

Effects of Integrated Water-Fertilizer Management on Growth, Root Morphology, Physiology, and Photosynthetic Characteristics of Flue-cured Tobacco in Northern Tobacco-Growing Regions Postprint

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Abstract

Drought inhibits the growth and development of flue-cured tobacco in northern tobacco-growing regions, causing declines in leaf yield and quality. To investigate the effects of water-fertilizer integration on field growth, root morphology, and photosynthetic characteristics of flue-cured tobacco in northern tobacco-growing regions, ‘Yunyan 87’ was used as the experimental material to study differences in tobacco agronomic traits, dry matter accumulation, root morphology and physiological activity, photosynthesis, chlorophyll fluorescence characteristics, and economic traits of cured leaves under two different treatments: water-fertilizer integration and conventional furrow irrigation with fertilization. The results showed that, compared with the conventional furrow irrigation and fertilization treatment, water-fertilizer integration promoted the growth and development of flue-cured tobacco, resulting in favorable field agronomic trait performance. Water-fertilizer integration significantly increased dry matter accumulation in both roots and shoots, reduced the root-to-shoot ratio, and markedly enhanced root volume, total absorption area, active absorption area, specific surface area, as well as root activity, ATPase, and other related root morphological and physiological activities ($P < 0.05$). Under water-fertilizer integration, the photosynthetic indices of flue-cured tobacco leaves—including net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and water use efficiency (WUE)—as well as chlorophyll fluorescence parameters such as PSII maximum photochemical efficiency (F_v/F_m), actual photochemical quantum efficiency (Φ_{PSII}), and photochemical quenching coefficient (q_p) were all significantly higher than those under conventional furrow irrigation and fertilization ($P < 0.05$), whereas transpiration rate (Tr)

and non-photochemical quenching coefficient (NPQ) were significantly lower ($P < 0.05$); simultaneously, the economic traits of its cured leaves were significantly higher than those of the conventional furrow irrigation and fertilization treatment ($P < 0.05$). The study indicates that water-fertilizer integration can create favorable root morphology, enhance root physiological activity, improve photosynthesis and light energy utilization efficiency, thereby promoting the growth and development of flue-cured tobacco and contributing to the improvement of economic traits in cured leaves.

Full Text

Effects of Water and Fertilizer Integration on Growth, Morphology, Physiology, and Photosynthetic Characteristics of Flue-Cured Tobacco in Northern China

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Abstract: Drought stress inhibits the growth and development of flue-cured tobacco in northern China, resulting in reduced yield and quality. To investigate the effects of integrated water and fertilizer management on field growth, root morphology and physiology, and photosynthetic characteristics of flue-cured tobacco in northern China, we examined differences in agronomic traits, dry matter accumulation, root morphology and physiological activity, photosynthesis, chlorophyll fluorescence characteristics, and economic traits of cured leaves between integrated water-fertilizer treatment and conventional furrow irrigation with standard fertilization, using ‘Yunyan 87’ as the experimental material. The results showed that compared with conventional furrow irrigation and fertilization, integrated water-fertilizer management promoted tobacco growth and development, resulting in superior agronomic performance. This approach significantly increased dry matter accumulation in both roots and shoots while decreasing the root-to-shoot ratio, and substantially enhanced root morphology and physiological activity, including root volume, total absorption area, active absorption area, specific surface area, root vitality, and ATPase activity ($P < 0.05$). Under integrated water-fertilizer management, net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), water use efficiency (WUE), PSII maximum photochemical efficiency (F_v/F_m), actual photochemical quantum efficiency (Φ_{PSII}), and photochemical quenching coefficient (q_p) were all significantly higher than those under conventional irrigation and fertilization ($P < 0.05$), whereas transpiration rate (T_r) and non-photochemical quenching coefficient (NPQ) were significantly lower ($P < 0.05$). Additionally, the economic characteristics of cured tobacco leaves were significantly improved under integrated water-fertilizer management ($P < 0.05$). These findings indicate that integrated water-fertilizer management creates favorable

root morphology, enhances root physiological activity, and improves photosynthetic efficiency and light energy utilization, thereby promoting tobacco growth and development and contributing to higher economic returns from cured tobacco leaves.

Keywords: Water and fertilizer integration; Flue-cured tobacco; Root morphology and physiology; Photosynthetic characteristics; Chlorophyll fluorescence; Economic characteristics

1.1 Experimental Site Conditions

The experiment was conducted from 2015 to 2016 in Loushang Village, Zhaohe Town, Fangcheng County, Henan Province, using the flue-cured tobacco cultivar ‘Yunyan 87’. The experimental site is located at an elevation of 114 m (113°23 E, 33°15 N) with yellow-brown soil of uniform fertility and flat terrain. The basic chemical properties of the soil were: organic matter 15.11 g · kg⁻¹, available nitrogen 80.25 mg · kg⁻¹, available phosphorus 15.52 mg · kg⁻¹, available potassium 98.79 mg · kg⁻¹, and pH 7.35.

1.2 Experimental Design

Two treatments were established: integrated water-fertilizer management (T) and conventional furrow irrigation with standard fertilization (control, CK). Large field plots were used, with each treatment covering 1.67 ha (total experimental area 3.33 ha). Row spacing was 110 cm and plant spacing 55 cm, with topping performed 60 days after transplanting. Both treatments received identical total amounts of pure nitrogen (52.5 kg · ha⁻¹), phosphorus (105 kg · ha⁻¹), and potassium (277.5 kg · ha⁻¹).

In the conventional treatment, basal fertilization consisted of 450 kg · ha⁻¹ sesame cake fertilizer, 150 kg · ha⁻¹ calcium superphosphate [Ca(H₂PO₄)₂ · H₂O], and 300 kg · ha⁻¹ tobacco-specific compound fertilizer applied as row application before transplanting. Topdressing at the rosette stage included 75 kg · ha⁻¹ potassium nitrate (KNO₃) and 375 kg · ha⁻¹ potassium sulfate (K₂SO₄) applied via hole application. Irrigation was performed using conventional furrow irrigation.

In the integrated water-fertilizer treatment, a mobile water-fertilizer integrator (consisting of a gasoline engine water pump, filter, fertilizer tank, air valve, and other components) was used for fertilization and irrigation. The pipeline system comprised a main pipe (PE material, 63 mm diameter) connected to patch-type drip tape (PE material, 16 mm diameter, with emitter spacing of 30 cm). Basal fertilization included 450 kg · ha⁻¹ sesame cake fertilizer and 150 kg · ha⁻¹ calcium superphosphate applied as row application. A specially formulated liquid tobacco fertilizer (containing nitrogen, phosphorus, and potassium) developed by our research group was dissolved in water and applied through drip irrigation at 0, 20, 30, 40, and 50 days after transplanting, with pure nitrogen applications of 7.5, 7.5, 15, 18.75, and 3.75 kg · ha⁻¹, respectively. At 60 and 70 days, 75 kg ·

ha⁻¹ potassium sulfate was topdressed each time. Each drip fertigation event delivered 0.002 m³ of water over 1.5 hours, with approximately 30,000 emitters per hectare. The irrigation schedule and total water volume (630 m³ · ha⁻¹ for the entire growth period) were identical between treatments, with water supplied from a 500 m³ reservoir constructed as part of local tobacco-water infrastructure projects. All other cultivation practices followed local high-quality tobacco production management protocols.

At 75 days after transplanting, 200 representative plants from each treatment were selected using the five-point sampling method, tagged, and used for measurements of agronomic traits, root morphology and physiology, photosynthesis, chlorophyll fluorescence, and economic trait statistics. The 10th leaf from the bottom was selected for photosynthetic and chlorophyll fluorescence measurements. Whole plants were then excavated, and intact root systems were washed clean. After blotting dry, fresh weights of shoots and roots were measured, and root morphological parameters and root vitality and ATPase activity were determined. Samples were then killed at 105 °C for 20 minutes, dried to constant weight at 70 °C, and dry weights measured to calculate root-to-shoot ratios. All indices were measured with four replications.

1.3.1 Agronomic Trait Measurements

Agronomic traits including plant height, stem girth, internode distance, number of productive leaves, and maximum leaf length and width were measured according to the YC/T 142-1998 standard for agronomic trait recording.

1.3.2 Root Morphological Parameter Measurements

Root volume was measured using the water displacement method. Total root absorption area, active absorption area, and specific surface area were determined using the methylene blue adsorption method [16].

1.3.3 Root Vitality Measurement

Root vitality was measured using the triphenyltetrazolium chloride (TTC) method [17].

1.3.4 Root ATPase Activity Measurement

Fresh flue-cured tobacco roots (0.2 g) were homogenized with physiological saline at a 1:9 ratio to prepare a 10% homogenate, which was centrifuged at 4 °C and 6,000 g · min⁻¹ for 15 minutes. The supernatant was then diluted with physiological saline at a 1:4 ratio to prepare a 2% homogenate. ATPase activity was subsequently measured following the procedures of a commercial assay kit (Nanjing Jiancheng Bioengineering Institute).

1.3.5 Photosynthetic Parameter Measurements

Following the methods of Chen et al. [18], a LI-6400 portable photosynthesis system (Li-Cor Inc., USA) was used to measure net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (Tr). Water use efficiency (WUE) was calculated as $WUE = P_n/Tr$ [19]. Measurements were conducted using a red-blue light source leaf chamber with an open gas path, with chamber temperature set at 25 °C, relative humidity at 60-70%, CO_2 concentration at 400 $mol \cdot mol^{-1}$, light intensity at 1,000 $mol \cdot m^{-2} \cdot s^{-1}$, and photon flux density at 800 $mol \cdot m^{-2} \cdot s^{-1}$.

1.3.6 Chlorophyll Fluorescence Characteristics Measurement

Chlorophyll fluorescence parameters including initial fluorescence (F_0), maximum fluorescence (F_m), and minimum fluorescence (F_0') were measured at symmetrical points along the tobacco leaf vein using an FMS-2 pulse-modulated fluorometer. Variable fluorescence (F_v), PSII maximum photochemical efficiency (F_v/F_m), PSII actual photochemical efficiency (Φ_{PSII}), photochemical quenching coefficient (q), and non-photochemical quenching coefficient (NPQ) were calculated according to Demmig-Adams et al. [20].

1.3.7 Economic Trait Statistics of Cured Tobacco Leaves

Yield of cured leaves from tagged plants was recorded for each treatment. Leaves were graded according to the 42-grade national standard for flue-cured tobacco (GB2635-92), and output value, average price, and proportion of high-quality tobacco were calculated.

1.4 Data Processing

Statistical analysis was performed using Microsoft Excel 2010 and SPSS 16.0 software. Significance was tested using Duncan's new multiple range test.

2.1 Effects of Integrated Water-Fertilizer Management on Agronomic Traits of Flue-Cured Tobacco

Agronomic traits provide the most direct indication of growth coordination in tobacco plants. Table 1 shows that integrated water-fertilizer management significantly promoted tobacco growth and development, resulting in superior agronomic performance. Compared with conventional furrow irrigation and fertilization, integrated water-fertilizer management increased plant height, stem girth, and maximum leaf area by 1.09, 1.02, and 1.07 times, respectively, with significant differences. Internode distance and number of effective leaves were also higher under integrated water-fertilizer management, though differences were not statistically significant.

2.2 Effects of Integrated Water-Fertilizer Management on Dry Matter Accumulation in Flue-Cured Tobacco

Dry matter accumulation reflects the growth and development status of tobacco plants. As shown in Table 2, compared with the control, integrated water-fertilizer management significantly increased aboveground fresh weight, root fresh weight, aboveground dry weight, and root dry weight by 14.15%, 18.51%, 21.95%, and 18.68%, respectively. Additionally, integrated water-fertilizer management reduced the root-to-shoot ratio by 2.48%, which was significantly different from conventional furrow irrigation and fertilization.

2.3 Effects of Integrated Water-Fertilizer Management on Root Morphology of Flue-Cured Tobacco

Root volume directly reflects root development and affects water and mineral nutrient absorption and transport. Root morphological characteristics such as total absorption area, active absorption area, and specific surface area reflect root physiological activity and are closely related to photosynthetic activity, single leaf weight, and nicotine and potassium content. Table 3 shows that compared with conventional furrow irrigation and fertilization, integrated water-fertilizer management increased root volume, total absorption area, active absorption area, and specific surface area by 1.11, 1.25, 1.12, and 1.13 times, respectively, with significant differences.

2.4 Effects of Integrated Water-Fertilizer Management on Root Physiological Activity of Flue-Cured Tobacco

High root vitality indicates strong metabolic capacity and ensures adequate supply of nutrients and water for plant growth. ATPase is a key enzyme in energy metabolism that affects nutrient and water absorption and transport, with its activity representing the intensity of root metabolic activity. Table 4 shows that root vitality and ATPase activity were higher under integrated water-fertilizer management and lower under conventional furrow irrigation and fertilization. Compared with the control, integrated water-fertilizer management increased root vitality and ATPase activity by 43.08% and 31.84%, respectively, with significant differences.

2.5 Effects of Integrated Water-Fertilizer Management on Photosynthesis of Flue-Cured Tobacco

Photosynthesis is fundamental to crop growth, development, and yield and quality formation, with water and nutrient status being critical limiting factors. Table 5 shows that compared with conventional furrow irrigation and fertilization, integrated water-fertilizer management significantly increased net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and water use efficiency (WUE) by 31.44%, 59.09%, 21.75%, and 85.66%, respectively, while transpiration rate (Tr) decreased by 29.20%.

2.6 Effects of Integrated Water-Fertilizer Management on Chlorophyll Fluorescence Characteristics of Flue-Cured Tobacco

Chlorophyll fluorescence characteristics authentically reflect changes in photosynthetic activity, with fluorescence parameters playing a unique role in evaluating light energy absorption and transfer by the photosynthetic system. Table 6 shows that under integrated water-fertilizer management, F/F_0 , Φ_{PSII} , and q were 1.12, 1.34, and 1.65 times higher than those under conventional furrow irrigation and fertilization, with significant differences, while NPQ was significantly lower at 61.36% of the control value.

2.7 Effects of Integrated Water-Fertilizer Management on Economic Traits of Flue-Cured Tobacco

Economic traits are key indicators for evaluating tobacco production levels. As shown in Table 7, integrated water-fertilizer management produced superior economic characteristics, with significantly higher yield, output value, average price, and proportion of high-quality tobacco compared with conventional furrow irrigation and fertilization. Yield, output value, and average price increased by $312.43 \text{ kg} \cdot \text{ha}^{-1}$, $\text{¥}13,971.78 \text{ ha}^{-1}$, and $\text{¥}2.38 \text{ kg}^{-1}$, respectively, while the proportion of high-quality tobacco was 6.49 percentage points higher.

3 Discussion and Conclusion

The root system is the primary organ for water and nutrient absorption, with its function primarily influenced by root morphology and physiological characteristics [21]. Changes in environmental conditions such as water and fertilizer availability affect dry matter distribution between aboveground and belowground parts, ultimately influencing yield potential. Rational irrigation and fertilization promote aboveground morphological development and increase yield [22-23]. In this study, integrated water-fertilizer management resulted in higher root dry matter accumulation, significantly increased root volume and other morphological parameters, and stronger root vitality and ATPase activity compared with conventional furrow irrigation and fertilization. These improvements facilitated enhanced water and mineral nutrient absorption, promoting tobacco growth and yield formation. Crop leaf area shows a significant positive correlation with biomass accumulation [24], and the increased leaf area under integrated water-fertilizer management would consequently benefit dry matter accumulation and yield formation. The root-to-shoot ratio reflects both the growth status and coordination between roots and shoots, as well as crop adaptation to environmental changes [25]. The lower root-to-shoot ratio under integrated water-fertilizer management indicates that this approach benefits the growth and development of both root and shoot systems, establishing a foundation for optimal function. A well-developed root system enhances water and nutrient absorption, consistent with changes in root morphological and physiological indices [26]. Nejad [27] reported that crops exhibit optimal resource use efficiency when root structure and function are in balanced states. Under integrated water-fertilizer manage-

ment, tobacco root systems developed well, possibly due to improved soil aeration and optimized rhizosphere nutrient conditions. Enhanced soil permeability increased rhizosphere oxygen concentration, reducing damage to root cells from reductive substances, accelerating cell division in root meristems, increasing cell length, and promoting lateral and adventitious root formation. This facilitated root elongation and expansion in the soil profile, resulting in extensive root distribution. Simultaneously, integrated water-fertilizer management increased available nitrogen supply in the soil, ensuring adequate rhizosphere nutrients for root growth and development, enhancing nitrogen absorption and assimilation, and thereby improving nitrogen use efficiency [28]. In contrast, conventional furrow irrigation and fertilization resulted in lower root dry matter, root volume, and significantly reduced root vitality and ATPase activity, indicating that this approach is detrimental to root development.

Photosynthesis forms the basis of crop growth, development, yield, and quality, with water and nutrients being critical influencing factors [29]. Integrated water-fertilizer management significantly increased Pn in tobacco leaves, indicating balanced water and fertilizer absorption that improved physiological activity and enhanced CO₂ capture capacity, leading to increased photosynthetic intensity. Increased Gs under integrated water-fertilizer management reduced CO₂ diffusion resistance, facilitating stomatal CO₂ exchange and promoting higher Pn. Elevated Ci suggests that integrated water-fertilizer management regulated mesophyll cell function. Lower Tr under integrated water-fertilizer management demonstrated improved microclimate conditions in the tobacco field, reducing transpirational water loss and maintaining normal physiological activity. Higher WUE in tobacco leaves under integrated water-fertilizer management indicated enhanced water absorption and utilization efficiency. This likely occurred because integrated water-fertilizer management delivered water and nutrients timely and quantitatively to the rhizosphere with minimal soil losses, significantly increasing root systems and expanding the spatial domain for water and nutrient absorption, thereby improving water and nutrient use efficiency and photosynthesis for greater assimilation product accumulation.

Chlorophyll fluorescence enables rapid detection of authentic photosynthetic responses to environmental stress, providing evaluation of photosynthetic apparatus function and stress impacts [30-31]. F/F_m represents PSII maximum photochemical efficiency, which is species-independent and primarily affected by environmental factors and stress levels [32]. Φ_{PSII} indicates actual photochemical efficiency of PSII reaction centers under partial closure [33]. q represents the openness degree of PSII reaction centers [29], while NPQ measures non-radiative energy dissipation in PSII reaction centers [34]. Our results showed that F/F_m , Φ_{PSII} , and q were significantly higher under integrated water-fertilizer management compared with conventional furrow irrigation and fertilization, indicating that integrated water-fertilizer management enhanced PSII light energy capture and utilization, increased photosynthetic electron transport activity and PSII energy conversion efficiency, reduced excess excitation energy, and improved leaf light energy absorption and utilization. This promoted formation of assimilatory

power and ensured carbon fixation and assimilation. The significant decrease in NPQ demonstrated that integrated water-fertilizer management increased excitation energy capture efficiency in PSII reaction centers [35]. The higher PSII light use efficiency and photosynthetic potential of tobacco leaves under integrated water-fertilizer management represent the photosynthetic physiological basis for yield increase.

The adage “harvest depends on water, yield depends on fertilizer” reflects the direct impact of rational water and fertilizer management on crop growth and development [36-38]. Over 90% of crop yield originates from photosynthesis [39]. Williams et al. [40] noted that current yield-increasing technologies have been fully exploited, with photosynthetic efficiency improvement representing the remaining major potential for yield enhancement [41]. Root system development is closely linked to leaf photosynthetic physiology. Fu et al. [42] reported that enhancing root physiological activity during the late grain-filling stage in super rice and thereby increasing leaf photosynthesis is an important pathway for yield improvement. Our results demonstrated that integrated water-fertilizer management significantly promoted tobacco growth and development, increasing plant height, stem girth, and maximum leaf area, with higher dry matter accumulation in both roots and shoots and superior field agronomic performance. These benefits primarily resulted from enhanced leaf photosynthesis and improved PSII light use efficiency, providing abundant organic assimilates for optimal tobacco growth.

Economic traits provide the most direct measure of practical application effects. In this study, economic characteristics of cured tobacco leaves were significantly higher under integrated water-fertilizer management than under conventional furrow irrigation and fertilization, demonstrating that integrated water-fertilizer management contributes to higher yields and profits. These improvements likely resulted from optimized root morphology and physiological characteristics combined with enhanced photosynthetic activity, promoting efficient water and fertilizer absorption and utilization.

In summary, this study demonstrated that integrated water-fertilizer management significantly increased P_n , G_s , C_i , WUE, and chlorophyll fluorescence parameters F/F_0 , Φ_{PSII} , and q , while significantly decreasing Tr and NPQ compared with conventional furrow irrigation and fertilization. These results indicate that integrated water-fertilizer management confers distinct advantages in photosynthetic performance and light energy use efficiency, with well-developed root systems showing strong root vitality and ATPase activity. This provides adequate water and organic nutrients for plant development, fulfilling the principle of “regulating fertilizer with water and promoting growth with fertilizer” [43-44], increasing photosynthetic conversion efficiency, producing better agronomic performance, and ultimately establishing the foundation for increased yield and higher economic returns [45]. Field management of water and fertilizer are both critical factors affecting crop growth, development, and yield/quality improvement [46]. This study confirms that integrated water-fertilizer management

effectively combines water and fertilizer through synergistic effects, mitigating the adverse impacts of drought and low rainfall on tobacco production in northern China, promoting tobacco growth and development, and achieving higher production benefits. Therefore, the next phase of this research will involve larger-scale production demonstrations to further validate the effectiveness of integrated water-fertilizer management, providing solid and reliable theoretical and practical foundations for its widespread application in flue-cured tobacco production in northern China.

References

- [1] Ma X H, Zhang Z F, Rong F F, et al. Studies on nitrogen absorption, distribution and utilization in flue-cured tobacco under higher and lower fertility conditions[J]. Chinese Tobacco Science, 2009, 30(1): 1-4
- [2] Peng S B, Tang Q Y, Zou Y B. Current status and challenges of rice production in China[J]. Plant Production Science, 2009, 12(1): 3-8
- [3] Zhu Z L, Jin J Y. Fertilizer use and food security in China[J]. Journal of Plant Nutrition and Fertilizer, 2013, 19(2): 259-273
- [4] Liu S Q, Cao H X, Zhang J Q, et al. Effects of different water and nitrogen supplies on root growth, yield and water and nitrogen use efficiency of small pumpkin[J]. Scientia Agricultura Sinica, 2014, 47(4): 1362-1371
- [5] Wang H Y, Gao J L, Wang Z G, et al. Effects of high planting density on super high-yielding spring maize leaf senescence and root activity at anthesis and kernel stage[J]. Journal of Maize Sciences, 2012, 20(2): 75-81
- [6] Wei Z X, Liang Y L, Zhou M J, et al. Physiological characteristics of leaf growth and yield of cucumber under different watering and fertilizer coupling treatments in greenhouse[J]. Transactions of the CSAE, 2010, 26(3): 69-74
- [7] Xia J H, Wang C, Zhao J C, et al. The development status and application prospects of integrated management of water and fertilizer in tobacco[J]. Modern Agricultural Science and Technology, 2016, (19): 63-64
- [8] Li Z, Wang J M, Wang H J, et al. Problems with greenhouse and technology of integrated management of water and fertilizer[J]. Soils, 2006, 38(2): 223-227
- [9] Kang Y H, Wang F X, Liu S P, et al. Effects of water regulation under drip irrigation on potato growth[J]. Transactions of the CSAE, 2004, 20(2): 66-72
- [10] Du S N, Bai G S, Liang Y L. Effects of irrigation methods on cucumber growth, yield and water use efficiency[J]. Journal of Zhejiang University: Agriculture & Life Sciences, 2010, 36(4): 433-439
- [11] Chen Y S, Li M X, Dong Y, et al. New techniques of integration of water and fertilizer and its advantages[J]. Modern Agricultural Science and Technology, 2011, (19): 298

- [12] Courtois B, Ahmadi N, Khowaja F, et al. Rice root genetic architecture: Meta-analysis from a drought QTL database[J]. *Rice*, 2009, 2(2/3): 115-128
- [13] Li G H, Zhao B, Dong S T, et al. Effects of coupling controlled release urea with water on yield and photosynthetic characteristics in summer maize[J]. *Acta Agronomica Sinica*, 2015, 41(9): 1406-1415
- [14] Shi H Z, Fan Y K, Liu G S, et al. Advances of studies on tobacco water-fertilizer coupling and its application[J]. *Journal of Henan Agricultural Sciences*, 2008, (10): 5-10
- [15] Fan Y K. Implementation of precision management system of water and fertilizer for high quality tobacco[C]//Proceedings of annual academic meeting of China Tobacco Society in 2014. Beijing: China Tobacco Society, 2014: 171-177
- [16] Li H S, Sun Q, Zhao S J, et al. Principles and Techniques of Plant Physiological Biochemical[M]. Beijing: Higher Education Press, 2000
- [17] Zou Q. Instruction of Experiment on Plant Physiology[M]. Beijing: China Agriculture Press, 2000
- [18] Chen Z, Xu J Y, Fan Y K, et al. Response of morphological structure and photosynthetic parameters to water deficit in four flue-cured tobacco cultivar seedlings[J]. *Chinese Journal of Eco-Agriculture*, 2016, 24(11): 1508-1520
- [19] Berry J, Bjorkman O. Photosynthetic response and adaptation to temperature in higher plants[J]. *Annual Review of Plant Physiology*, 1980, 31: 491-543
- [20] Demmig-Adams B, Adams W W, Baker D H, et al. Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation[J]. *Physiologia Plantarum*, 1996, 98(2): 253-264
- [21] Chu G, Zhou Q, Xue Y G, et al. Effects of cultivation patterns on root morph-physiological traits and aboveground development of japonica hybrid rice cultivar Changyou 5[J]. *Acta Agronomica Sinica*, 2014, 40(7): 1245-1258
- [22] Jiao J Y, Yin C Y, Chen K. Effects of soil water and nitrogen supply on the photosynthetic characteristics of *Jatropha curcas* seedlings[J]. *Chinese Journal of Plant Ecology*, 2011, 35(1): 91-99
- [23] Chen G P. Dry matter production and distribution in maize[J]. *Maize Science*, 1994, 2(1): 48-53
- [24] Qi H, Duan L S, Wang S L, et al. Effect of enhanced UV-B radiation on cotton growth and photosynthesis[J]. *Chinese Journal of Eco-Agriculture*, 2017, 25(5): 708-719
- [25] Shen X, Li H Y, Jia Q Z, et al. Influence of wheat (*Triticum aestivum* L.) stripe rust infection on photosynthetic function and expression protein D1 of wheat leaves[J]. *Acta Ecologica Sinica*, 2008, 28(2): 669-676

- [26] Huang B R, Fry J D. Root anatomical, physiological, and morphological responses to drought stress for tall fescue cultivars[J]. *Crop Science*, 1998, 38(4): 1017-1022
- [27] Nejad T S. Effect of drought stress on shoot/root ratio[J]. *World Academy of Science, Engineering and Technology*, 2011, 57: 598-600
- [28] Jiang D, Dai T, Jing Q, et al. Effects of long-term fertilization on leaf photosynthetic characteristics and grain yield in winter wheat[J]. *Photosynthetica*, 2004, 42(3): 439-446
- [29] Bilger W, Björkman O. Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*[J]. *Photosynthesis Research*, 1990, 25(3): 173-185
- [30] Krause G H, Weis E. Chlorophyll fluorescence and photosynthesis: The basics[J]. *Annual Review of Plant Physiology and Plant Molecular Biology*, 1991, 42: 319-359
- [31] Liu L Q, Zhang Y Q, Li X, et al. Influence of seed soaking with uniconazole on growth and root physiological characteristics of adzuki bean under drought stress[J]. *Acta Botanica Boreali-Occidentalia Sinica*, 2017, 37(1): 144-153
- [32] Aroca R, Irigoyen J J, Sánchez-Díaz M. Drought enhances maize chilling tolerance. . Photosynthetic traits and protective mechanisms against oxidative stress[J]. *Physiologia Plantarum*, 2003, 117(4): 540-549
- [33] Santos C V. Regulation of chlorophyll biosynthesis and degradation by salt stress in sunflower leaves[J]. *Scientia Horticulturae*, 2004, 103(1): 93-99
- [34] Lin L, Tang Y, Zhang J T, et al. Effects of different water potentials on leaf gas exchange and chlorophyll fluorescence parameters of cucumber during post-flowering growth stage[J]. *Chinese Journal of Applied Ecology*, 2015, 26(7): 1985-1992
- [35] Luo H H, Zhang H Z, Tao X P, et al. Effect of irrigation and nitrogen application regimes on senescent characters of roots and leaves in cotton with under-mulch-drip irrigation[J]. *Scientia Agricultura Sinica*, 2013, 46(10): 2142-2150
- [36] Yang J C. Relationships of rice root morphology and physiology with the formation of grain yield and quality and the nutrient absorption and utilization[J]. *Scientia Agricultura Sinica*, 2011, 44(1): 36-46
- [37] Sun Y J, Ma J, Sun Y Y, et al. The effects of different water and nitrogen managements on yield and nitrogen use efficiency in hybrid rice of China[J]. *Field Crops Research*, 2012, 127: 85-98
- [38] Zhao H, Zhang M, Qin S, et al. Response of Chinese cabbage growth, quality, photosynthesis and nitrogen utilization to new fertilizers in Guizhou yellow soil[J]. *Chinese Journal of Eco-Agriculture*, 2016, 24(10): 1320-1327

- [39] Ji L, Li T X, Zhang X Z, et al. Root morphological and activity characteristics of rice genotype with high nitrogen utilization efficiency[J]. *Scientia Agricultura Sinica*, 2012, 45(23): 4770-4781
- [40] Williams B A, Gurner P J, Austin R B. A new infra-red gas analyser and portable photosynthesis meter[J]. *Photosynthesis Research*, 1982, 3(2): 141-151
- [41] Raines C A. Increasing photosynthetic carbon assimilation in C_3 plants to improve crop yield: Current and future strategies[J]. *Plant Physiology*, 2011, 155(1): 36-42
- [42] Fu J, Chen L, Huang Z H, et al. Relationship of leaf photosynthetic characteristics and root physiological traits with grain yield in super rice[J]. *Acta Agronomica Sinica*, 2012, 38(7): 1264-1276
- [43] Aqueel M A, Leather S R. Effect of nitrogen fertilizer on the growth and survival of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) (Homoptera: Aphididae) on different wheat cultivars[J]. *Crop Protection*, 2011, 30(2): 216-221
- [44] Sandhu S S, Mahal S S, Vashist K K, et al. Crop and water productivity of bed transplanted rice as influenced by various levels of nitrogen and irrigation in northwest India[J]. *Agricultural Water Management*, 2012, 104: 32-39
- [45] Yuan S H. Effects of interaction of water and nitrogen on uptake and utilization of nitrogen and yield and quality of flue-cured tobacco[D]. Zhengzhou: Henan Agricultural University, 2008
- [46] Ma Z M, Du S P, Xue L. Coupling effects of water and fertilizer on melon in plastic greenhouse of gravel-mulched field under drip fertigation[J]. *Scientia Agricultura Sinica*, 2016, 49(11): 2164-2173

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