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Allelopathic effects of leaf litter leachates of *Ulex europaeus* on other species and its own seed germination

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ABSTRACT

We determined the allelopathic effects of leaf litter leachates of *U. europaeus* from 7-habitats in USA and New Zealand, on its own seed germination and that of *Abutilon theophrasti*. We found that the allelopathy of *U. europaeus* leaves depended on its habitats. The *U. europaeus* leaves leachate at 1 and 10% were auto-toxic to its own and hindered the germination. Thus *U. europaeus* use allelochemicals released from its leaves to compete with other species and to regulate the germination of its own seeds. It may be one of the important strategies for better adaptation to new environment.

Keywords: *Abutilon theophrasti*, adaptation, allelopathic effects, different habitats, Invasive species, *Lactuca sativa*, leaf litter leachates, lettuce, mother trees, seed germination, seedlings growth, *Ulex europaeus*

INTRODUCTION

Ulex europaeus is a serious invasive weed specie, and one of the 100 most noxious species (17). Its origin is from Iberian Peninsula (13,22) and was introduced as hedge row of ranch and ornamental use from Western Europe (18). Owing to its vigorous propagation, it has successfully adapted and propagated in the new environments in temperate, subtropical and tropical regions (4,6,24).

Photograph 1. *Ulex europaeus* in flowering stage in Hawaii Island.

It hinders the growth of native plant species due to its strong allelopathic potential (1,2,19), which also helps in its adaptation to new environments. Allelopathy is defined as harmful or beneficial effects of one plant (including microorganisms) on another plant through release of chemical compounds from the plant tissues as volatile compounds or leachates from the litter (2,3,28). Allelopathy is one of the survival strategies for the plant species in the new environments (7,15,20). Exotic plants often hinder the growth of native species, which do not have counter measures against the allelopathy of exotic plants (1,5)

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Cytisus scoparius, taxonomically close specie to *U. europaeus*, exudes allelochemicals from the roots against other species to expand its niche (10). Although *U. europaeus* is noxious weed in many regions, its allelopathy has not been well studied. The previous studies have reported that it releases allelochemicals from several parts (25), but the allelopathic effects are not well documented. In this study, we focused on the allelopathic effects of leaf litter leachates of *U. europaeus.* Allelochemicals are also released from its leaf litter (25,28), which directly influences other plants through soil (29). This study aimed to assess (i). The allelopathic effects of *U. europaeus* leaf litter compared to those of weed *Abutilon theophrasti* (11), (ii). Allelopathic potential of its leaf litters collected from different habitats in USA and New Zealand and (iii). Effects of its litter leachate on its own seed germination. Besides, we also conducted Head Space-Gas Chromatography/Mass Spectrometry (H/S-GC/MS) analysis on the hydrosol of fresh leaves of *U. europaeus* to identify the chemical components in its leaf oils.

MATERIALS AND METHODS

The leaves and seeds of *U. europaeus* used in this study were collected from July 2016 to March 2018 from 7- places [5 in USA (Hawaii Island, Maui Island, San Mateo, Bandon and Coos Bay) and 2- in New Zealand (North and South Island)] (Table 1). At each place, leaves and seeds were collected from 2-5 sites. First, the allelopathic potential of *U. europaeus* leaves from Hawaii Island was studied, to see if there is allelopathy in its leaf litter leachates. The habitat of sampling sites of New Zealand North Island 2, New Zealand South Island 1 and Bandon 2 were the natural forest with many short grasses, and that of Hawaii Island, Maui Island, San Mateo, New Zealand South Island 2 and Coos Bay was a ranch, fallow land and dune with almost no other species.

The sampling places were chosen based on the most successful adaptation and propagation sites of *U. europaeus.* The 5- cm samples from the tips of the twigs were collected and air dried. Seeds were taken out from the pods and the damaged seeds were discarded. Only healthy seeds were used in studies.

Allelopathic potential of *U. europaeus*

To test the allelopathic effects of *U. europaeus*, we used sandwich method (8). The air-dried 50 mg leaves were sandwiched between the 5 ml of 0.5 % agar layers (Wako Pure Chemical Industries, Ltd.) made with purified water in plastic cups (3 cm diameter with lid, sterilized with 95% of ethanol). Five seeds of lettuce (*Lactuca sativa*, Asteraceae) variety ‘Great Lakes’ seeds (cv. Great Lakes) per cup were sown on top of agar. The leaf leachates gradually dissolve in the agar and start to affect the radicle and hypocotyl growth of the lettuce seeds. In control, 5- lettuce seeds received only 0.5% agar (8). These cups were incubated (25 ℃ for 72 h, in dark). Afterwards, the length of hypocotyl and radicle of the lettuce seedlings were measured with scale.

(a) North Island 2 (New Zealand): small *U. europaeus* bushes mixed in some other species including *Cytisus scoparius* (also listed in 100 noxious species by IUCN), *Leptospermum scoparium* (manuka in common, indigenous) and *Kunzea ericoides* (kanuka in common, endemic to New Zealand).

(b) Bandon 1 (USA): some short grass species and *Hedela helix* L. are mixed with *U. europaeus*.

(c) Coos Bay (USA): one isolated *U. europaeus* bush in a huge dune.

Photograph 2. Habitats of the 3-Sampling sites of *U. europaeus* in USA and New Zealand.

Table 1. Details of the locations of *Ulex europaeus* leaves and seeds sampled and their sampling time.

Site No.	GPS coordinate	Annual mean temp (°C)	Annual rainfall (mm)	Elevation (msl)	Number of Mother tree	Replicates	Habitat	Sampling Time
USA: Hawaii Island								
1	19.69°N-155.45 °E	10.8	1193	1844	1	15	Ranch	Aug. 2017
2	19.73°N-155.39°W	10.3	1872.4	1952	1	15	Ranch	Aug. 2017
3	19.73°N-155.39°W	10.3	1872.4	2011	1	15	Ranch	Aug. 2017
4	19.73°N-155.38°W	10.8	1996.6	2010	1	15	Ranch	Aug. 2017
5	19.77°N-155.36°W	10.1	1819.1	2072	1	15	Ranch	Aug. 2017
	USA: Maui Island							
1	20.76°N-156.27°W	12.4	967.5	1823	1	25	Ranch	Mar. 2017
2	20.77°N-156.26°W	11.9	1159.4	1767	1	25	Ranch	Mar. 2017
3	20.77°N-156.26°W	11.9	1159.4	1763	1	25	Ranch	Mar. 2017
4	20.77°N-156.26°W	11.9	1159.4	1763	1	25	Ranch	Mar. 2017
5	20.78°N-156.25°W	11.9	1159	1773	1	25	Ranch	Mar. 2017
6	20.79°N-156.25°W	12.7	1880.6	1656	1	25	Ranch	Mar. 2017
	USA: San Mateo							
1	37.15°N-122.34°W	14.0	524	31	1	25	Fallow	Jul. 2016
2	37.15°N-122.34°W	14.0	524	33	1	25	Fallow	Jul. 2016
	USA: Bandon							
1	43.12°N-124.43°W	16.1	1492	33	1	25	Cliff	Mar. 2018
2	43.11°N-124.43°W	16.1	1492	2	1	25	Beach	Mar. 2018
	USA: Coos Bay							
1	43.45°N-124.28°W	14.2	1900.7	-1	2	25	Dune	Mar. 2018
	New Zealand: North Island							
1	37.86°S-176.39°E	14.9	1702.2	97	2	25	Grass land	Nov. 2017
2	38.9°S-175.76°E	12.1	1754.2	538	2	25	Forest	Nov. 2017
	New Zealand: South Island							
1	43.8°S-173E	11.7	557.4	623	2	25	Forest	Nov. 2017
2	43.5°S-172.52E	11.1	740.2	38	2	25	Hedge row	Nov. 2017

The number of replicated tests by the sandwich method are also shown. The climate data for Hawaii and Maui was taken from Online rainfall atlas of Hawaii (9), for Bandon and Coos Bay from Western Regional Climate Center (31), and for New Zealand from National Institute of Water and Atmospheric Research (26). The air temperature difference caused by the gap of altitude between weather station and site was adjusted by the rule of ICAO (16).

To determine the allelopathic potential, leaves of mother trees [6 from Hawaii, 2 each from Maui, San Mateo, Bandon and Coos Bay (USA), 4 from North Island and 4 from South Island (New Zealand) (Table 1)] were used. The habitats of 2-mother trees from North and South Island (New Zealand) and Bandon (USA) were different (Table 1), hence, distinguished by numbering 1 and 2. Data size was 75 lettuce seeds for Hawaii, 150 for Maui, 50 for San Mateo, and 25 each for Bandon 1 and 2, 50 for Coos Bay, 50 each for North Island 1 and 2, and South Island 1 and 2 respectively. After 72 h incubation, hypocotyls and radicles lengths of lettuce seedlings were measured and compared to control. Data size difference in the sampling sites was according to the number of mother trees except Hawaii. First the allelopathic potential of *U. europaeus* leaves from Hawaii Island was studied from August 7 and August 10, 2017 and results were compared with *Abutilon theophrasti* weed (11) because it is highly allelopathic. These studies were done in Komohana Research and Extension Center, University of Hawaii at Manoa in Hilo (Hawaii, USA). While, the samples from Maui Island and San Mateo were studied from April 3 to April 6, 2018 and the samples from Bandon, Coos Bay and New Zealand were studied from October 29 to November 1, 2017 in Kyoto University, Kyoto, Japan.

Allelopathy test on *U. europaeus* seeds

U. europaeus seeds have hard seed coat, thus, not able to germinate like lettuce seeds, hence, agar was not used to test their seed germination. Hence, we followed the method of Sato and Takahashi (29) to prepare the leaf leachates for bioassays (29). The air-dried *U. europaeus* leaves (3.3 g) were put in 100 mL purified water and boiled for one minute. The leaf litter leachate was identified as 100 %. To assess the magnitude of allelopathy, the 100 % leachates was diluted with purified water, to prepare 3-concentrations of 10, 1.0, 0.1 % for bioassays. The sterilized (with 95% ethanol) petri dishes, plastic beads (growth medium) and filter papers were used. The leaf litter leachates were filled to the top level of beads and the filter papers were put on top of the beads. The quantity of leachates was adjusted to prevent the submergence of seeds which affects the seeds germination of *U. europaeus*. The *U. europaeus* seeds were sown equidistant and incubated for 7- days (20 ^{0}C in complete darkness) (30). All *U. europaeus* seeds used for the bioassay were physically scarified with sterilized knife at 18 h before the hot water treatment. The scarification as to make an opening for entry of water in impermeable seeds coat. To increase imbibition, the seeds were pre-soaked in hot water at 90 ^{0}C for 24 h in total before the experiments. To see the allelopathic effects of leaves litter leachates on the germination of seeds from the same mother tree, samples of North Island 2 and South Island 2 (Table 1) were used. We studied the effects of leaf litter leachates on the germination of seeds from different mother trees, leaves from Bandon 2 (Table 1) and seeds from two mother trees on Hawaii Island (same coordinates: N19.69, W155.45 from different altitudes: 1,793 m and 1,862 m (not included in Table 1), collected in March 2018) were used. The germination tests were done on 4 - combination of leaves and seeds (two types of seed germination tests on the leaves of same mother trees and two types of tests on the leaves of other mother trees). All germination tests were done with 3 concentrations (10%, 1%, 0.1%) of leachates and control. Thirty seeds for each concentration and control were used; 120 seeds for each combination of the experiment were used. The experiments were done from June 15 to 22, 2018 in Kyoto University, Kyoto, Japan.

H/S-GC/MS analysis of the leaf samples

Fresh leaves sampled in the southeast flank of Mauna Kea on Hawaii Island, USA in July 2018 (GPS coordinates: 19.69N and 155.45W, altitude:1945m) were distilled by purified water to take hydrosol soon after sampling. The weight of the leaf samples and distillation time was not recorded because the objective of the experiment was to take the data of qualitative analysis. Hydrosol in the vial was kept at the temperature of 90℃ for 20 minutes to make the headspace and distilled water equivalent by TurboMatrix HS40 (PerkinElmer Japan Co., Ltd. Kanagawa, Japan). Analysis was carried out on QP2010 plus (Shimadzu Co., Kyoto Japan) in a column of Stabilwax. Helium was used as the carrier gas (flow rate 1 ml/min). The oven temperature program range was 40℃ to 240℃ with an increase in the rate of 10℃/min. The identity of the constituents of the oil was conducted by computer matching with NIST (National Institute of Standards and Technology) library.

Statistical analyses

To compare the allelopathic effects of leaves from Hawaii Island on hypocotyl and radicle lengths of the lettuce seeds with controls by sandwich method, those of the leaves of *U. europaeus* from 7- sites with *Abutilon theophrasti*, and to assess the differences in magnitude of allelopathy, t-test was used.

The habitat of each mother tree in North Island, South Island (New Zealand) and Bandon (USA) differed, hence, they were divided into North Island 1 and 2, South Island 1 and 2, and Bandon 1 and 2. The effects of litter leachates from the leaves of 10 types of habitats in sandwich method were studied on the hypocotyl and radicle lengths of lettuce seeds using the Linear Model analysis and Multi Comparison analysis.

To assess the allelopathic effects of the leaf litter leachates on the seed germination of *U. europaeus* itself, the results were analyzed using the Generalized Linear Model analysis with Binomial Distribution analysis (used two indications in the data sets of the seeds: 1 for germinated and 0 for not germinated). The statistical analyses of data were done by software of R, version 3.5.1 (27) and the package, Multcomp (14), and StatPlus (AnalystSoft Inc).

RESULTS AND DISCUSSION

Allelopathical potential of *U. europaeus*

The leaf litter leachates of 5-different mother trees from Hawaii Island significantly reduced the hypocotyls and radicles length of lettuce seeds than controls (Fig. 1).

The results showed the strong allelopathic effects of *U. europaeus* on the seed germination of lettuce. Though many previous studies on invasive weeds species have reported their allelopathic effects (7), studies on the allelopathic effects of *U. europaeus* leaf litter leachates are very rare.

In addition, the results were compared to those of the previous study of the allelopathic effect of wild type of *Abutilon theophrasti* conducted by the same method (11). *A. theophrasti* weed originally from India decreased corn yield and the substances exuded from the leaves were also harmful to livestock. It is one of the serious invasive weeds in Japan with very strong allelopathic effects (11). The leaf litter leachates of *U. europaeus* and *A. theophrasti* had similar effects on the lettuce seedlings hypocotyl elongation ($P = 0.09$) (Fig. 2). However, the leaf leachates of *U. europaeus* were more inhibitory to radicle length of lettuce seedlings than *A. theophrasti* ($P < 0.001$) (Fig. 2).

The allelopathic effects of leaf litter leachates of *U. europaeus* were very inhibitory to seedlings growth of lettuce because the effect of leaf litter leachates strongly appears to the radicle growth of seedlings (12). It suggested that the allelopathic effects of *U. europaeus* leaves were strong among the weed species.

In addition, the lengths of hypocotyls and radicles of the lettuce seeds tested on the leaves sampled in 10 different kinds of habitats were compared (Fig. 3).

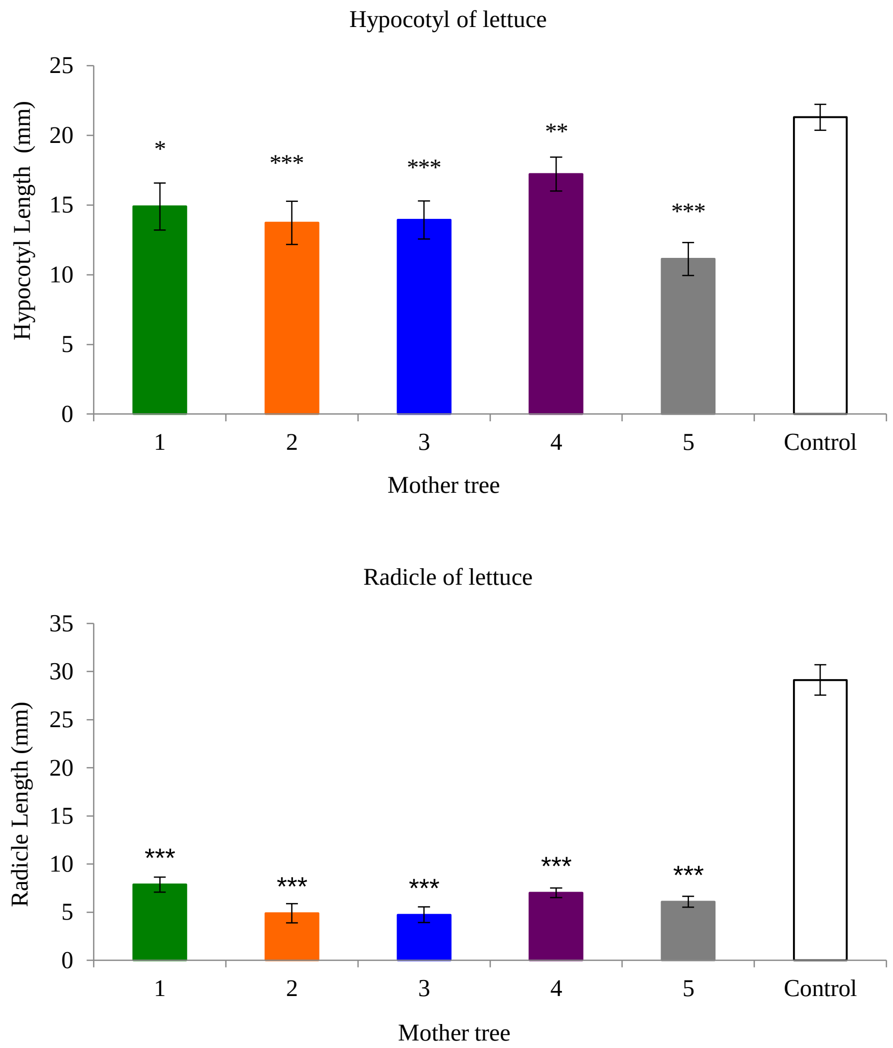

Figure 1. Effects of leaf litter leachates of five mother trees from Hawaii Island on the length of hypocotyls and radicles of lettuce seedlings.
The numbers (1-5) on X-axis indicate 5- different mother trees. The bars represent standard error, and the asterisks indicate the significant differences at the 5% level with respect to the control ('*' <0.05, '**' <0.01, '***'<0.001).

The magnitude of the allelopathic effects of the leaves was compared by Multiple Comparison Analysis, and they were divided to 3-groups (Fig. 3). The habitat of Group-I was mostly the natural forest with many species of plants, the habitat of Group-II was with some sorts of short grasses, and that of Group-III was a ranch, fallow land and dune with almost no other species (Table 1). For example, the sampling site of North Island 2 in the first group was in the natural forest with many mixed species of plants including some native species [Photograph 2 (a)], the sampling site of Bandon 1 in the second group was on the cliff overlooking the beach with some sorts of short grass species and invasive *Hedera helix* L. [Photograph 2 (b)], and that of Coos Bay in the last group was dune, where the large bush of *U. europaeus* (5 m diameter) had comparatively a long distance from a few other species [Photograph 2 (c)].

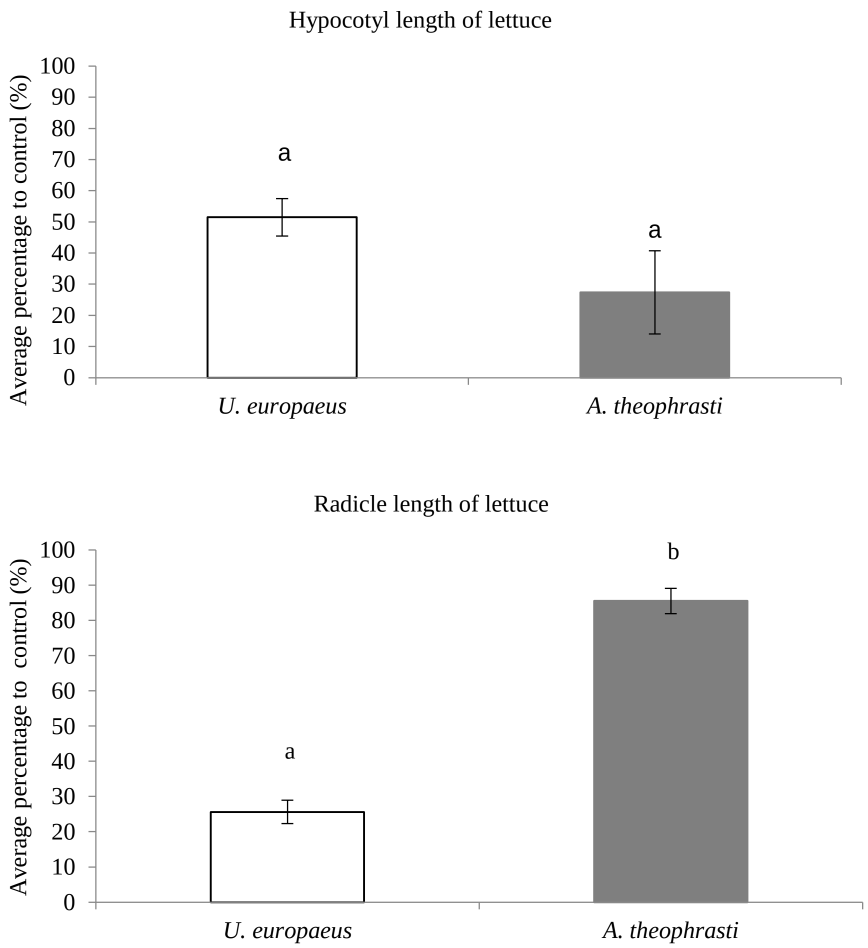

Figure 2. Effects of leaf litter leachates of *Ulex europaeus* collected from 7 different locations on the inhibition (%) over control of hypocotyl and radicle length of the lettuce seedlings and *Abutilon theophrasti* (the data of *Abutilon theophrasti* was from the previous study by Hattori *et al.* 2003). The bars represent standard error, and the different letters above the bars indicate statistical difference at 5% level.

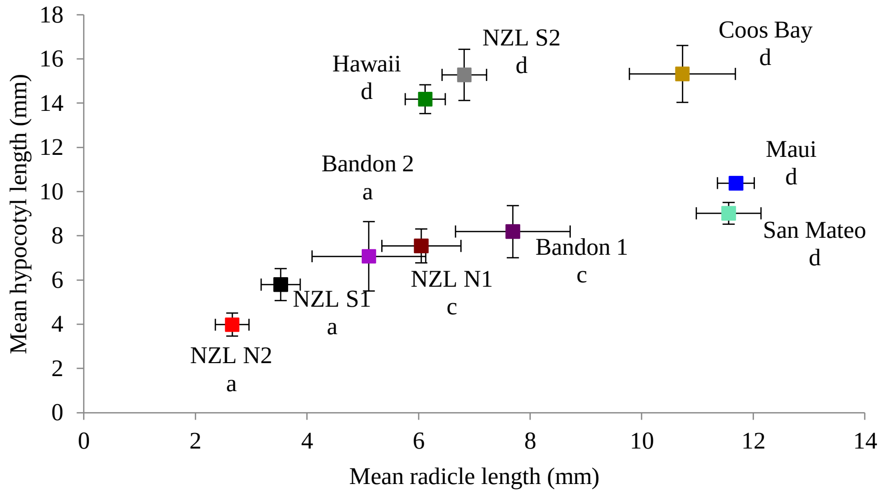

Figure 3. The effects of leaf litter leachates of *U. europaeus* on the elongation of hypocotyls and radicles of lettuce seedlings. The bars represent standard error and the different letters under the site names indicate statistical difference at 5% level by Tukey's Test. a : Group I, c : Group II and d : Group III.

Table 2. Effects of leaf litter leachates to the seed germination of *U. europaeus* (a) of the same mother tree and (b) other mother trees.

(a) Effects of leaf litter leachates on the seed germination of *U. europaeus* than control

Leaf litter leachates Conc	Estimated Standard. Error		Z value	P value	
(Intercept)	2.51	0.6	4.19	<0.001	***
10.0%	-1.54	0.7	-2.21	<0.05	*
1.0%	-1.51	0.7	-2.17	<0.05	*
0.1%	0.43	0.94	0.46	0.65	

(b). Effects of leaf litter leachates of mother trees on seed germination of *U. europaeus* than control

Leaf litter leachates Conc	Estimated Standard. Error		Z value	P value	
(Intercept)	0.16	0.28	0.565	< 0.001	***
10.0%	-1.98	0.5	-3.978	< 0.001	***
1.0%	-0.82	0.41	-2.0	< 0.05	*
0.1%	-0.08	0.4	-0.2	0.84	

The asterisks indicate the significant differences at the 5 % level ('*' <0.05, '**' <0.01, '***'<0.001).

These results inferred that the allelopathic effects of the leaf litters of *U. europaeus* depended on the sampling habitats, especially the number of the plant species mixed in each habitat and the interactions. Assessing the allelopathic effects according to the invaded sites by this method may help in identifying the appropriate species, which can be planted with *U. europaeus.* The detailed vegetation data of each site was not available, but comparing the vegetation and the magnitude of their allelopathy may help to control *U. europaeus* in future.

Allelopathy test using *U. europaeus* seeds

The leaf leachates from other mother trees at 10 % and 1 % concentrations significantly inhibited the seed germination of *U. europaeus* than control (Table 2). Besides the allelopathic effects of leaf leachates at 10 % and 1 % concentrations of the mother trees were also inhibitory to its own seed germination.

The leaf litter leachates of *U. europaeus* hindered the germination of its own seeds and it was stronger to the seeds from other mother trees. The seeds of *U. europaeus* are usually popped out from the pods on a sunny, dry day, and the seeds often jumped about 5 m away from the mother trees (23). The seeds are suggested to jump as far as away from mother plant to survive from the inhibitory allelopathic effects of mature mother trees. The mature mother trees of *U. europaeus* produce seeds for > 30 years (21), their survival also depends on competition with *U. europaeus* itself, as its leaves release the inhibitory allelochemicals. It is important strategies of *U. europaeus'*s adaptation to new environments.

Table 3. Peak table TIC of the hydrosol distilled from the fresh leave of *U. europaeus.*

Peak	Compound	Common name	Retention time (min)	Area	Area (%)	Height	Height (%)	A/H
1	Eucalyptol	1,8-Cineole	15.625	92955	3.09	32655	3.75	2.85
2	2-Hexanal	Leaf aldehyde	15.685	83080	2.76	28657	3.29	2.9
3	3-Hexen-1-ol, acetate, (Z)-	cis-3-Hexenyl Acetate	16.79	158813	5.28	63897	7.34	2.49
4	3-Hexen-1-ol		17.567	216076	7.18	65836	7.56	3.28
5	1-Octen-3-ol	Morillol	18.183	2133939	70.91	621890	71.43	3.43
6	2-Hexene, 3,5,5-trimethyl-		18.642	226709	7.53	41191	4.73	5.5
7	2-Cyclohexen-1-on e, 2-methyl-5-(1-methylethenyl) -, (S)-	D-Carvone	22.307	97655	3.25	16458	1.89	5.93
Total				3009227	100	870584	100	

H/S-GC/MS analysis of the fresh leaf samples of *U. europaeus*

The chemical composition of the hydrosol by H/S-GC/MS is summarized in Table 3. Morillol was found the most, and two other interesting components, 1,8 cineol and aldehyde from the previous studies about allelochemicals were found. One of them, 1,8 cineol is known to hinder the seed germination (7), and the other one, aldehyde, is known as an allelochemical to hinder the growth of seedlings (7). The roles of these compounds found in the hydrosol of *U. europaeus* fresh leaves should be investigated in the future.

CONCLUSIONS

To conclude, the results of this study all suggested the advantageous usage of leaf allelopathy of *U. europaeus* for itself. The exuded allelochemicals from the leaf litter leachates of *U. europaeus* strongly inhibited the seed germination to expand its niche. The mature mother trees of *U. europaeus* that have produced healthy seeds were protected by other individuals of *U. europaeus* itself, and even with the individuals from the seeds of the same mother tree by its leaves allelopathic effects. These results suggested that the *U. europaeus* for invasion used the allelopathic effects of its leaf litter. *U. europaeus* released allelochemicals from its roots in addition to leaves, hence, the relations between the root allelopathy and other organisms (viz., rhizospheric bacteria) should be investigated in future to understand the mechanism of allelopathy. Furthermore, in future studies, the allelopathic effects of chemical components found in oils of *U. europaeus* leaves, 1, 8-cineole and another compound (aldehyde), should be studied on its own and other species seeds germination and seedling growth. This will greatly help to control the *U. europaeus* in the future.

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