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Competing interests

No competing interests have been declared.

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ORIGINAL RESEARCH PAPER

Mutual effects between *Pinus armandii* and broadleaf litter during mixed decomposition

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Abstract

Mixed-decomposition effects are commonly observed in natural and planted forests and affect nutrient cycling in a forest ecosystem. However, how one litter type affects the decomposition of another is still poorly understood. In this study, *Pinus armandii* litter was mixed with *Betula albosinensis*, *Catalpa fargesii*, *Populus purdomii*, *Eucommia ulmoides*, and *Acer tsinglingense* litter. The mixtures were placed in litterbags and buried in soil with consistent moisture for a 180-day indoor simulated decomposition experiment. The litterbags were periodically harvested during decomposition; the litter residues of different species were separated, and the biomass dynamics of each litter type were simulated. In addition, the soil sucrose, cellulase and polyphenol oxidase activities were also detected three times. The mutual effects of needle and broadleaf litter during mixed decomposition and the possible underlying mechanisms were investigated. The results indicated that (i) during the decomposition experiment, *P. armandii* needles significantly inhibited the decomposition of broadleaf litter in the first 3 months, while the broadleaf litter accelerated the decomposition of *P. armandii* needles in only approximately 40% of the cases. However, the inhibitory effects of needles on broadleaf litter decomposition subsequently exhibited significant weakening, while the accelerating effects of broadleaf litter were significantly enhanced. The effects of mixed decomposition on the activities of three enzymes can only partially explain the interactions between different litter types; (ii) the prediction by the decomposition model showed that most of the broadleaf litter types could continuously accelerate the decomposition of *P. armandii* needles throughout the mixed decomposition process, while the decomposition of broadleaf litter would be significantly inhibited at least in the short term. In general, four of the five broadleaf litter types (excluding *E. ulmoides*) could accelerate the early decomposition of *P. armandii* needles and consequently accelerate nutrient cycling in *P. armandii* pure forests. These species could be used for the transformation of pure *P. armandii* pure forests to mixed forests.

Keywords

Pinus armandii pure forests; soil enzymatic activities; mixed litter decomposition

Introduction

The Qinling Mountains are the climatic and biogeographic boundary between Northern and Southern China. The Qinling Mountains are also one of the most important water sources in China. However, after historical long-term deforestation of the natural forests, the eco-environment in this area was seriously damaged. Fortunately, after the

implementation of several national forest projects such as the “Grain to green” project and natural forest protection projects, large areas of natural secondary forests and artificial forests had been recovered. *Pinus armandii* is one of the most widely disturbed species in the secondary and artificial forests in the Qinling region. However, this species exhibits considerable self-renewal ability; thus, it is difficult for other species to expand into *P. armandii* forests, leading to low biodiversity of these pure forests [1]. Due to the long-term selective utilization of nutrients and the specific characteristics of litter decomposition and nutrient release, *P. armandii* forests have exhibited unique soil degradation patterns, such as the loss of available N, P, and microelements and remarkable decreases in urease, sucrase, phosphatase, and protease activities [2].

According to previous studies, mixed forests of coniferous and broadleaved species usually exhibit higher productivity than pure coniferous forests [3]. In addition, the mixed decomposition of leaves and needle litter usually caused significantly synergistic effects [4], that is, accelerating the overall decomposition and nutrient release [5]. Consequently, a feasible approach to transform pure *P. armandii* forests might include planting broadleaved species with increased litter production, higher litter nutrient content, and complementary litter substrate quality [5], thus accelerating litter decomposition, adjusting the nutrient balance of forest soil, promoting nutrient cycling, improving the quality of soil organic matter via mixed litter decomposition [4,6], and finally alleviating the soil degradation of pure coniferous forest ecosystems [7].

Previous studies have indicated that the mixed decomposition of coniferous and broadleaf litter usually leads to a higher overall decomposition rate (the synergistic nonadditive effect) due to the nutrient transfer between litter, increased suitability of microhabitats for soil geobionts and microbes, and an increase in litter chemical diversity [8–10]. However, most investigations only studied the decomposition of litter mixtures, while how the decomposition of each litter type in the mixtures was affected remains less understood. During mixed decomposition, nutrients might be transferred from high-quality leaf litter to coniferous litter, thus alleviating the nutrient limitations and consequently accelerating litter decomposition, while the decomposition of themselves were hindered as nutrient loss. On the other hand, the secondary metabolites released from litter with poor substrate quality would inhibit the decomposition of broadleaf litter while increasing the decomposability of coniferous litter [11,12]. These undetected mutual effects might lead to misjudgment about the actual effects of mixed decomposition on material cycling even when overall additive effects are detected, and the decomposition of a given litter species in a mixture might still be accelerated or inhibited [8,13]; thus, the specific degradation tendency of the forest could not be controlled.

Little is known about the mutual effects between litter types during mixed decomposition, and these effects are largely affected by the litter species in the mixtures (or their substrate quality characteristics) [11,14,15]. Consequently, simulated mixed decomposition is still needed when selecting broadleaved species for the transformation of *P. armandii* forests to mixed forests to analyze the possible effects of mixed plantation on nutrient cycling. Hence, *P. armandii* litter and litter from five broadleaved species that are commonly used in mixed plantations were collected for a 180-day indoor mixed decomposition experiment, aiming to detect their mutual effects on the decomposition of each other and to analyze the mechanism causing these mutual effects. This study also aimed to provide a scientific basis for the transformation of pure *P. armandii* forests into mixed forests in the Qinling region. We hypothesized that during mixed decomposition, the broadleaf litter would significantly accelerate the decomposition of needle leaf litter (*P. armandii* litter), whereas the decomposition of themselves will be simultaneously hindered in turn. The observed mixed decomposition effects depend on the extent of these opposite effects, and the consequent apparent additive effects cannot reflect the actual mutual effects during mixed litter decomposition.

Material and methods

Sampling of litter and soil

Well-grown mature forests of *Pinus armandii*, *Betula albo-sinensis*, *Catalpa fargesii*, *Populus purdomii*, *Eucommia ulmoides*, and *Acer tsinglingense* were selected at the Houzhenzi forestry station of Zhouzhi County, China (108°44'~108°57' E, 33°46'~33°57' N, altitude: 1,300~2,650 m). The climate in this area is a warm temperate humid continental monsoon climate with an average annual temperature of 6.4°C and an average annual precipitation of approximately 1,000 mm. The soil in this area is classified as dark brown forest soil.

In late fall, 10 trees were randomly selected in each forest, and the senescent leaves or needles were collected with litter traps by knocking tree branches. Each type of foliar litter was uniformly mixed and air-dried after removing the vermiculated or decayed leaves. A portion of the litter was oven-dried at 60°C to convert the air-dried and oven-dried weight. Subsequently, the prepared litter was digested according to the methods of Bao [16], and then the C, N, and P contents were determined by the potassium dichromate oxidation method, a continuous flow analyzer and phosphomolybdate spectrophotometry, respectively, and the C/N and C/P ratios were calculated accordingly. The Mn contents were detected with an atomic absorption spectrophotometer. The detected litter substrate qualities are given in Fig. 1.

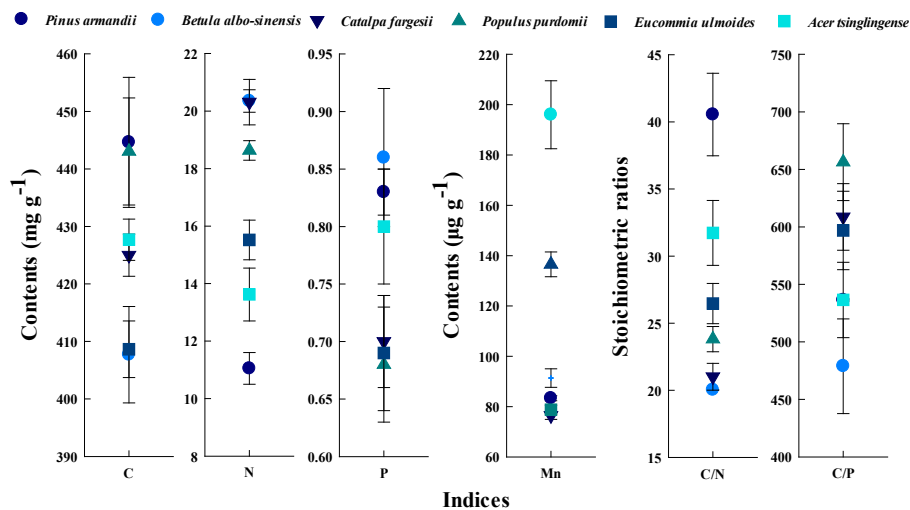


Fig. 1 Substrate qualities of the different tested litter types.

To avoid the spatial variation in soil properties and home field effects [17,18], the decomposition in an in situ experiment was simulated in indoor conditions. The soil used as the decomposition substrate was sampled in the tree-free wasteland near the studied forests. The soil from the 0–10 cm surface layer was collected, and then the soil was passed through a sieve with 5-mm mesh after the visible plant residues and stones were removed. In addition, the saturated water-holding capacity and the actual soil moisture were determined for the moisture control during decomposition. The soil that was used in this study had an organic matter content of 21.93 g kg⁻¹ and available N, P, and K contents of 110.37, 2.23, and 146.59 mg kg⁻¹, respectively.

Litter decomposition

The prepared litter types were uniformly mixed with a weight proportion of 1:1 (needle litter : each type of broadleaf litter), and 12 g of each mixture (oven-dried weight) was placed into 10 × 12-cm nylon litterbags (mesh size: 0.5 mm). Each type of mixture was prepared for 15 bags. In addition, 15 litterbags containing 12 g of each single-species

litter were also prepared. The filled litterbags were sealed, and five bags of each litterbag type were separately buried in a 30 × 40 × 20-cm plastic pot containing 4 kg soil to appropriately speed the decomposition. Each type of litter had three pots, and based on this, three independent decomposition processes were simulated (three replications).

Subsequently, the pots containing litter were watered with a sprayer. According to a previous study [19], the soil moisture was adjusted to 50% of the saturated water-holding capacity, which was slightly higher than the actual soil moisture. Subsequently, the pots were covered with ventilated and moisturizing film to avoid extreme changes in soil moisture. In the following incubation, the pots were weighed twice a month, and distilled water was sprayed according to the mass loss. The litter pots were incubated at 20–25°C for 180 days.

Residue sampling and biochemical analysis

The litterbags in each pot were harvested five times during the first, second, third, fourth, and sixth months during decomposition. During each sampling, three litterbags were retrieved from the three pots containing the same litter, and the residues were cleaned with a brush, oven-dried at 60°C and weighed. For the mixtures, the needles and broadleaf leaves were separated according to the differences in form and weighed. In addition, the soil around the litterbags was sampled during the first, third, and sixth months, air-dried and passed through a 1-mm sieve. The activities of soil sucrose, cellulase, and polyphenol oxidase were determined by 3,5-dinitrosalicylic acid colorimetry and pyrogallol colorimetry [20]. The soils sampled from the three pots containing the same litter were considered replicates.

Data processing

The weights of the litter residues or mixtures were converted into mass remaining rates R , and then the decomposition processes were fitted with a modified Olson decomposition model (Eq. 1) according to Berg and McClaugherty [21] using SigmaPlot 12.5.

$$R = ae^{-k_1t} + be^{-k_2t} \quad \text{Eq. 1}$$

where a , b , k_1 , and k_2 are the parameters of the model, t is the decomposition time (independent variable), and e is the Napierian base.

In this model, the litter decomposition process was seen as the superposition of two classical Olson models, which simulate the decomposition of labile and recalcitrant components [21]. Thus, two decomposition constants (k_1 and k_2) and the theoretical calculated relative abundances of these two litter components (a and b) were obtained after fitting. This model also exhibited much higher fitting precision (r^2 and significance) than the traditional Olson model [19,21]. However, it is difficult to use a single constant k to indicate the decomposition rate. Hence, the elapsed times for the first- and second-half of decomposition ($t_{\text{former50\%}}$ and $t_{\text{later50\%}}$) of each litter type or litter mixture were calculated with the analyzing module in SigmaPlot 12.5 to show the decomposition rate [19].

Assuming that each litter type did not affect the decomposition of the other type, the predicted mass remaining rates R_{PM} , $t_{\text{former50\%PM}}$ and $t_{\text{later50\%PM}}$ of the litter mixtures, and the predicted soil enzymatic activities EA_{PM} of could be calculated using Eq. 2–Eq. 5:

$$R_{\text{PM}} = 0.5R_{\text{OPa}} + 0.5R_{\text{OBroadleaved}} \quad \text{Eq. 2}$$

$$t_{\text{former50\%PM}} = 0.5t_{\text{former50\%,OPa}} + 0.5t_{\text{former50\%,OBroadleaved}} \quad \text{Eq. 3}$$

$$t_{\text{later50\%PM}} = 0.5t_{\text{later50\%,OPa}} + 0.5t_{\text{later50\%,OBroadleaved}} \quad \text{Eq. 4}$$

$$EA_{\text{PM}} = 0.5EA_{\text{OPa}} + 0.5EA_{\text{OBroadleaved}} \quad \text{Eq. 5}$$

where the subscripts OPa and OBroadleaved indicate the detected values of the mentioned indices of *P. armandii* and broadleaf litter or soil in single-species decomposition, 0.5

is the mass fraction of the litter types in the mixtures, and the subscript PM indicates the predicted values of the mixtures.

A *t* test was employed to detect the differences between the predicted and observed decomposition indices of the decomposition of mixtures and the differences between the decomposition indices of needle and broadleaf litter. One-way ANOVA and subsequent LSD tests were used to analyze the significance of the differences between the observed and predicted enzymatic activities in the decomposing media (soil) of the litter mixtures and those in the decomposing media of the needle and broadleaf litter. All statistical analyses were performed with SPSS 23.0, and the level of significance test was $\alpha = 0.05$. SigmaPlot 12.5 was employed for drawing figures.

Results

Mutual effects between litter types and the overall nonadditive effects during early decomposition

During the first 3 months of decomposition, significant slower overall decomposition was observed in the mixed decomposition treatment. However, these effects exhibited continuous weakening and turned to synergistic effects for the mixtures of *P. armandii* and *B. albo-sinensis* or *P. purdomii* or additive effects for the mixtures of *P. armandii* and *C. fargesii* or *A. tsinglingense* at 4–6 months. Only the mixed decomposition of *P. armandii* and *E. ulmoides* exhibited continuous antagonistic effects until the sixth month (Fig. 2A–E).

Regarding the actual mutual effects, when synergistic effects were observed, the decomposition of *P. armandii* litter was usually significantly accelerated in the mixtures, while that of broadleaf litter was not affected (Fig. 2A,F and Fig. 2C,H). Only the decomposition of *P. armandii* litter was significantly accelerated while that of broadleaf litter was significantly inhibited when additive effects were observed (Fig. 2B,G, Fig. 2E,J). Only the decomposition of broadleaf litter was significantly inhibited when antagonistic effects were observed (Fig. 2D,I). Specifically, *P. armandii* × *B. albosinensis* mixing significantly accelerated the decomposition of the former species in the second month, while it significantly inhibited that of the latter species in the second–sixth months. *Pinus armandii* × *P. purdomii* mixing significantly accelerated the decomposition of the former species in the fourth–sixth months, while it significantly inhibited that of the latter species in the third month. *Pinus armandii* × *E. ulmoides* mixing significantly accelerated the decomposition of the latter species in the third month, while it turned to significant inhibitory effects in the fourth–sixth months. *Pinus armandii* × *A. tsinglingense* mixing significantly inhibited the decomposition of the former species in the first–third months, and it turned to significant promoting effects in the fourth–sixth months, while the mixing significantly inhibited the decomposition of the latter species in the third–fourth months.

The effects of early mixed decomposition on the soil enzymatic activities

According to a previous study [22], the first–third months, sixth month, and first month were regarded as the main period when sucrase, cellulase, and polyphenol oxidase participated in the decomposition of litter in the present study. The results indicated that during the response periods, mixed decomposition (Fig. 3) led to significantly higher activities than those in the decomposition media for *P. armandii* and broadleaf litter (for *P. purdomii*, *E. ulmoides*, *A. tsinglingense* litter) or at least equal to them (*B. albosinensis* and *C. fargesii* litter). Mixed decomposition usually exhibited overall additive effects on cellulase activity; however, the activities were still significantly higher than those in the decomposition medium for *P. armandii* litter and equal to those in the broadleaf litter media (*C. fargesii*, *P. purdomii*, and *A. tsinglingense* litter). For polyphenol oxidase activities, mixed decomposition exhibited significant synergistic effects, leading to significantly higher activities than those in the *P. armandii* and broadleaf litter decomposition media (*B. albo-sinensis*, *C. fargesii*, and *P. purdomii* litter).

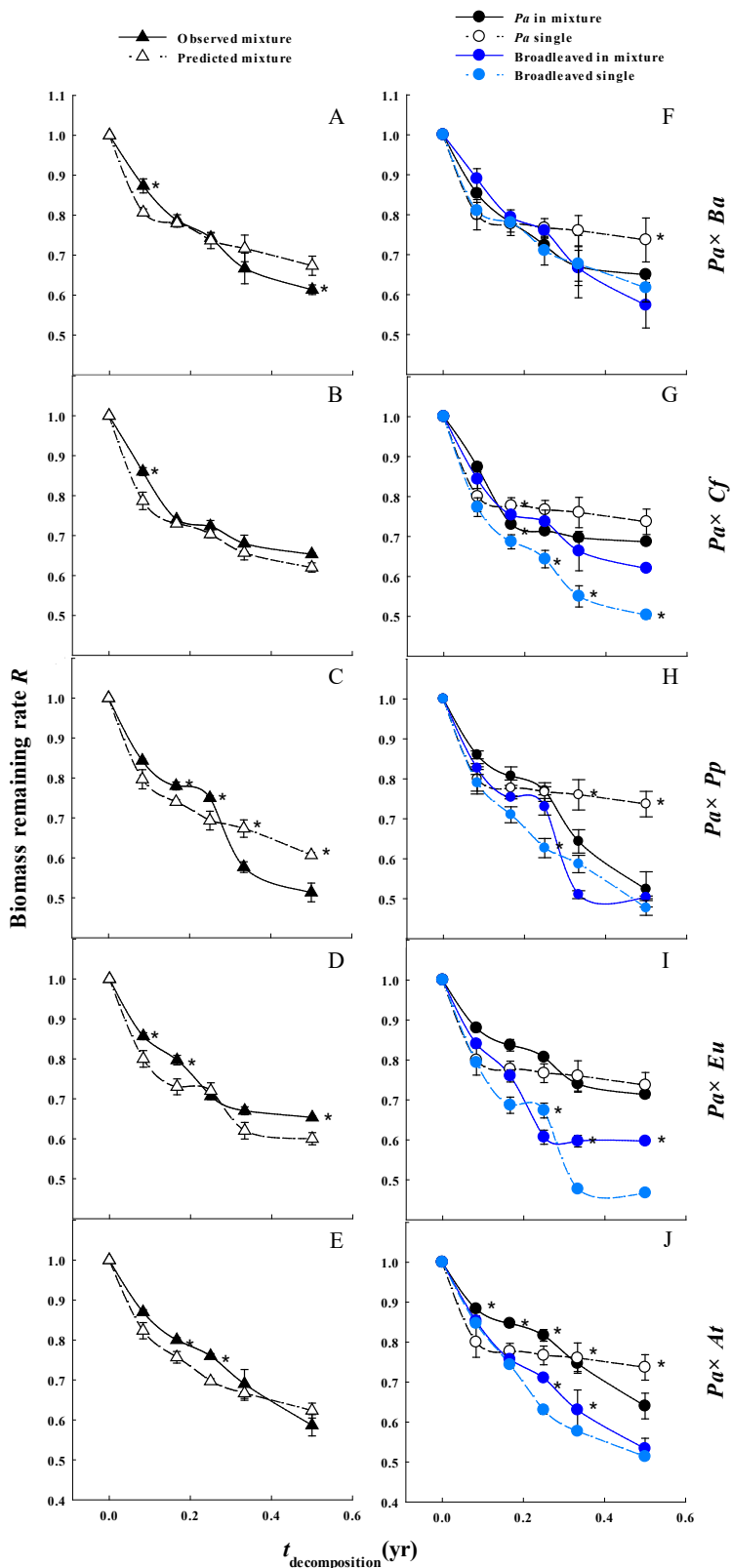


Fig. 2 The overall nonadditive effects of mixed decomposition and the mutual effects between litter types during early decomposition. * Indicates significant differences between the observed and predicted remaining masses of the litter mixtures or significant differences between the litter masses in the monospecific and mixed decomposition treatments ($p < 0.05$). Pa – *Pinus armandii*; Ba – *Betula albo-sinensis*; Cf – *Catalpa fargesii*; Pp – *Populus purdomii*; Eu – *Eucommia ulmoides*; At – *Acer tsinglingense*; × – indicates mixed decomposition; $t_{\text{decomposition}}$ – decomposition time.

or at least equal to them (*E. ulmoides* and *A. tsinglingense* litter).

Long-range prediction of the mutual effects between litter types and the overall nonadditive effects

The long-range prediction based on the decomposition model indicated that *P. armandii* × *B. albo-sinensis*, *P. armandii* × *P. purdomii*, and *P. armandii* × *A. tsinglingense* mixed decomposition exhibited significant overall synergistic effects during the first and second half decomposition (Tab. 1), while the *P. armandii* × *C. fargesii* and *P. armandii* × *E. ulmoides* mixing only exhibited significant synergistic effects during the first-half decomposition. Specifically, the first and second halves of decomposition of *P. armandii* litter and the second half of decomposition of *B. albosinensis* and *P. purdomii* litter were significantly accelerated in the mixtures, while the first and second halves of decomposition of *C. fargesii*, *E. ulmoides*, and *A. tsinglingense* litter were significantly inhibited (Tab. 2).

Discussion and conclusions

The results indicated that during early decomposition (first–sixth months), the decomposition of mixed coniferous and broadleaf litter exhibited significant overall nonadditive effects, which was in line with the findings of Xiao et al. [5], Zeng et al. [23], and Chen et al. [4]. However, the overall effects could not reflect the actual mutual effects between the different litter types in the mixtures. In fact, during the first 3 months, the decomposition of broadleaf litter was generally inhibited, which was in line with our hypothesis. First, the bacteriostatic secondary metabolites released from *P. armandii* litter might be responsible for this result. According to a previous study [19], *P. armandii* litter contains large amounts of phenolic acids and terpenes, such as benzoic acid, dibutyl phthalate, α -pinene, and β -pinene. These components could be leached with the addition of water during incubation, inhibiting the growth and activities of decomposers [24,25] and thus leading to significant decreases in the decomposition rate of broadleaf litter. A previous study stating that coniferous needle extracts inhibited the activities of several types of litter-decomposing enzymes and that the decomposition of broadleaf litter also confirmed this hypothesis [26]. However, in the present study, no significant

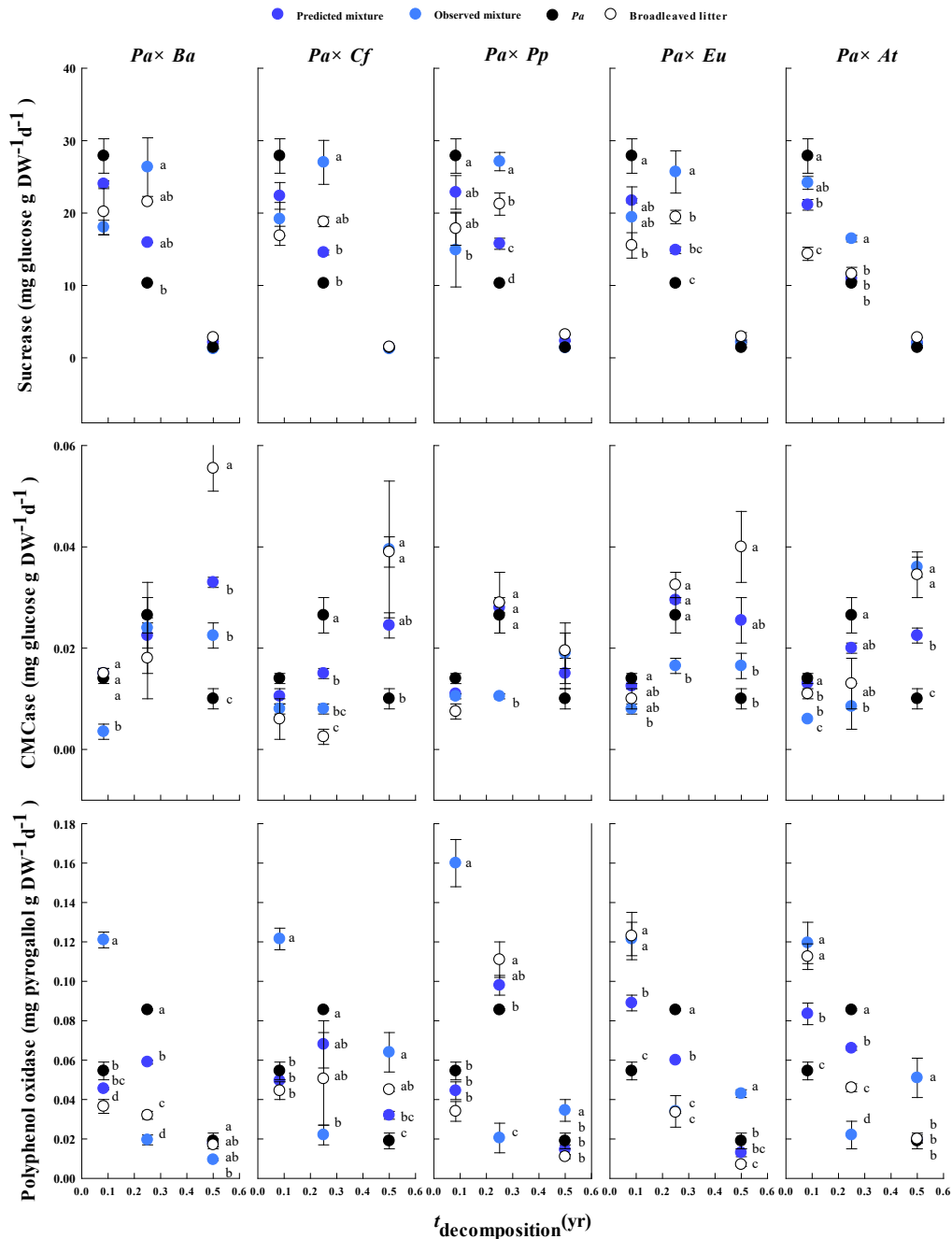


Fig. 3 The effects of mixed decomposition on related enzyme activities. The lowercase letters indicate significant differences ($p < 0.05$). Abbreviations: see Fig. 2.

decreases in the activities of related enzymes participating in this decomposition period (such as sucrase and polyphenol oxidase; Fig. 3) were observed, which was conflicted with the inhibited decomposition. This result might be attributed to the rapid adaptation of microbes to alterations in litter substrate quality [27]. Based on these adaptations, microbes might secrete large amounts of enzymes to obtain carbon sources and degrade phenolic compounds; however, these increases in enzymatic activities did not contribute to the decomposition of litter. Second, nutrients, especially N, would be transferred from nutrient-rich broadleaf litter to *P. armandii* needles by water envelopes or hyphae [28]; thus, nutrient loss might inhibit the decomposition of broadleaf litter at relatively low nutrient contents because sufficient nutrients might not be supplied to the decomposers. The decomposition of *P. armandii* needles was significantly accelerated in approximately 40% of the cases, which was similar to the findings of Yuan et al. [29] and Liu et al. [28], who stated that the decomposition of coniferous needles would be accelerated when broadleaf litter decomposition was inhibited in mixed litter. These

Tab. 1 Observed and predicted time required for the decomposition of litter mixtures.

Litter mixture	Method	$t_{\text{former50\%}}$ (yr)	$t_{\text{later50\%}}$ (yr)
<i>P. armandii</i> × <i>B. albo-sinensis</i>	Observed	0.66 (0.03)*	2.38 (0.1)*
	Predicted	1.56 (0.18)	7.78 (1)
<i>P. armandii</i> × <i>C. fargesii</i>	Observed	0.98 (0.13)*	6.1 (2.07)
	Predicted	1.38 (0.16)	7.21 (0.87)
<i>P. armandii</i> × <i>P. purdomii</i>	Observed	0.48 (0.02)*	1.55 (0.08)*
	Predicted	1.38 (0.18)	6.92 (0.99)
<i>P. armandii</i> × <i>E. ulmoides</i>	Observed	0.98 (0.01)*	7.17 (0.32)
	Predicted	1.35 (0.15)	7.39 (0.87)
<i>P. armandii</i> × <i>A. tsinglingense</i>	Observed	0.66 (0.01)*	2.38 (0.01)*

* Indicates significant differences ($p < 0.05$) between the observed and predicted values.

Tab. 2 Time required for litter decomposition in mixed or monospecific decomposition.

Litter	Form in decomposition	$t_{\text{former50\%}}$ (yr)	$t_{\text{later50\%}}$ (yr)
<i>P. armandii</i>	Monospecific	2.27 (0.33)	11.77 (1.91)
	× <i>B. albo-sinensis</i>	0.76 (0.11)*	2.93 (0.43)*
	× <i>C. fargesii</i>	0.82 (0.03)*	4.19 (0.44)*
	× <i>P. purdomii</i>	0.59 (0.05)*	2.06 (0.23)*
	× <i>E. ulmoides</i>	1.28 (0.07)*	5.14 (0.40)*
	× <i>A. tsinglingense</i>	0.86 (0.11)*	3.04 (0.50)*
<i>B. albo-sinensis</i>	Monospecific	0.84 (0.08)	3.79 (0.42)
	× <i>P. armandii</i>	0.68 (0.05)	2.15 (0.12)*
<i>C. fargesii</i>	Monospecific	0.49 (0.01)	2.65 (0.17)
	× <i>P. armandii</i>	0.86 (0.07)*	3.95 (0.43)*
<i>P. purdomii</i>	Monospecific	0.48 (0.05)	2.06 (0.07)
	× <i>P. armandii</i>	0.39 (0.01)	1.32 (0.02)*
<i>E. ulmoides</i>	Monospecific	0.44 (0.03)	3.01 (0.17)
	× <i>P. armandii</i>	0.62 (0.07)*	5.04 (0.14)*
<i>A. tsinglingense</i>	Monospecific	0.39 (0.01)	1.32 (0.01)

* Indicates significant differences ($p < 0.05$) between the values obtained in the monospecific and mixed decomposition.

accelerating effects on needle decomposition might be attributed to the nutrient supply from broadleaf litter and the attenuation of the decomposition inhibitors caused by mixing [13,23,28]. However, in most cases, mixed decomposition did not accelerate the decomposition of *P. armandii* needles in this period (Fig. 2A,C,D) and even led to significant inhibition (Fig. 2E), which was contrary to the above-mentioned studies. One possible reason for this difference might be the rapid release of N from the broadleaf litter [30]. Although this N would accelerate the growth of microbes and increase the activities of related enzymes to some extent, it might also combine with the lignin in *P. armandii* needles to form recalcitrant compounds, consequently inhibiting litter decomposition [31,32].

Subsequently (fourth–sixth months), most (approximately 4/5) of the antagonistic effects caused by mixed decomposition exhibited continuous weakening and turned to synergistic or additive effects. In view of the mutual effects between coniferous and broadleaf litter, the main causes of the mentioned alterations might be the continuous weakening of the inhibitory effects on the decomposition of broadleaf litter and the

promoting effects on the decomposition of *P. armandii* needles (Fig. 2). The following reasons might be responsible for these differences. First, secondary metabolites, especially liable and soluble compounds, could be rapidly leached, degraded and diffused into the soil. For instance, Qin et al. [33] stated that the phenolic compounds in *P. armandii* needles exhibited significant degradation after only 3 months of decomposition. The decreases in the concentrations of these compounds alleviated their inhibitory effects or even led to accelerating effects on decomposers [34,35]. In the present study, the enzymatic activities in the decomposition media for the mixtures remained at the levels in those for the broadleaf litter (Fig. 3), which confirmed the mentioned speculations. Second, the possible inhibitory effects of N on needle decomposition weakened with the decomposition of broadleaf litter. In contrast, nutrient transfer [28], the priming effects of liable carbon sources from broadleaf litter on the decomposition of recalcitrant compounds in coniferous needles [36], and the accelerating effects on the growth of microbes [37] would lead to faster decomposition of *P. armandii* needles. The significantly higher cellulase activities in mixed decomposition media in the third–sixth months also confirmed these speculations (Fig. 3). Finally, mixed decomposition could provide variable substrate, food sources, and habitat conditions (humidity, temperature, or spatial structures); these alterations would accelerate the growth of decomposers and thus promote the decomposition of litter mixtures [10,38]. Noticeably, the antagonistic effects caused by *P. armandii* and *E. ulmoides* mixing continued to the end of incubation. The decomposition inhibitors, such as chlorogenic acid and aucubin, found in *E. ulmoides* litter might be responsible for the continuous mutual inhibitions [39,40].

Due to relative short incubation period in the present study, the modified Olson decomposition model [21] was used to predict the entire decomposition process. The predicted effects of mixed decomposition on the first half of decomposition were basically the same as those observed in the present study, indicating that this model could accurately reflect the decomposition tendency. According to the prediction and related calculations, broadleaf litter would significantly accelerate the decomposition of *P. armandii* needles throughout the decomposition process, while the decomposition of broadleaf litter would be inhibited at least in the short term. However, mixed decomposition could accelerate the overall decomposition at least in the first half of decomposition, especially the decomposition of *P. armandii* needles. As most of the nutrient release also occurred during this period, the planting of mixed broadleaved species except for *E. ulmoides* with *P. armandii* might be a feasible approach to accelerate litter decomposition and compounds cycling in pure forests.

Noticeably, broadleaf litter with the best substrate quality did not improve the promoting effects on the decomposition of *P. armandii* needles, which was in line with the findings of Zhao et al. [41]. According to previous studies [42], the alterations in litter chemical diversity caused by mixing rather than the nutrient supply ability of a given litter species in a mixture might be the main factor affecting the mixed decomposition effects. Consequently, more chemical indices of litter should be measured in the following studies to further assess the chemical diversity changes caused by mixed decomposition. Accordingly, the underlying mechanisms of the mutual effects of litter during mixed decomposition should be further analyzed.

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