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Allelochemical mediated invasion of exotic plants in China

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ABSTRACT

Invasion of exotic species is a global ecological problem and has tremendous impact on economy, environment and human health. The success of invasion for exotic plants depends on many mechanisms and in recent years the novel weapons hypothesis has been argued as an important mechanism to elucidate the invasion process. This review summarizes a large body of research including the observations of potential allelopathic phenomenon, isolation and identification of allelochemicals and the role of allelopathy in invasion of common exotic invasive plants in China such as *Eupatorium adenophorum, Eucalyptus spp., Spartina anglica, Chromolaena odoratum, Eichhornia crassipes, Solidago canadensis, Alternanthera philoxeroides, Ambrosia artemisiifolia, Ambrosia trifida, Lantana camara, Wedelia trilobata, Bidens pliosa, Ageratum conyzoides and Mikania micrantha*. We suggest that allelopathy plays a vital role in successful invasion of alien species in new areas. The allelochemicals of invasive alien species also serve as defence chemical weapons against native plant pathogen and herbivorous insects.

Key words: Allelochemical, allelopathy, chemical defence, invasive plants

1. INTRODUCTION

Many invasive species are introduced exotic species that thrive in areas beyond their natural range of dispersal. Invasion of exotic species has become a global problem causing a tremendous impact on economy, ecosystems and human health. It is one of the

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main reasons to cause current biodiversity loss (41,111). Invasive plants threaten the integrity of natural ecosystems worldwide by displacing native plant communities and establishing monocultures in new habitats. Most invasive plants are characteristically widely-adaptable, aggressive and have a high reproductive capacity. Their vigour combined with a lack of natural enemies often leads to their outbreak in new habitats. The successful invasion of exotic plants has been explained by many mechanisms (75).

A growing number of invasive exotic plant species are causing significant economic and environmental impacts in China (133). Annual economic losses caused by few important invasive plant species was over US$ 7.4 billions (69). These species include *Eupatorium adenophorum*, *Eucalyptus spp.*, *Spartina anglica*, *Chromolaena odoratum*, *Eichhornia crassipes*, *Solidago canadensis*, *Alternanthera philoxeroides*, *Ambrosia artemisiifolia,* *Ambrosia trifida*, *Lantana camara*, *Wedelia trilobata*, *Bidens pliosa*, *Ageratum conyzoides* and *Mikania micrantha.*

To be a successful invader in a new region, a plant species must overcome an array of obstacles and encounter a series of new biotic interactions with new natural enemies, mutualists and competitors (48,83,95). How the introduced plant populations survive, widely spread and exclude native species in the new environment has puzzled ecologists for many years. Many researches expounded this question from diverse aspects as under:

(I). The enemy release hypothesis, which states that invasive populations are less exposed to herbivores, pathogens and other natural enemies in native region, resulting in attaining wider distribution and greater abundances (18,19,74).

(II). The mutualist facilitation hypothesis, which suggests that the replacement of their native mutualists with new mutualists in their introduced ranges plays a vital role in invaders establishment and spread (95). Mutualisms including pollinators, seed dispersal animals, and mycorrhizal symbioses often facilitate invasions. Some alien plants are easy to gain generalist pollinators (insects and birds), seed dispersed animals and non-obligate arbuscular mycorrhizal fungi. Lack of symbionts often results in invasion failure (76,95).

(III). The empty niche hypothesis, which argues that invaders may take advantage of unutilized resources and occupy empty niche when introduced into new communities (24). Low diversity may provide some vacant niche to accept new invaders (97).

(IV). The novel weapons hypothesis, which proposes that some invaders possess novel biochemical compounds that function as unusually powerful allelopathic agents, or as mediators of new plant–soil microbial interactions (1,6-8,112). The novel phytochemical compounds, to which native plants and soil organisms are not adapted, give some exotic plants a dramatic advantage in their new range (7). Furthermore, competitive plants in their native range are more tolerant to allelopathic compounds of invasive species than those in the introduced range that lack a coevolutionary-based tolerance (1). Allelopathy may be an important mechanism driving the enormous success of invasive species (43, 67,109).

Many of these hypotheses consider only one single factor for invader success. Mitchell *et al.* (75) proposed multifactor hypotheses which considers joint effects of enemies, mutualists and competitors, including interactions between them on introduced populations on invader success, and claims that plant invasion alter plant interactions with enemies, mutualists and competitors and these altered interactions jointly influence the invader success. Understanding the mechanisms through which some exotic plants are able to become invasive could assist in the control and management of these species and also provide insight into how plant species interact and how plant communities are organized.

This paper reviews the research done on above exotic plants in China to evaluate the role of allelopathy in the success of invasion and establishment. We also review the role of allelochemicals of invasive alien species in plant defense against native herbivorous insects and microbial pathogens.

2. ALLELOPATHY AND CHEMICAL DEFENCE OF INVASIVE SPECIES

2.1. COMPOSITE SPECIES

2.1.1. *Ambrosia artemisiifolia* and *Ambrosia trifida*

Ragweed (*Ambrosia artemisiifolia*) is native to Northern American (9) and was introduced into China during 1920-1930 (102). Since then it has become most noxious weeds spreading in more than 15 provinces in the North, Northeast, East and Central China. Millions of Chinese people suffer from pollen allergy and hay fever caused by it. Ragweed becomes so problematic that Municipal Government of Beijing has to organize local people to weed them out by hands prior to flowering in May-June. The biological and ecological characteristics, bio-control and pollen hypersusceptibility mechanism of the species have been extensively studied (113). Its allelopathic effects have attracted attention of many researchers in China since 1990's.

The volatiles from *A. artemisiifolia* show significant inhibitory effects on the seed germination and primary root growth of soybean and maize. Leaf and stem aqueous leachates of ragweed inhibit seed germination and seedling growth of all tested crops e.g. soybean, maize, wheat and rice (114), radish (*Raphanus sativus*), mungbean (*Vigna radiate*), tomato (*Lycopersicon esculentum*), melon (*Cucumis melo*), Chinese cabbage (*Brassica pekinensis*) (13). However, aqueous leachates of the underground parts and growth soil show no allelopathic effects (114). Putative allelochemicals such as α-pinent, β-pinene, cineole, camphene, spanthueol were identified from its underground parts (114).

Aqueous leachates of giant ragweed (*A. trifida*), another invasive species, are also inhibitory to the seed germination and seedling growth of soybean, maize, wheat and rice, while its volatiles are not inhibitory (115). Nodulation of soybean was significantly inhibited when soybean and giant ragweed grew together, or the soybean plants were watered with aqueous extracts of giant ragweed (170). Potent allelochemicals in *A. trifida* are organic acids, terpenoids and polyynes (170). Volatile allelochemicals of *A. trifida* include camphor, camphene, α- pinene, β-pinene, cineole, decane, nonane, hornylene, germacrene D, limonene and myrcene (9,115).

Previous bioassays showed that aqueous leachates of the whole ragweed plant inhibit seed germination of test plants (4). Fisher and Quijano (29) isolated phenolic acids and sesquiterpene-lactones from ragweed root. α-Amyrin acetate, β-amyrin acetate, chlorogenic and 3,5-dicaffeoylquinic acids from methanolic extracts of *A. artemisiifolia* have been identified as feeding stimulants for *O. communa*. When mixed together triterpenoid derivatives (α-amyrin acetate or β-amyrin acetate) and caffeic acid derivatives show feeding stimulant activity (107).

The wide spread of this invasive plant species attribute not only to its alleloapthy but also to facilitation by arbuscular mycorrhizal fungi (AMF) (30). Biodiversity of animals in ragweed grown soil was remarkably less than that in other similar habitats without ragweed. Ragweed plants showed selectivity to soil animals, especially to Nematoda and Enchytraeidae (102).

2.1.2. *Eupatorium adenophorum*

Crofton weed (*Eupatorium adenophorum*) is an aggressive perennial weed with a woody rootstock and numerous upright branching stems. This weed is a shallow-root herb with funicular root (168). A native to Central America (100), this plant was introduced into Yunnan Province of China in the 1940s, and now spreads in southwest China including Yunnan, Guizhou, Xizang (Tibet), Guangxi, Sichuan, Taiwan, Hubei provinces and Chongqing Municipality (106). Meng *et al.* (73) suggested that the invasion of *E. adenophorum* mainly depends on three principal factors, i.e. general ecological characteristics, humidity and light and plant biodiversity. Further studies show that allelopathy serves as an important mechanism for interacting with native plants.

The water leachates of *E. adenophorum* inhibit seed germination of several plants such as maize, ryegrass and white clover (31,158). The scanning electron microscopy observation showed that the leachates restrained development of root cells and destroyed cells between epidermis and cortex of corn roots (158). Zheng and Feng (165) investigated the allelopathic potentials of this invasive plant on five native species encountered at its early invasive stage and found that its aqueous leaf leachates inhibit seed germination and seedling growth of *Chloris gayana*, *Trifolium repens, Ixeridium gracile* and *Mariscus cyperinusll*, and the effects were concentration dependent. Aquatic leaf leachates of *E. adenophorum* grown in different sites have differential allelopathic potentials (144). The inhibitory effects were roadside > deciduous broad-1eaved forests > evergreen broad-1eaved forest.

The chloroform extracts of *E. adenophorum* are toxic to cotton aphid (*Aphis gossypii*) and eupatorin A was identified as the main allelochemical responsible for the toxicity (123). Eupatorin A at 2 mg/ml can kill 81% of cotton aphids in 48 h (123). This compound also inhibits the enzymatic activity of AChE (123) and NaK-ATPase (124) of the cotton aphids *in-vitro* and *in-vivo*. Zhou *et al.* (169) reported that A-1, P-1, Zi-2 and the leachates of *E. adenophorum* had anti-feeding activity to the fourth instars of *Pieris rapae.* The leachates of this weed are very toxic and could be used to control *Panonychus citri* (50). The weed extracts have strong insecticidal activity against four stored grain insects, rice weevil, maize weevil, Chinese bean weevil and European bean weevil (52). The ethanol and methanol extracts of *E. adenophorum* have insecticidal effects on the fifth instars of cabbage white butterfly (*Pieris rapae*) (15,51,53).

Epifriedelinol, stigmasterol, octacosanoic acid, 8-daucos tero1, 2- isopropeny1-5-acetyl-6-hydrxybenzofuran aceate and o-hydroxy einnamic acid were isolated from the *E. adenophorum* (171). The esential oil of *E. adenophorum* contains 1-methyl-2(1-methy1) benzene, endobornytcl-letate, hedycaryol, citra1, copaene, lonipinene, p-cymene and bornyl acetate (130,20). Ding *et al.* (22) isolated a new sesquiterpenene lactone – euprtoranolide and 11 known compounds from the flowers of *E. adenophorum*. Xu *et al.* (136) isolated a-dotriacontane, β-sitosterol, stigmasterol and taraxasteryl palmitate teraxasteryl acetate from this weed.

2.1.3. *Mikania micrantha*

This is a herbaceous perennial vine native to tropical Central and South America and has nicknames “mile-a-minute weed” and “plant-killer” because of its vigorous, fast growing and rampant growth habit. It is one of the world’s worst weeds and spreads in tropical Africa, Asia, Australia, the islands of the South Pacific Ocean and many subtropical countries. The plant was first introduced to Hong Kong in 1984 and then widely dispersed in the late 1980s and 1990s in the eastern coastal areas of the Guangdong Province, China, especially in the Pearl River Delta, causing severe damage to forests and crops (26,146).

Its allelopathic potentials were investigated and the volatile oil showed inhibitory effects on six tested plant species (157). The aqueous leachates of *M. micrantha* had allelopathic potentials on radish (*Raphanus sativus*), rye grass (*Lolium multiforum*) and white clover (*Trifolium repens*) (96). It also inhibits the growth of Chinese cabbage (*Brassica parachinensis*) and radish (*Raphanus sativus*) (56).

Ou *et al.* (80) reported that the methonal extract of *M. micrantha* had significant repellent effects on oriental fruit fly in the field. The volatile oil of this plant significantly deters oviposition of *Plutella xylostella, Phyllotretast riolata* and *Phaedon brassicae* at dose of 5-10 μL/plant (156). Antifeedant effects of crude extract of *M. micrantha* on l-2 instars of *Pieris rapae* and 2-3 instars of *Plutella xylostella* were 80% and 70%, respectively (28).

M. micrantha also has antimicrobal activity. Ethyl ether extracts of this plant inhibit the growth of bacteria *Escherichia coli* and *Staphylococcus aureus* (55). The volatile oil of this plant at 200, 400, 800, 1600 mg/l suppresses the growth of pathogens such as *Pyricularia grisea, Fusarium oxysporum* and *Phytophthora nicotianae* (157).

Allelochemicals such as mikanin, eupalitin, eupafolin, (3,4′,5,7-tetra-hydroxy 6-methoxyflavone 3-*O*-β-D-glucopyranoside, luteolin, 3,5-di-*O*-caffeoylquinic acid *n*-butyl ester and 3,4-di-*O*-caffeoylquinic acid *n*-butyl ester were identified from *M. micrantha* (128). β-Cubebene, terpinolene, β-caryophyllene, 1imonene, β-farnesene, ocimene, δ-cadino1, γ-terpinene, ethylnaphthalene, a-caryophy11ene, β- cadinene + isocaryophyllene, δ-bisabolene, β-bisabolene+cubebo1 were determined as the main compounds in essential oil of *M. micrantha* (27).

2.1.4. *Solidago canadensis*

Canada Goldenrod (*Solidago canadensis*), a perennial Composite species originating from North America, was introduced to China as a garden flower in 1935. Since then it has become an aggressive invasive weed in eastern China, and caused serious damage to agricultural production and ecosystems in several provinces of China (38). *S. canadensis* has high reproductive capacity with large number of seeds The plant also has strong clonal reproduction through underground rhizomes and stem base sprouting. It has long germination season lasting from March to October. A mature plant can produce over 20,000 seeds. The light-winged seeds disperse readily by air, water, vehicles, human or animal activity. These special reproductive traits provide effective mechanisms for dispersal, colonization and establishment (38). However, allelopathy provides an additional mechanism for the species to invade novel ranges.

The growth of wheat, maize and rice, and germination of barley, corn, tomato, wheat, maize, rice and rape seeds were severely inhibited by its water leachates (25,88). The leachates also inhibit seed germination of some weeds, e.g. *Echinochloa crusgalli*, *Digitaria sanguinalis*, *Setaria viridis*, *Eclipta prostrate* and *Amaranthus ascendens* (87). Growth of *Trifoliumrepens, Trifoliumpretense, Medicago lupulina, Lolium perenne, Suaeda glauca, Plantago virginica, Kummerowia stipulacea, Festuca arundinacea, Ageratum conyzoides, Portulaca oleracea* and *Amaranthus spinosus* was inhibited by the root and rhizome extracts of *S. canadensis* (72). Zhou and Guo (167) also found that the aquaous extract of roots and rhizosphere soil of this plant inhibit seed germination, root extension and elongation of seedlings of Chinese cabbage (*Brassica campestris*) and radish. The extract of aerial and underground parts of *S. canadensis* and that of rhizosphere soil displayed inhibitory effects on seed germination and seedling growth of tested plants (119,140). The essential oil has significant antimicrobial activity on growth of *Thanatephorus cucumeris* and *Rhizoctonia solani* (120). Allelochemicals of this plant also inhibit mycorrhizal colonization of several native species (71).

Iso-germacrene D was isolated from the essential oil of leaves and flowers of *S. Canadensis* (132). (+)-Germacrene D (28.64%), α-pinene (15.08%) and limonene (11.80%) were identified as the main components in the oil of *S. canadensis* (120).

2.1.5. *Chromolaena odoratum*

Siam weed (*Chromolaena odoratum*, Compositae) is an upright and perennial shrub native to Central America (125). The weed is aggressive in new habitats and spreads quick1y. It seriously interferes with native plants in forest, pasture and crop fields (35,46). It has become a major weed in Hainan, Guangxi, Guangdong, Hong Kong, Guizhou, Yunnan and Taiwan of China (84).

Volatile oil from *C. odoratum* inhibits the growth of ryegrass, Chinese cabbage, radish, soybean and rice (60). He *et al*. (34) found that the alcohol extracts (0.1 g/mL) inhibit seed germination and seedling growth of *Brassicae parachinensis, B. chinensis* and *B. perkinensis.*

The volatile oil of *C. odoratum* is a strong oviposition deterrent of striped flea beetle (*Phyllotreta striolata*) and diamondback moth (DBM) (*Plutella xylostella*) at dose 10-20 µL/plant (60). The alcohol extract and its chloroform fraction exhibited strong repellent effects (80%) against DBM (85). The alcohol extracts of *C. odoratum* were effective to deter the oviposition of DBM, and the active compounds were identified as chalkones and flavonol (32). Crude extracts of *E. odoratum* showed 73.8% antifeeding effects and 69.13 % mortality within 48 h on third instars of *Helicoverpa armigera* at 20g/L (12).

Volatile oil of *C. odoratum* at 800 mg/l inhibits growth of *Pyricularia grisea, Phytophthora nicotianae* and *Fusarium axysporum* (60). Liu *et al.* (64) found that ethanol and acetone extracts of *C. odoratum* had broad resistance against microbial pathogens such as *Exserohilium turcicum, Colletotrichum musae*, *Fusarium oxysporum* and *Colletotrichum gloeosporioides*. The acetone extracts of stems and leaves of this plant strongly inhibit *Colletotrichum gloeosporioides* (33). Several studies also demonstrated that leaf leachates of *C. odoratum* had antimicrobial effects on many bacteria (*Pseudomonas aeroginosa*, *Escherichia coli*, *Staphylococcus aureus* and *Neisseria gonorrhoea*) (5,42).

Trans-caryophyllene, β-cadinene, a-copaene, caryophyllene oxide, germacrene-D and n-humuhne were found to be the major components of the volatile oil of *C. odoratum* (59). Odoratin, dillenetin, pectolinarigenin, quercetin-7, 4'-dimethyl ether, kaempferol 4'-methyl ether, isosakuranetin, acacetin, dotriacontanic acid, β-sitosterol and daucossterol were isolated from its ethanol extract (145).

2.1.6. *Ageratum conyzoides*

Tropical Ageratum (*Ageratum conyzoides,* Composite) is widely distributed in roadsides, old fields, degraded sites and gardens in tropical and subtropical areas in West Africa, Asia and South America. Its seeds are achene and easily dispersed (70). It was introduced to China as an ornamental plant and soon became an important weed in the South and Southwest China (89). Successful invasion of *A. conyzoides* is attributed to its wide range of environmental adaptability, higher reproductive potentials and allelopathy (127,150,152).

Zeng (150) demonstrated that its aqueous leachates and root exudates have strong allelopathic effects on cucumber, radish and rice. Root exudates collected by XAD-4 resin in undisturbed root system significantly inhibited seedling growth of rice and radish (154). Ageratochromene (6, 7-dimethoxy-2, 2-dimethylchromene) was identified as the main allelochemical of *A. conyzoides* (127). Later several studies confirmed its allelopathic effects on crops and weeds (99,137). Aqueous leachates of *A. conyzoides* showed a strong allelopathic potential on *Merremia hederacea* and *Cajanus cajan* (86). Xu *et al.* (135) found that its volatiles decreased the contents of chlorophy b, protein and activity of POD in the test plant sharply, while they increase the relative plasma membrane permeability and MDA content.

Allelochemicals of *A. conyzoides* not only interfere with neighbour plants, but also resist herbivory attack. 6-Demethyoxyageratochromene (precocene I) and ageratochromene (precocene II) were isolated from *A. conyzoides* and these compounds showed strong insecticidal effects (66). Methanol extracts of the plant produced strong antifeeding effects on *Preris rapae* and *Plutella xyloaella* (157). Volatile oil and agemtochromene of this plant greatly reduced reproductive ability of *Plutella xyloaella* (39). Ageratochromene was highly toxic to *Aphis gossypii* with an LD-50 of 11.42 ppm in vitro studies (37). The compound has antifeeding effects on *Diaphania indica* (92). Extract of *A. conyzoides* at 1 % had antifeeding effects on *Plitella xylostella* and *Pitris rapae* with antifeeding ratio of 85% and 62%, respectively (160).

Bowers *et al.* (3) isolated ageratochromene (precocene II) and 6-demethyoxyageratochromene (precocene I) from *Ageratum houstonianum.* Lu *et al.* (66) isolated and identified the two compounds from *A. conyzoides.* Ageratochromene killed all rice weevil (*Sitophilus oryzae*) 6 d after treatment at 10 $\mu g/cm^2$ and 6-demethyoxyageratochromene killed all rice weevil within 24 h at 120 $\mu g/cm^2$. Wei et al. (126) identified agerato-chromene as the main allelochemical of *A. conyzoides.* The compound inhibit seedling growth of barnyardgrass at 25 µg/mL. Other studies confirmed these findings (47,135). Xu et al. identified 16 compounds from volatile oil of *A. conyzoides* and found that precocene (36.85%), precocene (26.41%) and caryophyllene (19.84%) were the main components of the volatile oil. Nutrient stress increaed the allelopathic potentials of volatile oil of *A. conyzoides* (135).

2.1.7. *Wedelia trilobata*

Yellow dots (*Wedelia trilobata*) is a perennial weed in tropical and subtropical regions. This plant was native in tropical Central and South America. It was introduced to China as an ornamental groundcover in gardens and roadsides. Currently it is widely distributed in South China. The plant propagates mainly vegetatively with climbing stems (131).

Its water leachates inhibits the seed germination and seedling growth of peanut and rice (77), and reduced dry root weight, numbers of nodules, leaf chlorophyll content, net photosynthetic rate and the dry weight per plant. They also decrease the activities of nitrate reductase and glutamine synthetase (79). Water leachates of *W. trilobata* had strong inhibitory effects on seed germination and seedling growth of several vegetable crops such as *Vigna radiata, Raphaus sativus* and *Brassica chinensis* (14). Watering rice seedlings with the aqueous extracts resulted in the reduced plant height, tillers, root activity, dry rootweight, leaf chlorophyll content, net photosynthetic rate and dry weight per plant (78).

Chen *et al.* (16) isolated 2-endesmanolides from the volatile oil of *W. trilobata.* Six sesquiterpene lactones were isolated from *W. trilobata.* They were identified as trilobolide-6-O-isobutyrate, 1β-acetoxy-4α,9α-dihydroxy -6β-isobutyroxyprostatolide, 1β,9α-diacetoxy-4α-hydroxy-6β-isobuty-roxy-prostatolide, 1β,9α-diacetoxy-4α- hydroxy-6β-methacryloxyprostatolide, 1β, 4α-dihydroxy-9α-tigloyloxy-6β-methylpropanoyl-prostatolide and 9α-angeloyloxy-1β,4α- dihydroxy-6β- methylpro-panoylprostatolide

(159). These compounds and their mixtures showed inhibitory effects on seedling growth of radish, cabbage and tomato (159).

2.1.8. *Bidens pilosa*

Beggar's ticks (*Bidens pilosa*, Compositae) is an annual herb native to South America and now can be found in almost all countries in tropical, subtropical and temperate regions (36). It was found in Hong Kong in 1857 and introduced to mainland China by livestocks and human casually. Because high invasive capacity, it has become a common weed in east China, southern China, and Hebei province (54).

Allelopathic effects of *B. pilosa* was first demonstrated by Zeng (150). Root exudates of *B. pilosa* showed allelopathic potential against *Raphanus sativus, Cucumis sativus* and *Oryza sativus* (154). *B. pilosa* displayed strong allelopathic effects under drought stress (153). Water leachates of this plant at 0.05g/ml displayed strong inhibitory effects on germination and growth of *Ligularia virgaureajournal* and *Elymus nutans* (121). Chen *et al*. (12) found that flavonoids isolated from *B. pliosa* strongly inhibited infection of *Tobacco mosaic viru*s (TMV) on *Nicotiana glutinosa*. The flavonoids had no direct viricidal effect but could bind TMV coat protein.

The main constituents of the essential oil of *B. pilosa* were tetradyne, trans-aryophyllene and germacrene-D (91). Salicylic acid, octadecadienoic acid and glucopyranoside, as well as flavonoids have been isolated from this plant (49,117,118). Coumaric acid, luteolin and butanedioic acid were also found in *B. pilosa* (44).

2.2. *EUCALYPTUS SPP.*

There are more than 500 species in genus *Eucalyptus* and most of them are native to Australia. The *Eucalyptus* plants are fast-growing species in tropics and subtropics. They are widely used as fire wood and paper making. The total plantation area is over 670,000 ha in Guangdong province and over 2,000,000 ha in China. But debate still continues about whether or not *Eucalyptus* should be planted in Guangdong. In *Eucalyptus* plantations the enzymatic activities of urease, inverease proteinas and peroxidase were found to decline with the increase of soil depth (0-20 cm, 20-40 cm and 40-60 cm) and the largest soil enzymatic activities occur in 0-20 cm. Compared with Chinese fir plantations, the soil enzymatic activities of *Eucalyptus* plantations were much lower (51). Continuous cropping of *Eucalyptus* plantation resulted in not only a reduction of species diversity but also changes in species composition and characteristics of plant community (148,129). Liu *et al*. (65) and Liang (57) found that the quantities of *Fusarium, Cephalosporium, Rhizoctonia* were higher in mixed forest than in pure *Eucalyptus* plantation.

The seedling growth of radish (*Raphanus sativus*), *Acacia mangium*, *Lactuca sativa* and *Leucaena leucocephala* was inhibited by leaf volatiles and aqueous extracts of *Eucalyptus citriodora*, *E. urophylla, E. exserta* and *E. tereticornis* (147,151). Leaf leachates of *E. urophylla* strongly inhibit root initiation, root number and root length of hypocotyl cuttings of mungbean

(*Phaseolus aureus*) and pea (*Pisum sativum*) (40). These leachates also suppressed the seed germination of Indian mustard (*Brassica juncea*) and wild cabbage (*Brassica oleracea* var. *caulorapa*) (40). Zhan *et al.* (155) found that the crude stem extracts of *Eucalytus* LH_{22} inhibit the root formation and root growth of mungbean cuttings.

Aqueous leachates of both fresh and withered leaves and branches of *E. grandis* × *E. urophylla* inhibit the seed germination of *Brassica parachinensis* and wheat, and seedling growth of wheat (58,162). *Eucalytus* 12 ABL plants have stronger allelopathic potentials on peanut and mung bean under resource stress conditions than that under normal resource supply (11). Intercropping is often recommended to minimize the negative effects of *Eucalytus* planting. However, inter-cropping between *Eucalytus* and *Litchi chinensis* resulted in withering of *L. chinensis* two years later and the death of all pants in three years (151).

The essential oil of *E. citriodora* and *E. globulus* produced a strong repellent effects against the adults of *Apriona germari*, *Psacothea hislari* and *Monochamus alternatu* (138). Turpentine oil and citriodore oil at 1g/kg produced antifeeding effects on *Diaphania indica* (92). Zhi *et al.* (166) isolated cineole, a-pinene, β-pinen, sabinene, α-3-carene, tert-butybenzene from the essential oil of *Eucalyptus*. Palmitic, palmitoleic, stearic, oleie, linoleic and eleosetearic acids were isolated from the leaves of *E. camaldulensis* (103). Citronellal, citronellol, citronellyl acetate, cis-p-Menthane-3, 8-diol and trans-p-menthane-3,8-diol were isolated from the essential oil of *Eucalyptus* (110). Methylnathaphalene, eudesmol, anthracene, heptacosane, 3-methyl-eicosane, biphenyl, cardynene, dibenzofuran, fluorene, dodecane and eudesmol are present in the root tissue of *Eucalyptus*12ABL and its surrounding soil (10). Wang *et al.* (116) found that the main allelopathic volatile in leaves of *E. grandis* are α-pinene, spathulenol, α-eudesmol and other terpenes.

2.3. OTHER INVASIVE EXOTIC SPECIES IN TERRESTRIAL ECOSYSTEMS

2.3.1. *Lantana camara*

Common lantana (*Lantana camara*, *Verbenaceae*) is an evergreen aromatic shrub native to Central and South America. This plant has been introduced in many countries as an ornamental shrub and is now a serious invasive weed (2). It was introduced to China as a garden plant and has been completely naturalized throughout the highlands in Guangdong, Guangxi and Fujian provinces.

The aqueous leachates of its fresh leaves inhibits the growth of water hyacinth (*Eichhornia crassipes*) (143). Zheng *et al.* (164) also found that the foliar spraying with leaf extract of *L. camera* suppresses the emergence of leaf buds of water hyacinth and resulted in increase in superoxide dismutase (SOD) activity, accumulation of H_2O_2 and increase in membrane peroxidation. Volatile oils and water leachates of *L. camara* inhibit the growth of tomato, radish, cucumber (*Cucumis sativus*) and barnyardgrass (63). The aqueous leachates from fruits, stems and leaves of *L. camara* has a strong inhibitory effect on seed germination and seedling growth of *Salvia splendens* (93).

Zeng *et al.* (149) found that alcohol extract of *L. camara* protect kidney bean (*Phaseolus vulgaris*) against *Liriomyza sativae*, but had no effect on the parastioids of *L. sativae*. The deterent rates and the antifeedant rates of the ethanol extracts of *L. carnara* on striped flea beetle and *Phyllotreta striolata* were 95% and 85%, respectively after 48 h treatment (139). Ren *et al.* (94) also found that chloroform extract of *L. camara* was oviposition deterrent and it has antifeeding effect on lettuce. The crude lantadene from *L. camara* leaves at 1.6mg/mL showed antifeeding effects on the second instars of *Plutella xylostella* and first instars of *Spodoptera litura* with the antifeeding rate of 62% and 33%, respectively within 48 h (23). Zhao *et al.* (161) found that the volatile of *L. camara* has strong repellence against *Phyllotreta striolata* adults. Methanol crude extracts of *L. camara* have strong nematicidal activity against the second instars of *Meloidogyne* spp (142).

Salicylic acid, gentisic acid, β- resorcylic acid, coumarin, ferulic acid, p-hydroxybenzoic acid and 6- methyl coumarin were indentified from *L. camara* (143). α-Caryophyllene and β-caryophyllene (164), as well as germacreme D, β-pinenc, and β-careue (63) were isolated from this plant. Lantadene A, lantadene B with cytotoxic activity were found in leaves of *L. camara* (69). Pan et al. (81,82) isolated lantadene A, B, oleanolic acid, lantanolic acid, icterogenin and 4',5-dihydroxy-3,7-dimethoxy-flavone-4'-O-β-D-gluco-pyranoside from leaves, and lantanolic, oleanolic and ursolic acids from roots of *L. camara*. Oleanolic acid in the roots of *L. camara* had hepato-protective activity (61).

2.4. INVASIVE SPECIES IN AQUATIC ECOSYSTEMS

2.4.1. *Eichhornia crassipes*

Water hyacinth (*Eichhornia crassipes*) originating from the tropical regions of South America, is a floating aquatic macrophyte that often jams rivers and lakes with thousands of tons of floating plant matter. This invasive plant has become the most serious weed in many tropical, warm and temperate freshwater habitats. Water hyacinth thrives in polluted or nutrient rich waters, particularly those rich in nitrogen, phosphorus and potassium. The weed causes serious environmental problems in China and manual removal of the weed in the country alone cost an estimated 13 million US dollars each year but was neither economic nor effective (21).

Hydroponic water of this plant suppressed algal growth (105). N-Phenyl-1-naphthylamine, linoleic acid and glycerol-1,9-12 (ZZ)-octadecadienoic ester were isolated from roots of water hyacinth (141). The N-phenyl-1-naphthylamine was also found in the hydroponic water and its antialgal activity was stronger than that of the common algaecide $CuSO_4$. Hydrophobic root exudates collected by XAD-2 resin showed strong algaecidal activity and were identified as N-phenyl-1-naphthylamine and N-phenyl-2-naphthylamine (104). The root exudates of water hyacinth inhibit the growth of *Slaphylococcus aureus* (108,163). Root extracts of water-hyacinth had strong growth inhibitory effects on *Alexandrium tamareme* (HK strain) (17). After the algae was treated with root exudates of water hyacinth chloroplast lamella of *S. arcuatu* swelled and disintergrated, mitochonria cristea disappeared, plasmolemma and nuclear were destroyed (108). Acetone extract of water-hyacinth roots suppresses the growth of *A. tamarense* and its main allelochemical, N-phenyl-2-naphthylamine inhibits the growth by more than 50% at 5 mg/l (65). The compound increased contents of soluble protein and MDA and decreased SOD activity in *A. tamarense*. Growth of *Prorocentrum donghaiense* was strongly inhibited by the aqueous leachates of water-hyacinth at□2 g/l and the alga was killed at 8 g/l (98). The acetone extract of the plant was inhibitory to *Lexandrium tamarense* (62).

2.4.2. *Alternanthera philoxeroides*

Alligatorweed (*Alternanthera philoxeroides*, Amaranthaceae) is an aquatic and wetland perennial herb native to South America. It is an aggressive weed in many parts of the world. The plant rarely produces viable seeds in the field and reproduces mainly by vegetative propagation with stolons and roots (45,122). It was first introduced in Shanghai as a horse forage by Japanese during 1930s (90). Its ability to compete with other native plants and to impede waterways has made it a serious threat to aquatic ecosystems.

The water leachates of its stems inhibit the germination of *Juncellus serotinus*, *Leptochloa chinensis*, *Celosia argentea*, *Brassica campestris* and *Echinochloa crusgalli* (101). Xiong et al. (134) isolated oleanolic acid, pyroglutamic acid and betaine from aquatic extract of *A. philoxeroides*.

3. CONCLUSIONS

Many invasive exotic plants have become the most noxious agricultural weeds. There are many factors influencing dispersal and establishment of exotic species in novel ranges. Various biotic interactions with enemies, mutualists and competitors can influence the dynamics of biological invasions by plants. Multifactor hypothesis which considers the joint effects of biotic and abiotic interactions on invader success was proposed by Mitchell *et al*. (75). Numerous studies in China outlined in this paper have shown that allelopathic potentials and chemical defense by allelochemicals of most notorious invasive weeds against native pathogens and herbivores play an important role in invader success. Recent studies outside China also suggest that allelochemicals in invasive exotic species may provide them with extra advantages to compete with native plants, defense them against native plant pathogens and herbivorous insects (7,67,68). More convincing evidences and well-designed experiments are required to determine the actual role of allelochemicals in biological invasion in China.

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