



# Soil microbes alleviate allelopathy of invasive plants

Yang-Ping Li · Yu-Long Feng · Ya-Jun Chen ·  
Yao-Hua Tian

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**Abstract** Soil microbes are one of the most important determinants of allelopathic effects in the field. However, most studies testing the role of allelopathy in biological invasions did not consider the roles of soil microbes. Here we tested the hypothesis that soil microbes which can degrade allelochemicals may accumulate in soils over time by adaptation and therefore increase the degradation of allelochemicals and alleviate the allelopathic effects in biological invasions. As expected, soil microbes significantly decreased the allelopathic effects of leaf leachates of eight in the nine invasive plant species studied. In addition, *Ageratina adenophora* showed lower allelopathic effects in soil with long or intermediately invasion history than those in soil with short invasion history. The two main allelochemicals of the invader were degraded more rapidly with increasing invasion history in the soil. Correspondingly,

biomass and activity of the soil microbes were higher in the soils with long invasion history than in that with short invasion history. Our results indicate that soil microbes may gradually adapt to the allelochemicals of *Ageratina* and alleviate its allelopathic effects and thus support the above hypothesis. It is necessary to consider the effects of soil microbes when testing the roles of allelopathy or the novel weapons hypothesis in biological invasions.

**Keywords** Adaptation · Allelopathy · Degradation of allelochemicals · Soil microbes · Invasive plants

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Y.-P. Li (✉) · Y.-J. Chen  
Key Laboratory of Tropical Forest Ecology, Xishuangbanna  
Tropical Botanical Garden, Chinese Academy of Sciences,  
Kunming 650032, China  
e-mail: liyp@xtbg.org.cn

Y.-P. Li  
University of Chinese Academy of Sciences, Beijing 100039,  
China

Y.-L. Feng (✉)  
College of Bioscience and Biotechnology, Shenyang  
Agricultural University, Shenyang 110866, China  
e-mail: fyl@xtbg.ac.cn

Y.-H. Tian  
Yunnan Tropical Crops Science Research Institute,  
Jinghong 666100, China

## 1 Introduction

Allelopathy has been widely accepted as a mechanism underlying invasion success of introduced plants [1–5]. Introduced plants may succeed due to possessing unique allelochemicals, to which naïve natives have not adapted (the novel weapons hypothesis) [1]. However, the hypothesis was only tested using a few invasive exotic plants, and some of the studies were carried out in laboratories, not considering potential influences of other biotic and abiotic factors [6–8]. To show allelopathic effects, allelochemicals must be released into soils by leaves leaching, root exudation, or degradation of plant residues, accumulate, and persist at phytotoxic levels in the field and come in contact with target plants [9]. Many factors influence accumulation of allelochemicals in soils, such as soil texture, chemical character, and microbial community [7, 10–12]. Without considering the effects of these factors, we could not accurately evaluate the importance of allelopathy in invasion success of introduced plants, and evidence for the role of allelopathy in biological invasions is controversial [13, 14]. Thus, understanding how biotic and abiotic factors affect

allelopathic effect between invasive and native plants may yield important insight into the role of allelopathy in biological invasions.

Of these factors, soil microbes are an important determinant factor of allelopathic effect [15–17]. It has been reported that allelopathic activity of carvacrol is stronger in sterilized soils than that in unsterilized soils [18]. Blum [19] found that soil microbes are able to degrade phenolic acid and then decrease its phytotoxicity and duration. Chen et al. [20] isolated a fungus, *Trichoderma harzianum* SQR-T037, which rapidly degrades allelochemicals released into rhizospheres by cucumber.

Short generation times and high genomic plasticity allow microbes to evolve new genes at a relatively high rate [21]. Soil microbial communities are able to adapt to the novel chemicals applied into environments by human via mutation, horizontal gene transfer, and DNA rearrangement [22, 23]. Aelion et al. [24] found that soil microbes acquire the ability to degrade p-nitrophenol after exposing to this compound for a time, and the rate of mineralization of p-nitrophenol and the amount of specific degrader increase with time. It has been widely reported that soil microbes evolve the ability of rapid degradation of many xenobiotic compounds including pesticides, fungicides, and herbicides, which were synthesized by human and did not exist previously in soils. For example, biodegradations of herbicide 2,4-dichlorophenoxy and nematicide fenamiphos are faster in soils previously experienced these chemicals than in naïve soils [21, 25, 26]. In this study, we hypothesized that naïve soil microbes may evolve the ability to degrade allelochemicals of invasive plants (natural products) more rapidly compared with the human-synthesized xenobiotic compounds and that the ability may increase with increasing invasion time. Little effort has been made to study the effects of soil microbes on accumulation of allelochemicals of invasive plants in soils, and the results in allelopathy of invasive plants are inconsistent [15, 16]. For example, Perry et al. [27] found that catechin was potential allelochemicals of *Centaurea maculosa* and maintain high concentration in field soil near *C. maculosa*. Perry et al. [28] collected 402 soil samples from 11 sites with invasive *C. maculosa* in two growing seasons and detected low level of catechin ( $0.65 \pm 0.45 \text{ mg g}^{-1}$ ) in only 20 samples collected from one site at one sampling time [28]. Similarly, Inderjit et al. [29] found that catechin is dynamic in natural soils, but inhibit *Koeleria macrantha* at low concentration in some soils. These results suggest that allelopathy is context dependent [29].

Here we studied the generality of allelopathic effect using nine invasive plant species, the effects of invasion history using one invader, and the ability of soil microbes to degrade allelochemicals of the invader. First, we studied the effects of soil microbes (with or without) on allelopathy

of nine invasive species. We also measured the effects of the amount of soil microbes on allelopathy using five of the nine invaders. Then we studied how invasion history influences the effects of soils on allelopathy and degradation of allelochemicals using a subtropical invader. We also estimated biomass and activity of the microbes that are able to degrade the allelochemicals by measuring soil substrate-induced respiration rate [30]. We predicted that soil microbes may decrease allelopathic effects for all invasive plants studied here (a general phenomenon), and the effects of soil microbes may increase with increasing invasion history by accumulating allelochemical-degrading soil microbes.

## 2 Materials and methods

### 2.1 Plant materials

To test the effects of soil microbes on allelopathic effects of leaf leachates, nine noxious invasive plant species were used in this experiment. They are *Ageratina adenophora* (Sprengel) R. M. King and H. Robinson (a perennial herb or subshrub native to Mexico and Central America; Asteraceae), *Ageratum conyzoides* L. (an annual herb native to Tropical America, especially Brazil; Asteraceae), *Bidens pilosa* L. (an annual herb native to Central and Tropical America; Asteraceae), *Chromolaena odorata* (L.) R. M. King and H. Robinson (a perennial herb or subshrub native to Americas; Asteraceae), *Gynura crepidioides* Benth. (an annual herb native to Tropical Africa; Asteraceae), *Lantana camara* L. (a perennial subshrub native to Mexico and Central America; Verbenaceae), *Mikania micrantha* (L.) Kunth. (a perennial creeper native to the subtropical zones of North, Central, and South America; Asteraceae), *Tithonia diversifolia* (Hemsl.) Gray (a perennial herb native to eastern Mexico and Central America; Asteraceae), and *Wedelia trilobata* (L.) Hitchc (a spreading, mat-forming perennial herb native to Mexico, Central America; Asteraceae). These invaders have allelopathic potential (Table S1).

### 2.2 Leaf leachate preparations

In July 2012, fully expanded leaves were collected from more than ten individuals of a natural population for each of the nine invasive species in Xishuangbanna ( $21^{\circ}41'N$ ,  $101^{\circ}25'E$ , 570 m asl), Yunnan Province, southwest China. Fresh leaves of each species were immersed in distilled water (2.5 % based on leaf dry mass) for 36 h. The 2.5 % aqueous leaf leachates were concentrated to 5 % for *A. conyzoides*, *B. pilosa*, *C. odorata*, *G. crepidioides*, *M. micrantha*, and *T. diversifolia* and to 10 % using rotary

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