Effects of Drought Stress and Rewatering on Hydraulic Characteristics of Drought-Tolerant Goji Berry (Lycium barbarum) Postprint

Authors: Xu Shengrong, Zhang Enhe, Ma Ruili, Wang Qi, Liu Qinglin, Wu Rui

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Abstract

Drought-resistant goji berry is an important economic crop in the arid regions of northwestern China. To further elucidate the water transport characteristics of goji berry and enhance agricultural production potential, a study was conducted at the Gulang County Agricultural Demonstration Base in Gansu Province (37.09°N, 102.79°E) using two-year-old seedlings of three goji berry cultivars ('Ningqi 1' , 'Ningqi 5' , and 'Mengqi 1') as experimental materials. Three treatments were designed [N: normal water; M: moderate drought; S: severe drought] to investigate the effects of drought stress on photosynthetic rate, stomatal conductance, canopy and root hydraulic conductivity, as well as the impact of rewatering after drought stress on branch hydraulic conductivity. The results showed that with increasing drought severity, the hydraulic conductivity of goji berry canopy, branches, and root system all decreased. 'Ningqi 5' exhibited the most significant reduction in plant hydraulic conductivity after drought stress and the greatest increase in the proportion of root hydraulic resistance within the whole plant. By fitting xylem vulnerability curves, it was found that the xylem water potential at 50% loss of hydraulic conductivity in 'Ningqi 1' was significantly higher than that in 'Ningqi 5' and 'Mengqi 1' . The net photosynthetic rate and stomatal conductance of goji berry leaves showed significant correlations with leaf hydraulic conductance. Plant growth after drought stress and rewatering depended primarily on the root system' s ability to recover water uptake. Four days after rewatering following drought stress, seedling hydraulic conductivity showed varying degrees of recovery. 'Mengqi 1' demonstrated the fastest recovery rate of hydraulic conductivity and exhibited a significant compensatory effect, while 'Ningqi 5' showed the slowest recovery rate. Comprehensive analysis indicated that drought resistance characteristics of goji berry are related to hydraulic capacity. The sensitivity of root hydraulic conductivity to drought stress can reflect the plant' s sustained drought resistance capacity.

The recovery capacity and compensatory effect of root hydraulic conductivity after drought stress and rewatering have significant impacts on soil water utilization under adverse conditions, and regulating root hydraulic conductivity is of great importance for improving soil water use efficiency.

Full Text

Hydraulic Characteristics of Lycium barbarum L. Seedlings Under Drought Stress and Re-watering Conditions

XU Shengrong[1],[3], **ZHANG Enhe**[1], MA Ruili[1], WANG Qi[2], LIU Qinglin[1], WU Rui[1]**

[1]College of Agronomy, Gansu Agricultural University, Lanzhou 730070, China
[2]College of Grass Industry, Gansu Agricultural University, Lanzhou 730070, China
[3]Gulang County Forestry Bureau, Wuwei 733100, China

Abstract

Drought-resistant goji berry (*Lycium barbarum* L.) is an important economic crop in the arid regions of northwestern China. To further elucidate the water transport characteristics of goji berry and enhance agricultural productivity potential, we conducted a pot experiment at the agricultural demonstration site in Gulang County, Gansu Province (37.09°N, 102.79°E). Using two-year-old seedlings of three goji berry varieties ('Ningqi 1' , 'Ningqi 5' , and 'Mengqi 1') as experimental materials, we designed three water treatments [N: normal water; M: moderate drought; S: severe drought] to investigate the effects of drought stress on photosynthetic rate, stomatal conductance, and hydraulic conductivity of canopy and root systems, as well as the impact of post-drought re-watering on shoot hydraulic conductivity. The results demonstrated that hydraulic conductance of canopy, shoot, and root all decreased with increasing drought severity. 'Ningqi 5'exhibited the most significant reduction in plant hydraulic conductance and the greatest increase in the proportion of root hydraulic resistance within the whole plant following drought stress. Fitting xylem vulnerability curves revealed that the xylem water potential at 50% loss of hydraulic conductance in 'Ningqi 1' was significantly higher than that in 'Ningqi 5' and 'Mengqi 1' . Leaf net photosynthetic rate and stomatal conductance showed significant correlations with leaf hydraulic conductance. Plant growth after drought stress and re-watering depended primarily on the root system' s capacity to recover water uptake. Four days after re-watering, seedling hydraulic conductance exhibited varying degrees of recovery, with 'Mengqi 1' showing the fastest recovery rate and significant compensation effects, while 'Ningqi 5' displayed the slowest recovery. Comprehensive analysis indicated that drought tolerance characteristics in goji berry are related to hydraulic capacity. The sensitivity of root hydraulic conductance to drought stress reflects the plant' s sustained drought resistance capacity, while root hydraulic recovery ability and compensation effects after re-watering significantly influence soil water utilization under adverse conditions. Regulating root hydraulic conductance is therefore crucial for improving soil water use efficiency.

Keywords: *Lycium barbarum* L.; Drought stress; Re-watering; Compensation effect; Hydraulic conductance; Xylem embolism

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Introduction

Drought stress has become a primary factor limiting the development of ecological agriculture and constraining crop growth and the full expression of plant stress resistance. Plant drought resistance represents the adaptive and defensive capacity of plants to drought stress, which is regulated and controlled by multiple environmental conditions and genetic factors [1]. Woody plants possess well-developed water transport systems that efficiently deliver soil water to various organs, thereby ensuring normal water supply to the plant [2]. Xylem vessel transport constitutes the main pathway for water movement from roots to aboveground parts in plants, and xylem vessel structure and embolism occurrence directly affect plant water transport and utilization. Drought can induce xylem vessel embolism, increase water transport resistance, and reduce water transport capacity, consequently affecting tree growth [3]. Therefore, maintaining the continuity of the root-stem-leaf xylem water transport system is crucial for plant growth and development [4]. The physiological changes associated with xylem vessel embolism occurrence and recovery are related to plant drought resistance characteristics. Plant drought resistance may not be manifested solely in the ability of xylem to resist embolism; other physiological strategies may also assist in resisting xylem vessel embolism [5]. For example, leaf stomatal opening and closing can reduce internal water loss through transpiration.

Root absorption represents the primary pathway for soil water entry into plants, and root hydraulic conductance can indicate changes in plant water relations under stress conditions [6]. When soil water deficit occurs, the root system' s capacity to absorb soil water directly affects the overall water status of the plant, while the hydraulic capacity of root xylem also directly influences root water absorption. Consequently, root hydraulic conductance plays a critical role in water transport and utilization within the soil-plant-atmosphere continuum (SPAC) system. Plant growth following drought stress and re-watering depends primarily on the recovery of root water absorption capacity; if the required recovery time is shortened, plant productivity can be improved. The recovery of plant root water absorption capacity is related to both the degree and duration of soil water stress. Secchi et al. [7] found in *Populus trichocarpa* that embolism could be rapidly repaired under moderate water stress, but repair time was longer under extreme water stress, significantly affecting root water absorption recovery. Xylem embolism and repair represent intrinsic plant regulatory mechanisms rather than spontaneous processes, requiring physiological activities to promote water flow into embolized vessels, and are therefore related to root development degree and root vigor [8-11]. Plants generally exhibit certain compensation effects after drought stress relief, which can manifest in root growth and water absorption, strengthening root absorption function and serving as an adaptive mechanism for resisting drought stress [12]. Whether the water transport process within plants can rapidly return to pre-stress levels after drought stress relief has become an important criterion for evaluating plant drought resistance [13].

Goji berry (*Lycium barbarum*) belongs to the Solanaceae family of perennial deciduous shrubs, with well-developed root systems, heat resistance, drought resistance, and strong adaptability. It also improves soil structure, enhances soil fertility, and reduces saline-alkali damage, making it an excellent species for desertification control. In recent years, numerous studies have investigated water utilization in goji berry, but research on internal water transport remains relatively scarce, and water transport and utilization characteristics of goji berry in arid regions have not been clearly defined. This experiment employed potted simulated drought stress to analyze changes in photosynthetic characteristics and plant water transport properties under drought stress and post-stress rewatering conditions, aiming to systematically understand the effects of drought stress on water transport and utilization in goji berry and provide important scientific basis for establishing standardized cultivation and breeding drought-resistant new varieties in arid and semi-arid regions.

Materials and Methods

1.1 Experimental Materials and Design

The experiment was conducted in August 2016 at the Goji Berry Demonstration Garden in Gulang County, Gansu Province (37.09°N, 102.79°E). Two-year-old potted seedlings of three main cultivated varieties in arid regions (‘Ningqi 1’ , ‘Ningqi 5’ , and ‘Mengqi 1’) were used as experimental materials. The test materials were planted in growth barrels measuring 30 cm in diameter and 45 cm in height, with one plant per barrel. The planting soil consisted of a mixture of 0-20 cm topsoil from the nursery, fine sand, and substrate at a ratio of 3:1:1. Soil organic matter content was 14.5 $g \cdot kg^{-1}$, nitrate nitrogen 38.1 $mg \cdot kg^{-1}$, ammonium nitrogen 1.34 $mg \cdot kg^{-1}$, available phosphorus 28.5 $mg \cdot kg^{-1}$, and available potassium 396.9 $mg \cdot kg^{-1}$, with uniform soil fertility and a maximum water-holding capacity of 26.3%.

In August 2016, when seedlings were in the vigorous growth stage, drought treatments were initiated. Water stress treatments were applied at three soil moisture levels: 75%-80% of field capacity (normal water, N), 50%-55% (moderate drought, M), and 40%-45% (severe drought, S). Each treatment had 10 replicates arranged in a randomized block design, with all test materials receiving consistent management practices. Soil initial water content was determined using the oven-drying method, and soil water content during the water control period was monitored using the weighing method. Before drought treatment, conventional irrigation maintained soil water content above 75% of saturated water content. After treatment initiation, soil water content was measured daily. When control water content fell below 75%, irrigation was applied to maintain 75%-80% water content. For drought treatments, soil was allowed to lose water naturally. When moderate and severe drought treatments reached 50%-55% and 40%-45% water content respectively, the stable drought stress state was maintained for 5 days. Measurements began on day 6, and drought-stressed plants were re-watered on day 10 to achieve water content above 75%. Measurements resumed on day 11, with treatment water content maintained above 75% during this period.

After each treatment' s soil water content (moisture gradient) reached the target value and continued for 5 days, when the physiological status of test seedlings stabilized, three healthy, pest-free seedlings with consistent growth were selected from each variety under each water stress gradient. Three to five mature leaves and current-year shoots measuring 0.4-0.6 cm in diameter and approximately 10 cm in length were randomly selected from around the canopy to determine photosynthesis and hydraulic characteristics.

1.2 Index Measurement

Water potential measurement: Mature leaves and vigorous, pest-free one-year-old shoots were selected from the canopy, and leaf and shoot water potential were measured using a MODEL-1000 pressure chamber (PMS Instrument Company, USA).

Leaf net photosynthetic rate (Pn) and stomatal conductance (Gs) measurement: Before hydraulic conductance measurement, mature, pest-free leaves were selected to determine leaf net photosynthetic rate and stomatal conductance using a CIRAS-2 portable photosynthesis system (PP-system, UK).

Leaf area and diameter measurement: Leaf area was measured using a Li-3000 leaf area meter (LI-COR, USA), and shoot diameter was measured using precision digital calipers.

Hydraulic conductance and resistance measurement: In-situ field measurements were conducted using a high pressure flow meter (HPFM) produced by Dynamax Company, USA. Current-year shoots were selected and connected to HPFM to measure shoot hydraulic conductance (Kshoot). The aboveground portion was cut at 5 cm above ground to measure canopy hydraulic conductance (Kcanopy), then all leaves were removed to measure stem hydraulic conductance (Kstem). After removing the aboveground portion, the root system was connected to measure root hydraulic conductance (Kroot). Absolute hydraulic conductance (Kh) and corresponding hydraulic resistance are reciprocals (R=1/Kh), thus: Rcanopy=1/Kcanopy, Rstem=1/Kstem. Plant hydraulic resistance can be calculated through vector operations, i.e., leaf hydraulic resistance in the plant canopy is Rleaf=Rcanopy-Rstem [4]. Leaf specific conductivity (Kl) is the absolute hydraulic conductance (Kh) per unit leaf area (Sleaf), calculated as: Kl=Kh/Sleaf.

Xylem embolism vulnerability curve construction: PLC (percentage loss of hydraulic conductivity) indicates the degree of xylem vessel embolism. During measurement, the initial hydraulic conductance (P) of test shoots was measured under low pressure, then after flushing for 20 minutes at pressures greater than 200 kPa, maximum hydraulic conductance (P0) was measured under high pressure. Shoot embolism was expressed as percentage loss of conductivity (PLC, %), with 5 replicates for each variety at each water potential, calculated as:

$$PLC(\%) = (1 - P/P0) \times 100$$

1.3 Data Analysis and Processing

Data were processed using SPSS 17.0 statistical analysis software. Analysis of variance was first performed among different treatments, and if differences were significant, LSD multiple comparisons were further conducted. SigmaPlot was used for graphical presentation.

Results

2.1 Effects of Drought Stress on Hydraulic Conductivity of Goji Berry Plants

Drought stress reduced plant water potential, induced xylem vessel embolism, and caused varying degrees of hydraulic conductivity reduction in goji berry organs. As shown in [Figure 1: see original paper], after different degrees of drought stress, ‘Ningqi 5’ exhibited the greatest reduction in canopy hydraulic conductivity, while ‘Ningqi 1’ showed the smallest reduction. ‘Mengqi 1’ had the smallest reduction in shoot and leaf hydraulic conductivity. Under normal conditions, root hydraulic conductivity was highest in ‘Ningqi 5’ , reaching 2.11$×10^{-5}$ $kg\cdot MPa^{-1}\cdot s^{-1}$. After moderate drought stress, root hydraulic conductivity was roughly equal among the three varieties with no significant differences. After severe drought stress, ‘Ningqi 1’ had the highest root hydraulic conductivity. The whole-plant hydraulic conductivity of ‘Ningqi 1’ , ‘Ningqi 5’ , and ‘Mengqi 1’ decreased to 42.41%, 39.76%, and 41.17% of normal treatment under moderate drought, and to 28.29%, 25.68%, and 26.35% under severe drought, respectively, with ‘Ningqi 5’ showing the greatest reduction in whole-plant hydraulic conductivity.

2.2 Effects of Drought Stress on Hydraulic Resistance Changes in Different Organs

Structural differences in xylem among leaves, stems, and roots result in varied responses to drought stress. As shown in [Figure 2: see original paper], after drought stress, ‘Ningqi 5’ exhibited the most significant change in the proportion of root hydraulic resistance within the whole plant, increasing from 36.2% under normal irrigation to 64.3% under severe drought stress. ‘Ningqi 1’ showed the next most significant change, while ‘Mengqi 1’ had the smallest change, with root hydraulic resistance proportion increasing from 44.9% to 55.1%. All three varieties showed increased hydraulic resistance in roots, canopy, and leaves after drought stress, but the proportion of canopy and leaf hydraulic resistance within the whole plant decreased, primarily due to the significant increase in root hydraulic resistance.

2.3 Xylem Embolism Vulnerability Curves in Goji Berry

There is a close relationship between xylem vessel embolism degree and water potential, described by the “vulnerability curve” of xylem embolism. The ability of plants to maintain continuous water transport under different water stress conditions can be expressed by the pattern of xylem hydraulic conductivity changes with water potential. Plants have a water potential threshold; when water potential reaches this threshold, hydraulic conductivity decreases significantly and xylem vessel embolism increases substantially. Higher thresholds indicate greater xylem vulnerability. [Figure 3: see original paper] shows the xylem embolism vulnerability curves for goji berry canopy. As xylem water potential decreased, hydraulic conductivity reduced to varying degrees, and the water potential at 50% loss of hydraulic conductivity (P50) differed among varieties. Significant differences existed between ‘Ningqi 1’ and both ‘Ningqi 5’ and ‘Mengqi 1’ , while no significant difference was observed between ‘Ningqi 5’ and ‘Mengqi 1’ . ‘Ningqi 5’ had the highest P50 value, while ‘Ningqi 1’ had the lowest.

Pammenter et al. [14] proposed an S-shaped exponential equation based on the “air-seeding hypothesis” mechanism of embolism vulnerability, which can simulate plant xylem embolism vulnerability curves. The vulnerability is measured by the water potential corresponding to 50% PLC. The vulnerability curve equation is:

$$PLC = 100 / (1 + e^{(S(P50 - P))})$$

where P50 is the xylem water potential causing 50% loss of hydraulic conductivity, S is the curve slope at this point, and P is the instantaneous water potential corresponding to PLC. [Figure 3: see original paper] presents the canopy xylem embolism vulnerability curve equations for the three goji berry varieties, all reaching significance levels of $P<0.01$. Based on P50 values to evaluate xylem vulnerability, the P50 values for ‘Ningqi 1’ , ‘Ningqi 5’ , and ‘Mengqi 1’ were -1.259 MPa, -1.005 MPa, and -1.012 MPa, respectively, with ‘Ningqi 1’ differing significantly from the other two varieties.

2.4 Relationship Between Net Photosynthetic Rate, Stomatal Conductance, and Leaf Specific Hydraulic Conductivity

Water is the raw material for photosynthesis in plant leaves. Under water deficit, plants generally have maximum stomatal conductance near the water threshold; when exceeding the water limitation point, plants close leaf stomata to prevent water loss from affecting normal physiological activities, thereby reducing leaf net photosynthetic rate (Pn) [8]. Correlation analysis between leaf net photosynthetic rate (Pn), stomatal conductance (Gs), and leaf specific hydraulic conductance (Kl,leaf) yielded correlation coefficients of 0.763 and 0.797, respectively, both reaching significant levels ($P<0.05$) ([Figure 4: see original paper]).

2.5 Effects of Re-watering After Drought Stress on Shoot Specific Hydraulic Conductivity in Goji Berry

When plants are re-watered after drought stress to reach suitable moisture conditions, various physiological activities and indices gradually recover, reducing adverse effects caused by drought. This recovery can sometimes reach or exceed levels of plants under normal growth conditions, showing obvious compensation or over-compensation effects. [Figure 5: see original paper] illustrates the recovery of shoot specific hydraulic conductivity in goji berry plants after drought stress and re-watering. The results show that after re-watering, shoot hydraulic conductivity recovered at different rates in the three varieties. On the fourth day of re-watering, the hydraulic conductivity of drought-stressed 'Ningqi 1' and 'Mengqi 1' plants exceeded that of normal treatment plants, showing compensation effects. Moreover, the hydraulic conductivity of severely drought-stressed 'Mengqi 1' plants exceeded both normal and moderately drought-stressed plants, reaching 106.4% of normal treatment. The shoot specific hydraulic conductivity of 'Ningqi 5' also approached normal treatment levels, reaching 98.4% and 97.1% of normal treatment.

Discussion

When plants experience drought stress, water potential decreases, leaf stomata close, net photosynthetic rate reduces, and consequently leaf hydraulic conductivity declines. The hydraulic architecture of goji berry shows different sensitivities to drought stress, with changes in xylem embolism vulnerability and hydraulic capacity related to drought tolerance characteristics. 'Ningqi 5' xylem was most sensitive to drought stress, showing the most significant changes in hydraulic conductivity after drought stress and re-watering, making it less suitable for planting in severely drought-stricken areas compared to 'Ningqi 1' and 'Mengqi 1' . Plant hydraulic resistance primarily originates from the root system, and roots are the most sensitive organ to drought stress among all plant parts. Regulating root hydraulic conductance is crucial for improving water use efficiency in goji berry. Appropriate water deficit treatment and reasonable soil moisture regulation can induce compensation or over-compensation effects, effectively promoting goji berry growth, improving soil water use efficiency under water-limited conditions, and enhancing drought resistance potential.

The hydraulic conductivity (Kh) of various plant organs or tissues reflects the relationship between plants and environmental water absorption and transport. Xylem vessel structure and differentiation degree both affect xylem hydraulic capacity [15]. Drought stress can alter root internal structure, causing air to enter water-filled conduits through pit membranes and resulting in xylem embolism, or accelerating suberization or lignification of endodermal and exodermal cells and thickening of Casparian strip cell walls, thereby affecting xylem hydraulic capacity [15]. After different degrees of drought stress, 'Ningqi 5' showed the greatest reduction in canopy and root hydraulic conductivity, while 'Ningqi 1' showed the smallest reduction. 'Mengqi 1' exhibited the smallest reduction in both shoot and leaf hydraulic conductivity. These differences may be attributed to variations in xylem vessel and pit membrane differentiation structures, or differences in aquaporin (AQP) activity on cell membranes [15]. The most significant structural changes occurred in the cortex cells or Casparian strip cell walls of 'Ningqi 5', while the smallest changes in xylem cell structure occurred in roots of 'Ningqi 1' and shoots and leaves of 'Mengqi 1', leading to differential changes in hydraulic conductivity of canopy, leaves, shoots, and roots after drought stress.

The root system is the most important organ for soil water entry into plants and directly affects water absorption, with root hydraulic conductance representing plant root water absorption capacity and directly reflecting the relationship between plant water and soil water [15]. Nardini et al. [19] found that root hydraulic resistance constitutes the main portion of whole-plant hydraulic resistance, with roots being the primary site of increased hydraulic resistance under stress conditions. This study found that root hydraulic resistance in goji berry accounted for 36.2%-64.3% of whole-plant hydraulic resistance, representing the main component of plant hydraulic resistance. After drought stress, the proportion of root hydraulic resistance within the whole plant increased to varying degrees in all three varieties, with 'Ningqi 5' showing the most significant increase. This occurred primarily because roots are more sensitive to water stress than shoots and leaves, causing the proportional value to change with water stress. Thus, due to structural differences in 'Ningqi 5' root systems or the highest sensitivity of aquaporin (AQP) activity on cell membranes to soil water supply conditions, this variety showed the greatest change in root hydraulic resistance. Numerous factors may cause changes in root hydraulic resistance, including suberization of root exodermal and endodermal cells during drought stress [20] and changes in water channel proteins in root cell membranes, both potentially contributing to root hydraulic sensitivity to drought stress.

Xylem vulnerability curves represent the relationship between percentage loss of hydraulic conductivity and water potential, providing a theoretical basis for studying plant physiological changes and drought resistance under water stress conditions [21]. Xylem resistance to embolism is closely related to drought resistance, with drought-resistant plants maintaining relatively high xylem hydraulic capacity under low plant water potential conditions [22-24]. This study found that the xylem water potential at 50% loss of hydraulic conductivity in goji berry ranked as 'Ningqi 1' < 'Mengqi 1' < 'Ningqi 5' , suggesting drought resistance capacity in the order of 'Ningqi 1' > 'Mengqi 1' > 'Ningqi 5' , which is consistent with characteristics observed in production practice. Some studies suggest that the relationship between xylem embolism vulnerability and drought resistance is not always clear, as different plants employ various drought resistance strategies. Appropriate xylem embolism may assist plant stress responses and could represent a water-saving drought tolerance strategy [25], though xylem vulnerability can serve as a research indicator for drought resistance characteristics within the same species.

Plants typically have maximum stomatal conductance near water thresholds. When exceeding water thresholds, plants coordinate physiological activities to minimize drought damage by closing leaf stomata to prevent transpirational water loss, thereby directly or indirectly affecting photosynthetic reaction centers [26-27]. The primary impact of water stress on photosynthesis is related to stomatal closure, with photosynthetic rate decreasing when water deficit causes stomatal closure [28]. This study found significant correlations between leaf net photosynthetic rate, stomatal conductance, and leaf specific hydraulic conductance in goji berry. Under water deficit, plants reduce water loss by regulating leaf stomatal closure, thereby preventing rapid water potential decrease and hydraulic resistance increase, and mitigating xylem embolism exacerbation, though this also reduces leaf net photosynthetic rate. Leaf net photosynthetic rate can thus reflect leaf hydraulic conductivity to some extent.

During long-term evolution, plants have developed adaptability to environmental changes and stress conditions, with physiological functions capable of recovery when adverse conditions improve. This recovery can sometimes reach or exceed levels of plants under normal conditions, showing obvious compensation or over-compensation effects [29]. Compensation effects represent physiological responses of plants to adapt to stress conditions and are manifestations of stress resistance. After drought stress and re-watering, 'Mengqi 1' showed the fastest hydraulic capacity recovery and most significant compensation effects, while 'Ningqi 5' had the slowest recovery. Research indicates that moderate water stress can delay leaf and root senescence in maize, direct water and nutrient supply preferentially to roots, greatly enhance root vigor, and ensure improved soil water absorption capacity [30-31]. Appropriate regulated deficit irrigation in wine grape cultivation can significantly improve water production efficiency, achieve efficient water use, and enhance fruit quality [32]. Therefore, 'Mengqi 1' showed the strongest root vigor recovery after drought stress and re-watering, indicating strong adaptability to drought stress, while 'Ningqi 5' had weaker root vigor recovery. Appropriate deficit irrigation can effectively improve water use efficiency.

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