Response of Cultivated Buddleja alternifolia Seedlings to Water and Salt Stress in the Desert Hinterland: Postprint

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Date: 2021-02-13T15:57:16+00:00

Abstract

To investigate the changes in plant growth and physiological characteristics under salt, drought, and their interactive stresses, understand the adaptability of Buddleja alternifolia seedlings in the extreme habitats of desert hinterlands, determine reasonable irrigation regimes, and provide a theoretical basis for the introduction of B. alternifolia in desert hinterlands. Through field control experiments, a randomized combination experiment with three water gradients and four salt gradients was designed, growth increments and biochemical indices were measured in situ, and the drought and salt tolerance of B. alternifolia was comprehensively evaluated based on the membership function method. The results showed that: (1) Under drought stress or low-concentration salt stress, the ground diameter, new shoot, and crown width growth increments of B. alternifolia all showed an increasing trend, whereas they all decreased under high-concentration salt stress; under water-salt interactive stress, the interactive effects differed with different salt concentrations—when low salt concentration interacted with drought (W1S1, W2S1), plant growth increments all increased, whereas when high salt concentration interacted with drought (W1S3, W2S3), plant growth increments all decreased. (2) Whether under salt stress, drought stress, or salt-drought interactive stress, the free proline (Pro) content of B. alternifolia showed a significant increasing trend with increasing stress intensity. (3) The changes in superoxide dismutase (SOD) activity and peroxidase (POD) activity of B. alternifolia were relatively complex; except under drought stress, where both SOD activity and POD activity decreased significantly, their respective changes under salt stress and interactive stress were not consistent. Under salt stress, interactive stress, and drought stress, the osmotic adjustment substances and enzyme activities of B. alternifolia changed correspondingly without obvious synchrony, suggesting the possibility of mutual coordination; meanwhile, the sensitivity of plant cells was far stronger than the changes in phenotypic growth—damage from high salt concentration was not manifested in plant external morphology, but enzyme activities and osmotic adjustment substances showed significant changes. Membership function analysis revealed that the optimal water-salt conditions for B. alternifolia growth were a salt concentration of 8 $g \cdot L^{-1}$ and an irrigation amount of 25 L per application, and the ranking of drought and salt tolerance was: drought stress > interactive stress > salt stress.

Full Text

Abstract

To investigate changes in plant growth and physiological characteristics under salt stress, drought stress, and their interactive effects, and to understand the adaptability of *Buddleja alternifolia* seedlings to extreme habitats in desert hinterlands while determining rational irrigation practices, this study provides a theoretical basis for introducing this species to desert hinterland areas. Through field control experiments, three water gradients and four salt gradients were designed in a randomized combination experiment to measure growth parameters and biochemical indicators. The drought resistance and salt tolerance of *Buddleja alternifolia* were comprehensively evaluated using the membership function method. The results showed: (1) Under drought stress or low-concentration salt stress, the ground diameter, new shoot length, and crown width growth of *Buddleja alternifolia* all showed an increasing trend, whereas they decreased under high-concentration salt stress. Under water-salt interactive stress, plant growth decreased. When low salt concentration was combined with drought stress, plant growth increased, but when high salt concentration was combined with drought stress, plant growth decreased. (2) Regardless of whether the stress was salt, drought, or their interaction, the free proline (Pro) content of *Buddleja alternifolia* showed a significant upward trend with increasing stress intensity. (3) The activity changes of superoxide dismutase (SOD) and peroxidase (POD) were relatively complex. Except under drought stress where SOD activity and POD activity both decreased significantly, inconsistent changes were observed under salt stress and interactive stress. Under salt stress, cross stress, and drought stress, osmotic adjustment substances and enzyme activities changed correspondingly without obvious synchronization, suggesting possible mutual coordination. Meanwhile, plant cell sensitivity was far stronger than phenotypic growth changes. Damage from high salt concentration was not manifested in external plant morphology, but enzyme activities and osmotic adjustment substances showed significant changes. Membership function analysis revealed that the optimal water-salt conditions for *Buddleja alternifolia* growth were a salt concentration of 8 $g \cdot L^{-1}$ and an irrigation amount of 25 $L \cdot time^{-1}$. The ranking of drought and salt tolerance was: drought stress > interactive stress > salt stress.

Keywords: drought stress; salt stress; interactive stress; *Buddleja alternifolia*; physiological characteristics

Introduction

Buddleja alternifolia, also known as purple-flowered butterfly bush, belongs to the Loganiaceae family and *Buddleja* genus. It is a typical native tree species in arid and semi-arid regions of northwest China, serving as an excellent shrub for landscaping and ecological restoration, with graceful plant form and fragrant flowers offering high ornamental value. Its native habitat is the semi-desert zone at the eastern foot of Helan Mountain in Ningxia, characterized by drought resistance, cold tolerance, barren resistance, salt-alkali resistance, rapid growth, freedom from pests and diseases, and extremely strong adaptability. It has no special soil requirements and grows well in sandy, sandy loam, and loam soils, making it suitable for integration with desert forestry ecological construction in arid regions to create large-scale ecological landscapes. Different plants have different response mechanisms and adaptive capacities under adverse conditions, and the same species shows varying morphological growth and physiological metabolism under different degrees of stress. Introducing appropriate plant species to specific environments can enrich plant diversity distribution and improve local ecological environments. Current research on *Buddleja* primarily focuses on introduction, propagation, cultivation techniques, and biochemical components, with limited studies on environmental responses and adaptability under stress conditions.

The study area is located at the Taklamakan Desert Research Station in the hinterland of the Taklamakan Desert, the only special environmental monitoring and research base that penetrates deep into the mobile desert in China, and an excellent site for studying plant adaptability and plant-environment interactions under special conditions. The climate in the desert hinterland is extremely arid with scarce precipitation and no surface runoff; the main irrigation water source is high-mineralization groundwater. Consequently, water and salt have become the primary threats to plant growth. Severe drought and high salt concentrations induce extremely complex response processes within plants, leading to metabolic disorders, inhibited growth, and even death. Many plants growing in this environment exhibit unique adaptive characteristics distinctly different from those in other environments. This study investigates the phenotypic growth characteristics of *Buddleja alternifolia* and changes in intracellular antioxidant enzyme systems and osmotic adjustment substances under drought, salt, and their interactive stresses to understand the plant's drought and salt resistance mechanisms, determine rational irrigation amounts and salt tolerance ranges, provide a reasonable basis for plant introduction under extreme conditions, and strongly promote the functional extension of desert plants' ornamental value.

1. Study Area Overview

The Taklamakan Desert Research Station's Central Desert Botanical Garden [FIGURE:N] is located in the hinterland of the Taklamakan Desert (39°00 N, 83°40 E) at an elevation of 1,100 m. The average annual temperature is 12.4°C, with an average temperature of 28.2°C in the hottest month and -22.2°C in the coldest month. The extreme maximum temperature is 45.6°C, and the extreme minimum temperature is -22.2°C. Annual sunshine hours total 2,571.3 h, average relative humidity is 35.34%, annual precipitation is only 36.6 mm, and annual potential evaporation reaches 3,638.6 mm. The average wind speed is 2.5 $m \cdot s^{-1}$, with maximum instantaneous wind speeds of 24.0 $m \cdot s^{-1}$ and intense aeolian activity. The garden soil is predominantly mobile aeolian sandy soil with loose structure, water content below 3%, and salt content of 1.26–1.63 $g \cdot kg^{-1}$. Groundwater mineralization reaches 4.04 $g \cdot L^{-1}$. The garden has introduced various plants adapted to arid environments from different regions, mainly including multiple species of *Tamarix* and *Haloxylon ammodendron*, irrigated with groundwater at a quota of 165 $m^3 \cdot hm^{-2}$ and an average irrigation cycle of 8 days, using drip irrigation.

2. Materials and Methods

2.1 Experimental Materials

Uniformly growing *Buddleja alternifolia* seedlings from the botanical garden were selected as experimental materials. They were transplanted into experimental plots in March for acclimation, and control experiments were conducted from the following May to September. The seedlings had an average height of 50 cm, average ground diameter of 0.662 mm, and were planted at a spacing of 1 m × 1 m.

2.2 Experimental Methods

A two-factor equal-replication experimental design was adopted. Based on the multiple mineralization levels of groundwater at the experimental site and conventional irrigation practices, industrial salt (composition detailed in Table 1) was used to configure four salt concentration gradients: 0 (CK), 8, 13, and 17 $g \cdot L^{-1}$. Three drought stress gradients were established: 25, 40 (CK), and 55 $L \cdot time^{-1}$. This resulted in 12 treatments, each with three replicates. Freshwater and normal irrigation measures at the experimental site (40 $L \cdot time^{-1}$) served as the control (Table 2). Anti-seepage membranes were buried 1.2 m deep between adjacent treatments to prevent mutual infiltration of irrigation water and salt. Irrigation was applied according to the experimental station's practices with full irrigation between May and June. After seedlings resumed normal growth, irrigation control experiments were conducted from July to September with a weekly irrigation cycle.

2.2.1 Growth Index Measurement

At the end of each irrigation cycle, the labeled branches and crown width of *Buddleja alternifolia* were measured with a tape measure, and ground diameter was measured with vernier calipers.

2.2.2 Physiological Index Measurement

Sampling was conducted after the control experiment ended. Leaf sampling was performed between 08:00–10:00. Three samples were taken from each treatment to determine relevant indicators. Superoxide dismutase (SOD) activity was measured using the nitroblue tetrazolium method, peroxidase (POD) activity was measured using the guaiacol method, and proline (Pro) content was measured using the ninhydrin colorimetric method.

2.3 Data Processing

Experimental data were analyzed using SPSS 19.0 software for general linear model bivariate analysis and Duncan's multiple comparison method for significance testing at $\alpha = 0.05$. Excel 2013 and Sigmaplot 12.5 were used for chart creation.

Note: The main chemical components of groundwater salts are shown in Table 1.

Industrial salt composition analysis

Note: Although industrial salt contains many chemical components, the main components are listed above.

Experimental design

Note: Different letters indicate significant differences between treatments ($P < 0.05$).

3. Results and Analysis

3.1 Changes in Phenotypic Growth Characteristics of *Buddleja alternifolia* Under Water-Salt Stress

As shown in Table 3, under salt stress, all phenotypic growth increments increased at low salt concentration, began to decrease at moderate salt concentration, and reached their minimum at high salt concentration. Differences among indicators varied under different treatments. At low salt stress, ground diameter and crown width growth increments increased by 37.43% and 84.08% respectively compared with the control (CK), showing significant differences ($P < 0.05$), while new shoot growth increment was not significant. At high salt stress, all growth increments were lower than the control, with new shoot and crown width growth increments showing significant differences ($P < 0.05$), decreasing by 63.13% and 64.54% respectively compared with the control. Although ground diameter growth increment decreased significantly, it showed no significant difference from the control ($P > 0.05$). These results indicate that salt stress has a significant stimulating effect on plant growth, with low salt stress significantly promoting growth. However, as salt concentration increases, the promoting effect weakens, and high salt stress significantly inhibits growth, demonstrating that *Buddleja alternifolia* possesses certain salt tolerance but limited capacity, with a definite salt tolerance threshold.

Under drought stress, all treatment phenotypic growth increments showed an initial increase followed by a decreasing trend, but all remained higher than the control. At W1, all growth increments were significantly higher than the control, increasing by 132.18%, 44.55%, and 55.75% respectively, but decreased with increasing drought severity. Compared with the control, ground diameter and crown width growth increments still increased by 71.63% and 46.98% at W2, with significant differences ($P < 0.05$), indicating that water stress stimulates plant growth and that *Buddleja alternifolia* has strong drought adaptability.

Under interactive stress of drought and different salt concentrations, all phenotypic growth increments showed an initial increase followed by a decreasing trend with increasing salt concentration. Under the same drought condition, growth increments increased when combined with low-concentration salt stress, but showed no significant differences ($P > 0.05$). When combined with high-concentration salt stress, all growth increments decreased and showed significant differences from the control ($P < 0.05$), with ground diameter, new shoot, and crown width growth increments decreasing by 51.56–65.99%, 62.57%, and 33.98–40.43% respectively. This indicates that low-concentration salt stress can improve plant salt tolerance under drought stress, while moderate and high-concentration salt stress reduces plant salt tolerance under drought conditions, with greater drought severity causing stronger reduction. Under interactive salt-drought stress, plants show cross-adaptability, with salt stress playing the primary role. General linear model bivariate analysis showed that different salt concentrations and salt-drought interactive stress had extremely significant effects on ground diameter ($F_{salt} = 22.48$, **$F_{drought} = 1.76$, $F_{interaction} = 4.31$**), new shoot ($F_{salt} = 57.09$, **$F_{drought} = 0.22$, $F_{interaction} = 5.18$**), and crown width ($F_{salt} = 34.18$, **$F_{drought} = 1.25$, $F_{interaction} = 1.76$**) growth increments ($P < 0.01$), while drought stress alone had no significant effect on plant growth.

Changes in growth indexes of *Buddleja alternifolia* under drought, salt stress, and interaction stress

Note: Same letters indicate no significant difference between treatments, different letters indicate significant difference ($P < 0.05$).

3.2 Physiological Responses of *Buddleja alternifolia* Under Water-Salt Stress

3.2.1 Effects of Water-Salt Stress on Superoxide Dismutase (SOD) Activity As shown in Figure 1, under single salt stress, SOD activity showed a decreasing then increasing trend with increasing salt concentration, but remained significantly lower than the control ($P < 0.05$). Compared with the control, SOD activity decreased by 41.50%, 14.34%, and 13.32% under low, moderate, and high salt concentrations respectively, with significant differences

($P < 0.05$). Under single drought stress, SOD activity gradually decreased with increasing drought severity, decreasing by 24.11% at W1, with significant difference ($P < 0.05$). Under interactive stress, SOD activity showed no significant change at low salt concentration but significantly decreased at moderate and high salt concentrations ($P < 0.05$), decreasing by 24.11% at W2S3. This suggests that the enzyme protection system may be damaged and enzyme activity inhibited under moderate and high salt stress, insufficient to scavenge oxygen free radicals and causing damage to cell membranes. Under the same salt stress, SOD activity showed no obvious change under different drought and salt cross-stresses. Under the same drought condition, SOD activity first decreased then increased with increasing salt concentration, significantly decreasing when interacting with low and moderate salt concentrations ($P < 0.05$), with reductions of 13.29% and 46.82% respectively, but significantly increasing when interacting with high salt concentration ($P < 0.05$), though still 10.60% lower than the control with no significant difference ($P > 0.05$). Notably, the control group with the largest irrigation amount showed significantly higher SOD activity than all treatment groups under both single salt and single drought stresses, indicating that water stress primarily alleviates salt stress damage to plants.

[Figure 1: see original paper] Changes in SOD activity under single stress and interaction stress

Note: Different letters indicate significant difference between treatments ($P < 0.05$).

3.2.2 Effects of Water-Salt Stress on Peroxidase (POD) Activity As shown in Figure 2, under salt stress, POD activity showed a decreasing then increasing trend with increasing salt, reaching its minimum at S2, decreasing by 27.55% compared with the control ($P < 0.05$). Although no significant difference was observed at S3 compared with the control ($P > 0.05$), it was significantly higher than at low and moderate salt concentrations. This indicates that under high salt stress, plants maintain higher POD enzyme activity to effectively scavenge reactive oxygen species, reduce damage to membrane structure and function, and maintain certain salt tolerance. Under drought stress, POD activity first increased then decreased with increasing drought severity, but all values were higher than the control. Compared with the control, POD activity increased by 55.10% at W1, with significant difference ($P < 0.05$). Under interactive stress, POD activity first increased then decreased with increasing salt concentration, showing no significant difference from the control when interacting with low salt concentration ($P > 0.05$), but significantly decreasing when interacting with high salt concentration ($P < 0.05$), with a reduction of 18.40% compared with the control. Under the same drought condition, POD activity first decreased then increased with increasing salt concentration, significantly decreasing when interacting with low and moderate salt concentrations ($P < 0.05$), with reductions of 13.29% and 46.82% respectively, but increasing when interacting with high salt concentration, though still 17.34% lower than the control without significant difference ($P > 0.05$). This suggests that POD activity is most sensitive to drought stress, and the degree of water stress damage is greater than that of salt and drought stresses alone. Although no obvious damage symptoms appeared in plant phenotypes, cells were highly sensitive to this stress, requiring more enzymes to scavenge harmful substances.

[Figure 2: see original paper] Changes in POD content under single stress and interaction stress

Note: Different letters indicate significant difference between treatments ($P < 0.05$).

3.2.3 Effects of Water-Salt Stress on Proline Content As shown in Figure 3, under single salt stress, proline content in leaves significantly increased with increasing salt concentration ($P < 0.05$), with increases of 38.58%, 27.29%, and 29.81% respectively, showing significant differences from the control ($P < 0.05$). Although proline content slightly decreased under high salt stress compared with moderate salt stress, it indicates that excessively high salt concentration exceeded the regulatory capacity of proline. Under drought stress, proline content also gradually increased, rising by 32.39% at W1, with significant difference from the control ($P < 0.05$), demonstrating that proline accumulates with deepening drought stress. Under water-salt interactive stress, proline content significantly increased with increasing stress intensity ($P < 0.05$), increasing by 95.92% compared with the control, with significant differences from other treatments ($P < 0.05$). This indicates that proline, as an important osmotic adjustment substance, is highly sensitive to external stress, especially salt stress. The massive accumulation of proline during stress processes regulates intracellular osmotic balance, prevents cell damage, and enhances *Buddleja alternifolia*'s stress resistance. When drought stress interacts with salt stress, the significant increase in proline content compared with single drought stress indicates that salt stress can enhance proline accumulation under drought conditions.

[Figure 3: see original paper] Changes in Pro content under single stress and interaction stress

Note: Different letters indicate significant difference between treatments ($P < 0.05$).

3.3 Comprehensive Evaluation of Drought and Salt Tolerance of *Buddleja alternifolia* Under Salt, Drought, and Interactive Stresses

The membership function method was used to evaluate the drought and salt tolerance of *Buddleja alternifolia* under single and interactive stresses to determine the effects of different treatments. The membership function formula is:

$$U(X_i) = (X_i - X_{min}) / (X_{max} - X_{min})$$

Where Xi is the measured value of a certain indicator for the test sample, and X_{max} and X_{min} are the maximum and minimum values of this indicator among all samples. The membership function values of each indicator for each sample were accumulated and averaged for ranking. A larger average value indicates stronger adaptability of *Buddleja alternifolia* under that treatment.

Membership function comprehensive evaluation revealed that under salt stress, the mean membership function value was highest at 8 $g \cdot L^{-1}$ and lowest at 17 $g \cdot L^{-1}$. Under drought stress, the mean membership function value was highest at 25 $L \cdot time^{-1}$ (W1) and lowest at 55 $L \cdot time^{-1}$ (W3). Under salt-drought interactive stress, the mean membership function values ranked as: W1S1 > W2S1 > W1S0 > W2S0 > W3S1 > W1S2 > W2S2 > W3S0 > W1S3 > W2S3 > W3S2 > W3S3. Overall, under single stress, *Buddleja alternifolia* showed the most sensitive drought and salt tolerance at salt concentration of 8 $g \cdot L^{-1}$ and irrigation amount of 25 $L \cdot time^{-1}$. Comparing the maximum mean membership function values among single salt stress, single drought stress, and interactive stress, drought stress was most prominent, followed by interactive stress and salt stress.

Comprehensive evaluation of drought and salt tolerance of *Buddleja alternifolia* under single stress and interaction stress

4. Discussion

Plant ground diameter, new shoot length, and crown width are the most commonly used indicators to characterize plant growth status. Changes in external morphological characteristics represent a comprehensive manifestation of stress response strategies and a direct measure of plant stress tolerance. Stress effects on plants can be intuitively reflected through growth and relative growth rates, with larger values indicating stronger stress resistance. Research has shown that plant growth is often inhibited under salt stress conditions, but moderate salt stress can promote growth in salt-resistant plants. As salt concentration increases, seed germination and plant vegetative and reproductive growth are inhibited, morphological and anatomical structures are altered, and even death may occur. This study found that under both single and interactive stresses, *Buddleja alternifolia* showed different growth increments in ground diameter, new shoots, and crown width under different water-salt treatments. Low salt stress significantly promoted growth, moderate salt stress showed varying effects, and high salt stress significantly inhibited growth. The magnitude of these effects varied with irrigation amount. As salt stress concentration increased and irrigation amount decreased, all growth increments of *Buddleja alternifolia* decreased, indicating that under severe drought conditions, the plants were affected by both salt and drought stresses, with the dual stress severely inhibiting growth. This primarily occurs because the same soil salt content leads to different soil solution concentrations due to varying soil water content. When soil water content is high, soil solution salt concentration is low, soil water potential is high, and plants do not experience water deficit, thus low salt concentration reduces ion toxicity to seedlings and minimally affects *Buddleja alternifolia* growth. However, when soil water content is too low and soil solution salt concentration is too high, low soil water potential makes water absorption difficult for plants, and excessive salt absorption causes ion toxicity, thereby limiting plant growth and reducing growth increments. Drought stress promotes plant growth, though the stimulation effect varies with drought severity—significant growth increments occur under low drought stress but not under severe drought stress. In summary, both salt and drought stresses affect *Buddleja alternifolia* growth, with salt stress having a more significant impact than drought stress.

Under stress conditions, plant cells generate large amounts of reactive oxygen species that damage cell membranes, interfere with metabolism, cause loss of membrane protective function, induce membrane lipid peroxidation, and damage membrane systems. However, during biological system evolution, cells have developed protective systems to scavenge these free radicals and active oxygen, including catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR), which work synergistically to remove excess reactive oxygen, maintain metabolic balance, and protect membrane structures, enabling plants to tolerate or resist stress to some degree. This study showed that SOD activity did not follow the general pattern of first increasing then decreasing with salt concentration under salt and interactive stresses, and the two enzymes (SOD and POD) did not show obvious synchronization. Under single drought stress, SOD activity significantly decreased while POD activity significantly increased with increasing drought severity. Under both single salt and interactive stresses, SOD activity significantly decreased under severe salt stress while POD activity significantly increased. Both enzymes slightly decreased under low salt stress but significantly decreased under moderate salt stress. Drought severity under interactive stress did not significantly alleviate salt concentration effects. However, this suggests that during drought and salt stress, plants may have coordinated relationships in their cross-adaptation processes, with SOD and POD showing certain differences in drought and salt resistance mechanisms, and salt stress being the main factor disrupting *Buddleja alternifolia*'s cellular metabolic balance.

Proline is a common osmotic adjustment substance that accumulates massively in plant cells under adverse conditions to reduce intracellular osmotic potential and maintain water balance. Current research holds different views on proline's physiological mechanisms under drought, salt, and other stresses. Li Hesheng considers massive proline accumulation as an active adaptation to stress, where proline acts as an osmotic regulator to reduce cell osmotic potential and enhance stress resistance. This study found that under salt stress, drought stress, and their interaction, proline content in *Buddleja alternifolia* continuously increased with increasing salt concentration and drought severity, significantly higher than the control. This demonstrates that proline is an important osmotic adjustment substance highly sensitive to environmental stress, and *Buddleja alternifolia* accumulates large amounts of proline to adapt to salt and drought stresses—a crucial protective regulatory measure in response to adverse conditions.

5. Conclusion

(1) *Buddleja alternifolia* shows hierarchical responses to salt stress: low salt stress (8 g·L^{-1}) promotes growth, with maximum values for ground diameter, new shoot, and crown width growth increments; high salt stress (17 g·L^{-1}) inhibits growth, with significant reductions in all growth indicators, though plants can still survive. Drought stress promotes *Buddleja alternifolia* growth, with lower drought severity showing more obvious growth stimulation. The species is not suitable for growth under excessive water conditions. Therefore, when planting *Buddleja alternifolia* locally using saline groundwater irrigation, irrigation amount should be reduced to approximately 25 L·$time^{-1}$ to better meet local ecological construction needs.

(2) The response sequence of *Buddleja alternifolia* leaf components differs under different stress conditions: SOD activity is most sensitive to salt stress, POD activity is most sensitive to drought stress, and proline content is most sensitive to interactive stress, followed by salt stress.

(3) *Buddleja alternifolia* has strong adaptability and can grow well under certain salt stress conditions. It exhibits different response mechanisms to different stresses and can serve as an alternative species for plant introduction in desert hinterlands, with moderate interactive stress potentially enhancing plant adaptability to adverse conditions.

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Note: Figure translations are in progress. See original paper for figures.