Effects of Soil Microbial Films on Photosynthetic and Fluorescence Characteristics of Psammophyte Seedlings: Postprint

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Abstract

To reveal the effects of soil microbial films on the photosynthetic and fluorescence characteristics of desert plant seedlings, pot experiments were conducted using seedlings of Ammopiptanthus mongolicus and Astragalus laxmannii as test subjects, with different application methods (spraying, mixing) and dosages (0, 1, 3, 5, 7 g · kg-1 and 10 g · kg-1) of microbial agents, to compare and analyze the plant gas exchange and chlorophyll fluorescence characteristics after soil microbial film formation. The results showed that: (1) When the microbial agent dosage was >3 g · kg-1, the hardness and thickness of the consolidated layer and the activities of soil urease and sucrase were all significantly higher than those of the control group (P<0.05). (2) In the 3~7 g · kg-1 microbial agent treatment groups, the net photosynthetic rate of Astragalus laxmannii was significantly higher than that of the control group (P<0.05), and the transpiration rate (Tr), net photosynthetic rate (Pn), and intercellular CO2 concentration (Ci) were all significantly higher than those of Ammopiptanthus mongolicus (P<0.05). (3) When the microbial agent dosage was >5 g · kg-1, the maximum photochemical efficiency (Fv/Fm) of Astragalus laxmannii was significantly higher than that of the control group (P<0.05). Except for the 3 g · kg-1 treatment group, the Fv/Fm and photochemical quenching coefficient (QP) of Ammopiptanthus mongolicus were both higher than those of Astragalus laxmannii. (4) Soil characteristics, photosynthetic gas exchange, and chlorophyll fluorescence constituted a partial mediation model, and changes in soil characteristics could directly affect the chlorophyll fluorescence characteristics of Ammopiptanthus mongolicus and Astragalus laxmannii. The soil microbial film increased the hardness and thickness of the consolidated layer by 3.84% and 152.85% on average, respectively, and enhanced the activities of soil catalase, urease, and sucrase by 93.37%, 170.68%, and 256.03% on average, respectively. It enhanced the photosynthetic

efficiency and capacity of Ammopiptanthus mongolicus and Astragalus laxmannii by improving soil quality and increasing leaf stomatal conductance, resulting in an average increase of 28.48% in net photosynthetic rate and 0.84% in Fv/Fm for both species.

Full Text

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Abstract

To reveal the effects of soil microbial films on photosynthetic and fluorescence characteristics of psammophyte seedlings, pot experiments were conducted using *Ammopiptanthus mongolicus* and *Astragalus laxmannii* seedlings as test subjects. Different bacterial agent application methods (spraying, mixing) and application rates (0, 1, 3, 5, 7, and 10 $g \cdot kg^{-1}$) were employed to compare and analyze plant gas exchange and chlorophyll fluorescence characteristics following soil microbial biofilm formation. The results demonstrated that: (1) When bacterial agent application exceeded 3 $g \cdot kg^{-1}$, the hardness and thickness of the consolidated layer, along with soil urease and sucrase activities, were significantly higher than those in the control group ($P < 0.05$). (2) The net photosynthetic rate of *Astragalus laxmannii* in the 3–7 $g \cdot kg^{-1}$ treatment was significantly higher than the control ($P < 0.05$), and its transpiration rate, net photosynthetic rate, and intercellular CO_2 concentration were all significantly higher than those of *Ammopiptanthus mongolicus* ($P < 0.05$). (3) For *Astragalus laxmannii* treated with >5 $g \cdot kg^{-1}$, the maximum photochemical efficiency (Fv/Fm) was significantly higher than the control ($P < 0.05$). Except for the 3 $g \cdot kg^{-1}$ treatment group, *Ammopiptanthus mongolicus* exhibited higher Fv/Fm and photochemical quenching coefficient (QP) values than *Astragalus laxmannii*. (4) Soil properties, photosynthetic gas exchange, and chlorophyll fluorescence parameters formed a partial mediation model, wherein changes in soil characteristics directly affected

the chlorophyll fluorescence properties of both species. Soil microbial films increased consolidation layer hardness and thickness by 73.84% and 152.85%, respectively, while enhancing catalase, urease, and sucrase activities by 93.37%, 170.68%, and 256.03% on average. By improving soil quality and increasing leaf stomatal conductance, the technology enhanced photosynthetic efficiency and capacity, raising the net photosynthetic rate of *Astragalus laxmannii* and *Ammopiptanthus mongolicus* by 28.48% on average and increasing Fv/Fm by 0.84%.

Keywords: soil microbial films; psammophyte; photosynthesis; chlorophyll fluorescence

Introduction

Soil microorganisms serve as critical linkages between aboveground and belowground ecological processes, participating directly or indirectly in soil nutrient cycling through their metabolic activities, thereby influencing plant physiological growth. Soil microbial communities are essential for maintaining plant community diversity and stability. Soil microbial films, formed by the accumulation of microbial communities and their secretions, adhere to soil particle surfaces and perform vital ecological functions such as soil consolidation and water retention. These biofilms effectively promote soil aggregate formation, enhance soil organic matter content, and increase plant net photosynthetic rates. The extracellular polymeric substances produced during biofilm formation can form hydrogen bonds with soil water molecules, improving soil water retention capacity and water use efficiency, which helps reduce photoinhibition. Furthermore, soil microbial films can enhance soil microbial activity, reduce soil bulk density, and promote the stabilization of mobile sand dunes.

Currently, extensive exploratory research on soil microbial film sand fixation technology has been conducted both domestically and internationally, yielding promising results in soil wind erosion control. Studies have found that microbial sand fixation can cement loose aeolian sand particles, forming a consolidated layer with high strength and hardness that enhances soil erosion resistance. The technology can also cover and protect exposed sand particles, reducing wind erosion impacts and decreasing soil erodibility. However, post-fixation plant physiological growth and vegetation recovery issues have often been overlooked, particularly regarding effects on psammophytes. This knowledge gap constrains comprehensive evaluation of the technology' s impact on desert ecosystems and limits its broader application.

Ammopiptanthus mongolicus is a unique xerophytic broadleaf shrub and relict species in desert regions, exhibiting strong cold, drought, and saline-alkali tolerance, making it an excellent species for windbreak and sand fixation. *Astragalus laxmannii* is a versatile herbaceous plant used for forage, green manure, and soil and water conservation, with high wind erosion control capacity and

nutritional value. This study selected these two typical psammophyte seedlings for controlled experiments to compare their photosynthetic and fluorescence characteristics, aiming to reveal the impacts of soil microbial film sand fixation technology and provide theoretical support for its improvement.

Materials and Methods

1.1 Experimental Materials

The experiment utilized seeds of *Ammopiptanthus mongolicus* and *Astragalus laxmannii* as plant materials, with aeolian sandy soil from the Mu Us Desert in Yanchi, Ningxia as the growth medium. The microbial agent powder was purchased from the National Microbial Fertilizer Technology Research and Extension Center (Registration No.: GT012KC011), primarily containing *Bacillus subtilis* supplemented with *B. pumilus*, with viable bacteria counts of approximately 10^9 cfu $\cdot$ g^{-1}. Mineral substances (diatomaceous shale) were used as adsorbents to support bacterial survival.

1.2 Experimental Design

Rectangular plastic containers (40.00 cm × 15.50 cm × 10.00 cm) served as potting vessels, sterilized with 75% ethanol and autoclaved at 120°C for 25 minutes. Aeolian sandy soil was sieved through a 2 mm mesh, and 0.40 kg (dry weight) of sterilized soil was placed in each container as the cultivation substrate. Seeds were disinfected with 10% sodium hypochlorite solution for 10 minutes and germinated in darkness. Ten uniformly germinated seeds were sown per pot with a covering depth of 1 cm, then thinned to three seedlings per pot after emergence. Environmental conditions including temperature, humidity, and light were strictly controlled to ensure consistency across all pots.

Two application methods were established: spraying (dissolving agent in 150 mL distilled water then applying) and mixing (directly mixing agent with soil before adding 150 mL distilled water). Six application rates were set: 0, 1, 3, 5, 7, and 10 g $\cdot$ kg^{-1}, with three replicates per treatment. A control group received no bacterial agent but equivalent amounts of distilled water and aeolian sandy soil. Plants received water twice weekly, with amounts based on average annual precipitation in the study area.

1.3 Measurement of Photosynthetic and Fluorescence Parameters

After seedling growth stabilized, three healthy seedlings per pot were selected. On clear, windless days between 9:00–11:00 AM, three fully expanded, healthy leaves from the upper-middle portion of each seedling were measured using a Li-6800 portable photosynthesis system (LI-COR, USA). Parameters included net photosynthetic rate (Pn), transpiration rate (Tr), intercellular CO_2 concentration (Ci), and stomatal conductance (Gs). Chlorophyll fluorescence parameters

were measured simultaneously, including initial fluorescence (F_0), maximum photochemical efficiency (Fv/Fm), photochemical quenching coefficient (QP), and non-photochemical quenching coefficient (NPQ).

1.4 Soil Property Measurements

Soil microbial film morphology was observed and photographed using a BK6000-FL electron microscope (Cnoptec, China) to verify biofilm formation. A soil hardness meter and vernier caliper measured consolidated layer hardness and thickness. Soil catalase, urease, and sucrase activities were determined using potassium permanganate titration, phenol-sodium hypochlorite colorimetry, and 3,5-dinitrosalicylic acid colorimetry methods, respectively.

1.5 Data Processing and Analysis

Excel software was used for statistical analysis and structural equation modeling. Model fit indices including Comparative Fit Index (CFI), Tucker-Lewis Index (TLI), and Root Mean Square Error of Approximation (RMSEA) were employed to evaluate model adaptation. One-way ANOVA, two-way ANOVA, and least significant difference (LSD) tests compared differences between treatment groups.

Results

2.1 Soil Microbial Film Characteristics and Soil Properties

2.1.1 Soil Microbial Film Morphology Scanning electron microscopy revealed smooth, loosely structured sand particles in the control group without bacterial agent application [Figure 1: see original paper]. Following agent application, adhesion points appeared on sand particle surfaces, with particles becoming coated by microorganisms and sand debris. Bacterial cells were visibly attached around sand particles, confirming successful soil microbial film formation with important cementing functions.

2.1.2 Consolidated Layer Development Two-way ANOVA indicated that both application method and rate had extremely significant effects on consolidated layer thickness and hardness ($P < 0.01$) . Hardness and thickness increased with application rate [Figure 2: see original paper]. When application exceeded 3 $g \cdot kg^{-1}$, both parameters were significantly higher than the control ($P < 0.05$). The spray application produced significantly greater hardness and thickness than mixing at rates >5 $g \cdot kg^{-1}$ ($P < 0.05$). At 1 $g \cdot kg^{-1}$, spray-treated thickness was significantly higher than the control ($P < 0.05$).

2.1.3 Soil Enzyme Activity Application method, rate, and their interaction significantly affected catalase, urease, and sucrase activities ($P < 0.05$) . All

three enzyme activities increased with application rate [Figure 3: see original paper]. Spray application at >3 $g \cdot kg^{-1}$ significantly elevated all enzyme activities compared to the control ($P < 0.05$). Mixing only significantly affected urease and sucrase at >5 $g \cdot kg^{-1}$. At equivalent application rates, spray treatments showed higher enzyme activities than mixing treatments, with significant differences appearing at >5 $g \cdot kg^{-1}$ ($P < 0.05$).

2.2 Photosynthetic Characteristics of Psammophyte Seedlings

With increasing bacterial application, transpiration rates of both species showed an initial increase followed by decrease, while net photosynthetic rates increased overall. Stomatal conductance and intercellular CO_2 concentration first rose then declined [Figure 5: see original paper]. Bacterial application had no significant effect on *Ammopiptanthus mongolicus* net photosynthetic rate ($P > 0.05$). However, at >7 $g \cdot kg^{-1}$, *Astragalus laxmannii* showed significantly higher net photosynthetic rate than the control ($P < 0.05$). At 3–7 $g \cdot kg^{-1}$, *Astragalus laxmannii* exhibited significantly lower intercellular CO_2 concentration than the control ($P < 0.05$). Under identical application conditions, *Astragalus laxmannii* demonstrated significantly higher transpiration rate, net photosynthetic rate, and intercellular CO_2 concentration than *Ammopiptanthus mongolicus* ($P < 0.05$) [Figure 4: see original paper].

2.3 Chlorophyll Fluorescence Characteristics

Maximum photochemical efficiency (Fv/Fm) in both species showed a fluctuating upward trend with increasing application rate, while non-photochemical quenching (NPQ) and photochemical quenching (QP) coefficients initially decreased then increased [Figure 7: see original paper]. At 1 $g \cdot kg^{-1}$, *Ammopiptanthus mongolicus* Fv/Fm was significantly lower than the control ($P < 0.05$), then gradually increased. Application rates >5 $g \cdot kg^{-1}$ produced significantly higher Fv/Fm than the control ($P < 0.05$). Except for the 3 $g \cdot kg^{-1}$ treatment, *Ammopiptanthus mongolicus* maintained higher Fv/Fm and QP values but lower NPQ than *Astragalus laxmannii* ($P < 0.05$) [Figure 6: see original paper].

2.4 Relationships Between Soil Properties, Photosynthesis, and Fluorescence

Structural equation modeling of soil properties, photosynthetic gas exchange, and chlorophyll fluorescence parameters revealed acceptable model fit after modification, with all path coefficients passing significance tests ($P < 0.05$) [Figure 8: see original paper]. Soil characteristics showed positive correlations with chlorophyll fluorescence parameters but negative correlations with photosynthetic gas exchange, which in turn negatively correlated with fluorescence parameters. This partial mediation model indicated that soil microbial film formation altered soil properties, directly affecting fluorescence characteristics while indirectly influencing them through changes in photosynthetic gas exchange.

Bootstrap confidence interval testing of mediation effects showed that at 0–3 $g \cdot kg^{-1}$ application, both indirect effects (through gas exchange) and direct effects on fluorescence were extremely significant ($P < 0.01$). At 5–10 $g \cdot kg^{-1}$, the mediating effect remained significant but weaker, indicating that soil property changes primarily exerted direct effects on fluorescence characteristics, with relatively minor indirect effects mediated through photosynthetic gas exchange.

Discussion

3.1 Effects on Seedling Photosynthesis

Photosynthesis represents the fundamental material and energy metabolism foundation of plants, with gas exchange serving as a critical indicator of photosynthetic efficiency and capacity. This study demonstrated that low bacterial application rates (1–3 $g \cdot kg^{-1}$) initially increased stomatal conductance in both species, facilitating greater CO_2 diffusion into leaves to provide more substrates for photosynthesis. Stomatal conductance is highly sensitive to soil moisture, which directly affects turgor pressure in leaf guard cells. At 1–3 $g \cdot kg^{-1}$, the consolidated layer' s increased hardness and thickness inhibited soil water evaporation, improving water retention and increasing soil moisture availability. Simultaneously, soil microbial films improved soil structure, enhancing leaf quality and promoting photosynthesis.

However, at application rates of 5–10 $g \cdot kg^{-1}$, net photosynthetic rate, stomatal conductance, and transpiration rate all declined, indicating photosynthetic reduction caused by stomatal limitation. The structural equation model revealed low-effect negative correlations between soil properties and photosynthetic gas exchange, suggesting that excessive bacterial application created overly thick and hard consolidated layers that inhibited water infiltration, causing soil water deficit and stomatal closure. Additionally, excessive bacterial agents may have damaged root systems, inhibiting water absorption and causing stomatal closure. Spray application produced harder, thicker consolidated layers than mixing, resulting in greater and faster declines in photosynthetic rates. The technology proved more effective in improving photosynthetic efficiency and capacity in *Astragalus laxmannii* than in *Ammopiptanthus mongolicus*, likely due to interspecific differences in photosynthetic physiological adaptation strategies.

3.2 Effects on Chlorophyll Fluorescence Characteristics

Chlorophyll fluorescence is intimately connected with various photosynthetic reactions and serves as an intrinsic probe of the relationship between photosynthesis and environmental conditions. The structural equation model showed high-effect negative correlations between photosynthetic gas exchange and fluorescence characteristics, with NPQ and Fv/Fm showing opposite trends in both species. At 1 $g \cdot kg^{-1}$, *Astragalus laxmannii* Fv/Fm significantly increased while

NPQ decreased, indicating that appropriate bacterial application enhanced photosynthetic electron transport activity and light energy utilization efficiency. However, at 5–7 $g \cdot kg^{-1}$, Fv/Fm in *Astragalus laxmannii* decreased significantly while NPQ increased ($P < 0.05$), suggesting environmental stress induced photoinhibition and activated self-protection mechanisms.

The positive correlation between soil properties and fluorescence characteristics indicates that soil microbial films improved the soil environment, altering root growth and resource use efficiency, thereby enhancing photosynthetic capacity and increasing photosystem center activity and light energy conversion efficiency. As application rates increased, QP initially rose then fell in both species, indicating that moderate bacterial application promoted photosynthetic electron transfer, while excessive amounts caused inhibition without damaging the photosynthetic apparatus. The technology demonstrated greater enhancement of photosynthetic electron transfer capacity in *Ammopiptanthus mongolicus* than in *Astragalus laxmannii*, possibly because the latter possesses weaker light energy conversion and photosynthetic apparatus protection capabilities.

Conclusion

Soil microbial film sand fixation technology successfully formed microbial biofilms that increased consolidated layer hardness and thickness by 73.84% and 152.85%, respectively, while enhancing catalase, urease, and sucrase activities by 93.37%, 170.68%, and 256.03% on average. The technology primarily improved photosynthetic efficiency and capacity in both species by enhancing soil quality and leaf stomatal conductance, resulting in average net photosynthetic rate increases of 28.48% and Fv/Fm increases of 0.84%. The optimal application range for both species was 1–5 $g \cdot kg^{-1}$. While application rates exceeding 5 $g \cdot kg^{-1}$ inhibited photosynthetic electron transfer, no damage to the photosystem apparatus occurred. These findings provide theoretical foundations and technical support for improving soil microbial film sand fixation technology.

References

[1] Adomako M O, Xue W, Du D L, et al. Soil microbe mediated N:P stoichiometric effects on solidago canadensis performance depend on nutrient levels[J]. Microbial Ecology, 2021, 83(4): 960-970.

[2] Yan B, Lu Q, Xia S, et al. An overview of advances in soil microbial diversity of urban environment[J]. Biodiversity Science, 2022, 30(8): 191-204.

[3] Bever J D, Dickie I A, Facelli E, et al. Rooting theories of plant community ecology in microbial interactions[J]. Trend in Ecology and Evolution, 2010, 25(8):

468-478.

[4] Ala S, Gao G L, Ding G D, et al. Eco-physiological functions of soil microbial biofilms: A review[J]. Chinese Journal of Applied Ecology, 2022, 33(7): 1885-1892.

[5] Kuzyakov Y, Blagodatskaya E. Microbial hotspots and hot moments in soil: Concept and review[J]. Soil Biology and Biochemistry, 2015, 83: 184-199.

[6] Du Y J, Gao G L, Chen L H, et al. Effects of soil microbial films on sand fixation and water retention characteristics of aeolian soils[J]. Transactions of the Chinese Society of Agricultural Engineering, 2020, 36(17): 98-105.

[7] Meng Q Y, Zou H T, Han Y Y, et al. Effects of straw application rates on soil aggregates, soil organic carbon content and maize yield[J]. Transactions of the Chinese Society of Agricultural Engineering, 2019, 35(23): 119-125.

[8] Zheng N, Shao Y, Luo M, et al. Effects of soil aggregate preparation methods on the stability and carbon sequestration potential evaluation[J]. China Environmental Science, 2022, 42(6): 2821-2827.

[9] Li J Y, Yuan X L, Ge L, et al. Rhizosphere effects promote soil aggregate stability and associated organic carbon sequestration in rocky areas of desertification[J]. Agriculture, Ecosystems and Environment, 2020, 304: 107126.

[10] Tian K L, Wu Y Y, Zhang H L, et al. Increasing wind erosion resistance of aeolian sandy soil by microbially induced calcium carbonate precipitation[J]. Land Degradation and Development, 2018, 29(12): 4271-4281.

[11] Fattahi S M, Soroush A, Huang N, et al. Biocementation control of sand against wind erosion[J]. Journal of Geotechnical and Geoenvi-ronmental Engineering, 2020, 146(6): 04020045.

[12] Zhang M X, Wang R Q, Liu F F, et al. Anti-wind erosion and anti-dust mechanisms of microbial consolidation of bare soil[J]. Environmental Engineering, 2020, 146(6): 04020045.

[13] Wang J J, Yan H B, Wang Z X, et al. Effects of root cutting and IBA treatment on the root quality and growth of *Ammopiptanthus mongolicus* seedlings[J]. Arid Zone Research, 2022, 39(1): 230-239.

[14] Zhang J, Ma Y M, Wang S S, et al. Physiological responses of young *Ammopiptanthus mongolicus* to soil water loss and rehydration under different temperature[J]. Journal of Arid Land Resources and Environment, 2023, 37(3): 150-161.

[15] Duan Y J, Wang B T. Effect of different fertilizers and AM fungi on quality of *Astragalus adsurgens* Pall.[J]. Journal of Northwest A & F University (Natural Science Edition), 2019, 47(5): 118-124.

[16] Wang Y, Liu Z T, Gao G L, et al. Effects of *Bacillus subtilis* on seed germination and seedling growth of *Caragana korshinskii* and *Ammopiptanthus*

mongolicus under drought stress[J]. Journal of Desert Research, 2022, 42(5): 73-81.

[17] Jin C, Zha T S, Jia X, et al. Dynamics of chlorophyll fluorescence parameters under drought condition for three desert shrub species[J]. Journal of Beijing Forestry University, 2020, 42(8): 72-80.

[18] Chang W, Li X, Zhou Y F, et al. Screening of drought resistance indices and comprehensive evaluation of Alfalfa germplasm resources based on leaf morphology and photosynthetic characteristics at seedling stage[J]. Journal of Northwest A & F University (Natural Science Edition), 2020, 48(5): 57-68.

[19] Zhao L L, Deng R, Xiang Q H, et al. Effects of high temperature stress on gas exchange and chlorophyll fluorescence parameters of *Fagopyrum dibotrys*[J]. Pratacultural Science, 2015, 32(4): 560-569.

[20] Wang Q C, Sun J, Shu S, et al. Effects of microbial agents on growth and photosynthesis of pepper in solar greenhouse[J]. Journal of Nanjing Agricultural University, 2012, 35(6): 7-12.

[21] Zhu H Y, Li H Y, Wang X L, et al. Characteristics and modeling of canopy stomatal conductance and transpiration of *Pinus tabuliformis* on the Loess Plateau[J]. Acta Ecologica Sinica, 2022, 42(22): 9130-9142.

[22] Zhang L G, Zeng F J, Liu B, et al. Study of the photosynthesis characteristics and physical signs of four plants at the desert-oasis ecotone[J]. Acta Prataculturae Sinica, 2012, 21(1): 103-111.

[23] Xu L, Gao Z Q, An W, et al. Flag leaf photosynthetic characteristics, change in chlorophyll fluorescence parameters, and their relationships with yield of winter wheat sowed in spring[J]. Chinese Journal of Applied Ecology, 2016, 27(1): 133-142.

[24] Yang Z Q, Li L L, Yin J M, et al. Effects of different duration of high temperature stress during filling stages on leaf photosynthetic and fluorescence parameters of early rice[J]. Chinese Journal of Agrometeorology, 2014, 35(1): 80-84.

[25] Lu G C, Xu J X, Xue L, et al. Comprehensive evaluation on photosynthetic and fluorescence characteristics in seedlings of 4 drought resistance species[J]. Acta Ecologica Sinica, 2013, 33(24): 7872-7881.

[26] Wang M, Yin C M, Sun M M, et al. Effect of fulvic acid microbial agent on leaf photosynthesis and fluorescent parameters of apple (*Malus hupehensis*) under replant condition[J]. Plant Physiology Journal, 2019, 55(1): 99-106.

[27] Wang C X, He F Y, Yang M, et al. Effects of three *Bacillus* agents on growth and photosynthetic characteristics of *Parashorea chinensis* seedlings[J]. Journal of Tropical and Subtropical Botany, 2022, 30(2): 213-223.

[28] Jin K M, White P J, Whalley W R, et al. Shaping an optimal soil by root-soil interaction[J]. Trends in Plant Science, 2017, 22(10): 823-829.

[29] Grace J B. Structural Equation Modeling and Natural Systems[M]. New York: Cambridge University Press, 2006.

[30] Hu L T, Bentler P M. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives[J]. Structural Equation Modeling: A Multidisciplinary Journal, 1999, 6(1): 1-55.

[31] Alimu A, Yao H Z, Song Y F, et al. Effects of soil structure improvement on chlorophyll fluorescence parameters and yield of rice in a coastal reclamation region[J]. Chinese Journal of Applied Ecology, 2019, 30(10): 3435-3442.

[32] Zhang Q Q, Zhou Z Z, Wang X Y, et al. Effects of fertilization on photosynthetic and chlorophyll fluorescence characteristics of *Tectona grandis*[J]. Journal of Central South University of Forestry & Technology, 2021, 41(4): 31-38.

[33] Li Y L, Jin Z X, Guan M, et al. Effects of soil microbes on photosynthetic characteristics and chlorophyll fluorescence parameters of *Elsholtzia splendens* under copper stress condition[J]. Bulletin of Botanical Research, 2013, 33(6): 684-689.

[34] Bai J J, Wu J W, Li J Y, et al. Effects of drought stress on chlorophyll fluorescence parameters of two fast-growing tree species[J]. Journal of South China Agricultural University, 2015, 36(1): 85-90.

[35] Yang R, Lang Y, Zhang G C, et al. Responses of photosynthesis and fluorescence of *Ziziphus jujuba* var. *spinosa* to drought stress[J]. Acta Botanica Boreali Occidentalia Sinica, 2018, 38(5): 922-931.

[36] Huang Y L, Zheng L W, Huang Y A, et al. Effects of different application methods of *Bacillus subtilis* agent on soil microbial diversity and growth of muskmelon[J]. Chinese Journal of Biotechnology, 2020, 36(12): 2644-2656.

[37] Tang J W, Liang W B, Zou H, et al. Effects of water stress on photosynthesis and chlorophyll fluorescence parameters of *Polygonatum cyrtonema*[J]. Journal of Central South University of Forestry & Technology, 2019, 39(5): 110-118.

[38] Wang M H, Li M, Gao Q, et al. Effects of amendments on growth and physiological characteristics of maize seedlings on saline-alkali soil[J]. Chinese Journal of Ecology, 2016, 35(11): 2966-2973.

[39] Bai W Y, Tie L H, Feng M S, et al. Photosynthesis and chlorophyll fluorescence characteristics of grafted *Alnus cremastogyne* seedlings from different provenances[J]. Journal of Sichuan Agricultural University, 2020, 38(6): 670-676, 692.

[40] Zhang Z Z, Qu Y P, Wang H J, et al. Inhibiting water evaporation of sand soil with clay modified by linear alkylbenzene sulfonates[J]. Transactions of the Chinese Society of Agricultural Engineering, 2014, 30(18): 168-175.

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