Canadian Journal of Forest Research
Revue canadienne de recherche forestière

**Thinning effect on understory community and
photosynthetic characteristics in a subtropical *Pinus
massoniana* plantation**

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2017-0082.R1
Manuscript Type:	Article
Date Submitted by the Author:	18-Apr-2017
Complete List of Authors:	Cheng, Chuanpeng; Institute of Geographic Sciences and Natural Resources Research, ; Wang, Yidong; Tianjin Normal University, Tianjin Key Laboratory of Water Resources and Environment Fu, Xiaoli; Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Xu, Mingjie; Institute of Geographic Sciences and Natural Resources Research Chinese Academy of Sciences Dai, Xiaoqin; Institute of Geographic Sciences and Natural Resources Research Chinese Academy of Sciences Wang, HuiMin; Qianyanzhou Ecological Station,
Keyword:	Thinning, Forest management, Understory diversity, Photosynthesis, <i>Pinus massoniana</i> plantation
Is the invited manuscript for consideration in a Special Issue? :	N/A

SCHOLARONE™
Manuscripts

1 **Thinning effect on understory community and photosynthetic**
2 **characteristics in a subtropical *Pinus massoniana* plantation**

3 Chuanpeng Cheng^{1,2}, Yidong Wang³, Xiaoli Fu¹, Mingjie Xu^{1,4}, Xiaoqin Dai¹,
4 Huimin Wang^{1,2,5*}

5 ¹ Qianyanzhou Ecological Research Station, Key Laboratory of Ecosystem Network
6 Observation and Modeling, Institute of Geographic Sciences and Natural Resources
7 Research, Chinese Academy of Sciences, Beijing 100101, China

8 ² College of Resources and Environment, University of Chinese Academy of
9 Sciences, Beijing 100190, China

10 ³ Tianjin Key Laboratory of Water Resources and Environment, Tianjin Normal
11 University, Tianjin 300387, China

12 ⁴ College of Agronomy, Shenyang Agricultural University, Shenyang 110866, China,

13 ⁵ Jiangxi Provincial Key Laboratory of Ecosystem Processes and Information, Ji'an
14 343725, China

15 *Corresponding author: Huimin Wang, Address: Key Laboratory of Ecosystem
16 Network Observation and Modeling, Institute of Geographic Sciences and Natural
17 Resources Research, No. 11A, Datun Road, Chaoyang District, Beijing 100101,
18 China. Tel: +86 10-64888896, Fax: +86 10-64888896.

19 E-mail address: wanghm@igsnr.ac.cn (H. Wang).

20

Abstract: Thinning forest stands changes biotic and abiotic conditions, subsequently altering understory communities including their photosynthetic characteristics. We investigated the effects of thinning (25% basal area decrease) in a subtropical *Pinus massoniana* plantation at two post-thinning times: 0.5 (PT_{0.5-yr}) and 2.5 years (PT_{2.5-yrs}). Thinning (PT_{0.5-yr} and PT_{2.5-yrs}) significantly increased understory density (+104.9% and +142.4%), aboveground biomass (+191.1% and +239.2%), Shannon-Wiener index and Pielou index, and decreased the Simpson index ($p < 0.05$). Species richness significantly increased at PT_{0.5-yr}, and decreased at PT_{2.5-yrs} ($p < 0.05$). Photosynthetic characteristics of three dominant species (*Woodwardia japonica*, *Dryopteris championii* and *Dicranopteris dichotoma*) new-leaf and old-leaf showed different variation after 0.5 and 2.5 years post-thinning depending on their various adaptive strategies. Generally, thinning improved leaf carbon fixation capacity of these dominant plants (except *W. japonica* old-leaf). Leaf photosynthetic characteristics of these species exhibited some common changes with respect to leaf morphological attributes and chlorophyll content. Thinning increased new-leaf length (or width) and reduced old-leaf chlorophyll b concentration at PT_{0.5-yr}, while reduced new-leaf length, specific leaf area, and all-leaf chlorophyll concentration at PT_{2.5-yrs}. In conclusion, thinning is a useful tool for increasing understory abundance and carbon fixation capacity of some fern species.

Keywords: Thinning, Forest management, Understory diversity, Photosynthesis, *Pinus massoniana* plantation, Subtropical China

Introduction

Understory plays an important role in providing wildlife habitat and conserving biodiversity in forests (Ishii et al. 2008; Sullivan et al. 2009). It affects both belowground and aboveground ecological processes, such as nutrient cycling, litter decomposition, and species succession (Nilsson and Wardle 2005; Liu et al. 2012). Although the biomass proportion of understory is small in most forests types (especially in mature plantation) around the world (Wang et al. 2006; Li et al. 2013), its impact on the forest carbon fixation and nutrients cycles should be highlighted (Nilsson et al., 2005). Understory usually distributes most of its productivity to the leaves and fine roots where carbon and nutrient turnover rates are significantly higher than in trees (Chiang and Brown 2010). So, understory community dynamics and carbon exchange capacity (carbon fix and release rate per biomass) is an important consideration for forest management (Hanley et al. 2006; Yan et al. 2013).

Thinning, an important forest management practice, has been found to have complex effects on understory biodiversity after different time post-thinning (He and Barclay 2000; Gajardo-Caviedes 2005; Raunikaar et al. 2010). Many factors (such as thinning intensities, thinning prescriptions, site-specific conditions and sampling time) have considerable influence on these uncertain results (Taki et al. 2010; Lindgren and Sullivan 2013). Research methods may account for important variations, because most research is based on surveys in the same plot at different times post-thinning (Wolk and Rocca 2009; Lindgren and Sullivan 2013). Species phenological differences and inter-annual variation of climate conditions have often been ignored (Yirdaw and Luukkanen 2004; Xu et al. 2014a). This could lead to

uncertainty in thinning effects, as these differences are important in forest structure and function (Yan et al. 2013). Therefore, it is necessary to consider the response of understory communities after various post-thinning times under the same climate conditions.

Thinning has the potential to impact leaf traits (such as nitrogen content, leaf mass per area, chlorophyll content, and leaf gas exchange) through alterations of microenvironments (especially light and soil conditions) (Moreno-Gutiérrez et al. 2011). Generally, leaf traits vary under different suites of environmental variables (Forrester et al. 2012). Different species also show various responses to same suites of environmental variables depending on their various adaptive strategies (variation of leaf traits, resource use pattern and efficiency difference and so on) (Chiang and Brown 2010; Gspaltl et al. 2013; Xu et al. 2014b). For example, *Dicranopteris dichotoma* (Thunb.) Bernh. possessed higher N and P utilization rates and higher leaf N and P content than *Woodwardia japonica* (Linn. f.) Sm) across a whole ecological restoration chronosequence in subtropical China (Wu et al. 2013; Chen et al. 2016). In addition, leaf physiological and morphological adaptations to the environments may different between foliar development stages (Catoni et al. 2012). Rodríguez-Calcerrada et al. (2008) investigated light acclimation of oak *Quercus petraea* from low-light exposure (LL: 5.3% of ambient irradiance) to high-light exposure (HL: 70% of ambient irradiance) either before leaf flushing (LL-HLBF plants) or after full leaf expansion (LL-HLAF plants), they found that morphological adaptation of leaves of LL-HLBF plants enhanced photosynthetic capacity per unit

leaf area, whereas leaves of LL-HLAF plants enhanced both mass- and area-based photosynthetic capacity. Thus, examining the influence of thinning on the different age leaf traits and physiological processes of various species can provide insights into the effects of thinning on understory communities and forest productivity.

Pinus massoniana, a native evergreen conifer, is commonly used as a pioneer species for degraded ecosystem restoration (Wang et al. 2015). Many pure *P. massoniana* plantations were established in subtropical China in the 1980s, and have provided many wood products and increased world carbon sinks (Peng et al. 2008; Piao et al. 2009). Piao et al. (2009) estimated a net carbon sink of 0.096 Pg carbons per year in this region, and this makes China's carbon sink comparable to that in geographic Europe. However, their development has led to many problems, such as declines in soil fertility, frequent pest outbreaks, and soil food web changes (Ji et al. 2011; Chen et al. 2016). Given the low carbon fixation capacity and poor crop quality of pure pine plantations, thinning has potential to increase forest productivity (Peng et al. 2008; Yan et al. 2013), while at the same time providing a useful model for studying the effects of thinning on understory communities and their photosynthetic characteristics.

In this study, we investigated the properties of understory communities (density, biomass, and species diversity) as well as the age-specific photosynthetic characteristics of the leaves (morphological attributes, chlorophyll content, and leaf gas exchange) of three dominant herbaceous species in a subtropical *P. massoniana* plantation under the same climate conditions 0.5 and 2.5 years after thinning. Our

goal was to assess the effects of thinning over time. We hypothesized that (i) understory community density, aboveground biomass, and species diversity will increase soon after thinning due to improvement in the light environment, and then will decrease with soil nutrient consumption and understory light environment recovery, and (ii) leaves of different ages will exhibit different gas exchange responses to environmental conditions, morphological attributes, and chlorophyll content 0.5 and 2.5 years post-thinning depending on their various adaptive strategies.

Materials and methods

Experimental site

This experiment was carried out at the Qianyanzhou Ecological Station of the Chinese Academy of Sciences (26°44'39"N, 115°03'33"E, and 102 m in elevation above sea level), which is located in a typical hilly red-soil region of subtropical China. The soil is classified as a Typic Dystrudept in the USDA system (Wen et al. 2010; Wang et al. 2012). The site is controlled by a warm and humid monsoon climate (annual mean air temperature: 18.0 °C; annual mean precipitation: 1509.0 mm). About 1980, coniferous trees, including Masson pine (*P. massoniana* Lamb.), Slash pine (*Pinus elliottii* Englem.), and Chinese fir (*Cunninghamia lanceolata* Hook.), were planted at a density of about 1460.0 stems ha⁻¹ to combat soil degradation. The *P. massoniana* plantation understory is dominated by *Loropetalum chinense* (R. Br.) Oliver, *Vaccinium bracteatum* Thunb., *Woodwardia japonica*, *Dryopteris championii* (Benth.) C. Chr., and *Dicranopteris dichotoma* (Fu et al.

2016). Our field studies did not involve endangered or protected species.

Experimental design

The experiment was a completely randomized design with three treatments and three replicate plots (30 × 30 m, located on moderately steep slopes and 15–20 m apart). The three treatments were: Unthinned; PT_{0.5-yr}, with thinning treatments in December 2014; and PT_{2.5-yrs}, with thinning treatments in December 2012. Before thinning, in December 2012, *P. massoniana* trees in the plots had a mean diameter at breast height of 15.9 cm, a mean stand density of 1329.0 stems ha⁻¹ and a basal area of 26.4 m² ha⁻¹. The shrubs in all the plots were cut down for ease of operation, following standard practice, but the herbs were retained. Approximately 25% of the basal area was reduced when the thinning treatments were applied, and most of the slash (except for the woody parts of trees) was left on the site. 0.5 and 2.5 years after thinning, the stands had a mean diameter at breast height of 17.3 and 17.6 cm, a mean stand density of 849.0 and 825.0 stems ha⁻¹, and a basal area of 19.9 and 20.1 m² ha⁻¹, respectively. Effects of thinning on understory communities and their photosynthetic characteristics were assessed in July 2015, when 0.5 and 2.5 years had passed after the two thinning treatments (PT_{0.5-yr} and PT_{2.5-yrs}). We choose this time because there was a clear summer drought (with intense solar irradiation and little precipitation) in this month, and the understory community was likely to respond acutely (Chiang and Brown 2010; Yan et al. 2015). We also analyzed soil chemical properties, canopy structure and light transmittance, as well as understory community structure and species diversity before thinning in December 2014. There

153 were no significant differences (soil chemical properties, canopy structure and light
154 transmittance, as well as understory community structure and species diversity)
155 between Unthinned and PT_{0.5-yr} before thinning, except with respect to understory
156 community species diversity (Table A1, A2).

157 **Soil sampling and analyses**

158 Soil samples were collected in December 2014 and July 2015 (before and after
159 thinning was applied for PT_{0.5-yr}) using a 45-mm-diameter hand auger at depths of
160 0–10 cm and 10–20 cm in each plot. One soil core was randomly collected in each of
161 the nine 10 × 10 m subplots, and then the nine soil cores combined into one
162 composite soil sample for each depth in each plot (Fig. A1). One part of the sample
163 was air-dried for soil pH measurement in a 1:2.5 soil:water suspension. The other
164 was extracted in 2 M KCl solution for inorganic nitrogen (IN) content, including
165 measurement of ammonium nitrogen (NH₄⁺-N) and nitrate nitrogen (NO₃⁻-N), by
166 continuous flow on an auto analyzer (Bran + Luebbe, Germany).

167 **Measurement of canopy structure and light transmittance**

168 Canopy structure and light transmittance were measured with TRAC (Tracing
169 Radiation and Architecture of Canopies, Canada) and hemispherical photography
170 above the understory on sunny days before (24 November 2014) and after (25 July
171 2015) thinning was applied at PT_{0.5-yr}. The TRAC measurements and hemispherical
172 photographs were taken in the morning and evening, respectively.

173 The leaf area index (LAI) and effective plant area index (PAI_e) in each plot
174 were calculated from the TRAC measurements by TRACWIN. Canopy openness,

total solar radiation transmittance (T_{tot}), direct solar radiation transmittance (T_{dir}), and diffuse solar radiation transmittance (T_{dif}) of the canopy were analyzed from the digital hemispherical photographs by Sidelook and GLA (Gap Light Analyzer).

Analysis of understory community

Understory was surveyed in December 2014 and July 2015 (before and after thinning was applied for $PT_{0.5\text{-yr}}$). Five permanent square subplots (5×5 m) in each plot were demarcated to survey the shrub layer. In each subplot, one 1×1 m permanent quadrat was delimited for the herb survey (Fig. A1). Species composition and number were surveyed for the shrub and herb layers, and representative plants of the surveyed species were collected outside the permanent survey plots for long-term study. The plants were oven-dried at 65°C for 48 h and weighed to calculate aboveground biomass.

Density and aboveground biomass were calculated as the average density and aboveground biomass. Density sum and aboveground biomass sum were the sum of the total density and aboveground biomass per species in all the treatments at the two sampling dates. Total density and total aboveground biomass were calculated as the total density and aboveground biomass of all the species in each treatment at each sampling date. Species richness (S) was calculated as the mean number of species (Magurran 1988). The Shannon-Wiener index (H'), Simpson index (D), and Pielou index (J) were calculated according to equation 1-3:

$$H' = \frac{N \ln N - \sum n \ln n}{N} \tag{1}$$

$$D = \sum (n/N)(n/N) \tag{2}$$

197
$$J = \frac{H'}{\ln S} \quad (3)$$

198 where N is the total number of understory species and n is the number of individuals
199 of each species per plot. Variation in the density, aboveground biomass, and species
200 diversity between December 2014 and July 2015 were also estimated by calculating
201 the difference between the two sampling dates.

202 **Analysis of leaf morphological attributes and chlorophyll content**

203 Leaf morphological attributes and chlorophyll content of the three dominant plant
204 species (*W. japonica*, *D. championii*, and *D. dichotoma*) (Table A2) in each plot were
205 measured in July 2015 after thinning. For each species, three new and three old
206 representative leaves (same location on stem and similar size and growth state for
207 every leaf type) of three representative plants (plants with average size and growth
208 state on the basis of understory surveys) were collected (except *D. championii* new
209 leaves due to their smaller number).

210 Leaf morphological attributes were measured by scanning six leaves of each
211 type in every plot on an A3 flatbed scanner (HP M1522n) to obtain leaf length (L),
212 width (W), and surface area (SA). The images were analyzed by Sidelook and Image
213 J. The leaves were then oven-dried at 65 °C for 48 h and weighed to calculate
214 biomass. Specific leaf area (SLA) was the ratio of leaf surface area to biomass.

215 The three leaves of each type for chlorophyll content measurement in every plot
216 were cut into pieces and extracted (0.100 g) in 10 ml dimethyl sulfoxide for 72 h in
217 darkness. OD645 and OD663 of the extracts were analyzed using a UV-Visible
218 spectrophotometer (UV-1601, Shimadzu Corporation, Japan). Chlorophyll a (Chl_a), b

(Chl_b), and total (Chl_{tot}) concentrations were calculated using equation 4-6 (Arnon 1949):

$$\text{Chl}_a = 0.3 \times (12.70 \times \text{OD}_{663} - 2.69 \times \text{OD}_{645}) \quad (4)$$

$$\text{Chl}_b = 0.3 \times (22.90 \times \text{OD}_{645} - 4.68 \times \text{OD}_{663}) \quad (5)$$

$$\text{Chl}_{\text{tot}} = 0.3 \times (20.21 \times \text{OD}_{645} + 8.02 \times \text{OD}_{663}) \quad (6)$$

Analysis of leaf gas exchange

Leaf gas exchange of the three dominant herbaceous plants in each plot was measured in July 2015 after thinning. The net photosynthetic rate and the light response curve of new and old representative leaves were measured between 09:00 and 12:00 hours on sunny days with a portable photosynthesis system (LI-6400XT, Li-Cor, Inc., USA) equipped with a LED Source Leaf Chamber and a CO₂ injector. The airflow was 500 $\mu\text{mol s}^{-1}$, leaf temperature was 29.5–30.5 °C, and humidity was 50–60%. Leaves were acclimated to a saturating photosynthetic photon flux density (PPFD) of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a CO₂ concentration [CO₂] of 400 $\mu\text{mol mol}^{-1}$ until photosynthetic rates stabilized. Under these conditions, the net photosynthetic rate (*A*) was defined as the mean of three consecutive measurements. Photon irradiances were then decreased in sequence to 1500, 1200, 1000, 900, 800, 700, 600, 500, 400, 300, 200, 100, 80, 50, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Leaf sections enclosed in the chamber were digitized with an A3 flatbed scanner to obtain leaf surface area.

Dark respiration rate (*R_d*), light saturation point (*LSP*), light compensation point (*LCP*), apparent quantum efficiency (*AQE*), and maximum net photosynthetic rate (*A_{max}*) were calculated by fitting the light response curves to a Mitscherlich

241 nonlinear function using Photosynthesis Work Bench Software (Potvin et al. 1990).

242 **Statistical analyses**

243 Independent sample *t*-tests were used to examine the differences (soil chemical
244 properties, canopy structure and light transmittance, and understory community
245 structure) before thinning, and the differences (leaf gas exchange, morphological
246 attributes, and chlorophyll content) of the two leaf types. Multiple comparisons were
247 performed using a one-way ANOVA with a Duncan's HSD post hoc test. Stepwise
248 multiple linear analyses examined the relationships between the understory
249 community parameters and the environmental conditions, the relationships between
250 the leaf gas exchange and the environmental conditions, the relationships between
251 the leaf gas exchange with the leaf morphological attributes and chlorophyll content
252 for all the treatments. The assumptions of the ANOVA and linear regression for the
253 data set were verified prior to analysis. The data were $\ln(x)$ -transformed during the
254 regression analysis. Significant differences were assessed at the $p < 0.05$ level. These
255 analyses were processed with SPSS Version 10.0 (SPSS Inc., USA).

256 **Results**

257 **Soil chemical properties**

258 Thinning significantly decreased soil nitrate nitrogen (NO_3^- -N) and inorganic
259 nitrogen (IN) in the 0–10 cm layer at $\text{PT}_{0.5\text{-yr}}$ and $\text{PT}_{2.5\text{-yrs}}$ in July 2015, and these two
260 properties at $\text{PT}_{0.5\text{-yr}}$ were significantly lower than at $\text{PT}_{2.5\text{-yrs}}$ (Table 1). This may
261 indicate that the values of the soil chemical properties had decreased significantly
262 after 0.5 year, and then partially recovered, coming close to the original level after

263 2.5 years post-thinning.

264 **Canopy structure and light transmittance**

265 Thinning significantly decreased leaf area index (LAI) and effective plant area index
266 (PAIe), and increased canopy openness, total solar radiation transmittance (T_{tot}),
267 direct solar radiation transmittance (T_{dir}), and diffuse solar radiation transmittance
268 (T_{dif}) at $PT_{0.5\text{-yr}}$ in July 2015 (Table 1). These variables were not significantly
269 different at $PT_{2.5\text{-yrs}}$ from those in the Unthinned. T_{tot} , T_{dir} , and T_{dif} at $PT_{0.5\text{-yr}}$ were
270 also significantly higher than at $PT_{2.5\text{-yrs}}$. These results indicate that light availability
271 in the understory increased significantly after 0.5 year, and then partially decreased
272 again, close to the original level after 2.5 years post-thinning.

273 **Understory structure and species diversity**

274 *W. japonica*, *D. championii*, and *D. dichotoma* were the dominant species in the
275 understory community. Together they accounted for 53.0% and 67.0% of the total
276 density and aboveground biomass in all the treatments at the two sampling dates,
277 respectively (Table A2).

278 Thinning significantly led to an increase of understory density and aboveground
279 biomass ($PT_{0.5\text{-yr}}$: +104.9% and +191.1%; $PT_{2.5\text{-yrs}}$: +142.4% and +239.2%) in July
280 2015, and their values at $PT_{0.5\text{-yr}}$ were still significantly lower than at $PT_{2.5\text{-yrs}}$. The
281 density increases of the two treatments ($PT_{0.5\text{-yr}}$: 81.7 plants m^{-2} ; $PT_{2.5\text{-yrs}}$: 79.4 plants
282 m^{-2}) were not significantly different, while the aboveground biomass increase at
283 $PT_{0.5\text{-yr}}$ (467.0 g m^{-2}) was greater than at $PT_{2.5\text{-yrs}}$ (388.1 g m^{-2}).

284 Comparing the values of the species diversity indexes in July 2015 and their

variation between December 2014 and July 2015, thinning significantly increased the understory communities' Shannon-Wiener index (H') and Pielou index (J), and decreased their Simpson index (D) at $PT_{0.5-yr}$ and $PT_{2.5-yrs}$. Thinning significantly increased the communities' Species richness (S) at $PT_{0.5-yr}$ but significantly decreasing again at $PT_{2.5-yrs}$ (Table A1, Fig. 1).

Leaf morphological attributes and chlorophyll content of the three dominant herbaceous plants

For *W. japonica*, thinning significantly increased new-leaf length (L) (8.3%), and decreased new-leaf chlorophyll b concentrations (Chl_b) (25.0%) and old-leaf L (12.3%) at $PT_{0.5-yr}$. However, thinning significantly increased old-leaf specific leaf area (SLA) (16.6%), and decreased old-leaf surface area (SA) (19.3%), all-leaf (new and old) L (10.7% and 6.6%), chlorophyll a concentrations (Chl_a) (23.8% and 21.6%), Chl_b (8.3% and 18.2%), chlorophyll total concentrations (Chl_{tot}) (21.2% and 20.2%) at $PT_{2.5-yrs}$ (Table 2). Thinning promoted *W. japonica* new-leaf elongation 0.5 year post-thinning, and then it made the leaves smaller and thicker, thereby reducing length and chlorophyll concentration.

For *D. championii*, thinning significantly decreased old-leaf SLA (12.5%) at $PT_{0.5-yr}$, and also width (W) (14.8%) and Chl_b (6.9%) at $PT_{2.5-yrs}$. The results show that thinning led *D. championii* to produce narrow and thick leaves.

For *D. dichotoma*, thinning significantly increased new-leaf W (15.6%), and decreased new-leaf SLA (12.2%), Chl_a (30.3%), Chl_b (21.9%), Chl_{tot} (27.8%), and old-leaf Chl_b (8.2%) at $PT_{0.5-yr}$. At $PT_{2.5-yrs}$, thinning significantly increased old-leaf L

(6.1%), and decreased new-leaf SA (17.0%), old-leaf W (11.1%), all-leaf SLA (31.0% and 23.2%), Chl_a (31.7% and 45.7%), Chl_b (29.7% and 44.9%), and Chl_{tot} (31.9% and 45.3%). The results indicate that thinning promotes *D. dichotoma* leaf elongation 0.5 year post-thinning. After 2.5 years post-thinning, thinning makes leaves broader and thicker, but doesn't change leaf size, and thus chlorophyll concentration is low.

Leaf gas exchange in the three dominant herbaceous plants

For *W. japonica*, thinning significantly increased new-leaf dark respiration rate (R_d) (40.5%), and decreased old-leaf apparent quantum efficiency (AQE) (23.6%) at $\text{PT}_{0.5\text{-yr}}$. At $\text{PT}_{2.5\text{-yrs}}$, thinning significantly increased new-leaf net photosynthetic rate (A) (66.6%), light saturation point (LSP) (50.9%), old-leaf R_d (30.0%), and light compensation point (LCP) (100.0%), and decreased old-leaf A (38.3%), maximum net photosynthetic rate (A_{max}) (27.1%), and all-leaf AQE (26.6% and 48.6%) (Fig. 2, 3, and 4). These results show that thinning promoted *W. japonica* new-leaf carbon emissions after 0.5 year, and improved carbon fixation potential 2.5 years post-thinning. For old leaves, however, thinning promoted carbon emission and reduced carbon fixation potential and light use efficiency at both times.

For *D. championii*, thinning significantly increased new-leaf R_d (209.7%), old-leaf AQE (29.6%), all-leaf A (80.9% and 48.3%), LSP (120.3% and 66.1%), and A_{max} (126.9% and 91.6%) at $\text{PT}_{0.5\text{-yr}}$. At $\text{PT}_{2.5\text{-yrs}}$, thinning significantly increased new-leaf A (39.4%) and AQE (127.4%), and decreased old-leaf AQE (31.8%). Thinning improved *D. championii* leaf carbon fixation ability after 0.5 year, but only

329 increased new-leaf light use efficiency 2.5 years post-thinning.

330 For *D. dichotoma*, thinning significantly increased new-leaf *A* (43.8%), *Rd*
331 (29.8%), and old-leaf *Amax* (16.0%) at $PT_{0.5-yr}$. Thinning also significantly increased
332 old-leaf *AQE* (253.7%), all-leaf *A* (46.6% and 75.6%), *LSP* (28.7% and 42.2%), and
333 *Amax* (45.4% and 68.1%), and decreased new-leaf *Rd* (17.0%), *AQE* (28.6%), and
334 old-leaf *LCP* (63.6%) at $PT_{2.5-yr}$. These results indicate that thinning improved *D.*
335 *dichotoma* old-leaf carbon fixation potential after 0.5 year, and increased all-leaf
336 carbon fixation ability 2.5 years post-thinning.

337 Discussion

338 Effects of thinning on understory communities

339 Our results showed that thinning increased understory density and aboveground
340 biomass, supported by previous studies (Lindgren et al. 2006; Sullivan et al. 2009).
341 However, other studies reported little or negative effects after thinning (He and
342 Barclay 2000; Wolk and Rocca 2009). Factors such as ecosystem-specific conditions
343 (e.g., level of competition from other plants, plant community structure and
344 diversity), thinning intensity, sampling time and time post-thinning, and responses to
345 environmental conditions have a considerable influence on the results (Wolk and
346 Rocca 2009; Taki et al. 2010).

347 Our results showed different responses to environmental conditions at the two
348 post-thinning times (Table 1 and 3). The sudden changes in environmental conditions
349 (especially light availability) post-thinning can be quickly used by certain species
350 (such as *D. championii* and *D. dichotoma*) for propagation and growth (Zhang et al.

2012; Gang et al. 2015). But the rapid growth of the remaining trees within 2.5 years (reclosed the canopy) may limit the growth of new understory. This may be the reason why plant density and aboveground biomass at $PT_{2.5\text{-yrs}}$ was higher than at $PT_{0.5\text{-yr}}$, but aboveground biomass increase at $PT_{2.5\text{-yrs}}$ was lower than at $PT_{0.5\text{-yr}}$. Furthermore, nutrient availability may create competition among plants over the long term (Lochhead and Comeau 2012). Disturbance caused by thinning can change the photosynthetic capacity of understory (Fig. 2, 3 and 4); this may produce more complex understory communities. Adaptive strategy variation of different plant species may be another important reason led to these results, such as *D. championii* and *D. dichotoma*, although mean daily net photosynthetic rate of *D. championii* was maximum when total solar radiation transmittance was 50% like *D. dichotoma*, *D. championii* growth was the most robust when total solar radiation transmittance was 15-30% (not 50%) (Lv 2014; Wang 2014).

The significant diversity results we obtained were surprising given that other studies reported no response a short time post-thinning (Ishii et al. 2008; Taki et al. 2010). In those previous studies, it took more than three years before changes were observed in species diversity, although the canopy structures were altered by thinning. These differences may be related to thinning intensity, thinning time, or site-specific conditions (Wolk and Rocca 2009; Lindgren and Sullivan 2013). Our results suggested that canopy structure and light transmittance determined species number and richness, while soil conditions in the surface layer and light transmittance determined community dominance and uniformity (Table 3). Moreover,

clean-up of shrubs may play an important role in relation to the immediate diversity change, because herbs responded faster than shrubs and dominated the understory after thinning (Lindgren and Sullivan 2013). The role of the dominate fern species as an ecological filter that influences the emergence and establishment of the other understory species and their patterns of seedling spatial distribution may be another important influencing factors of understory diversity, and the mechanism of fern interference was species-specific (George and Bazzaz 1999; Xu et al. 2014b). Additional long-term surveys are required here to evaluate when the understory diversity would become stable post-thinning.

Effects of thinning on the leaf photosynthetic characteristics of the dominant herbaceous plants

Photosynthetic characteristics of the three dominant species showed different variation after 0.5 and 2.5 years post-thinning (Fig. 2, 3 and 4). Thinning significantly increased photosynthetic carbon sequestration ability of *W. japonica* new-leaf, *D. championii* all-leaf and *D. dichotoma* old-leaf, and decreased photosynthetic carbon sequestration ability of *W. japonica* old-leaf and breathing carbon loss ability of *D. dichotoma* new-leaf. Thinning influence on *D. championii* becomes smaller with time passing while its influence on *D. dichotoma* becomes bigger. This may explain why thinning significantly increased understory aboveground biomass at different rates. In July 2015, the aboveground biomass of three dominant herbaceous plants significantly increased by 169.2 and 418.1 g m⁻² at PT_{0.5-yr} and PT_{2.5-yr}, this accounted for 47.9% and 94.7% of the total aboveground

395 biomass increase, respectively (data not shown).

396 Leaf photosynthetic characteristics of the three species could not be explained
397 in terms of the differences in environmental conditions (Table 3). Inter-specific
398 differences may be the most important factors contributing to observed patterns
399 depending on their various adaptive strategies (Ma et al. 2008; Wang et al. 2014;
400 Chen et al. 2016). Generally, photosynthesis rate of most understory plants increases
401 with light intensity enhancement after thinning within certain limits (Brouwer et al.
402 2012; Catoni et al. 2012). *D. dichotoma* is a light-demanding heliophyte, its growth
403 was more robust when total solar radiation transmittance was higher (such as 50%)
404 (Lv 2014; Chen et al. 2016). So, *D. dichotoma* in our site grow better with time
405 passing after thinning, because the total solar radiation transmittance were high after
406 thinning (44.45% and 42.94%) (Table 1). *W. japonica* is a shade fern, too high light
407 transmittance confined its photosynthesis rate increase and growth in the long run
408 (Ma et al. 2008). *D. championii* is photophilous, but its growth was the most robust
409 when total solar radiation transmittance was 15-30% and it always has a very
410 significant positive correlation with *W. japonica* in the understory communities
411 (Wang 2014; Wang et al. 2014). Then, *D. championii* in our site cannot always grow
412 better with time passing after thinning. Light quality difference between the two time
413 post-thinning may be another important factor due to its important role in fern spore
414 germination and gametophyte growth (Brum and Randi 2002; Gang et al. 2015).
415 Finally, intense competition between the three species may confuse their various
416 photosynthetic responses to environmental conditions because of their similar

resource usage and overlapping niches (Wu et al. 2013). Further investigations are needed to understand the deep effect of thinning on particular species (especially include multiple functional plant groups, such as shrub) photosynthesizes attributes and in favor of protection of plant diversity in subtropical China.

Leaf morphological attributes and chlorophyll content can partly explain the difference of leaf photosynthetic characteristics (Table 3). Generally, leaf size and chlorophyll a concentrations of most understory plants decreases with light intensity enhancement after thinning within certain limits (Brouwer et al. 2012; Wang 2014). At $PT_{0.5\text{-yr}}$, greater new-leaf length (or width) and lower old-leaf chlorophyll b concentration may show that understory produced bigger new leaves and reduced old-leaf chlorophyll photooxidative damage in order to acclimate to the higher light levels (Atanasova et al. 2003; Forrester et al. 2012). At $PT_{2.5\text{-yrs}}$, old-leaf chlorophyll content was low due to the larger surface area and thicker cellular structure (Oguchi et al. 2003), and new-leaf size was small in support of direction adjustment to improve the light utilization efficiency of less light quantum on account of canopies reclose.

Conclusion

Understory density and aboveground biomass increased significantly 0.5 years after thinning and increased further 2.5 years post-thinning. The Shannon-Wiener index and Pielou index increased significantly, while the Simpson index decreased markedly after 0.5 and 2.5 years post-thinning. Species richness increased significantly after 0.5 year, and then decreased markedly 2.5 years post-thinning.

439 Different age leaf photosynthetic characteristics of the three dominant species
440 changed differently after 0.5 and 2.5 years post-thinning. Their photosynthetic
441 characteristics cannot be together explained by environmental conditions depending
442 on their various adaptive strategies, while these characteristics had some common
443 responses to thinning in leaf morphological attributes and chlorophyll content.
444 Generally, new-leaf sizes increased first, and then decreased to adapt to the new light
445 regime, while old leaves chlorophyll content gradually reducing. These results
446 provide new insights into forest biodiversity and photosynthetic characteristics
447 response to thinning in the short-term, and may be successfully used in a carbon
448 balance algorithm for carbon model parameterization. We also suggest that other
449 study pay close attention to the response of different functional plant groups to
450 thinning in the future.

451 **Acknowledgments**

452 This research was funded by the NSFC Projects of International Cooperation and
453 Exchanges (31210103920), the National Key Research and Development Program
454 (2016YFD0600202), and the Project of Jiangxi Provincial Department of Science
455 and Technology (20144BBB70005).

References

- Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts-Polyphenoloxidase in
Beta-vulgaris. Plant physiology, 24(1): 1-15.
- Atanasova, L., Stefanov D., Yordanov, I., Kornova, K., and Kavardzikov, L. 2003.
Comparative characteristics of growth and photosynthesis of sun and shade

- leaves from normal and pendulum walnut (*Juglans regia* L.) trees. *Photosynthetica*, 41(2): 289-292.
- Brouwer, B., Ziolkowska, A., Bagard, M., Keech, O., Gardeström, P. 2012. The impact of light intensity on shade-induced leaf senescence. *Plant, Cell and Environment*, 35: 1084-1098. doi: 10.1111/j.1365-3040.2011.02474.x.
- Brum, F.R., and Randi, Á.M. 2002. High irradiance and temperature inhibit the germination of spores of the fern *Rumohra adiantiformis* (Forst.) Ching (Dryopteridaceae). *Brazilian Journal of Botany*, 25(4): 391-396.
- Catoni, R., Gratani, L., and Varone, L. 2012. Physiological, morphological and anatomical trait variations between winter and summer leaves of *Cistus* species. *Flora*, 207(6): 442-449. <http://dx.doi.org/10.1016/j.flora.2012.02.007>.
- Chen, Z.Q., Chen, Z.B., Yan, X.Y., and Bai, L.Y. 2016. Stoichiometric mechanisms of *Dicranopteris dichotoma* growth and resistance to nutrient limitation in the Zhuxi watershed in the red soil hilly region of China. *Plant Soil*, 398(1-2): 367-379. doi: 10.1007/s11104-015-2670-7.
- Chiang, J.M., and Brown, K.J. 2010. The effects of thinning and burning treatments on within-canopy variation of leaf traits in hardwood forests of southern Ohio. *Forest Ecology and Management*, 260(6): 1065-1075. doi:10.1016/j.foreco.2010.06.033.
- Forrester, D.I., Collopy, J.J., Beadle, C.L., Warren, C.R., and Baker, T.G. 2012. Effect of thinning, pruning and nitrogen fertilizer application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation.

- Forest Ecology and Management, 266: 286-300.
doi:10.1016/j.foreco.2011.11.019.
- Fu, X.L., Wang, J.L., Wang, H.M., Dai, X.Q., Yang, F.T., and Zhao, M. 2016. Response of the fine root production, phenology, and turnover rate of six shrub species from a subtropical forest to a soil moisture gradient and shading. *Plant Soil*, 399(1-2): 135-146. doi:10.1007/s11104-015-2686-z.
- Gajardo-Caviedes, P.A., Espinosa, M.A., González, U.T., Ríos, and Darcy.G. 2005. The influence of thinning and tree size on the sapwood area / leaf area ratio in coigue. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 35(7): 1679-1685. doi: 10.1139/X05-098.
- Gang, Q., Yan, Q.L., and Zhu, J.J. 2015. Effects of thinning on early seed regeneration of two broadleaved tree species in larch plantations: implication for converting pure larch plantations into larch-broadleaved mixed forests. *Forestry*, 88(5): 573-585. doi:10.1093/forestry/cpv025.
- George, L.O. and Bazzaz, F.A. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology*, 80(3): 833-845.
- Gspaltl, M., Bauerle, W., Binkley, D., Sterba, H. 2013. Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age classes. *Forest Ecology and Management*, 288: 49-59.
doi:10.1016/j.foreco.2011.11.044.
- Hanley, T.A., Deal, R.L., and Orlikowska, E.H. 2006. Relations between red alder composition and understory vegetation in young mixed forests of southeast

- Alaska. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 36(3): 738-748. doi:10.1139/X05-290.
- He, F.L., and Barclay, H.J. 2000. Long-term response of understory plant species to thinning and fertilization in a Douglas-fir plantation on southern Vancouver Island, British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 30(4): 566-572.
- Ishii, H.T., Maleque, M.A., and Taniguchi, S. 2008. Line thinning promotes stand growth and understory diversity in Japanese cedar (*Cryptomeria japonica* D. Don) plantations. Journal of forest research, 13(1): 73-78. doi: 10.1007/s10310-007-0051-7.
- Ji, L.Z., Wang, Z., Wang, X.W., and An, LL. 2011. Forest insect pest management and forest management in China: an overview. Environmental Management, 48(6): 1107-1121. doi: 10.1007/s00267-011-9697-1.
- Li, X.F., Chen, Z.B., Chen, Z.Q., Zheng, L.D., Zhang, X.Y., and Li, R.L. 2013. Response of *Disranopteris dichotoma* growth to environmental factors in eroded red-soil region of southern China. Bull Soil Water Conserv, 33(3): 33-37.
- Lindgren, P.M.F., Ransome, D.R., Sullivan, D.S., and Sullivan, T.P. 2006. Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 36(1): 48-61. doi:10.1139/X05-228.
- Lindgren, P.M.F., and Sullivan, T.P. 2013. Influence of stand thinning and repeated fertilization on plant community abundance and diversity in young lodgepole

- pine stands: 15-year results. *Forest Ecology and Management*, 308: 17-30.
<http://dx.doi.org/10.1016/j.foreco.2013.07.020>.
- Liu, Z.F., Wu, J.P., Zhou, L.X., Lin, Y.B., and Fu, S.L. 2012. Effect of understory fern (*Dicranopteris dichotoma*) removal on substrate utilization patterns of culturable soil bacterial communities in subtropical *Eucalyptus* plantations. *Pedobiologia-International Journal of Soil Biology*, 55(1): 7-13.
[doi:10.1016/j.pedobi.2011.07.014](https://doi.org/10.1016/j.pedobi.2011.07.014).
- Lochhead, K.D., and Comeau, P.G. 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. *Forest Ecology and Management*, 284: 12-22.
doi.org/10.1016/j.foreco.2012.07.029.
- Lv, C.X. 2014. The photosynthetic physiological and ecological response of *Dicranopteris dichotoma* under the light intensity and 4 kinds of tree litter cover. Dissertation for the Degree of Master, Zhejiang A&F University(in Chinese with English abstract).
- Ma, Z.Q., Liu, Q.J., Xu, W.J., Li, X.R., and Liu, Y.C. 2008. A preliminary study on biomass of *Woodwardia japonica* community under a coniferous plantation in subtropical China. *Chinese Journal of Plant Ecology*, 32(1): 88-94(in Chinese with English abstract).
- Magurran A.E. 1988. *Ecological Diversity and its Measurements*. Princeton, USA: Princeton University Press.
- McDowell, N.C., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic

- maintenance of *Ponderosa pine* gas exchange in response to stand density changes. *Ecological Applications*, 16(3): 1164-1182. doi: 10.1890/1051-0761(2006)016[1164:HMOPPG]2.0.CO;2.
- Moreno-Gutiérrez, C., Barberá, G.G., Nicolás, E., Luis, M.D., Castillo, M.V., Martínez-fernández, F., and Querejeta, J.I. 2011. Leaf $\delta^{18}\text{O}$ of remaining trees is affected by thinning intensity in a semiarid pine forest. *Plant, Cell and Environment*, 34(6): 1009-1019. doi: 10.1111/j.1365-3040.2011.02300.x.
- Nilsson, M.C., and Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in ecology and the environment*, 3(8): 421-428.
- Oguchi, R., Hikosaka, K., and Hirose, T. 2003. Does the photosynthetic light-acclimation need change in leaf anatomy? *Plant, Cell and Environment*, 26(4): 505-512.
- Peng, S.L., Wang, D.X., Zhao, H., and Yang, T. 2008. Discussion the status quality of plantation and near nature forestry management in China. *Journal of Northwest Forestry University*, 23(2): 184-188(in Chinese with English abstract).
- Piao, S.L., Fang, J.Y., Ciais, P., Peylin, P., Huang, Y., Sitch, S., and Wang, T. 2009. The carbon balance of terrestrial ecosystems in China. *Nature*, 458(7241): 1009-U82. doi:10.1038/nature07944.
- Potvin, C., Lechowicz, M.J., and Tardif, S. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, 71(4): 1389-1400.

- Raunika, R., Buongiorno, J., Turner, J.A., and Zhu, S.S. 2010. Global outlook for wood and forests with the bioenergy demand implied by scenarios of the Intergovernmental Panel on Climate Change. *Forest Policy and Economics*, 12(1): 48-56. doi:10.1016/j.forpol.2009.09.013.
- Rodríguez-Calcerrada, J., Reich, P.B., Rosenqvist, E., Pardos, J.A., Cano, F.J., and Aranda, I. 2008. Leaf physiological versus morphological acclimation to high-light exposure at different stages of foliar development in oak. *Tree Physiology*, 28(5): 761-771. <http://treephys.oxfordjournals.org/>.
- Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Ransome, D.B. 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *Forest Ecology and Management*, 258(S): S127-S141. doi:10.1016/j.foreco.2009.06.001.
- Taki, H., Inoue, T., Tanaka, H., Makihara, H., Sueyoshi, M., Isono, M., and Okabe, K. 2010. Responses of community structure, diversity, and abundance of understory plants and insect assemblages to thinning in plantations. *Forest Ecology and Management*, 259(3), 607-613. doi:10.1016/j.foreco.2009.11.019.
- Wang, L.F., Ji, H.B., Bai, K.Z., Li, L.B., and Kuang, T.Y. 2006. Photosystem 2 activities of hyper-accumulator *Dicranopteris dichotoma* Bernh from a light rare earth elements mine. *Photosynthetica*, 44(2): 202-207.
- Wang, X.Q. 2014. Study on *In vitro* culture and shade tolerance of *Dryopteris championii*. Dissertation for the Degree of Master, Beijing Forestry University(in Chinese with English abstract).

- Wang, X.Q., Zhang, T.T., Meng, Z., and Dong, L. 2014. In vitro Culture of *Dryopteris championii* (Benth.) C. Chr. from Spores. Plant Physiology Journal, 50(2): 159-163.
- Wang, Y.D., Wang, Z.L., Wang, H.M., Guo, C.C., and Bao, W.K. 2012. Rainfall pulse primarily drives litterfall respiration and its contribution to soil respiration in a young exotic pine plantation in subtropical China. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 42(4): 657-666. doi:10.1139/X2012-017.
- Wang, Y.D., Wang, H.M., Xu, M.J., Ma, Z.Q., and Wang, Z.L. 2015. Soil organic carbon stocks and CO₂ effluxes of native and exotic pine plantations in subtropical China. Catena, 128: 167-173. <http://dx.doi.org/10.1016/j.catena.2015.02.003>
- Wen, X.F., Wang, H.M., Wang, J.L., Yu, G.R., and Sun, X.M. 2010. Ecosystem carbon exchanges of a subtropical evergreen coniferous plantation subjected to seasonal drought, 2003–2007. Biogeosciences, 7(1): 357-369. doi:10.5194/bg-7-357-2010, 2010.
- Wolk, B., and Rocca, M.E. 2009. Thinning and chipping small-diameter ponderosa pine changes understory plant communities on the Colorado Front Range. Forest Ecology and Management, 257(1): 85-95. doi:10.1016/j.foreco.2008.08.014.
- Wu, X.J., Zhang, Z.W., Meng, X.F., Li, Z., and Wang, Y.J. 2013. Dynamics of diversity, distribution patterns and interspecific associations of understory herbs in the city-suburb-exurb context of Wuhan city, China. Archives of biological

- sciences, 65(4): 1619-1628. doi:10.2298/ABS1304619W.
- Xu, M.J., Wen, X.F., Wang, H.M., Zhang, W.J., Dai, X.Q., Song, J., Wang, Y.D., Fu, X.L., Liu, Y.F., Sun, X.M., and Yu, G.R. 2014a. Effects of Climatic Factors and Ecosystem Responses on the Inter-Annual Variability of Evapotranspiration in a Coniferous Plantation in Subtropical China. PLOS ONE, 9(1): e85593. doi:10.1371/journal.pone.0085593.
- Xu, X.L., Li, Q.K., Wang, J.Y., Zhang, L.M., Tian, S.N., Zhi, L., Li, Q.R., and Sun, Y. 2014b. Inorganic and Organic Nitrogen Acquisition by a Fern *Dicranopteris dichotoma* in a Subtropical Forest in South China. PLoS ONE, 9(5): e90075. doi:10.1371/journal.pone.0090075.
- Yan, J.H., Li, K., Peng, X.J., Huang, Z.L., Liu, S.Z., and Zhang, Q.M. 2015. The mechanism for exclusion of *Pinus massoniana* during the succession in subtropical forest ecosystems: light competition or stoichiometric homeostasis? Scientific Reports, 5: 10994. doi:10.1038/srep10994.
- Yan, J.H., Zhang, Y.P., Yu, G.R., Zhou, G.Y., Zhang, L.M., Li, K., Tan, Z.H., and Sha, L.P. 2013. Seasonal and inter-annual variations in net ecosystem exchange of two old-growth forests in southern China. Agricultural and Forest Meteorology, 182(SI): 257-265. <http://dx.doi.org/10.1016/j.agrformet.2013.03.002>.
- Yirdaw, E., and Luukkanen, O. 2004. Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecology and Management, 188(1-3): 17-24. doi:10.1016/j.foreco.2003.07.024.

Zhang, M., Zhu, J.J., and Yan, Q.L. 2012. Review on influence mechanisms of light in seed germination. Chinese Journal of Plant Ecology, 36(8): 899-908(in Chinese with English abstract).

Draft

Table 1. Soil chemical properties, canopy structure and light transmittance after thinning in July 2015. The values are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among treatments.

Item		Unthinned	PT _{0.5-yr}	PT _{2.5-yr}
Soil depth	Chemical properties			
0-10cm	pH	4.22 $\pm$ 0.02b	4.23 $\pm$ 0.03b	4.12 $\pm$ 0.02a
	NH ₄ ⁺ -N(mg kg ⁻¹)	8.15 $\pm$ 0.34b	5.66 $\pm$ 0.22a	8.14 $\pm$ 0.01b
	NO ₃ ⁻ -N(mg kg ⁻¹)	2.90 $\pm$ 0.12c	1.53 $\pm$ 0.08a	1.91 $\pm$ 0.06b
	Inorganic N(mg kg ⁻¹)	11.05 $\pm$ 0.22c	7.60 $\pm$ 0.33a	9.70 $\pm$ 0.09b
10-20cm	pH	4.23 $\pm$ 0.01a	4.21 $\pm$ 0.02a	4.20 $\pm$ 0.01a
	NH ₄ ⁺ -N(mg kg ⁻¹)	3.17 $\pm$ 0.07a	3.38 $\pm$ 0.21a	3.25 $\pm$ 0.42a
	NO ₃ ⁻ -N(mg kg ⁻¹)	1.28 $\pm$ 0.12b	1.09 $\pm$ 0.02ab	0.84 $\pm$ 0.06a
	Inorganic N(mg kg ⁻¹)	4.45 $\pm$ 0.15a	4.46 $\pm$ 0.18a	4.23 $\pm$ 0.26a
Leaf area index (LAI)		3.15 $\pm$ 0.05b	2.56 $\pm$ 0.15a	3.08 $\pm$ 0.15ab
Effective plant area index (PAIe)		3.02 $\pm$ 0.04b	2.55 $\pm$ 0.07a	2.80 $\pm$ 0.10ab
Canopy openness (%)		37.57 $\pm$ 1.42a	44.45 $\pm$ 1.80b	42.94 $\pm$ 1.30ab
Total solar radiation transmittance (T _{tot}) (%)		37.94 $\pm$ 1.10a	55.15 $\pm$ 1.53b	39.13 $\pm$ 2.97a
Direct solar radiation transmittance (T _{dir}) (%)		35.43 $\pm$ 0.83a	55.20 $\pm$ 1.09b	37.01 $\pm$ 3.10a
Diffuse solar radiation transmittance (T _{diff}) (%)		35.43 $\pm$ 1.37a	55.10 $\pm$ 1.97b	41.24 $\pm$ 2.85a

Table 2. Effects of thinning on leaf morphological attributes and chlorophyll content of *W. japonica*, *D. championii*, and *D. dichotoma* in July 2015. The values are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among thinning treatments for the same leaf type. Different capital letters represent significant differences among leaf types for the same thinning treatment.

Species	Leaf type	Treatment	Length (L) (cm)	Width (W) (cm)	Surface area (SA) (cm ²)	Specific leaf area (SLA) (cm ² g ⁻¹)	Chlorophyll a concentration (Chl _a) (mg g ⁻¹ FW)	Chlorophyll b concentration (Chl _b) (mg g ⁻¹ FW)	Chlorophyll total concentration (Chl _{tot}) (mg g ⁻¹ FW)
<i>W. japonica</i>	New	Unthinned	15.86 $\pm$ 0.31Ab	2.79 $\pm$ 0.11Aa	36.58 $\pm$ 0.76Aa	199.09 $\pm$ 16.89Ba	1.01 $\pm$ 0.08Ab	0.60 $\pm$ 0.01Bc	1.56 $\pm$ 0.05Ab
		PT _{0.5-yr}	17.18 $\pm$ 0.35Ac	2.69 $\pm$ 0.11Aa	36.93 $\pm$ 1.41Aa	183.56 $\pm$ 2.86Ba	1.05 $\pm$ 0.02Ab	0.45 $\pm$ 0.01Aa	1.52 $\pm$ 0.01Ab
		PT _{2.5-yr}	14.17 $\pm$ 0.18Aa	2.82 $\pm$ 0.03Aa	34.15 $\pm$ 0.51Aa	201.08 $\pm$ 6.69Ba	0.77 $\pm$ 0.02Aa	0.55 $\pm$ 0.01Bb	1.23 $\pm$ 0.02Aa
	Old	Unthinned	20.56 $\pm$ 0.21Bc	3.32 $\pm$ 0.14Ba	50.22 $\pm$ 0.73Bb	134.55 $\pm$ 5.83Aa	1.53 $\pm$ 0.03Bb	0.55 $\pm$ 0.01Ab	2.18 $\pm$ 0.10Bb
		PT _{0.5-yr}	18.03 $\pm$ 0.26Aa	3.23 $\pm$ 0.10Ba	48.25 $\pm$ 0.52Bb	131.92 $\pm$ 1.86Aa	1.41 $\pm$ 0.04Bb	0.51 $\pm$ 0.02Bb	1.93 $\pm$ 0.06Bab
		PT _{2.5-yr}	19.20 $\pm$ 0.29Bb	2.95 $\pm$ 0.31Aa	40.54 $\pm$ 0.52Ba	156.91 $\pm$ 3.96Ab	1.20 $\pm$ 0.03Ba	0.45 $\pm$ 0.01Aa	1.74 $\pm$ 0.05Ba
<i>D. championii</i>	Old	Unthinned	17.71 $\pm$ 0.23a	3.99 $\pm$ 0.08b	48.16 $\pm$ 2.29ab	131.2 $\pm$ 6.59b	2.13 $\pm$ 0.02ab	0.72 $\pm$ 0.01b	2.86 $\pm$ 0.02a
		PT _{0.5-yr}	17.73 $\pm$ 0.26a	3.98 $\pm$ 0.02b	51.98 $\pm$ 3.91b	114.75 $\pm$ 3.00a	1.94 $\pm$ 0.11a	0.70 $\pm$ 0.01b	2.74 $\pm$ 0.04a
		PT _{2.5-yr}	16.93 $\pm$ 0.35a	3.40 $\pm$ 0.07a	40.59 $\pm$ 0.79a	121.71 $\pm$ 1.70ab	2.33 $\pm$ 0.05b	0.67 $\pm$ 0.01a	2.96 $\pm$ 0.15a
<i>D. dichotoma</i>	New	Unthinned	14.40 $\pm$ 0.60Aab	2.71 $\pm$ 0.08Aa	30.96 $\pm$ 1.04Ab	262.28 $\pm$ 2.51Bc	2.08 $\pm$ 0.05Bb	0.64 $\pm$ 0.01Bc	2.70 $\pm$ 0.07Bb
		PT _{0.5-yr}	15.95 $\pm$ 0.47Ab	3.21 $\pm$ 0.13Ab	34.39 $\pm$ 1.38Ab	233.81 $\pm$ 1.32Bb	1.45 $\pm$ 0.01Aa	0.50 $\pm$ 0.01Bb	1.95 $\pm$ 0.01Aa
		PT _{2.5-yr}	13.05 $\pm$ 0.80Aa	2.66 $\pm$ 0.07Aa	25.69 $\pm$ 1.18Aa	180.89 $\pm$ 0.97Ba	1.42 $\pm$ 0.04Ba	0.45 $\pm$ 0.01Ba	1.84 $\pm$ 0.06Ba
	Old	Unthinned	14.23 $\pm$ 0.07Aa	4.33 $\pm$ 0.06Bb	43.03 $\pm$ 2.38Ba	188.60 $\pm$ 1.04Ab	1.51 $\pm$ 0.05Ab	0.49 $\pm$ 0.01Ac	2.01 $\pm$ 0.06Ab
		PT _{0.5-yr}	14.58 $\pm$ 0.17Aa	4.51 $\pm$ 0.09Bb	43.71 $\pm$ 0.16Ba	181.22 $\pm$ 3.66Ab	1.38 $\pm$ 0.05Ab	0.45 $\pm$ 0.01Ab	1.84 $\pm$ 0.05Ab
		PT _{2.5-yr}	15.10 $\pm$ 0.10Ab	3.85 $\pm$ 0.09Ba	40.07 $\pm$ 2.33Ba	144.88 $\pm$ 2.02Aa	0.82 $\pm$ 0.01Aa	0.27 $\pm$ 0.01Aa	1.10 $\pm$ 0.01Aa

Table 3. Results of multiple stepwise regression analysis for the relationships of the understory community parameters (density, aboveground biomass, Species richness, Shannon-Wiener index, Simpson index and Pielou index) with the environmental conditions (soil inorganic nitrogen (IN), $\text{NH}_4^+\text{-N}$, and $\text{NO}_3^-\text{-N}$ in the 0-10 cm layer, canopy LAI, direct solar radiation transmittance (T_{dir}), diffuse solar radiation transmittance (T_{dif}) and total solar radiation transmittance (T_{tot}); the relationships of the leaf gas exchange (net photosynthetic rate (A), dark respiration rate (R_d), light saturation point (LSP), light compensation point (LCP), apparent quantum efficiency (AQE), maximum net photosynthetic rate (A_{max})) with the environmental conditions; and the relationships of the leaf gas exchange with the leaf morphological attributes and chlorophyll content (width (W), length (L), surface area (SA), specific leaf area (SLA), chlorophyll a concentration (Chl_a), chlorophyll b concentration (Chl_b) and chlorophyll total concentration (Chl_{tot})) for all the treatments in July 2015. No correlations were found between the all-leaf ($n=45$) (or same-type-leaf, $n=18$ or 27) leaf gas exchange of the three plant species with the environmental conditions for all the treatments.

Dependent variable		Regression equation	<i>n</i>	<i>R</i> ²	<i>P</i> value
Density		$y=2.37\text{NH}_4^+\text{-N}-1.77\text{NO}_3^-\text{-N}+0.85$	18	0.73	≤ 0.001
Aboveground biomass		$y=2.12\text{NH}_4^+\text{-N}-2.14\text{NO}_3^-\text{-N}+3.22$	18	0.62	≤ 0.001
Species richness		$y=1.35\text{LAI}+1.46$	18	0.34	0.011
Shannon-Wiener index		$y=-0.66T_{\text{dif}}+3.05$	18	0.35	0.008
Simpson index		$y=0.49\text{IN}+1.08T_{\text{dif}}-6.34$	18	0.61	0.001
Pielou index		$y=-0.33\text{NH}_4^+\text{-N}-0.33T_{\text{dir}}+1.35$	18	0.80	≤ 0.001
New	<i>A</i>	$y=-1.62L-0.79\text{Chl}_b+1.56W+3.88$	18	0.66	0.001
	<i>R_d</i>	$y=2.08\text{SA}-0.73\text{SLA}-3.84$	18	0.82	≤ 0.001
	<i>LCP</i>	$y=-1.13\text{Chl}_a+2.62$	18	0.58	≤ 0.001
	<i>AQE</i>	$y=2.03\text{SA}-1.60W-8.34$	18	0.76	≤ 0.001
	<i>A_{max}</i>	$y=-0.74\text{Chl}_a-0.88L+3.62$	18	0.57	0.002
Old	<i>A</i>	$y=-1.66\text{SLA}-4.26L+21.61$	27	0.71	≤ 0.001
	<i>R_d</i>	$y=-1.63W+0.59\text{Chl}_a+0.66\text{SLA}-2.39$	27	0.59	≤ 0.001
	<i>LSP</i>	$y=-0.52\text{Chl}_a+0.78\text{SA}+3.27$	27	0.40	0.002
	<i>LCP</i>	$y=7.25L+3.11\text{SLA}-34.45$	27	0.77	≤ 0.001
	<i>AQE</i>	$y=-1.56\text{Chl}_a-2.30\text{SLA}+1.49W+7.12$	27	0.73	≤ 0.001
	<i>A_{max}</i>	$y=-2.65L-0.77\text{Chl}_a+1.53\text{SA}-0.94\text{SLA}+8.13$	27	0.74	≤ 0.001

Fig. 1. Species richness (S), Shannon-Wiener index (H'), Simpson index (D), and Pielou index (J) after thinning in July 2015, and their variation between December 2014 and July 2015. The data are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among treatments.

Fig. 2. Effects of thinning on net photosynthetic rate (*A*) and dark respiration rate (*Rd*) of new and old leaves of *W. japonica* (A, D), *D. championii* (B, E), and *D. dichotoma* (C, F) in July 2015. The data are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among thinning treatments for the same leaf type. Different capitals letters represent significant differences among leaf types for the same thinning treatment.

Fig. 3. Effects of thinning on light saturation point (*LSP*) and light compensation point (*LCP*) of new and old leaves of *W. japonica* (A, D), *D. championii* (B, E), and *D. dichotoma* (C, F) in July 2015. The data are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among thinning treatments for the same leaf type. Different capitals letters represent significant differences among leaf types for the same thinning treatment.

Fig. 4. Effects of thinning on apparent quantum efficiency (*AQE*) and maximum net photosynthetic rate (*Amax*) of new and old leaves of *W. japonica* (A, D), *D. championii* (B, E), and *D. dichotoma* (C, F) in July 2015. The data are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among thinning treatments for the same leaf type. Different capitals letters represent significant differences among leaf types for the same thinning treatment.

Table A1. Soil chemical properties, canopy structure and light transmittance, and understory community structure before thinning in December 2014. The values are means $\pm$ SE ($n = 3$). Different lowercase letters represent significant differences among treatments.

Item		Unthinned	PT _{0.5-yr}
Soil depth	Chemical properties		
0-10cm	pH	4.19 $\pm$ 0.02a	4.21 $\pm$ 0.05a
	NH ₄ ⁺ -N(mg kg ⁻¹)	3.54 $\pm$ 0.06a	3.91 $\pm$ 0.30a
	NO ₃ ⁻ -N(mg kg ⁻¹)	1.78 $\pm$ 0.09a	1.76 $\pm$ 0.23a
	Inorganic N(mg kg ⁻¹)	5.66 $\pm$ 0.37a	5.67 $\pm$ 0.53a
10-20cm	pH	4.30 $\pm$ 0.02a	4.30 $\pm$ 0.03a
	NH ₄ ⁺ -N(mg kg ⁻¹)	2.33 $\pm$ 0.07a	2.19 $\pm$ 0.06a
	NO ₃ ⁻ -N(mg kg ⁻¹)	1.52 $\pm$ 0.20a	1.20 $\pm$ 0.18a
	Inorganic N(mg kg ⁻¹)	3.85 $\pm$ 0.13a	3.45 $\pm$ 0.23a
Leaf area index (LAI)		3.62 $\pm$ 0.08a	3.80 $\pm$ 0.06a
Effective plant area index (PAIe)		3.38 $\pm$ 0.08a	3.64 $\pm$ 0.03b
Canopy openness (%)		35.19 $\pm$ 2.48a	37.03 $\pm$ 1.09a
Total solar radiation transmittance (T _{tot}) (%)		38.04 $\pm$ 4.54a	37.13 $\pm$ 2.08a
Direct solar radiation transmittance (T _{dir}) (%)		36.33 $\pm$ 5.37a	36.46 $\pm$ 2.48a
Diffuse solar radiation transmittance (T _{dir}) (%)		36.33 $\pm$ 3.70a	37.81 $\pm$ 1.86a
Species richness (<i>S</i>)		13.50 $\pm$ 0.87b	7.50 $\pm$ 0.87a
Shannon-Wiener index (<i>H'</i>)		2.17 $\pm$ 0.00b	1.41 $\pm$ 0.10a
Simpson index (<i>D</i>)		0.16 $\pm$ 0.01a	0.32 $\pm$ 0.01b
Pielou index (<i>J</i>)		0.84 $\pm$ 0.02b	0.70 $\pm$ 0.01a

Table A2. Density and aboveground biomass of the understory communities in December 2014 and July 2015. The values are means ($n = 3$). Different lowercase letters represent significant differences among thinning treatments at the two investigate dates. Different capital letters represent significant differences between the two investigate dates for the same thinning treatment.

Species	Density (Plants m ⁻²)						Density sum (Plants m ⁻²)	Above-ground biomass sum (g m ⁻²)
	Dec-2014			July-2015				
	Unthinned	PT _{0.5-yr}	PT _{2.5-yrs}	Unthinned	PT _{0.5-yr}	PT _{2.5-yrs}		
<i>Woodwardia japonica</i> (L. f.) Sm.	1.10	2.50	14.40	2.60	11.95	21.80	54.35	677.71
<i>Dryopteris championii</i> (Benth.) C. Chr.	6.90	3.20	7.87	7.30	9.20	14.20	48.67	269.63
<i>Dicranopteris dichotoma</i> (Thunb.)Bernh.	0.50	5.47	5.70	2.00	10.80	36.40	60.87	218.94
<i>Adiantum flabellulatum</i> L. Sp.	1.40	0.10	1.10	1.00	0.73	2.40	6.73	6.10
<i>Parathelypteris glanduligera</i> (Kze.) Ching	0.13			1.47			1.60	3.50
<i>Pteridium aquilinum</i> (Linn.) Kuhn var. latiusculum (Desv.)Underw.ex Heller				0.80	0.33	0.04	1.17	5.93
<i>Lophatherum gracile</i> Brongn.				10.30	34.30	27.70	72.30	135.51
<i>Isatis indigotica</i> Fortune					0.20	0.07	0.27	0.67
<i>Imperata cylindrica</i> (Linn.) Beauv.				10.60	0.60		11.20	31.66
<i>Amorphophallus rivieri</i> Durieu						0.07	0.07	0.01
<i>Glycyrrhiza uralensis</i> Fisch.					2.80	0.47	3.27	8.76
<i>Oplismenus undulatifolius</i> (Arduino) Beauv.					0.27	0.10	0.37	0.47
<i>Carex parva</i> Nees	0.50		0.07				0.57	0.21
<i>Arundo donax</i> Linn.			0.07			0.40	0.47	1.07
<i>Bupleurum chinensis</i> DC.		0.07	0.07	3.00	0.60	0.53	4.27	9.68
<i>Melastoma dodecandrum</i> Lour.	0.07			0.10	0.07		0.23	0.90
<i>Cyperus rotundus</i> L.	0.07						0.07	0.03

<i>Cyrtomium fortunei</i> J.Sm.		0.13					0.13	0.02
<i>Rosa multiflora</i> Thunb. Var. Cathayensis Rehd. Et Wils.	0.13			0.07			0.20	0.82
<i>Spatholobus suberectus</i> Dunn	0.07			0.07	0.07	0.13	0.33	0.41
<i>Uncaria rhynchophylla</i> (Miq.) Miq. ex Havil.	0.07			0.27			0.33	2.13
<i>Vitis amurensis</i> Rupr.				0.07	0.13		0.20	0.69
<i>Morinda umbellata</i> Linn. subsp. obovata Y.Z.Ruan	0.07		0.10	0.20	1.60	0.40	2.37	5.59
<i>Paederia scandens</i> (Lour.) Merr.						0.07	0.07	0.03
<i>Premna microphylla</i> Turcz.					0.13		0.13	0.55
<i>Viburnum dilatatum</i> Thunb.					0.13		0.13	0.32
<i>Glochidion puberum</i> (Linn.) Hutch.				0.60			0.60	0.13
<i>Psilopogon sinense</i> Hemsl.						0.07	0.07	0.29
<i>Lonicera japonica</i> Thunb.						0.07	0.07	0.08
<i>Eurya muricata</i> Dunn	0.50	0.13	0.30	0.10	0.40	0.13	1.57	22.73
<i>Rubus corchorifolius</i> Linn. f.				0.13	0.13		0.27	0.70
<i>Smilax china</i> Linn.	0.10		0.13	0.90	0.20	0.07	1.40	11.13
<i>Smilax corbularia</i> Kunth var. woodii (Merr.) T.Koyama	0.30		0.20	0.90	0.50	0.33	2.23	7.33
<i>Ilex asprella</i> (Hook. et Arn.) Champ. ex Benth.			0.07		0.20	0.20	0.47	1.00
<i>Phlomis umbrosa</i> Turcz.	0.07			0.07	0.27	0.13	0.53	2.30
<i>Ficus pumila</i> Linn.			0.07				0.07	0.50
<i>Loropetalum chinense</i> (R. Br.) Oliver	0.27	0.10	0.80	0.60	12.70	3.00	17.47	229.79
<i>Vaccinium bracteatum</i> Thunb.	0.20	0.13	0.07		0.20		0.60	4.67
<i>Ardisia crenata</i> Sims		0.13			0.13		0.27	2.36
<i>Gardenia jasminoides</i> Ellis	0.30	0.07		0.30	0.53		1.20	3.60
<i>Camellia oleifera</i> Abel.		0.07			0.07	0.40	0.60	6.67
<i>Berchemia floribunda</i> (Wall.) Brongn.					0.33		0.33	1.70
<i>Symplocos paniculata</i> (Thunb.) Miq.			0.07	0.07			0.13	0.50

<i>Vitex negundo</i> Linn. var. <i>cannabifolia</i> (Sieb.et Zucc.) Hand.-Mazz.			0.13				0.13	1.99
<i>Syzygium grijsii</i> (Hance) Merr. et Perry			0.07			0.40	0.47	3.11
<i>Rhaphiolepis indica</i> (Linn.) Lindl.	0.90	0.07	0.20	0.40	0.30	0.10	1.97	10.67
<i>Acer palmatum</i> Thunb.					0.07	0.07	0.13	2.87
<i>Rhamnus utilis</i> Decne.				0.10	0.13		0.23	0.46
<i>Rhus chinensis</i> Mill.				0.07	0.07		0.13	0.98
<i>Aralia chinensis</i> Linn.				0.07			0.07	0.04
<i>Sapium sebiferum</i> (Linn.) Roxb.				0.07			0.07	1.84
<i>Symplocos sumuntia</i> Buch.-Ham. ex D. Don					1.20		1.20	1.15
<i>Quercus fabri</i> Hance				0.07			0.07	0.08
<i>Choerospondias axillaria</i> (Roxb.) Burt et Hill					0.07	0.40	0.47	3.55
<i>Sapindus mukorossi</i> Gaertn.				1.50	2.10	0.90	4.50	22.87
<i>Liquidambar formosana</i> Hance		0.07		0.07	0.20		0.33	4.34
<i>Michelia maudiae</i> Dunn		0.13			0.07		0.20	1.84
<i>Schima superba</i> Gardn. et Champ.	0.07		0.30	0.07	0.20	0.20	0.83	6.74
<i>Cinnamomum camphora</i> (L.) Presl					0.07		0.07	0.24
Total density (Plants m ⁻²)	13.70Aa	12.37Aa	31.83Ab	45.90Ba	94.05Bb	111.24Bc	309.09	
Total density variation (Plants m ⁻²)				32.20a	81.68a	79.41b		
Total aboveground biomass (g m ⁻²)	82.42Aa	70.48Aa	238.19Ab	184.66Ba	537.52Bb	626.32Bc		1739.59
Total aboveground biomass variation (g m ⁻²)				102.24a	467.03c	388.13b		

Fig. A1. Sketch map of the understory survey.