African Journal of Biotechnology Vol. 10(77), pp. 17748-17754, 5 December, 2011
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB11.2208
ISSN 1684–5315 © 2011 Academic Journals

Full Length Research Paper

Critical responses of photosynthetic efficiency in *Campsis radicans* (L.) Seem to soil water and light intensities

Xia Jiang-bao[1], Zhang Shu-Yong[2*], Zhang Guang-Can[3*], Xie Wen-Jun[1] and Lu Zhao-Hua

[1]Binzhou University, Shandong Provincial Key Laboratory of Eco-Environmental Science for Yellow River Delta, Binzhou 256603, China.
[2]Resources and Environmental Sciences College, Northeast Agricultural University, Harbin 150030, China.
[3]Shandong Provincial Key Laboratory of Soil Erosion and Ecological Restoration; Key Laboratory of Agricultural Ecology and Environment, Forestry College, Shandong Agricultural University, Taian 271018, China.

Accepted 28 October, 2011

Campsis radicans **(L.) Seem is one of the main forestation tree species in semi-arid loess hilly region. Using the CIRAS-2 portable photosynthesis system, the light-response of the photosynthetic efficiency parameters of three-year-old *C .radicans* leaves, such as net photosynthetic rate (P_N), transpiration rate (Tr), water use efficiency (WUE), and light use efficiency (LUE), were studied under different soil water conditions in order to explore the effects of soil water stress on photosynthesis and the suitable soil water content for water-saving irrigation of this liana. Soil water and light intensity needed by the growth and development of *C .radicans* were analyzed. The results show that P_N, Tr, WUE, and LUE of the leaves had threshold value to soil water and photosynthetically-active radiation (PAR). The non-rectangular hyperbola model was used to simulate light-response curve and the convexity was about 1. With the increase of soil relative water content of field capacity (Wr, ranged from 20.1% to 71.1%), the light compensation point declined while light saturation point, the maximum P_N and apparent quantum yield increased. When Wr was about 71.7%, the light compensation point was at the minimum (21.61μmol/m^2/s) and the light saturation point was at the maximum (1400 μmol/m^2/s). In order to maintain the normal plant growth and have higher P_N, LUE, and WUE synchronously, the range of Wr was from 49.5 to 71.1%. The optimum Wr was 71.1%, and the minimum Wr was 28.2% for the normal growth of *C .radicans*. The high P_N and WUE were recorded when PAR ranged from 800 to 1600 μmol/m^2/s and the light saturation points ranged from 800 to 1400 μmol/m^2/s. The peak value of LUE was found when PAR ranged from 100 to 300 μmol/m^2/s, indicating that the *C. radicans* had high adaptability to light conditions.**

Key words: *Campsis radicans*, soil water content, photosynthetically-active radiation, photosynthetic efficiency, water use efficiency.

INTRODUCTION

In loess hilly region of China, soil water and light intensity are important ecological factors influencing plant growth and distribution. Both have effects on photosynthesis and transpiration as shown in the levels of water and solar energy utilization efficiency among plants (Mitton et al., 1998; Sobrado, 2000; Ashraf and Arfan, 2005; Lavinsky et al., 2007; Islam et al., 2008; Fu et al., 2010). Light has become an important environment factor with the reductions in ozone (Bertamini and Nedunchezhian, 2003; Lavinsky et al., 2007; Guan et al., 2010). Meanwhile, soil drought is the most critical ecological factor restraining vegetation restoration and affecting agricultural and forestry productivity. As problems caused by water crisis and drought worsen, the need to develop ways of saving water for use in agriculture and forestry has become urgent. How vegetation could best adapt to soil drought and light stress caused by global climate change has

*Corresponding authors. E-mail: zhsyong@126.com, xiajb@163.com. Tel.:86-543-3195586

been the focus of research in the fields of agriculture and forestry in recent years. Photosynthetic characteristics and space-time dynamics of ecological factors have become primary components of recent studies, some of which look into the characteristics of gas exchange under soil water stress merely involving three or four moisture gradients (Bertamini and Nedunchezhian, 2003; Zhu et al., 2006; Tong et al., 2007; Sofo et al., 2009). However, there has been no systematic study on photosynthetic and physiological indexes, as well as the fitting soil water and light conditions for vegetation growth. Hence, knowledge on photosynthetic and physiological changes remains inadequate.

A liana called *Campsis radicans* with vigorous roots, whose provenance is northern America, is now planted in many areas of China. *C. radicans* is a main liana species of conserving soil and water, improving ecological environment on the Loess Plateau, especially its semi-arid loess hilly region. The liana has great potential in that it can be used to help restore vegetation in semi-arid loess hilly area. Previously, research on *C. radicans* mainly focused on its development and utilization (such as gardening, planting technique, etc.) (Chen et al., 2005; Wang and Ma, 2004). The study, however, on its ecophysiological characteristics is still at the preliminary stage. The objectives of this study were to understand the ecophysiological processes and responses to light intensity of *C. radicans* under different soil water conditions, indicate the effects of soil water deficits and strong light stress on net photosynthetic rate (P_N), transpiration rate (Tr), water use efficiency (WUE), and light use efficiency (LUE), and confirm the range of appropriate soil water and light intensity which keeps the plant's higher photosynthetic capacity and WUE. The study also provide a scientific basis and technical standard for field water management and water-saving irrigation of restoring vegetation in loess hilly region of China.

MATERIALS AND METHODS

Study area

The experimental site is located in Chemingyu forest station, Zhongyang County, Shanxi province, China, a part of the gully-hilly area of the Loess Plateau in the middle reaches of the Yellow River. It lies at north latitude 37°03′ 14″, east longitude 110°04′ 15″, and belongs to warm temperature zone with a drought and obvious continental monsoon climate. The average annual precipitation is 525 mm, and the precipitation in June, July, August and September is more than 70%. The annual potential evaporation is 1019.7 mm. The average temperature is about 6°C and the extremely highest and lowest temperature is 35.6°C (June 16th, 1994) and -24.3°C (Jan 30th, 1980), respectively. Frostless season is about 135 days, and annual accumulated temperature over 10°C is 2750°C The soil is classified as brown and cinnamon soil, with inferior development and severe water and soil erosion. The vegetation type is forest-steppe and shrub zones with little shrub species and most of woodland is open forest with low stability.

Experimental materials and soil water disposal

Six pieces of three-year-old *C. radicans* seedlings (12±1.4 mm in diameter at the base) grown at the field of study area were transplanted to buckets (120 cm depth, 60 cm diameter, one plant per bucket) containing 15 kg well-mixed forest soil. The plants were potted on March 2 (the pots were buried chronically in the soil to make same temperature). The field capacity and bulk density, measured by a ring sample, was about 27.3% and 1.22 g/cm^3 respectively. A one-meter-long aluminum tube of LNW-50A neutron probes (CAS, Nanjing, Jiangsu, CHN) was buried about 0.2 m away from the *C. radicans* seedlings. Three months later (June 9), the soil water gradient was obtained by providing water supply and natural water consumption. The detailed method we used was as follows: first, two days before the experimental observation, we selected three potted materials at random denoted by 1, 2 and 3. We provided same water supplies to three seedlings, and then monitored the change of soil mass water content (Wm) and soil Wr by the neutron probes. Two days later, we obtained the early soil water gradient and carried out the first observation, with Wm measured with a LNW-50A neutron probe (CAS, Nanjing, Jiangsu, CHN) in three seedlings (average of three seedlings). According to D-optimum law (Kiefer and Wolfowitz, 1952), after producing a continuous degree of soil water stress (Table 1) by evapo-transpiration every two or three days, the second and third observations were carried out. The soil water treatment lasted for three days (from June 9 to 11), and eight soil water stress grades were obtained (Table 1).

Observation of photosynthetic responses to light intensity

Photosynthetic parameters were taken on mature leaves (from an intermediate position on the stem) in each of the three replicate plants during the soil water period, using a programmable open-flow gas exchange portable system (CIRAS-2, PP System, UK). To reduce the effect of light fluctuation, the measurements of photosynthetic light-response of every soil water gradient was carried out on clear days at 09:00 to 11:30 h in all the eight soil water stress grades. The photosynthetic light-response curves were measured at a range of photosynthetically-active radiation (PAR), which was changed every 120 s in a sequence of 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 250, 200, 150, 100, 50 and 20 µmol/m^2/s, with controlled CO_2 (370 µmol/mol) and artificial light, and leaf-chamber temperature was maintained at about 30±0.5°C, which was close to air temperature. The photosynthesis system automatically recorded gas exchange parameters, such as P_N, PAR and Tr etc., the following two ratios were calculated: WUE = P_N / Tr (Nijs et al., 1997), and LUE = P_N /PAR (Long et al., 1993).

Calculation and statistical analysis

The non-rectangular hyperbola model was used to fit light-response curves (Graham, 2001).

$$P_N = \frac{(AQY)(PAR) + P_{N\,max} - \sqrt{((AQY)(PAR) + P_{N\,max})^2 - 4(AQY)(PAR)KP_{N\,max}}}{2K} - R_D$$

In the formula, P_N is the net photosynthetic rate, AQY is the apparent quantum yield, PAR is the photosynthetic active radiation, $P_{N\,max}$ is the maximum photosynthetic rate, K is the curvature of the light response curve (convexity), and R_D is the dark respiration rate. R_D, AQY, and light compensation points (LCP) were calculated by carrying through linear regression to the beginning parts of response curves (PAR < 200 µmol/m^2/s), and the light saturation

Table 1. Light-response of photosynthetic parameters of *C. radicans* under different soil water conditions.

W_m (%) (W_r, %)	K	$P_{N\ max}$ (μmol/m^2/s)	AQY (μmol/mol)	R_D (μmol/m^2/s)	LCP (μmol/m^2/s)	LSP (μmol/m^2/s)
23.1 (84.6)	0.92±0.02^b	7.01±1.11^b	0.024±0.002^c	0.71±0.03^a	29.51±1.32^b	1000±150^a
21.4 (78.4)	0.92±0.01^b	10.91±0.98^d	0.031±0.001^d	1.17±0.02^e	37.36±2.12^c	1400±104^c
19.4 (71.1)	0.93±0.01^b	17.13±1.21^g	0.049±0.002^f	1.05±0.01^d	21.61±0.98^a	1400±150^c
16.5 (60.4)	0.95±0.02^c	14.80±1.23^f	0.037±0.002^e	0.82±0.05^b	21.87±1.57^a	1400±100^c
13.5 (49.5)	0.95±0.02^c	12.41±1.97^e	0.033±0.003^d	0.76±0.03^a	22.82±2.78^a	1000±150^a
10.7 (39.2)	0.93±0.02^b	8.58±0.95^c	0.031±0.001^d	0.86±0.03^b	28.04±2.86^b	1200±150^b
7.7 (28.2)	0.80±0.03^a	6.37±1.08^b	0.020±0.002^b	0.93±0.02^c	45.80±1.57^d	1000±100^a
5.5 (20.1)	0.96±0.01^c	3.12±0.98^a	0.012±0.002^a	1.09±0.04^d	95.11±1.85^e	800±100^a

$P_{N\ max}$, maximum of net photosynthetic rate; AQY, apparent quantum yield; R_D, dark respiration rate; LCP, light compensation points; LSP, light saturation point; K, convexity; Wm, soil mass water content; Wr, soil relative water content. Means (n=3) with the same letter within columns are not significantly different at $P < 0.05$.

points (LSP) value could be estimated after fitting the light-response curves of photosynthesis (Zhang et al., 2000). The light response simulation process was analyzed by carrying out cluster analysis and variance analysis using statistics analysis software. All statistical analyses were performed with SPSS 12.0 and Excel 2003 for windows. Repeated measurement analysis of variance (ANOVA) was used and mean differences were considered using Duncan's multiple range test significant at P<0.05.

RESULTS

Parameters of light-response curves under different soil water content

In Figure 1A, the light-response curves shows that the P_N fitted value and factual value were almost similar under different soil water conditions, and all R^2 of the fitted equation were over 0.97, indicating that the model could better fit the light response process of leaf P_N. The fitted value of $P_{N\ max}$ was higher than the factual value; was correlated to the character of this curve style, with P_N slowly decline after exceeding LSP. The calculated LSP according to the fitted value of $P_{N\ max}$, was higher than the factual value. Therefore, the LSP could be estimated by fitting the light-response curves of photosynthesis.

The convexity K represented the shape of light-response curves. The values of K had little discrepancy under different soil water conditions, and kept a higher level approaching 1(Table 1 and Figure 1A). The light-response curves of *C. radicans* ascended faster before LSP, and were similar basically after LSP with P_N maintaining a ascending trendy. Leaf $P_{N\ max}$ and AQY were important parameters indicating plant photo-synthetic capacity. R_D, the source of material and energy to maintain normal plant growth and development, also played an important role (Liu et al., 2003; Isam et al., 2008). $P_{N\ max}$ and AQY increased, to some extent, with the increase in soil water and reached the highest level when W_m was 19.4%. The potential of photo-assimilation was maximal and, in W_m of 19.4%, both AQY and leaf physiological activity were higher. Therefore, it was easy to obtain higher photosynthetic rate in high light intensity. After that, $P_{N\ max}$ and AQY descended sharply with the increase of soil water, and P_N reached the highest level approximating the intermediate water stress (W_m was about 10.7%). Notably, under different soil water conditions, the value of AQY was lower than the theoretic maximum quantum efficiency (which is 0.125), which was reasonable (Table 1). However, the change of R_D was very complicated, and the consumption of photosynthetic product under different moisture conditions resulted in greater discrepancy. Under higher soil water (W_m was about 21.4%) and severe soil water stress (W_m was about 5.5%), the consumption of photosynthetic product was higher; however, in middle soil water stress (W_m was about 13.5%), because of R_D, the consumption of photosynthetic product through respiration was reduced, indicating that it was propitious to dry matter accumulation and for laying the benign foundation to improve biomass.

The LCP of *C. radicans* was 21.61 to 95.11μmol/m^2/s between sciophyte (LCP<20 μmol/m^2/s) and h eliophyte (50 μmol/m^2/s<LCP<100 μmol/m^2/s) in the range of 5.5 to 23.1% (W_m). When W_m was less than 19.4%, LCP decreased as W_m increased, whereas under higher or lower soil water conditions, LCP tended to increase, indicating that the ability of utilizing low light diminished. When soil water was low (W_m was about 5.5%, W_r was about 20.1%), LSP was about 800 μmol/m^2/s; otherwise, LSP was about 1000 to 1400 μmol/m^2/s. The above mentioned results suggest that *C. radicans* has a strongly apricus photophilic character and puts up plasticity and adaption to light intensity to some extent under different soil water conditions. *C. radicans* also showed its better ability to utilize high light and low light under fitting soil water conditions.

The light-response of net photosynthesis rate to soil water content

As seen in Figure 1A, to a certain extent, P_N increased as

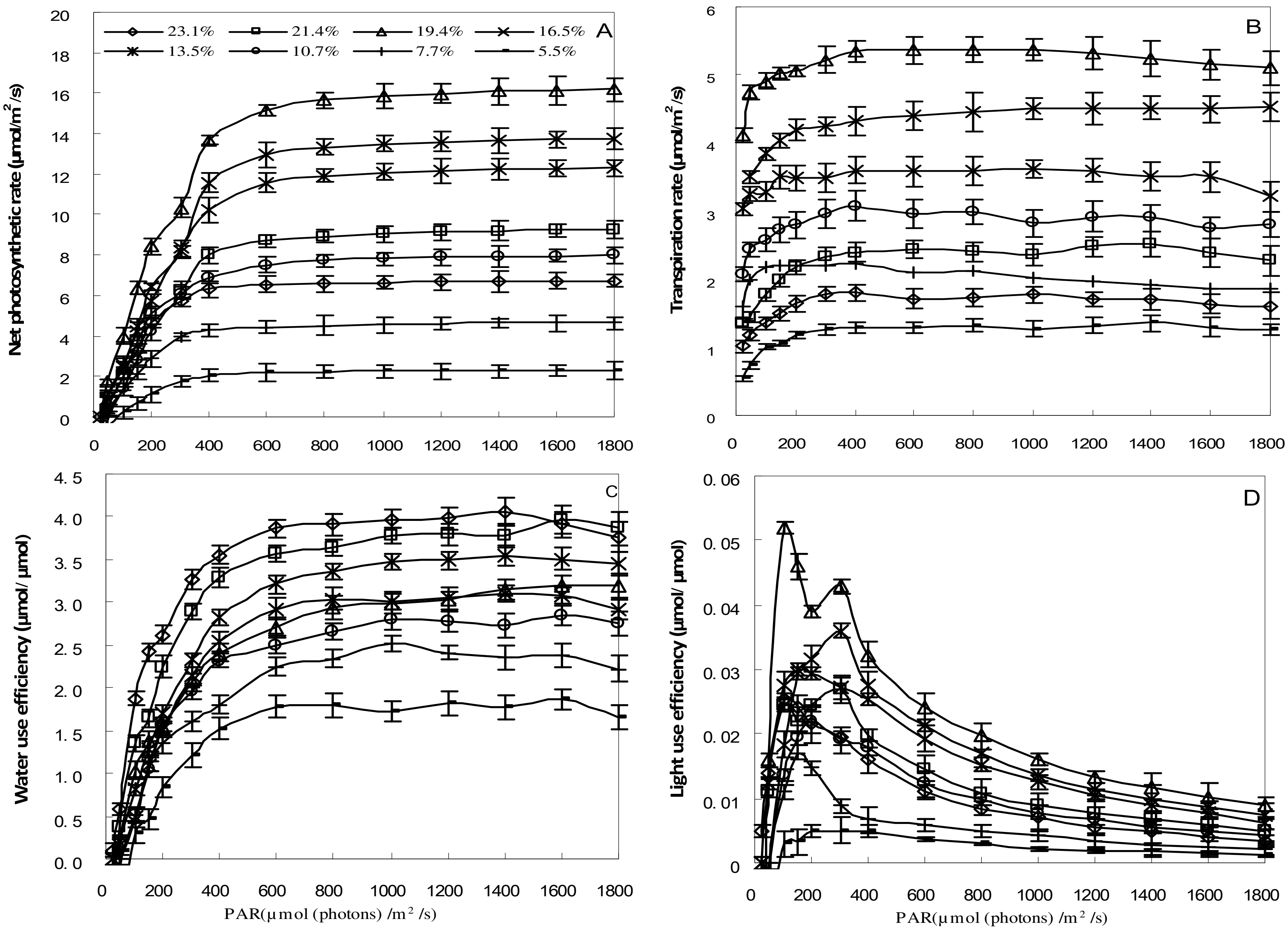

Figure 1. Light-response curves of net photosynthetic rate (P_N). (A), transpiration rate(Tr); (B), water use efficiency (WUE); (C) light use efficiency (LUE); (D) *C. radicans* leaves under different soil water conditions (soil mass water content (Wm)) (Means+SD, n=3).

PAR strengthened within the range of light intensity under different soil water conditions; when light intensity was out of range, the increscent trend gradually weakened. Concrete reflection was as follows: P_N was hypersensitive to the response of PAR change under different soil water conditions in low light intensity (PAR < 400 μmol/m^2/s) and P_N ascended swiftly with PAR strengthening. In this research, P_N had an obvious discrepancy under different soil water conditions in the same light intensity. P_N reached the highest level with PAR continuously strengthened, such that when the PAR reached LSP, P_N tended to fall with the increase of PAR, maintaining a high level when the PAR ranged from 600 to 1600 μmol/m^2/s. P_N in response to Wm indicate that the mean value of P_N increased with the increase of Wm range from 5.5 to 19.4%; out of this range, P_N then tended to decline with the increase of Wm. Therefore, the Wm of 19.4% (Wr was about 71.1%) could be considered as the turning point of P_N change.

Analyses suggest that in order to improve the photosynthetic productivity of *C. radicans*, there must be fitting soil water (Wm) at about 13.5 to 19.4% to maintain higher photosynthetic productivity, and corresponding fitting PAR was about 800 to 1600 μmol/m^2/s. When Wm was about 19.4%, P_N was at the maximum (17.13 μmol/m^2/s), and corresponding PAR was about 1400 to 1600 μmol/m^2/s.

The light-response of transpiration rate to soil water content

Light-response curves of Tr tended to be similar even under different soil water conditions (Figure 1B). Tr obviously ascended with the increase of PAR in low light intensity (PAR<200 μmol/m^2/s), and then ascended slowly as PAR increased. The change of PAR (PAR>500 μmol/m^2/s) had very little influence on the Tr under the same soil water conditions. There was obvious difference in Tr under different soil water conditions. When Wm was below 19.4%, Tr obviously increased with the rise of Wm. The fitting soil water (Wm), which gives the leaves a high Tr value, was about 10.7 to 19.4%, whereas out of this range, Tr descended whether Wm increased or decreased. When Wm was about 19.4%, Tr maintained the highest level. It indicated that Tr of *C. radicans* was more influenced by soil water than by the change in light intensity.

The light-response of water use efficiency to soil water content

The light-response change trend of WUE resembled that of P_N (Figure 1C). WUE was hypersensitive to PAR in low light intensity (PAR<400 μmol/m^2/s), and ascended slowly to reach LSP (600 to 1400 μmol/m^2/s). After that, the change of PAR had little influence on WUE, and only in low soil water and high light intensity, WUE decreased largely, showing that *C. radicans* adapted to light intensity in a wide range (WUE reached the same level when PAR ranged from 600 to 1600 μmol/m^2/s). There was obvious difference about WUE under different soil water conditions, tending to rise with the increase of Wm and reaching the highest level at saturated soil water conditions. WUE in the Wm of 13.5% was obviously larger than that of 19.4%, perhaps correlative to the fact that the decline range of Tr was larger than that of P_N in the Wm of 13.5%. Whether the soil water was mild stressed or severe stressed, the WUE of *C. radicans* maintained high level, indicating there was a wide adapting range about soil water. In order to maintain the high WUE, the range of Wm was from 10.7 to 23.1% and the range of Wr was from 39.2 to 84.6%.

The light-response of light use efficiency to soil water content

The light-response of LUE, which was obviously unimodal curve changing in the range of 0.001 to 0.05, was similar under different soil water conditions (Figure 1D). In low light intensity (PAR<200 μmol/m^2/s), as PAR strengthened, LUE (which was hypersensitive to responses of light intensity) sharply ascended and reached peak value in the range of 100 to 300 μmol/m^2/s; thereafter, LUE gradually descended but had little difference in high light intensity (PAR>1000 μmol/m^2/s). LUE was more influenced by soil water, and LUE increased as Wm ranged from 5.5 to 19.4% increased. LUE rose to its highest level when Wm was 19.4%. Thereafter, LUE tended to diminish at the increase of Wm. The value of LUE was lower at the high (Wm was 23.1%) or low soil water (Wm was 10.7%). Under the conditions of soil water deficiency or oversaturation, the LUE fell to a certain extent. The range of Wm maintaining higher LUE was about 10.7 to 23.1% and the fitting PAR was about 100 to 800 μmol/m^2/s.

DISCUSSION

The processes of photosynthesis and transpiration were hypersensitive to changes in the environment for plants (Moutinho-Pereira et al., 2004). The environment responses of leaf P_N showed that plants could live and grow under different light conditions and adapt to continual environment changes (Mielke et al., 2000; Montanaro et al., 2009). The fitting soil water and light conditions of WUE and LUE were ascertained by improving high photosynthetic productivity and effective transpiration for *C. radicans*. P_N was lower when Wm was less than 7.7%, in severe soil water stress. At soil water oversaturation (Wm was over 19.4%), P_N tended to descend with the improvement of soil water conditions. In view of the range of fitting soil water and light intensity for maintaining higher LUE, the Wm turning zone of P_N, LUE, and WUE combined with change of soil water were in the range of 10.7 to 19.4% (39.2%<Wr<71.1%). P_N, Tr, LUE, and WUE maintained higher levels when Wm was about 13.5 to 19.4% (49.5%<Wr<71.1%). Out of this range, higher or lower soil water was unfavorable for improvement of the P_N, LUE, and WUE. This range of Wm could be considered as the fitting soil water for growth of *C. radicans* seedlings, and the fitting PAR ranged from 800 to 1600 µmol/m^2/s. The range of soil water and light intensity not only ensured higher photosynthesis, restricted water consumption due to transpiration, but also maintained higher WUE, prevented the defective growth and development due to severe soil water stress. When Wm was below 7.7% (Wm was about 5.5%), severe soil water stress and high light intensity might have led to the photodamage in the photosynthetic apparatus, decreased the value of P_N, LUE, and WUE, thus influencing the growth and development of *C. radicans*. The Wm of 7.7% (Wr was about 28.2%) was the minimum of soil water, which maintained *C.radicans* normal growth. Compared with studies made on other plants under the same environment conditions, the ranges of Wr for maintaining higher P_N, and WUE were as follows: agriculture crops (*Triticum aestivum*) were about 60 to 80% (Zhang et al., 2001), *Parthenocissus quinquefolia* Planch was about 45.2 to 65.7% (Zhang et al. 2006), and *Wisteria sinensis* was about 46.4 to 80.3% (Zhang et al., 2007). The aforementioned indicate that *C. radicans* not only has a strong resistance to drought, but also has a better waterlogging tolerance.

The vegetation with a low LCP and high LSP usually had a strong adaptability to light environment (Sofo et al., 2009; Montanaro et al., 2009). This study indicate that LCP and AQY of *C. radicans* were about 21.6 to 22.8 µmol/m^2/s and 0.033 to 0.049 µmol/m^2/s respectively. The LCP of *C. radicans* was less than that of lower threshold of typical heliophytes (50 to 100 µmol/m^2/s) and its AQY was close to the value for normal plant growth (0.04 to 0.07) (Jiang, 2004; Long et al., 1994). Most leaves of *C. radicans* reached LSP in the range of 800 to 1400 µmol/m^2/s, and could maintain a high P_N and WUE in a wide light range (about 600-1600 µmol/m^2/s). It indicate that *C. radicans* has shade tolerance to some extent and adaptability to high light intensity, and has a wider light ecological amplitude.

Water use efficiency is not only a comprehensive index for confirming a plant's physiological function and adaptability to water environment, it is also useful in ascertaining a plant's water supply during its development and growth (Montanaro et al., 2009; Sobrado, 2000). When *C. radicans* suffered from water shortage or waterlogging stress (Wm was over 21.4% or below 10.7%), P_N and Tr both fell to low levels under high light intensity, while WUE stayed at a high level. It indicate that *C. radicans* has a better physiological character of water efficient, has a higher adaptive ability to the change of soil water and light intensity under soil water stress by regulating its physiological function (for example, diminishing transpiring water-consumption by a large margin), and then relieve the photodamage in the photosynthetic apparatus in order to maintain higher P_N and WUE.

A total of 90% of vegetation dry matter derives from photosynthesis, and the value of LUE is an important factor for determining plant productivity (Penuelas et al., 1998; Huang, 2004; Ganji and Shekarriz, 2010). LCP decreased while LSP and AQY ascended with the increase in Wm (5.5 to 19.4%), such that when Wm was about 19.4%, LCP was at its lowest (21.61µmol/m^2/s) and LSP was at its highest (1400 µmol/m^2/s). Under these soil water conditions, *C. radicans* had a better ability to utilize light levels of low and high, which was propitious to accumulating organic matter and adapting to multiple light conditions. Soil water deficiency obviously influenced LSP and AQY of photosynthesis in leaves of *C. radicans*, so that LUE in leaves decreased under the same PAR conditions. Fitting soil water could also improve LUE and light ecological amplitude of *C. radicans*. Therefore, in order to improve the LUE of *C. radicans*, it should be planted under fitting soil water conditions and a shed must be built to improve the plant's spatial collocation structure and enrich its biological production and competitive ability.

The aforementioned results show that photosynthesis, transpiration, and resource-use efficiency of *C. radicans* were closely correlative to soil water and light intensity and had a notable threshold of responses. Light responses of physiological parameters exhibited higher plasticity, indicating that *C. radicans* had better adaptability to light and soil water conditions, which is vital for *C. radicans* to grow and develop under different soil water and light regimes.

ACKNOWLEDGEMENTS

The work was financially supported by the National Natural Science Foundation of China, Project No. 31100468 and No. 30872003 ; by Important National Basic Research Program of China (973 Program-2012CB416904); by the National Key Science and Technology item in "11th Five Year" period, Project No. 2009BADB2B0502 and No. 2011BAC02B01-05.

Abbreviations:

P_N, Net photosynthetic rate; $P_{N\ max}$, maximum of net photosynthetic rate; AQY, apparent quantum yield; R_D, dark respiration rate; LCP, light compensation points; LSP, light saturation point; K, convexity; Wm, soil mass water content; Wr, soil relative water content; Tr, transpiration rate; WUE, water use efficiency; LUE, light use efficiency; PAR, photosynthetically-active radiation.

REFERENCES

Ashraf M, Arfan M (2005). Gas exchange characteristics and water relations in two cultivars of *Hibiscus esculentus* under waterlogging. Biologia Plantarum, 49: 459-462.

Bertamini M, Nedunchezhian N (2003). Photoinhibition of photosynthesis in mature and young leaves of grapevine. Plant Sci. 164: 635-644.

Chen HX, Tang QR, Jiang H (2005). The application of climbing shrub species in Changsha city virescence. Hunan Forest. Sci. Technol. 32: 48-49.

Fu QS, Zhao B, Wang YJ, REN S, GUO YD (2010). Stomatal development and associated photosynthetic performance of capsicum in response to differential light availabilities. Photosynthetica, 48: 189-198.

Ganji A, Shekarrizfard M (2010). A modified constrained state dormulation of stochastic soil moisture for crop water allocation. Water Resour. Manage. 24: 547-561.

Graham DF (2001). Models of photosynthesis. Plant Physiol. 125: 42-45.

Guan WC, Lu SH (2010). The short- and long-term response of *Scrippsiella trochoidea* (Pyrrophyta) to solar ultraviolet radiation. Photosynthetica, 48: 287-293.

Huang GH (2004). Modeling soil water regime and corn yields considering climatic uncertainty. Plant Soil, 259: 221-229.

Islam MR, Hamid A, Karim MA, Haque MM, Khaliq QA, Ahmed JU (2008). Gas exchanges and yield responses of mungbean (*Vigna radiata* L. Wilczek) genotypes differing in flooding tolerance. Acta . Physiol. Plant, 30: 697-707.

Jiang GM (2004). Plant Ecophysiology. Beijing: Higher Education Press, 65-68: 161-169.

Kiefer J, Wolfowitz J (1952). Stochastic estimation of the maximum of a regression function. Ann. Math. Stat. 23: 462-466.

Lavinsky AO, Sant'Ana CDS, Mielke MS, Almeida AFD, Gomes FP, Franca S, Silva DDC (2007). Effects of light availability and soil flooding on growth and photosynthetic characteristics of *Genipa Americana* L. seedlings. New Forests, 34: 41-50.

Liu MZ, Jiang GM, Li YG, Gao LM, Niu SL, Cui HX, Ding L (2003). Gas exchange, photochemical efficiency, and leaf water potential in three *Salix* species. Photosynthetica, 41: 393-398.

Long SP, Baker NR, Raines CA (1993). Analyzing the responses of photosynthetic CO_2 assimilation to long-term elevation of atmospheric CO_2 concentration. Vegetation, 104-105: 33-45.

Long SP, Humphries S, Falkowski PG (1994). Photoinhibition of photosynthesis in nature. Annu. Rev. Plant Physiol. Mol. Biol. 45: 633-662.

Mielke MS, Oliva MA, Barros NF, Penchel RM, Martinez CA, Fonseca Sda, Almeida AC (2000). Leaf gas exchange in a clonal eucalypt plantation as related to soil moisture, leaf water potential and microclimate variables. Trees, 14: 263-270.

Mitton JB, Garant MC, Yoshino AM (1998). Variation in allozymes and stomatal size in pinyou (*Pinusedulis,Pinaceae*), associated with soil moisture. Am. J. Bot. 85: 1262-1265.

Montanaro G, Dichio B, Xiloyannis C (2009). Shade mitigates photoinhibition and enhances water use efficiency in kiwifruit under drought. Photosynthetica, 47: 363-371.

Moutinho-Pereira JM, Correia CM, Goncalves BM, Bacelar EA, Torres-Pereira JM (2004). Leaf gas exchange and water relations of grapevines grown in three different conditions. Photosynthetica, 42: 81-86.

Nijs I, Ferris R, Blum H (1997). Stomatal regulation in a changing climate: A field study using free air temperature increase (FATI) and free air CO_2 enrichment. Plant, Cell Environ. 20: 1041-1050.

Penuelas J, Filella I, Llusia J (1998). Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees Quercus ilex and Phillyrea latifolia. J. Exp. Bot. 49: 229-238.

Sobrado MA (2000). Relation of water transport to leaf gas exchange properties in three mangrove species.Trees, 14: 258-262.

Sofo A, Dichio B, Montanaro G, Xiloyannis C (2009). Photosynthetic performance and light response of two olive cultivars under different water and light regimes. Photosynthetica, 47: 602-608.

Tong FP, Fang W, Ma LY (2007). Study on response to photosynthetic characters of Slash Pine's half-sib under water stress. J. of Nanjing Forestry University (Natural Sciences Edition). 31: 32-36.

Wang Y, Ma WC (2004). Comparative studies on light utilization characteristics and shade tolerance of 7 climbing shrub species. Forest Res. 17: 305-309.

Zhang GC, Liu X, He KN (2001). Fitting soil moisture environment of trees Growthon Loess Plateau in semi-arid region. J. Soil Water Conserv. 15: 1-5.

Zhang SY, Xia JB, Zhou ZF, Zhang GC (2007). Photosynthesis responses to various soil moisture in leaves of *Wisteria sinensis*. J. Forest. Res. 18: 217-220.

Zhang SY, Zhou ZF, Zhang GC, XIA JB, Zhan HX (2006). Ecophysiological Characteristics of *Parthenocissus quinquefolia* Planch under different soil moisture condition. Forest. Sci. Technol. 5: 76-81.

Zhang XQ, Xu DY (2000). Seasonal changes and daily courses of photosynthetic characteristics of 18-year-old *Chinese fir* shoots in relation to shoot ages and positions within tree grown. Scientia Silvae Sinicae, 36: 19-26.

Zhu JJ, Kang HZ, Li ZH (2006). Comparison of different types of drought stresses affecting photosynthesis of *Mongolian pine* seedlings on sandy soils. J. Beijing Forest. Univ. 28: 57-63.