Effects of Overbank Flooding on Leaf Osmotic Adjustment Substances and Antioxidant Enzyme Activities in Natural Populus euphratica Forests in the Middle Reaches of the Tarim River (Postprint)

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Abstract

This study investigated natural Populus euphratica forests in the middle reaches of the Tarim River basin subjected to seasonal flood inundation, examining changes in leaf osmotic adjustment substances and antioxidant enzyme activities under flooding conditions using field in-situ sampling methods, to provide scientific evidence for preliminary research on the physiological mechanisms of flood tolerance in natural Populus euphratica forests. The results indicated that: (1) In the early stage of flood inundation (8 d), the contents of Na+, K+, free proline (Pro), soluble sugars (SS), and superoxide dismutase (SOD) activity in Populus euphratica leaves decreased, while Cl- content, soluble protein (SP) content, and peroxidase (POD) and catalase (CAT) activities increased, suggesting that in the early stage of flood inundation, Populus euphratica maintained leaf osmotic potential by increasing the contents of osmotic adjustment substances such as Cl- and SP, while simultaneously scavenging reactive oxygen species accumulated due to waterlogging stress through elevated POD and CAT activities, thereby collectively enhancing plant resistance; (2) With prolonged flood inundation duration (18 d), the contents of K+, Cl-, SS, SP, and SOD activity in Populus euphratica leaves all increased, whereas Na+ content, Pro content, POD activity, and CAT activity all decreased, indicating that as waterlogging stress intensified, the plant enhanced its stress resistance by increasing the contents of K+, SS, and SP and elevating SOD activity; (3) With further extension of flood inundation duration (35 d), Na+ content in leaf tissues increased, while SS content, SOD activity, POD activity, and CAT activity all decreased, but remained comparable to pre-inundation levels. In summary, under flood inundation stress, Populus euphratica enhanced plant resistance through the combined action of osmotic adjustment substances and the antioxidant enzyme system. Among the osmotic adjustment substances, Na+, K+, and SP played important roles in osmotic regulation throughout the entire flood inundation process, whereas Cl- and SS primarily functioned in the early and middle stages to maintain vacuolar osmotic potential balance in leaves. In the antioxidant enzyme system, POD and CAT played important roles in scavenging reactive oxygen free radicals accumulated in Populus euphratica leaves under stress during the early stage of flood inundation, while SOD exhibited a strong scavenging effect during the late stage of flood inundation.

Full Text

Effects of Flood Overtopping on Leaf Osmotic Adjustment Substances and Antioxidant Enzyme Activities of Natural Populus euphratica Forest in the Middle Reaches of the Tarim River

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Abstract

This study examined natural *Populus euphratica* forests in the middle reaches of the Tarim River subjected to seasonal flood overtopping. Using field in situ sampling, we investigated changes in leaf osmotic adjustment substances and antioxidant enzyme activities under flooding conditions to elucidate the physiological mechanisms of waterlogging resistance in natural forests. The results showed that: (1) During the initial stage of flood overtopping (8 days), superoxide dismutase (SOD) activity in *P. euphratica* leaves decreased, while Cl^- content, soluble protein (SP) content, free proline (Pro) content, soluble sugar (SS) content, peroxidase (POD) activity, and catalase (CAT) activity increased. This indicates that during early flooding, *P. euphratica* maintained leaf osmotic potential by increasing osmotic adjustment substances such as Cl^- and SP, while enhancing POD and CAT activities to eliminate reactive oxygen species accumulated from waterlogging stress, thereby jointly improving plant resistance. (2) As flooding duration extended (18 days), K^+ content, Cl^- content, SS content, SP content, and SOD activity in leaves increased, while Na^+ content, Pro content, POD activity, and CAT activity decreased, suggesting that as waterlogging stress intensified, plants enhanced stress resistance by increasing K^+ and SS content and improving SOD activity. (3) With further extension of flooding (35 days), Na^+ content and SS content in leaves increased, while SOD, POD, and CAT activities decreased to levels comparable with pre-flooding values. In summary, *P. euphratica* enhances plant resistance through coordinated action

of osmotic adjustment substances and antioxidant enzyme systems under flood overtopping stress. Among osmotic adjustment substances, Na^+, K^+, Cl^-, and SP played important roles throughout the flooding process, while SS contributed primarily during early and middle stages to maintain leaf vacuole osmotic potential balance. In the antioxidant enzyme system, POD and CAT played major roles in scavenging reactive oxygen species during early flooding stages, whereas SOD exhibited stronger scavenging capacity during the late stage.

Keywords: *Populus euphratica*; flood overtopping; osmotic adjustment substances; antioxidant enzyme activities; Tarim River

Introduction

Waterlogging is one of the major abiotic stresses affecting plants worldwide. This stress occurs in many ecosystems and is characterized by periodic or long-term anaerobic or hypoxic conditions that interfere with normal plant respiration at the electron transport level, severely affecting plant growth and development. Waterlogging stress impacts plants in multiple ways, particularly affecting cellular membrane systems and their functions. Under prolonged waterlogging, the balance between reactive oxygen species (ROS) formation and scavenging is disrupted, causing molecular oxygen to be reduced into toxic ROS such as superoxide anion radicals, hydroxyl radicals ($\cdot$OH), and hydrogen peroxide (H_2O_2), which accumulate in cells and trigger membrane lipid peroxidation. To cope with waterlogging stress, plants undergo a series of physiological, biochemical, and morphological changes. They regulate osmotic substance content to maintain osmotic potential balance and increase various antioxidant enzyme activities. Plants typically develop a complete antioxidant chain through their antioxidant enzyme systems and antioxidants (such as ascorbic acid) to scavenge excess free radicals and enhance stress resistance.

Previous research on waterlogging stress has primarily focused on laboratory simulations and agricultural crops, with fewer studies investigating changes in osmotic adjustment substances and antioxidant enzyme systems of trees under long-term field flooding conditions. *Populus euphratica*, belonging to the genus *Populus* in the family Salicaceae, is the oldest and most primitive subgenus of *Populus*, mainly distributed in arid desert regions of central and western Asia, North Africa, and southern Europe. It is a typical phreatophytic xerophyte to mesophyte and the only tree species capable of forming forests in desert and semi-desert areas, playing a crucial role in improving ecological environments in its distribution regions. *P. euphratica* is a typical desert riparian forest, and the Tarim River basin hosts the world' s largest natural *P. euphratica* forest. During summer, melting snow and ice from upstream mountains inject floodwater into the river channel, subjecting natural *P. euphratica* forests along the riverbanks to waterlogging conditions with obvious seasonal flood overtopping processes. While numerous studies have investigated the physiological and biochemical characteristics of *P. euphratica* under drought and salt stress, research on its physiological adaptation mechanisms under flood overtopping conditions remains scarce. This study focuses on *P. euphratica* riparian forests in the Tarim River basin, using waterlogging stress as the dominant factor during typical seasonal flood overtopping processes to investigate physiological responses of osmotic adjustment substances and antioxidant enzyme activities. The findings aim to reveal the physiological adaptation mechanisms of *P. euphratica* under waterlogging stress, providing a theoretical basis for ecosystem restoration and scientific implementation of ecological water conveyance projects in the Tarim River basin.

1 Study Area Description

The study area is located in the *P. euphratica* public welfare forest area of Luntai County in the middle reaches of the Tarim River, Xinjiang. The region has a warm temperate continental arid climate with abundant light and heat resources, receiving 2,574 hours of annual sunshine. The extreme minimum temperature is -25.5°C, while the extreme maximum temperature reaches 40.1°C. Precipitation is scarce, with an annual average of only 52.5 mm, while evaporation is intense at 1,085 mm annually. The area experiences prevailing northeasterly winds with an average speed of 7.6 $m \cdot s^{-1}$, and frequent sand and dust storms. The dominant tree species is *Populus euphratica*, with shrubs 主要包括柽柳 (*Tamarix ramosissima*), 铃铛刺 (*Halimodendron halodendron*), and 琵琶柴 (*Reaumuria songonica*), and herbaceous plants mainly consisting of 芦苇 (*Phragmites communis*), 芨芨草 (*Achnatherum splendens*), and 蒿草 (*Kobresia myosuroides*). The soil type is aeolian sandy soil.

2 Methods

2.1 Plot Establishment and Sample Tree Selection

Observation plots were established in *P. euphratica* public welfare forest compartments in the middle reaches of the Tarim River in Luntai County. The observation plot measured 200 m × 200 m. A steel-wood monitoring platform was constructed perpendicular to the north side of the Tarim River flood control dike, consisting of three branch channels. The main channel was 5.5 m above ground, with branch channels at 3.0 m height and 100.0 m length. The platform channels were 2.5 m wide. A 2.4 m high fence was installed around the plot to prevent entry by unauthorized personnel and wildlife. Seven healthy, pest-free middle-aged trees with good growth were marked as observation subjects, with an average height of 7.5 m, average DBH of 8.2 cm, and average crown size of 2.4 m × 2.6 m. The flooding period in 2016 lasted from June 15 to August 30, with complete water recession.

2.2 Sample Collection

P. euphratica leaf samples were manually collected before flooding (June 15), and on days 8, 18, and 35 of flooding. During sampling, healthy, pest-free leaves were collected from upper, middle, and lower positions in the east, south, west, and north directions of each sample tree, with samples from the three positions in each direction mixed into one composite sample. The collected samples were divided into two portions: one portion was placed in sample bags, returned to the laboratory, killed at high temperature, and oven-dried; the other portion was wrapped in aluminum foil, placed in a liquid nitrogen tank, and returned to the laboratory for testing.

2.3 Measurement Indicators and Data Processing

The measurement indicators included: Na^+ and K^+ content determined by ethanol solution protection method; soluble protein (SP) content by Coomassie brilliant blue staining method; free proline (Pro) content by acidic ninhydrin method; soluble sugar (SS) content by anthrone method; superoxide dismutase (SOD) activity by nitroblue tetrazolium (NBT) method; peroxidase (POD) activity by guaiacol method; and catalase (CAT) activity by potassium permanganate titration method. Differences in physiological and biochemical indicators of *P. euphratica* under flood overtopping were analyzed using one-way ANOVA in SPSS 22.0, with significance set at $P < 0.05$. Data were processed using Excel 2010.

3 Results

3.1 Effects of Flooding on Inorganic Osmotic Adjustment Substances in *P. euphratica* Leaves

With extended flooding duration, Na^+ and K^+ contents showed a trend of initial decrease followed by increase. Before flooding, Na^+ content in *P. euphratica* leaves was 3.01 $g \cdot kg^{-1}$, which decreased by 17.32% and 67.43% on flooding days 8 and 18, respectively. However, as flooding continued, Na^+ content increased to 5.05 $g \cdot kg^{-1}$ on day 35, representing a 12.93% increase compared with pre-flooding levels. This value was significantly different from pre-flooding, early flooding (day 8), and middle flooding (day 18) ($P < 0.05$). Overall, K^+ content was highest before flooding, decreasing by 18.97%, 17.36%, and 23.80% on flooding days 8, 18, and 35, respectively ($P > 0.05$), with no significant differences between periods. However, during the flooding period, Cl^- content in *P. euphratica* leaves showed an increasing trend with prolonged flooding, with middle (day 18) and late (day 35) flooding stages showing 6.34% and 8.45% increases, respectively, compared with early flooding. Cl^- content under flooding was significantly higher than before flooding ($P < 0.05$), increasing by 90.23% on day 8, 98.15% on day 18, and 113.45% on day 35 compared with pre-flooding levels.

[Figure 1: see original paper]

3.2 Effects of Flooding on Organic Osmotic Adjustment Substances in *P. euphratica* Leaves

Variance analysis showed that SP content before flooding and on day 8 was significantly higher than on days 18 and 35 ($P < 0.05$). SP content decreased by 25.06% on day 8 compared with pre-flooding levels. As flooding continued, SP content increased rapidly, reaching 9.81% on day 18, then decreased to levels comparable with pre-flooding by day 35. Pro content was significantly higher before flooding than during flooding ($P < 0.05$). With prolonged flooding, Pro content gradually decreased, reaching its lowest point on day 35 at only 21.12% and 35.56% of pre-flooding levels on days 18 and 35, respectively. The trend of SS content was opposite to that of Pro content. Before flooding, SS content was significantly lower than after flooding ($P < 0.05$). After flooding, SS content increased with flooding duration, with significant differences between day 8 and days 18 and 35 ($P < 0.05$), though no significant differences existed between days 18 and 35.

[Figure 2: see original paper]

3.3 Effects of Flooding on Antioxidant Enzyme Activities in *P. euphratica* Leaves

Before flooding, SOD activity in *P. euphratica* leaves was higher than during early flooding ($P < 0.05$). As the trees adapted to flooding, SOD activity decreased by 29.66% compared with pre-flooding levels. However, as flooding continued, SOD activity increased again. On day 18, SOD activity was roughly equivalent to pre-flooding levels. With further extension of flooding to day 35, SOD activity decreased again. In the antioxidant system of *P. euphratica* leaves, POD and CAT activities showed consistent trends during flooding, initially increasing then decreasing. Both POD and CAT activities on day 18 were significantly higher than in other periods ($P < 0.05$). As flooding continued, POD and CAT activities gradually decreased. By day 35, POD and CAT activities were comparable to pre-flooding levels, having decreased by 39.11% and 41.99%, respectively, compared with day 18.

[Figure 3: see original paper]

4 Discussion

4.1 Osmotic Adjustment Response in *P. euphratica* Leaves Under Flooding

Osmotic adjustment is a primary physiological mechanism for desert plants to adapt to environmental stress. When plants experience waterlogging, low oxygen stress inhibits respiration, directly affecting energy supply. During early waterlogging, *P. euphratica* had relatively low K^+ content. To maintain survival energy, the trees likely consumed stored sugars through glycolysis to alleviate the energy crisis and provide ATP. With prolonged flooding, soluble salts in the soil were dissolved and transferred, and hypoxic conditions intensified, damaging root cell membranes and increasing Na^+ absorption. Energy supply deficiencies impeded the sodium pump, leading to excessive Na^+ accumulation. In this study, Na^+ and K^+ accumulated rapidly during middle and late flooding stages, consistent with ion change characteristics in sunflowers and rice under hypoxic stress. The large accumulation of Na^+ and K^+ served as osmotic adjustment substances, regulating vacuole osmotic potential, maintaining cellular turgor, and improving stress tolerance. *P. euphratica* is a salt-secreting plant with strong salt rejection and vacuolar compartmentalization capacity, sequestering excess Na^+ in vacuoles and ultimately secreting it through leaves. The accumulated Na^+ and K^+ did not cause significant adverse effects on physiological activities, demonstrating that *P. euphratica* enhances resistance through coordinated osmotic adjustment and antioxidant protection under long-term waterlogging.

Free proline (Pro) is an important organic osmotic adjustment substance existing in free state in plants. Numerous studies show that proline content correlates closely with plant stress resistance. However, this study found that Pro content decreased with extended flooding duration, indicating Pro did not play a major osmotic adjustment role under waterlogging conditions. The low Pro content may result from either strong waterlogging adaptation mechanisms in *P. euphratica* or damage to Pro synthesis systems under anaerobic conditions, requiring further investigation.

Soluble sugar (SS) is an important energy substance and organic osmotic adjustment material. Under waterlogging, *P. euphratica* root systems shift from aerobic to anaerobic respiration. Hypoxic stress reduces ATP synthesis, decreasing energy for active transport and preventing the ion transport system that creates water potential gradients in root inner cortex, ultimately reducing active absorption and transport of ions like K^+. However, as flooding continued, SS content increased significantly, indicating that appropriate flooding duration benefits *P. euphratica* energy reserves. The accumulation of SS effectively improved waterlogging tolerance and enhanced survival capacity under temporary root hypoxia.

4.2 Antioxidant Enzyme System Response in *P. euphratica* Leaves Under Flooding

Plants have evolved complex antioxidant defense systems. Within certain stress ranges, protective enzymes activate antioxidant mechanisms to eliminate excess ROS and protect membrane systems. The antioxidant enzyme system primarily includes SOD, POD, and CAT. SOD rapidly dismutates superoxide anion radicals into H_2O_2 and molecular oxygen, while POD and CAT are key enzymes that quickly clear H_2O_2, reducing oxidative status and preventing H_2O_2 accumulation damage.

Studies show that in waterlogging-sensitive plants, antioxidant enzyme activities like SOD, POD, and CAT increase initially as a stress response. In this study, SOD activity decreased during early flooding (day 8), but POD and CAT activities increased significantly, indicating *P. euphratica* is waterlogging-sensitive. As flooding extended (day 18), SOD activity increased rapidly, dismutating superoxide anion radicals, while POD and CAT activities decreased, suggesting ROS caused some enzyme system damage. As waterlogging stress intensified (day 35), large amounts of ROS accumulated in leaf tissues. At this stage, SOD, POD, and CAT activities all decreased, likely because long-term waterlogging stress hindered antioxidant enzyme synthesis. Although *P. euphratica* tissues experienced some damage under long-term waterlogging, they remained within normal physiological tolerance ranges and could still reduce and scavenge excess ROS through non-enzymatic antioxidant systems to maintain normal growth. The mechanism of non-enzymatic antioxidant systems in *P. euphratica* under long-term waterlogging requires further research.

5 Conclusion

Under long-term flood overtopping conditions, *P. euphratica* experiences hypoxic stress and enhances resistance by increasing organic and inorganic substances (Na^+, K^+, Cl^-, SP, SS) in leaves to improve cell solute concentration and maintain normal osmotic potential, thereby preventing cell damage. Simultaneously, antioxidant enzymes in *P. euphratica* coordinate and cooperate: POD and CAT play major roles in early and middle flooding stages, while SOD contributes more in late stages, jointly scavenging excess free radicals and enhancing stress resistance. This study provides preliminary research on physiological and biochemical indicator changes in *P. euphratica* leaves under long-term flooding, but further in-depth studies on physiological and structural adaptation mechanisms are needed to provide technical support for ecosystem restoration and management of *P. euphratica* forests in the Tarim River basin.

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