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Groundwater Altered Water Balance and Plant Water Use Efficiency in Desert Ecosystems

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Key Points:

- Groundwater replenishment changed soil water storage toward a new hydrostatic equilibrium, as well as actual evapotranspiration and drainage loss
- Semi-shrub was recommended for vegetation restoration in desert ecosystems without groundwater due to higher water use efficiency, compared to other replanting configurations
- Semi-shrub monoculture, shrub monoculture and a mixture of semi-shrub and shrub were recommended as the preferred replanting configurations in desert ecosystems with groundwater

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Groundwater is an important water source in water-limited desert ecosystem. Less attention has been paid to how the water balance and plant performance in such ecosystems vary with the presence or absence of groundwater. Appropriate replanting strategies play a pivotal role in preventing desertification. In this study, we used twelve large-scale weighing lysimeters with different replanting configurations, ranging from bare soil to various monocultures and mixtures of shrubs and semi-shrubs, to quantify water balance components and plant growth dynamics in contrasting desert ecosystems (groundwater-dependent vs. groundwater-independent) during 2019–2023. The results indicated that actual evapotranspiration in groundwater-dependent desert ecosystems was greater than in groundwater-independent ones. Linear mixed-effects models showed that groundwater had a significant effect on the water balance components and enhanced plant growth performance. Boosted regression tree models indicated that groundwater alleviated the influence of drought and sparse rainfall on the water balance components in deserts. The water use efficiency (WUE) of the semi-shrub *A. ordosica* (*Ao*) in monoculture was 6.74 and 3.10 kg m^{-3} in desert ecosystems with and without groundwater, respectively. The WUE of the *C. korshinskii* shrub (*Ck*) in monoculture and in a mixture with the semi-shrub *A. ordosica* (*Ao* & *Ck*) in groundwater-dependent desert ecosystems was 3.05 and 2.64 kg m^{-3}, respectively. Vegetation restoration in arid areas serves as an effective nature-based solution for desertification control, where tailored replanting strategies are key to ensuring long-term sustainability.

1. Introduction

Drylands approximately occupy 45% of the earth's terrestrial surface (Koppa et al., 2024), and about 3 billion people inhabit here (D' Ettorre et al., 2024). Desertification has become one of the main environmental challenges in drylands due to climate and anthropogenic factors (D' Ettorre et al., 2024). Territories affected by desertification are usually characterized by a negative water balance owing to low rainfall and high potential evapotranspiration (PET). Thus water is the main limiting factor for plant survival and growth in these areas (Li et al., 2016; Wang et al., 2008). The ecological restoration and recovery, predominantly based on revegetation establishment (Fan et al., 2023), are of great national importance for preventing desertification (UNCCD, 2017). The presence of groundwater can mitigate soil water deficit during dry periods, such as in spring and summer, when plants exhibit a pronounced water requirement for their accelerated growth (Condon & Maxwell, 2019). In drylands, the water balance under groundwater-dependent ecosystems (GDEs) and ecosystems without groundwater is closely related to plant growth, which in turn determines the sustainability of ecological restoration (Liu et al., 2017).

The soil water balance, defined as the net difference between the total amount of water entering an area and the total amount leaving it over a given period, is a direct measure of the change in soil water storage. Water input components to soil ecosystems include precipitation, non-rainfall water (e.g., dew), irrigation, and capillary rise from available groundwater (Groh et al., 2018; Li et al., 2024; Milly, 1994). Desert ecosystems are heavily reliant on the limited availability of water from precipitation and non-rainfall events (Arenas-Díaz et al., 2022; Yang et al., 2021). Meanwhile, the groundwater table in desert varies, and some areas are devoid of groundwater

(Cheng et al., 2013; He et al., 2023). Generally, GDEs are located along the river corridors, around the terminal lakes in arid inland river basins, and mountain foot slopes (Huang et al., 2020; Yang et al., 2021). Water that leaves the soil ecosystem includes the following components, that is, evapotranspiration (ET, comprises of plant transpiration and soil evaporation), surface runoff, and drainage loss (DL) (He et al., 2023; Li et al., 2024). Soil functions include the regulation and storage of water, and soil serves as a buffer to mitigate the effects of drought on plants and to delay the recovery of soil water under long-term drought conditions (Krevh et al., 2022; Milly, 1994). According to Liu et al. (2017), groundwater can be an important source of soil water for supporting plant survival and growth. Under very dry and warm conditions, ecosystems typically have little or no vegetation because an increase in vapor pressure deficit (VPD) and evaporation or ET leads to a decrease in soil water storage, thereby further restricting the availability of water in the root zone, and thus preventing better coverage of vegetation on the soil surface (Zhao et al., 2016). Sand stabilized plants species are more likely to survive and grow in wet years (Zhao et al., 2024). Accessible groundwater plays an important role in facilitating primary production and increasing actual evapotranspiration (ET_a) through capillary rise (Han et al., 2015; Liu et al., 2017; Vanslycken & Vereecken, 1990). According to Liu et al. (2017), ET_a in arid northwestern China exhibited significant spatial heterogeneity, decreasing sharply from GDEs (riparian forest: 550 mm; wetland: 505 mm) to transition zones (oasis edge: 283 mm; desert-oasis ecotone: 127 mm) and finally arid deserts (sandy desert: 103 mm). There is a critical groundwater table threshold in drylands depending on the variability of land cover and soil profile characteristics (e.g., soil texture), thus influencing land surface process by changing the energy and water balance (Kollet & Maxwell, 2008). Excessively shallow groundwater tables induced root-zone oxygen stress (Soylu et al., 2014), which would consequently restrict plant transpiration. This suppressive effect was, however, highly dependent on the ecosystem's adaptive capacity (Garcia-Vila et al., 2025). In contrast, deep groundwater tables caused a hydraulic decoupling between the soil profile and the aquifer, minimizing the interaction between surface processes and groundwater (Condon et al., 2020). The relationships between groundwater and vegetation were studied widely (Han et al., 2015; Kollet & Maxwell, 2008; Liu et al., 2017), but there is a lack of studies that provide observation on soil water balance components, especially in desert ecosystems.

Although numerous studies have investigated the interaction of plant growth and water balance under varying groundwater conditions, the underlying mechanisms are still poorly understood. As a key trait integrating carbon-water coupling, water use efficiency (WUE) quantitatively reflects the trade-off between plant productivity and water consumption in terrestrial ecosystems (Liu et al., 2017). For example, Poplars (*Populus spp.*) were once the primary species used for vegetation restoration in arid and semi-arid regions of China, covering an area of 920,000 km^2. However, solid evidence showed that such afforestation exacerbated groundwater decline and reduced WUE (Lu et al., 2018). Shrubs and semi-shrubs are the primary sand-fixing plant species in deserts due to their unique morphological and water use characteristics (Schenk et al., 2003). On the one hand, taller shrubs serve to block sand and dust and reduce the wind velocity, while shorter semi-shrubs grow close to the ground and are more effective at fixing sand (Schenk et al., 2003). On the other hand, shrubs with deeper root systems consume more water, predominantly utilizing water from deeper soil layers and potentially groundwater, whereas semi-shrubs with shallower root systems consume less water, primarily using soil water from the upper layers (Shamsutdinova et al., 2022). Studies on different replanting configurations in different ecosystems are sometimes conflicting. For example, the relationships between semi-shrub and shrub have been reported to segregate (Schenk et al., 2003) or coexist (Shamsutdinova et al., 2022) in various desert ecosystems. These conflicting findings may be associated with different plant species, edaphic conditions, or water availability.

The reported ET_a in such studies was mostly estimated using the Bowen ratio energy-balance method (Liu et al., 2017), or the Penman-Monteith model (Han et al., 2015), as well as some other indirect methods. Lysimeters are high-precision instruments designed for the continuous measurement of weight change, which can be used to estimate water balance components (Pütz & Groh, 2023), making them key tools in the study of water balance (Dietrich et al., 2016; Zhang, Zhao, et al., 2021). However, studies using large-scale weighting lysimeters to investigate the water balance in deserts, both with and without the influence of groundwater on the ecosystem, remain scarce. In this study, we investigate how water balance components and plant growth properties vary in the presence or absence of groundwater. We also evaluated the contributions of groundwater, replanting configuration, and meteorological factors to the water balance components of desert ecosystems with and without groundwater. We hypothesized that (a) The output water (e.g., ET_a and DL): will increase with groundwater replenishment from an environment with a −2.5 m water table compared to an environment without groundwater;

(b) Different replanting configurations (shrub monoculture, semi-shrub monoculture, and mixture of shrub and semi-shrub) will result in different plant individual sizes, leading to differences in the water balance; (c) Plant growth responses of different replanting configurations to groundwater conditions will be different due to differences in plant growth performance and WUE.

2. Materials and Methods

In this section (Figure 1), we first introduce the study site, the measuring devices used, and the experimental setup. We then present the methods for analyzing the data. The linear mixed-effects models (LMMs) were fitted to assess the impacts of groundwater and replanting configuration on water balance components and plant growth properties. The boosted regression tree (BRT) models were implemented to quantify the relative contributions of meteorological factors, groundwater conditions, and replanting configurations to water balance components (Elith et al., 2008). Finally, we analyzed the relationships between biomass increment with cumulative ET_a and ratio between ET_a and the PET.

2.1. Study Site

The study site is located at the Shapotou Desert Research and Experiment Station of the Chinese Academy of Sciences (37°47′N, 105°01′E, 1,250 m above sea level) in the Ningxia Hui Autonomous Region on the southeastern edge of Tengger Desert. The area is distributed by high and dense reticulated chains of barchan dunes. Some natural psammophytes, like *Hedysarum scoparium* and *Agriophyllum squarrosum* sporadically grow and cover about 1% of this area (Zhang, Liu, et al., 2008). The main soil is aeolian sandy soil (Ari-Sandic Entisols, USDA) and the long-term mean gravimetric water content lies between 3% and 4% (Li et al., 2010; Zhang, Xu, et al., 2021). The average annual temperature is 9.6°C (1955–2023), and the daily temperature ranges between −25.1 and 38.1°C, respectively. The groundwater table from the Helan Mountains to the eastern Tengger Desert ranges from 0.8 to 200 m (Ding et al., 2013). The mean annual precipitation is 185 mm (1955–2023), and approximately 80% of it falls between July and September. The annual apparent evaporation (observed by an evaporation pan of type E-601) and the mean annual wind velocity are 2,900 mm and 2.9 m s^{-1}, respectively (Li et al., 2010). The mean annual humidity is 40% (Huo et al., 2024).

2.2. Large-Scale Weighing Lysimeters

To determine the soil water balance and study eco-hydrological interaction mechanisms, a unique lysimeter setup was established at Shapotou site. It was named *Automatic Simulating and Monitoring System for Water Balance of Sandy Areas of Northern China: Shapotou Lysimeter Group* and it was established in 2018 (Figure S1 in Supporting Information S1). Thirty-six large-scale weighing lysimeters are installed, backfilled with different soil types and planted with various sand-fixing shrubs and semi-shrubs from different bioclimatic zones of Northern China, indicating Horqin Sandy Land (42°35′N, 120°45′E), Tengger Desert (37°47′N, 105°01′E), and Gurbantunggut Desert (44°′17′N, 87°56′E). In this study, we considered 12 lysimeters that were backfilled with soil (aeolian sandy soil) from the Tengger Desert. Each lysimeter consists of a 3.35 m deep stainless-steel cylinder (MSL-G4-10, range 40, 000 kg, Xi'an Simon's Electronic Technology Co, Ltd, China) containing a 0.3 m thick filter layer backfilled with gravel of different particle sizes at the bottom of the lysimeter, and a soil monolith that is 3 m deep with a surface area of 4 m^2, with a distance of 0.05 m from the top edge. Changes in soil water storage over time were estimated by the weight change of the lysimeter, which was measured for each lysimeter by three weighing sensors (VC3500, range 15,000 kg, precision 0.16 kg (0.04 mm), Thames Side Co. Ltd, UK). The bottom of each lysimeter was reserved with channels connected to DL gravimeter (L6D-Cx-05kg-0.4 B, range 5 kg, precision 0.01 mm, Zhonghang Electronic Measuring Instruments (Xi'an) Co, Ltd, China), as well as an automatic groundwater control system (LabV1, range 0–3,000 mm, groundwater table precision 0.1 mm, water replenishment rate 0.007–570 ml min^{-1}, Baoding Shenchen Precision Pump Co., Ltd, China). Lysimeter weight, groundwater replenishment and DL were automatically recorded at one-hour interval. All lysimeter data were collected using an automated data logger (CR6, CampbellSCI Co. Ltd, USA). Data collection was not initiated until the soil monoliths in each lysimeter had stabilized for 1 year. For more detailed information about the *Shapotou Lysimeter Group*, see Zhang, Zhao, et al. (2021).

2.3. Experimental Design

Twelve lysimeters were included in this study, all of which represents the conditions from the Tengger Desert (Figure S1 and Table S1 in Supporting Information S1). The experimental design of the 12 lysimeters comprises two groundwater conditions and five replanting configuration patterns, with bare soil serving as a control (Figure S1b in Supporting Information S1). The two groundwater conditions were defined by the presence or absence of groundwater. Six lysimeters had groundwater with a constant depth of the groundwater table of −2.5 m, and the other six lysimeters had no groundwater (Figure S1b in Supporting Information S1). The replanting configurations consisted of monocultures of the following species *Artemisia ordosica* (*Ao*; semi-shrub), *Caragana korshinskii* (*Ck*; shrub), and *Ceratoides latens* (*Cl*; semi-shrub), a mixture of *A. ordosica* and *C. korshinskii* (*Ao* & *Ck*), and a mixture of *C. latens* and *C. korshinskii* (*Cl* & *Ck*). Given that lysimeters are primarily employed for long-term experimental measurements (Zhang, Xu, et al., 2021) and represent a substantial financial investment in infrastructure and maintenance, replicate treatments were not included in the experimental design. Notably, different replanting configurations included monoculture and mixture of *A. ordosica, C. korshinskii, C. latens*, which are common plant species in Tengger Desert (Li et al., 2016). Only plant combinations of deep-rooted shrubs and shallow-rooted semi-shrubs were used due to niche differentiation. Lysimeter data were collected in this study from May 2019 to October 2023 (Table S2 in Supporting Information S1).

The two-year old seedlings of shrubs and semi-shrubs with a height of 15 cm were replanted in lysimeters in April of 2018. Plant growth properties were measured in May 2020 and October 2023. Plant height, crown diameters, and new branch length were measured by tapelines. Plant ground diameter was measured by vernier calipers. The crown projected area was calculated as oval shape using crown diameters, and crown volume was calculated as ellipsoidal structure using the plant height and crown diameters. The WUE (kg m^{-3}) was defined as a ratio between total biomass increment (kg m^{-2}) and cumulative ET_a (m^3 m^{-2}) from May 2020 to October 2023 (Groh et al., 2020). Plant biomass was estimated to use allometric equations in Table S3 in Supporting Information S1, as plants in the long-term experimental design could not be harvested.

2.4. Meteorological Data Collection

Meteorological factors, including precipitation, air temperature (T_a), relative humidity (RH), wind speed (WS), and net radiation (R_n) at 10-min intervals, were obtained from the weather station (Vaisala Automatic Weather Station, Helsinki, Finland). Daily VPD was calculated from T_a and RH (Wang et al., 2004). Daily water surface evaporation was measured using an evaporation pan (E601 B, range 70 mm, precision 0.1 mm, Nanjing Automation Institute of Water Conservancy and Hydrology, Ministry of Water Resources, China) from March to October each year, as water surface evaporation in cold seasons is negligible. Uncertainty in PET estimates could be caused by different approaches, like Penman-Monteith equation, and their complicated parameterization (Peng et al., 2019), thus we used water surface evaporation to indicate PET to improve the accuracy of the results. The weather station and the water surface evaporation pan were located approximately 20 m from the lysimeters. Mean annual daily values of T_a, RH, WS, R_n, VPD, and PET were calculated based on daily values for each year that were obtained from 10-min observations.

2.5. Data Analysis

2.5.1. Water Balance Components Calculations

Lysimeter data were first manually filtered for periods of known mechanical failure, instrument maintenance, power outages and management activities such as weeding. Missing lysimeter weight values for periods of less than 3 days were filled using an average interpolation method (Wang et al., 2004; Zhang, Xu, et al., 2021), while the gap periods of more than 3 days were not included due to the possible inaccuracy of gap-filling method. The data set was harmonized to compare the water balance components of the 12 lysimeters. Therefore, only measurements for which data were available from all 12 lysimeters were considered. The lysimeter weight changes caused by groundwater replenishment and drainage were corrected using formulas that were derived specifically for the calibration of the lysimeter data (Zhang, Zhao, et al., 2021). The data in our article are all from the observation periods, but the observation periods per year differ (see Table S2 in Supporting Information S1). For the sake of simplicity, we refer to the data for the respective years in the following. Mean daily ET_a of the respective year was the average of daily ET_a (Equation S1 and S2 in Supporting Information S1), and it could be represented as follows (Zhang, Xu, et al., 2021):

$$ET_a + DL = P + G - \Delta S$$

where ET_a is the mean daily actual evapotranspiration, DL is the mean daily volumetric DL, P is the mean daily precipitation, G is the mean daily groundwater replenishment, which was set to 0 for the configuration without groundwater, ΔS is the mean daily change in soil water storage and all units are in mm d^{-1}.

Water balance components mainly consisted of three parts: P and G as the water input component; ET_a and DL as the water output components; ΔS as the water regulator component. $ET_a/(P + G)$ and $DL/(P + G)$ represented the water consumed proportions, and the former referred to evaporative index in Budyko theory (Anderson et al., 2016). If $ET_a/(P + G)$ is >1, ET_a is greater than the water supply and the system is water-limited (Condon et al., 2020). ET_a/PET is an empirical stress factor, which represents the water availability (Peng et al., 2019). DL/PET exhibited the proportion of extra water. P + G-DL represented an available water supply, and $ET_a/(P + G-DL)$ was the proportion of available water loss via ET_a.

2.5.2. Statistical Analysis

The LMMs were fitted to evaluate the effects of groundwater and replanting configuration on water balance components and plant growth properties, accounting for temporal autocorrelation in repeated measurements (Wu et al., 2022). The analysis was performed using the nlme package version 3.1–168 (Pinheiro et al., 2025). Groundwater treatment and replanting configuration were included as fixed effects, while individual lysimeters were specified as random intercepts to account for variability between units. A first-order autoregressive (AR1) covariance structure was applied to model temporal autocorrelation, with sampling year (year_numeric) nested within lysimeters. To validate model assumptions, we conducted a comprehensive residual diagnosis. This included examining plots of residuals versus fitted values (to assess homoscedasticity and linearity), normal Q-Q plots (to assess normality), a histogram of the residuals, and the autocorrelation function (ACF) of residuals (to verify the adequacy of the AR1 structure). Diagnostic checks confirmed that the key model assumptions were well satisfied. The relationships between the biomass increment with cumulative ET_a and ET_a/PET from May 2020 to October 2023 were fitted using linear, exponential, logarithmic, power, and parabolic functions, respectively. The optimal fitting function was selected based on the Akaike Information Criterion. The statistical analyses were conducted using SPSS 23.0 (International Business Machines Corp., Armonk, NY, USA), and *R* studio 4.0.3 (The *R* Foundation for Statistical Computing, Vienna, Austria). In addition, the graphs were plotted using Origin 2017 (Origin Lab Corp., Northampton, MA, USA).

2.5.3. Influence Factor and Its Relative Contribution

Many factors influence the water balance, and we used BRT to explore the relative contributions of precipitation, groundwater replenishment, available water supply, replanting configuration, and meteorological factors such as T_a, RH, WS, R_n, and VPD to water balance components. We used BRT to capture complex nonlinearities and interactions among ecological drivers, and evaluate the contribution rates of environmental variables, which outperformed conventional models in prediction (Elith et al., 2008). Only variable with relative contributions higher than 5% was displayed for the sake of brevity. We first used linear regression to remove collinearity factors, and then utilized BRT to investigate the relative contributions. During the BRT analysis, different replanting configurations were parameterized, including 1 for bare soil, 2 for *Ao*, 3 for *Ck*, 4 for *Cl*, 5 for *Ao* & *Ck*, and 6 for *Cl* & *Ck*. Parameter tuning and model construction of BRT utilized caret package version 6.0–92 (Kuhn, 2022) and gbm package version 2.1.8 (Greenwell et al., 2020) in *R* Studio, respectively. All the data was divided into a training set and a test set, used for the construction and performance evaluation of models, respectively. In the process of parameter tuning, interaction depths were set to 1, 2, and 3. Shrinkage was set to 0.0001, 0.0005, 0.001, 0.005, and 0.01. The number of trees was in the range of 1–2,000, with a step length of 50. The n. minobsinnode was in the range of 1–10, with a step length of 1. The cross-validation fold was set to 5. Coefficient of determination (R^2), mean absolute error, normalized mean bias, and normalized mean error were used to perform model evaluation and testing (Elith et al., 2008; Ge et al., 2017; Ou et al., 2018).

3. Results

First, we investigated the impact of groundwater and replanting configuration on water balance components. Next, we quantified the contributions of these factors to the components of the water balance. Finally, we

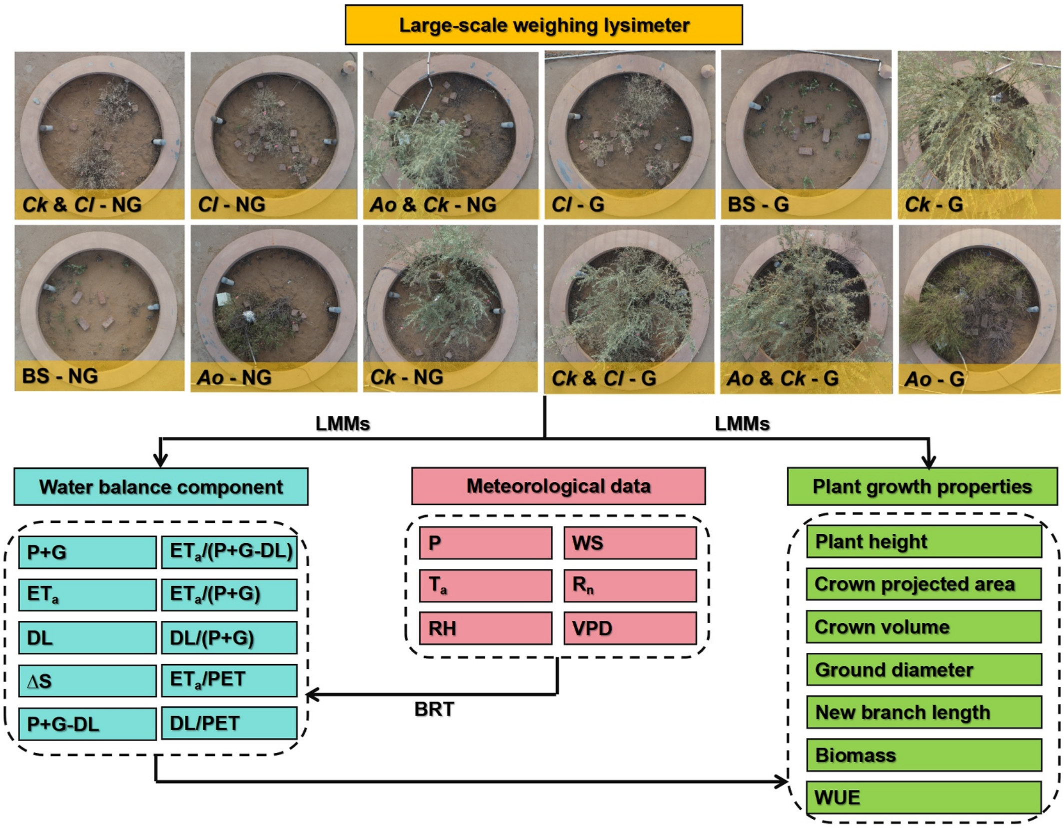

Figure 1. Schematic of the analytical framework combining large-scale weighting lysimeter data, meteorological data, and plant growth properties. *Ao*: monoculture of *Artemisia ordosica* (semi-shrub); *Ck*: monoculture of *Caragana korshinskii* (shrub); *Cl*: monoculture of *Ceratoides latens* (semi-shrub); *Ao* & *Ck*: mixture of *A. ordosica* and *C. korshinskii*; *Cl* & *Ck*: mixture of *C. latens* and *C. korshinskii*; BS: bare soil; NG: condition without groundwater; G: groundwater condition; P + G: precipitation and groundwater replenishment; DL: drainage loss; PET: potential evapotranspiration; ΔS: change in soil water storage; WS: wind speed; T_a: air temperature; R_n: net radiation; RH: relative humidity; VPD: vapor pressure deficit; WUE: water use efficiency.

presented how plant growth performance responds to groundwater, as well as the relationships between water balance and plant biomass (Figure 1).

3.1. The Impact of Groundwater and Replanting Configuration on the Components of the Water Balance

During the observation period (2019–2023), the average daily precipitation was 0.513 ± 0.0458 mm d^{-1}, ranging from 0.101 mm d^{-1} (2022) to 0.777 mm d^{-1} (2019, Figure 2a, Table S2 in Supporting Information S1). The LMMs revealed that groundwater had a significant effect on the water balance components, whereas no significant effects were detected for the replanting configurations (Figure S2 in Supporting Information S1). We combined five replanting configurations (*Ao*, *Ck*, *Cl*, *Ao* & *Ck*, and *Cl* & *Ck*) as planted lysimeters, and focused on how replanting and groundwater more generally influence the variation patterns of the water balance components (Figures 2 and 3). The results indicated that under conditions without groundwater, the mean daily water loss by ET_a of the planted lysimeters (0.694 ± 0.0855 mm d^{-1}) was 1.35 times higher than evaporation loss (0.513 ± 0.110 mm d^{-1}) of the bare soil lysimeter (Figures 2b and 3a, 3b). The mean daily DL of the bare soil lysimeter (0.0929 ± 0.0583 mm d^{-1}) was 1.53 times higher than that of the planted lysimeters (0.0606 ± 0.0317 mm d^{-1}) (Figures 2c and 3a, 3b). The mean daily ΔS of the planted lysimeters had a deficit of −0.241 ± 0.0661 mm d^{-1}, while the ΔS of the bare soil lysimeter had a surplus of 0.00341 ± 0.0405 mm d^{-1} (Figures 2d and 3a, 3b). While mean daily available water (P-DL) was comparable between bare soil (0.451 ± 0.096 mm d^{-1}) and vegetated lysimeters (0.453 ± 0.046 mm d^{-1}) (Figure 2e), the ratio of ET_a to available water reached 1.84 ± 0.34 in planted lysimeters, higher than the evaporation ratio (0.98 ± 0.07) observed in bare soil (Figure 2f).

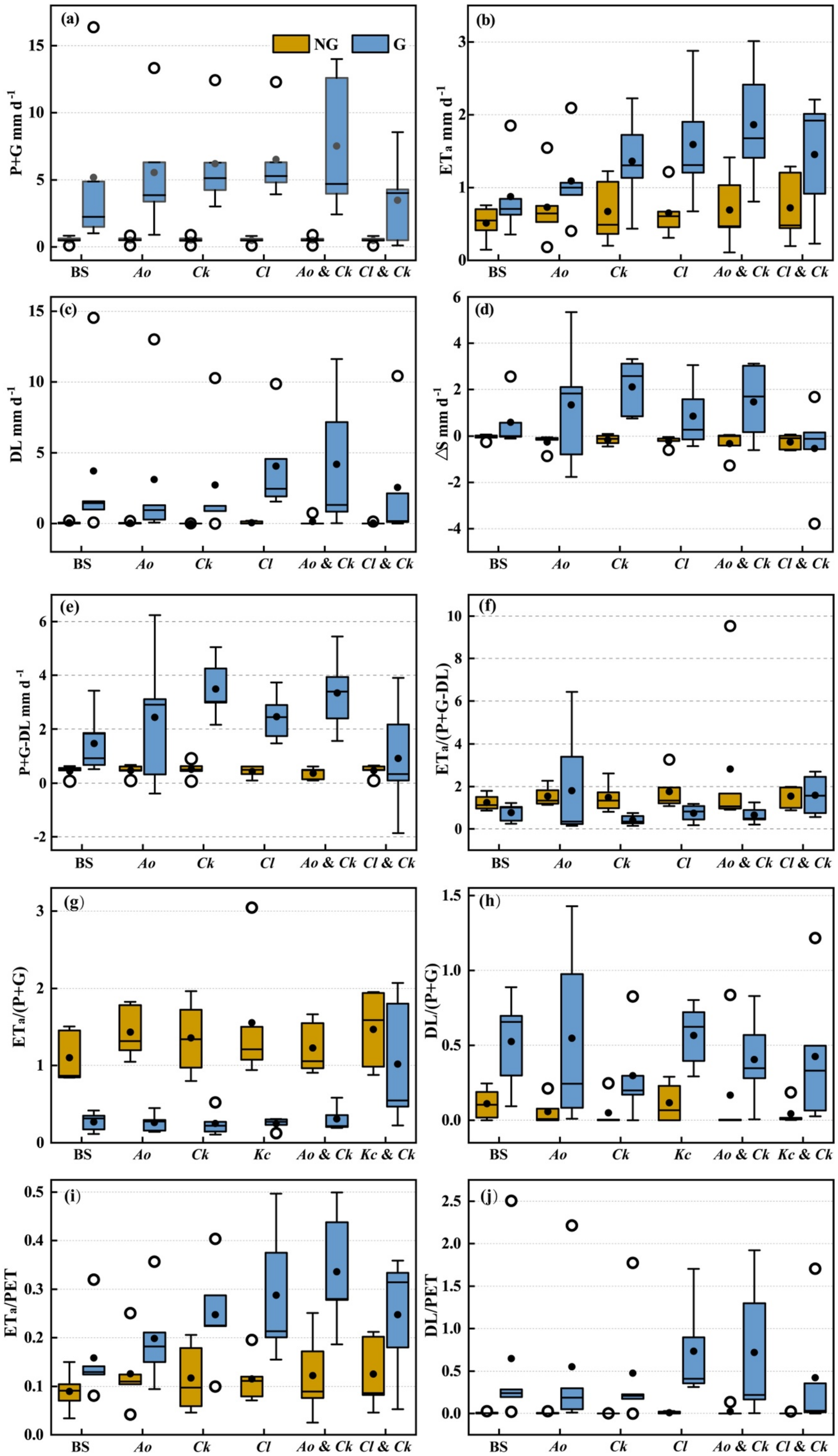

Figure 2. Box plots of daily water balance components and relevant ratios, grouped by six replanting configurations and groundwater present and absent conditions. Each box indicates the interquartile range (top: the third quartile; bottom: the first quartile), with a horizontal black line indicating the median and a black filled dot referring to the mean value. The upper and lower whiskers extended to 1.5 times the interquartile range.

Under groundwater conditions, the mean daily water loss by ET_a of the planted lysimeters (1.47 ± 0.151 mm d^{-1}) was 1.67 times higher than that of the bare soil lysimeter by evaporation (0.878 ± 0.257 mm d^{-1}) (Figures 2b and 3c, 3d). The mean daily DL of the bare soil lysimeter (3.73 ± 2.71 mm d^{-1}) was 1.12 times higher than that of

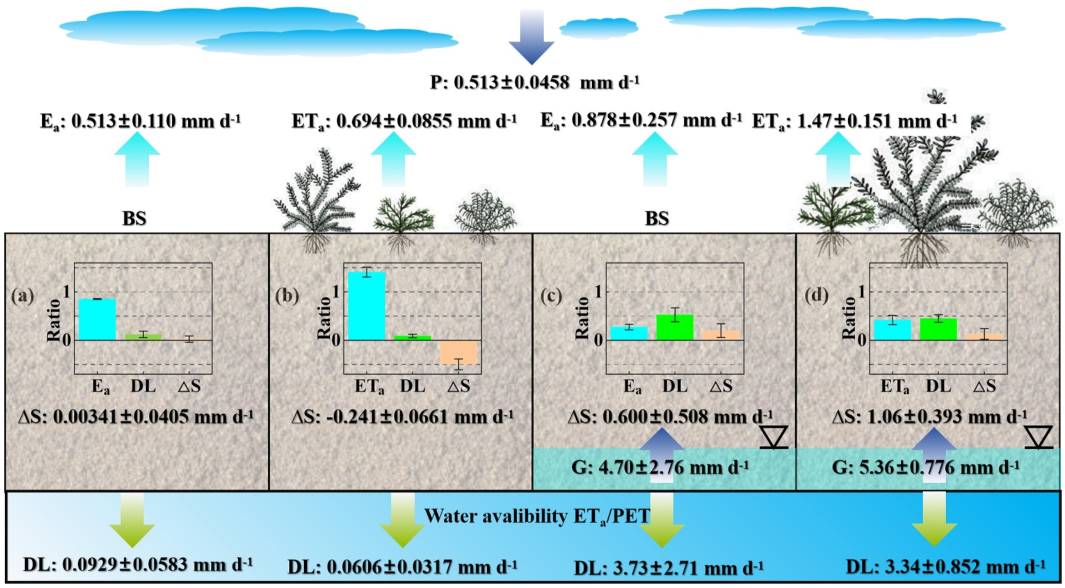

Figure 3. The influence of groundwater and replanting on the water balance components. E_a: actual soil evaporation. The water balance for bare soil is shown in (a) and (c), and for planted lysimeters in (b) and (d) under conditions with (c), (d) and without (a), (b) groundwater.

planted soil lysimeter (3.34 ± 0.852 mm d^{-1}) (Figures 2c and 3c, 3d). Mean daily ΔS of bare soil and planted lysimeters had 0.600 ± 0.508 and 1.06 ± 0.393 mm d^{-1} water surpluses, respectively (Figures 2d and 3c, 3d). The mean daily available water (P + G-DL) of planted lysimeters and bare soil was 2.53 ± 0.376 and 1.48 ± 0.538 mm d^{-1} (Figure 2e), respectively, the ratio of ET_a to available water reached 0.990 ± 0.281 in planted lysimeters, higher than the evaporation ratio (0.778 ± 0.193) observed in bare soil (Figure 2f). Notably, water partitioning exhibited contrasting patterns: ET_a dominated water loss in systems without groundwater access, whereas DL exceeded ET_a under groundwater presence (Figures 2g, 2h and 3). Both available water (ET_a/PET) and extra water (DL/PET) in groundwater conditions were higher than those in non-groundwater conditions (Figures 2i and 2j).

3.2. The Contributions of Groundwater and Replanting Configuration to Water Balance Components

The BRT fitted the effects of influence factors on the water balance components well (Figure 4, Table S4–S5 and Figure S3 in Supporting Information S1). In the absence of groundwater, Figure 4a–4e showed that P and P + G-DL were the main influencing factors, explaining 29.1% and 24.1% of the variation in components of the mean daily water balance, respectively. These were followed by RH (18.6%), T_a (8.07%), and WS (6.75%). The main influencing factors under groundwater conditions were *G* and P + G-DL, contributing 23.5% and 18.8% respectively to the variation in the mean daily water balance components. The next most important factors were

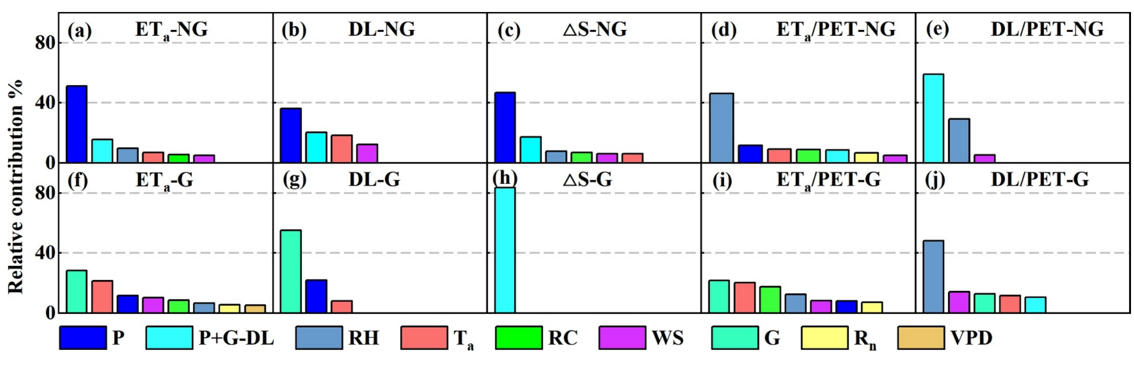

Figure 4. Summary of the relative contributions (%) of predictor variables. RC: Replanting configuration.

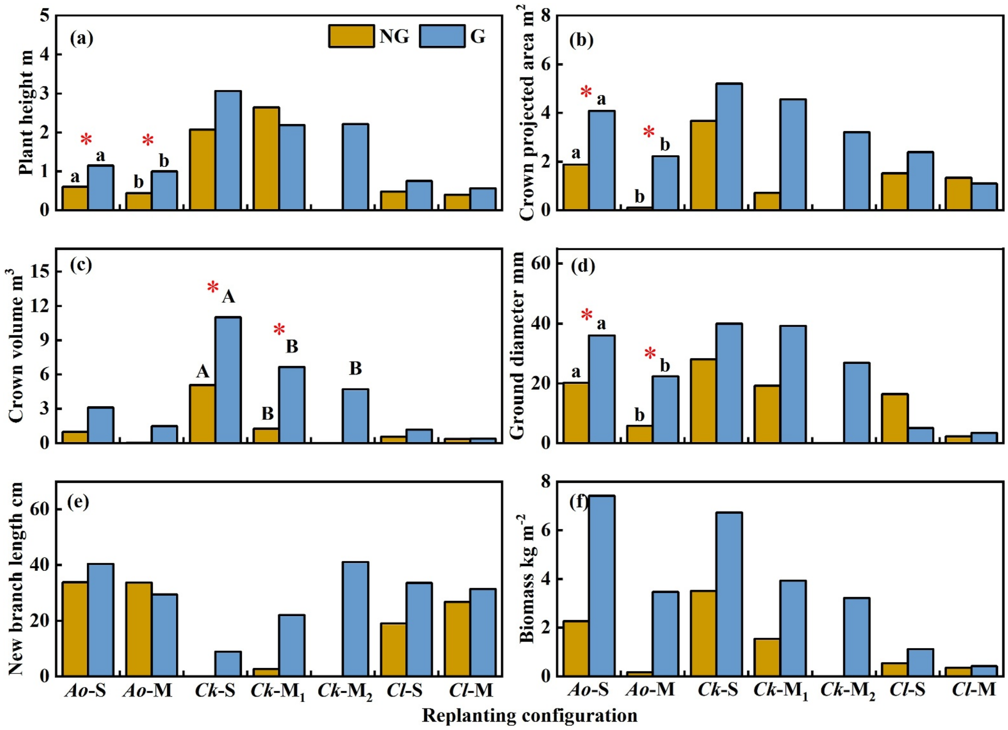

Figure 5. Plant growth characteristics under conditions with groundwater (G) and without groundwater (NG) and different replanting configurations in 2023. S represents monoculture, and M represents mixture. *Ao*-M: the growth characteristics of *A. ordosica* under mixed conditions (i.e., *Ao* & *Ck*); *Ck*-M_1: the growth characteristics of *C. korshinskii* under mixed conditions (i.e., *Ao* & *Ck*); *Ck*-M_2: the growth characteristics of *C. korshinskii* under mixed conditions (i.e., *Cl* & *Ck*); *Cl*-M: the growth characteristics of *C. latens* under mixed conditions (i.e., *Cl* & *Ck*). Absence of *Ck*-M_2 values under conditions without groundwater was due to *C. korshinskii* died. Statistically significant differences between G and NG are shown by "*" above each bar. * Significant difference with $p < 0.05$. The growth characteristics differences of *A. ordosica and C. korshinskii* under different replanting configurations are shown by lowercase and capital letters, respectively.

RH (13.4%), T_a (12.3%), P (8.31%), WS (6.54%), and replanting configuration (RC, 5.25%) (Figures 4f–4j). In summary, the relative contributions of P and RH to mean daily water balance components under conditions without groundwater were 3.50 and 1.39 times higher than those under conditions with a groundwater table.

3.3. Plant Growth Response to the Groundwater and Replanting Configuration

The LMMs demonstrated that, in 2023 (Figure S4 in Supporting Information S1), the growth performance of *A. ordosic*a was significantly enhanced by the presence of groundwater, as evidenced by increased plant height ($p = 0.0112$), crown projected area ($p = 0.0204$), and ground diameter ($p = 0.0142$). The crown volume of *C. korshinskii* was also increased by groundwater ($p = 0.0273$). However, when grown in mixed stands, *A. ordosica* exhibited significant reductions in plant height ($p = 0.0392$), crown projected area ($p = 0.0244$), and ground diameter ($p = 0.0164$) compared to monoculture. Similarly, the crown volume of *C. korshinskii* was significantly lower in mixtures with *A. ordosica* ($p = 0.0378$) and *C. latens* ($p = 0.0331$) than in monoculture. In contrast, neither groundwater nor replanting configuration had a substantial effect on *C. latens*. Notably, these effects were absent in 2020, with no significant influence of groundwater or replanting configuration on the plant growth (Figure S5 in Supporting Information S1). Under conditions without groundwater, the crown projected area, crown volume, and biomass of *A. ordosica* under mixed stand (*Ao* & *Ck*) declined from 2020 to 2023. Ground diameter of *A. ordosica*, *C. korshinskii*, and *C. latens* in both conditions with and without groundwater increased dramatically (2020–2023), compared to other plant growth characteristics (Figure 5, Figure S6 in Supporting Information S1).

Under conditions without groundwater, WUE values of *Ao* (3.10 kg m^{-3}) and *Cl* (0.831 kg m^{-3}) were higher than that of *Ck* (0.193 kg m^{-3}) (Figure 6a). However, the biomass of *Cl* was low (Figure 5f). Under mixed stand of *Ao*

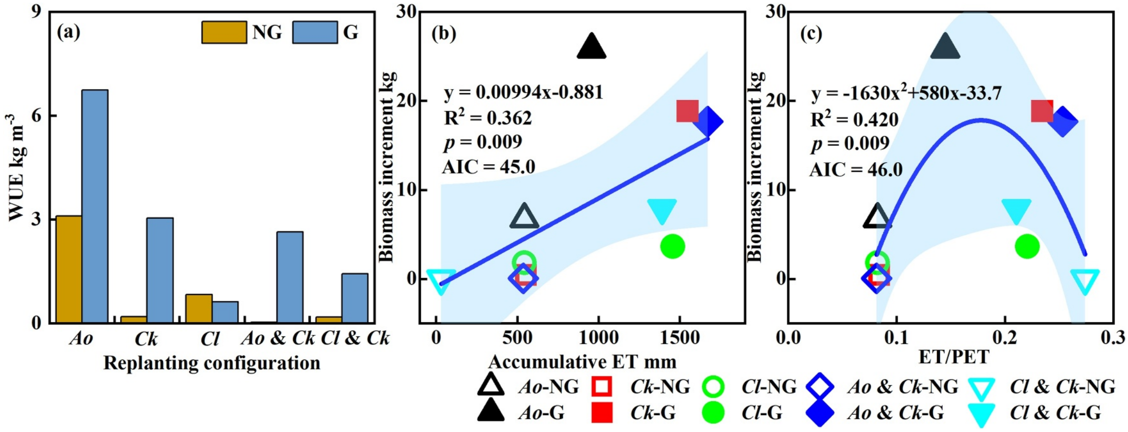

Figure 6. Water use efficiency under two groundwater conditions and different replanting configurations during 2020–2023 (a) and relationships between the variations in plant biomass increment and cumulative ET_a (b) and ET_a/PET (c). Shades of blue represent 95% confidence intervals.

& *Ck*, the biomass of *A. ordosica* and *C. korshinskii* decreased and increased from 2020 to 2023, respectively (Figure 5f, Figure S6f in Supporting Information S1), leading to the low WUE of *Ao* & *Ck* (0.0315 kg m^{-3}) due to the offset effect. *Cl* & *Ck* under conditions without groundwater had high water availability (ET_a/PET) but low increment in biomass, because *C. korshinskii* died in the dry year (2022). Therefore, *Ao* was recommended under conditions without groundwater.

Under groundwater conditions, WUE of *Ao* was the highest (6.74 kg m^{-3}), followed by *Ck* (3.05 kg m^{-3}), *Ao* & *Ck* (2.64 kg m^{-3}), *Cl* & *Ck* (1.43 kg m^{-3}), and *Cl* (0.624 kg m^{-3}) (Figure 6a). After the comparisons of fitting (Table S6 and Figure S7 in Supporting Information S1), increment in biomass linearly increased with cumulative ET_a and the slope in Figure 6b represented WUE. Figure 6c showed a parabolic relationship between biomass increment and ET_a/PET. Figure 6c showed ET_a/PET of *Ao* & *Ck* was the highest (0.253). Both *Cl* and *Cl* & *Ck* had higher water availability ET_a/PET but lower increment in biomass, compared to *Ao* (Figure 6c). Thus, *Ao*, *Ck*, and *Ao* & *Ck* were recommended under groundwater conditions.

4. Discussion

4.1. The Impacts of Groundwater on Water Balance Components

Consistent with the first hypothesis, this study confirmed that the mean daily ET_a for the variants without access to groundwater resources was significantly lower than for variants with a groundwater table of −2.5 m. Our findings on ET_a are in line with previous observations from Liu et al. (2017), which showed that ET was lower in sandy desert with deeper groundwater tables (103 mm), compared to oasis edge with shallower groundwater tables (283 mm). According to Condon et al. (2020), deeper groundwater tables suppressed ET_a relative to shallower groundwater ecosystems. During the observation period, planted ecosystems with groundwater maintained a higher DL and a soil water storage surplus, whereas those without groundwater exhibited a low DL and a soil water storage deficit (Figure 3), indicating that groundwater replenishment changed soil water storage toward a new hydrostatic equilibrium. Under groundwater conditions, plant roots utilized groundwater and reduced water uptake from vadose zone, which in turn likely resulted in the moisture increase in vadose zone and consequently drainage. Conversely, under conditions without groundwater, a greater proportion of infiltrated water is subjected to ET_a loss within the vadose zone, leading to the decrease in DL (Chen et al., 2020). Lower ET_a/PET in ecosystems without groundwater indicated that plants implement a conservative water use strategy, while higher ET_a/PET in ecosystems with groundwater suggested that plants adopt a profligate water use strategy (Peng et al., 2019). BRT results spotlighted that the groundwater replenishment alleviated the influence of drought and sparse rainfall on the water balance components in arid deserts. Condon et al. (2020) also showed that ET_a in the arid western US exhibited greater sensitivity to precipitation and warming rate variability compared to the humid eastern regions.

Increasing studies highlight the alarming groundwater depletion, especially under arid and semi-arid climatic conditions (Gurdak, 2017), consequently threatening plant growth and survival. The sustainability of groundwater depends on the balance between the groundwater consumption rate and the natural recharge rate (Gurdak, 2017). In our case, the DL ranged from 0 to 0.763 mm d^{-1} with no groundwater for the different replanting configurations, providing information on local recharge dynamics. Huang et al. (2013) found that the recharge rate in the desert was lower than those in the riparian and the oasis zones. Our results showed that biomass increment linearly increased with cumulative ET_a (Figure 6b). Groundwater replenishment provides a pivotal soil water source for supporting plant root water uptake and enhancing net primary production (Soylu et al., 2014). Our lysimeter observations demonstrated that, under steady-state groundwater table conditions, the water supply could support an increase in ET_a. However, under natural field conditions where groundwater tables typically exhibit dynamic fluctuations, high ET_a may potentially lead to groundwater depletion risks. Therefore, our results indicated that WUE had to be prioritized over biomass maximization in sustainable vegetation management.

4.2. The Impacts of Replanting Configuration on Water Balance Components

We also assumed that replanting configuration changed the water balance components based on different plant morphological characteristics. This hypothesis diverged from the experimental measurements. Except bare soil, the ET_a values among other five replanting configurations were similar, which could be explained that arid areas are characterized by high soil evaporation and low vegetation cover (Montoro et al., 2016). Montoro et al. (2016) found that evaporation of grapevine in an arid area ranged from 81% to 30% of ET_a per year. While Benettin et al. (2021) showed that ET_a rates of grass-planted and bare soil lysimeters were 5 and 2 mm d^{-1}, respectively. A previous study showed that the response of ET_a in savannah and grassland ecosystems was more sensitive to water deficit, compared to forest ecosystems (Giardina et al., 2023), as most of the water supply in arid ecosystems were consumed by ET_a (Li et al., 2016; Wang et al., 2008). The high ratios of ET_a/(P + G-DL) underscored that evaporation drove available water depletion in arid areas, with vegetation amplifying this process. These results were consistent with previous studies (Wang et al., 2004; Zhang, Xu, et al., 2021). Less DL/P (0.122) of the bare soil ecosystem without groundwater was found in this study, compared to the results (0.230) of Zhang, Xu, et al. (2021). The discrepancy between these might be attributable to weed growth, which consumed soil water through root water uptake, thereby increasing plant transpiration and decreasing DL in bare soil lysimeter. In addition, the difference could be elucidated by the distinct depths of soil monoliths, with 3 m depths in this study and 2.2 m depths in Zhang, Xu, et al. (2021). We were surprised that there was DL (0.0606 ± 0.0317 mm d^{-1}) under planted ecosystems without groundwater, compared to Zhang, Xu, et al. (2021), which had no DL. Such differences were mainly attributed to the limited plant biomass and underdeveloped root systems during the early vegetation establishment stage (2019).

4.3. Plant Response to the Groundwater and Replanting Configuration

Aligning with our third hypothesis, replanting configuration under different groundwater conditions is quite important, which is related to the sustainability of ecological restoration in arid deserts. Previous studies showed that the unsuitable afforestation in arid and semi-arid regions might reduce the groundwater recharged, which was mainly fed by precipitation, and jeopardized the already vulnerable ecological environment (Lu et al., 2018). Replanting configurations using limited water to realize the maximum of sand stabilization effect (i.e., high WUE) were recommended (Antunes et al., 2018; Lu et al., 2018). Our study highlighted the importance of semi-shrubs on vegetation restoration in deserts. In this study the semi-shrub *A. ordosica* had the highest WUE in both ecosystems with and without groundwater and could, therefore, be a better option for replanting. Especially in ecosystems without groundwater, *C. latens* semi-shrub also had a relatively high WUE compared to other replanting configurations (Figure 6a). However, less attention was paid to semi-shrubs. Dwarf semi-shrub *A. ordosica* is a typical xerophyte and psammophyte (Zhang, Li, et al., 2008). Our findings were consistent with those of Palmquist et al. (2021), who found that the plant stand structure consisted of many small plant individuals and fewer but larger individuals on water-limited sites. In addition, small individuals require less water resources and subsequently reduced the intraspecific and interspecific competition to acclimate the limited water supply settings (Huang et al., 2013; Palmquist et al., 2021). Besides, non-rainfall events (e.g., dew and soil water vapor absorption) were of high importance for shallow-rooted semi-shrubs, it improves the microhabitat (Pan & Wang, 2014) and intercepted water from dew formation could be directly taken up by plants (Gui et al., 2021), reducing water stress and leading to evaporative cooling of the canopy (Ghafarian et al., 2022; Groh et al., 2018), especially in ecosystems without groundwater.

Since the WUE of *Ck*, *Ao* & *Ck* is higher than those of other replanting configurations, our study advocated semi-shrub monoculture, shrub monoculture and a mixture of semi-shrub and shrub as the preferred replanting configurations in ecosystems with groundwater. Biomass increment first increased and then decreased with water availability (ET_a/PET), which might be due to species limitation (Figure 6). *C. korshinskii* shrub was also a typical xerophyte. These results also supported the two-layer theory in dry climates (Schenk & Jackson, 2002). Replanting configurations with deep and shallow root systems in arid deserts occupy different depths, realizing the hydraulic redistribution (Zhao et al., 2024). However, our study showed that in ecosystems without groundwater, neither shrub monoculture nor mixture were recommended due to low WUE. Other plant growth characteristics (plant height, crown projected area, crown volume, biomass) were not changing a lot from 2020 to 2023 compared to ground diameter (Figure 5, Figure S6 in Supporting Information S1). Shrub *C. korshinskii* of *Cl* & *Ck* even died in an extremely dry year (2022) because younger plants didn't have an established deep rooting system. Therefore, long-term observations of ecological restoration effects merit considerations to make vegetation restoration robust and sustainable.

In this study, our analysis focused primarily on the mean daily water balance components, with limited consideration of seasonal variations. Additionally, groundwater depth was treated as constant, while actual seasonal fluctuations were not accounted for. The findings were based on only 5 years of observational data; longer-term monitoring could yield more robust conclusions and further support strategies for desert prevention. Future studies should integrate high-frequency (e.g., weekly) above- and below-ground plant observations (Xi et al., 2018) to more accurately characterize plant development dynamics under varying management strategies and groundwater regimes. We also propose investigating how foliar uptake of non-rainfall water varies among plant species (Groh et al., 2018; Gui et al., 2021). A key challenge remains to partition ET_a in these diverse ecosystems, which could be addressed using methods such as mechanistic modeling (Tu et al., 2021) and stable isotope techniques (Liu et al., 2021).

5. Conclusions

We conclude that: (a) access to shallow groundwater (−2.5 m) alleviated the stress of drought and scarce precipitation in arid deserts. Plants in desert ecosystems with access to groundwater consumed more water than those in ecosystems without groundwater. (b) A large amount of available water supply was consumed as evaporation or actual evapotranspiration (ET_a) in desert ecosystems with and without groundwater. (c) Semi-shrubs played an important role in desert ecosystems under conditions with and without groundwater. *A. ordosica* semi-shrub monoculture was recommended in desert ecosystems without groundwater while *A. ordosica* monoculture, *C. korshinskii* shrub monoculture, and a mixture of *A. ordosica* and *C. korshinskii* were the preferred replanting configurations in desert ecosystems with groundwater. This study quantifies the impact of groundwater and different replanting configurations on the water balance components. The plant growth performance was evaluated mainly based on WUE, which gave direct evidence to the recommended replanting configuration in desert ecosystems with or without access to groundwater.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All experimental data, including lysimeter measurements and meteorological observations, along with the corresponding analysis codes, are openly available in the Figshare repository [https://figshare.com/s/c2f5a9615164f10dac81]. The data set is permanently preserved with doi: 10.6084/m9.figshare.29482313 and distributed under a CC BY 4.0 license, ensuring full transparency and reproducibility of our findings. Data processing and statistical analyses were performed using industry-standard software packages: Origin 2017 [https://www.originlab.com], *R* Studio 4.0.3 [https://posit.co/download/rstudio-desktop/], and SPSS 23.0 [https://spssau.com]. All software was utilized according to the manufacturers' recommended protocols.

Acknowledgments
All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Yicong Nan, Zhishan Zhang, and Jannis Groh. The first draft of the manuscript was written by Yicong Nan and all authors commented on previous versions of the manuscript. All of the authors read and approved the final manuscript. This work was supported by the National Key Research and Development Program of China (2024YFF1306903), the National Natural Science Foundation of China (U23A20223, 32301314, and 32171630), and the Postdoctoral Fellowship Program of CPSF (GZC20232954).

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