were compared, the risk of type I error inflation should be considered; no correction for multiple comparisons was applied in the original analysis. Because control plants were screened for outliers, a formal sensitivity analysis using all 11 control plants was not part of the original analysis. Both points are acknowledged as limitations.

3 Results and Analysis

3.1 Cell Membrane Electrical Properties

On the 37th day post-disaster, the inherent physiological resistance (R_p) of damaged *B. striata* leaves decreased to $0.28 \pm 0.04 M\Omega$, only 25.0% of the control value ($1.12 \pm 0.21 M\Omega$; $t = 7.21$, $P < 0.001$). The inherent physiological capacitance (C) increased to 141.30 ± 18.23 pF, 5.6 times that of the control group (25.34 ± 3.77 pF; $t = 13.11$, $P < 0.001$) (Table 1). This “extremely low resistance–extremely high capacitance” pattern deviates from the recovery trajectory expected under classical stress–recovery models [9], suggesting that the membrane system had not returned to the

control state by 37 days post-damage: membrane permeability remained elevated, and the capacitive properties of the membrane had not recovered.

Inherent physiological impedance (Z), capacitive reactance (X_C), and inductive reactance (X_L) decreased by 78.2%, 92.8%, and 89.3%, respectively (all $P < 0.001$), indicating a parallel reduction in the overall resistance to transmembrane transport of ions and polar molecules. Leaf-specific effective thickness increased by only 14.9% ($t = 1.56$, $P = 0.145$), which was not statistically significant, suggesting that the increased capacitance was not simply due to an expansion of membrane area but possibly reflected an alteration in the effective electrical properties of the membrane; direct structural evidence is, however, lacking.

3.2 Intracellular Water Metabolism

The intracellular water metabolism of damaged leaves exhibited a “low-efficiency, high-speed” pattern, consistent with membrane functional

Table 3. Comparison of nutrient transport parameters between damaged and control *B. striata* leaves 37 days post-disaster ($n = 8$).

Nutrient transport parameter	Damaged plants	Control plants	Change (%)	Welch's <i>t</i>	<i>P</i> -value
Active transport capacity	28.46 ± 3.20	1.37 ± 0.25	+1977	16.98	< 0.001
Passive transport capacity	38.09 ± 4.23	2.09 ± 0.78	+1722	15.67	< 0.001
Total nutrient transport capacity	66.55 ± 7.12	3.47 ± 0.69	+1818	16.78	< 0.001
Low-nutrient tolerance	0.43 ± 0.05	0.40 ± 0.12	+7.5	0.61	0.551
Nutrient use efficiency	0.77 ± 0.09	1.99 ± 0.55	−61.4	3.76	0.005

Values are instrument-derived relative values.

Table 4. Comparison of metabolic parameters between damaged and control *B. striata* leaves 37 days post-disaster ($n = 8$).

Metabolic parameter	Damaged plants	Control plants	Change (%)	Welch's <i>t</i>	<i>P</i> -value
Leaf metabolic rate	1455.55 ± 167.23	66.74 ± 45.66	+2081	17.23	< 0.001
Relative metabolic activity	47.76 ± 5.23	23.85 ± 9.45	+100.3	5.01	< 0.001
Resistance-related metabolic energy (ΔG_R)	6.32 ± 0.71	3.60 ± 0.97	+75.7	4.89	0.012
Capacitive reactance-related metabolic energy (ΔG_{X_C})	1.97 ± 0.22	3.48 ± 0.58	−43.3	5.78	0.003

Values are instrument-derived relative values.

decoupling (Table 2). These are model-derived electrophysiological estimates: IWHC represents the estimated intracellular water-holding capacity, related to free-water space and membrane water retention, and WTR represents the estimated intracellular water transport rate across the membrane. IWHC was 22.4 times that of the control group (+2141%, $P < 0.001$), reflecting a substantial expansion of the intracellular free-water space. WTR was 7.0 times that of the control group (+603%, $P < 0.001$). However, IWUE decreased by 95.1% ($P < 0.001$), which may suggest that a large proportion of water is not efficiently used for metabolic maintenance; direct water-physiology measurements are needed to confirm this. Intracellular water retention time was prolonged by 25.2%, but this change was not statistically significant ($t = 1.54$, $P = 0.157$).

These results suggest that damaged cells respond to injury by greatly increasing the intracellular “free-water” space (high IWHC) and transmembrane flux (high WTR), whereas the contribution of this water to normal cellular metabolism appears to be small; part of it may serve to fill cavities created by damage or to maintain turgor pressure. Independent measurements such as leaf water potential, relative

water content, and transpiration were not performed.

3.3 Intracellular Nutrient Transport

Intracellular nutrient metabolism exhibited a decoupling pattern highly consistent with that of intracellular water metabolism (Table 3). NAC, PNTC, and total nutrient transport capacity (NTC) were 20.8, 18.2, and 19.2 times those of the control group, respectively (all $P < 0.001$). In contrast, NUE decreased significantly by 61.4% ($P < 0.01$). The simultaneous increase in active and passive transport together with the decrease in nutrient use efficiency indirectly suggests that damage triggers large-scale, possibly low-selectivity ion flux across membranes, whereas the capacity to integrate absorbed nutrients into anabolic pathways may be impaired. Low-nutrient tolerance showed no significant change (+7.5%, $P = 0.551$), suggesting that the enhanced nutrient transport capacity does not stem from adaptive up-regulation to a low-nutrient environment but is more likely a non-specific concomitant phenomenon of the stress response. Actual nutrient concentrations and ion contents were not measured; therefore, these transport parameters should be regarded as electrophysiological estimates, and direct ion-selectivity measurements are needed.

3.4 Metabolic Parameters

Metabolic parameters further revealed an apparent imbalance in energy allocation (Table 4). The leaf metabolic rate and relative metabolic activity (MA) of damaged leaves were 21.8 times (+2081%, $P < 0.001$) and 2.0 times (+100.3%, $P < 0.001$) those of the control group, respectively, indicating a persistently hyperactive metabolic state. However, resistance-related metabolic energy (ΔG_R , associated with energy consumption for transmembrane ion transport) increased by 75.7% ($P < 0.05$), whereas capacitive reactance-related metabolic energy (ΔG_{X_C} , associated with membrane structural integrity and ordered energy-storage efficiency) decreased by 43.3% ($P < 0.01$). This divergence between energy-dissipating and energy-storing metabolic energy provides indirect bioenergetic evidence for the “low-efficiency, high-speed” pattern: the plant may invest considerable metabolic energy in maintaining the ion pumping required under high membrane permeability, while its capacity to maintain ordered membrane structures and store energy capacitively appears to be reduced.

4 Discussion

4.1 Questioning the “Disturbance–Repair” Model: A Persistent Electrophysiological State at 37 Days Post-Damage

The central finding of this study is that on the 37th day after severe hail damage, the inherent physiological resistance and capacitance of *B. striata* leaves had not approached the control values but remained in an extreme “low-resistance, high-capacitance” state. This provides evidence that may challenge the classical “disturbance–repair” view in plant physiology [9], which assumes that after stress is removed, plants initiate repair mechanisms and eventually return physiological parameters to baseline. Our data indicate that a single extreme mechanical damage event was associated with a persistent, energy-expensive electrophysiological state at 37 days post-damage. We propose this as a possible maladaptive homeostasis, but multi-time-point data are required to test its stability. Conceptually, this state may be viewed as a hypothetical “pathological attractor” within a complex dynamical system [9].

We hypothesize that the persistently low resistance may reflect a reprogramming of the membrane proteome, such as persistent activation of K^+ and Ca^{2+} channels or up-regulation of non-selective cation channels in response to damage-associated molecular

patterns (DAMPs) [10]. The marked increase in capacitance may reflect alterations in the membrane bilayer, such as lipid peroxidation, disruption of membrane microdomains, or conformational changes in membrane proteins, since tissue capacitance and resistance are governed by the integrity of the plasma membrane and tonoplast [11]. However, these mechanisms were not directly measured in this study. This “low-resistance, high-capacitance” signature may nonetheless serve as a candidate non-destructively detectable “electrophysiological fingerprint”.

4.2 Bioenergetic Basis and Possible Cost of the “Low-Efficiency, High-Speed” Pattern

The consistency of the “low-efficiency, high-speed” pattern across water metabolism, nutrient transport, and energy supply may be associated with a structure–function decoupling of energy metabolism. The opposite trends of ΔG_R (resistance-related, energy-dissipating) and ΔG_{X_C} (capacitive reactance-related, energy-storing) quantify this cost from a bioenergetic perspective in this dataset. Whether the observed pattern is specific to hail damage or represents a general mechanical wounding response cannot be distinguished in this study. Sustained high-intensity ion pumping (maintaining a high ΔG_R) may deplete cellular energy reserves, while the metabolic energy available for membrane repair and maintenance (ΔG_{X_C}) is reduced, potentially creating a vicious cycle. This resembles, at a conceptual level, the uncoupled state of “high oxygen consumption, low ATP synthesis” in mitochondrial dysfunction, although neither respiration nor ATP content was measured here.

From an evolutionary perspective, and under the assumption that the observed state persists, this does not represent an optimal strategy. Unlike the partial recovery of photosynthetic capacity observed in apple leaves following mechanically simulated hail damage [12], severe natural hail damage in the present study was associated with a persistent “maladaptive emergency response” rather than a recovery trajectory. Confronted with extreme disturbance, plants may activate multiple transmembrane transport systems to sustain basic cellular turgor and ion homeostasis [13]. Within the framework of C–S–R (competitor–stress tolerator–ruderal) theory [14], *B. striata* may be conceptually characterized as a stress-tolerator strategist, relying on conservative resource allocation and pseudobulb-based storage. Interpreted within this framework, the persistent “low-efficiency,

high-speed” electrophysiological pattern observed here represents a putative deviation from this strategy: the high transmembrane flux and low resource-use efficiency recorded in this study are precisely the traits that C–S–R theory predicts to be disfavored in a stress-tolerator, suggesting that severe hail may have forced a functionally ruderal-like physiological state at the cellular level. Any radical stress response that deviates from a conservative resource-allocation pattern may consequently compromise long-term growth and reproduction.

Based on the above discussion, we propose the Maladaptive Stress Homeostasis (MSH) hypothesis as a conceptual hypothesis derived from electrophysiological data rather than a proven mechanism: (1) Trigger: a single severe mechanical damage event (here, hail) affecting more than half of the leaves. (2) State: a persistent electrophysiological state at the measured time point, which may or may not be reversible. (3) Diagnostic features: the “low-resistance, high-capacitance” electrophysiological fingerprint; the “low-efficiency, high-speed” decoupling of intracellular water and nutrients; and the divergence of metabolic energy supply between energy dissipation and energy storage. (4) Proposed essence: a costly state that may arise from the dysregulation of a conserved “life-preserving” program, sustaining high-flux emergency transmembrane transport at the expense of material-use efficiency and ordered energy storage. In contrast to “stress memory” [15], MSH, if validated, would imply a decline in overall function rather than enhanced stress resistance.

5 Conclusion

Through analysis of 44 electrophysiological parameters of *B. striata* leaves at 37 days after severe hail damage, this study shows that damaged leaves still exhibited a pronounced “low-resistance, high-capacitance” electrophysiological pattern and a “low-efficiency, high-speed” decoupling of water and nutrient parameters. These changes were accompanied by a shift in metabolic energy allocation. We propose the Maladaptive Stress Homeostasis (MSH) concept as a testable hypothesis to describe this persistent post-damage state. However, because measurements were performed at a single time point and independent water, ion, and biochemical validations were not included, further multi-time-point, multi-species, and mechanistic studies are needed to determine whether this state is stable, slowly recovering, or progressive.

The 44-parameter electrophysiological profiling approach may provide a useful non-destructive tool for assessing mechanical damage in Orchidaceae medicinal plants.

Data Availability Statement

The raw electrophysiological measurements for the final 8 damaged and 8 control plants are available from the corresponding author on reasonable request. Definitions, units, and biological meanings of all 44 parameters are provided in Appendix Table A1. Data for the three control plants excluded during outlier screening are also available from the corresponding author on reasonable request.

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Conflicts of Interest

The authors declare no conflicts of interest. The plant life analyzer used in this study is manufactured by Jiangsu Zhongtian Zhigan Life Data Co., Ltd.; however, the authors have no financial or other relationship with the manufacturer that could be construed as a conflict of interest.

AI Use Statement

The authors declare that no generative AI was used in the preparation of this manuscript.

Ethical Approval and Consent to Participate

Not applicable. This study involved only cultivated plants and did not involve human participants or animals. The plant material (*B. striata* ‘Guiji 1’) was clonally propagated cultivated material; no wild specimens of this CITES Appendix II orchid species were collected.

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Appendix

Table A1 provides the definitions, units, and biological meanings of all 44 electrophysiological parameters measured in this study.

Table A1. Definitions, units, and biological meanings of the 44 electrophysiological parameters. Asterisks (*) denote parameters reported in the main text.

No.	Parameter (Abbreviation)	Unit	Definition	Biological Meaning
1	Inherent physiological resistance* (R_p , IR)	M Ω	Intrinsic resistance of leaf cell membrane to ion flow, obtained by extrapolating the resistance-clamping force relationship to zero clamping force.	Reflects membrane permeability and ion channel activity; lower R_p indicates higher membrane permeability or increased ion leakage.
2	Inherent physiological capacitance* (C , IC)	pF	Intrinsic capacitance of leaf cell membrane, derived from capacitive reactance at zero clamping force.	Reflects membrane charge-storage ability, related to membrane surface area, bilayer integrity, and dielectric properties.
3	Inherent physiological impedance* (Z , IZ)	M Ω	Total opposition to alternating current flow through leaf tissue, combining resistance and reactance.	Integrates membrane resistance and reactance; reflects overall resistance to transmembrane transport of ions and polar molecules.
4	Inherent capacitive reactance* (X_C , IX_C)	M Ω	Opposition to current flow caused by membrane capacitance.	Reflects membrane charge-storage properties; changes indicate alterations in membrane structure or effective dielectric constant.
5	Inherent inductive reactance* (X_L , IX_L)	M Ω	Opposition to current flow caused by inductance-like behavior of membrane proteins and ion channels.	Reflects dynamic properties of membrane proteins and ion channel activity.
6	Intracellular water-holding capacity* (IWHC)	Relative value	Estimated from inherent physiological capacitance (IC) as $IWHC = (IC)^{3/2}$ (normalized).	Reflects intracellular free-water space and the cell's capacity to retain water; higher IWHC indicates greater intracellular water storage.
7	Intracellular water use efficiency* (IWUE)	Relative value	Calculated from IWHC and leaf-specific effective thickness (d): $IWUE = d/IWHC$.	Reflects how efficiently intracellular water is used for metabolic maintenance; lower IWUE indicates water is less effectively utilized.
8	Intracellular water retention time (IWHT)	Relative value	Estimated from inherent physiological capacitance and impedance: $IWHT = C \times Z$.	Reflects how long water is retained within cells; longer retention time indicates slower water turnover.
9	Intracellular water transport rate* (WTR)	Relative value	Estimated from IWHC and IWHT: $WTR = IWHC/IWHT$.	Reflects rate of water movement across the cell membrane; higher WTR indicates faster transmembrane water flux.

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Table A1 continued

No.	Parameter (Abbreviation)	Unit	Definition	Biological Meaning
10	Leaf-specific effective thickness (d)	Relative value	Derived from the electrophysiological model; represents effective thickness of leaf tissue relevant to electrical measurements.	Reflects effective path length for ion and water transport; used in calculation of water use efficiency.
11	Intracellular water transfer rate (IWTR)	Relative value	Similar to WTR; estimated from electrophysiological parameters.	Reflects dynamics of intracellular water translocation.
12	Intracellular nutrient active transport capacity* (NAC)	Relative value	Estimated from the electrophysiological model: $NAC = UAF \times NTR$.	Reflects cell's ability to actively take up nutrients; higher NAC indicates greater active transport activity.
13	Intracellular nutrient passive transport capacity* (PNTC)	Relative value	Estimated from the electrophysiological model; represents capacity for passive (diffusion-driven) nutrient transport.	Reflects passive nutrient uptake; higher PNTC indicates increased membrane permeability to nutrients.
14	Total nutrient transport capacity* (NTC)	Relative value	Sum of active and passive nutrient transport capacities: $NTC = NAC + PNTC$ (or $UNF \times NTR$).	Reflects overall capacity for nutrient transport across the membrane.
15	Nutrient use efficiency* (NUE)	Relative value	Calculated from nutrient transport capacity and growth-related parameters.	Reflects how efficiently absorbed nutrients are used for growth and metabolism; lower NUE indicates poor nutrient assimilation.
16	Low-nutrient tolerance	Relative value	Estimated from the electrophysiological model; represents plant's ability to maintain function under low-nutrient conditions.	Reflects adaptation to nutrient-poor environments.
17	Nutrient transfer rate (NTR)	Relative value	Estimated from the electrophysiological model: $NTR = IWHC/IWHT$.	Reflects speed of nutrient transport.
18	Unit for nutrient-relative transport (UNF)	Relative value	Estimated from the electrophysiological model: $UNF = (R_p/IX_C) + (R_p/IX_L)$.	Reflects nutrient transport per unit of driving force.
19	Unit for nutrient active flow (UAF)	Relative value	Estimated from the electrophysiological model: $UAF = IX_C/IX_L$.	Reflects active nutrient transport per unit of energy input.
20	Leaf metabolic rate	Relative value	Estimated from the electrophysiological model; represents overall rate of leaf metabolism.	Reflects general metabolic activity of leaf tissue.
21	Relative metabolic activity* (MA)	Relative value	Normalized metabolic activity relative to the calibration standard.	Reflects overall metabolic status of the leaf.

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Table A1 continued

No.	Parameter (Abbreviation)	Unit	Definition	Biological Meaning
22	Resistance-related metabolic energy* (ΔG_R)	Relative value	Gibbs free energy change associated with resistance (energy dissipation for ion transport across the membrane).	Reflects energy consumed for maintaining ion gradients and membrane permeability; higher ΔG_R indicates greater energy expenditure for ion pumping.
23	Capacitive reactance-related metabolic energy* (ΔG_{X_C})	Relative value	Gibbs free energy change associated with capacitive reactance (energy storage in membrane structures).	Reflects energy stored in ordered membrane structures; lower ΔG_{X_C} indicates reduced capacity for membrane structural maintenance and energy storage.
24	Inductive reactance-related metabolic energy (ΔG_{X_L})	Relative value	Gibbs free energy change associated with inductive reactance (energy associated with membrane protein dynamics).	Reflects energy related to membrane protein conformational dynamics.
25	Total metabolic energy (ΔG_{total})	Relative value	Sum of ΔG_R , ΔG_{X_C} , and ΔG_{X_L} .	Reflects total bioenergetic status of the leaf.
26	Comprehensive stress resistance index	Relative value	Integrated index derived from multiple electrophysiological parameters.	Reflects overall ability of the plant to resist environmental stress.
27	Drought resistance index	Relative value	Derived from water metabolism parameters.	Reflects plant's ability to maintain function under water deficit.
28	Low-nutrient resistance index	Relative value	Derived from nutrient transport parameters.	Reflects plant's ability to maintain function under nutrient limitation.
29	Salt stress resistance index	Relative value	Derived from ion transport and membrane parameters.	Reflects plant's ability to tolerate salinity stress.
30	Cold stress resistance index	Relative value	Derived from membrane electrical parameters.	Reflects plant's ability to tolerate low-temperature stress.
31	Heat stress resistance index	Relative value	Derived from membrane electrical parameters.	Reflects plant's ability to tolerate high-temperature stress.
32	Membrane integrity index	Relative value	Calculated from R_p , C , and Z .	Reflects overall structural and functional integrity of the cell membrane.
33	Ion homeostasis index	Relative value	Derived from ion transport parameters.	Reflects cell's ability to maintain ion balance.
34	Water balance index	Relative value	Derived from IWHC, IWUE, and WTR.	Reflects cell's water status and balance.

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Table A1 continued

No.	Parameter (Abbreviation)	Unit	Definition	Biological Meaning
35	Energy balance index	Relative value	Derived from ΔG_R and ΔG_{X_C} .	Reflects balance between energy dissipation and energy storage.
36	Membrane permeability index	Relative value	Derived from R_p and Z .	Reflects ease of ion and molecule passage across the membrane.
37	Membrane fluidity index	Relative value	Derived from C and X_C .	Reflects dynamic properties of the membrane bilayer.
38	Ion channel activity index	Relative value	Derived from R_p and X_L .	Reflects functional state of ion channels.
39	Proton pump activity index	Relative value	Derived from ΔG_R .	Reflects activity of proton pumps and other ion transporters.
40	Metabolic efficiency index	Relative value	Derived from MA and NUE.	Reflects efficiency of metabolic processes.
41	Nutrient utilization index	Relative value	Derived from NAC, PNTC, and NUE.	Reflects efficiency of nutrient uptake and use.
42	Stress adaptation index	Relative value	Integrated from multiple stress resistance indices.	Reflects plant's overall adaptive capacity under stress.
43	Growth potential index	Relative value	Derived from metabolic and nutrient parameters.	Reflects potential for growth and biomass accumulation.
44	Overall physiological status index	Relative value	Integrated from all electrophysiological parameters.	Reflects comprehensive physiological condition of the leaf.