Allelopathic Research in China

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Abstract: Allelopathic phenomena had been recorded in ancient Chinese literature. Since 1990’s allelopathy involved in natural and managed ecosystems has been widely investigated in China and substantial progress has been achieved. In recent years, allelopathic research in China has focused on staple food crops of rice and wheat, and the use and management of allelopathic weeds. Many allelochemicals have been isolated and identified from a wide variety of allelopathic plants. The Chinese Allelopathy Society was established with the approval from the government in 2005 and organized successfully 4 national conferences on allelopathy. Allelopathy in China should make its potential impact worldwide.

Keywords: Aquatic ecosystem, allelopathy, allelochemical, rice, plant invasion, forestry, weed management

1. Introduction

China is a large and old country with over 5000-years of history. Allelopathic phenomena had been repeatedly recorded in ancient Chinese literature. Since 1970’s, Professor C.H. Chou and his co-workers have done remarkable research on allelopathy in agro-ecosystems in Taiwan province, while allelopathic research in other provinces started late. Since 1990’s, allelopathy in China has received a great deal of attention of both the scientists and the government. More and more interdisciplinary scientists have been joining this exciting research field. In parallel, proposals for allelopathic research have been funded by the National Natural Science Foundation of China (NSFC) and other funding agencies. An ever increasing number of papers from Chinese scientists have been delivered in international journals in past decade (Fig. 1). The Chinese Allelopathy Society was established with the approval from the government in 2005 and each organized national conference on allelopathy within every two years. The fourth Chinese Allelopathy Conference was held in August 14-17, 2009 in Qingdao.

![Fig.1 Allelopathic papers published in past decade. Data were collected from Web of Science](image)

The occurrence of allelopathy in both terrestrial and aquatic ecosystems, natural or managed ecosystems in China has been widely investigated in recent years and substantial progress has been made. Many allelochemicals have been isolated and identified from a wide variety of allelopathic plants. Here is an outlook of the recent advances in allelopathic research in China, (a) crop allelopathy, (b) the use and management of allelopathic weeds, (c) allelopathy in forestry, (d) allelopathy in aquatic systems, (e) allelopathy and plant invasion.

2. Crop Allelopathy

Allelopathy of rice, wheat, soybean, maize and other crops has been studied since 1990’s. In recent years, crop allelopathy has focused on the staple food crops of rice and wheat. Allelopathic rice and wheat accessions were evaluated and screened from Chinese germplasm collections [19,46].
Numerous compounds have been identified as potent allelochemicals from the rice tissues and root exudates. Flavones, cyclohexenone, and momilactones play a key role in rice allelopathy [14,21], while phenolic acids were not among the primary allelochemicals [13]. Among these allelochemicals, 5,4′-dihydroxy-3′,5′-dimethoxy-7-O-β-glucopyranosylflavone is particularly interesting because a significant amount could be exuded from the roots to the rhizosphere and then rapidly transformed into aglycone 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone [20]. This aglycone interacts with soil organisms to generate many biological effects [15,18]. Furthermore, allelopathic rice not only releases allelochemicals to suppress the growth of paddy weeds, but also detects the presence of interspecific neighbours and responds through increased release of certain allelochemicals [13,21]. Accordingly, the mechanism of allelopathic rice interference with paddy weeds is not only a phytotoxic process, but also involves their species chemical recognition (Fig.2).

The inheritance pattern and genes involved in rice allelopathy have been conducted in China. Molecular approaches indicated that a population of 147 RILs derived from a cross between allelopathic rice Zhong 156 and non-allelopathic rice Gumei 2 were employed to map the genes responsible for the allelopathic effect on barnyard grass. The map contained 168 DNA markers, covering all 12 chromosomes with 1447.9 cM spans. Three main-effect QTLs, mapped on chromosomes 5, 5 and 11, explained 13.6% phenotypic variations. Five pairs of digenic epistatic loci were also found. The main QTLs and epistatic loci totally explained 55.1% of the phenotypic variation of allelopathic activity [45]. Recent study showed that the distribution of allelopathy in F2 populations of N2S/PI312777 was continuous but not normal. There were two maximal distribution frequencies of 22 F2 plants with inhibition of 20-29 % and 35 F2 plants with inhibition of 60-69 %, respectively. Over 90 % inhibition of 20 F2 plants indicated that allelopathic traits were not unidirectional gene controlling chromosome segregation but were controlled by multiple genes [3].

Variatel improvement is an essential prerequisite for the practical application of rice allelopathy for paddy weed management and thus much effort has been done to develop commercially acceptable allelopathic rice cultivars [3]. Significant results are leading to a large scale application of allelopathic rice cultivars in China. However, paddy weed control by using allelopathic rice cultivars alone may not be adequate. Several management options will need to be combined with the suppressive effect of the allelopathic rice cultivars and facilitate effective weed control at reduced herbicide rates. Recent study has clearly shown that allelopathic rice cultivars combined with integrated cultural management practices can reduce the quantity of herbicides used in paddy ecosystems [11].

It was found that planting wheat or mulching with wheat straw can effectively control weeds in fields and orchards. Growing allelopathic wheat varieties significantly decreased weed infestation in the wheat field and their stubble greatly reduced the weed biomass in the following corn crops. Mulching of wheat straw effectively controlled the weeds in corn fields and it is now becoming a common practice for weed management in the crop fields of North China [22]. Major allelochemical 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) was found in tissues and root exudates of 26 allelopathic wheat varieties from Chinese germplasm collections [42,43]. DIMBOA concentration in allelopathic wheat is not only related to weed inhibition and pathogen resistance, but also was induced by associated with weeds and other environmental factors [44].

Allelopathy of wheat genotypes was also studied. All genotypes, excluding Secale cereale L., had allelopathic effects. Inhibition caused by the wheat genotypes increased as their genome changed from 2n to 4n to 6n [46]. Triticum boeoticum L., French, Secale cereale L., Aegilops.tauschii Cosson Syn, Triticum dicoccoides K., Triticum aestivum L. Var. Shaan 160 and T. aestivum Var. No.1 Ningdong had a weak effect, Triticum monococcum L., Aegilops.speltoides L. and Triticum dicoccum S. had an intermediate effect, whereas T. aestivum Var. common wheat had a strong effect.

The essence of allelopathy and the genomes of wheat with allelopathic traits were constructed to make available allelopathic bioinformation on wheat [24]. More recently, allelopathy variation in dryland winter wheat accessions grown on the Loess Plateau of China for about fifty years has been investigated [47]. Consequently, wheat
allelopathy is genetically controlled. The genetic variation of allelopathic property in dryland winter wheat showed significant differences between accessions. Allelopathic effects exhibited high heritability (55-95%) throughout the life cycle of wheat. Heritability was highest in the tillering stage and weakest in the seed filling stage. Allelopathic potential varied and was discontinuous throughout the wheat life cycle.

3. The Use and Management of Allelopathic Weeds

Weeds pose an important biological constraint to crop productivity. Many weeds release allelochemicals to interfere with crop plants. These allelopathic weeds are economically destructive and attempts to control them have met with limited success. However, their allelopathic action and allelochemicals may also be used as an important part of crop and weed management systems, or employed for other uses. A few studies have shown that allelopathic weeds could be put into use for pest management in certain managed ecosystems in China. *Ageratum conyzoides* L. and *Lantana camara* L. are American in origin and have spread to other regions of the world including China. Both weeds can use allelopathic mechanism to interfere with crops and other organisms in natural and managed ecosystems. *A. conyzoides* infestation of cultivated fields reduces crop productivity, but it is also beneficial to some crops in certain agro-ecosystems. In south China, *A. conyzoides* is intercropped as under-storey in citrus orchards to make the orchards more favorable for predatory mites (*Amblyseius spp.*) that are natural enemies of citrus red mite (*Panonychus citri*). Intercropping with *A. conyzoides* in citrus orchards increased the *A. newsami* population to make the population density of *P. citri* at non-injurious levels [23]. The volatile allelochemicals released from *A. conyzoides* regulated the population of *A. newsami* and *P. citri*. In intercropped citrus orchard, *A. conyzoides* plants continuously released volatile allelochemicals to stabilize the *A. newsami* population [10].

Intercropping of *A. conyzoides* also controls weeds and pathogenic fungi in citrus orchards. Several allelochemicals, such as ageratochromene and its two dimmers, were identified from the *A. conyzoides* intercropped citrus orchard soil. Ageratochromene could inhibit weeds and soil pathogenic fungi, but two dimers had no inhibition. There was a reversibly dynamic transformation between ageratochromene and two dimers in the *A. conyzoides* intercropped citrus orchard soil. Ageratochromene released to the soil by *A. conyzoides* plants might be transformed into its dimers and the dimers might be re-monomerized [12]. The reversible transformation can be an important mechanism maintaining allelochemicals at effective concentrations in the soil. Because of its multifunction in the field, *A. conyzoides* is intercropped in citrus orchards in >150,000 ha in South China [23]. This resulted into substantial ecological and economic benefits and provides an excellent example of applied aspects of allelopathy in agro-ecosystems.

The phytochemicals of *L. camara* has attracted considerable interest. These phytochemicals have been related to *L. camara* defense against a wide variety of organisms including microbes, insects and other plants. Particularly, allelochemicals of *L. camara* could be used against *Eichhornia crassipes* (water hyacinth) in freshwater systems [39].

Over 50% of areas in freshwater systems have been severely infested with *E. crassipes* in South China since 1990’s. Commonly used herbicides for controlling of *E. crassipes* are harmful for the utilization and supplies of water resources, so it is essential to develop safe methods for *E. crassipes* management. Aqueous extract of *L. camara* leaves completely killed *E. crassipes* and the highly inhibitory compounds toward the growth of *E. crassipes* were subsequently identified as lantadene A and lantadene B [17]. When over 5 kg *L. camara* leaves were floated in a static water body, lantadenes A and B concentrations with over the inhibition threshold (10.8–13.7 mg/L) for *E. crassipes* were detected in the water body after 5 days. The maximal concentration was reached after 15-20 days and then decreased rapidly [17]. These results showed that lantadenes A and B released from decomposition *L. camara* leaves into the water body could inhibit the growth of neighbouring *E. crassipes*. Therefore, using *L. camara* mulches or planting *L. camara* in riversides has been employed for small bodies of water to improve the management of *E. crassipes* in South China.

4. Allelopathy in Forestry

Many tree species have been planted commercially in China for industrial wood production. However, the establishment and productivity-decline of replanted tree ecosystems has remained a significant problem in China. Autotoxicity, a type of intra-specific allelopathy, is a major reason why managed tree ecosystems fail to regenerate, causing replant problems.

_Eucalyptus exserta* and *E. urophylla* was introduced in 1960’s and become dominant species in man-made forest communities in South China. Due to their fast growing, they are very important for the paper industry of the country. However, because of allelopathic interactions, there are problems in the communities formed. Aqueous leaf leachate and leaf volatile of *Eucalyptus urophylla* showed allelopathic effects on several native tree species including *Cinnamomum burmanni*, *Cryptocarya concinna*, *Machilus chinensis*, *Photinia benthamiana*, *Pygeum topengii*,...
Diospyros morrisiana and Pterospermum lanceaefolium. The allelochemical effects of these native tree species varied with the dose applied, and species respond differently to allelochemical released by the Eucalyptus [4].

Chinese fir [Cunninghamia lancealata (Lamb.) Hook] trees are a native species that has been widely planted in mountainous tropical and subtropical areas in South China for more than 1000 years. *C. lancealata* is an endemic fir with rapid growth and high timber yields, but a declination always occurs in replanted Chinese fir tree ecosystems. Various factors that could be responsible for this decline have been considered and examined. An increasing number of studies have shown that autotoxicity plays an important role in the replant problem from Chinese fir tree ecosystems. Several phenolic acids including *p*-hydroxybenzoic, gallic, coumaric, ferulic, vanillic, and protocatechuic acids were regarded as allelochemicals to be responsible for the autotoxicity in replanted Chinese fir tree systems in early studies [2,8]. However, such phenolic acids-based allelochemicals have been argued due to the effects of known phenolic acids with arbitrary concentrations and the neglect of other potent phytotoxins in Chinese fir tree systems. More recently, a novel cyclic dipeptide (6-hydroxy-1,3-dimethyl-8-nonadecyl-[1,4]-diazocane-2,5-diketone) was obtained by using bioassay-guided isolation technique from toxic soils of replanted Chinese fir tree ecosystem. The cyclic dipeptide inhibited Chinese fir growth at soil concentrations determined in replanted Chinese fir tree ecosystem. Therefore phenolic acids are not key allelochemicals since they are weakly phytotoxic and detected low concentrations in replanted Chinese fir tree ecosystem, while cyclic dipeptide is a highly active allelochemical with phytotoxic effect that limit offspring growth in replanted Chinese fir tree ecosystem [9].

![6-Hydroxy-1, 3-dimethyl-8-nonadecyl-[1, 4]-diazocane-2, 5-diketone](image)

Interestingly, productivity-decline and replant problem of managed tree plantations can be improved by inter-planted with certain tree species in long-term practices in China. In Northeast China, larch (*Larix gmelini* Rupr.) has been advocated for inter-planting in Manchurian walnut (*Juglans mandshurica* Maxim.) plantation that becomes a successful mixed-species plantation. There is positive interference of larch with Manchurian walnut in mixed-species plantation. Larch root exudates stimulated the biomass, chlorophyll contents and soluble sugar of Manchurian walnut seedlings [37]. In particular, larch root exudates could increase soil microbial populations including bacteria, actinomycetes, azotobacter and cellulose-decomposing microorganisms and enzyme activities of urease and polyphenol oxidase, and led to rapid degradation of phytotoxic juglone root-exuded from Manchurian walnut [38].

5. Allelopathy in Aquatic Systems

Given the harmful algae and aquatic weeds boom in various freshwater bodies, allelopathy in aquatic systems has been seriously studied in China. It was found that macrophytes and algae were antagonistic to each other in several aquatic ecosystems. Several submerged macrophytes showed allelopathic potential on the harmful algae. *Phragmites communis* could effectively inhibit the growth of *Microcystis aeruginosa* [36]. *Potamogeton malaianus* had significant allelopathic effects on the growth and physiological processes of *Scenedesmus obliquus* [35]. The growth of *S. obliquus* was significantly suppressed by the two macrophytes *P. malaianus* and *Najas minor*, but *P. malaianus* showed the stronger growth inhibition effect on *S. obliquus* than *N. minor*. *P. malaianus* obviously inhibited the photosynthetic rate of *S. obliquus*, while *N. minor* did not [5]. The novel allelochemical, ethyl 2-methylacetoacetate (EMA), isolated from the reed (*Phragmites australis*), inhibited the growth of three common species of algae, *S. obliquus*, *Selenastrum capricornutum* and *Chlamydomonas reinhardtii* [25]. In particular, EMA had multiple effects on the growth of *S. capricornutum* under different initial algal densities (IADs). The algal growth was inhibited by EMA at low IADs, but stimulated at high IADs [6]. EMA significantly inhibited the growth of *M. aeruginosa* in a concentration-dependent way. The cellular structure and metabolic activity of *M. aeruginosa* were influenced by EMA and the oxidative damage induced by EMA may be an important factor responsible for the inhibition of EMA on the growth of *M. aeruginosa* [7]. Similar results were found in another potent allelochemical pyrogallol on *M. aeruginosa*. The gene expressions and the main antioxidant enzymes measurement indicated that the oxidant damage is an important mechanism for the allelopathic effect of pyrogallol on *M. aeruginosa* [28].
Red tide occurs frequently in inner seas in China and thus allelopathy involved in species of causative bloom dinoflagellates has been investigated. Interactions between Prorocentrum donghaiense and Alexandrium tamarense, two bloom-forming dinoflagellates, were investigated using bialgal cultures. Consequently, A. tamarense could affect the growth of co-cultured P. donghaiense by producing allelochemicals [33]. Similarly, in the interactions between P. donghaiense and Scrippsiella trochoidea, P. donghaiense or S. trochoidea would release allelochemicals into the bialgal culture medium [31]. These species of microalgae interfere with each other mainly by releasing allelopathic agents into the culture medium, and a direct cell-to-cell contact was not necessary for their mutual interaction. It also was found that several marine macroalgae, such as Ulva pertusa, U. linza, U. lactua, Corallina pilulifera, Sargassum thunbergii and Gracilaria lemaneiformis, showed negative allelopathic effects on harmful bloom-forming microalgae. The fresh thalli of either U. pertusa or G. lemaneiformis significantly inhibited the growth of the red tide microalga, or caused mortality [32]. The growth of P. donghaiense was strongly inhibited by using fresh tissues and dry powder of the three macroalgae U. linza, C. pilulifera and S. thunbergii. The cells of P. donghaiense are sensitive to the allelochemicals with relatively high polarities released from these three macroalgae [30]. In nutrient replete semicontinuous co-cultures with U. lactua, red tide microalgae, Heterosigma akashiwo was completely dead in 12 days, and the growth of A. tamarense and Skeletonema costatum was reduced by 48 and 46%, respectively [26].

6. Allelopathy and Plant Invasion

Several exotic plants, such as Mikania micrantha H.B.K., Solidago canadensis L., Ambrosia trifida L. and Ageratina adenophora Spreng. (Eupatorium adenophorum Spreng.), are spreading to threat both native plant communities and agriculture in China. Allelopathic mechanism and allelochemicals of these invasive plants have are investigated in recent years.

The aqueous extracts from M. micrantha had inhibitory effects on the seed germination and seedling growth of two co-occurring woody plants (Lagerstroemia indica L. and Robinia pseudoacacia L.) in south China. Allelopathic activity depended on the concentration of the extracts, target species, and the extract sources. In particular, root extract had greater allelopathic effects on roots than leaf extract, which might greatly promote the invasion success of M. micrantha due to more direct and effective allelopathy of root [34]. Furthermore, M. micrantha could influence soil nutrients and N transformation through allelopathy. Soil beneath M. micrantha had inhibitory effects on seed germination and seedling growth of plant species, and had significantly higher C, N, ammonia, net nitrification rate than those of open soil. The water soluble allelochemicals of M. micrantha improve soil nutrient availability, through which the invasive plant M. micrantha may successfully invade and establish in new habitats [1].

S. canadensis may acquire spreading advantage in non-native habitat by using allelopathy to inhibit not only local plants but also soil-borne pathogens. Extracts from root and rhizome of S. canadensis significantly suppressed the growth and pathogenic activity of two soil-borne pathogens Pythium ultimum and Rhizoctonia solani, while native plant Calendula officinalis L. did not have allelopathic effects on these soil pathogens through root and rhizome exudation. The results from field soil experiments showed that mortality and damping-off rate of tomato seedlings were significantly lower under the soils collected from the fields dominated by S. canadensis than that dominated by native plants at both sampling sites, suggesting that suppression of pathogens also occurs in the field [40].

A. trifida infestation interferes with the growth and establishment of crop plants. Particularly in wheat fields, a heavy infestation of A. trifida resulted in adverse effects on the growth and yield of wheat in Northeast China. A. trifida-infested soils caused phytotoxicity to wheat growth. Two carotane-type sesquiterpenes, 1α-angeloyloxycarotol and 1α-(2-methylbutyroyloxy)-carotol, were subsequently isolated and identified from the toxic soils. Both sesquiterpenes at concentrations of 11.5 -16.3 μg/g soil inhibited the growth of wheat, while their amounts ranged from 13.7 to 43.2 μg/g in the A. trifida-infested soils and reached the inhibition thresholds for inhibition of wheat growth [16].

The invasive plant A. adenophora has caused great economic loss in Southwest China in recent years. A. adenophora released allelochemicals of sesquiterpenes into the habitats to interfere with the crops and native plants [41]. The allelochemicals released from A. adenophora remained in the soil and suppressed other plant species for 2 years after removal of the plants. Allelochemicals of A. adenophora can not only facilitate its invasion but also influence the efforts of ecological restoration of invaded habitats [29]. Furthermore, A. adenophora invasion strongly increased the abundance of soil VAM (vesicular-arbuscular mycorrhizal fungi) and the fungi/bacteria ratio. A. adenophora is more positively affected by the soil community associated with native communities than are resident natives, and once the invader becomes established it further alters the soil community in a way that favors itself and inhibits natives, helping to promote the invasion. Soil biota alteration after A. adenophora establishment may be an important part of its invasion process to facilitate itself and inhibit native plants [27].
7. Conclusions

The development and research of allelopathy is striving toward a future for sustainable agriculture. China is the largest agricultural country with over 800 million farmers who have very limited lands to plough. This giant challenge has made allelopathy very important in agricultural production in China. Currently, agricultural production is characterized by heavy use of synthetic herbicides. Allelopathy can definitely reduce the amount of herbicide use. However, the adoption of allelopathy and allelochemicals has to be based on our understanding of ecological principles and mechanisms. The Chinese scientists have made progress toward developing allelopathy to use as an important part of crop and weed management in several agro-ecosystems. Significant results are leading to the development of successfully ecological pest control. Even if the effectiveness and manipulation of using allelopathy and allelochemicals for pest management practices are being debated and tested, allelopathy-based research and technique offer many potential implications and applications for sustainable agriculture, especially for the low-input crop-farming systems prevailing throughout China and other Asian countries.

References


