

Original Research

How Soil Moisture Affects Photosynthetic Characteristics of *Aralia elata* Leaves

Jie Zhao, Rui Yang, Xiaohua Liu, Guangcan Zhang, Shuyong Zhang*

Shandong Province Key Laboratory of Soil Erosion and Ecological Restoration,
Key Laboratory of Agricultural Ecology and Environment, Forestry College, Shandong Agricultural University,
Taian, 271018, China

Received: 20 July 2017

Accepted: 18 September 2017

Abstract

Using a CIRAS-2 portable photosynthesis system, the photosynthesis, transpiration, and light responses of *Aralia elata* were studied under different soil moisture values with the aim of understanding the adaptability of this species to different light and soil water conditions. The results showed that the net photosynthetic rate (P_n), transpiration rate (T_r), and water use efficiency (WUE) of *A. elata* varied in response to different levels of photon flux density (PFD). When PFD was between 800 and 1,800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, P_n changed little in response to the increasing light intensity, whereas T_r decreased gradually and WUE increased significantly. Light saturation point (LSP) and light compensation point (LCP) were approximately 800 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The soil water content had little effect on LSP and LCP , but significantly affected photosynthetic quantum efficiency (Φ) and dark respiratory rate (R_d). By defining the P_n and WUE as the indexes of plant productivity and soil water efficiency, respectively, the soil moisture availability and productivity of *A. elata* were graded and evaluated, and six types of soil water grading were established. Thus, at RWC values between 44.5% and 79.2% in which both P_n and WUE were maintained at a high level, the results can provide theoretical support for highly productive and efficient water management in *A. elata*.

Keywords: net photosynthetic rate, WUE , availability of soil moisture, evaluation of photosynthetic productivity, *Aralia elata*

Introduction

Light and water are important ecological factors in plant physiology and growth [1-4]. In recent years, with the changes in the global climate and the aggravation of environmental problems such as soil erosion and desertification, environmental stress factors have

clearly limited plant growth and development [5-7]. In a natural environment, soil moisture in different regions is obviously influenced by rainfall, runoff, leakage, and evaporation, which in turn affect a series of physiological changes in plants such as water status, photosynthesis, and material transport [8-11]. Therefore, we explored the photosynthetic, transpiration, and light responses of plants under different soil water conditions [12-14]. These results contributed to our understanding of the adaptive characteristics of plant physiological processes to light and water, and provide physiological and ecological

*e-mail: zhsy@sdaa.edu.cn

evidence for the scientific introduction, cultivation, and management of this species.

Photosynthesis is not only related to structure and physiological function of the genetic characteristics of the species themselves [15], but it is also affected by ecological factors such as light, temperature, and soil moisture [16-18]. Under drought stress, plants can regulate and adjust the physiological pathways of leaf movement through stomatal regulation so as to achieve a balance between carbon assimilation and water loss [19]. To improve the *WUE* is the main adaptation strategy for plant survival and reproduction in arid areas. According to the limiting factors of ecology, it can be seen that there are different levels of threshold values of the plant physiological processes with reference to soil moisture, and what extremely high or low water levels can affect [20-21]. In recent years the changes of plant anatomical structure, physiological and biochemical factors under different water conditions, and its adaptation characteristics and mechanism to water stress were investigated and discussed [22-23]. However, the study of physiological processes under different soil water conditions was limited to PEG habitat and single potting simulation under 3-4 water stresses. Also, the studies on the quantitative relationships between photosynthesis, transpiration, moisture, and light are limited.

A. elata, which belongs to the *Araliaceae* family, is a perennial deciduous small arbor species with a high medicinal and edible value [24] that is also used in landscaping to conserve water and soil [25]. With decreases in wild resources and increases in market demand of this species, people are paying more attention to resource protection, introduction, and cultivation. Thus far, most of the studies performed on *A. elata* have been confined to its pharmacological action, edible value, artificial breeding, and cultivation techniques [26-27]. The physiological and ecological processes, photosynthetic productivity, and suitable water conditions for the growth of *A. elata* under different soil water conditions were still not clear. Therefore, in this paper, the light responses of photosynthetic physiological parameters of 2-year-old *A. elata* were studied and the quantitative relationships between photosynthetic physiological parameters and soil water content as well as light intensity were analyzed to investigate the physiological adaptability of *A. elata* to environmental changes. Meanwhile, P_n and *WUE* as the indexes of plant productivity and soil water efficiency at light saturation point, respectively, were defined. Based on photosynthetic and physiological parameters, soil moisture availability and productivity of *A. elata* were graded and evaluated. Moreover, the high productivity and high efficiency water range of plants were determined, which could provide the theoretical basis and technical guidance for the introduction, cultivation, and management of *A. elata*.

Experimental Procedures

Experimental Site Description

The experimental site is located at the forestry experimental station, Shandong Agricultural University, Taian City, at north latitude 35°38'~36°33' and east longitude 116°02'~117°59'. This area has a semi-humid, warm temperate, continental monsoon climate with four hot rainy seasons. The average annual precipitation is 741.8 mm, most of which falls in July, August, and September. The annual average temperature is 12.9°C, with the highest temperature on record in July (26.4°C on average) and the lowest temperature on record in January (-2.6°C on average). The extreme highest temperature on record was 41°C and the lowest temperature was -27.5°C. The annual accumulated temperature over 10°C is 2,350°C~4,777°C, and the average frost-free period is 195 days. The main soil types are cinnamon soil and brown soil.

Experimental Material and Humidity Control

Nine two-year-old *A. elata* seedlings were used as the experimental samples. These plants exhibited strong growth vigor and were not infected with disease or insect pests. In late March 2016, nine pots (0.6 m in diameter and 1.2 m deep, with drainage holes at the bottom; the shape of the pot is cylindrical, and the volume per pot is 0.34 m³) containing brown soil were prepared to conduct the pot experiment, the average height of the plants was 58.6±1.3 cm and the average diameter at chest height was 1.62±0.32 cm, and the management was underway by July. When the experiment was finished, the soil around the plant root was dug up by ring sampling, and each pot was measured three times. The average field capacity and soil density of the pots were 26.1±1.3% and 1.34±0.12 g cm⁻³, respectively.

Different degrees of soil water stress were imposed by changing the water content in the field environment (the pots were buried in the soil for a long time to ensure that the pot and field soil were at the same temperature). First, two days before the experimental observations we provided sufficient water until moisture saturation was reached and we determined gravimetric water content (*MWC*; %) using an oven-drying method with an *LNW-50A* neutron probe (*CAS*, Nanjing, Jiangsu, CHN). For comparability with other tree species over the literature, relative soil water content (*RWC*) was calculated as the ratio of *MWC* and field capacity (*FC*; %) by ring sampling [28]. Two days later we obtained the initial water content (*MWC* of 26.0%, *RWC* of 99.6%) and for the first time the physiological parameters of photosynthesis and transpiration were measured. Then, based on natural water consumption, we obtained the soil water content every two days. When the *MWC* values were 22.7%,

19.6%, 17.2%, 14.6%, 12.8%, 9.8%, and 7.3% (*RWC* values were 87.0%, 75.1%, 65.9%, 55.9%, 49.0%, 37.5%, and 28.0%, respectively), we measured photosynthesis, transpiration, and light.

Photosynthetic Response to Light

Three strong seedlings of pot-cultured *A. elata* were selected from the nine seedlings, and three strong mature leaves were selected from the top of each seedling. We repeatedly measured each sample leaf three times and calculated the mean value for further analysis. Photosynthesis, transpiration, and light responses of *A. elata* under different soil conditions were measured using a portable photosynthesis system (CIRAS-2, PP System, UK). To reduce the effect of light fluctuations, all measurements were collected between 09:00 and 11:00 in all of the soil moisture treatments. During this time environmental factors, for example external light intensity, air temperature, atmospheric moisture and atmospheric CO_2 concentration, were similar.

During each measurement, CO_2 concentration, air temperature, and relative humidity were maintained at 375 ± 6.0 ppm, $25\text{--}26^\circ\text{C}$, and $65 \pm 3.0\%$, respectively, by using a CIRAS-2 portable photosynthesis system. For each observation, *PPFD* was controlled at 1,800, 1,600, 1,400, 1,200, 1,000, 800, 600, 400, 250, 150, 100, 50, and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The measuring time was 120 s under each *PPFD*. The photosynthesis system automatically recorded the physiological indexes, such as the net photosynthetic rate (P_n), *PPFD*, transpiration rate (T_r), stomatal conductance (G_s), and intercellular CO_2 concentration (C_i), etc. Leaf *WUE* was calculated as follows [29]:

$$WUE = P_n / T_r$$

Data Processing and Regression Analysis

The experimental data were analyzed using SPSS 12.0 software and statistical techniques such as variance analysis and logistic analysis were carried out. A nonrectangular hyperbolic model was used to fit the photosynthetic light response curves of *A. elata* under the different water contents and to calculate the specific parameters.

The model expression is [30-31].

$$P_n = \left[\left(\Phi PFD + P_{n\max} - \sqrt{(\Phi \cdot PFD + P_{n\max})^2 - 4 \cdot \Phi \cdot PFD \cdot k \cdot P_{n\max}} \right) / 2k - R_d \right]$$

...where P_n is net photosynthetic rate, *PPFD* is photon flux density, $P_{n\max}$ is maximum net photosynthetic rate, Φ is photosynthetic quantum efficiency, R_d is dark respiration

rate, and k is inflection point of the photosynthetic light-response curve.

The light compensation point (*LCP*) of photosynthesis was calculated using the following formula [32]:

$$LCP = \frac{R_d \cdot P_{n\max} - k \cdot R_d^2}{\Phi(P_{n\max} - R_d)}$$

The light saturation point (*LSP*) of photosynthesis can be directly obtained from the light response curve [33].

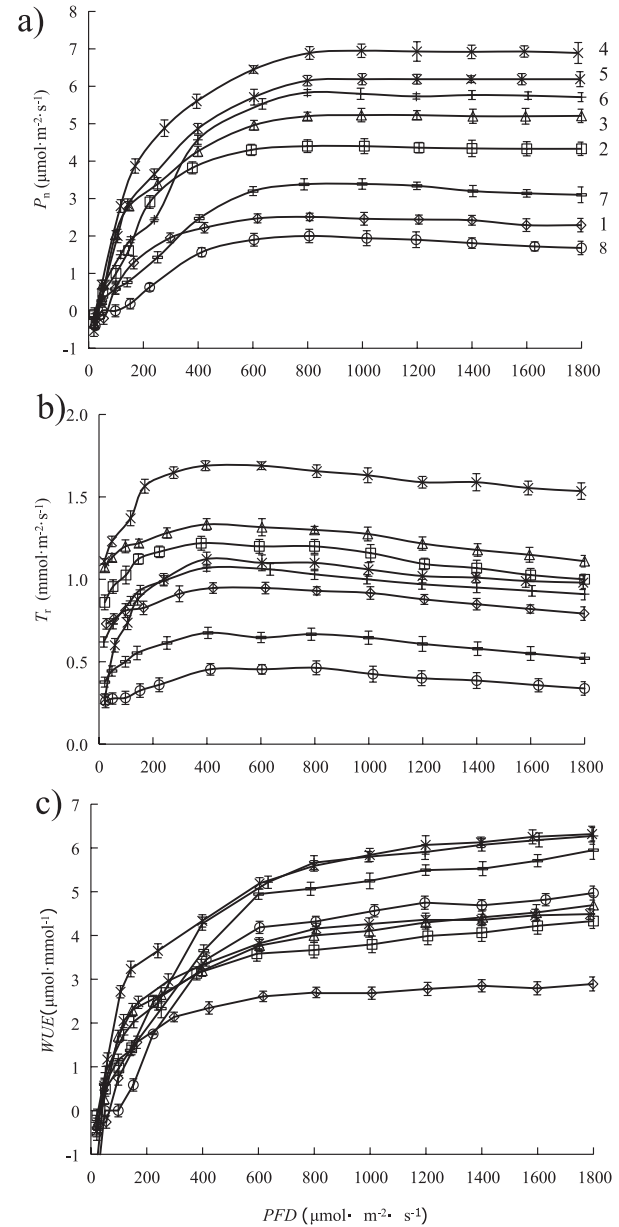


Fig. 1. Light response processes of net photosynthetic rate (P_n), transpiration rate (T_r), and water use efficiency (*WUE*) of *A. elata* under different relative soil water contents with: 1) 99.6%, 2) 87.0%, 3) 75.1%, 4) 65.9%, 5) 55.9%, 6) 49.0%, 7) 37.5%, and 8) 28.0%. Points are the mean of at least 27 replicate P_n , T_r , and *WUE* responses for each light. Vertical bars indicate ± 1 SE of the means. Lines are fitted to the response of P_n , T_r , and *WUE* to light.

Results

Photosynthetic Response of *A. elata* Leaves to Light

The photosynthetic light response of *A. elata* was similar under different soil water contents (Fig. 1). Below a PFD of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, the P_n exhibited a significant increasing trend with an increase in PFD . However, when the PFD was higher than this value, P_n stabilized at a certain level. This showed that the light intensity threshold of *A. elata* photosynthesis was the LSP , and

the corresponding P_n value was the maximum net photosynthetic rate ($P_{n\text{max}}$) of *A. elata*. This also showed that the adaptability of *A. elata* photosynthesis to light intensity was strong, and under the same water content photosynthesis was maintained at a high level within a PFD range of 800 to $1,800 \mu\text{mol m}^{-2} \text{s}^{-1}$. The LSP was little affected by the changes in soil moisture, and stabilized at a PFD value of approximately $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (or approximately $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ when the RWC was 99.6% or 28.0%).

The variance analysis showed that $P_{n\text{max}}$ and Φ of *A. elata* differed significantly under different soil

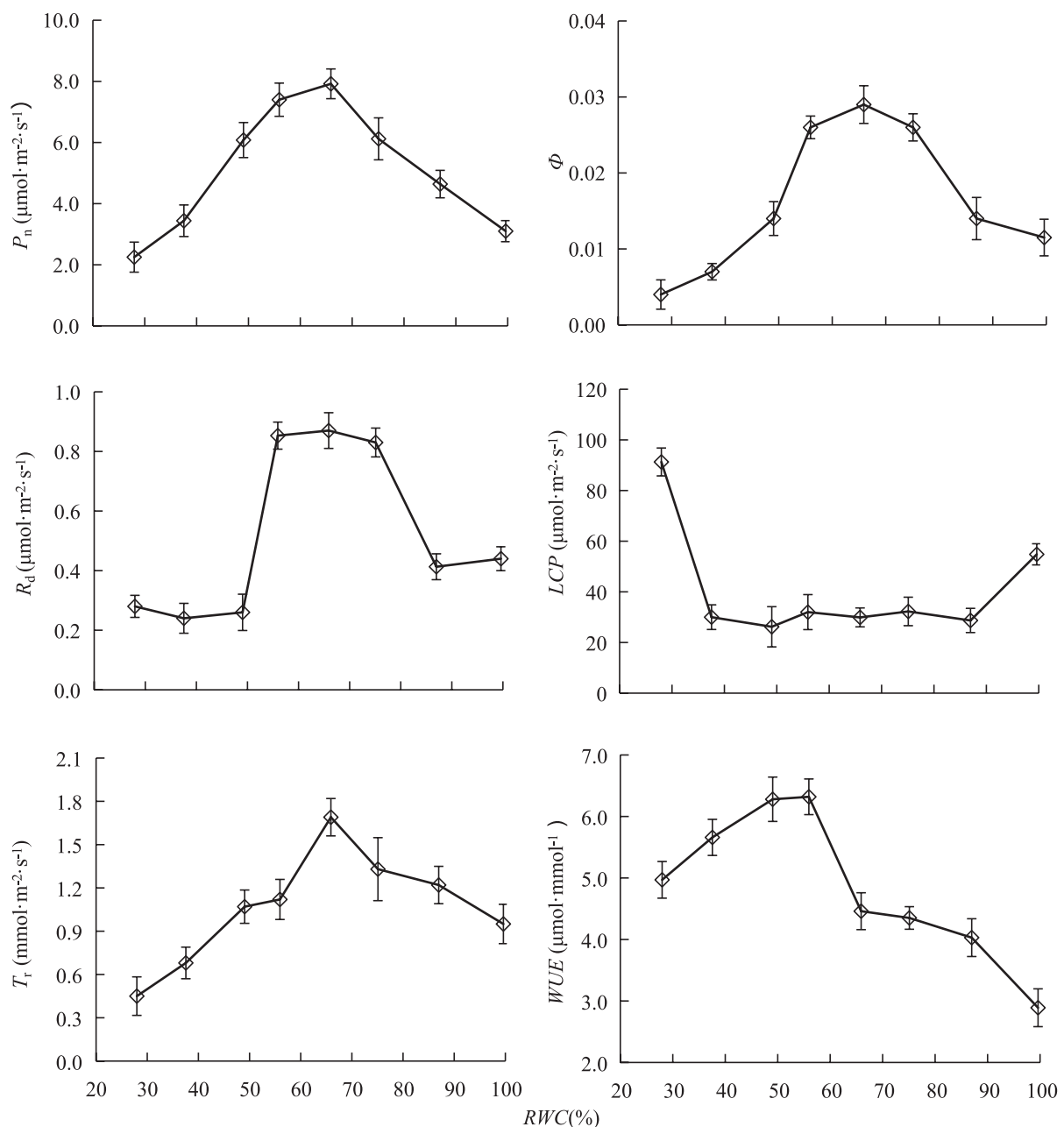


Fig. 2. The net photosynthesis rate (P_n), apparent photosynthetic quantum yield (Φ), dark respiratory rate (R_d), light compensation point (LCP), transpiration rate (T_r), and water use efficiency (WUE) of *A. elata* under different soil moisture conditions. Each point represents the mean of at least three plants with 27 replicate P_n , Φ , R_d , LCP, T_r and WUE for each RWC. Regression lines were fit using a polynomial expression. Error bars represent ± 1 SE of the mean.

moisture contents ($P < 0.01$); the maximum photosynthetic rate ranged $2.2\text{--}7.91 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the Φ ranged $0.004\text{--}0.029 \mu\text{mol m}^{-2} \text{s}^{-1}$. The $P_{n\text{max}}$ and Φ of *A. elata* decreased significantly with a change (increase or decrease) in soil water content (Fig. 2). As the soil water content increased, $P_{n\text{max}}$ and Φ increased rapidly. When RWC reached a certain threshold (RWC was approximately 65.9%), $P_{n\text{max}}$ and Φ reached their highest levels of $7.92 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $0.029 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. After reaching the maximum, these variables gradually decreased with an increase in the RWC .

The dark respiration rate (R_d) of *A. elata* ranged $0.24\text{--}0.86 \mu\text{mol m}^{-2} \text{s}^{-1}$ and exhibited clear threshold value responses to RWC (Fig. 2). When RWC was between 55.9% and 75.1%, R_d was maintained at a high level of approximately $0.85 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, when $RWC < 55.9\%$ or $> 75.1\%$, R_d decreased significantly to respective values of approximately $0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $0.26 \mu\text{mol m}^{-2} \text{s}^{-1}$. The LCP of *A. elata* ranged from $26.2\text{--}91.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ and was less influenced by the changes in soil moisture. When RWC was between 37.5% and 87.0%, LCP was maintained at approximately $30 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, when RWC was 99.6% or 28.0%, LCP increased significantly to respective values of $54.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $91.2 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Transpirational Response of *A. elata* to Light

Under different soil water contents, response of transpiration in *A. elata* similar to changes in PFD (Figs 1 and 2). When PFD was less than $400 \mu\text{mol m}^{-2} \text{s}^{-1}$, T_r increased rapidly with an increase in PFD ; when RWC was higher than this value, T_r showed a gradual decreasing trend. The maximum transpiration rate ($T_{r\text{max}}$) of *A. elata* was measured at a PFD of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$; above this value, T_r exhibited a decreasing trend. $T_{r\text{max}}$ maximum rate of transpiration measured under the various soil moisture contents was in the range $0.45\text{--}1.69 \mu\text{mol m}^{-2} \text{s}^{-1}$. The variance analysis showed that $T_{r\text{max}}$ differed significantly under the various soil water contents ($P < 0.01$). When $RWC = 65.9\%$, T_r reached a maximum value of $1.69 \text{ mmol m}^{-2} \text{s}^{-1}$, and an increase or decrease in the soil water content led to a decrease in T_r .

Leaf WUE of *A. elata* in Response to Light

Under different soil moisture contents, the leaf WUE of *A. elata* showed a gradual increasing trend with an increase in PFD , and no asymptote was reached (Fig. 1). At a $PFD < 400 \mu\text{mol m}^{-2} \text{s}^{-1}$, the WUE increased considerably with an increase in PFD . However, when the PFD exceeded this value, the WUE increased slowly with an increase in PFD . This showed that *A. elata* leaf WUE can be improved under strong light. However, this response varied significantly under different soil moisture conditions. Under the highest light intensity ($PFD = 1,800 \mu\text{mol m}^{-2} \text{s}^{-1}$), the maximum water use

efficiency (WUE_{max}) was in the range of $2.9\text{--}6.3 \mu\text{mol mol}^{-1}$. WUE_{max} gradually increased with an increase in the soil water content and reached a maximum value ($WUE_{\text{max}} = 6.3 \mu\text{mol mol}^{-1}$) when $RWC = 55.9\%$. At RWC values higher than this value, WUE_{max} decreased obviously. This showed that higher soil moisture will lead to lower WUE in *A. elata*.

Net Photosynthetic Rate and Water Use Efficiency of *A. elata* in Responses to Soil Moisture

We analyzed the photosynthetic response of *A. elata* to soil moisture using the RWC value that corresponded to P_n at $PFD = 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (i.e., light-saturating conditions; Fig. 3). (This PFD value exceeded the LSP , and under various soil moisture conditions, P_n of *A. elata* remained basically unchanged with increasing light intensity.) The fitting results were in agreement with the quadratic equation. Thus, the value of RWC that corresponded to $P_{n\text{max}}$ was 65.9%; the values of RWC that corresponded to $P_n = 0$ were 21.0% and 108%. When the RWC exceeds 100%, it has no actual biological significance and 108% should be replaced by the measured maximum of 99.6%. The integration according to the fitting equation was:

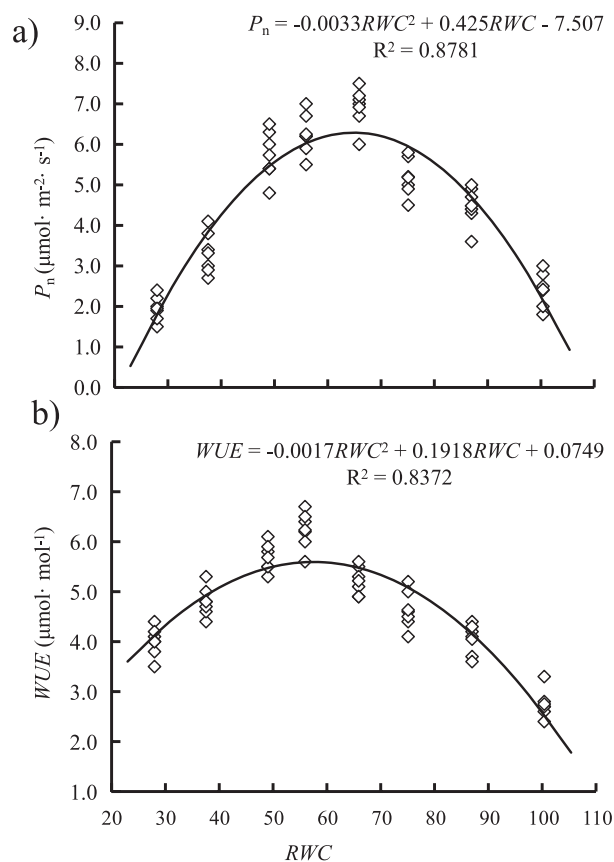


Fig. 3. The responses of net photosynthetic rate (P_n) and water use efficiency (WUE) of *A. elata* to soil moisture under $PFD = 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Regression lines were fit using a polynomial expression. Lines are fitted to the response of P_n and WUE to RWC .

$$\overline{P_n} = \frac{1}{99.6 - 28.0} \int_{28.0}^{99.6} [-0.0033x^2 + 0.425x - 7.507] dx$$

When *RWC* was in the range of approximately 28.0~99.6%, the values of P_n were calculated using the integral fitting equation. The mean P_n value was $4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the corresponding *RWC* values were 44.5% and 85.1%. Therefore, *A. elata* photosynthesis stabilized at a high *RWC* that ranged from 44.5% to 85.1%. The most suitable *RWC* was 64.5%, and the minimum *RWC* that sustained photosynthesis was 21.3%.

The response of *WUE* to soil moisture were also in agreement with the quadratic equation under the saturated light intensity of photosynthesis ($PF_D = 1,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Thus, the value of *RWC* that corresponded to WUE_{max} was 55.9%. The integration according to the fitting equation was:

$$\overline{WUE} = \frac{1}{99.6 - 28.0} \int_{28.0}^{99.6} [-0.017x^2 + 0.1918x + 0.0749] dx$$

When *RWC* was in the range of approximately 28.0~99.6%, the values of *WUE* were obtained from the integral fitting equation. The mean *WUE* value was $4.6 \text{ mol}\cdot\text{mol}^{-1}$, and the corresponding *RWC* values were 34.6% and 79.2%, respectively. Therefore, *A. elata* photosynthesis was stabilized at a high *RWC* in the range 34.6-79.2%.

Grading and Evaluating Soil Water Availability and Productivity

Grading criteria of soil moisture were based on plant water physiology theory and the results of moisture threshold analysis combined with the response rule of photosynthetic process to soil moisture. Based on the physiological significance of determining the critical water points, the classification and evaluation criteria of soil water availability of *A. elata* were studied (Table 1). The water point at $P_n = 0$ was taken as a critical water

point, and a water point lower than this value was considered as non-productive and non-efficient. The water point corresponding to $P_{n\text{max}}$ and WUE_{max} was taken as the high productivity and high efficiency water point, respectively. The mean values of P_n and *WUE* that corresponded to *RWC* values were calculated using the integral fitting equation. Water points above average were considered as the medium productivity and medium efficiency water points, and water points below average were considered as the low productivity and low efficiency water points. In this study, six types of the soil water gradings of *A. elata* were established based on the size of P_n and *WUE* under different soil water contents. The *RWC* of less than 21.3% corresponded to non-productivity and non-efficiency water; the *RWC* of 21.3-34.6% and 85.1-99.6% corresponded to low productivity and low efficiency water; the *RWC* of 34.6-44.5% and 79.2-85.1% corresponded to low productivity and medium efficiency water, and medium productivity and low efficiency water, respectively; the *RWC* of 44.5-55.9% and 64.5-79.2% corresponded to medium productivity and medium efficiency water. The *RWC* of 55.9-64.5% corresponded to high productivity and high efficiency water. In this range (55.9-64.5%), *A. elata* had the highest photosynthetic capacity and efficient physiological characteristics for water consumption. As a result, the soil water should be maintained in the range of 44.5-79.2%, in which P_n and *WUE* can reach their maximum values of 60% and 70%, respectively, so that the *A. elata* can attain higher productivity and efficiency.

Discussion

The factors that affect Φ of plant photosynthesis are internal physiological factors such as the carbon metabolism pathway, respiration, pigment content, etc., and environmental factors such as light, temperature, water, etc. [34-37]. Studies have shown that an unsuitable soil moisture level (too high or too low) can lead to a decrease in plant Φ [38-40], but the quantitative

Table 1. critical water point of photosynthetic efficiency and its threshold grade in leaves of *A. elata*.

Critical index of soil water	Critical point of <i>RWC</i>	Grading of soil water availability	Threshold grade of <i>RWC</i>
WCPP _n	21.3%, 99.6%	NPNEW	<21.3%
WSP _n	64.50%	LPLEW	21.3-34.6%; 85.1-99.6%
WSPWUE	55.90%	LPMEW	34.6-44.5%
MVPP _n	44.5%, 85.1%	MPLWEW	79.2-85.1%
MVPWUE	34.6%, 79.2%	MPMEW	44.5-55.9%; 64.5-79.2%
		HPHEW	55.9-64.5%

1) WCPP_n, water compensation point of net photosynthetic rate; WSP_n, water saturation point of net photosynthetic rate; WSPWUE, water saturation point of water use efficiency; WVPP_n, mean value point of net photosynthetic rate; WVPWUE, mean value point of water use efficiency. 2) NPNEW, no-productivity and no-efficiency water; LPLEW, low-productivity and low-efficiency water; LPMEW, low-productivity and medium-efficiency water; MPLWEW, medium-productivity and low-efficiency water; MPMEW, medium-productivity and medium-efficiency water; HPHEW, high-productivity and high-efficiency water

relationship between soil moisture and Φ has not been reported for different plants. This study shows that the Φ of *A. elata* that corresponded to changes in soil moisture ranged between 0.004 and 0.029; an approximate “ \cap ”-shaped quantitative relationship existed between these variables (Fig. 2). When *RWC* was in the range 55.9–75.1%, the Φ of *A. elata* was higher than 0.26 (approximately 90% of its maximum level); however, when *RWC* was outside of this range, Φ decreased obviously. When *RWC* ranged 49.0–87.0%, Φ was 0.014 (approximately 48% of its maximum level). This indicates that soil moisture has a significant effect on the Φ of *A. elata*.

Φ is an index that reflects a plant's capacity to absorb, transform, and utilize light under low-light conditions [41]. Measurements of plant Φ generally range from 0.03 to 0.05 under suitable conditions. The maximum value of Φ of *A. elata* was approximately 0.029, i.e., less than Φ of plants in general. The results show that the Φ of *A. elata* is low under low-light conditions, i.e., light use efficiency is low.

The *LSP* and the *LCP* are two main indexes that reflect the light requirement characteristics of plants [42–45]. The study shows that the *A. elata* *LSP* and *LCP* were little affected by variation in the soil moisture content. When the water content was within the range 37.5–87.0%, *LSP* and *LCP* were 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1) and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2), respectively. Plants can be divided into heliophilous species and sciophytes according to their light intensity requirements. *LSP* of heliophilous species is generally above 540 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and *LCP* is in the range of 13–36 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while *LSP* of sciophytes is generally 90–180 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and *LCP* is below 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [46]. The *A. elata* *LSP* and *LCP* were similar to typical heliophilous plants. When *PFD* was in the range 800–1,800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and light intensity was increased, *A. elata* photosynthetic rate did not decrease significantly, but T_r decreased continuously and leaf *WUE* obviously increased (Fig. 1). This indicates that *A. elata* photosynthesis responds strongly to light, and the ability of this plant to use low levels of light is poor. Therefore, *A. elata* has a strong adaptability to high light conditions, it can improve *WUE* to adapt to strong light stress.

Research has shown that plants have a certain degree of adaptability and resistance to soil water deficits, and various physiological activities are increased in the moderate water deficit range [47–50]. This range varies in different plant species and for different physiological processes. P_n of *A. elata* stabilized at a high soil water content that ranged 44.5–85.1%; an *RWC* of 64.5% was the optimum soil moisture content for photosynthesis (Fig. 3). Within this *RWC* range, *A. elata* transpiration was maintained at a high level (Fig. 2), and an *RWC* of 65.9% was the optimum soil moisture content for transpiration. As the leaf *WUE* is affected by photosynthetic and transpiration rates, the suitable soil water content of *WUE* was different from that of photosynthesis. *A. elata* *WUE* stabilized at a high soil water content that ranged 34.6–79.2%; an *RWC* of 55.9% resulted in the highest *WUE* (Fig. 3). At present, one of the most important

problems in the water management of *A. elata* is to achieve highly efficient utilization of water resources and to improve photosynthetic productivity. Therefore, we quantified the “productivity” (biomass) and “efficiency” (root resistance to water absorption) in traditional agricultural research, and graded the soil water of *A. elata* into non-productivity and non-efficiency water (NPNEW), low-productivity and low-efficiency water (LPLEW), low-productivity and medium-efficiency water (LPMEW), medium-productivity and low-efficiency water (MPLEW), medium-productivity and medium-efficiency water (MPMEW), and high-productivity and high-efficiency water (HPHEW). As a result, the soil water should be maintained in the range of 44.5% to 79.2%, in which P_n and *WUE* can reach their maximum values of 60% and 70%, respectively, so that the *A. elata* can obtain higher productivity and efficiency. The results can provide theoretical support for water management of *A. elata*. Relevant results show a suitable *RWC* of 40.6–60.4% for *Juglans regia* [51], 47.5–64.2% for *Robinia pseudoacacia* [52], 40.5–52.0% for *Platycladus orientalis* [52], and 58.8–76.6% for *Syringa oblata* [53]. Compared with the moderate soil water deficit range of these plants, *A. elata* can maintain a high photosynthetic rate and high *WUE* under a relatively higher soil water deficit.

Conclusions

The results show that photosynthesis, transpiration, and water use efficiency of *A. elata* were closely correlative to soil moisture and light intensity and had a notable threshold of responses. Light responses of physiological parameters exhibited higher plasticity, indicating that *A. elata* had better adaptability to light and soil water conditions.

At $44.5\% \leq RWC \leq 79.2\%$ was the economic water threshold value that maintained higher productivity and efficiency. Therefore, it can provide theoretical support for highly productive and highly efficient water management in *A. elata*.

Acknowledgements

This work was financially supported by research and demonstration of the key technology of vegetation restoration and reconstruction in the open pit of the eastern Shandong hilly area (201504406), and the National Natural Science Foundation of China (No. 31370702).

References

1. XIA J.B., ZHANG G.C., SUN J.K., LIU X. Threshold effects of photosynthetic and physiological parameters in *Prunus sibirica* to soil moisture and light intensity. *Acta Pharmacol. Sin.* **35** (3), 322, 2011.

2. RAKIĆ T., GAJIĆ G., LAZAREVIĆ M., STEVANOVIĆ B. Effects of different light intensities, CO₂ concentrations, temperatures and drought stress on photosynthetic activity in two paleoendemic resurrection plant species *Ramonda serbica* and *R. nathaliae*. *Environ. Exp. Bot.* **109** (109), 63, **2015**.
3. HAZRATI S., TAHMASEBI-SARVESRANI Z., MODARRES-SANAVY S.A., MOKHTASSI-BIDGOLI A., NICOLA S. Effects of water stress and light intensity on chlorophyll fluorescence parameters and pigments of *Aloe vera* L. *Plant. Physiol. Bioch.* **106**, 141, **2016**.
4. CELIA S.E., BENJAMÍN V.P., JOSÉ A.C. Assessing differences in water- and light-use efficiency in two related fir species under contrasting light conditions: gas exchange instantaneous rates vs. integrated C fixation and water loss. *Environ. Exp. Bot.* **122**, 49, **2016**.
5. XIA J.B., ZHANG S.Y., ZHANG G.C., XIE W.J., LU Z.H. Critical responses of photosynthetic efficiency in *Campsis radicans* (L.) Seem to soil water and light intensities. *Afr. J. Biotechnol.* **10** (77), 17748, **2011**.
6. HU J.C., CAO W.X., ZHANG J.B., JIANG D., FENG J. Quantifying responses of winter wheat physiological processes to soil water stress for use in growth simulation modeling. *Pedosphere*. **14** (4), 509, **2004**.
7. LAMCHIN M., LEE J.Y., LEE W.K., LEE E.J., KIM M., LIM C.H., CHOI H.A., KIM S.R. Assessment of land cover change and desertification using remote sensing technology in a local region of Mongolia. *Adv. Space. Res.* **57** (1), 64, **2016**.
8. LIU X.P., FAN Y.Y., LONG J.X., WEI R.F., KGELGREN R., GONG C.M., ZHAO J. Effects of soil water and nitrogen availability on photosynthesis and water use efficiency of *Robinia pseudoacacia* seedlings. *J. Environ. Sci-China*. **25** (3), 585, **2013**.
9. SOFO A., DICHIO B., MONTANARO G., XILOYAN-NIS C. Photosynthetic performance and light response of two olive cultivars under different water and light regimes. *Photosynthetic*. **47** (4), 602, **2009**.
10. RIVAS R., Falcão H.M., RIBEIRO R.V., MACHADO E.C., Pimentel C., Santos M.G. Drought tolerance in cowpea species is driven by less sensitivity of leaf gas exchange to water deficit and rapid recovery of photosynthesis after rehydration. *S. Afr. J. Bot.* **103**, 101, **2016**.
11. FUENTEALBA M.P., ZHANG J., KENWORTHY K., ERICKSON J., KRUSE J., TRENHOLM L. Transpiration responses of warm-season turfgrass in relation to progressive soil drying. *Sci. Hortic-Amsterdam*. **198**, 249, **2016**.
12. ZHANG Z.Z., ZHAO P., NI G.Y., ZHU L.W., ZHAO X.H. Water use of re-vegetation pioneer tree species *Schima superba* and *Acacia mangium* in hilly land of South China. *Chinese Journal of Applied Ecology*. **25** (4), 931, **2014**.
13. ZHANG W.Q., ZENG L.H., WANG M.H., YIN Z.Y., ZHOU P., CHEN S.G. The photosynthetic physiological characteristics of main tree species in the upper and middle reaches of Dongjiang watershed. *Ecology and Environmental Sciences*. **20** (1), 51, **2011**.
14. ZHANG S.Y., ZHANG G.C., LIU X., XIA J.B. The responses of photosynthetic rate and stomatal conductance of *Fraxinus rhynchophylla* to differences in CO₂ concentration and soil moisture. *Photosynthetic*. **51** (3), 359, **2013**.
15. SAJAD M.Z., NANCY G., MUSLIMA N., REETIKA M., FIRDOSE A.M., NAGEEBUL R.S., ASIF B.S., SALGOTRA R.K. Impact of drought on photosynthesis: Molecular perspective. *Plant. Gene*. **2017**.
16. BEATRYCZE N., KRUK J. Powered by light: Phototrophy and photosynthesis in prokaryotes and its evolution. *Microbiol. Res.* **186**, 99, **2016**.
17. OSWALDO F., AURÉLIE M., JACQUES W. Differential effect of regulated deficit irrigation on growth and photosynthesis in young peach trees intercropped with grass. *Eur. J. Agron.* **81**, 106, **2016**.
18. GREER D.H. Responses of biomass accumulation, photosynthesis and the net carbon budget to high canopy temperatures of *Vitis vinifera*, L. cv. Semillon vines grown in field conditions. *Environ. Exp. Bot.* **138**, 10, **2017**.
19. RIZWAN Z., HAORAN D., MUHAMMAD A., WEN-QING Z., YOUHUA W., ZHIGUO Z. Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and carbohydrate metabolism. *Environ. Exp. Bot.* **137**, 73, **2017**.
20. LIU E.K., MEI X.R., YAN C.R., GONG D.Z., ZHANG Y.Q. Effects of water stress on photosynthetic characteristics, dry matter translocation and WUE in two winter wheat genotypes. *Agr. Water. Manage.* **167**, 75, **2016**.
21. LI J.H., CANG Z.M., JIAO F., BAI X.J., DING Z., ZHAI R.C. Influence of drought stress on photosynthetic characteristics and protective enzymes of potato at seedling stage. *Journal of the Saudi Society of Agricultural Sciences*. **16** (1), 82, **2015**.
22. DANIELE C., LIOR R., ELISABETTA B., MARCO C. Xylem anatomical traits reveal different strategies of two Mediterranean oaks to cope with drought and warming. *Environ. Exp. Bot.* **133**, 128, **2017**.
23. CAO Y.N., MA C.X., CHEN G.C., ZHANG J.F., XING B.S. Physiological and biochemical responses of *Salix integra* Thunb. under copper stress as affected by soil flooding. *Environ. Pollut.* **225**, 644, **2017**.
24. HUANG F.S., ZHAO H.T., ZHOU K.Q., LI F.H., ZHANG K.W. Study on Distribution Characteristics of the Total Aralosides Content in *Aralia elata* (Miq.) Seem. *Chinese Wild. Plant. Resources*. **33**, 1, **2014**.
25. ZHANG M.P., GAO Y.G. Study on cutting root reproduction of *Aralia elata*. *Chinese Agricultural Science Bulletin*. **21**, 237, **2005**.
26. ZHANG X.P., YIN L.Y., NIU W.Y., LIU J.W., XIAO H.B. Antitumor effect of congmyue total saponins on tumor cells in vitro. *Lishizhen Medicine and Materia Medica Research*. **23** (12), 2966, **2012**.
27. ZHANG P., SHEN H.L. Cultivation techniques of *Aralia elata* planted for edible and medicinal purposes. *Nonwood Forest Research*. **29**, 69, **2011**.
28. LANG Y., WANG M., XIA J.B., ZHAO Q.K. Effects of soil drought stress on photosynthetic gas exchange traits and chlorophyll fluorescence in *Forsythia suspensa*. *Journal of Forestry Research*. **4**, 1, **2017**.
29. FARQUHAR G.D., SHARKEY T.D. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*. **33** (33), 317, **1982**.
30. LANG Y., ZHANG G.C., ZHANG Z.K., LIU S.S., LIU D.H., HU X.L. Light response of photosynthesis and its simulation in leaves of *Prunus sibirica* L. under different soil water conditions. *Acta. Ecologica. Sinica*. **31**, 4499, **2011**.
31. ZHOU H.H., CHEN Y.N., LI W.H., CHEN Y.P., FU L.X. Photosynthesis of *Populus euphratica* and its response to elevated CO₂ concentration in an arid environment. *Progress in Natural Science*. **19** (4), 443, **2008**.
32. LANG Y., ZHANG G.C., ZHANG Z.K., LIU S.S., LIU D.H., HU X.L. Light response of photosynthesis and its simulation in leaves of *Prunus sibirica* L. under different soil water conditions[J]. *Acta Ecologica Sinica*, **31** (16), 4499, **2011**.

33. LANG Y., WANG M., ZHANG G.C., ZHAO Q.K. Experimental and simulated light responses of photosynthesis in leaves of three tree species under different soil water conditions. *Photosynthetica*. **51** (3), 370, **2013**.
34. KAKANI V.G., VU J.C., ALLEN L.H.Jr., BOOTE K.J. Leaf photosynthesis and carbohydrates of CO₂-enriched maize and grain sorghum exposed to a short period of soil water deficit during vegetative development. *J. Plant. Physiol.* **168** (16), 2169, **2011**.
35. VERCAMPT H., KOLEVA L., VASSILEV A., HOREMANS N., BIERMANS G., VANGRONSVELD J., CUYPERS A. The functional role of the photosynthetic apparatus in the recovery of *Brassica napus* plants from pre-emergent metazachlor exposure. *J. Plant. Physiol.* **196-197**, 99, **2016**.
36. LIU C.G., WANG Y.J., PAN K.W., JIN Y.Q., LI W., ZHANG L. Effects of phosphorus application on photosynthetic carbon and nitrogen metabolism, water use efficiency and growth of dwarf bamboo (*Fargesia rufa*) subjected to water deficit. *Plant. Physiol. Bioch.* **96** (9), 20, **2015**.
37. SEKHAR K.M., SREEHARSHA R.V., REDDY A.R. Differential responses in photosynthesis, growth and biomass yields in two mulberry genotypes grown under elevated CO₂ atmosphere. *J. Photoch. Photobio. B.* **151**, 172, **2015**.
38. DAVIES F.S., FLOER J.A. Short-term flooding effects on gas exchange and quantum yield of rabbiteye blueberry (*Vaccinium ashei* Reade). *Plant. Physiol.* **81** (1), 289, **1986**.
39. ZHU Y.Y., HE K.N., TANG D.F., GONG Y.X. Response to light of *Ulmus pumila* in different soil moisture. *Research of Soil and Water Conservation*. **14**, 92, **2007**.
40. ZHANG S.Y., ZHOU Z.F., XIA J.B., ZHANG G.S. The responses of *Euonymus fortunei* var. *radicans* sieb. leaf photosynthesis to light in different soil moisture. *Acta. Botanica. Boreali-Occidentalia. Sinica*. **27** (12), 2514, **2007**.
41. LI H.S. MODERN plant physiology. Beijing Higher Education Press. Beijing. **2002**.
42. LIU G., ZHANG G.C., LIU X. Responses of *Cotinus coggygia* var. *cinerea* photosynthesis to soil drought stress. *Chinese Journal of Applied Ecology*. **21** (7), 1697, **2010**.
43. LANG Y., WANG M. Effects of soil water on photosynthesis of *Forsythia suspensa* (Thunb.) Vahl in spring and summer. *Acta. Ecologica. Sinica*. **35** (9), 3043, **2015**.
44. COLLIER C.J., ADAMS M.P., LANGLOIS L., WAYCOTT M., O'BRIEN K.R., MAXWELL P.S., MCKENZIE L. Thresholds for morphological response to light reduction for four tropical seagrass species. *Ecol. Indic.* **67**, 358, **2016**.
45. AASAMAA K., APHALO P.J. Effect of vegetational shade and its components on stomatal responses to red, blue and green light in two deciduous tree species with different shade tolerance. *Environ. Exp. Bot.* **121**, 94, **2016**.
46. MENG F.J. Plant Physiology. Huazhong University of Science and Technology Press, Wuhan, **2000**.
47. XU D.Q. Efficiency of photosynthesis. Shanghai Science and Technology Press. Shanghai, **2002**.
48. PEI B., ZHANG G.C., ZHANG S.Y., WU Q., XU Z.Q., XU P. Effects of soil drought stress on photosynthetic characteristics and antioxidant enzyme activities in *Hippophae rhamnoides* Linn. seedlings. *Acta. Ecologica. Sinica*. **33** (5), 1386, **2013**.
49. XIA J.B., ZHANG S.Y., ZHAO X.M., LIU J.H., CHEN Y.P. Effects of different groundwater depths on the distribution characteristics of soil-*Tamarix* water contents and salinity under saline mineralization conditions. *Catena*. **142**, 166, **2016**.
50. ABEGUNRIN T.P., AWE G.O., IDOWU D.O., ADEJUMOBI M.A. Impact of wastewater irrigation on soil physico-chemical properties, growth and water use pattern of two indigenous vegetables in southwest Nigeria. *Catena*. **139** (3), 167, **2016**.
51. LI X.L., ZHANG G.C., ZHOU Z.F., LIU X., CHEN X.J., ZHANG S.Y. Response to light of water utilization efficiency of *walnut* leaf in different soil moisture in loess hilly region. *Science of Soil and Water Conservation*. **3** (1), 43, **2005**.
52. ZHANG G.C., LIU X., HE K.N. Grading of *Robinia pseudoacacia* and *Platycladus orientalis* woodland soil's water availability and productivity in semi-arid region of Loess Plateau. *Chinese Journal of Applied Ecology*. **14** (6), 858, **2003**.
53. CHEN X.J., ZHANG G.C., ZHOU Z.F., MA S.S., LI X.L., ZHANG S.Y. Diurnal variations and response to light of gas exchange parameters of clove (*Syringa oblata* Lindl.) leaf in loess hilly region. *Science of Soil and Water Conservation*. **2** (4), 102, **2004**.

