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Thinning promotes litter decomposition and nutrient release in poplar plantations via altering the microclimate and understory plant diversity

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Abstract: Thinning is widely employed in forest management to improve productivity, protect forest biodiversity and maintain ecosystem functions. Here a thinning experiment with four treatments (unthinned, CK; 30% tree removal from below, MB; 50% tree removal by interlaced thinning, HI; and 50% tree removal from below, HB) was set up in the poplar plantation, while a followed decomposition experiment with four litter types was conducted under the poplar plantations of undergoing four thinning treatments using the litterbag technique. Thinning affected the microclimate, but only the heavy thinning (HI and HB) significantly enhanced photosynthetic photon flux density (PPFD) and soil moisture in the plantations during the growing season. Thinning promoted understory vegetation biomass and vegetation diversity via modifying the microclimate parameters. Pearson correlation analysis showed that PPFD and understory herbaceous biomass were significantly correlated to Shannon-Weiner diversity index. Both thinning intensity and litter type significantly affected the litter remaining mass over times. Overall, increasing thinning intensity and litter complexity enhanced decay rate, while reduced half live ($t_{0.5}$) and $t_{0.95}$ values. Correlation analysis showed that air relative humidity, soil temperature, air temperature and soil moisture significantly influenced the litter mass loss rates. Non-additive (synergistic) effects were observed when different litters were mixed, but the non-additive effect was most pronounced when more herbaceous species litter were mixed with poplar leaves and 50% thinning intensity was applied. Dynamics of nutrient release from different litter types were similar to those on the litter mass lose, depending on the litter quality and microclimatic conditions. Our results suggest that a thinning operation with 50% tree removal from below (HB) would maintain the structural and functional features of the poplar plantations at the similar sites.

Keywords: thinning intensity, litter type, environmental factor, vegetation biomass, decay rate, nutrient content.

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Introduction

Poplars (*Populus*), as one of the major tree species in the plantation of China, have received growing interests due to their characteristics with rapid early growth rates, large woody biomass production and adaptability to different environmental conditions. It was reported that the total area of poplar plantations has reached 8.54 million ha (Tun et al. 2018), approaching one third of total poplar plantations in the world, and now poplars have become preferred tree species for various solid wood and panel products, paper and fiber products, carbon sequestration and as a source of energy fast-growing plantations in the world (Liu et al. 2015, Eisenbies et al. 2017).

In recent years, the researches and technical extensions on production systems and cultivation of poplar plantations have generally been concentrated on further improving stand productivity and economic benefits of the plantations through clone selection, planting density control, site preparation, fertilizing, and thinning so as to develop the cultivation patterns that satisfy diversified purposes (Eisenbies et al. 2017, Niemczyk et al. 2018). However, degradation of soil fertility, ecological deterioration, decline of forest productivity and the spread of forest pests and diseases in pure poplar plantations after successive planting are serious problems in China (Fang et al. 2011). Therefore, how to maintain the long-term site productivity and improve the environmental roles of poplar plantations is the key issue to be solved for its sustainable management in the future.

Density adjustment via thinning is widely employed in forest management to protect forest biodiversity, improve the quality of timber production, and maintain ecosystem function (Jandl et al. 2007, Trentini et al. 2017). Thinning regulates the distribution of open growing space so that remaining trees may benefit from reduced competition, increasing growth and tree health (Jandl et al. 2007, Wang et al. 2019). Thinning practice can also affect understory biodiversity due to changes in canopy densities and forest microclimate parameters (Ares et al. 2010, Taki et al. 2010), which directly affects litter composition and plant exudates that indirectly affects soil microbial community, and nutrient cycling (Chen et al. 2016, Salerni et al. 2020).

Litter, as a part of photosynthesis production from green plant, is an essential pathway to return nutrient in forest ecosystem, while litter decomposition is a critical step linking ecosystem processes with plant productivity (Edmonds & Tuttle, 2010). It is reported that nutrients released from litter decomposition could meet 69–87% forest growth required (Song et al. 2010), therefore the process of litter decomposition plays an important role in tree growth especially in poor soil. Due to the importance of litter decomposition in the function of terrestrial ecosystems, factors affecting litter decomposition have been extensively studied (Aerts 1997, Gartner & Cardon 2004, Wang et al. 2014, Santos et al. 2019). For example, litter decomposition is known to be affected by the initial nutrient concentrations, lignin content, and C/N ratio (Berg 1986, Bani et al. 2018), and environmental conditions (Cortez 1998). Various studies focusing on litter decomposition of tree species have been conducted using litter of the same species (Kasurinen et al. 2006, Duboc et al. 2012). The decomposition rates of litter with different initial N concentrations can be very different under the same environmental conditions (Zhang et al. 2008). However, litter from different species returns to the ground and forms a mixture in natural ecosystems. Such litter mixtures may dramatically change the litter quality and can markedly change the decomposition rate as well as the nutrient release pattern, which ultimately affect the availability as well as the timing of the release of nutrients in the soil (Lecerf et al. 2011).

In plantation systems, mixed litter types occur when mixed species plantations are established or when litter from trees is mixed

with that of understory vegetation. Thinning not only alters the environmental conditions, but also the understory vegetation in the stands. Therefore, understanding the rate of decomposition of mixed litter and nutrient release pattern under different environmental conditions become very important for forest thinning research. Despite the studies on effects of thinning on understory plants have been done (Ares et al. 2010, Taki et al. 2010, Trentini et al. 2017), the effects of thinning treatments on understory vegetation varied because of variations in deforestation time and intensity, thinning site conditions, and stand ages (Lei et al. 2007, Dang et al. 2018). Thinning effects on the understory vegetation of monoculture plantations have been investigated mostly for coniferious trees in the mountain regions (He & Barclay 2000, Haughian & Frego 2016, Trentini et al. 2017, Dang et al. 2018), with fewer studies in broadleaf tree plantations or in the plain regions (Fang et al. 2016, Wei et al. 2020). Especially how thinning intensity affects decomposition and nutrient release of litters mixed with understory vegetation are still unclear. The objectives of this study is to test a hypothesis that thinning would promote litter decomposition and nutrient release via altering the microclimate parameters and understory vegetation in the stands, to see if and how mixed litter contributed to litter decomposition and nutrient cycling in poplar plantations under different thinning practices.

Materials and methods

Study site

The study site, a plain area, is located at Baoying Agriculture Farm (119°15' E, 33°22' N) in Lixiahe Region of Jiangsu Province, China. The main forested areas consist of poplar and dawn redwood (*Metasequoia glyptostroboides*) plantations established on marginal agricultural lands in the middle of the 1980s. The area has a warm temperate climate with four distinct seasons, spring from March till May, summer from June till Augest, fall from Semptember till November, and winter from December till February. The annual frost-free period is about 225 days, the annual rainfall of the area is about 996 mm, and the average radiant intensity is 494.04 kJ cm^{-2}. Mean annual air temperature is 14.3 °C, with average temperatures of 0.4 °C in January and 27.6 °C in July. Soils at this site were formed on fine sediments of Gaoyou Lake and have a clay-loam texture with a moderate fertility (Fang et al. 2016).

Plantation establishment and experiment design

The poplar plantation under study was established in 2006 with one-year-old seedlings of clone 35 (*Populus deltoides* cv. 35) over an area of about 45.0 ha. The initial density of the plantation was 500 trees ha^{-1} (spacing: 4 × 5 m).

The thinning trial was set up after 6 years of the plantation established in order to compare the thinning effect on microclimate, decomposition of mixed litters, nutrient cycling, and plantation growth. Before thinning, the mean diameter at breast height (1.3 m) of the plantation was 16.6 cm (averaged over all trees on the trial area), while the tree height was 18.2 m (averaged over trees sampled by 15% of all trees on the trial). The experiment involved four treatments: unthinned (CK), medium intensity thinning (30% removal of trees) from below (from the lower end of the diameter distribution) (MB, removing about 2.9 m^2 ha^{-1} in basal area), high intensity (50% removal of trees) interlaced thinning (HI, removing about 6.0 m^2 ha^{-1} in basal area), and high intensity thinning (50% removal of trees) from below (HB, removing about 3.6 m^2 ha^{-1} in basal area), using a randomized complete-block design with three replications. Each plot size was about 4200 m^2 (75 m long × 56 m width) with a buffer row of trees between plots, and total area of the trial was about 5.2 ha. After thinning, all the thinned stems and branches were removed from the site, and the mean basal areas of the remaining trees were 11.08, 8.23, 7.54, and 5.03 m^2 ha^{-1} for CK, MB, HB, and HI, respectively.

Litter decomposition experiment

According to the collection of the poplar leaf litters during the first-two years after thinning, it was calculated that the drop mass of unthinned experimental field (CK) was about 350 g m^{-2} $year^{-1}$. From late November to early December, poplar leaves were collected on experimental sites, and the fallen leaves were collected on a mesh sheet that was placed on the ground beneath the trees to prevent soil contamination. Based on the survey of plant diversity in 2013, the herbaceous layer naturally presented at experimental field after thinning treatments was mainly consisted of *Conyza canadensis* and *Bidens pilosa* and other sparsely distributed species (e.g., *Setaria viridis, Rostellularia procumbens, Paederia scandens*), and these plant materials were cut at ground level from the same plantation site in the fall. Collected plant materials were homogenized, air-dried, and then stored at room temperature prior to the experiment.

By reference to the survey results of plant diversity and understory plant biomass after thinning, four litter composition treatments (litter types) were installed: 1) pure poplar leaves (P), 2) poplar leaves mixed with *C. canadensis* (11:7 mass to mass ratio, PC), 3) poplar leaves mixed with *C. canadensis* and *B. pilosa* (11:4:3 mass to mass ratio, PB), 4) poplar leaves mixed with *C. canadensis*, *B. pilosa*, *S. viridis,* and *R. procumbens* (11:3:2:1:1 mass to mass ratio, PV). We constructed 20 × 20 cm litter bags using 0.5 × 0.5 mm mesh nylon cloth on the bottom and 1.5 × 1.5 mm mesh nylon cloth on the top. Each bag contained 18.0 g of air-dried litter, which is equal to 14.0 g of the litter at oven-dried at 60 °C for 48 hours.

The litterbag technique was used to quantify the litter decomposition rate. The litter bags were randomly deposited on the soil surface (not overlapped) in experimental field in January 2014. Three replications of each litter type were deposited in the CK and HI treatments, while five replications were set for each litter treatments in MB and HB treatments because the distribution of trees in the plantation was uneven in the MB and HB treatments. Within each replication, ten bags for each treatment were installed to accommodate the sampling requirement, and totally 640 bags were deposited. The bags were retrieved in the days of 104, 160, 226, 290, 362, 469, 580, and 684 after incubation, respectively. For each sampling date, three bags for each litter type were retrieved in the CK and HI treatments, while five bags for each litter type were retrieved in the MB and HB treatments. After the litter bags were retrieved from the field, they were cleaned of soils by brushing. The remaining litter in each litter bag was dried in an oven at 60 °C until constant weight and weighed. Dry weight of litter remaining was calculated as the difference between the initial dry mass and the actual dry mass of the litter at each sampling date, while the mass loss percentage of each period was calculated as the difference between the two sampling dates. The litter was then ground to pass a 0.5-mm sieve to determine the nutrient concentrations.

Monitoring of microclimate parameters

A wireless sensor network (WSN) was set up to monitor microclimate parameters in different thinning treatments automatically (Fang et al. 2016). Five sensors were installed randomly in each thinning treatment for each environmental factor within the plots. During the experimental periods of the three years, photosynthetic photon flux density (PPFD), air temperature (T) and relative humidity (RH) at 1.5 m height, as well as soil temperature and moisture content at the 5 cm and 15 cm depths were recorded in the plantations of each thinning treatment at intervals of 5 min. However, only soil temperature and moisture content at the 5 cm depth were used in the present study.

Understory vegetation investigation

The understory vegetation investigation in four thinning treatments was conducted in each spring (in May), summer (in August) and fall (in November) for three consecutive years. Five 1 × 1 m quadrats were only established

in each plot to assess the plant diversity of the herb layers at each season, because almost no shrub was observed under the poplar plantation at this site. Totally, forty-five 1 × 1 m quadrats were surveyed for each thinning treatment every year. In each quadrat, the number of plant species was counted, and plant coverage and frequency were measured separately for each species. Shannon–Weiner diversity of herbaceous diversity (Hp) was calculated for each thinning treatment using the following equation:

$Hp = -\sum(p_i)\ln(p_i)$, where p_i = the proportion of the *i*th species.

After the investigation, only two 1 × 1 m quadrats were selected in each plot to assess the biomass of the herb layers at each season, and totally, eighteen 1 × 1 m quadrats were sampled for each thinning treatment every year (e.g. six 1 × 1 m quadrats at each season). Herbaceous biomass was estimated by harvest method in each thinning treatment at different seasons, where the herb plants within the sampled quadrats were clipped at ground level and sorted out into shoots and roots components. Fresh weights of the two components for each one-meter-square quadrat were determined in the field, and sub-samples for each component were collected for moisture analysis (dried in an oven at 60 °C until constant weight). From the biomass sampling measurement, herbaceous biomass was expanded to an area basis in the field as a whole.

Chemical analysis

Plant materials were digested using 5 mL concentrated H_2SO_4 and 1 mL concentrated $HClO_4$ for 30 min at 120 °C (Wang et al., 2014). The digestion continued at 360 °C until the digest is clear. After digestion, the N and P concentrations in the digest were determined using a flow-injection analyzer (Bran+ Luebbe AA3), while the K, Ca and Mg concentrations in the digest were analyzed using a Hitachi 108-80 atomic adsorption spectrometer (Hitachi Ltd., Japan).

Calculations and statistical analysis

The percent of litter remain (Y) was calculated as $Y = X_t/X_0 \times 100$, where X_0 is the initial litter sample weight and X_t is the amount of litter remaining after t days of incubation in the field. The litter decomposition process was modeled using the negative exponential decay model of Olson (1963), expressed as $Y=ae^{-kt}$, where a is a fitting parameter and k is the decay rate (gram per day). Half life ($t_{0.5}$) and time for 95% decomposition ($t_{0.95}$) of mixed litter were estimated from its regression equation of biomass decomposition. The percentage of nutrients remaining in the litter relative to the initial contents were estimated by the method of Fang et al. (2008).

All data were expressed as mean ± standard deviation (SD), and were analyzed by using a one-way or two-way ANOVA to test the differences between the treatments except for daily variation in microclimate parameters. When ANOVA results indicated that there were significant differences, the Tukey test was performed to separate the means. Pearson correlation analysis was conducted between the paired parameters tested in each corresponding period. All statistical analyses were performed by using SPSS 19.0 software (SPSS, Chicago, IL, USA).

Results

Variation in microclimate parameters

Microclimatic parameters were affected by the thinning treatments, but the impact degree varied for the different parameters. Based on the dynamics of daily photosynthetic photon flux density (PPFD, daytime 6 a.m.−6 p.m.) recorded, the mean monthly PPFD variation in different thinning treatments was calculated during experimental periods (Fig. 1). A one-way ANOVA result indicated that thinning intensity significantly affected the monthly PPFD during the growing season ($p \leq 0.05$). Compared to CK, the mean annual PPFD in MB, HB and HI increased by 29.5, 56.6 and 96.7% respectively.

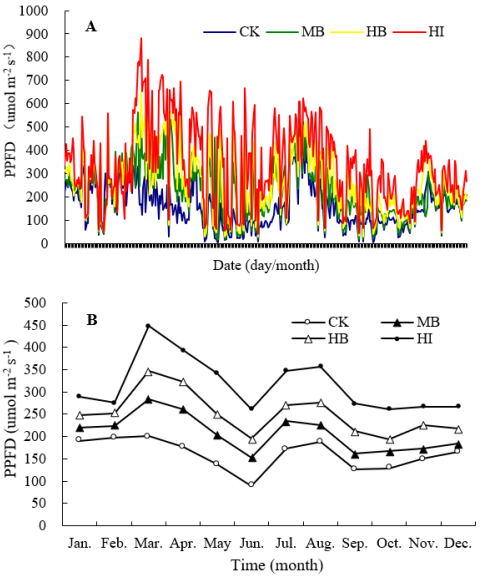

Figure 1 Variation in photosynthetic photon flux density (PPFD) under four thinning treatments. A: Daily variation during experimental periods (the first three consecutive years after the thinning) : Mean monthly variation during the experimental periods. CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning.

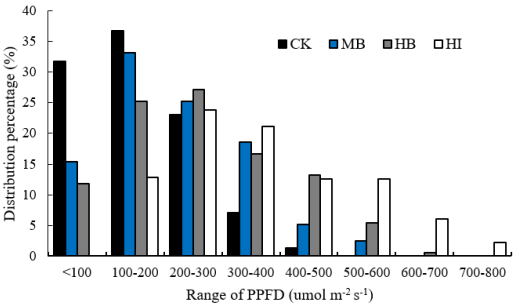

Figure 2 Distribution percentage of photosynthetic photon flux density (PPFD) at different PPFD ranges under four thinning treatments for the first year after thinning. CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning.

Furthermore, a great difference in the range of PPFD was observed among the thinning treatments (Fig. 2). For example, the distribution of PPFD in CK was 68.5% in 0−200 μmol m^{-2} s^{-1}, 30.0% in 200−400 μmol m^{-2} s^{-1}, 1.4% in 400−600 μmol m^{-2} s^{-1}, 0.0% in 600−800 μmol m^{-2} s^{-1} during the 3 years, whereas the PPFD in HB ranged from 0 to 800 μmol m^{-2} s^{-1}, and the distribution was 37.0% in 0−200 μmol m^{-2} s^{-1}, 43.8% in 200−400 μmol m^{-2} s^{-1}, 18.7% in 400−600 μmol/m^2/s, and 0.5% in 600−800 μmol m^{-2} s^{-1} in the same periods (Fig. 2). The greatest PPFD distribution in MB and HI was in 0−200 μmol m^{-2} s^{-1} (accounting for 48.5%) and 200−400 μmol m^{-2} s^{-1} (accounting for 44.9%), respectively.

A similar dynamic of daily soil temperature and moisture at the 5 cm depth was recorded in the four thinning treatments during the experimental period, and mean monthly variations were calculated (Fig. 3 and 4). One-way ANOVA analysis indicated that thinning intensity had a significant effect on the monthly soil moisture except for November and December (Fig. 4B, $p \leq 0.05$), but in most months no significant effects were observed for soil temperature (Fig. 3B). Compared to CK, the mean annual soil moisture in HB and HI increased by 4.4% and 35.9% respectively, whereas decreased by 5.3% in MB. However, mean annual soil temperature in the thinning treatments was only about 1.0 °C higher than the CK.

During the 3-year period, there were no significant differences in air temperature (T) and relative humidity (RH) at 1.5 m height among the four thining treatments ($p \leq 0.05$). The ranking of mean air temperature during the growing season (from March to November) by thinning treatment was HI (22.8°C) > HB (22.7°C) > MB (22.4°C) > CK (22.3°C), whereas the mean RH value during the growing season was in the order of CK (65.1%) > MB (64.9%) > HB (64.5%) > HI (63.9%).

Variation in understory vegetation

The total species richness of understory vegetation enhanced with increase of the thinning intensity in the first three consecutive

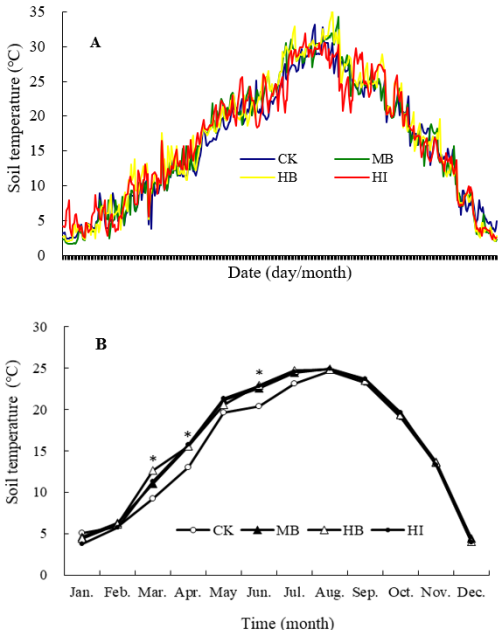

Figure 3 Variation in soil temperature at the depth of 5 cm under four thinning treatments. A: Daily variation during experimental periods (the first three consecutive years after the thinning). B: Mean monthly variation during the experimental periods. CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning. * indicates significant differences among the treatments for the same month ($p < 0.05$).

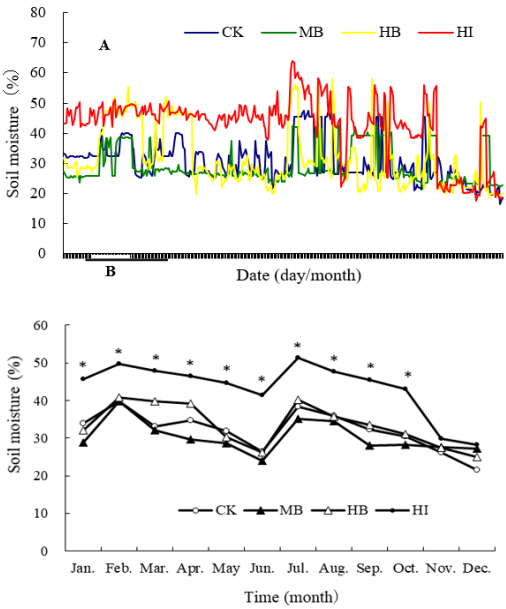

Figure 4 Variation in soil moisture at the depth of 5 cm under four thinning treatments. A: Daily variation during experimental periods (the first three consecutive years after the thinning). B: Mean monthly variation during the experimental periods. CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning. * indicates significant differences among the treatments for the same month ($p < 0.05$).

years after the thinning, and showed a seasonal variation. Differences in the species richness among the thinning treatments were considerable with the highest in HI and the lowest in CK, even if no significant variation was detected. The total species richness in spring, summer and fall ranged from 15 to 18, 11 to 16, and 9 to 14 respectively, showing a decreasing tendency over the season. There were some differences in the abundant species among the thinning treatments and three seasons, but the most abundant species of understory vegetation over the thinning treatments were *Conyza canadensis*, *Bidens pilosa*, *Paederia scandens* and *Setaria viridis* at the research site.

Seasonal variation in Shannon–Weiner index and understory vegetation biomass under four thinning treatments were presented in Fig. 5. Generally, Shannon–Weiner diversity, where three seasons averaged within thinning classes, was 2.265 for HI > 2.149 for HB > 1.968 for MB > 1.860 for CK, showing significantly higher in HB and HI than in CK (Fig. 5A, $p \leq 0.05$). Moreover, the diversity tended to be higher in the spring than in the summer and fall for all thinning treatments (Fig. 5A), which was 2.230 in spring, 1.904 in summer and 2.047 in fall (where four thinning treatments averaged within season classes), respectively.

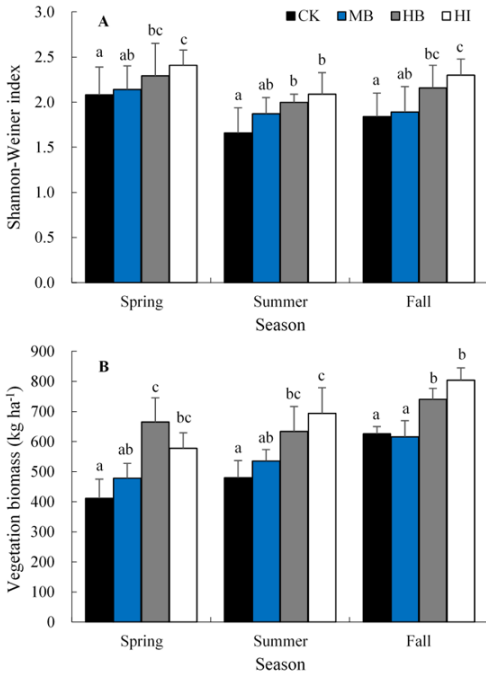

Figure 5 Seasonal variation in Shannon-Weiner index and understory vegetation biomass under four thinning treatments. A: Mean Shannon-Weiner index during experimental periods (the first three consecutive years after the thinning). B: Mean understory vegetation biomass during the experimental periods. CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning. Significant differences among the treatments for the same season are indicated by different lower case letters ($p < 0.05$).

Similar to the Shannon–Weiner diversity, the understory vegetation biomass was also significantly affected by the thinning treatments (Fig. 5B, $p \leq 0.05$), and showed a seasonal variation. Total herbaceous biomass varied from 350 to 900 kg ha^{-1} year^{-1} during the investigation period, with the highest biomass appearing in the fall of HI and the lowest in the spring of CK. Overall, total herbaceous biomass, where three seasons averaged within thinning classes, was 692.0 kg ha^{-1} for HI > 679.6 kg ha^{-1} for HB > 543.3 kg ha^{-1} for MB > 505.7 kg ha^{-1} for CK, showing significantly higher in HB and HI than in CK and MB. However, total herbaceous biomass where four thinning treatments averaged within season classes was 553.2 kg ha^{-1} in spring, 585.8 kg ha^{-1} in summer and 696.5 kg ha^{-1} in fall, respectively.

Variation in litter decomposition

A two-way ANOVA result indicated that both thinning intensity and litter type significantly affected the dry weight of litter remaining over times (Table 1), whereas no significant interaction was detected except for sampling at 104 days. The detailed dynamics of residual biomass retention with time are presented in Tables S1-S4. For describing the processes of decomposition, the Olson model was fitted for each treatment, and decomposition parameters of various litter types under different thinning treatments are presented in Table 2.

Table 1 The result summary of two-way ANOVA significance tests for the dry weight of litter remaining over times under different treatments.

Sources	Df	Decomposition time (days)							
		104	160	226	290	362	469	580	684
Thinning (A)	3	***	***	***	***	**	***	***	***
Litter type (B)	3	*	***	***	***	***	***	***	***
A×B	9	**	ns	ns	ns	ns	ns	ns	ns

Note: Significance levels: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), $p > 0.05$ (ns).

Both thinning and litter type obviously affected the decay rate (k), half live ($t_{0.5}$) and $t_{0.95}$ values. Overall, increasing thinning intensity and litter complexity enhanced k values (ranging from 0.003 to 0.006 g day^{-1}), but reduced $t_{0.5}$ (ranging from 231 to 116 days) and $t_{0.95}$ (ranging from 999 to 499 days) values. For example, $t_{0.5}$ values of poplar leaf litter (P) in thining treatments of CK and MB were 33.5 % greater than the HI and HB treatments, while the $t_{0.5}$ values of PV litterer in the CK and MB were 49.1 % longer than the HI and HB treatments. A similar trend was also observed for k and $t_{0.95}$ values (Table 2).

Table 2 Olson models and decomposition parameters of various litter types under different thinning treatments.

Thinning treatment	Litter type	Olson model		$t_{0.5}$ (day)	$t_{0.95}$ (day)
		Equation	R^2		
CK (unthinned)	P	$y=131.095e^{-0.003t}$	0.938	231	999
	PC	$y=126.923e^{-0.003t}$	0.945	231	999
	PB	$y=128.110e^{-0.003t}$	0.943	231	999
	PV	$y=139.761e^{-0.004t}$	0.920	173	749
MB (30% tree removal from below)	P	$y=130.986e^{-0.003t}$	0.939	231	999
	PC	$y=132.039e^{-0.004t}$	0.938	173	749
	PB	$y=129.398e^{-0.004t}$	0.941	173	749
	PV	$y=141.779e^{-0.004t}$	0.920	173	749
HI (50% tree removal by interlaced thinning)	P	$y=132.446e^{-0.004t}$	0.912	173	749
	PC	$y=142.727e^{-0.004t}$	0.886	173	749
	PB	$y=142.104e^{-0.004t}$	0.889	173	749
	PV	$y=151.311e^{-0.005t}$	0.868	139	599
HB (50% tree removal from below)	P	$y=144.975e^{-0.004t}$	0.881	173	749
	PC	$y=149.485e^{-0.004t}$	0.860	173	749
	PB	$y=145.934e^{-0.004t}$	0.863	173	749
	PV	$y=174.169e^{-0.006t}$	0.817	116	499

Note: y: percentage of biomass remaining (%); t: time of decomposition (day); $t_{0.5}$ (half life) and $t_{0.95}$ (the days to decompose 95% of the litter biomass) of the mixed litter was estimated from Olson equations of biomass decomposition. P: pure poplar leaves; PC: poplar leaves mixed with *C. canadensis*; PB: poplar leaves mixed with *C. canadensis* and *B. pilosa*; PV: poplar leaves mixed wih *C. canadensis*, *B. pilosa*, *S. viridis,* and *R. procumbens*.

Variation in litter nutrient release

The initial nutrient concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were significantly different among four litter types prior incubation ($p < 0.05$, Table S5). Mean N concentration was highest in the poplar leaves (P), followed by the PV and lowest in the PB. Mean P concentration was ranked as PB > PV > PC > P, while mean K concentration was in the order of PB > PC > PV > P. Ca concentration in the poplar leaves was about 13.0% higher than that of the mixed litters. PB and PV had higher Mg concentrations than the other two litter types.

As a general pattern, K content in all litter types declined most rapidly with time, while slight differences were detected for the remaining contents of N and P in the residual litter among the treatments (Tables 3 and 4). When evaluating the effect of mixing litter with poplar leaf litter or thinning intensity on nutrient release, it was shown that in the initial stage of litter decomposition (about 3 months), the percent nutrient remaining of N, P and K, in most cases, were not significantly different regardless of the litter types or thinning treatments. However, after 23 months of litter decomposition, both thinning and litter types significantly affected the observed percent nutrient remaining of N, P and K (Tables 3 and 4).

Table 3 Mean percentage of nutrient remaining in the thinning treatments over four litter types at different decomposition stages (%).

Decomposition times (day)	Nutrient types	Thinning treatments			
		CK	MB	HI	HB
104	N	83.95±6.65a	84.27±10.76a	85.70±13.36a	90.41±6.39a
	P	69.51±14.39b	79.27±14.93ab	83. 44±5.55a	98.52±4.05a
	K	33.53±10.53a	37.42±7.14a	25.65±4.58a	33.89±13.15a
362	N	57.74±3.49a	51.17±1.29b	53.72±7.54ab	53.11±8.13ab
	P	39.55±9.31a	39.13±5.80a	39.07±4.93a	37. 43±8.59a
	K	22.69±7.12a	27.02±8.27a	23.74±5.13a	17.95±4.30a
684	N	9.44±2.01a	6.89±1.68b	4.70±1.11bc	3.45±1.30c
	P	9.69±2.15a	9.66±4.89a	4. 06±1.83b	3.39±1.71b
	K	2.46±0.54a	2.182±0.83ab	1.17±0.71bc	0.83±0.55c

Note: For each nutrient, significant differences among the treatments at the same decomposition time are indicated by different lower case letters ($p < 0.05$). CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning.

Table 4 Mean percentage of nutrient remaining in the litter types over four thinning treatments at different decomposition stages (%).

Decomposition times (day)	Nutrient types	Litter types			
		P	PC	PB	PV
104	N	85.35±15.07b	80.56±13.64b	95.34±5.98a	84.79±9.19b
	P	92.60±6.59a	84.95±12.03a	72.97±18.33a	80.22±16.22a
	K	35.54±6.76a	33.98±10.38a	25.41±4.99a	35.56±10.65a
362	N	48.20±6.51c	56.81±7.09ab	59.20±4.61a	54.04±5.01b
	P	47.26±4.03a	41.23±2.04b	34.82±2.32c	31.86±2.74c
	K	30.68±6.37a	18.63±4.97b	19.44±3.99b	22.64±2.06b
684	N	7.02±2.64a	6.70±3.13a	6.85±2.75a	3.91±2.08b
	P	9.97±5.37a	7.02±3.50a	5.72±3.10a	4.08±2.62a
	K	2.60±0.82a	1.35±0.75ab	1.54±0.81ab	1.14±0.80b

Note: For each nutrient, significant differences among the treatments at the same decomposition time are indicated by different lower case letters ($p < 0.05$). CK: unthinned; MB: 30% tree removal from below; HB: 50% tree removal from below; HI: 50% tree removal by interlaced thinning.

Discussion

Microclimate conditions

Thinning practices, widely employed in forest management, modify microclimate conditions (Fang et al. 2016, Trentini et al. 2017, Wang et al. 2019) and consequently may exert positive effects on understory vegetation, soil physico-chemical properties and biological activity (Baba et al. 2011, Dang et al. 2018). A meta-analysis result from Zhang et al. (2018) showed that overall, forest thinning significantly increased soil temperature by 8.7%, whereas only moderate and heavy thinning significantly increased soil moisture by 34.5% and 35.1% respectively. Results from this study indicated that the thinning effects on microclimate in the poplar plantations varied for the different parameters, such as air temperature (T) and relative humidity (RH) were not significantly affected by the thinning treatments, while significant differences in the PPFD and soil moisture were observed among the treatments during the growing season (Figs. 1 and 4), supporting the point that a heavy thinning intensity significantly increased soil moisture (Dang et al. 2018, Wang et al. 2019). However, variation in soil temperature at the 1.5 cm depth among the thinning treatments (Fig. 3) is not consistent with the meta-analysis of Zhang et al. (2018). It should be indicated that the mean monthly soil moisture at the 5 cm depth was much greater in HI than in HB (Fig. 4), although the thinning intensity is 50% removal of trees both in the HB and HI treatments. The possible reason is more evapotranspiration caused by changes in poplar trees in the thinning treatments, because the mean basal areas of the remaining trees after thinning were 7.54, and 5.03 m^2/ha in HB and HI respectively, and no significant difference in understory vegetation biomass was detected between HB and HI (Fig. 5B). Meanwhile, the soil moisture showed a seasonal variation with the highest in summer (34.8%, from March to May) and spring (34.7%, from June to Auguest), and the lowest in fall (30.6%, from Semptember to November) (Fig. 4), which may be caused by the combined effects of temperature, PPFD, rainfall and vegetations during the study periods.

Thinning enhanced photosynthetic photon flux density (PPFD) (Fig. 1). However, no significant differences were found among the thinning treatments at non-growing season (from Dec. to Feb.), and only significant difference in the mean PPFD were found between CK and HI treatments during the growing season (from Mar. to Nov., $p < 0.05$). Meanwhile, decreased differences in PPFD were observed between thinning plots and CK plots two years after thinning, which is consistent with other studies (Seiwa et al.

2012, Trentini et al. 2017), probably owing to crown size increasing in the thinned plots and self-thinning in the CK plots over time.

Understory vegetation

Understanding the key environmental factors to affect forest understory diversity is a theoretical basis for sustainable management practices of the plantations. Some studies reported that fast-growing plantations do not decrease understory plant diversity if sustainable practices are implemented (Carle & Holmgren 2008, Royer-Tardif et al. 2018). Our results confirmed that thinning is in general associated with increasing understory vegetation biomass and vegetation cover duo to increment of resources availability after thinning, in agreement with the previous studies (Thomas et al. 1999, Trentini et al. 2017, Zhang et al. 2018). As expected, species richness was higher in thinning than in CK plots. However, Pearson correlation analysis between microclimate parameters and understory vegetation indexes indicated that only PPFD is significantly correlated to Shannon-Weiner diversity index (Fig. 6, $p \leq 0.001$), while a close relationship between understory herbaceous biomass and Shannon-Weiner diversity index is also observed (Fig. 6, $p \leq 0.05$) in this study. Total herbaceous biomass in the present study, ranged from 350 to 900 kg/ha/year, contributes little to stand biomass and carbon stores, but can improve carbon and nutrient cycling because of high turnover rates and litter production (Elliott et al. 2015, Zhang et al. 2018, Wang et al. 2019).

As indicated, the extent to which a canopy gap affects establishment, growth, death and reproduction of understory species is a function of both the degree to which the opening alters the local physical environment, and the sensitivity of individual species to that environmental change (Collins & Pickett 1988, Gálhidy et al. 2006). Thinning is the artificial way to create canopy gaps, but the gap size and its distribution pattern varied among the thinning intensities and thinning methods. In our study, both gap size created by the thinning treatments and its distribution in the plantation seem to greatly affect microclimate parameters and understory vegetation, mainly as a consequence of the release of light resources. Based on the results in diversity and biomass of understory plants from this study as well as the poplar growth after thinning (not presented in this study), we found thinning operation with 50% tree removal from the lower end of the diameter distribution (HB) to better increase poplar basal areas and understory vegetation biomass in the plantations, suggesting that a thinning operation with 50% tree removal from below (HB) would maintain structural and functional features of poplar plantations at the similar sites as the HB can increase the heterogeneity of the habitat for understory vegetation growth.

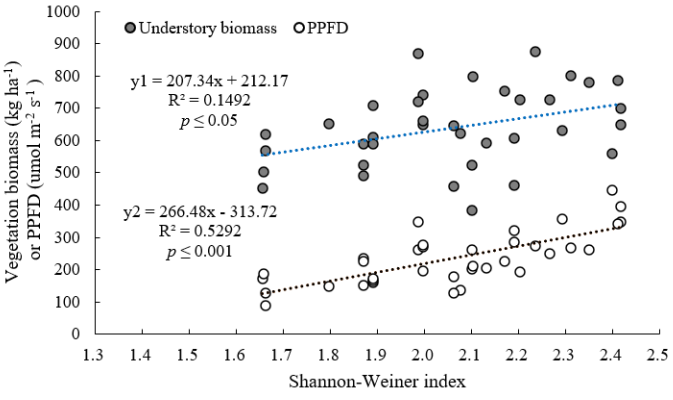

Figure 6 Relationship of herbaceous biomass of understory (y1) and photosynthetic photon flux density (PPFD, y2) to Shannon-Weiner index (n=36).

Litter decomposition

Litter decomposition is largely a function of ecological factors (moisture, temperature, and biological activity) and chemical properties of litter (i.e., cellulose or lignin content, N content and C:N ratio) (Coûteaux et al. 1995, Fang et al. 2008, Bani et al.

2018). Our result showed that the dry weight of litter remaining over times was significantly affected by thinning treatments (including thinning intensity and thinning method via modifying microclimatic conditions) and litter types (Table 1), confirming that decomposition in forest ecosystems is a complex process resulting from the interaction of abiotic and biotic drivers that cause physical and chemical changes of the substrate (Freschet et al. 2012).

Pearson correlation analysis showed that the litter mass loss rates had positively significant correlation with air relative humidity, soil temperature, air temperature and soil moisture (x4) ($p \leq 0.05$), whereas were not significantly correlated with PPFD (Table 5). However, the response extents of different litter types to the environmental factors varied in the mass lose (Fig. 7). For instance, the response of mixed litter (PC, PB and PV) in the decomposition to air relative humidity and soil temperature was more efficient than a single species litter (poplar leaves), as indicated by the parameter estimates of the exponential functions (Fig. 7A and 7B). Furthermore, a stepwise regression analysis indicated air relative humidity and PPFD were the best two variables for predicting the litter mass lose rate ($y = -45.639+0.822x1+0.018x5$, $r=0.741$, $p \leq 0.0001$), suggesting that PPFD would be a very important indirect factor to affect litter decomposition.

Previous studies indicated that litter decomposition is mainly governed by the rate of lignin decomposition (Jin et al. 2003, Isaac & Nair 2006, Leppert et al. 2017), and litter with high C:N ratio is considered a poor substrate (Cleveland et al. 2014, Bani et al. 2018), which means that litter decomposition rates are highly species-specific. Unfortunately, C:N-ratio, lignin content and biological activity were not measured in this study. Therefore, further research is needed for the effects of litter chemistry properties on litter decomposition in the field to better understand the decomposition processes. However, it seems that litter species richness affected litter mass loss rate, but these effects were time-dependent (Tables S1-S4). For example, the mean litter mass loss in PC (five species mixtures) over four thinning treatments was slower compared to two (PC) and three (PB) species richness levels at day 104 of decomposition, whereas the positive species richness effects on litter mass loss appeared after 290 days of incubation. A simillar result was also reported by Leppert et al. (2017), where they did not observe general positive litter species richness effects on litter decomposition dynamics.

It is worthy noting that the enhanced litter decompositions were observed when poplar leaf litter was mixed with various understory herbaceous litters (Table 2 and Tables S1-S4). There have been few reports of such synergistic effects of mixing more than two litter types that are both low in N concentrations (Montané et al. 2013, Wang et al. 2014). This

Table 5 Pearson correlation coefficients (r) between the mass loss rate and mean values of microclimate parameters in each corresponding period as well as between the paired parameters of the microclimate tested (n=128).

Varuables	Variables				
	ST	SM	PPFD	T	RH
Litter mass loss rate	0.525**	0.244*	0.092	0.518**	0.697**
Soil temperature at 5 cm depth (ST)	1	0.109	-0.123	0.966**	0.797**
Soil moisture at 5 cm depth (SM)		1	0.813**	0.161	0.061
Photosynthetic photon flux density (PPFD)			1	-0.073	-0.220*
Air temperature (T)				1	0.677**
Air relative humidity (RH)					1

Note: ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

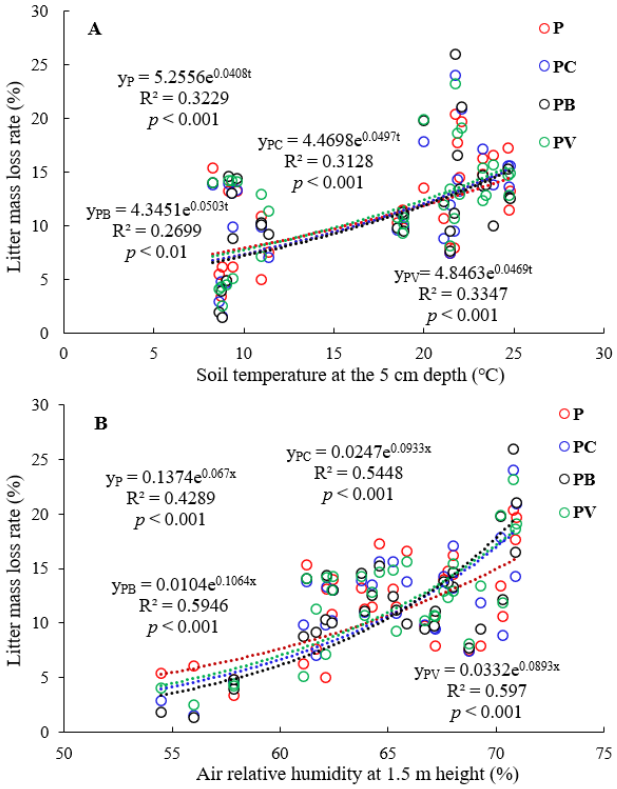

Figure 7 Relationship between the litter mass loss rate and mean values of soil temperature at the 5 cm depth (A) and air relative humidity at 1.5 m height (B) during the corresponding period for each litter type (n=32). P: pure poplar leaves; PC: poplar leaves mixed with *C. canadensis*; PB: poplar leaves mixed with *C. canadensis* and *B. pilosa*; PV: poplar leaves mixed wih *C. canadensis, B. pilosa, S. viridis*, and *R. procumbens*.

finding indicates that the synergistic effect of mixing different types of litter together may not only limit to mixing litter types with a high N concentration.

Nutrient release

Dynamics of nutrient release from litter decomposition depend on the litter quality and environmental conditions. Our results indicated that nutrient release from the decomposition is closely linked with thinning treatments via modifiing microclimatic conditions and litter quality (Tables 4 and 5). The dynamics of total nutrients (N + P + K) in different litter types showed that nutrient contents in litter residues declined with weight losses of the materials (Fig. 6), in agreement with the results reported by Fang et al. (2008) and Wang et al. (2014). However, the nutrient release rates of N and P in the initial stage of litter decomposition (i.e., the first 3 months) were relatively low over the thinning and litter types (Tables 4 and 5). This was likely affected by a range of factors, such as taking time for the break down of the litter to form smaller-sized litter particles (Loecke & Robertson 2009) and for the microbial populations to colonize the litter (Wang et al. 2014). However, the key factor to lead to the low initial rate of litter decomposition and nutrient release is the temperature in the present study as the litter bags were installed in January (the coldest month of the year at the study region) (Fig. 3), and temperature is known to be an important factor regulating litter decomposition and nutrient release rates (Aerts 1997).

Species richness effects on nutrient release among litter types were similar to those on mass loss in the present study, but to which extent leaf litter species richness affects these processes of nutrient cycling remains unclear. Our results suggest the positive effects of nutrient enrichment after increasing litter complexity and possibly a positive effect of the litter species richness. However, it should be mentioned that litter species richness seems to be relevant for nutrient dynamics in decomposing litter, but may have no direct implications on plant nutrition, because plant

nutrition is mainly determined by species specific nutrient contents which are released during decomposition (Leppert et al. 2017).

Conclusions

In conclusion, thinning is the artificial way to create canopy gaps, but the gap size and its distribution pattern varied among the thinning intensities and thinning methods, which consequently affects microclimate parameters and understory vegetation greatly. Thinning effects on the microclimate varied for the different parameters, but heavy thinning (HI and HB) significantly enhanced PPFD and soil moisture in the poplar plantations during the growing season. Thinning promoted understory vegetation biomass and vegetation diversity via modifying the microclimate parameters. Pearson correlation analysis showed that PPFD and understory herbaceous biomass were significantly correlated to Shannon-Weiner diversity index. Both thinning intensity and litter type significantly affected the dry weight of litter remaining over times. Overall, increasing thinning intensity and litter complexity enhanced decay rate, but reduced half live ($t_{0.5}$) and $t_{0.95}$ values. Correlation analysis showed that air relative humidity, soil temperature, air temperature and soil moisture significantly impacted the litter mass loss rates, while positive species richness effects on litter mass loss were observed. Non-additive (synergistic) effects were observed when different litters were mixed, but the non-additive effect was most pronounced when more herbaceous species litter were mixed with poplar leaf litter and 50% thinning intensity was applied. Dynamics of nutrient release from different litter types decomposition were similar to those on the litter mass, depending on the litter quality and microclimatic conditions. Our results confirm the hypothesis that thinning promotes litter decomposition and nutrient release in the plantation via altering the microclimate parameters and understory vegetation, and suggest that a thinning operation with 50% tree removal from below (HB) would maintain the structural and functional features of the poplar plantations at the similar sites.

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