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EDITED BY
Qi Wu,
Shenyang Agricultural University, China

REVIEWED BY
Junxiao Zhang,
Xinjiang Academy of Agricultural Sciences, China
Evandro Franklin De Mesquita,
State University of Paraíba, Brazil

*CORRESPONDENCE
Dezhi Sun
sdzcf@163.com
Junying Jia
jjy509628@163.com

†These authors share first authorship

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# Effects of drip irrigation regimes on leaf structure, photosynthesis, yield, and quality in *Atractylodes chinensis* (DC.) Koidz

Guoshuai Lv[1,2†], Yunlong Wu[1†], Zhijun Li[1,2], Defeng Zhuang[1,2], Yuan Guo[1,2], Zicheng Wang[3], Chunxue Gao[1,2], Dezhi Sun[2,4*] and Junying Jia[1,2*]

[1]College of Agronomy, Inner Mongolia Minzu University, Tongliao, China, [2]University Engineering Research Center of Chinese (Mongolia) Ecological Planting Medicinal Materials in Inner Mongolia Autonomous Region, Tongliao, China, [3]Tongliao Agriculture and Animal Husbandry Development Center, Tongliao, China, [4]College of Grassland, Inner Mongolia Minzu University, Tongliao, China

**Introduction:** *Atractylodes chinensis* (DC.) Koidz, a medicinal herb in the Chinese Pharmacopoeia, is grown in sandy soils. However, water scarcity in the Horqin Sandy Land limits its growth, and the effects of irrigation remain poorly studied. This research aimed to determine how irrigation levels affect its yield and quality through leaf structure, physiology, and secondary metabolism.

**Methods:** A field experiment tested five irrigation rates (4500–2500 $m^3 \cdot hm^{-2}$). We measured leaf anatomy, photosynthetic parameters, yield, and quality indicators.

**Results and discussion:** Irrigation altered leaf anatomy (palisade and spongy tissue thickness). Photosynthetic pigment content showed a initial increase then decrease with reduced irrigation. An irrigation rate of 3500 $m^3 \cdot hm^{-2}$ maintained high electron transfer efficiency, carbon assimilation, and key enzyme activity for alkaloid synthesis. While yield declined with less water, quality peaked at moderate irrigation. Moderate irrigation (3500 $m^3 \cdot hm^{-2}$) best balances yield and quality by supporting both physiological function and secondary metabolism. These findings offer a theoretical basis and practical guidance for cultivating *A. chinensis* in water-limited sandy lands under climate change.

KEYWORDS

***Atractylodes chinensis* (DC.) Koidz, drip irrigation, quality, water deficit, yield**

## Introduction

*Atractylodes chinensis* (DC.) Koidz is a perennial herb belonging to the genus *Artemisia* of the family Asteraceae. It is suitable for planting in well-drained sandy soil (Lv et al., 2022) and has ecological benefits such as wind prevention and sand fixation, as well as pharmacological effects. The dried rhizomes of *A. chinensis* are used in medicine and are among the sources of *Atractylodes*-derived medicinal materials included in the Chinese

Pharmacopoeia (National Pharmacopoeia Commission, 2020). Modern pharmacological studies have shown that *A. chinensis* has hepatoprotective, diuretic, anti-inflammatory, antibacterial, antiviral, and inhibitory effects on cancer cell growth; its pharmacological effects are related to the content of its major active ingredients (Zhuang et al., 2021). Atractylodin content is an important standard for measuring the quality of *A. chinensis*. It is synthesized in plants via the acetic acid-pimelic acid (AA-MA) pathway with acetyl-CoA as the direct raw material. Acetyl-CoA carboxylase (ACC) is the key and rate-limiting enzyme in this biosynthetic pathway (Sun et al., 2021, 2020). As a medium connecting the soil–plant–atmosphere system, water is an important ecological factor affecting the quality of medicinal materials and dry matter accumulation (Wang, 2004). The response of medicinal plants to changes in external water conditions includes changes in leaf morphology and physiological and biochemical reactions (Ennajeh et al., 2010; Thakur et al., 2024). Previous studies have shown that in response to drought stress, the diameter of spongy tissue and veins in the leaves of *Cyclocarya paliurus* showed a decreasing trend with an increase in drought intensity, whereas the proportion of palisade and spongy tissue, along with leaf thickness, exhibited an increasing trend (Li et al., 2022). Further, waterlogging stress negatively affects leaf anatomical structure. For example, prolonged waterlogging reportedly significantly increased the thickness of the epidermis, as well as that of the palisade and spongy tissue, in *Chrysanthemum* (Yin et al., 2012). This indicates that water is an important factor affecting the anatomical structure of medicinal plant leaves. Leaf morphology and structure are closely related to photosynthesis; therefore, when plants are under water stress, their morphology and structure are affected, which in turn affects photosynthetic processes (Han and Zhao, 2010; Wang et al., 2019). For example, drought stress reduces photosynthetic pigment content in the leaves of *Atractylodes macrocephala*, impairing the efficiency of the respiratory electron transport chain and RuBisCO enzyme activity. This results in decreased photosynthetic parameters, including net photosynthetic rate (Pn) and stomatal conductance (Gs), which negatively affects the yield and quality of *Atractylodes lancea* (Zhang et al., 2021). Waterlogging stress can seriously limit photosynthesis in *Zingiber officinale* by reducing the content of photosynthetic pigments in leaves and inhibiting the assimilation efficiency rate and Photosystem II (PSII) electron transport efficiency (Liu et al., 2023).

Photosynthesis can be linked to the secondary metabolism of medicinal plants through the formation of three-carbon compounds during the Calvin cycle (Li et al., 2024a); therefore, photosynthesis is the basis for the quality and yield of medicinal plants (Liu Z. et al., 2022; Song et al., 2023). Several studies have shown that water stress is not conducive to improving medicinal plants; however, moderate water stress can activate a series of physiological and biochemical reactions to activate secondary metabolism in plants, thereby promoting the formation and accumulation of active ingredients in medicinal plants (Xue et al., 2018). Hosseini et al. showed that an appropriate reduction of water can stimulate sugar metabolism in the plant body of *Glycyrrhiza glabra* L, accelerate the decomposition of substances, or promote the expression of glycyrrhizin synthesis genes, thereby promoting the synthesis and accumulation of glycyrrhizin. However, excessive water loss leads to a decrease in glycyrrhizin content (Hosseini et al., 2018; Liu and Wang, 2008; Nasrollahi et al., 2014). Although waterlogging stress is beneficial to rhizome yield in *Curcuma kwangsiensis*, endogenous volatile oils such as geraniol decrease with increasing soil water content (Tan et al., 2012). This indicates that excessive or insufficient water is not conducive to the synthesis of the active substance.

*A. chinensis* has considerable market demand in eastern Inner Mongolia as a major authentic medicinal material (Li et al., 2021). The traditional supply of *A. chinensis* mainly depends on wild resources. However, due to excessive harvesting, the availability of medicinal materials has decreased sharply. The implementation of a national ecological environmental protection strategy has strictly restricted the harvesting of wild *A. chinensis*. Therefore, the artificial large-scale and standardized cultivation of northern *A. chinensis* has gradually become the main source of *A. chinensis* medicinal materials (Liu C. et al., 2022). However, the content of medicinal components during the cultivation process of *A. chinensis* is one of the bottlenecks in the intensive production of *A. chinensis.* The soil in Horqin Sandy Land is severely decertified. Meanwhile, under the national policy for controlling the "non-grain use" of cultivated land, *A. chinensis*, as an ecological restoration type of medicinal material, has the functions of sand fixation and wind prevention. Therefore, planting *A. chinensis* in Horqin Sandy Land is advantageous (General Office of the State Council, 2020). However, the low water retention capacity of Horqin Sandy Land and water availability affect the growth process of *A. chinensis*, which in turn influences its medicinal quality by regulating the activity and content of key enzymes in the metabolic pathway.

While extensive research has confirmed the influence of water supply on the yield and quality of medicinal plants, studies on how water regulation modulates *A. chinensis*, from leaf structure and photosynthetic function to the biosynthesis of its bioactive compounds, are still scarce. Therefore, we examined the synergistic relationships among leaf structure, plant physiology, and secondary metabolism to understand how irrigation levels in the Horqin Sandy Land affect *A. chinensis* yield and quality. The findings provide theoretical foundations for optimizing ecological and economic benefits in cultivating *A. chinensis* in the Horqin Sandy Land, while offering data-driven insights to enhance climate resilience and mitigate drought stress in this medicinal plant.

# Materials and methods

## Test site overview

The trial was conducted in 2022 at the Chinese-Mongolian Medicinal Materials Research Base in Naiman Banner, Inner Mongolia (42°14′17″N, 120°20′35″E). The experimental area is characterized by a temperate continental monsoon climate, with an average temperature of 6°C and precipitation of 300 mm in 2022.

The soil in the experimental field was sandy loam with a pH of 8.2, containing 63.3 mg/Kg of alkaline nitrogen, 75.9 mg/kg of available potassium, and 26.4 mg/Kg of available phosphorus.

## Test material and methods

The experiment employed five irrigation treatments: ① T1: 4500 $m^3$/ha; ② T2: 4000 $m^3$/ha; ③ T3: 3500 $m^3$/ha; ④ T4: 3000 $m^3$/ha; and ⑤ T5: 2500 $m^3$/ha. Fifteen 20-$m^2$ plots were established, with three replicates conducted. Using the 2011–2020 meteorological data from Tongliao City (average rainfall of 300 mm from June to September, as recorded in the Inner Mongolia Statistical Yearbook), monthly rainfall was converted into irrigation volume ($m^3$). Drip irrigation was implemented with water meters monitoring each plot's consumption. Irrigation schedules for different growth stages are detailed in Table 1. During the experiment, mobile rain shelters were installed, and 60-cm-deep liners were buried between plots to prevent water infiltration. Two-year-old high-quality *A. chinensis* macrocephala seedlings (originally sourced from Zhalute) with uniform quality were planted at 25 × 40 cm spacing (125,000 plants/ha) in the research base. The cultivation cycle involved six annual weeding sessions without chemical fertilization, with the plants maintained until reaching 5 years of growth for experimental evaluation.

## Determination index and method

Samples were collected from the entire plant during the leaf expansion peak (June 25), flowering (July 25), and fruiting (August 25) periods. For each treatment, five well-grown *A. chinensis* plants were dug from each plot and replicated thrice. After washing, organs were separated, and the rhizomes of some plants were chopped, mixed, rapidly frozen in liquid nitrogen, and stored at -80°C for subsequent physiological measurements. The other samples were oven-dried at 65°C for use in other related measurements.

To determine the anatomical structure, samples were collected during the flowering period (July 25), and nine randomly selected *A. chinensis* plants with healthy mid-to-upper leaves were used. After rinsing thoroughly with clean water and drying on filter paper, the leaves were placed in an FAA fixative (70%). Next, the mid-leaf sections were cut into 1-$cm^2$ pieces, embedded in paraffin, and sectioned (Xu, 1999). Under a 200× microscope, the sections were measured using a micrometer and photographed. The data obtained included the average values from five fields of view across different sections. The measured indicators were epidermal cell thickness, wax layer thickness of epidermal cells, dermal cell thickness, wax layer thickness of dermal cells, palisade tissue thickness, spongy tissue thickness, and main vein diameter. The anatomical-related parameters were calculated using Equations 1-3 formulas (Li et al., 2024b):

$$\text{P/S ratio} = \text{palisade tissue thickness}/\text{sponge tissue thickness} \quad (1)$$

$$\text{Organization structure tightness} = \text{palisade organization thickness}/\text{leaf thicknes} \times 100\,\% \quad (2)$$

$$\text{Degree of tissue structureloosening} = \text{spongetissue thickness}/\text{leaf thickness} \times 100\,\% \quad (3)$$

To determine photosynthetic pigment content, fresh samples of the upper and middle leaves of *A. chinensis* were cut and mixed, and the photosynthetic pigments were extracted with ethanol and measured using a Hitachi High-Tech U-2900 spectrophotometer (Gao, 2006). For chlorophyll fluorescence determination, a FluorPen FP110/D handheld chlorophyll fluorometer (Photon Systems Instruments, Drásov, Czech Republic) was used to select clear mornings between 8:00 and 11:00. Before measurement, a light shield was used to acclimate the healthy and intact leaves at the same position on *A. chinensis* for 15 min in the dark. The saturation pulse intensity and duration were set to 3000–5000 μmol $m^{-2}$ $^{-1}$ and 0.7 s, respectively. The initial fluorescence (Fo), maximum fluorescence (Fm), maximum photochemical quantum yield of PSII (Fv/Fm), and activity of PSII (Fv/Fo) were measured, among other chlorophyll fluorescence parameters. RuBisCO activity was determined using a 1,5-diphosphonucleoside carboxylase/oxygenase (RuBisCO) enzyme-linked immunosorbent assay kit (catalog number: YJ094788; Shanghai Enzyme Biotechnology Co., Ltd., Shanghai, China). To determine photosynthetic gas exchange parameters, Pn, Gs, and Tr during the peak flowering period were measured at 8:30–11:30 on a clear and windless day using an Li-6400 portable photosynthesis instrument (LI-COR Biosciences, Lincoln, NE, USA) to determine the photosynthetic physiological indices of the same leaf position. The instrument is set to a $CO_2$

TABLE 1 Irrigation scheme used in the study.

| Treatment | Single irrigation volume ($m^3$ $hm^{-2}$)/ Irrigation frequency in the current month | | | Total irrigation frequency | Irrigation quota ($m^3$ $hm^2$) |
|---|---|---|---|---|---|
| | June | July | August | | |
| T1 | 650/2 | 640/3 | 640/2 | 7 | 4,500 |
| T2 | 575/2 | 570/3 | 570/2 | 7 | 4,000 |
| T3 | 500/2 | 500/3 | 500/2 | 7 | 3,500 |
| T4 | 425/2 | 430/3 | 430/2 | 7 | 3,000 |
| T5 | 350/2 | 360/3 | 360/2 | 7 | 2,500 |

concentration of 400 μmol/mol, flow rate of 500 μmol/s, and temperature of 25°C. Subsequently, the instantaneous water use efficiency (WUE) of the leaf was calculated as follows: WUE = Pn/Tr.

## Determination of key enzymes and substance content in atractylodin synthesis

The pyruvate content was determined using a pyruvate testing kit. An enzyme-linked immunosorbent assay (ELISA) kit was used to determine the pyruvate dehydrogenase (PDH), plant dihydrothioctic acid transacetylase (DLAT), and plant dihydrothioctic acid dehydrogenase (DLD) activities in roots. The acetyl coenzyme A (A-COA) content in roots was determined using an ELISA kit. At the beginning of October, the method of measuring yield in small areas was adopted. Three representative unsampled 5 $m^2$ areas were selected in each treatment for yield measurement. The *A. chinensis* rhizome was treated at 110°C for 10 min to deactivate enzymes, then dried at 65°C until constant weight. The atractylodin content was measured by high-performance liquid chromatography (HPLC). A Venusil MP C18 column (4.60 × 300 mm, 5 μm; Bonna-Agela Technologies Inc., Newark, DE, USA), was employed with methanol:water (81:19) elution at 1 mL/min. Detection was conducted at 340 nm with column temperature maintained at 35°C and a 10 μL injection volume. The standard curve was calculated as y=372.03x-3.5049 ($R^2$ = 0.9999).

## Statistical analysis and plotting

The experimental data were processed and calculated using Microsoft Excel 2010. Statistical analysis was performed with SPSS 20.0 software using one-way analysis of variance (ANOVA), followed by Duncan's new multiple range test for significance analysis (P< 0.05). Graphs were generated using GraphPad Prism 8. The comprehensive index evaluation was conducted using the CRiteria Importance Through Intercriteria Correlation (CRITIC) method. The leaf thickness to main vein diameter ratio, upper epidermis thickness to lower epidermis thickness ratio, Fv/Fo, Fv/Fm, Gs, PDH, DLD, acetyl-CoA, acetyl-CoA carboxyl synthase, schizonepeta content, and dry weight were selected as evaluation indicators. Correlation analysis was performed on the required evaluation indicators in line with the CRITIC method to obtain the correlation coefficient matrix R = ($R_{ij}$) 11 × 11. The weight calculation was performed according to Equation 4 (Zhou and Ma, 2004):

$$C_j = sj\sum_{i=1}^{n}(1 - R_{ij}),\ \ (j = 1, 2, 3, \ldots,\ \ n), \tag{4}$$

where $C_j$ is the information contained in the *j*th evaluation index, and $R_{ij}$ is the correlation coefficient between evaluation indexes *i* and *j*. The larger the $C_j$, the more information the *j*th evaluation index contains and the greater its relative importance. Therefore, the objective weight of the *j*th evaluation index can be expressed as follows (Equation 5):

$$W_{ij} = C_j/\sum_{i=1}^{n} C_j(j - 1, 2, 3, \ldots, n) \tag{5}$$

# Results

## Leaf characteristics

The cross-sectional anatomical structure of *A. chinensis* leaves included the epidermis, mesophyll, and vascular bundles (veins) (Figure 1). The upper and lower epidermis were composed of a layer of cells. The palisade tissue was distributed on the inner side of the upper epidermis, whereas the sponge tissue was distributed on the inner side of the lower epidermis.

With reduced irrigation, *A. chinensis* leaf thickness first increased and then decreased. No significant difference was observed in leaf thickness between treatments T4 and T5, but their values were significantly higher than those of treatments T1, T2, and T3 ($p<0.05$). The main vein diameter of *A. chinensis* followed the same trend as its leaf thickness, with a variation range of 430.65–515.12 μm. While treatments T4 and T5 showed significantly higher values than T1, T2, and T3 ($p<0.05$), no significant difference was found between T4 and T5 (Table 2).

With reduced irrigation, both the upper and lower epidermal layers and their respective cuticle thicknesses in the leaves of *A. macrocephala* showed a gradual decrease. The upper epidermal thickness varied from 22.95 to 28.43 μm, with no significant difference observed between treatments T3 and T4, while other treatments showed significant differences ($p<0.05$). The lower epidermal thickness showed no significant difference between treatments T2 and T3 but was significantly higher than those in treatments T4 and T5 ($p<0.05$). The cuticle thickness of the upper epidermis differed significantly only between treatments T1 and T5 ($p<0.05$). Both treatments T4 and T5 exhibited significantly lower epidermal cuticle thickness compared with other treatments ($p<0.05$), though no significant difference was found between them (Table 3).

The trends in the tightness of the guard cell structure, guard cell ratio, and leaf structure were consistent, with T5 treatment showing significantly higher values than T3, T2, and T1 treatments ($p<0.05$). Conversely, both the thickness of the spongy tissue and looseness of the leaf tissue decreased with reduced drip irrigation volume. The thickness of the spongy tissue was significantly higher in T1 treatment than in T5 treatment ($p<0.05$), while no significant differences were observed in other treatments. Additionally, the looseness of the leaf tissue was significantly higher in T1 treatment than in T3, T4, and T5 treatments ($p<0.05$). This indicates that the leaves of *A. chinensis* can respond to varying drip irrigation volumes by altering their anatomical structure (Table 4).

## Effects of different irrigation levels on the photosynthetic physiological characteristics of *A. chinensis*

Under different drip irrigation systems, the chlorophyll changes in the leaves of *A. chinensis* were similar. During the peak leaf

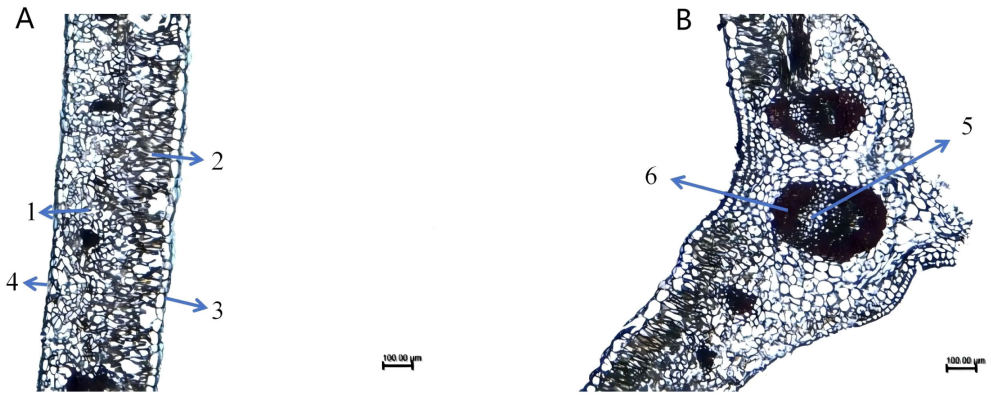



FIGURE 1
Leaf anatomical structure of *A. chinensis;* **(A)** mesophyll structure, **(B)** main vein and mesophyll structure; 1: sponge tissue, 2: fence organization, 3: upper epidermis, 4: lower epidermis, 5: main vein phloem, 6: xylem of the main vein.

expansion period, the T3 treatment showed significantly higher chlorophyll levels than other treatments ($p<0.05$). In the fruiting stage, there was no significant difference in chlorophyll content between the T3 and T4 treatments, but their chlorophyll a contents were significantly higher than those in the other treatments ($p<0.05$). However, during the flowering stage, the trend of chlorophyll b changes was opposite to that of the total chlorophyll content, with the T2 treatment showing significantly higher levels than T1, T4, and T5 treatments ($p<0.05$; Figures 2A–C). The carotenoid content in each treatment showed no significant difference during the peak leaf expansion period, but it was significantly higher in the T4 treatment during both the flowering and fruiting stages ($p<0.05$; Figure 2D). This indicates that different drip irrigation amounts had varying degrees of impact on the synthesis and accumulation of chlorophyll and carotenoids in the leaves of *A. chinensis*.

During the peak leaf expansion period, the Fv/Fo and Fv/Fm ratios of *A. chinensis*. showed consistent trends across treatments. While T1 and T2 treatments showed no significant differences in these ratios, they were significantly higher than those of other treatments ($P<0.05$). At flowering stage, the Fv/Fo ratio in T3 treatment increased by 20.46% and 25.30% compared with those of T1 and T5 treatments, respectively, reaching statistical significance ($P<0.05$); whereas no significant differences were observed in Fv/Fm ratios among treatments. In fruiting stage, T1 and T3 treatments exhibited significantly higher Fv/Fo values than other treatments ($P<0.05$; Figure 3A). The Fv/Fm ratio in T1 treatment was notably higher than that in T3, T4, and T5 treatments ($P<0.05$), with T3, T4, and T5 treatments showing reductions of 10.61, 12.31, and 21.67% compared to T1, respectively (Figure 3B). These results demonstrate that different drip level treatments significantly affect the maximum photochemical efficiency and plant's potential photosynthetic capacity in *A. chinensis*.

The RuBisCO activity in the leaves of *A. chinensis*. showed consistent trends with the fruiting stage. This activity was the highest in T3 treatment at the leaf expansion peak; it was significantly higher than those T1, T4, and T5 treatments ($P<0.05$), while no significant difference was observed between T2 and T3 treatments. During the fruiting stage, it was only significantly higher than that of T4 treatment ($P<0.05$). At flowering, T3 treatment demonstrated significantly higher RuBisCO activity than other treatments ($P<0.05$; Figure 4). This indicates that enhancing RuBisCO activity under moderate water deficit conditions facilitates the dark reaction.

In addition to water use efficiency, the trends of photosynthetic gas exchange parameters during the flowering period of *A. chinensis*. were similar, with all of them reaching peak values under the T3 treatment. The net photosynthetic rate of leaves in T3 and T4 treatments showed significant differences compared with those in T1 and T5 treatments ($P<0.05$), with T3 treatment increasing by 72.05% and 38.37%, respectively. The stomatal conductance in T3 treatment was significantly higher than those in other treatments ($P<0.05$), while no significant differences were observed between treatments. Transpiration rates in T3 and T2 treatments were significantly higher than those in T1 and T5 treatments ($P<0.05$), with T3 treatment showing 34.49% and 41.67% increases compared with T1 and T5 treatments, respectively. Instantaneous water use efficiency increased initially and then decreased as irrigation volume decreased, with T3, T4, and

TABLE 2 Changes of leaf thickness and main vein diameter of *A. chinensis* under water regulation.

| Treatment | Blade thickness (μm) | Main vein diameter (μm) |
|---|---|---|
| T1 | 372.10 ± 1.90c | 430.65 ± 5.82d |
| T2 | 379.68 ± 4.98c | 455.87 ± 5.92cd |
| T3 | 389.55 ± 4.90b | 474.82 ± 9.90bc |
| T4 | 398.46 ± 2.77a | 515.12 ± 25.30a |
| T5 | 396.65 ± 2.92ab | 503.16 ± 14.11ab |

In this article, lowercase letters indicate a significance level of p=0.05 for the same sampling period under different drip irrigation amounts.
The lowercase letters denote significant differences at $p<0.05$.

TABLE 3 Changes of epidermal characteristics of *A. chinensis* under water regulation.

| Treatment | Upper skin thickness | Lower skin thickness | Upper epidermal cuticle thickness | Lower epidermal cuticle thickness |
|---|---|---|---|---|
| T1 | 28.43 ± 0.34a | 21.80 ± 0.92a | 9.16 ± 0.16a | 12.77 ± 0.19a |
| T2 | 26.63 ± 0.38b | 20.07 ± 0.27ab | 8.09 ± 0.58b | 11.82 ± 0.63ab |
| T3 | 25.00 ± 0.59c | 19.37 ± 0.33b | 7.77 ± 0.20b | 10.98 ± 0.28b |
| T4 | 23.74 ± 0.67c | 17.42 ± 1.35c | 7.45 ± 0.29b | 9.48 ± 0.27c |
| T5 | 21.95 ± 0.83d | 16.49 ± 0.84c | 6.52 ± 0.12c | 9.47 ± 0.68c |

The lowercase letters denote significant differences at p<0.05.

T5 treatments significantly higher than T2 treatment (P<0.05). Notably, T3 treatment demonstrated 31.69% and 41.67% improvements over T1 and T2 treatments (Figure 5). These results indicate that photosynthetic gas exchange parameters of flowering *A. chinensis* were significantly affected under different irrigation treatments. The T3 treatment notably enhanced leaf net photosynthetic rate and stomatal conductance while maintaining high water use efficiency, effectively boosting both photosynthetic capacity and water balance capabilities in leaves.

## Effects of different irrigation levels on the synthesis of key atractylodin substances

The pyruvic acid content in the rhizomes of *A. chinensis* showed no significant differences among treatments during the peak leaf expansion and flowering periods (Figure 6). During the fruiting stage, pyruvic acid content peaked in treatment T2, with a significant difference (P<0.05), compared with that in treatment T3, showing a 44.11% higher level (Figure 6A). Acetyl-CoA content exhibited significant differences only during peak leaf expansion, with treatments T2, T4, and T5 exhibiting significantly higher values than T1 and T3 (P<0.05); treatment T4 increased by 31.48% and 10.16% compared with T1 during peak leaf expansion and flowering periods, respectively (Figure 6B). This indicates that under different irrigation conditions, *A. macrocephala* produces varying amounts of photosynthetic products through its photosynthetic characteristics, which further influences the synthesis and accumulation of precursor substances in its secondary metabolism.

## Enzyme activities of PDH, DLAT, and DLD in rhizome of *A. chinensis*

During the peak leaf expansion stage, the PDH enzyme activity in the rhizomes of *A. chinensis* was highest under T4 treatment, showing a significant 18.34% increase compared with T1 treatment (P<0.05), with no significant difference between T4 and T5. At flowering stage, PDH activity was higher under T2 and T5 treatments, with significant increases of 16.44% and 15.30%, respectively, compared with T1 (P<0.05). In fruiting stage, PDH activity in T5-treated rhizomes was the highest, significantly exceeding that in T1 treatment (P<0.05) (Figure 7A). DLATase activity was the highest under T2 treatment during the leaf expansion peak and flowering period (Figure 7B). Specifically, the that under T2 treatment at leaf expansion peak was significantly higher than those in other treatments (P<0.05), while that of T2 treatment at flowering period was significantly higher than those of T3 and T4 treatments (P<0.05). During the fruiting stage, the T4 treatment achieved the peak DLATase activity, which was significantly higher than those of the other treatments (P<0.05). At each sampling stage, the DLD enzyme activity under T4 treatment was the highest at the peak leaf expansion stage, with significantly higher activity (21.34% and 12.75%) than those of T1 and T5 treatments (P<0.05), respectively. During flowering, T4 treatment demonstrated significantly higher DLD activity than T2, T3, and T5 treatments, with a 17.40% increase over T5. No significant differences were observed among treatments during fruiting (Figure 7C). This indicates that moderate water deficit effectively activates the pyruvate dehydrogenase system (PDH, DLAT, and DLD), collectively promoting the conversion of

TABLE 4 Changes of mesophyll tissue of *A. chinensis* under water regulation.

| Treatment | Palisade mesophyll thickness (μm) | Sponge tissue thickness (μm) | Pt/St | Compactness of leaf structure (%) | Looseness of leaf structure (%) |
|---|---|---|---|---|---|
| T1 | 167.19 ± 2.36c | 162.48 ± 4.62a | 1.03 ± 0.04c | 44.93 ± 0.40c | 43.67 ± 1.38a |
| T2 | 171.65 ± 2.84bc | 160.20 ± 2.48ab | 1.07 ± 0.02c | 45.21 ± 0.40c | 42.19 ± 0.43ab |
| T3 | 176.19 ± 3.54b | 159.46 ± 2.67ab | 1.11 ± 0.03b | 45.23 ± 0.81c | 40.93 ± 0.50b |
| T4 | 187.57 ± 3.50a | 157.30 ± 1.98ab | 1.19 ± 0.04ab | 47.07 ± 0.55b | 39.66 ± 0.76c |
| T5 | 193.97 ± 5.01a | 154.26 ± 3.79b | 1.26 ± 0.06a | 48.90 ± 1.13a | 38.71 ± 1.12c |

The lowercase letters denote significant differences at p<0.05.

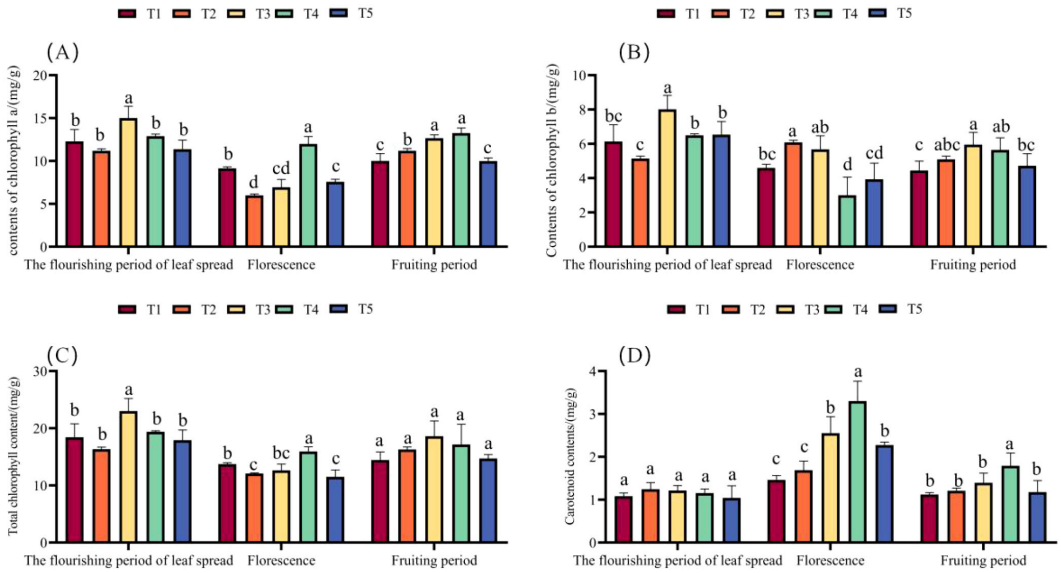



FIGURE 2
Changes in photosynthetic pigment content under different irrigation amounts: **(A)** chlorophyll a, **(B)** chlorophyll b, **(C)** chlorophyll, **(D)** carotenoid. The lowercase letters denote significant differences at $p<0.05$.

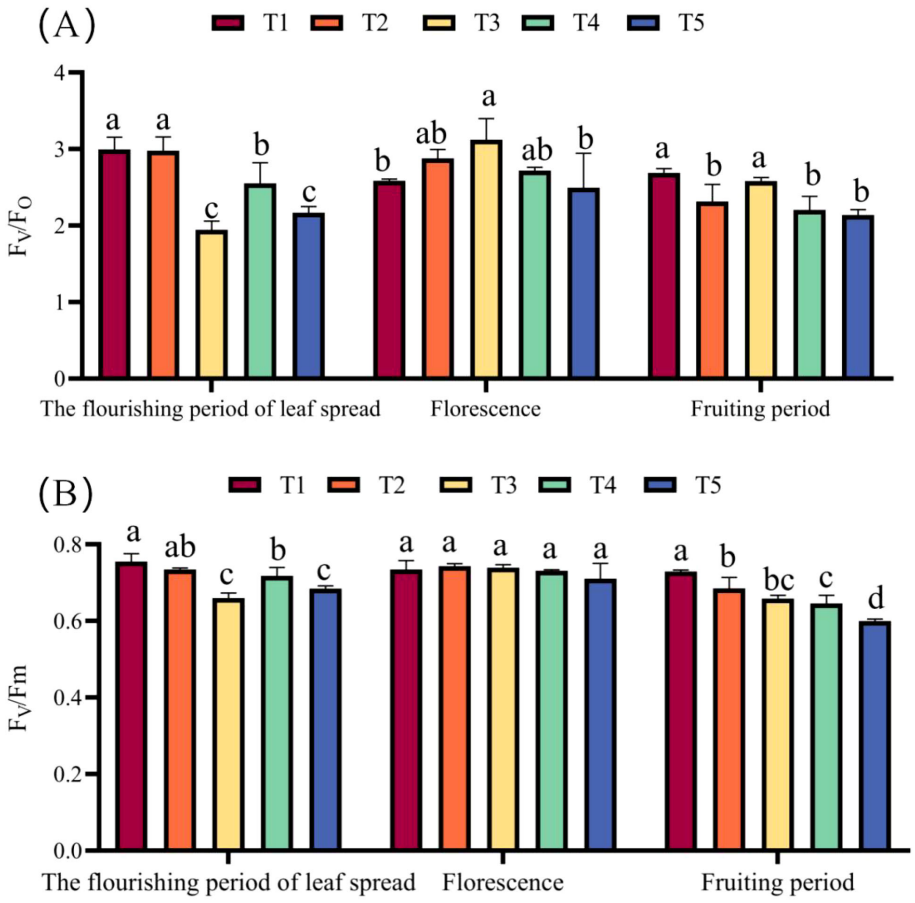



FIGURE 3
Changes of leaf fluorescence parameters of *A. chinensis* under different drip irrigation rates : **(A)** Fv / Fo : PSII quantum efficiency; **(B)** Fv / Fm : Photochemical quantum efficiency. The lowercase letters denote significant differences at $p<0.05$.

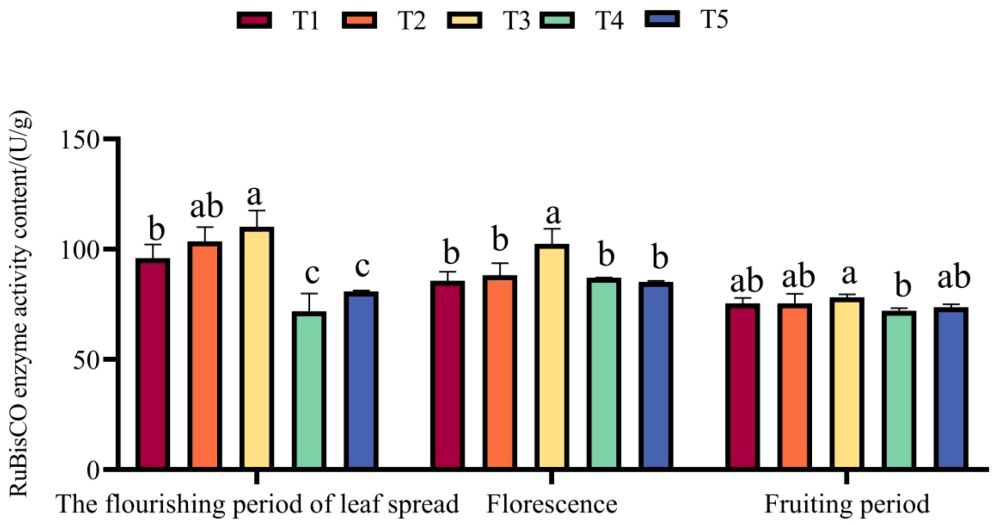



FIGURE 4
Effect of different irrigation amount on RuBisCO activity in leaves of *A. chinensis* during different sampling periods. The lowercase letters denote significant differences at p<0.05.

pyruvate to acetyl-CoA, thereby providing key precursor substances for the synthesis of atractylodesine in *A. chinensis* rhizomes.

## ACC enzyme activity

The T3 treatment exhibited the highest ACC enzyme activity during both the leaf expansion peak and flowering period (Figure 8). At the leaf expansion peak, T3 treatment showed a significant 9.49% increase in ACC enzyme activity, compared with T5 treatment (P<0.05), while T4 treatment also outperformed T2 (P<0.05). During flowering, T3 treatment demonstrated significant increases of 14.29%,14.42%, and 18.57%, in ACC enzyme activity, over T2, T4, and T5 treatments, respectively (P<0.05). In the fruiting stage, T4 treatment achieved the highest ACC enzyme activity, with significant increases of 8.64% and 18.10% over T3 and T5 treatments, respectively (P<0.05). These results indicate that moderate water deficit enhances ACC enzyme activity, thereby effectively promoting the synthesis and accumulation of atractylodesine.

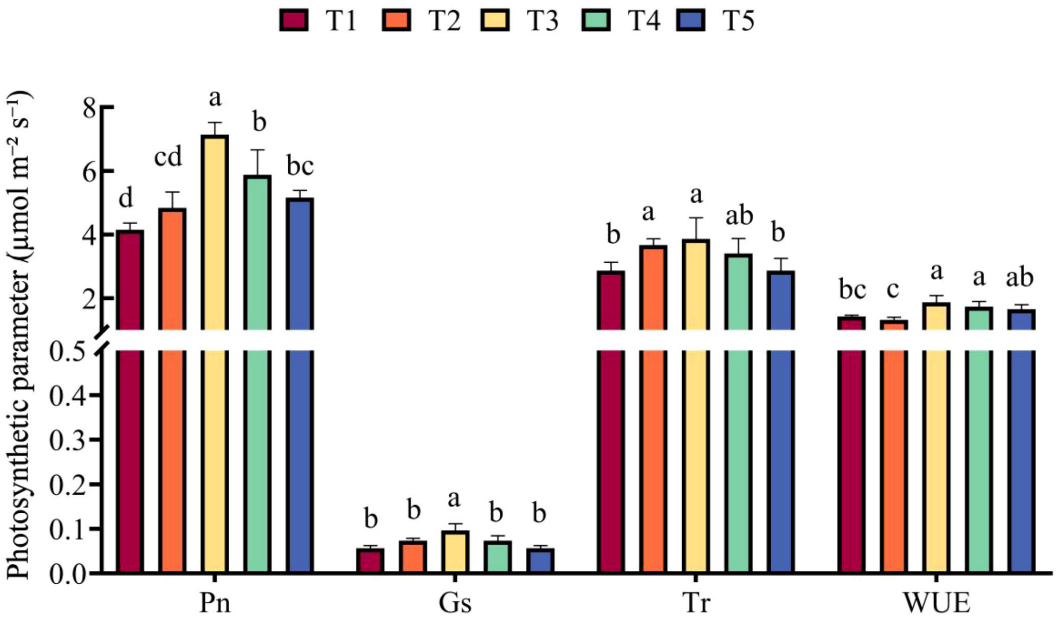



FIGURE 5
Effect of different drip irrigation amounts on the photosynthetic parameters of leaves of *A. chinensis* during the florescence. The lowercase letters denote significant differences at p<0.05.

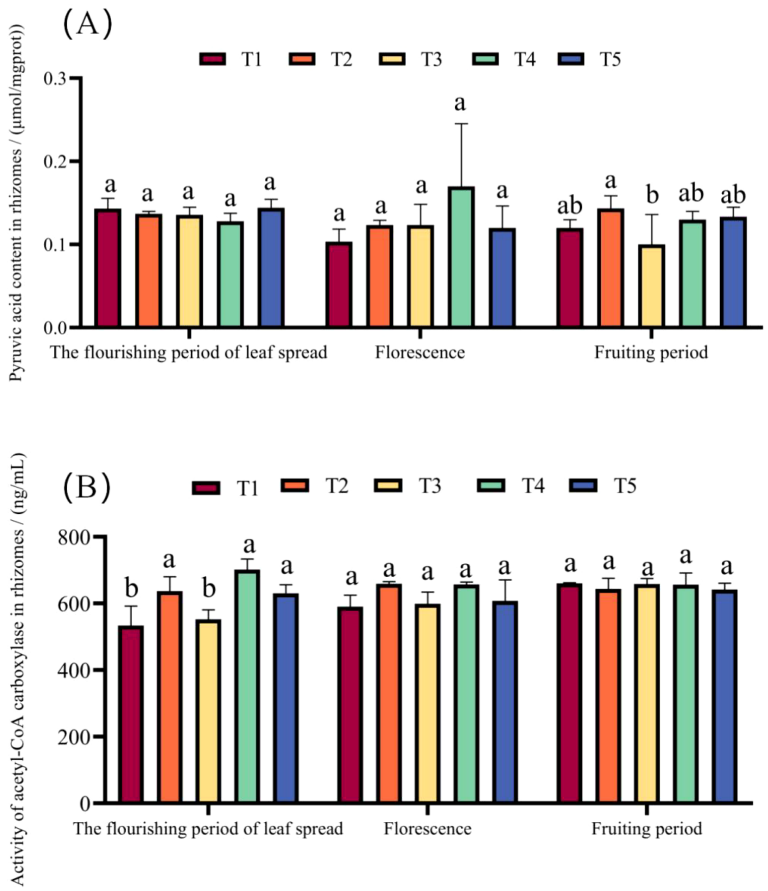



FIGURE 6
Effects of different drip irrigation on the content of pyruvic acid and Acetyl CoA Content in rhizomes of *A chinensis* **(A)** pyruvic acid; **(B)** Acetyl CoA Content. The lowercase letters denote significant differences at p<0.05.

## Effects of different irrigation levels on yield and content of atractylodin content in *A. chinensis*

The yield of *A. chinensis* showed a downward trend with decreasing irrigation volume, with the highest yield in T1 treatment and the lowest in T5 treatment. There was no significant difference between T2 and T3 treatments, while the differences among other treatments were significant (P<0.05). Atractylodesine content peaked in T4 treatment, reaching the levels specified in the "China Pharmacopoeia" except for T1 treatment. Notably, the atractylodesine content in T3, T4, and T5 treatments was significantly higher than those in T1 and T2 treatments (P<0.05; Table 5).

## Correlation among between yield, quality, and physiological mechanisms

Correlation analysis showed that Fv/Fo and Fv/Fm ratios and net photosynthetic rate were positively correlated with plant dry weight. The activity of key enzymes involved in secondary metabolism and the content of key substances such as PA and DLAT were negatively correlated with *A. chinensi* yield. Atractylodin content was negatively correlated with leaf anatomical structure, fluorescence parameters, and net photosynthetic rate, with Fv/Fm ratio and net Pn rate showing significant correlations (P<0.05). The contents of PA and Acetyl-CoA, which are related to secondary metabolism in *A. chinensis*, were positively correlated with atractylodin. Additionally, the activity of enzymes involved in atractylodin synthesis, such as DLAT and ACC, was positively correlated with atractylodin synthesis (*p<=0.05; Figure 9).

## CRITIC method to evaluate the yield and quality of *A. chinensis* under different irrigation treatments

To determine the optimal irrigation volume for cultivating *A. chinensis* in the Horqin Sandy Land, we employed the CRITIC weighting method to conduct an objective, comprehensive evaluation of multiple indicators related to yield and quality under different irrigation levels. Compared with traditional subjective weighting methods or objective methods that consider only internal indicator variability, the CRITIC method is a more

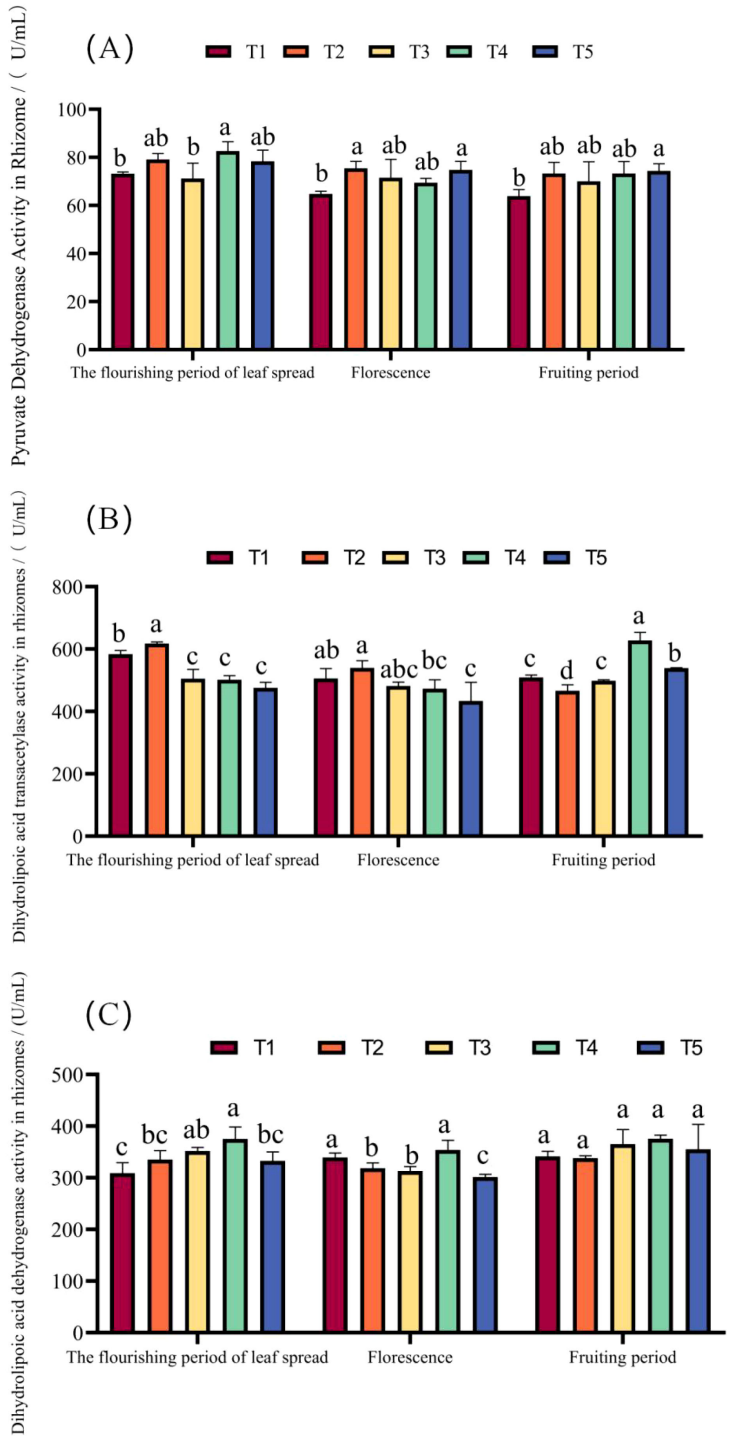



FIGURE 7
Effect of different drip irrigation rates on pyruvate dehydrogenase system in rhizomes; **(A)** PDH; **(B)** DLAT; **(C)** DLD. The lowercase letters denote significant differences at $p<0.05$.

comprehensive objective weighting approach (Diakoulaki et al., 1995). By calculating total information content based on indicator variability and conflict, the method assigns weights to avoid errors caused by high inter-indicator correlations, thereby enhancing the reliability of the results. First, homogenization processing was applied to all indicators to ensure their relative importance in the comprehensive evaluation, with the homogenization results shown in the Table 6.

The weight calculation results are presented in Table 7, showing differences in variability, conflict, and weights among the indicators. The variability of the indicators measured the fluctuation in relative values across different treatments. The variability of Tr, PDH

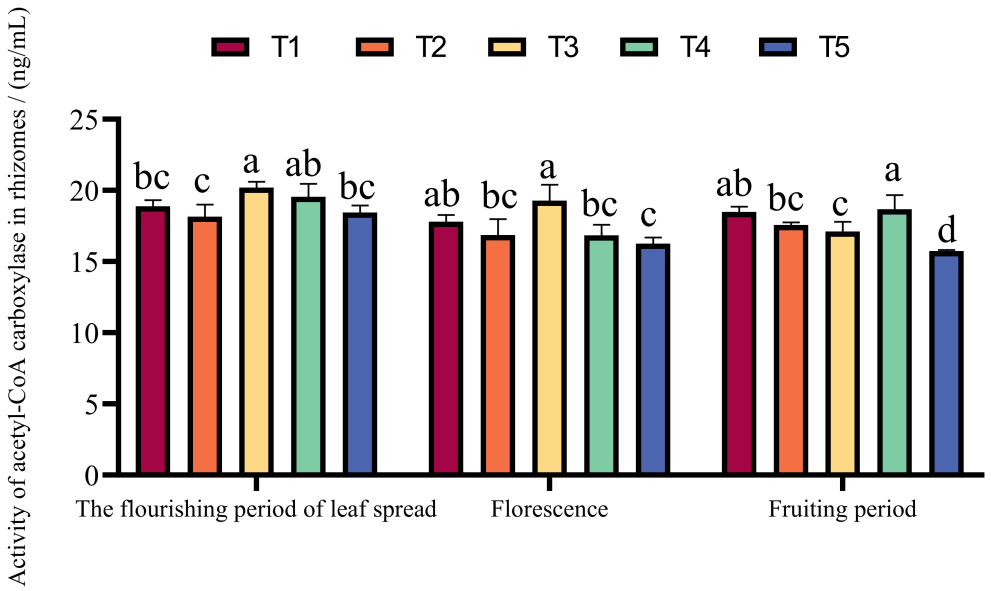



FIGURE 8
Effects of different drip irrigation on ACC enzyme activity in rhizomes of *A. chinensis*. Lowercase letters indicate a significance level of p<0.05 for the same sampling period under different drip irrigation amounts.

activity, and acetyl-CoA content was higher than that of other indicators, suggesting greater susceptibility to water regulation. Conflict indicators measure the correlations and mutual constraints between one indicator and other indicators. The results showed significant conflict among leaf anatomical structure, PDH activity, and atractylodin content. This suggests that during later production processes, the relationship between water regulation and these factors should be carefully evaluated to minimize indicator conflicts. The weights were determined based on the information content of each indicator, reflecting their relative importance in the entire evaluation system. Leaf anatomical structure, PDH activity, and atractylodin content had higher weights, indicating that they are key indicators in the cultivation of *A. chinensis*. Therefore, they require more precise and effective management during production. In terms of overall scores, the comprehensive scores for T5 and T1 were 0.34 and 0.48, respectively, suggesting that excessive irrigation and drought are detrimental to *A. chinensis* production. In contrast, the score for T4 reached 0.64, which was relatively high among all treatments, indicating that moderate water deficiency might be more beneficial to the formation of *A. chinensis* quality.

TABLE 5 Effect of different irrigation amount on yield and quality of medicinal materials.

| Treatment | Yield/ (kg hm$^{-2}$) | Atractylodin content/ (mg/g) |
|---|---|---|
| T1 | 8,226.95 ± 123.25a | 0.0027 ± 0.0001c |
| T2 | 7,761.16 ± 122.53b | 0.0032 ± 0.0001b |
| T3 | 7,695.24 ± 101.76b | 0.0043 ± 0.0003a |
| T4 | 5,557.91 ± 110.25c | 0.0047 ± 0.0001a |
| T5 | 5,172.29 ± 109.86d | 0.0043 ± 0.0001a |

The lowercase letters denote significant differences at p<0.05.

## Discussion

As vital organs for environmental stress perception, plant leaves demonstrate anatomical structures that directly reflect adaptive strategies (Liu et al., 2020). Beyond serving as primary sites for photosynthesis, leaves play crucial regulatory roles in plant growth, development, and physiological/chemical reactions (Deans et al., 2020). The well-developed guard tissue not only shields plants from intense light radiation but also facilitates photosynthesis by using diffused light, thereby enhancing water retention and internal structure to improve survival and growth under stress conditions (He et al., 2021). As the main photosynthetic tissue, the thickness ratio of guard tissue to spongy tissue in leaf mesophyll directly influences chloroplast distribution and light energy utilization efficiency. A higher guard-to-sponge ratio indicates stronger drought adaptation (Li et al., 2022). This study revealed that moderate drought (T4 treatment) significantly altered the leaf structure of *A. chinensis*, characterized by increased leaf thickness, guard tissue thickness, and Pt/St ratio, while upper and lower epidermal thickness decreased with reduced drip irrigation volume. The compact leaf structure suggests enhanced guard tissue development and improved drought resistance in *A. chinensis*, a response strategy consistent with drought adaptation in species such as *Nicotiana tabacum* L. and *Machilus thunbergii* Sieb. et Zucc (Wang et al., 2014; Khan et al., 2023; Shi et al., 2025). However, *Vigna unguiculata* (L.) Walp. is known to respond differently to drought stress compared to *A. chinensis*, with drought stress reducing leaf thickness, Pt/St value, and leaf

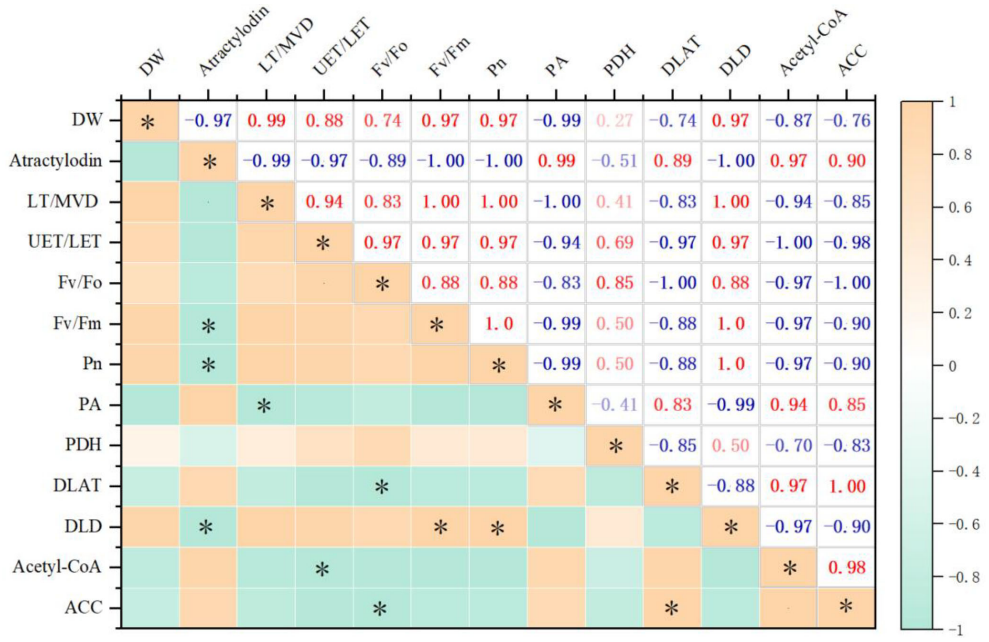



FIGURE 9
Correlation analysis among yield, quality, and physiological mechanism. DW, yield; LT/MVD, blade thickness to main vein diameter ratio; UET/LET, upper epidermis thickness to lower epidermis thickness ratio; Pn, net photosynthetic rate; PA, pyruvate content; PDH, pyruvate dehydrogenase; DLAT, diheme acetyltransferase; DLD, diheme dehydrogenase; ACC, acetyl-CoA carboxyl synthase.

thickness (Merwad et al., 2018). This demonstrates that species differences modify plants' responses to water stress. Furthermore, the main vein of plants plays an important role in water transport and structural protection (Bartlett et al., 2012). This study found that the main vein diameter of *A. chinensis* leaves under T4 treatment was significantly higher than that under other treatments, indicating that the plant increased the main vein diameter to adapt to water deficiency and reduce water transport resistance. In conclusion, the leaf anatomical structure and water transport system of *A. chinensis* can be coordinated to optimize the leaf structure and water transport, thus enhancing the ability of adaptation to adversity.

TABLE 6 Homogenization results.

| Treatment | T1 | T2 | T3 | T4 | T5 |
|---|---|---|---|---|---|
| LT/MVD | 1.00 | 0.67 | 0.56 | 0 | 0.11 |
| UET/LET | 0.10 | 0.30 | 0 | 0.70 | 1.00 |
| Fv/Fo | 1.00 | 0.50 | 0.75 | 0.25 | 0 |
| Fv/Fm | 1.00 | 0.75 | 0.50 | 0.25 | 0 |
| Gs | 0.21 | 0.47 | 1.00 | 0.51 | 0 |
| Tr | 0 | 0.81 | 1.00 | 0.54 | 0 |
| PDH | 0 | 0.10 | 0.66 | 1.00 | 0.89 |
| DLAT | 0.26 | 0 | 0.20 | 1.00 | 0.45 |
| Acetyl-CoA | 1.00 | 0.12 | 0.90 | 0.81 | 0 |
| ACC | 0.96 | 0.64 | 0.48 | 1.00 | 0 |
| Atractylodin | 0 | 0.67 | 0.93 | 1.00 | 0.91 |
| Yield | 1 | 0.90 | 0.68 | 0.37 | 0 |

The experimental results demonstrate that moderate drought (T3 and T4 treatments) significantly increases photosynthetic pigment content in plant leaves, enhances potential photochemical efficiency (Fv/Fo) and maximum photochemical efficiency (Fv/Fm), effectively protects thylakoid membrane structures, activates photosystem II's electron transport capacity, and simultaneously boosts RuBisCO enzyme activity. Elevated RuBisCO activity effectively increases photosynthetic rate (Pn), stomatal conductance, and transpiration rate in *A. chinensis* leaves, thereby enhancing $CO_2$ fixation capacity, improving photosynthetic efficiency, and increasing accumulation of photosynthetic products. This aligns with the conclusion from Gardenia jasminoides under mild drought conditions, where both Fv/Fm and Fv/Fo in leaves increased, promoting intracellular electron transfer efficiency and elevating photosynthetic rate (Cai et al., 2023), demonstrating plants' physiological regulatory mechanisms for coping with stress. However, when water content exceeds the plant's self-regulation range, photosynthesis is significantly inhibited. Under extreme drought (T5) treatment, photosynthetic capacity was significantly suppressed, indicating that excessive water stress degrades photosynthetic pigments and effectively inhibits stomatal conductance, thereby affecting photosynthetic efficiency. When *Acorus calamus* L. and *Glycyrrhiza uralensis* Fisch. seedlings were subjected to drought stress, the photosynthetic pigment content in leaves decreased with reduced water content, stomatal conductance declined, the core function of Photosystem II (PSII) was impaired, the electron transport chain was disrupted, and Rubisco activity was directly

TABLE 7 CRITIC weight calculation results and scores.

| Item | Indicator variability | Conflict of indicators | Amount of information | Weight | Overall score |
|---|---|---|---|---|---|
| LT/MVD | 0.411 | 11.037 | 4.539 | 8.50% | / |
| UET/LET | 0.421 | 14.768 | 6.213 | 11.63% | / |
| Fv/Fo | 0.395 | 9.590 | 3.791 | 7.10% | / |
| Fv/Fm | 0.395 | 10.200 | 4.032 | 7.55% | / |
| Gs | 0.458 | 9.458 | 4.336 | 8.12% | / |
| Tr | 0.413 | 9.109 | 3.758 | 7.04% | / |
| PDH | 0.457 | 12.429 | 5.674 | 10.63% | / |
| DLAT | 0.381 | 11.454 | 4.362 | 8.17% | / |
| Acetyl-CoA | 0.470 | 8.714 | 4.098 | 7.67% | / |
| Atractylodin | 0.413 | 12.128 | 5.003 | 9.37% | / |
| ACC | 0.408 | 8.915 | 3.638 | 6.81% | / |
| Yield | 0.409 | 9.690 | 3.959 | 7.41% | |
| T1 | / | / | / | / | 0.48 |
| T2 | / | / | / | / | 0.48 |
| T3 | / | / | / | / | 0.62 |
| T4 | / | / | / | / | 0.64 |
| T5 | / | / | / | / | 0.34 |

inhibited, ultimately leading to reduced photosynthetic capacity. The results were consistent across all treatments (Cao and Wang, 2007; Hosseini et al., 2018). The study further demonstrated that excessive water (T1) induces root hypoxia in plants, disrupting physiological processes. This leads to inhibited chlorophyll synthesis and reduced RuBisCO activity, thereby impairing photosynthesis. These findings align with previous reports showing that short-term waterlogging stress in sorghum and cucumber reduces photosynthetic pigments, damages photosystems, and consequently diminishes photosynthetic capacity (Zhang et al., 2023; Olorunwa et al., 2022; Wang et al., 2022). Photosynthesis is a vital pathway for plants to obtain energy and synthesize organic compounds, directly influencing the synthesis and accumulation of their metabolic products (Saadat et al., 2023).

Through the Calvin cycle, plants convert the carbon fixed by photosynthesis into starch, 6-phosphofructose, and other metabolites, which are then transformed into pyruvate via glycolysis and phosphoglucoisomerase, participating in plant material synthesis and metabolic processes. The present study demonstrated that moderate water regulation (T3 and T4 treatments) effectively activates key enzymes and precursor accumulation in *A. chinensis* rhizomes. During the leaf expansion peak to fruiting stage, T3 and T4 treatments significantly increased pyruvate and acetyl-CoA levels, while markedly enhancing the activity of the pyruvate dehydrogenase system (including *PDH*, *DLAT*, and *DLD*). Concurrently, *ACC* activity remained elevated throughout the flowering-to-fruiting period. The combined effects of enhanced enzyme activity and precursor accumulation collectively promoted increased atractylodin content. These findings corroborate the "stress response" mechanism proposed by Huang et al. for the formation of quality in authentic medicinal herbs (Huang and Guo, 2007). However, when water content was reduced to the T5 treatment level, both pyruvate levels and related enzyme activities declined, indicating that excessive drought adversely affects primary metabolism and key enzyme activities involved in the synthesis of bioactive compounds in medicinal plants. This finding aligns with those of previous studies on drought stress in medicinal plants such as *Astragalus membranaceus* (Fisch.) Bunge and *Salvia miltiorrhiza* Bunge (Jia et al., 2015; Zhang et al., 2024). Excessive water content (T1 treatment) significantly inhibited the synthesis of key precursors and enzyme activity for *A. chinensis* alkaloid production, resulting in substantially lower alkaloid content, compared to other treatments ($P<0.05$). This indicates that oxygen deficiency under waterlogging stress suppresses both the electron transport chain and the tricarboxylic acid cycle (TCA) in aerobic respiration (Bailey-Serres and Voesenek, 2008). Additionally, the study revealed that the flowering-to-fruiting period of *A. chinensis* is a critical phase influenced by water availability. This finding aligns with those of Yang et al. (2024), who reported that moderate drought stress during the late reproductive growth stage can activate the biosynthetic pathway of secondary metabolites in this plant. While this study provides valuable insights into the effects of drip irrigation on A. chinensis, several limitations should be acknowledged. First, the experiment was conducted over a single

growing season. The interannual variability of climate factors may influence plant growth and secondary metabolism, thus multi-year trials are needed to confirm the stability of our findings. Second, the study was confined to a single location within the Horqin Sandy Land, which may limit the extrapolation of our results to other regions with different soil or climatic conditions. *A. chinensis* for the interpretation of our results lies in the scale of replication. The current study was conducted with 3 plots per treatment, which, while sufficient to identify statistically significant responses in numerous key parameters, results in a limited number of error degrees of freedom. As per contemporary statistical guidance (e.g., Piepho et al., 2003), aiming for a minimum of 12 error degrees of freedom would further enhance the reliability of the inferences and increase the power to detect more subtle treatment effects. Therefore, we propose that future work in this area prioritize larger plot numbers to build upon the foundational relationships observed here. Furthermore, the study primarily elucidated physiological mechanisms, while the underlying molecular regulatory networks, such as gene expression related to the key enzymes in the atractylodin biosynthesis pathway, remain to be explored.

## Conclusions

Moderate water deficit effectively modifies the leaf structure, physiology, and secondary metabolism of *A. chinensis*. By optimizing leaf anatomy, this stress condition enhances drought resistance and creates favorable conditions for photosynthesis. It significantly improves leaf photosynthetic performance and carbon assimilation efficiency, providing precursors for secondary metabolism. Additionally, it activates key enzymes in atractylodesine synthesis, thereby improving herb quality. This study elucidates the integrated mechanism by which moderate water deficit promotes adaptive growth and bioactive compound accumulation in *A. chinensis*. The findings not only provide scientific evidence for addressing future climate change and mitigating drought impacts on medicinal plant production, but also offer theoretical support for standardized cultivation practices of *A. chinensis* in the Horqin Sandy Land.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

## Author contributions

GL: Conceptualization, Data curation, Formal Analysis, Investigation, Writing – original draft. YW: Data curation, Formal Analysis, Investigation, Writing – original draft. ZL: Formal Analysis, Methodology, Project administration, Writing – review & editing. DZ: Conceptualization, Investigation, Methodology, Supervision, Validation, Writing – review & editing. YG: Conceptualization, Methodology, Validation, Visualization, Writing – review & editing. ZW: Funding acquisition, Supervision, Writing – review & editing. CG: Resources, Software, Visualization, Writing – review & editing. DS: Project administration, Visualization, Writing – review & editing. JJ: Project administration, Resources, Supervision, Visualization, Writing – review & editing.

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## Conflict of interest

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## Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fagro.2025.1711027/full#supplementary-material

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