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Allelopathic effects of common exotic plants on soil-conserving native grasses in Taiwan

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ABSTRACT

Invasive plant species, such as *Mikania micrantha* (*M. micrantha*), *Leucaena leucocephala* (*L. leucocephala*) and *Mimosa pigra* (*M. pigra*), often outcompete native vegetation, leading to biodiversity loss and ecological imbalance. These invasive species can negatively impact ecosystems by altering habitat structure, modifying nutrient cycling, and suppressing the growth of native plants, which can have significant ecological and economic consequences, particularly in agriculture. This study investigates the allelopathic effects of three invasive species on five soil-conserving grasses native to Taiwan: *Axonopus affinis* Chase (*A. affinis*), *Cynodon dactylon* (*C. dactylon*), *Dichondra repens* (*D. repens*), *Paspalum notatum* (*P. notatum*) and *Eremochloa ophiuroides* (*E. ophiuroides*). Results indicate that the root growth of *A. affinis*, *C. dactylon*, and *D. repens* was inhibited by extracts of *M. micrantha*, while *P. notatum* and *E. ophiuroides* showed no significant effects. In contrast, the root growth of all five grass species was inhibited by the *L. leucocephala* extracts. For *M. pigra*, the root growth of *A. affinis*, *E. ophiuroides*, and *D. repens* was inhibited, while *C. dactylon* and *P. notatum* were unaffected. Interestingly, the inhibitory effects were correlated with increased peroxidase (POD) activity in the plants, suggesting a potential mechanism of resistance or tolerance in some species, particularly *P. notatum*. This grass species exhibited notable resistance to allelochemicals from *M. micrantha* and *M. pigra* but appeared more vulnerable to those from *L. leucocephala*. The study also examined the effects of benzoic acid, the primary allelochemical in *M. micrantha*, and mimosine, the key compound in *L. leucocephala* and *M. pigra*. The growth inhibition caused by these compounds mirrored the effects of the plant extracts, highlighting the allelopathic potential of benzoic acid and mimosine, which be used as a natural herbicide to protect human health. These findings provide valuable insights into the complex interactions between invasive plant species and native grasses, particularly the potential resistance of *P. notatum* to certain allelochemicals, which could inform strategies for managing invasive species and conserving native vegetation in Taiwan.

Key words: Allelopathy; *Mikania micrantha*; *Leucaena leucocephala*; *Mimosa pigra*; soil-conserving grasses.

INTRODUCTION

Invasion plants grow with the development of transportation, some species are more likely to move around the world with various means of transportation (20). A part of exotic species can naturally grow and reproduce without artificial cultivation and even expand

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rapidly and increase the population in new habitats. These are the symptoms of invasive plants. Taiwan indigenous reserves is also affected by invasive alien species, such as *Mikania micrantha* (*M. micrantha*) and *Leucaena leucocephala* (*L. leucocephala*), which are common invasive plants in Taiwan (16).

The mechanism of allopathic chemical of invasive plants may be that the plants and microorganisms disperse compounds to the air through the volatile action, indirectly affecting other plants and microorganisms, or release compounds to the soil environment through direct exudate and plant residues decomposition, or wash various compounds, including competing compounds, from the surface of the plant body to the earth's surface to precipitate using external water through the Leaching action. This affects the growth and development of peripheral plants or soil microorganisms, so as to change the physical and chemical properties of the rhizosphere soil (1,11,39). Based on the meta-analysis results of Zhang *et al*. (39), the decomposition of plant residues has the greatest negative impact on other plants, and the negative impact mainly exists during the seed germination period. These are all manifestations of allelopathy.

Most of allelochemicals involved in allelopathy are produced in the secondary metabolic pathway of plants to improve the stress tolerance, competition for nutrients, and attract mutually beneficial soil microorganisms (1,8,9,23) and interfere with the germination or growth of peripheral plants, or deter the animals and insects (14).

The allelopathic compound in this study, benzoic acid, is an organic acid and a polyphenol (17). It is synthesized in plants through the shikimate pathway and provides the carbon skeleton basis for numerous metabolites and derived compounds such as hormones of plants (29), so as to defend against external stress and pathogenic bacteria (6,29). It is also the competing compound with the highest content in the aqueous extract of *M. micrantha* (21). Moreover, Mimosine, the allelochemical from the leguminous tree *L. leucocephala*, is toxic to most terrestrial animals and plants (31). It is also the allelochemicals in *Mimosa pigra* (*M. pigra*), and has a toxic effect on the growth of some plants (22). Allelopathy involves the release of chemicals by one plant species that affect the growth and development of neighboring plants. Therefore, this study explores the effects of invasive plants (*M. micrantha*, *L. leucocephala* and *M. pigra*) and their competing compounds on the five Taiwan naturalized and native grass species: *Axonopus affinis* Chase (*A. affinis*), *Cynodon dactylon* (*C. dactylon*), *Dichondra repens* (*D. repens*), *Paspalum notatum* (*P. notatum*), and *Eremochloa ophiuroides* (*E. ophiuroides*) (30), to investigate the natural defensive pathways inherent in Taiwanese grass species against invasive plants and in the future devise methods or even hybrid plant options to increase Taiwanese eco-systemic competition against current and other potential invasive plants.

MATERIALS AND METHODS

I. Collection of invasive plants and preparation of crude extracts

The invasive plant samples were collected from Dongshan District (Tainan City). 20 grams of fresh leaves of *M. micrantha* and fruit parts of *M. pigra* and *L. leucocephala* were put in 1 liter of distilled water respectively (10,31) and placed in a 37 °C incubator for 24 h dark light extraction to obtain the crude extract.

II. Test materials and plant growth

A. affinis and *D. repens* were purchased from Known You Seed Corp. *P. notatum*, *C. dactylon* and *E. ophiuroides* were purchased from Green Arts Horticulture Co.

(i). *C. dactylon*: The seeds were soaked in a 9 cm tray, filled with 20 ml of distilled water, and placed in a dark growth chamber at 27 °C for 60 h. A total of 21 seedlings with a radicle of more than 5 mm and similar root lengths were transferred to a 14 cm circular tray covered with a piece of 125 mm filter paper.

(ii). *P. notatum*: The seeds were soaked in a 9 cm circular tray, and cultured in a dark incubator at 37 °C. After 2 days, 49 seeds were evenly spaced as possible on a 12 cm square tray covered with a piece of filter paper, and 7ml of distilled water was dropped into each tray, 5 days in a growth chamber at 27 °C with 16 h of illumination and 8 h of dark light. Twelve seedlings with similar radicle lengths were transferred to a 14 cm circular tray covered with a piece of 125 mm filter paper.

(iii). *A. affinis*: After the seed coating was washed off with distilled water, Axonopus affinis Chase was placed in a growth chamber at 27 °C with 16 h of illumination and 8 h of dark light for 5 days, during which the water was changed every 2 days. Twenty-one rice seedlings with a radicle of more than 5 mm and similar root lengths were transferred to a 14 cm circular tray covered with a piece of 125 mm filter paper.

(iv). *E. ophiuroides*: Eremochloa ophiuroides was sterilized with 1.25 % NaClO solution for 5 min, and washed with distilled water 5 times. The seeds after surface sterilization were soaked in a 9 cm circular tray with 20 ml distilled water, and placed in a constant temperature growth chamber at 27 °C with 16 h of illumination and 8 h of dark light. After 2 days, 49 seeds were evenly spaced as possible on a 12 cm square tray covered with a piece of filter paper and 7 ml distilled water was dropped into each tray, 2 days in a constant temperature growth chamber at 27 °C with 16 h of illumination and 8 h of dark light. A total of 16 seedlings with a radicle of more than 5 mm and similar radicle lengths were transferred to a 14 cm circular tray covered with a piece of 125 mm filter paper.

(v). *D. repens*: After the seed coating was washed off the surface of Dichondra repens with distilled water, 36 seeds were placed equidistantly in a 12 cm square tray covered with a piece of filter paper. Each tray was filled with 7 ml distilled water, and placed in a dark light incubator at 27 °C for 2 days. Nine rice seedlings with a radicle of more than 5 mm and similar root lengths were transferred to a 14 cm circular tray covered with a piece of 125 mm filter paper.

III. Test plants for treatment of crude extracts of invasive plants (competing compounds)

Each tray was filled with 4 ml distilled water and three crude extracts of invasive plants (or competing compounds 0.02 g/L benzoic acid solution (21) or 0.01 g/L mimosine solution (16,24) and sealed with parafilm. Afterwards, it was placed in a constant-temperature growth chamber at 27 °C with 16 h of illumination and 8 h of dark light. The peroxidase activity was measured after 2 days of treatment; the growth was observed after 3 days of treatment.

IV. Antioxidant enzyme Peroxidase (POD) determination

The method of (Johnson and Cunningham, 1972) was referred to and adjusted, 0.075 g of the plant sample was weighed, and homogenized with an electric grinder, mixed with 1 ml of 50 mM (pH 5.8) phosphate buffer (potassium phosphate buffer), and centrifuged at 4 ℃ and 12000 rpm for 20 min. During the measurement, 30 µl supernatant, 300 µl of 50 mM (pH 5.8) phosphate buffer, 300 µl of 3.6 $\times 10^{-3}$M guaiacol solution and 2 70µl of 39 mM H_2O_2 solution were supplied in turn and mixed thoroughly. The change in the absorbance value at the first minute of wavelength 470 nm was measured with a spectrophotometer. The calculation method of POD activity is: POD activity (mM/min /g) = OD △ 470 ÷26.6 ($mM^{-1}cm^{-1}$) × 0.9 ÷ 0.03 ÷ 1 (min) ÷ fresh weight.

V. Statistical Analysis

Data obtained from various aspects of the experiment were analyzed using the Statistical Analysis System (SAS, 2014) software package. The two-sample t-test of two-tailed allocation is used, $P < 0.05$ denotes a significant difference.

RESULTS

Effects of *M. micrantha*, *L. leucocephala* and *M. pigra* on test grasses

ROOT GROWTH

(i). *M. micrantha*: Comparison with roots growth of these species (*A. affinis, C. dactylon, P. notatum, E. ophiuroides* and *D. repens*) treated with *M. micrantha* in figure 1A, the root growths of *P. notatum* and *E. ophiuroides* seedlings were not inhibited by the extract of *M. micrantha* (Fig 1A), while that of *A. affinis C. dactylon* and *D. repens* seedlings were significantly inhibited. Comparison with shoots growth of these species (*A. affinis, C. dactylon, P. notatum, E. ophiuroides* and *D. repens*) treated with *M. micrantha* in figure 1B, the Axonopus affinis Chase seedlings grown in the extract of *M. micrantha* showed significant increase in shoot height (Fig 1B). As shown in Fig. 1C, the POD activity of *A. affinis, C. dactylon, P. notatum* and *Dichondra repens* seedlings significantly increased with the extract of *M. micrantha* while *E. ophiuroides* seedling has no significantly affected.

Mikania micrantha

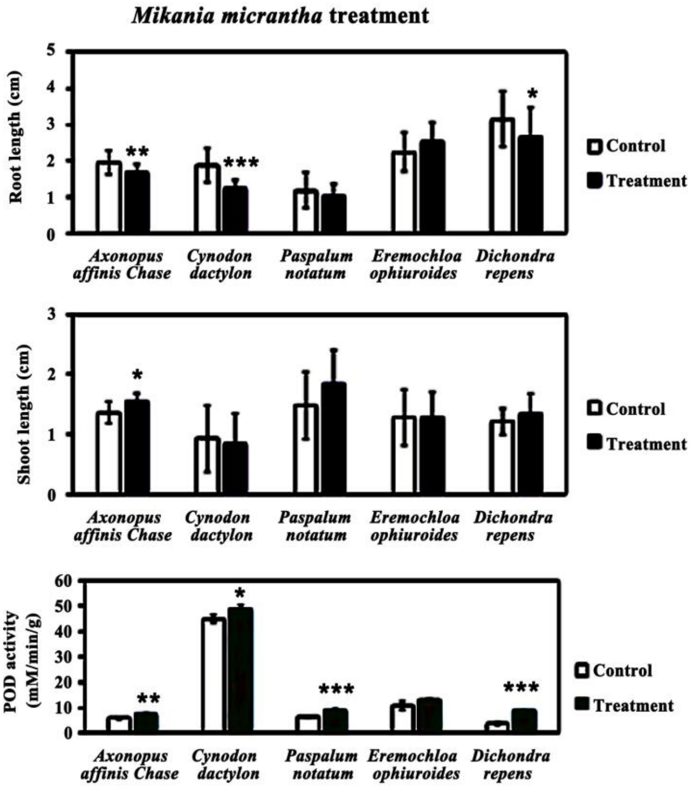

Figure 1. Effects of seed treatment of *M. micrantha* on (A) Root length (B) Seedling height (C) Peroxidase activity of Test Soil and water conservation grasses. Each data in the graph represents the experimental mean and standard error (SD). * represents P<0.05,** P <0.01, *** P <0.001 compared with the control group.

(ii). *L. leucocephala*: Comparison with roots growth of all native species treated with *L. leucocephala* in figure 2A, the root growth of all species seedlings were all inhibited by the extract of *L. leucocephala* (Fig 2A). Comparison with shoots growth in figure 3B the *A. affinis Chase* seedlings grown in the extract of *L. leucocephala* showed significant inhibit in shoot height (Fig 2B). As shown in Fig. 2C, the POD activity of

A. affinis, *C. dactylon*, *P. notatum*, *E. ophiuroides* and *Dichondra repens* seedlings significantly increased with the extract of *L. leucocephala*.

Leucaena leucocephala

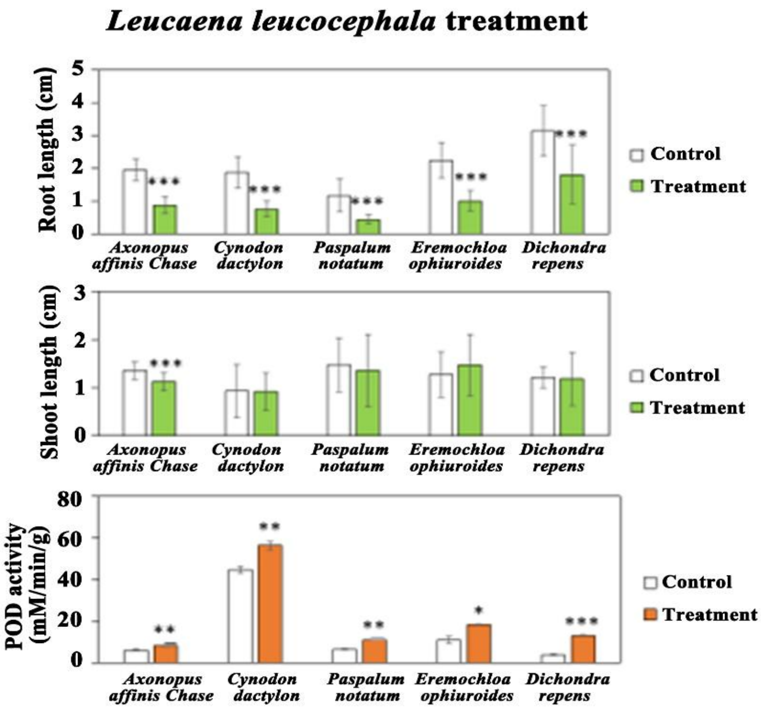

Figure 2. Effects of seed treatment of *L. leucocephala* on (A) Root length (B) Seedling height (C) Peroxidase activity of Test Soil and water conservation grasses. Each data in the graph represents the experimental mean and standard error (SD). * represents $P<0.05$,** $P <0.01$, *** $P <0.001$ compared with the control group.

(iii). *M. pigra*: Comparison with roots growth of all native species treated with *M. pigra* in figure 3A, the root growth of *C. dactylon* and *P. notatum* seedlings was not inhibited by the extract of *M. pigra* (Fig 3A), while that of *A. affinis, C. dactylon* and *D. repens* was significantly inhibited. Comparison with shoots growth in figure 3B, the *A. affinis* seedling grown in the extract of *M. pigra* showed significant increase in shoot height (Fig 3B). As shown in Fig. 3C, the POD activity of *A. affinis*, *C. dactylon*, *P. notatum*, *E. ophiuroides* and *D. repens* seedlings significantly increased with the extract of *M. pigra*.

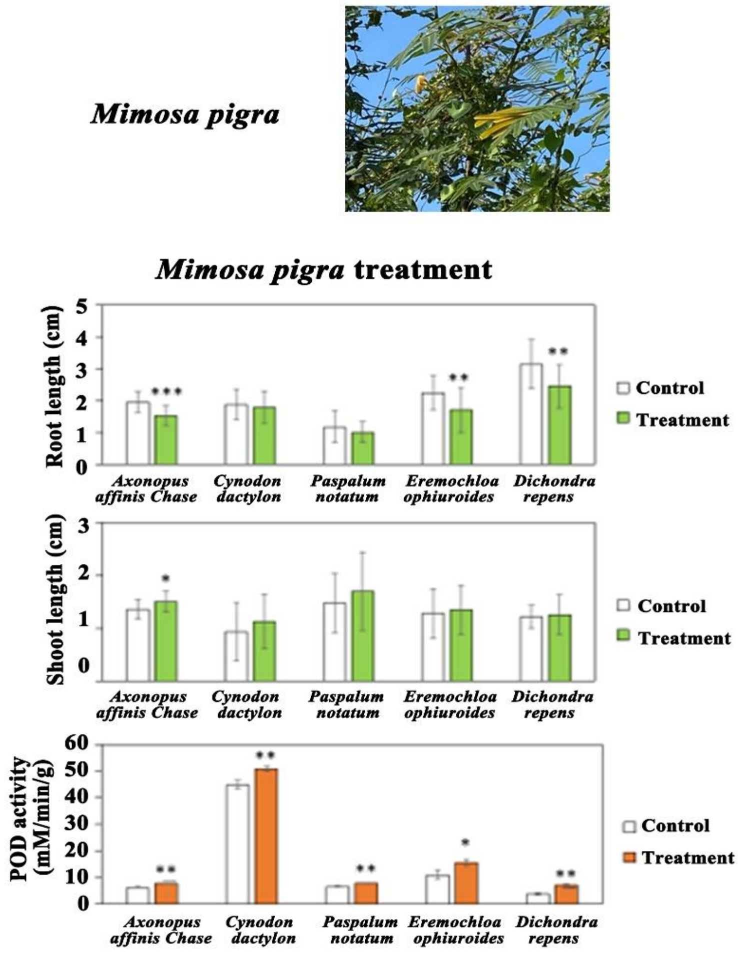

Figure 3. Effects of seed treatment of *M. pigra* on (A) Root length (B) Seedling height (C) Peroxidase activity of Test Soil and water conservation grasses. Each data in the graph represents the experimental mean and standard error (SD). * represents P <0.05,** P <0.01, *** P <0.001 compared with the control group.

(iv). Benzoic Acid: Comparison with roots growth of all native species treated with benzoic acid in figure 4A, benzoic acid not significantly inhibited *C. dactylon*, *P. notatum* and *E. ophiuroides* seedlings root growth (Fig 4A), while that of *A. affinis, E. ophiuroid*es and

D. repens was significantly inhibited. Comparison with shoots growth figure 4B, benzoic acid inhibited in *A. affinis* and increase in *D. repen*s. As shown in Fig. 4C, the POD activity of *C. dactylon, P. notatum, E. ophiuroides* seedlings were no significantly changed in the benzoic acid treatment while *A. affinis* seedlings was significantly increased and *D. repens* was significantly decreased.

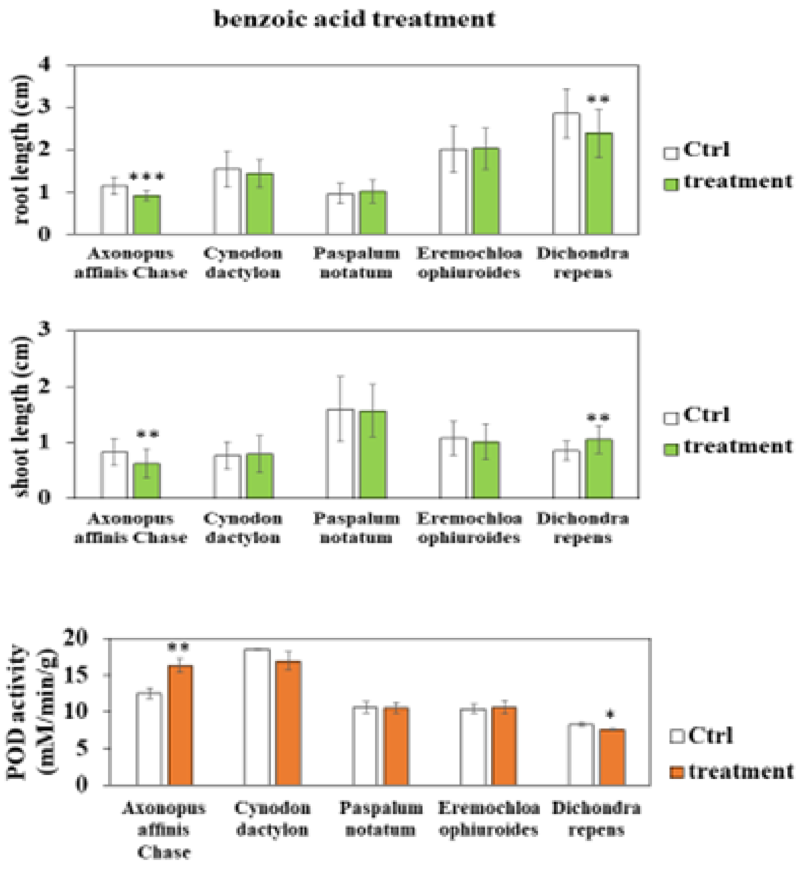

Figure 4. Effects of seed treatment of benzoic acid on (A) Root length (B) Seedling height (C) Peroxidase activity of Test Soil and water conservation grasses. Each data in the graph represents the experimental mean and standard error (SD). * represents P <0.05,** P <0.01, *** P <0.001 compared with the control group.

(v). Mimosine: Comparison with roots growth of all native species treated with mimosine in figure 5A, mimosine significantly inhibited most soil-conserving grasses seedlings root growth in this experiment (Fig 5A). However, *P. notatum* was not inhibited in root growth in the mimosine treatment (Fig 5A). Comparison with shoots growth in figure 5B, mimosine has no significantly affected on all soil-conserving grasses seedlings shoot growth in this experiment. As shown in Fig. 5C, the POD activity of *A. affinis, C. dactylon, E. ophiuroides* and *D. repens* were significantly increased while the POD activity of *P. notatum* was no significantly effect.

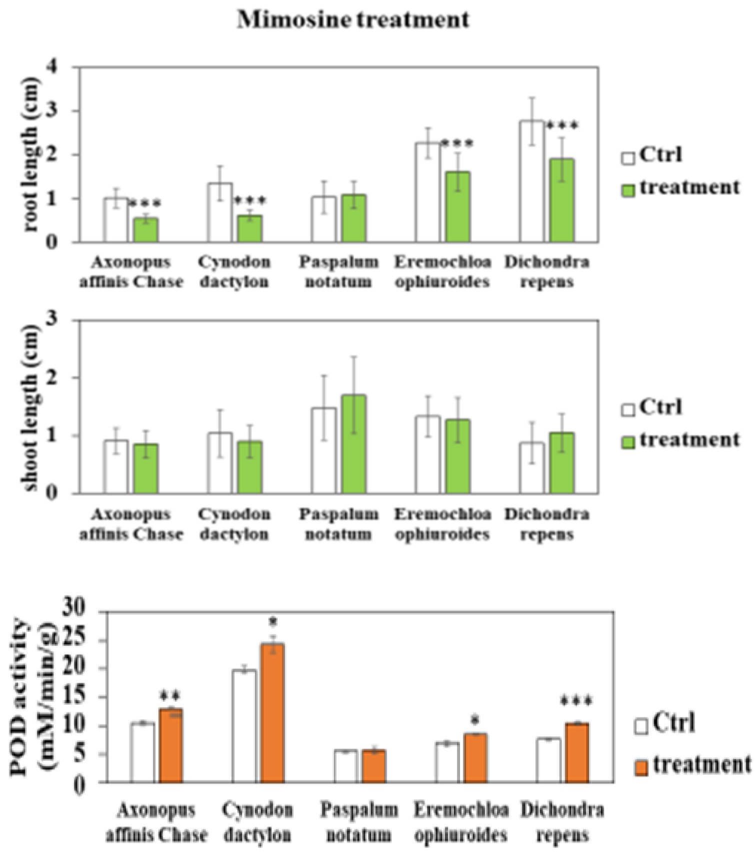

Figure 5. Effects of seed treatment of mimosine on (A) Root length (B) Seedling height (C) Peroxidase activity of Test Soil and water conservation grasses. Each data in the graph represents the experimental mean and standard error (SD). * represents P <0.05,** P <0.01, *** P <0.001 compared with the control group.

DISCUSSION

M. micrantha and benzoic acid effects on physiology and POD activity of test grasses

(i). *M. micrantha* and benzoic acid: Because benzoic acid is the competing compound with the highest content in the aqueous extract of *M. micrantha* (21). Both *M. micrantha* extracts and benzoic acid serve as plant immune responses and hormesis elicited in reaction to the disinfection reponse (18). Thus, they have a big impact on the stress response of *Axonopus affinis* Chase.

In the *M. micrantha* extracts treatment, *C. dactylon* exhibited inhibited root growth and increased POD activity. However, it has no significant effect on the plant growth and POD activity in the benzoic acid treatment. It might show that the others allelochemicals in *M. micrantha* can have allelopathic effect on *C. dactylon* or the concentration of benzoic acid in this experiment is insufficient to have an impact on the stress response of *C. dactylon*. Besides, it might also be related to the higher concentration of phenolic compounds in *C. dactylon* (28). Jenny *et al*. Major and minor phenolics such as glycerol (38.49 %) and phytol (4.89 %) were identified in the *C. dactylon* water extract (25).

P. notatum exhibited an increase in POD activity, without inhibiting root growth in *M. micrantha* extracts treatment. Furthermore, *P. notatum* demonstrated tolerance and hormesis to the allelopathic effect of *M. micrantha* simultaneously.

E. ophiuroides exhibited no effect on root growth and POD activity in both *M. micrantha* extracts and benzoic acid treatments. The result might be attributed to its high free radical scavenging ability as reported by Kang *et al*. (12) or the presence of specific channels or gene expressions in *E. ophiuroides* to reduce cellular damage.

D. repens exhibited inhibition of root growth and an increase in POD activity in *M. micrantha* extracts treatment, and it showed inhibition of root growth but promotion of shoot growth and a decrease in POD activity in benzoic acid treatment. This finding demonstrated that *M. micrantha* extracts has an allelopathic effect on *D. repens*. Moreover, benzoic acid exhibits allelopathic effects and hormesis on the root and shoot growth of *Dichondra repens* respectively.

These findings suggested that M. micrantha induced the physiological characteristics and POD activity of soil-conserving grasses seedlings in both *A. affinis* and *C. dactylon* may be correlated with the response in benzoic acid content.

(ii). *L. leucocephala* and Mimosine: Mimosine, the allelochemical from the leguminous tree *L. leucocephala,* is toxic to most terrestrial animals and plants (5,10,13,31). In the present study, *L. leucocephala* and mimosine significantly inhibit the root growth of *A. affinis, C. dactylon, P. notatum, E. ophiuroides,* and *D. repens*, similar to many previous studies (5,10,13,23). The result in the POD activity indicated that *L. leucocephala* and mimosine can induce stress and stimulate the plant antioxidants system of these plants. Besides, *L. leucocephala* significantly inhibit the shoot length of *A. affinis,* demonstrating that the toxicity of *L. leucocephala* is stronger in *A. affinis*. *P. notatum* exhibited inhibition of root growth and an increase in POD activity in *L. leucocephala* treatment. However, it showed no significant effect on the plant growth and POD activity in mimosine treatment. This finding might be demonstrated that mimosine don't pose a threat to *P. notatum* or the dose of mimosine in this experiment is insufficient to have an impact on the stress response of it.

(iii). *M. pigra* and Mimosine: Mimosine is also the allelochemical in *M. pigra*, and has a toxic effect on the growth of some plants (27). According to the result of *M. pigra* and mimosine on the physiological characteristics and POD activity of *A. affinis, E. ophiuroides,* and *D. repens*. Both *C. dactylon* and *P. notatum* exhibited no effect of root growth and an increase in POD activity in *M. pigra* extracts treatment, indicated that they could resist the allelopathy effect of *M. pigra* extracts with increase in POD activity. However, they exhibited inhibition of root growth and an increase in POD activity under mimosine treatment, suggesting that the concentration of mimosine in the extract of *M. pigra* in this experiment might be lower.

In the study involving treatments with *M. micratha* and *M. pigra* extracts, there was no observable effect on the root growth of *P. notatum*, but peroxidase (POD) activity increased. This suggests that while the growth of *P. notatum* was not hindered, it did trigger a defensive response, possibly due to oxidative stress or other underlying mechanisms. In contrast, treatments with benzoic acid and mimosine showed no impact on root growth and no change in POD activity in *P. notatum*, indicating that these compounds neither influenced its growth nor activated its stress response and suggesting an active stress response, which likely plays a role in its ability to resist or cope with allelopathic stress. Interestingly, *P. notatum* has not been observed invading intact native ecosystems (7). Its resilience under intense grazing, combined with its ability to store resources in rhizomes for up to 2-3 years, gives it a competitive advantage (2). In Taiwan, *P. notatum* thrives in low-altitude areas, where it has difficulty flowering and setting seeds but develops a deep root system, reaching depths of up to 1 meter. These characteristics make it an excellent species for soil and water conservation, ideal for use in orchard ground cover, turf, and grass planting along slopes and ditches. It is frequently employed in soil and water conservation on engineering slopes. Overall, the ability of *P. notatum* to withstand competition and allelopathic stress allows it to dominate in certain environments, demonstrating its value as a resilient and beneficial grass species in specific ecological and agricultural settings.

The study also revealed that allelopathy can alter various physiological processes in plants, such as cell membrane permeability, nutrient absorption, and hormone synthesis (1,32). These effects are often more pronounced in underground plant parts, as roots are more sensitive to environmental changes than aboveground structures (3,15,26,27). When allelopathy occurs, affected plants typically produce large amounts of reactive oxygen species (ROS), which activate the plant's antioxidant defense system. This triggers changes in the activity of several key enzymes, including POD, catalase (CAT), superoxide dismutases (SOD) and malondialdehyde (MDA) (4).

CONCLUSIONS

In conclusion, the findings provide valuable insights into the mechanisms by which *P. notatum* interacts with allelopathic compounds. This knowledge could inform land management strategies, particularly in grazing systems or disturbed areas where allelopathic invasives are common. The ability of *P. notatum* to tolerate oxidative stress without growth inhibition may make it a useful species in environments where allelopathic plants are prevalent. Further research could explore the use of *L. leucocephala* extracts as a bioherbicide, which reduce the use of chemical herbicides and protect human health. And investigate the resilience mechanisms of *P. notatum* in response to allelopathic stress, which could be applied in ecosystem restoration efforts aimed at promoting native species.

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AUTHORS' CONTRIBUTIONS

This work was carried out in collaboration with all authors. All authors finally approved and drafted the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest. All authors agree to publish it.

DECLARATION

We declare that all authors of this Ms. have made substantial contributions. We did not exclude any author who substantially contributed to this Ms. We have followed our ethical norms established by our respective institutions.

ETHICAL STATEMENT

This is to inform you that in this study, we have not been involved in any animal and human studies.

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