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Effects of decomposing leaf litter of *Leucaena leucocephala* on photosynthetic traits of *Cynodon dactylon* and *Medicago sativa*

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Abstract *Leucaena leucocephala* is an introduced species, which has been widely used in mountain ecological restoration in southwestern China. To investigate the allelopathic effects of decomposing *L. leucocephala* leaf litter, the photosynthetic physiology of seedlings of two recipient plants, *Cynodon dactylon* and *Medicago sativa*, were measured in this controlled study. As the amount of decomposing *L. leucocephala* leaf litter increased, the net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs) decreased continuously, and the intercellular CO_2 concentration (Ci) increased continuously in both recipient plants. In *M. sativa*, all abovementioned indices differed significantly compared with the control group: Pn, Gs, and Tr decreased by 41.69, 59.35, and 48.02%, respectively, and Ci increased by 28.53%. In *C. dactylon*, Gs decreased significantly by 27.27%. Analysis of the photosynthesis–light response curve indicated that the maximum net photosynthetic rate (Pn_{max}) and dark respiration rate (Rd) of *C. dactylon*,

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as well as Pn_{max} and light saturation point (Lsp) of *M. sativa*, decreased significantly as the amount of decomposing *L. leucocephala* leaf litter increased. These results indicated that the photosynthetic traits, light adaptation ability and physiological metabolism of recipient plants were affected by the treatment. The decreased photosynthesis was caused by the changes in pigments and soluble sugar contents induced by *L. leucocephala* leaf litter and is therefore considered to be associated with non-stomatal limitations. In addition, as the amount of decomposing *L. leucocephala* leaf litter increased, *M. sativa* showed decreased chlorophyll (Chl*a*) and carotenoid (Car) contents, while *C. dactylon* showed decreased Chl*a* and Chl($a+b$) contents. However, both recipient plants exhibited significantly increases in their soluble sugar content. Overall, *M. sativa* was more sensitive than *C. dactylon* to the allelopathic effects induced by decomposing *L. leucocephala* leaf litter.

Keywords Allelopathy · *Leucaena leucocephala* · Leaf litter · Pioneer species · Photosynthesis

Introduction

Introduced species usually affect the diversity of native ecosystems by releasing allelopathic chemicals; this phenomenon is known as allelopathy (Chu et al. 2014). Leaves are one plant part that have high allelopathic activity (Turk and Tawaha 2003; Li et al. 2013). Therefore, allelochemicals released from decomposing leaf litter hinder seed germination as well as seedling growth and the development of surrounding plants and communities (Meksawat and Pornprom 2010; Namkeleja et al. 2014; Huang et al. 2015). Photosynthesis is a fundamental physiological process in plants, and the organic compounds produced during photosynthesis provide energy and materials required for the growth and development of plants. Photosynthesis is sensitive to environmental changes; when the plant is under environmental stress, its photosynthesis is often affected (Feng et al. 2016; Liang et al. 2017). Studies show that most allelochemicals released from the leaf litter of introduced species adversely affect photosynthesis and transpiration and consequently inhibit the growth of surrounding plants (Sahoo et al. 2007; Lorenzo et al. 2011). However, some native species are resistant to allelopathic effects, and their photosynthesis is less affected by allelochemicals (Weir et al. 2004). When exposed to allelochemicals, the response of a recipient plant can be assessed by measuring the changes in photosynthetic indices, and this response can help us to determine whether the recipient plant is adversely affected by allelopathy (Zhang et al. 2016).

Leucaena leucocephala (Lam.) de Wit (*L. leucocephala*), indigenous to tropical America, is a species of the genus *Leucaena*, family *Leguminosae*, and is an evergreen, branched shrub or small tree. *L. leucocephala* has a deep root system, grow wells in poor soil, is fast growing, and is drought-resistant. Therefore, it has been widely used in the ecological restoration of seriously degraded ecosystems including engineering slopes, abandoned mines and abandoned farmlands in the western and southern region of China, such as Sichuan, Yunnan, Guangdong and Guangxi provinces (Fang et al. 2005). It is estimated that the application area has been more than 10,000 ha. However, field studies suggest a loss of biodiversity and bare soil in *L. leucocephala* plantations, which generally affect the soil conservation capability of the plant community (Lin et al. 2009). Current studies show that *L. leucocephala* has allelopathic effects on seed germination and seedling growth of some crops, and the inhibitory effects increase as the concentration of allelochemicals increase

(Ahmed et al. 2008; Khare and Bisaria 2000). Aqueous extracts of *L. leucocephala* fresh root and leaf litter inhibited seed germination and seedling survival of pioneer species used in ecological restoration (Liu et al. 2017). However, the allelopathic effects of decomposing leaf litter of *L. leucocephala* on the photosynthesis of pioneer herbaceous plants used in soil restoration have not been extensively studied. *Cynodon dactylon* L. and *Medicago sativa* L. are two native herbs with resistance to a variety of stresses, grow vigorously and spread easily. Therefore, they have been used widely as pioneer species for soil restoration in southwestern China (Liu et al. 2017). In this study, we investigated the effects of decomposing leaf litter of *L. leucocephala* on the photosynthesis of recipient plants *C. dactylon* and *M. sativa* in controlled potted experiments. The aims of this study were (1) To investigate whether *L. leucocephala* leaf litter has allelopathic effects on the photosynthesis of two recipient plant species: the net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs) and intercellular CO_2 concentration (Ci) of the recipient plants were measured under different *L. leucocephala* leaf litter treatments. (2) To investigate the mechanisms of allelopathic effects of *L. leucocephala*: light response curves of the two recipient plants under different *L. leucocephala* leaf litter treatments were plotted, and photosynthetic parameters including the maximum net photosynthetic rate (Pn_{max}), light saturation point (Lsp), light compensation point (Lcp), dark respiration rate (Rd), and apparent quantum efficiency (AQY) were calculated. (3) To investigate the biochemical mechanisms of allelopathic effects of *L. leucocephala*: the pigment contents and soluble sugar contents in the leaves of recipient plants were measured under different *L. leucocephala* leaf litter treatments.

Materials and methods

Experimental design

Cynodon dactylon and *Medicago sativa*, two widely used pioneer species for ecological restoration, were used as recipient plants in this study. Seeds were purchased from a commercial source and were surface sterilized with 0.3% $KMnO_4$ for 5 min, rinsed in distilled water 5–6 times and air dried before sowing. Leaf litter of *L. leucocephala* was collected in January 2016. The litter was air dried, cut into small pieces (less than 1 cm), and stored for future study.

This is a single factor randomized study. A pot experiment was conducted according literature (Wu et al. 2012). A field investigation showed that the annual litter production in a *L. leucocephala* plantation is approximately 7.03 metric tons per square hectometer per year (7.03 t hm^{-2} y^{-1}) (Fang et al. 2005). Considering the litter production under natural conditions and the size of the pot used in this study (top inner diameter: 20 cm; bottom inner diameter: 12 cm; and height 15 cm), approximately 20 g of litter was added to each pot. However, to mimic the natural conditions where the distribution of litter may be affected by plant growth and environmental interference, we used five treatment groups: seeds of recipient plants grown in a bed with soil only (control group, CK); seeds of recipient plants grown in a bed mixed with 10 g of litter (T1), seeds of recipient plants grown in a bed mixed with 20 g of litter (T2), seeds of recipient plants grown in a bed mixed with 30 g of litter (T3), and seeds of recipient plants grown in a bed mixed with 40 g of litter (T4). Each group had 20 repeats, and 100 pots were used for each recipient plant. The soil was sieved through a 1-cm mesh, mixed uniformly with different amounts of litter specified above, and then leveled in each pot. Each pot contained 2.5 kg of soil with a water content of 11.6%. The beds were thoroughly watered and allowed to sit for 2 days before the seeds of the recipient plants were sown. On April 7, 2016, fifty healthy and full seeds of *Cynodon dactylon* L. and *Medicago sativa* L. were sown evenly in each pot and then covered with a thin layer of soil. Each pot was considered an experimental unit. After sowing, the pots were watered thoroughly and were subsequently watered every other day. Ten seedlings were retained in each pot while the redundant seedlings were thinned out when all seeds had germinated. When the seedlings in the T4 group, which were treated with the highest amount of decomposing *L. leucocephala* leaf litter, had 3–4 true leaves, the photosynthetic physiological and biochemical indices were measured.

Measurement of photosynthetic physiological and biochemical indices

The net photosynthetic rate (Pn_{max}) and gas exchange (Gs) indices were monitored using a portable photosynthesis analyzer (Li-6400, Li-Cor Inc., USA). The experimental conditions were as follows: carbon dioxide (CO_2) concentration 400 μmol/mol, temperature 25 °C and light intensity 1200 $\mu mol/m^2$ s. The net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs) and intercellular CO_2 concentration (Ci) of leaves from two recipient plants were measured. Three pots were randomly selected from each treatment group. One plant was selected from each pot, and the third leaf from the top of each plant was used for measurements. After the measurements, the leaves were labeled and transported to the laboratory. The leaf area was measured using a portable leaf area meter and was adjusted using LI6400SIM simulation software.

Photosynthesis–light response curves (Pn–PAR) of the two recipient plants were measured using a portable photosynthesis analyzer (Li-6400, Li-Cor Inc., USA) equipped with a red and blue light source and a liquid CO_2 cylinder. The experimental conditions were as follows: chamber temperature 25 °C; reference CO_2 concentration 400 μmol/mol; and the in-chamber photosynthetic photon flux density (PPFDi) was 2000, 1600, 1200, 800, 600, 400, 200, 150, 100, 50, and 0 $\mu mol/m^2$. Three pots were randomly selected from each treatment group. One healthy intact plant was selected from each pot, and the third leaf from the top of each plant was used for measurements. The leaves were maintained in their natural positions during the measurements. After the measurements, the leaves were labeled and transported to the laboratory. The leaf area was measured and adjusted using the method mentioned above. All photosynthetic characteristics were measured between 8:30 and 11:30 a.m. on a sunny day.

Pigments were extracted using 80% acetone, and their contents were determined using a UV-5500PC UV/VIS Spectrophotometer. The soluble sugar content was determined using the anthrone method as previously described (Wang 2006). Each test included triplicates.

Data analysis

The light response curves were analyzed using photosynthesis software. The photosynthesis indices including Pn_{max}, Lsp, Lcp, Rd and AQY of the two recipient plants under different treatments were derived from the curves. One-way ANOVA and Duncan's post hoc multiple range test were used to compare the differences between treatments. The independent variables were the amount of *L. leucocephala* litter used in each treatment group, while the dependent variables included Pn, Tr, Gs, Ci, Pn_{max}, Lsp, Lcp, Rd, AQY, the pigment contents [i.e., the chlorophyll *a* (Chl*a*), chlorophyll *b* (Chl*b*), total chlorophyll (Chl $a+b$), and carotenoid (Car) contents], as well as the soluble sugar content.

Results and analysis

The effects of decomposing leaf litter on the net photosynthetic rate and gas exchange parameters in recipient plants

As the amount of *L. leucocephala* leaf litter increased, Pn, Gs, and Tr decreased continuously while Ci increased continuously in both recipient plants (Fig. 1). All of the tested photosynthetic indices of *M. sativa* differed significantly among different groups ($p < 0.05$). Compared with CK, the Pn, Gs, and Tr of the T4 group decreased by 41.69, 59.35, and 48.02%, respectively, while the Ci of the T4 group increased by 28.53%. In contrast, the Pn, Ci and Tr of *C. dactylon* in each treatment group did not differ significantly ($p > 0.05$), although Gs decreased significantly ($p < 0.05$), e.g., the Gs of *C. dactylon* L. in the T4 group decreased by 27.27% compared with CK. Overall, the inhibitory effects of *L. leucocephala* litter were more potent in *M. sativa* than in *C. dactylon*.

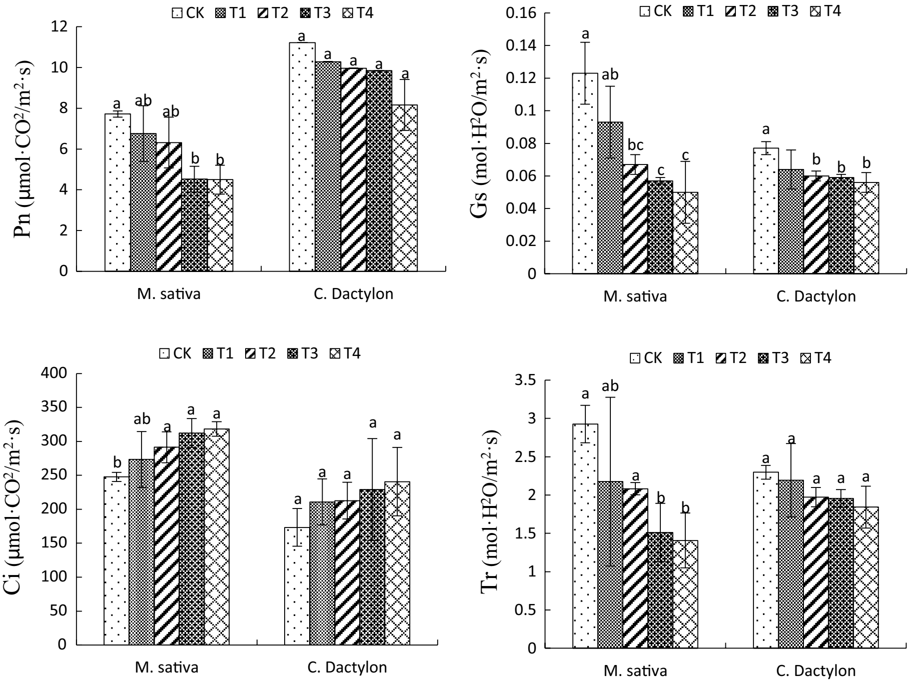

Fig. 1 Effects of decomposing *L. leucocephala* leaf litter on the photosynthetic rate and gas exchange parameters of two recipient plants

The photosynthesis–light response curves of two recipient plants under different litter treatments

The photosynthesis–light response curves showed that as the light intensity increased, the Pn of both recipient plants first increased gradually and then decreased to some extent. In addition, as the photosynthetically active radiation (PAR) increased, the difference in Pn between the treatment groups enlarged gradually (Fig. 2). The indices derived from the photosynthesis–light response curve are presented in Table 1. As the amount of *L. leucocephala* litter increased, the Pn_{max} and Lsp of both recipient plants decreased significantly ($p < 0.05$). In the *C. dactylon* treatment groups, Pn_{max} differed significantly, but the Lsp was comparable. The Pn_{max} and Lsp of the T4 group of *C. dactylon* L. decreased by 25.95 and 23.07%, respectively, compared with CK. However, the Pn_{max} and Lsp of *M. sativa* were significantly different among different treatment groups, e.g., Pn_{max} and Lsp of the T4 group of *M. sativa* decreased by 53.54 and 52.10%, respectively, compared with CK. The data suggested that the effects of decomposing *L. leucocephala* litter on photosynthesis were more potent in *M. sativa* than in *C. dactylon*. The AQY was not significantly different between the treatment groups of both recipient plants ($p > 0.05$). In *M. sativa*, the Lcp and Rd did not differ significantly between treatment groups, although Lcp showed an increasing trend ($p > 0.05$). However, the Lcp and Rd of *C. dactylon* differed significantly among different treatment groups ($p < 0.05$).

The effects of decomposing leaf litter on the pigment contents in the two recipient plants

As the amount of *L. leucocephala* litter increased, the pigment contents of both recipient plants showed a decreasing trend (Table 2). However, the recipient plants responded differently. In *C. dactylon*, the Chl*a* and Chl($a+b$) contents differed significantly among treatment groups ($p < 0.05$). For example, the Chl*a* and Chl($a+b$) contents of the T4 group were 40.78 and 42.26% lower, respectively, than the CK. The Chl*b* and Car contents did not differ significantly among groups ($p > 0.05$). In *M. sativa*, all pigments were affected significantly by *L. leucocephala* litter treatment ($p < 0.05$). For example, the pigment contents were inhibited significantly in the T2 treatment group, while the Chl*a*, Chl*b*, Chl($a+b$), and Car contents of the T4 treatment group were 33.33, 28.07, 32.71 and 29.17% lower, respectively, than those of CK. However, the Chl*a*/*b* and Chl($a+b$)/Car ratios were not significantly different among all treatment groups of both recipient plants ($p > 0.05$).

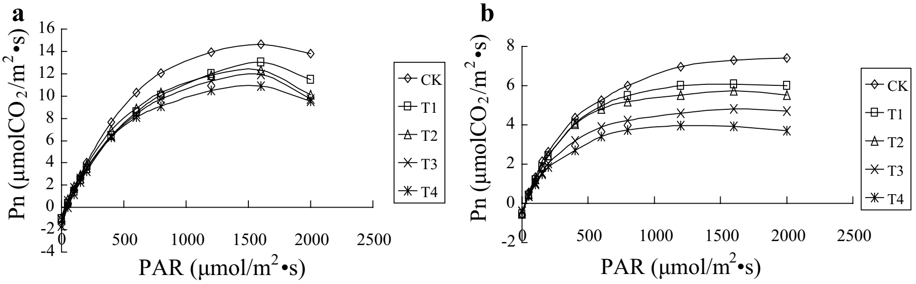

Fig. 2 Light response curves of *C. dactylon* (**a**) and *M. sativa* (**b**) leaves under different *L. leucocephala* leaf litter treatments

Table 1 Parameters of photosynthesis in response to light intensity measured in the leaves of two recipient plants under different *L. Leucocephala* leaf litter treatments

Recipient	Treatment	Parameters of photosynthesis				
		Pn$_{max}$ (μmol CO$_2$/m^2 s)	Lsp (μmol/m^2 s)	Lcp (μmol/m^2 s)	AQY (μmol CO$_2$/m^2 s)	Rd (μmol CO$_2$/m^2 s)
c. dactylon	CK	16.617 ± 0.781a	1536.000 ± 102.137a	36.667 ± 2.309ab	0.034 ± 0.002a	1.507 ± 0.031a
	T1	14.140 ± 0.356b	1489.333 ± 96.028a	29.333 ± 4.619b	0.032 ± 0.006a	1.500 ± 0.111a
	T2	13.429 ± 2.040b	1329.333 ± 375.496a	34.667 ± 2.309b	0.030 ± 0.003a	1.067 ± 0.116b
	T3	12.946 ± 1.510b	1325.333 ± 324.206a	36.000 ± 4.000ab	0.027 ± 0.001a	0.998 ± 0.124b
	T4	12.305 ± 0.310b	1149.333 ± 106.533a	43.333 ± 5.774a	0.031 ± 0.002a	0.911 ± 0.179b
Total	F; Sig	5.575; 0.013	1.273; 0.343	4.631; 0.022	1.500; 0.274	16.483; 0.000
M. sativa	CK	9.326 ± 0.813a	1391.667 ± 79.400a	21.333 ± 2.309a	0.026 ± 0.002a	0.541 ± 0.200a
	T1	7.273 ± 2.897ab	984.000 ± 462.636ab	25.333 ± 4.619a	0.022 ± 0.005a	0.563 ± 0.176a
	T2	6.370 ± 1.880ab	816.000 ± 116.207b	24.000 ± 4.000a	0.021 ± 0.002a	0.503 ± 0.150a
	T3	5.420 ± 0.870b	814.667 ± 200.013b	26.333 ± 8.505a	0.017 ± 0.005a	0.425 ± 0.096a
	T4	4.333 ± 1.007b	666.667 ± 50.332b	24.000 ± 4.000a	0.019 ± 0.012a	0.393 ± 0.184a
Total	F; Sig	3.701; 0.042	4.228; 0.029	0.405; 0.801	0.854; 0.523	0.837; 0.532

Different letters in the columns indicate significant differences ($p < 0.05$)

Table 2 Effect of decomposing *L. leucocephala* leaf litter on the pigment content of two recipient plants

Recipient	Treatment	Chl*a* content (mg/g)	Chl*b* content (mg/g)	Chl(*a*+*b*) content (mg/g)	Car content (mg/g)	Chl*a*/Chl*b*	Chl(*a*+*b*)/Car
c. dactylon	CK	1.79 ± 0.15a	0.60 ± 0.03a	2.39 ± 0.14a	0.27 ± 0.04a	2.98 ± 0.32a	8.85 ± 1.12a
	T1	1.68 ± 0.44a	0.54 ± 0.21a	2.22 ± 0.65a	0.28 ± 0.05a	3.11 ± 0.42a	7.93 ± 1.14a
	T2	1.66 ± 0.16a	0.54 ± 0.08a	2.20 ± 0.24a	0.25 ± 0.02a	3.07 ± 0.14a	8.80 ± 0.35a
	T3	1.46 ± 0.19ab	0.47 ± 0.07a	1.92 ± 0.26ab	0.23 ± 0.04a	3.11 ± 0.09a	8.35 ± 2.47a
	T4	1.06 ± 0.11b	0.35 ± 0.09a	1.38 ± 0.19b	0.21 ± 0.02a	3.03 ± 0.91a	6.57 ± 0.92a
Total	F; Sig	4.403; 0.026	2.069; 0.160	3.928; 0.036	2.071; 0.160	0.080;0.987	1.570; 0.256
M. sativa	CK	1.56 ± 0.17a	0.57 ± 0.09a	2.14 ± 0.08a	0.24 ± 0.04a	2.74 ± 0.76a	8.92 ± 1.17a
	T1	1.40 ± 0.20ab	0.49 ± 0.01ab	1.90 ± 0.19ab	0.23 ± 0.03a	2.86 ± 0.43a	8.26 ± 0.25a
	T2	1.28 ± 0.12bc	0.45 ± 0.02b	1.73 ± 0.13b	0.21 ± 0.02a	2.84 ± 0.16a	8.24 ± 0.64a
	T3	1.22 ± 0.17bc	0.41 ± 0.06b	1.60 ± 0.20bc	0.18 ± 0.02b	2.98 ± 0.51a	8.89 ± 0.64a
	T4	1.04 ± 0.06c	0.40 ± 0.06b	1.44 ± 0.03c	0.17 ± 0.03b	2.60 ± 0.36a	8.47 ± 1.92a
Total	F; Sig	5.007; 0.018	8.787; 0.003	10.313; 0.001	3.807; 0.039	0.245; 0.906	0.413; 0.796

Different letters in the columns indicate significant differences ($p < 0.05$)

The effects of decomposing leaf litter on the soluble sugar content in the two recipient plants

As the amount of *L. leucocephala* litter increased, the soluble sugar content of both recipient plants showed an increasing trend (Fig. 3), and the differences between groups were significant ($p < 0.01$). In *M. sativa*, the *L. leucocephala* litter treatment caused significant increases in the soluble sugar content, with T2, T3, and T4 increasing by 67.14, 94.64, and 219.49%, respectively, compared with CK. Similarly, the *L. leucocephala* litter treatment also caused significant increases in the soluble sugar content in *C. dactylon* with T2, T3, and T4 increasing by 60.42, 76.77, and 93.12%, respectively, compared with CK. However, the soluble sugar content of the T1 treatment group of *C. dactylon* was not different from CK. The results suggested that the soluble sugar content of *M. sativa* was affected more significantly by decomposing *L. leucocephala* litter treatment than *C. dactylon*.

Discussion

The Effects of decomposing *L. leucocephala* leaf litter on the photosynthesis of the two recipient plants

Plants usually respond to environmental stresses by reducing photosynthetic activity. Causes of decreased photosynthetic rate include stomata-related factors such as Gs, Tr, and Ci, as well as non-stomatal factors such as photochemistry and the chlorophyll content, etc. (Lu et al. 2017; Cheng and Cheng 2015). Farquhar and Sharkeyt (1982) proposed that the decrease in Pn is caused by stomatal limitations when Pn, Gs and Ci decreased simultaneously; however, when leaf Pn decreases but Ci increases, the causes may be associated with non-stomatal limitations. In our study, the Gs, Tr, Pn and Ci of both recipient plants were affected by decomposing *L. leucocephala* leaf litter, among which Gs, Tr and Pn decreased while Ci increased. These results indicated that the decomposing *L. leucocephala* litter-induced Pn decrease is associated with non-stomatal limitations. A possible explanation could be that allelopathic chemicals released from decomposing *L. leucocephala* leaf litter inhibit the photosynthetic activities in the leaves of recipient plants, reduce CO_2 utilization, increase intercellular CO_2 accumulation and eventually suppress photosynthesis (Wu et al. 2012; Li et al. 2013).

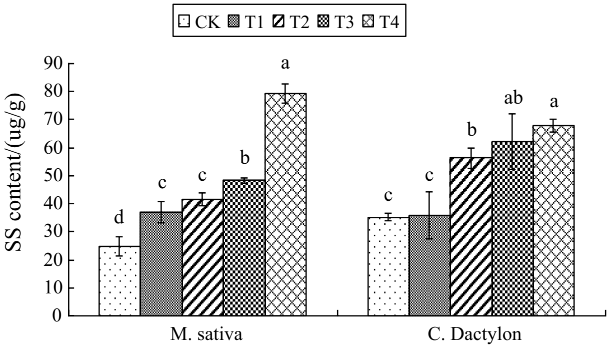

Fig. 3 Effects of decomposing *L. leucocephala* leaf litter on the soluble sugar (SS) content of two recipient plants

The two recipient plants responded differently to allelochemicals released from *L. leucocephala* litter. As the amount of *L. leucocephala* litter increased, *M. sativa* exhibited decreased Gs, Tr and Pn, and increased Ci, while *C. dactylon* only showed significantly affected Gs compared with CK. Therefore, *M. sativa* was more sensitive to allelochemicals released from *L. leucocephala* litter, and the reaction mechanisms between the two recipient plants were different. We further analyzed the light response curve-derived photosynthetic parameters. Compared with CK, the Pn_{max} and Lsp of *M. sativa* decreased significantly, while the Lcp, AQY and Rd were comparable. However, in *C. dactylon*, the Pn_{max} and Rd decreased significantly while Lsp, AQY and Lcp remained unaltered. With reference to the light response curve, Lsp and Lcp reflect how plants adapt to different light conditions; AQY reflects the light utilization efficiency, especially for low intensity light, while Rd reflects plant physiological metabolic intensity (Dong et al. 2007; Liang et al. 2017; Hej and Koster 2004). These results further indicated that the photosynthesis of both recipient plants was adversely affected by *L. leucocephala* litter with *M. sativa* being more sensitive to the allelopathic effects than *C. dactylon*. *L. leucocephala* litter significantly decreased Pn_{max} and reduced the light adaption ability of *M. sativa* and significantly decreased Pn_{max} and Rd in *C. dactylon*.

Other studies also showed that different plants respond to allelochemicals with distinct intensity and mechanisms (Weir et al. 2004). Li et al. (2013) and Wu et al. (2012) studied the effects of decomposing leaf litter of *Eucalyptus grandis* on *Lolium perenne* and *Cichorium intybus*. Their results showed that *E grandis* leaf litter significantly decreased Pnmax, Lsp, Lcp, AQY and Rd and consequently negatively affected the photosynthetic capacity, eventually inhibiting the growth of these two recipient plants. In Chen et al.'s report (2014), decomposing leaf litter of *Eucalyptus grandis* promoted the photosynthetic rate (Pnmax), Lsp, Lcp, and AQY of *Elymus sibiricus* and *Trifolium pratense*; however, their growth was limited throughout the experimental period because their energy consumption rate was also promoted. Genetic variation of receptors may explain the fact that responses to the same allelochemicals vary among different plant species (Zuo et al. 2005; Qiu et al. 2016). The enzymatic activities of receptors, protein expression levels, gene transcription levels, as well as hormones levels, may vary among different species, which may contribute to the different responses toward the same allelochemicals (Weir et al. 2004).

The effects of decomposing litter on the photosynthetic physiology and biochemistry of the two recipient plants

Photosynthetic pigments, which include chlorophyll and carotenoids, participate in the absorption and transmission of light energy, as well as primary photochemical reactions in higher plants. Chlorophyll is vital for photosynthesis; it allows plants to absorb light energy and transfer it to other parts of the photosystem, converting light energy into chemical energy. Therefore, the chlorophyll content will affect the intensity of photosynthesis (Li et al. 2013). Carotenoids absorb and transfer light energy, and they protect chlorophyll from photodamage (Zhang et al. 2016). Allelochemicals from introduced species usually affect photosynthetic activity in recipient plants by affecting photosynthetic pigment contents (Wu et al. 2012; Hussain and Reigosa 2016). Exposure to allelochemicals causes increased reactive oxygen species (ROS) in recipient organisms, which subsequently lead to the detachment of the plasma membrane from the cell well and the disruption of chloroplast structure (Qian et al. 2009; Zhang et al. 2016). Chloroplast deformity or decomposition reduces photons, electron donors and electron acceptors in the photosystem, reduces the quantum yield of PSII photochemistry, and consequently decreases the photosynthetic rate (Uddin et al. 2012; Hussain et al. 2017). Our study showed that allelochemicals released from decomposing *L. leucocephala* litter significantly reduced the photosynthetic pigment contents in both recipient plants. In *C. dactylon*, only the T4 group had significantly lower pigment contents compared with CK. In *M. sativa*, all treatment groups had significantly lower pigment contents compared with CK. The results suggested that the adverse effects of decomposing *L. leucocephala* litter on the leaf photosynthetic pigments were stronger in *M. sativa*. The ratio between the photosynthetic pigments reflects the stability of photosystem and the intensity of photosynthesis (Weir et al. 2004). In this study, the chlorophyll *a*/*b* ratio and Chl($a+b$)/Car ratio did not change significantly, which suggests that the photosystems in the recipient plants were still relatively stable.

Soluble sugar participates in the regulation of osmotic pressure in plant cells. Water stress, salinity stress, cold stress or other unfavorable environmental factors may significantly change the soluble sugar content (Chen et al. 2013). Ahmad et al. (2016) reported that allelochemicals increased the accumulation of soluble sugars in recipient plants. A possible mechanism is that allelochemicals inhibit the absorption and utilization of water and nutrients in recipient plants (Hej and Koster 2004; Cheng and Cheng 2015); consequently, the plant water content decreases, and the soluble sugar content increases relatively (Chen et al. 2013). On the other hand, allelochemicals induce the degradation of macromolecular saccharides and proteins into sucrose, glucose and other small molecular soluble sugars, thus leading to an increased soluble sugar content (Rossouw et al. 2017). Sugars are one of the most important regulators in many physiological processes, such photosynthesis, seed germination, flowering and senescence. The accumulation of carbohydrates would inhibit photosynthetic activity. Ding et al. (2014) investigated the effects of decomposing walnut leaf litter on antioxidant systems and the photosynthetic characteristics of lettuce. Their results showed that decomposing walnut leaf litter caused a significant increase in soluble sugar and a decrease in the net photosynthetic rate. The accumulation of a high sugar concentration may cause a delay in leaf development or even necrosis (Sami et al. 2016). In this study, exposure to allelochemicals caused an increase in the soluble sugar content in both recipient plants, which concurred with the decrease in the photosynthetic rate.

Our study suggested that *L. Leucocephala* litter significantly influenced the photosynthetic physiology of two native species, which further impacted their biomass accumulation and seedling growth. Our previous study also indicated that *L. Leucocephala* litter had significant allelopathic effects on seed germination and seedling establishment of native species (Liu et al. 2017). Therefore, the use of *L. Leucocephala* should be limited in ecological restoration to increase species diversity and enhance soil and water conservation of the restored ecosystems.

Conclusion

Decomposing *L. leucocephala* leaf litter exerted allelopathic effects on two common pioneer species used in ecological restoration: *C. dactylon* and *M. sativa*. The Pn, Gs, and Tr of both recipient plants decreased, while Ci increased continuously as the amount of decomposing *L. leucocephala* leaf litter increased. In *M. sativa*, the photosynthetic indices of all treatment groups changed significantly, while in *C. dactylon*, only Gs changed significantly. These results suggest that *M. sativa* is more sensitive than *C. dactylon* to the allelopathic effects induced by decomposing *L. leucocephala* leaf litter. Analysis of the photosynthesis–light response curve-derived parameters indicated that decomposing *L. leucocephala* leaf litter affected the photosynthetic process by inhibiting Pn_{max} and the light adaptation ability of *M. sativa* and Pnmax and Rd in *C. dactylon*. In the presence of decomposing *L. leucocephala* leaf litter, the pigment content in both plants decreased significantly. Because photosynthetic pigments are important for light energy absorption and transfer, the decrease in the pigment content result in reduced photosynthetic activity. Decomposing *L. leucocephala* leaf litter also increased the accumulation of soluble sugar in the leaves of the two recipient plants and consequently inhibited the photosynthesis. In summary, the inhibition of photosynthesis induced by decomposing *L. leucocephala* leaf litter was mainly associated with non-stomatal limitations, i.e., a decreased pigment content and increased accumulation of soluble sugar. The allelopathic effects of *L. leucocephala* litter on native species limits its use in ecological restoration.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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