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Non-additive allelopathic effects of decomposing mixed litters of *Eucalyptus urophylla* and *Acacia mangium on* radish, lettuce and *Paspalum notatum*

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ABSTRACT

We investigated the effects of decomposing leaf litters of *Eucalyptus urophylla* and *Acacia mangium* on plant growth, nitrogen (N) immobilization and allelopathy. We found that single and litter mixture of *E. urophylla* and *A. mangium* during decomposition inhibited the growth of test plants [radish (*Raphanus sativu*s), lettuce (*Lactuca sativa*) and *Paspalum notatum*)]. Non-additive effects on growth inhibition were observed in pure and mixture of decomposing leaf litters. After 0 days decomposition, the litter mixture showed antagonism (germination rate lower than expected value). After 5 days of decomposition, the mixture effect was synergistic, and the germination rate was higher than the expected value. Finally, 20 days after decomposition, the effects became additive. Litter mixture slightly inhibited the root length (8 %) in treatment of water (AC^-N^-) and by 21 % in treatment of mineral solution (AC^-N^+), but the non-additive effects disappeared after the activated carbon (AC) was added to medium. We propose that the changes in the composition, proportion and concentration of allelochemicals in litter mixture caused the non-additive allelopathic effects.

Keywords: *Acacia mangium,* activated carbon, AC, allelopathy, allelopathic effects, decomposition, *Eucalyptus urophylla,* growth, *Lactuca sativa,* lettuce, mixed litter, non-additive effects, *Paspalum notatum,* radish, *Raphanus sativus*

INTRODUCTION

Plant litter is major driver of many biotic interactions and nutrients cycling in ecosystems (13). Allelochemicals produced from plant litters play key role in the interactions (6). Some of these metabolites are produced directly from plant litters, whereas other metabolites might be produced by decomposer microbes in the soil.

Allelochemicals from plant litters are one of the drivers in the successional replacement of plant species. Many studies in both laboratory (3,4,5) and field (4,10) have indicated that the addition of plant litter to the soil can inhibit plant growth, leading to decreased plant growth and biomass. Many studies have shown that the presence of allelochemicals in soil or from the litter leachate inhibits the seed germination and seedling growth. Allelochemicals in the soil may affect the plant growth if they exceed the threshold concentrations (8,17,27,34). There are several mechanisms responsible for growth inhibition by plant litter. One mechanism is nitrogen (N) immobilization by microbial competition (2,3,29). It usually occurred in the early phase of litter decomposition if the N content in litter is < 2% (12,26) or the organic matter C: N ratio >

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30 (14). Owing to the very broad diversity of secondary metabolites, studying their effects on the decomposition process has remained a major challenge. Therefore, most studies on the effects of plant litter have focussed on single-specie leaf litter. However, in the forests most of the litter from above-ground plant production is supplied in the form of mixed-species leaf litter.

Recently some studies have been done to determine the potential interactions among leaves of different plant species during decomposition (11,33). These studies focus on patterns of mass loss (18,28,37) changes in nutrients concentration (22,23), decomposer abundance and activity (41). Most of these studies indicated that mixed-litter often exhibited different patterns than single-species (11,33,35) which are named non-additive effects (synergistic or antagonistic).

The *Eucalyptus urophylla* and *Acacia mangium* do not grow together naturally, these were introduced into China for landscape purposes > 110 years ago. Now, these have been planted on large scale in South China for production of pulpwood, flake board, plywood, construction poles and ties for railway lines tracks (20). Leaf litters of *E. urophylla* are allelopathic to *Brassica chinensis*, radish, cucumber and Chinese cabbage (20), while nothing is known about the allelopathic effects of litter of *A. mangium*.

This study aimed to determine the (i). inhibitory effects of single- and mixed-species litters on soil available N, seed germination and seedling growth of target plants, (ii). to test the hypothesis that mixed-litter have inhibitory effects and show non-additive patterns than single-specie and (iii). these non-additive inhibitory effects might be related to allelopathy instead of N immobilization.

MATERIALS AND METHODS

Collection of litters and soil

Fresh litters of *Eucalyptus urophylla* and *Acacia mangium* leaves were collected in May 2016 from the Botanic Garden, South China Agricultural University, Guangzhou, China (113°35’E, 23°16’N), altitude: 356 m, and mean annual precipitation: > 1800 mm. The leaves of *E. urophylla and A. mangium* were collected at the time of abscission by shaking the trees and collecting the falling leaves on cloth sheets (3 × 4 m).

The upper 20-cm soil layer collected from the same garden contained 1.69 % organic matter, 1.05 % total N, 1.05 g/kg total P,19.30 g/kg total K and pH of 5.72. It was air-dried, mixed thoroughly and then sieved through 1 mm sieve and stored at room temperature for two months as culture medium in seed germination assay and green house pot experiment.

Receiver plant species

Seeds of radish (*Raphanus sativus*), lettuce (*Lactuca sativa*) and *Paspalum notatum* (natural grass growing under *E. urophylla* and *A. mangium*) were purchased from Guangdong Academy of Agricultural Sciences, Guangzhou, China. They were used as the target species due to their fast and uniform germination and sensitivity to allelochemicals (36).

Seed germination Petri dish bioassays

Litters of *E. urophylla* and *A. mangium* were cut into 1 cm×1 cm pieces and air dried at 40 °C for 3 days. Dry litters of either *E. urophylla*, *A. mangium* alone or their mixture (1:1) were mixed at 1.0 g per 50 g soil and used in petri dishes (12 cm, dia). The soil without litter was used as control. Each petri dish was watered with 20 mL distilled water every 5 days. The dishes were incubated in a growth chamber (25 ± 2 ℃; 12 /12h light/dark photoperiod). The litters were decomposed for 0, 5 and 20 days. thereafter, 50 seeds of radish were sown in each dish and germinated in Incubator. Seeds were considered germinated when 1 mm radicle protruded from the seed coat Seed germination was recorded on 5th day when > 50% seeds germinated (24).

Seedlings root growth

To assess the allelopathic potential of litters (single- or mixed-species) on the growth of root, the 'root proliferation' experiment was conducted as described by Bonanomi *et al.* (2). The 2-cm-wide and 5-cm-long sterile filter paper strips were placed parallel in square petri dishes (size 10 × 10 × 1.0 cm, oriented at 45° slope on a horizontal surface), with 3 mm Gap in the middle (Figure 1). Ten lettuce seeds in each dish were placed over the higher side 2-cm-wide strip and different treatments were applied on the lower 5-cm-wide strip. Petri dishes were placed in growth chamber (25 ± 2 ℃; 12/12h light/dark photoperiod).

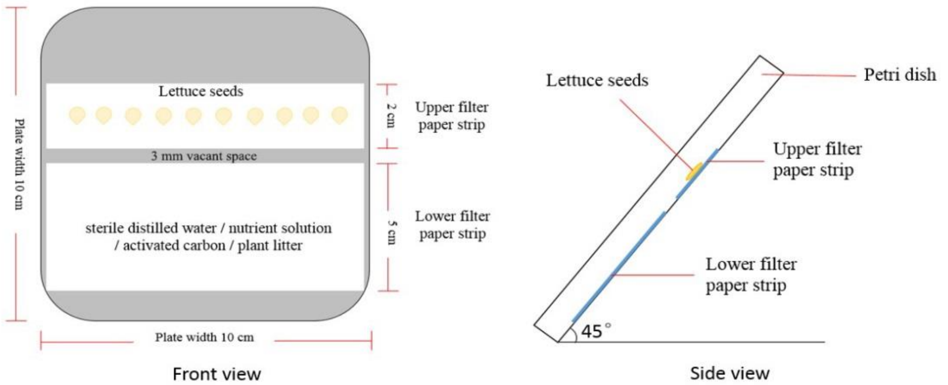

Figure 1. Graphical representation of experimental design for the "Litter allelopathic potential on root growth"

There were 4-experimental treatments as under:

(i). 1.5 ml sterile distilled water, AC^-N^-.
(ii). 1.5 ml nutrients solution (half strength Hoagland's nutrient solution), AC^-N^+
(iii). activated carbon (AC, purchased from Taishan Yueqiao Reagent Plastic Co., Ltd.) at 0.05 g per dish, AC^+N^-.
(iv). nutrient solution + activated carbon, AC^+N^+.

These four treatments were applied with 0.05 g dry powder litter [*E. urophylla*, *A. mangium* or mixed litter (1:1)] on the lower strip. The upper strip with the seeds was treated only with distilled water. The treatments were replicated four times in complete randomized Design. Root lengths of seedlings were measured with Ruler 5 days after germination. Data were expressed as root growth (*i.e.* per cent difference in root length) compared with control.

Greenhouse experiment

Seedling Growth: The seedlings of *P. notatum* were transplanted in 1.2 L plastic pots (3-seedlings per pot, 10 cm dia and 15 cm depth) filled with 400 g soil and 3 g leaf litter chips (1 cm × 1 cm). The experimental treatments were: (i). Non-litter (control), (ii), single litter of *E. urophylla,* (iii). single litter of *A. mangium* and (iv). Equal-mass mixed litter of both spp. Pots were placed in greenhouse (25 ± 2 ℃; 12/12 h light/dark photoperiod). To avoid errors caused by differences in photoperiod or light intensity, pots were moved randomly twice a week and irrigated daily with 5 mL water. Plants were harvested after 2, 3 and 5 weeks, respectively. Six replicates of each treatment were used in each sampling time. 3 plants per pot, therefore treatments were replicated 18 times. The roots were carefully separated from the pot soil and litter residue, shoot and root lengths were measured by Ruler**.**

Soil Nitrogen: To know if litter treatment influenced the available N in the soil, the same treatments as above were used for seedling growth, but without plants. Available N was determined 1, 2, 3, 5 and 7 weeks after treatments were applied. The litter residues were removed from the air-dried soil by sieving through 1 mm sieve. Thereafter analyzed using Alkali-hydrolyzable method as per Wallenstei *et al*. (47). Five replicates for each treatment were used in each sampling.

Data analysis

To further analyze the mix effects of litter mixtures, relative deviation between the observed (*O*) and expected (*E*) value in litter mixtures was calculated as difference (*O*-*E*)/*E* as per the method of Lecerf *et al.* (15,19,22). Values not different from zero, indicate additive, whereas positive or negative values indicate antagonistic or synergistic effects on decomposition, respectively (15,19,22). Expected value (*E*) in litter mixtures was calculated as under:

$$E = (O_{eu} + O_{am}) / 2$$

Where, O_{eu} : Observed value of *E. urophylla* and O_{am} : Observed value of *A. mangium*.

Allelopathic potential of litters on seed germination, biomass of seedlings and soil N dynamic were analyzed by two-way ANOVA. Generalized linear models (GLMs) were used to analyze bioassays of root proliferation. Significance was evaluated at $P< 0.05$. All statistical analysis was done using SPSS 13.0 (SPSS, Chicago, IL, USA).

RESULTS AND DISCUSION

Incubator studies

Seeds germination

All 3- types of litters of *Eucalyptus urophylla*, *Acacia mangium* and their mixture (1:1) during the different phases of decomposition (0-20 days) inhibited the seeds germination of *R. sativus* than control (Figure 2). However, their inhibitory effects decreased on the seed germination of *R. sativus* with increase of decomposition period. The litters treatment increased the seeds germination of *R. sativus* from 45.92 % to 69.12 % than control during the degradation of *E. urophylla* litter. While in *A. mangium* litter, the germination rate increased from 50.79 % to 82.38 % during the litter degradation time.

Litter mixture was most inhibitory to seeds germination (28.57 %) at 0 days after decomposition i.e. in the beginning (Figure 2). Litter mixture exhibited non-additive effects on *R. sativus* germination than single litter after the litters decomposed for 5 days. After 0 days decomposition, the mixed effect showed antagonism (germination rate lower than expected value about 19.79 %, *t*-test， $P < 0.001$). After 5 days of decomposition, the mixed effect was synergistic (*t*-test， $P = 0.037$) and the germination rate was higher than the expected value 24.48 %. Finally, additive effects occurred 20 d after decomposition.

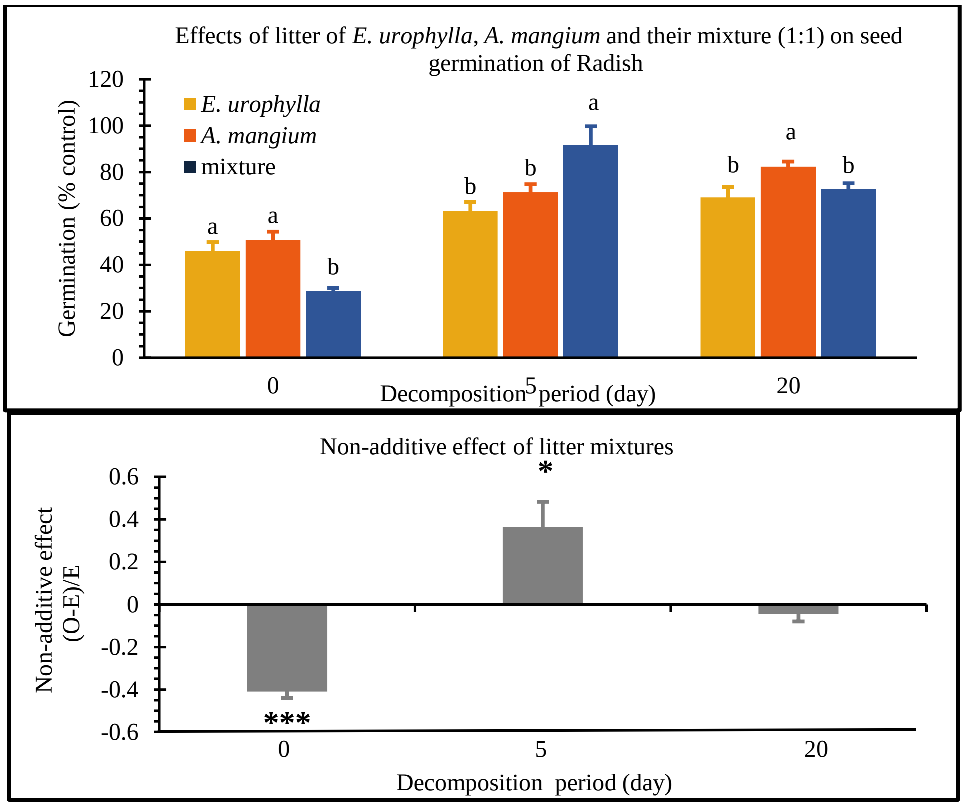

Figure 2. Effects of litter of *Eucalyptus urophylla*, *Acacia mangium* and their mixture (1:1) on seed germination of Radish and non-additive effect of the litter mixtures. The bioassays were conducted after the litters were decomposed for 0, 5 and 20 d, respectively.
Values shown are means ± SE ($n = 6$). Significant differences (Duncan test; $p < 0.05$) among treatments in a group are indicated by different letters above bars. Asterisk indicates significant non-additive effect (*t*-test: * $p < 0.05$, *** $p < 0.001$).

Seedlings root growth

All litter leachates significantly inhibited the root growth of *L. sativa* (Figure 3). Application of the mineral nutrients to the litter plates did not reverse the inhibitory effect on root growth. In contrast, the inhibitory effects of litters of *A. mangium* and mixed litters were substantially decreased, at a level comparable to water control, when AC was added to the medium. The inhibitory effects of litter of *E. urophylla* also decreased when activated carbon (AC) was added. The combined application of mineral solution and AC did not show any interactive effects.

When litter mixture alone or combined with nutrients was added to the petri plates, non-additive mixture effects on root length were observed (Figure 3). Litter mixture inhibited the root length slightly 8 % (AC^-N in treatment) and 21 % (AC^-N in treatment), whereas the non-additive effects disappeared when AC was added to the medium.

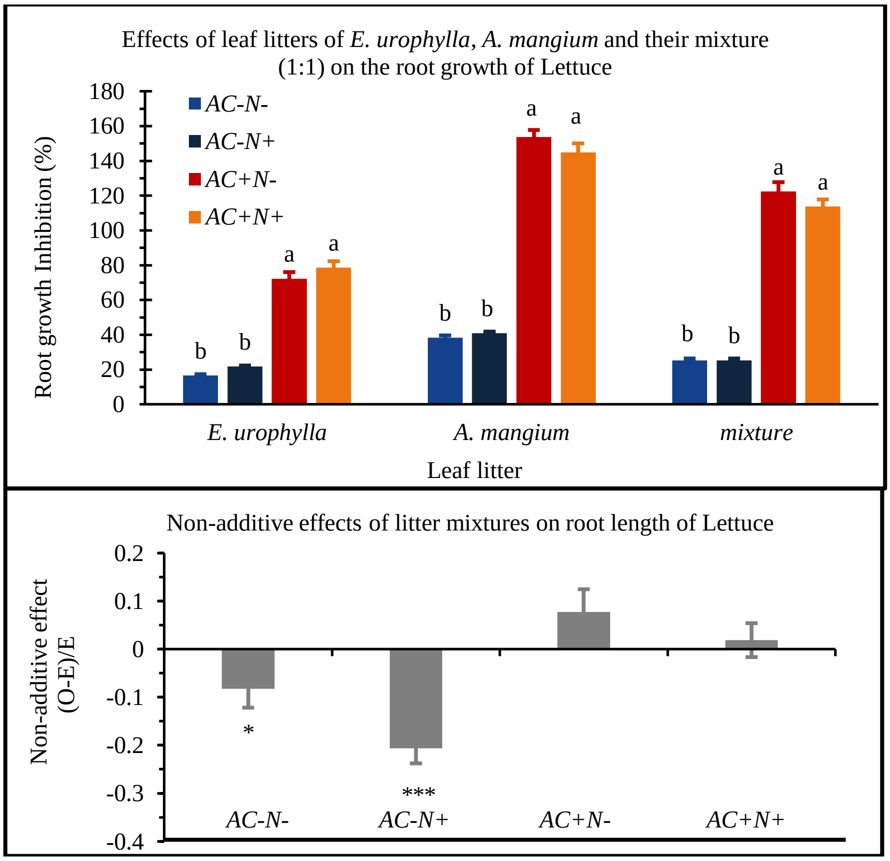

Figure 3. Effects of leaf litters of *Eucalyptus urophylla*, *Acacia mangium* and their mixture (1:1) on the root growth of *Lactuca sativa*. Results of the 'root growth' bioassay: root length of *L. sativa* compared with the control for different litter types (*E. urophylla* and *A. mangium* and their litter mixture, 0.05 g per dish) in the presence of water (AC^-N^-), mineral solution (AC^-N^+), activated carbon (AC^+N^-) and activated carbon plus mineral solution (AC^+N^+). Non-additive effects of litter mixtures on root length of *L. sativa*. Values shown are means ± SE (n = 40). Significant differences (Duncan test; $p < 0.05$) among treatments in a group are indicated by different letters above bars. Asterisk indicates significant non-additive effect (t-test: * $p < 0.05$, *** $p < 0.001$).

Greenhouse studies

Single and mixed species litter significantly inhibited the seedlings growth of *P. notatum* during decomposition (Figure 4). At the end of 3^{rd} and 5^{th} weeks, litter mixtures stimulated the root length (49 % and 8 % of cases respectively) (Figure 3c). Non-additive inhibitory effects on shoot length were observed in litter mixture experiments at the end of 2^{nd} and 3^{rd} weeks (17 % and 63 % inhibition, respectively).

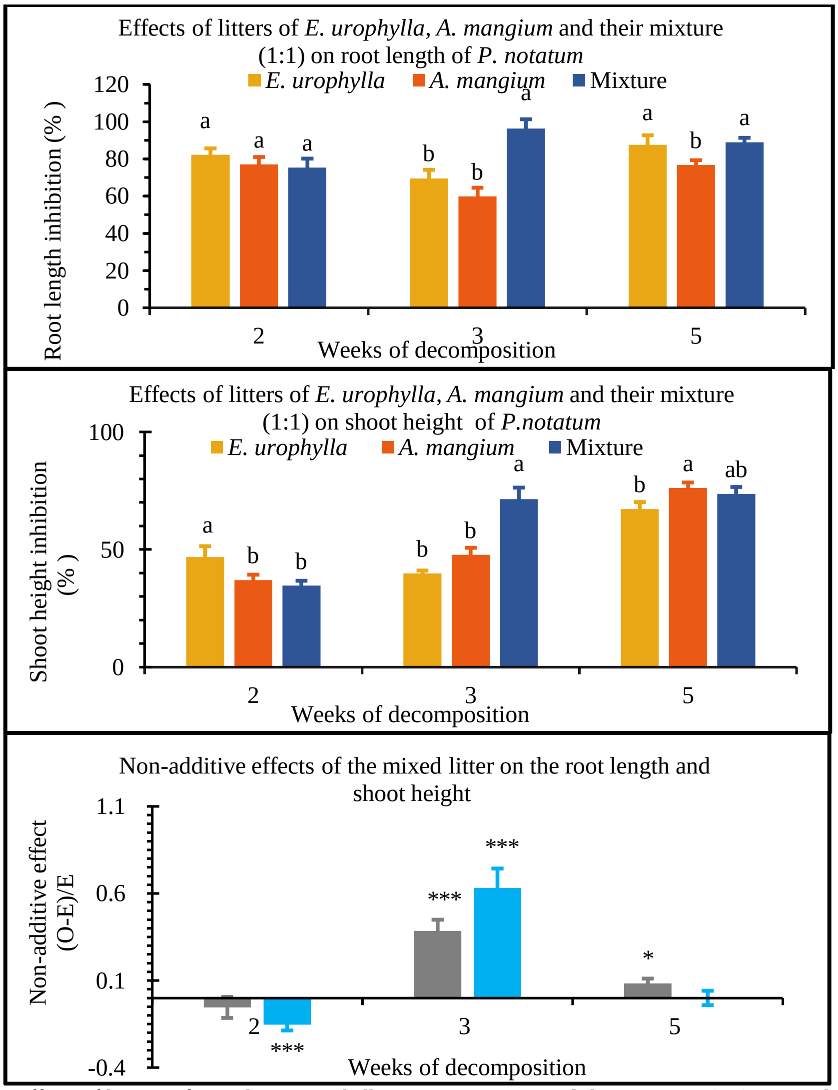

Figure 4. Effects of litters of *Eucalyptus urophylla*, *Acacia mangium* and their mixture (1:1) on root length and shoot height of *Paspalum notatum* and non-additive effects of the mixed litter on the root length and shoot length**.** Plants were harvested after 2, 3 and 5 weeks, respectively. Values shown are means ± SE (n = 18). Significant differences (Duncan test; p < 0.05) among treatments in a group are indicated by different letters above bars. Asterisk indicates significant non-additive effect (t-test: * p < 0.05, *** p <0.001).

Compared with control, available N decreased only in *E. urophylla* treatment in 1st week and then decreased in all litter treatments in 2nd and 3rd weeks. After 5th week, there were no significant differences between the control and treatments. Additive effects were observed in the mixed-litter treatments. Only in the 5th week, observed available N was 10.9 % lower in single-species litter treatments (Figure 5).

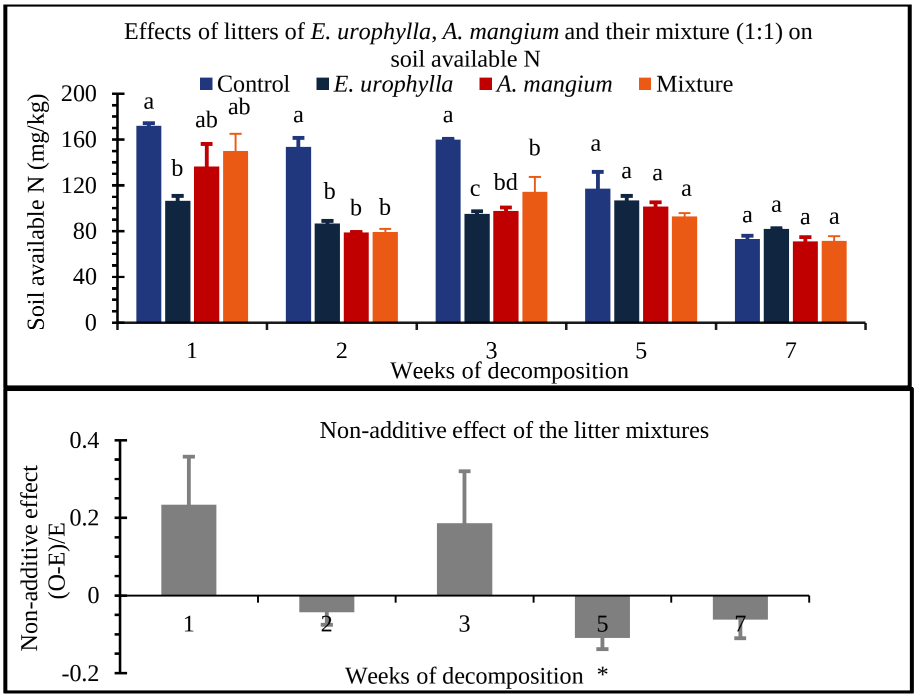

Figure 5. Effects of litters of *Eucalyptus urophylla*, *Acacia mangium* and their mixture (1:1) on soil available N **(a)** and non-additive effect of the litter mixtures **(b).** Available N was evaluated respectively after litters decomposed 1, 2, 3, 5 and 7 weeks, respectively. Values shown are means ± SE (n = 5). Significant differences (Duncan test; $p < 0.05$) among treatments in a group are indicated by different letters above bars. Asterisk indicates significant non-additive effect (*t*-test: * $p < 0.05$).

The N content of *E. urophylla*, *A. mangium* and their litter mixture were 1.56 %, 2.22 % and 1.89 %, respectively, lower or similar to the threshold of N immobilization (14,32). Thus, the decrease in available nitrogen was one of the reasons for the inhibitory effects on plant growth.

DISCUSSION

Allelopathic substances released into the soil by decomposition of litters can produce allelopathic effect and affect the growth of tested plants.

Firstly, in this paper, all the three types of litters displayed inhibitory effects on the seed germination of *R. sativus* compared with control (Figure 1a), as well as on the root growth of *L. sativa*. As activated carbon can adsorb allelopathic substances, the inhibitory effect was also decreased when activated carbon (AC) was added (Figure 2a). That means that the aqueous extract of litter contained water-soluble allelopathic substances, which had direct allelopathic effects. Since the inhibitory effect was not alleviated by the addition of nutrient solution, it can be assumed that the direct allelopathy had nothing to do with nutrients.

Secondly, litter mixing appears to enhance allelochemicals diversity. Mixtures of allelochemicals might be more phytotoxic than pure compounds and the composition of a natural allelochemical mixture is a more complex matter than the simple additive effect (1). The chemical changes would be more complex in mixed litter decomposition and might directly influence allelopathy patterns.

Thirdly, during decomposition process, the proportions of each individual allelochemical might change in mixed litter treatment, resulting in different biological activity. Litter mixture showed the strongest inhibitory effect and the smallest germination rate (28.57%) at 0 days after decomposition (Figure 1a). The combination of allelochemicals in equal proportions yielded less inhibition than the combination of allelochemicals in their natural proportions, even though the contribution to the mix of some compounds with high phytotoxicity had increased (1).

We supposed this phenomenon might relate to the change of allelochemicals. Further studies are needed to determine the mechanisms as well as whether these non-additive litter-diversity effects can occur in the field.

Other studies have shown that the presence of allelochemicals in the soil may be determined by physical factors (16,32). Because of continuous chemical and physical changes during decomposition, the full range of positive, negative and no effects of mixed litter on allelopathy would happen depending on decomposing phase. In our study, during litter decay, germination and seedling growth have changed similarly from positive, negative to little or no effects, indicating that non-additive effects were antagonistic in the beginning of decomposition, then became synergistic, and these mixing effects disappeared during the decomposition proceeded (Figure 1b). The inhibitory effects of litter mixture on seed germination, root growth and plant growth appeared to have non-additive effects (Figures 1b, 2b, 3c, 4b). Non-additive inhibitory effects on root growth had no relationship with nutrients and couldn't be relieved by nutrients addition, but it disappeared after the application of AC (Figures 1, 2, 3, 4). Diverse plant litter mixtures often exhibit non-additive effects on mass loss, net N immobilization and decomposer abundance (11,33), but it remains unclear what could have led to the negative or positive effects of the litter mixture treatment. Many studies demonstrated that litter quality such as N concentration of the individual constituent litter species (30), environmental factors (19,21,31), decomposer community (35), chemical composition and diversity (23) possibly determined whether the non-additive effects in litter mixtures occurred. These factors were also considered to determine whether the non-additive effects are antagonistic or synergistic. Therefore, the non-additive patterns of inhibition might probably due to the allelochemicals instead of physical factors (9,25) or N immobilization (7,38,39).

Further studies are needed to determine the mechanisms as well as whether these non-additive litter-diversity effects can occur in the field.

CONCLUSIONS

We investigated the effects of decomposition of mixed litters of *Eucalyptus urophylla* and *Acacia mangium* on plant growth and further determined the role of nitrogen (N) immobilization and allelopathy. The inhibitory effects of decomposing litters had no relationship with the soil nutrients status, but were decreased by AC addition. On the contrary, we observed additive effects of litter mixture on soil N dynamic. Our findings showed that non-additive inhibitory effects of decomposed litters of two species were related to their potential allelopathy rather than physical factors and N immobilization. We propose that the changes in composition, proportion and concentration of allelochemicals in litter mixture are responsible for non-additive allelopathic effects.

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