

PHOTOSYNTHETIC CARBON FIXATION CAPACITY OF BLACK LOCUST IN RAPID RESPONSE TO PLANTATION THINNING ON THE SEMIARID LOESS PLATEAU IN CHINA

YUAN ZHENG^{1,3}, JINGJING ZHOU^{2,3}, HUI ZHOU³ AND ZHONG ZHAO^{3*}

¹College of Forestry, Southwest Forestry University, Kunming, Yunnan 650224, P. R. China

²College of Horticulture & Forestry Sciences, Huazhong Agriculture University, Wuhan, Hubei, P. R. China

³Key Laboratory of Environment and Ecology in Western China of Ministry of Education, Northwest A & F University, Yangling, Shaanxi 712100, P. R. China

*Corresponding author's email: zhaozh@nwsuaf.edu.cn

Abstract

Black locust (*Robinia pseudoacacia* L.) has been widely planted throughout the semiarid Loess Plateau in China. However, black locust plantations likely induce stand degradation and soil desiccation because of high water consumption, high stand density, and insufficient stand management. In this study, five kinds of density types in 19-year-old black locust plantations, including three intact non-thinned control plantation types with different stand densities (1800, 2700, and 3600 trees ha⁻¹) and two thinned-treatment plantation types with the same stand densities (1800 trees ha⁻¹) were selected to calculate the responses to thinning intensity in the Maliantan catchment within the central Loess Plateau. Gas exchange, leaf area index, associated changes in the photosynthetic carbon fixation capacity (PCFC), and environmental variables (light radiation, air temperature, and soil moisture) were determined throughout the growing season in 2009. The growth, daily leaf-level net CO₂ assimilation rate (A_n), and tree-level PCFC were significantly different among the three intact black locust plantations in their annual growth period. A_n and PCFC increased as the stand density decreased because of enhanced environmental resource availabilities per individual tree, including the increased exposure to light radiation, canopy air temperature, and soil moisture level. Comparing thinned and non-thinned black locust plantations, we provided ecophysiological evidence that black locust trees could actively adjust their photosynthetic functions from the beginning of the first growing season after thinning to enhance their height, diameter, and canopy diameter during growth and development. This mechanism indicated that the rapid adaptability of black locust in response to plantation thinning on the semiarid Loess Plateau. Based on the same stand density (1800 trees ha⁻¹), the low thinning intensity of 33% was more suitable for the sustainable management and increased of photosynthetic carbon fixation capacities of black locust trees on the Loess Plateau in China. These findings can enrich our knowledge of forest plantation dynamics and provide valuable information regarding sustainable plantation management in this ecological fragile region.

Key words: Gas exchange, Leaf area index, Photosynthetic carbon fixation capacity, Thinning intensity, Black locust, Loess Plateau.

Abbreviations: LAI: leaf area index; A_n : net CO₂ assimilation rate; PCFC: photosynthetic carbon fixation capacity; PAR: photosynthetic active radiation; α : apparent quantum yield; A_{max} : maximum photosynthetic rate; R_a : dark respiration rate; LCP: light compensation point; LSP: light saturation point

Introduction

The Loess Plateau in China is a fragile ecosystem that belongs to a typical semiarid region (62.7×10^4 km²) (Li *et al.*, 2013), and this ecosystem has suffered from long-term water and soil erosion (He *et al.*, 2006; Li *et al.*, 2006). Revegetation campaigns, including forest recovery through afforestation, have been extensively applied since 1978 to prevent soil erosion and degradation (Cao *et al.*, 2009; Jiao *et al.*, 2016). Widely distributed plantations are important vegetation types that cover more than 70,000 ha on the Loess Plateau and are dominated by shade intolerant species, such as black locust (*Robinia pseudoacacia* L.) (Qiu *et al.*, 2010). This dominance is attributed to the combination of the ecophysiological plasticity and advantageous characteristics, such as rapid growth, drought tolerance, and nitrogen fixation, of black locust (Feldhake 2001; Li *et al.*, 2014; Mantovani *et al.*, 2015). Black locust plantations on the Loess Plateau can act as a large carbon sink for atmospheric CO₂ (Zheng *et al.*, 2011). However, black locust plantations can barely regenerate in this region and likely induce stand degradation and soil desiccation with the development of a dry soil horizon in deep soil

layers (Wang *et al.*, 2001). This phenomenon is mainly due to high water consumption, high stand density, and insufficient stand management (Wu *et al.*, 2015; Zhang *et al.*, 2015; Jiao *et al.*, 2016).

Stand density-related changes in the physiological characteristics of trees are essential contributing factors to variations in photosynthesis at leaf and tree scales (Forrester *et al.*, 2011). Endogenous and exogenous factors, such as tree morphology (White *et al.*, 2009), radiation interception (Boucher *et al.*, 2007), and water status (Moreno and Cubera, 2008; Martin-Benito *et al.*, 2010), with different stand density plantations can remarkably affect photosynthesis under field conditions. Small-scale variations in micro-environmental conditions may influence the photosynthetic and physiological characteristics related to carbon fixation and water use by woody species (Flexas *et al.*, 2001; Balaguer *et al.*, 2002). Discrepancies in tree photosynthesis within different stand densities also affect the tree carbon gains and ecosystem productivities. Despite the importance of stand density in tree dynamics and performance in semiarid regions and the effects of stand density on tree photosynthesis, the influence of stand density on the

photosynthetic carbon fixation capacities of black locust plantations on the Loess Plateau has been rarely evaluated.

As an effective silvicultural management practice, plantation thinning has been extensively applied to improve stand growth, renewal, and environmental productivity and avoid the strong intraspecific competition of residual trees (Misson *et al.*, 2003). Thus, this mechanism generally leads to long-term consequences on the functioning of individual trees in different areas, particularly water-limited regions (Moreno-Gutierrez *et al.*, 2011). The beneficial growth and physiological responses of residual trees are probably due to improvements in their crown characteristics (Medhurst and Beadle, 2001; Yu *et al.*, 2003) and the increased availability of environmental resources (Breda *et al.*, 1995; Blanco *et al.*, 2008; Stupak *et al.*, 2008). However, the expected degree and time of responses of different tolerant and intolerant species to thinning remarkably vary (Medhurst and Beadle, 2005; Han *et al.*, 2006; Gauthier and Jacobs, 2009; Goudiaby *et al.*, 2011), and the response sensibility of the same species to thinning differs in magnitude (Ginn *et al.*, 1991; Peterson *et al.*, 1997; Tang *et al.*, 1999, 2003). To our knowledge, the effects of plantation thinning on tree functioning and semiarid woodland productivity have been seldom explored, and the photosynthetic responses of trees have been examined mostly at a single-leaf level.

This study aimed to test the hypothesis that the gas exchange, leaf area index (LAI), and associated photosynthetic carbon fixation capacity of black locust increase proportionally to the enhanced environmental resource availability created by increasing the plantation thinning intensity. To achieve this objective, we compared single-leaf and whole-tree responses to low and high thinning intensities in different 19-year-old black locust plantations with various stand densities on the semiarid Loess Plateau. Our study may enrich our knowledge of forest plantation dynamics and provide valuable information regarding sustainable plantation management in this fragile and challenging region.

Materials and Methods

Site description and sample plots: This study was conducted in the Maliantan catchment (34°29′–34°59′ N, 107°56′–108°20′ E, altitude 1116–1276 m above sea level) within the central Loess Plateau, which is a typically loess hilly and gully region in northern China. The mean annual precipitation is 601.6 mm, the annual mean air temperature is 10.8 °C, and the annual average potential evaporation is 807.4 mm (Zhang *et al.*, 2016). The soil of the catchment is typical loess with 11.3 g kg⁻¹ organic matter content, 44.2 µg g⁻¹ available N, 164.5 µg g⁻¹ available P, and 189.1 µg g⁻¹ available K (Zhang *et al.*, 2007).

The study area is the main region where afforestation campaigns have been implemented and black locust has been planted over the past few decades to restore the abandoned hillslope farmlands. Currently, most of the black locust trees in this area are 19 years old. These 19-year-old black locust plantations are categorized into five kinds: intact non-thinned control plantation with a density of 1800 trees ha⁻¹ (ND1, 30 ha), intact non-thinned control plantation with a density of 2700 trees ha⁻¹ (ND2, 14 ha), intact non-thinned control plantation with a density of 3600 trees ha⁻¹ (ND3, 18 ha), thinned-

treatment ND2 with a density of 1800 trees ha⁻¹ (TD2, 14 ha), and thinned-treatment ND3 with a density of 1800 trees ha⁻¹ (TD3, 18 ha). In particular, one-third of the trees in ND2 (low thinning intensity of 33%) and one-half of the trees in ND3 (high thinning intensity of 50%) were removed in November 2008 by harvesting the trees at an interval of two rows and then at an interval of every other tree in the remaining rows to maintain an even spacing between the residual trees in TD2 and TD3. ND2 and ND3 with the same size were separated by buffer zones to avoid boundary or edge effects and left un-thinned. ND1 versus ND2 versus ND3 was used to determine the effects of stand density on gas exchanges and photosynthetic carbon fixation capacities. TD2 versus ND2, TD3 versus ND3, and ND1 versus TD2 versus TD3 were considered to calculate the responses to thinning intensity.

In each density type (treatment), three black locust stands were selected on sunny (southeast-facing) slopes of three parallel ridges with a distance of ca. 200 m from one another. In each stand, three sample plots (20 m × 20 m) were randomly selected. In each sample plot, the height of each tree was determined using a height gauge, the diameter at breast height (DBH) was measured with a caliper, and the canopy diameter was identified using a tapeline. Three average sample trees were selected to measure gas exchange, LAI, and photosynthetic carbon fixation capacity (PCFC) on the basis of the similarities of height, diameter, and canopy diameter to the average values of all trees in each sample plot. One average sample tree was selected to obtain photosynthetic light response (A/PAR) curves under field conditions. The light radiation and air temperature within the canopy of black locust trees were automatically recorded by using a portable gas exchange system (Li-Cor 6400; Li-Cor Inc., Lincoln, NE, USA), and the daily mean light radiation and air temperature within canopy were estimated by averaging the data across all time points within the day. The soil moisture in the top 10 cm soil near each sample tree was measured through gravimetric method (Fang *et al.*, 2008). The characteristics of black locust plantations are listed in Table 1.

Gas exchange measurements: Black locust exhibits pronounced seasonality characterized by bud break in April, leaf fall in November, and growth season of approximately six months (Zou, 1986; Feldhake, 2001). As such, gas exchange was determined for eight, ten, and twelve months (one year) after plantation thinning, that is, in June (early growth period), August (vigorous growth period), and October (late growth period) 2009 on sunny days. A scaffold was used to reach the canopy for the intact measurements of leaf photosynthesis. Our previous study found that the net CO₂ assimilation rate (A_n) in the west middle layer of the black locust tree canopy was the same as that of the whole canopy, that is, the mean value of different orientations (east, south, west, and north) and layers (upper, middle, and lower) within the crown of the black locust (Zheng *et al.*, 2010). In the present study, three mature leaves from a western orientation in the middle canopy layer of each sample tree were selected for leaf-level A_n measurements, which were performed *in situ* on the selected leaves under local irradiance by using an LI-6400 gas exchange system from 6:00 to 18:00 at a 2 h interval in the third to fourth week in June, August, and October 2009.

Table 1. Characteristics of black locust plantations, which include non-thinned control plantation 1 (ND1), non-thinned control plantation 2 (ND2), non-thinned control plantation 3 (ND3), thinned ND2 (TD2), and thinned ND3 (TD3). The height, diameter at breast height (DBH), canopy diameter, and canopy density were determined before plantation thinning (in October 2008) and for one year after thinning (in October 2009). The data for the light radiation, air temperature, and soil moisture for eight months (in June 2009), ten months (in August 2009), one year (in October 2009) after thinning are the means \pm SE ($n = 27$), respectively.

| Plantation | | ND1 | ND2 | ND3 | TD2 | TD3 |
|--|--------------|----------------|----------------|----------------|----------------|----------------|
| Stand density (trees ha ⁻¹) | | 1800 | 2700 | 3600 | 1800 | 1800 |
| Altitude (m) | | 1209 | 1237 | 1194 | 1237 | 1194 |
| Slope (°) | | 6.6 | 8.9 | 7.9 | 8.9 | 7.9 |
| Canopy density | October 2008 | 0.7 | 0.7 | 0.8 | 0.6 | 0.8 |
| | October 2009 | 0.7 | 0.7 | 0.8 | 0.7 | 0.5 |
| Height (m) | October 2008 | 12.1 \pm 0.4 | 8.6 \pm 0.3 | 5.9 \pm 0.2 | 8.6 \pm 0.5 | 5.9 \pm 0.3 |
| | October 2009 | 12.5 \pm 0.7 | 8.8 \pm 0.4 | 6.0 \pm 0.3 | 9.2 \pm 0.4 | 6.1 \pm 0.3 |
| DBH (cm) | October 2008 | 10.0 \pm 0.5 | 8.0 \pm 0.3 | 5.8 \pm 0.3 | 7.8 \pm 0.5 | 5.7 \pm 0.4 |
| | October 2009 | 10.5 \pm 0.6 | 8.3 \pm 0.4 | 5.9 \pm 0.3 | 8.6 \pm 0.4 | 6.1 \pm 0.3 |
| Canopy diameter (m) | October 2008 | 3.2 \pm 0.3 | 2.6 \pm 0.4 | 1.5 \pm 0.3 | 2.3 \pm 0.3 | 1.5 \pm 0.2 |
| | October 2009 | 3.4 \pm 0.2 | 2.7 \pm 0.4 | 1.5 \pm 0.2 | 2.8 \pm 0.2 | 1.7 \pm 0.1 |
| Light radiation within canopy ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$) | June 2009 | 1197 \pm 52 | 1026 \pm 47 | 834 \pm 39 | 1233 \pm 56 | 1245 \pm 54 |
| | August 2009 | 1378 \pm 61 | 1235 \pm 57 | 1050 \pm 49 | 1365 \pm 62 | 1417 \pm 68 |
| | October 2009 | 1098 \pm 43 | 885 \pm 38 | 726 \pm 32 | 1067 \pm 45 | 1034 \pm 40 |
| Air temperature within canopy (°C) | June 2009 | 26.0 \pm 1.6 | 24.8 \pm 1.4 | 23.7 \pm 1.2 | 26.2 \pm 1.8 | 25.9 \pm 1.8 |
| | August 2009 | 32.2 \pm 2.8 | 30.4 \pm 2.2 | 27.8 \pm 1.9 | 31.9 \pm 2.6 | 32.5 \pm 2.7 |
| | October 2009 | 21.5 \pm 1.5 | 20.1 \pm 1.0 | 18.6 \pm 0.8 | 21.2 \pm 1.3 | 20.9 \pm 1.4 |
| Soil moisture in top 10 cm soil (%) | June 2009 | 16.4 \pm 1.6 | 15.5 \pm 1.5 | 13.8 \pm 1.4 | 15.9 \pm 1.7 | 14.7 \pm 1.6 |
| | August 2009 | 14.0 \pm 1.5 | 13.6 \pm 1.2 | 11.4 \pm 1.1 | 14.3 \pm 1.4 | 12.2 \pm 1.3 |
| | October 2009 | 24.1 \pm 1.9 | 23.6 \pm 1.8 | 21.0 \pm 1.9 | 24.0 \pm 2.1 | 21.8 \pm 2.0 |

A/PAR curves were measured *in situ* in leaves by using a 6400-02B light source from 9:00 to 11:00. The leaf photosynthetic responses to the photosynthetic active radiation (PAR) were constructed by obtaining measurements at 14 PAR values ranging from 0 $\mu\text{mol m}^{-2}$

s^{-1} to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the measured leaves acclimated to each light level for 3 min before switching. The relationship between A_n and PAR was fitted by a non-rectangular hyperbolic model (Herrick and Thomas, 1999; Zheng *et al.*, 2012):

$$A_n = \frac{\alpha \times PAR + A_{\max} - \sqrt{(\alpha \times PAR + A_{\max})^2 - 4 \times \alpha \times PAR \times \theta \times A_{\max}}}{2 \times \theta} - R_d \quad (1)$$

where A_n is the net CO_2 assimilation rate, PAR is the photosynthetic active radiation, α is the apparent quantum yield, A_{\max} is the maximum photosynthetic rate, θ is the convexity, R_d is the dark respiration rate. The light saturation point (LSP) was estimated according to the trends of the A/PAR curves, and the light compensation point (LCP) was calculated using the following equation:

$$LCP = \frac{A_{\max} \times R_d - \theta \times R_d^2}{\alpha \times (A_{\max} - R_d)} \quad (2)$$

Determination of LAI: LAI (m^2 of leaves per m^2 of ground) is a good indicator to determine the levels of the photosynthetic capacity of trees. To determine LAI, we acquired the images of each sample tree at four

orientations (east, south, west, and north) by using a digital camera equipped with a hemispheric lens (Minolta DiMAGE X, Konica Minolta Inc., Tokyo, Japan) at sunset according to the protocol (Regent Instruments Inc., Québec, Canada). The images were subsequently analyzed with WinScanopy (WinScanopy-2005a, Regent Instruments Inc., Québec, Canada) to obtain LAI (Frazer *et al.*, 2001; Zheng *et al.*, 2011).

Estimation of PCFC: The tree-level PCFC in black locust plantations were estimated on the basis of the leaf-level A_n and LAI data of the sample trees in this study. The daily photosynthetic carbon fixation capacity for the unit stand area (PCFC_{daily}, $\text{g CO}_2 \text{m}^{-2} \text{d}^{-1}$) was evaluated according to the daily net CO_2 assimilation rate for unit leaf area (A_{ndaily} , $\text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$) of black locust (Zheng *et al.*, 2011):

$$A_{\text{ndaily}} = \sum_{i=1}^j [(A_{ni+1} + A_{ni}) \times (t_{i+1} - t_i) / 2 \times 3600 / 1000] \quad (3)$$

where A_{ni} is the instantaneous A_n at a determination time ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), A_{ni+1} is the instantaneous A_n at the next determination time (2 h interval), t_i is the determination time, and t_{i+1} is the next determination time, j is the times of A_n determination, and 3600 refers to 3600 seconds per hour.

$$PCFC_{\text{daily}} = A_{\text{ndaily}} \times LAI \times 44 / 1000 \quad (4)$$

where LAI is the leaf area index, the molar mass of CO_2 is 44 g mol^{-1} , and 1000 refers to 1 gram or 1000 mg.

Statistical analysis

Significant differences among various treatment means were determined through ANOVA and Duncan's multiple range test (i.e., each treatment, 3 stands \times 3 sample plots \times 3 sample trees = 27 sample trees) in SPSS version 13 (SPSS Inc., Chicago, USA). Normality was assessed visually and then quantitatively with Kolmogorov–Smirnov test. For each parameter, the values followed by different letters and asterisks indicated significant differences when the P -value of ANOVA F -test was less than 0.05.

Results

Effects of stand density on gas exchange, LAI, and PCFC: The leaf-level A_n data in ND1 (1800 trees ha^{-1}), ND2 (2700 trees ha^{-1}), and ND3 (3600 trees ha^{-1}) were analyzed to determine the effects of stand density on the daily gas exchanges of black locust trees. In June 2009, the daily A_n at leaf level in ND1 and ND2 slightly varies, but these values were significantly higher than those in ND3 (Fig. 1b). In August and

October, A_n in ND1 was markedly higher than its counterpart in ND2 and in turn pronouncedly greater than the value in ND3 (Fig. 1b). The height, DBH, and canopy diameter in intact black locust plantations was decreased as the stand density increased (Table 1). Although the A/PAR curves in ND1, ND2, and ND3 revealed similar trends, stand density significantly influenced the leaf-level photosynthetic sensibility to irradiance (Fig. 2), and α , A_{max} , and R_d of black locust showed similar patterns in June, August, and October 2009: ND1 > ND2 > ND3. For A_{max} in October, the following trend was observed: ND1 > ND3 > ND2 (Table 2). By contrast, the LCP values of the black locust among ND1, ND2, and ND3 changed slightly, and no significant variations for the LSP existed with different stand densities during the whole measurement periods (Table 2).

To estimate the PCFC at tree level in different stand-density black locust plantations, the LAI in ND1, ND2, and ND3 were analyzed. In June and August 2009, ND3 had marked and/or slightly higher LAI than ND1 and ND2, whereas no significant difference of LAI existed between ND1 and ND2 (Fig. 1a). In October, no obvious differences existed among ND1, ND2, and ND3 (Fig. 1a). The tree-level PCFC was estimated based on the A_n and LAI data, the PCFC in ND1, ND2, and ND3 present pronounced variations in June, August, and October, the PCFC in ND1 was significantly higher than that in ND2, which was significantly higher than that in ND3 (Fig. 1c). The growth, daily A_n , and PCFC of black locust trees increased as the stand density became lower possibly due to the increased canopy light radiation, canopy air temperature, and soil moisture level (Table 1).

Table 2. Calculations of the apparent quantum yield (α), maximum photosynthetic rate (A_{max}), dark respiration rate (R_d), light compensation point (LCP), and light saturation point (LSP) of black locust trees in ND1, ND2, ND3, TD2, and TD3. The mean values \pm SE (n = 9). Different letters in the columns indicate significant difference at $p \leq 0.05$.

| Month and year | Plantation type | α ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon) | A_{max} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | R_d ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | LCP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | LSP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) |
|----------------|-----------------|--|---|--|--|--|
| June 2009 | ND1 | 0.079 \pm 0.005 a | 9.03 \pm 0.29 b | 1.76 \pm 0.18 a | 23.57 \pm 2.72 ab | 866.67 \pm 33.33 a |
| | ND2 | 0.071 \pm 0.003 ab | 7.94 \pm 0.08 bc | 1.29 \pm 0.06 b | 19.27 \pm 1.29 b | 933.33 \pm 33.33 a |
| | ND3 | 0.041 \pm 0.002 d | 6.19 \pm 0.16 d | 0.82 \pm 0.09 c | 20.71 \pm 2.33 b | 933.33 \pm 33.33 a |
| | TD2 | 0.061 \pm 0.006 bc | 12.31 \pm 0.50 a | 1.26 \pm 0.27 b | 21.42 \pm 1.83 b | 955.56 \pm 29.40 a |
| | TD3 | 0.056 \pm 0.006 c | 6.85 \pm 0.12 cd | 1.33 \pm 0.09 b | 26.51 \pm 0.96 a | 955.56 \pm 29.40 a |
| August 2009 | ND1 | 0.089 \pm 0.013 a | 14.61 \pm 0.41 a | 1.20 \pm 0.26 a | 14.17 \pm 0.82 a | 911.11 \pm 35.14 a |
| | ND2 | 0.067 \pm 0.006 b | 12.96 \pm 0.27 a | 1.03 \pm 0.15 a | 16.25 \pm 0.94 a | 933.33 \pm 33.33 a |
| | ND3 | 0.052 \pm 0.005 c | 8.46 \pm 0.37 b | 0.72 \pm 0.19 b | 14.40 \pm 1.35 a | 911.11 \pm 35.14 a |
| | TD2 | 0.063 \pm 0.010 bc | 14.84 \pm 0.74 a | 0.94 \pm 0.28ab | 13.72 \pm 0.94 a | 933.33 \pm 33.33 a |
| | TD3 | 0.055 \pm 0.019 bc | 10.52 \pm 0.57 b | 0.77 \pm 0.32 b | 14.83 \pm 1.51 a | 933.33 \pm 33.33 a |
| October 2009 | ND1 | 0.078 \pm 0.014 a | 8.94 \pm 0.26 a | 0.52 \pm 0.17 a | 6.94 \pm 0.040 bc | 933.33 \pm 33.33 a |
| | ND2 | 0.058 \pm 0.016 b | 3.59 \pm 0.14 c | 0.41 \pm 0.10 b | 7.30 \pm 0.77 b | 955.56 \pm 29.40 a |
| | ND3 | 0.051 \pm 0.003 b | 3.76 \pm 0.04 c | 0.29 \pm 0.03 c | 5.75 \pm 0.36 cd | 933.33 \pm 33.33 a |
| | TD2 | 0.056 \pm 0.005 b | 6.52 \pm 0.14 b | 0.38 \pm 0.10 b | 5.01 \pm 0.35 d | 955.56 \pm 29.40 a |
| | TD3 | 0.060 \pm 0.014 b | 6.39 \pm 0.27 b | 0.49 \pm 0.16 a | 8.55 \pm 0.85 a | 933.33 \pm 33.33 a |

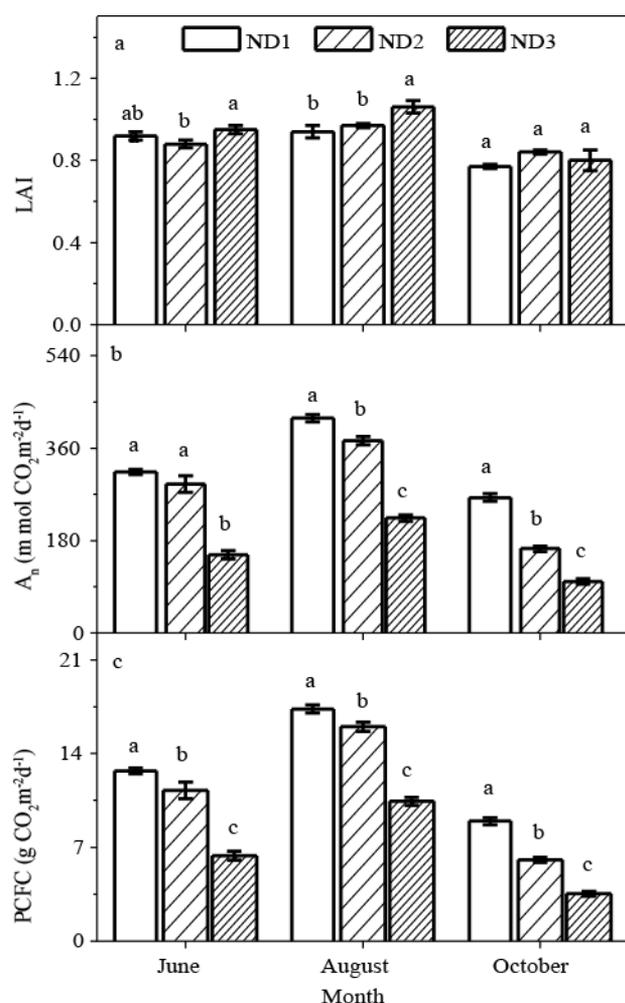


Fig. 1. Comparisons of the leaf area index (LAI), leaf-level net CO_2 assimilation rate (A_n), and tree-level photosynthetic carbon fixation capacity (PCFC) among ND1, ND2, and ND3. The mean values \pm SE ($n = 27$). Different letters on the bars indicate significant difference at $p \leq 0.05$.

Responses of gas exchange, LAI, and PCFC to thinning intensity: To obtain information on black locusts' responses of daily gas exchange, LAI, and PCFC to different thinning intensities, data recorded from field measurements in ND2 versus TD2, ND3 versus TD3, and ND1 versus TD2 versus TD3 were analyzed.

When comparing ND2 versus TD2 (low thinning intensity effect) in June (8 months after thinning) and October (12 months after thinning), the leaf-level daily A_n in TD2 were markedly higher than those in ND2, and in August (ten months after thinning), the leaf-level A_n in TD2 was slightly higher than that in ND2 (Fig. 3b). Thinning promoted the height, DBH, and crown of black locust trees, especially under the low thinning intensity (Table 1). In the whole annual growth periods, TD2 had slightly lower α and R_d but significantly higher A_{\max} than ND2, whereas the discrepancies for the LCP and/or LSP between ND2 and TD2 were weak (Table 2). The variation of LAI between ND2 and TD2 was limited in June and August but statistically significant in October (Fig. 3a). The tree-level PCFC comparative result was consistent with A_n between ND2 and TD2 (Fig. 3c); the

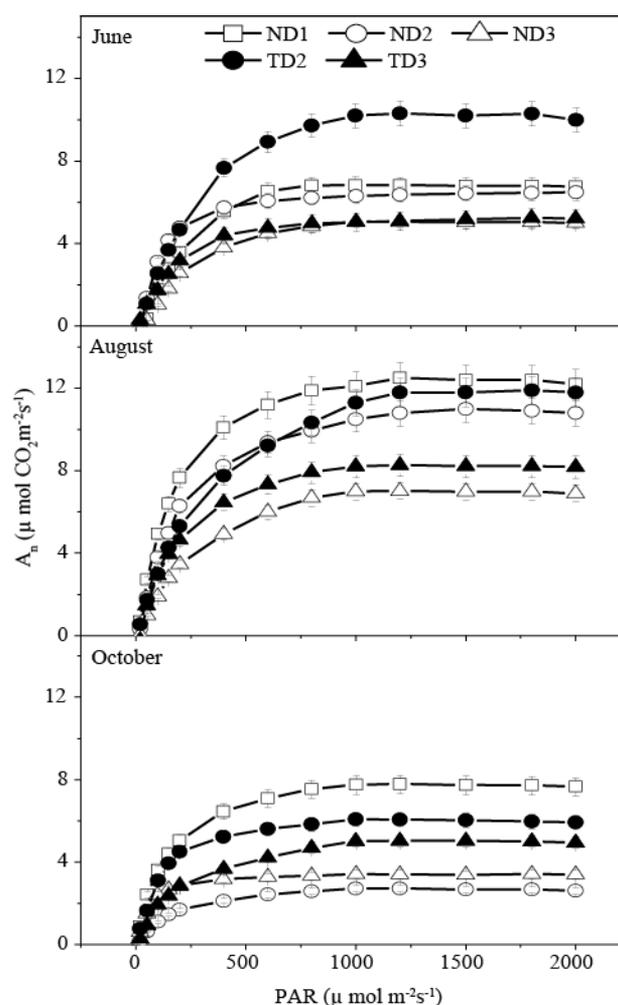


Fig. 2. Responses of the net CO_2 assimilation rate (A_n) to photosynthetic active radiation (PAR) of black locust trees in ND1, ND2, ND3, TD2, and TD3. The mean values \pm SE ($n = 9$).

daily PCFC value in TD2 was 34%, 5%, and 21% higher compared with that of ND2 in black locust tree's annual early, vigorous, and late growth period, respectively.

When comparing ND3 versus TD3 (high thinning intensity effect), the leaf-level daily A_n in TD3 were significantly greater compared with those in ND3 whether in June, August, and October (Fig. 4b). Moreover, the α , A_{\max} , R_d , and LCP values in TD3 were higher at different levels than the counterparts in ND3, but no considerable difference for the LSP value existed between ND3 and TD3 (Table 2). The LAI values in TD3 were 45%, 34%, and 24% markedly lower than that obtained in ND3 for 8, 10, and 12 months after thinning, respectively (Fig. 4a). Based on the A_n and LAI data, the tree-level daily PCFC in TD3 was pronouncedly lower than the counterpart in ND3 both in June and August (Fig. 4c) and was mainly caused by the pronounced decreases in thinning-related LAI and canopy density within TD3 (Table 1). However, the PCFC in TD3 started to increase significantly for one year after thinning mostly due to the negative effect on LAI in ND3 during leaf fall period.

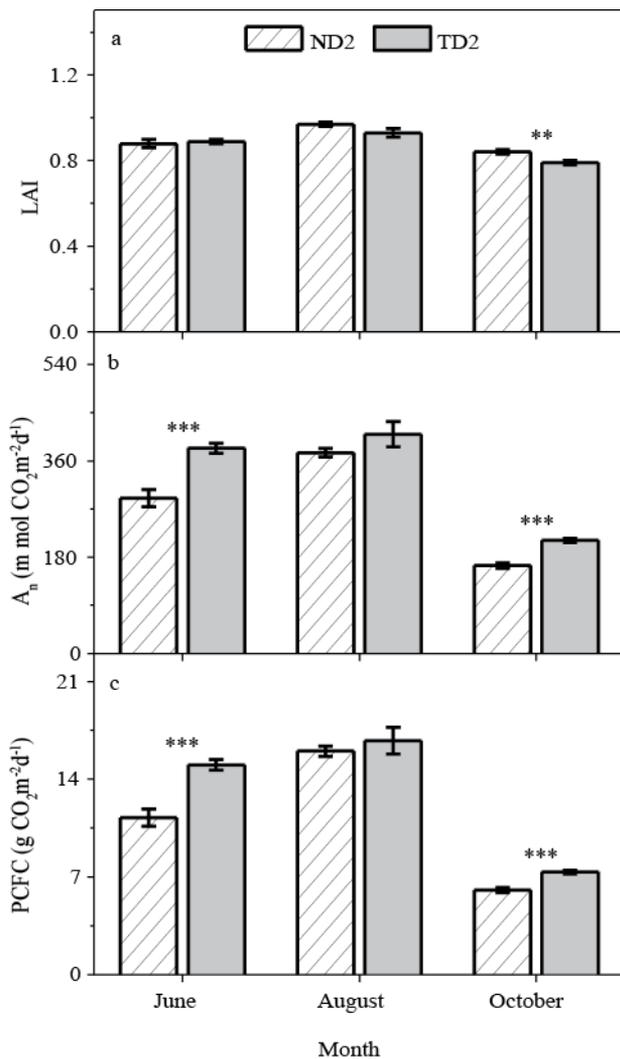


Fig. 3. Comparisons of the leaf area index (LAI), leaf-level net CO₂ assimilation rate (A_n), and tree-level photosynthetic carbon fixation capacity (PCFC) between ND2 and TD2. The mean values \pm SE ($n = 27$). Significant differences were tested and are indicated by asterisks. *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$.

ND1, TD2, and TD3 were compared on the basis of the same stand density (1800 trees ha^{-1}) to evaluate the thinning intensity effect. In June, August, and October 2009, the LAI values in ND1 and TD2 varied slightly (Fig. 5a). They were markedly higher than those in TD3 (Fig. 5a). Moreover, TD2 showed significantly higher A_n , LAI, and PCFC values compared with TD3 (Fig. 5). The leaf-level daily A_n and tree-level daily PCFC presented the coincident patterns as follows: TD2 > ND1 > TD3 for 8 months after thinning, TD2 \approx ND1 > TD3 for 10 months after thinning, and ND1 > TD2 > TD3 for one year after thinning (Fig. 5b, c). Results showed the black locust tree's rapid adaptability in response to low thinning intensity, although the decreases of A_n and PCFC in TD2 were more acute in autumn period than in spring and summer periods (Fig. 5). All these findings suggested that the low thinning intensity of 33% was more beneficial for the growth, leaf-level A_n , and tree-level PCFC of black locust.

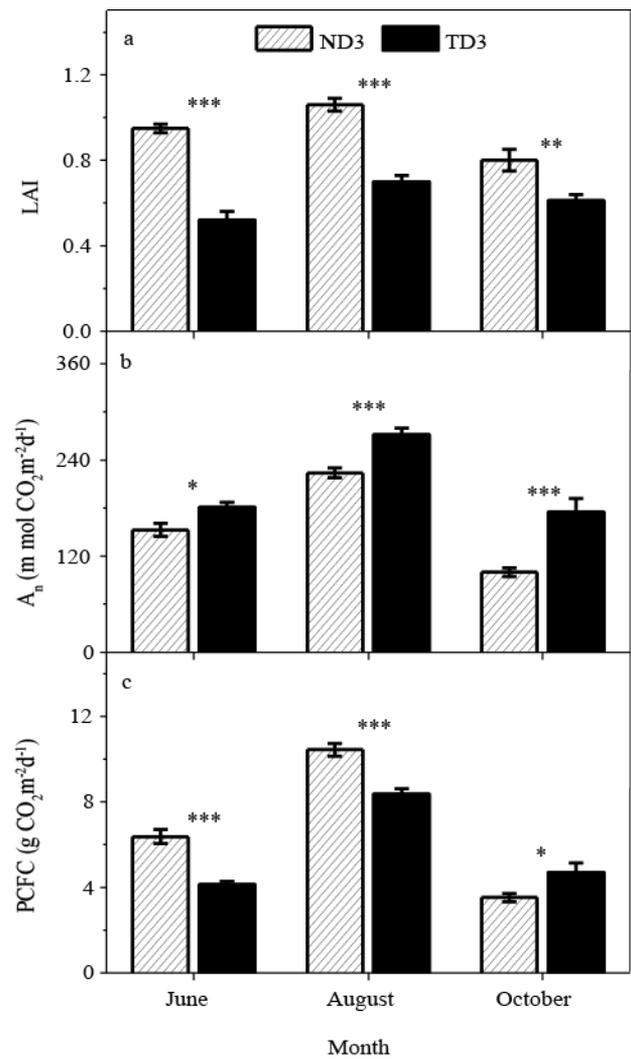


Fig. 4. Comparisons of the leaf area index (LAI), leaf-level net CO₂ assimilation rate (A_n), and tree-level photosynthetic carbon fixation capacity (PCFC) between ND3 and TD3. The mean values \pm SE ($n = 27$). Significant differences were tested and are indicated by asterisks. *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$.

Discussion

This study was mainly focused on the photosynthetic carbon fixation capacity of black locust trees in response to plantation thinning on the semiarid Loess Plateau. Results showed that the growth, A_n , and PCFC values were significantly different among the three stand densities in their annual growth period. Our data also implied that the adaptations of black locust to plantation thinning occurred at two levels: (i) gas exchange dynamics on the leaf level and (ii) canopy photosynthetic assimilation on the tree level. The leaf-level A_n and A_{max} of black locusts increased proportionally to the increasing thinning intensity. Contrary to our hypothesis, the tree-level photosynthetic carbon fixation capacity decreased in response to the increasing thinning intensity, which was mainly caused by the obvious decrease in thinning-related LAI and canopy density. On the basis of the same stand density (1800 trees ha^{-1}), we suggested that the photosynthetic carbon fixation capacities was improved in low 33% thinning intensity. This thinning intensity of 33% was more suitable for sustainable management of black locust plantations.

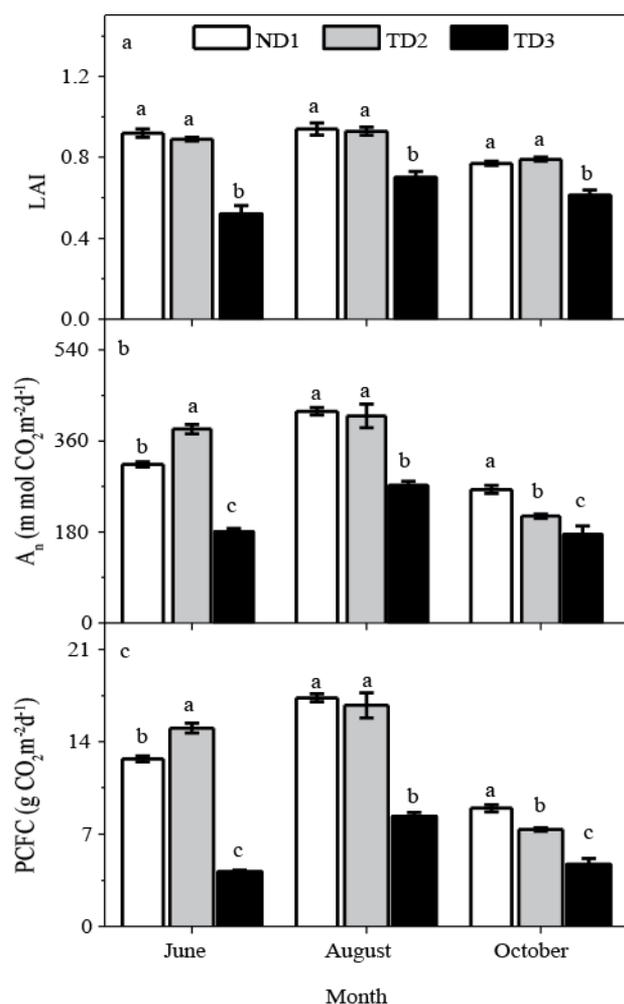


Fig. 5. Comparisons of the leaf area index (LAI), leaf-level net CO_2 assimilation rate (A_n), and tree-level photosynthetic carbon fixation capacity (PCFC) among ND1, TD2, and TD3. The mean values \pm SE ($n = 27$). Different letters on the bars indicate significant difference at $p \leq 0.05$.

The effects of stand density were further analyzed on both leaf- and tree-level photosynthesis of black locust in this study. Our results demonstrated that the daily leaf-level A_n and tree-level PCFC increase in intact plantations of deciduous black locust as the stand density decreases in the whole annual growth periods (Fig. 1). α , A_{\max} , and R_d exhibited a similar pattern in the most measurement period: ND1 > ND2 > ND3 (Table 2). Our findings were similar to previously conclusions described in the effects of stand density to photosynthesis. Previous studies reported that the diameter (Simard *et al.*, 2004), volume growth (de Moraes *et al.*, 2004), and the net photosynthetic rate on the single leaf scale (Will *et al.*, 2001) of individual trees were greater in the lower stand-density plantations. This phenomenon was mainly attributed to the improved environmental conditions and thus lengthened the growing season (Laurent *et al.*, 2003; White *et al.*, 2009). Although the light distribution patterns above and within a tree canopy change widely over time in a deciduous forest (Koike *et al.*, 2001; Sakai *et al.*, 2005). These conclusions in this study were probably due to the enhanced environmental resource availabilities per individual tree, including increased exposure to light radiation, canopy air temperature, and soil

moisture level (Table 1). This finding indicated that black locust trees with low stand densities were more sensitive to light environments and had more vigorous crowns than those with high stand densities. Given that black locust as a shade intolerant species possesses fast growth and high water-consuming characteristics (Du *et al.*, 2011; Yan *et al.*, 2013), the relatively low stand density of black locust plantations should be ecologically beneficial to arid and semiarid regions (Zhang *et al.*, 2015). Therefore, these observations implied that excessive stand densities possibly inhibited the growth and photosynthetic capacity of intact black locust plantations. Black locust should maximize photosynthetic-fixed carbon by optimizing leaf photosynthesis and tree canopy development based on a suitable stand density.

After plantation thinning residual trees constantly adapt to environmental changes by modifying the physiological and morphological characteristics of their leaves. However, the responses of residual trees to thinning vary in magnitude even among stands of the same species, such as *Pinus taeda* (Ginn *et al.*, 1991; Tang *et al.*, 1999, 2003). Plantation thinning has promoted the photosynthesis of residual trees since the first year after treatment. For example, A_n and A_{\max} of 19-year-old *Juglans nigra* in thinned plantation for 1 year after treatment were markedly higher than those in unthinned plantation (Gauthier & Jacobs, 2009). The photosynthetic carboxylation efficiencies was significantly different between the thinned and control *Chamaecyparis obtuse* stands in the first year after thinning (Han *et al.*, 2006). Thinning increased the photosynthesis and light use efficiency in a *Eucalyptus nitens* plantation in the first year after treatment (Forrester *et al.*, 2011). By contrast, the favorable photosynthetic and physiological responses to plantation thinning have been detected since the second year to the following year. For instance, A_{\max} , α , LCP, and R_d of *Pinus banksiana* and *Picea mariana* did not respond to plantation thinning within two years after treatment (Goudiaby *et al.*, 2011). Saunders *et al.*, (2012) reported that carbon stocks or fluxes did not exhibit significant responses for four years after thinning, although the range of inter-annual variability in NEE in a *Picea sitchensis* forest increased after thinning. The leaf net photosynthetic rate and annual carbon sink of pine species were reduced several years after thinning; some of these species are *Pinus ponderosa* (Campbell *et al.*, 2009), *P. halepensis* (Moreno-Gutierrez *et al.*, 2011), and *P. pinaster* (Ruiz-Peinado *et al.*, 2013). This result was probably due to the slow growth rate and long response time to thinning of pine. Consequently, considerable variations exist in the response times among tolerant and intolerant species.

It is well known that the harmonization of carbon and nitrogen could improve the photosynthetic assimilation and nitrogen production, because N metabolites needs C skeletons in plants (Luo *et al.*, 2013). Exogenous nitrogen availability influences N uptake and assimilation through the variation of root length and biomass, which may further regulate the photosynthesis and leaf area in poplar (Luo *et al.*, 2015). Black locust can actively improve soil nutrient concentrations due to its N-fixing ability (Tateno

et al., 2007), this species can fix nitrogen as much as 75 kg N ha⁻¹ y⁻¹ (Olesniewicz and Thomas, 1999). Previous studies proved that the black locust effectively increased soil organic carbon, total nitrogen and nitrate in the loess gully region of the Loess Plateau (Qiu *et al.*, 2010). Soil nitrogen stocks have been significantly enhanced in the 20-year-old black locust plantation in comparison with that of farmland on the Loess Plateau (Li *et al.*, 2013). Consequently, in this study, the good growth performance and rapid photosynthetic physiological response of black locust to plantation thinning in 1st-year after the treatment may be due to its larger biological nitrogen fixation in the increased soil moisture environment.

Overall, in the current study, black locust trees could actively adjust their photosynthetic functions from the first growing season after thinning to increase their height, diameter, and canopy diameter during growth and development. This result indicated that black locust could rapidly adapt in response to plantation thinning on the semiarid Loess Plateau. Therefore, the time interval from thinning to growth and development should be considered to evaluate the response and acclimation of the photosynthetic roles of different tree species. This study was conducted in one growing season. As such, variations in the long-term effects of thinning on the photosynthetic response, LAI, and growth of black locust trees among different stand density plantations in degraded semiarid regions should be further investigated.

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