

Allelopathy Research: Past, Present and Future--II. Managed Ecosystems

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ABSTRACT

Molish in 1937 coined Allelopathy from two Greek words, ‘allelo’ (means two organisms) and ‘pathy’ (means harm). The term defined as plant released metabolites into environment through ecological processes: volatilization, leaching, root exudation and decomposition of plant debris in soil, resulting in detrimental effects on understorey or neighbouring plants sharing the same habitat. This essay aimed to describe the allelopathy researches dealing with the allelopathy in natural and managed ecosystems in the past, present and future. The allelopathy plays an important role in managed ecosystems, particularly in agricultural productivity. The yield reduction of rice (*Oryza stiva* L.) in the second crop season was 25 to 50 % lower than the first crop season in Taiwan. This phenomenon was designated as *auto-intoxication*, which is another phase of allelopathy. The potential of allelochemicals are often modified by environmental stresses (temperature, soil pH, drought, nutrients deficiency, light and physiological or biochemical interactions) under varied environmental conditions. The action modes of allelochemicals on the structure and function of plants are via physiological and molecular interactions. Allelochemicals released from plants, microorganisms, or algae can be used as agro-chemicals (Herbicides, fungicides, nematicides and anti-pathogens), these are environmental friendly for sustainable agriculture. For example, the win-win strategy of pasture-forest intercropping results in the kikuyu grass suppresses the weed growth due to the allelopathic effects of kikuyu grass, but is good for the regeneration of chinese fir. Furthermore, the mechanisms of allelochemicals action on crops are discussed. The allelochemicals cover very broad aspects of chemical interactions among organisms, thus, the fundamental studies of natural products from organisms need trainings in multi-disciplinary sciences viz., Biology, ecology, biochemistry, organic chemistry, molecular biology, soil science and earth sciences. The authors coined a new scientific term called “*Allelochemicology*”, which hopefully, inspires young scientists in life sciences to explore this field to solve the most difficult tasks in ecology, sustainable agriculture, pharmaceutical and medicinal applications. The research finding of allelopathy, indeed, can be beneficial to human beings in reaching the Sustainable Development Goals.

Key Words: Allelochemicals, allelopathy, decomposition of plant residues, leaching, managed ecosystems, microorganisms, natural products, naturally occurring herbicide, plants, root exudation, sustainable agriculture, volatilization.

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1. INTRODUCTION

Plant secondary metabolites are released into environment by means of ecological processes; volatilization, leaching, decomposition of plant residues in soil and root exudation (8,9,60,74). Meanwhile, soil microorganisms are also involved in the decomposition of plant residues and biotransform the metabolites into other forms of products (30,106). These metabolites can directly or indirectly affect the growth of adjacent plants or microorganisms, resulting in the stimulation or inhibition of the associated plants or other organisms (94). Later, Molisch (72) studied the effects of ethylene on plant growth and coined a word “*Allelopathy*” from two Greek words “*Allelo*” (two organisms) and “*pathy*” (harm), meaning mutual harm. The definition was supported by Rice (94), who also enlarged the scope of allelopathy including microorganisms. Furthermore, Whittaker and Feeny (110) made an extensive review and created a new term “*Allelochemicals*” meaning that the chemical message between species inter- and intra- specifically. Thus, the chemical messages, such as pheromone and allomone released by insects are allelochemicals.

The definition of allelopathy seems to be not clear, thus Duke (32) and Putnam and Duke (90) pointed out the term might be technically erroneous. Muller (73) used “interference” to describe the phenomenon of plant-plant interactions, involving both competition and allelopathy. Muller defined competition as that one plant takes up a necessary physical factor(s) from habitat and hence, has deleterious effects on other plants that require the same factor(s). On the other hand, allelopathy is the process, whereby plant releases toxic compounds into the environment, resulting in detrimental effects on neighboring plants or its own plants sharing the same habitat, thus, autointoxication is another phase of allelopathy (19). Rice in 1984 published the second edition of his book *Allelopathy* based on update research in allelopathy, covering all chemical interactions between plants. Rice (1995) also published a book *Biological Control of Weeds and Plant Diseases* (95). Willis published a book on *The History of Allelopathy*, which is good for popular science and general education (111). Furthermore, Chou and Waller (20) firstly used “*Allelochemicals*” in all chemical interactions between species, thus the term has been increasingly recognized and used in recent literatures (16,20,49,52,59,66,87,105,113). Narwal (75) presented allelopathy in ecological sustainable organic agriculture and others. In fact, the allelopathy research has increasingly been attracted by scientists in different disciplinary areas (Biochemistry, microbiology, phycology, soil science, mathematics, molecular biology and biomedical sciences), to look into the complicated phenomenon of allelochemical interactions (51,109). Multiple disciplines of integrated research have to be carefully designed. Therefore, we suggest a new scientific term “*Allelochemicology*”, which will be a new scientific arena. Hopefully, it will attract young scientists in different science disciplines participation to solve the compound-complex interactions among organisms inter- and intra- specifically. For the sake of this exciting subject, we present a Series Review on the *Past, Present and Future of Allelopathy Research*, its Part I is published in *Allelopathy Journal* Volume **58 (1)** : 1-22 Januury 2023. This essay is emphasizing the

contributions of allelochemicals in managed ecosystems in particular to agriculture to meet Sustainable Development Goals (SDGs).

2. ALLELOPATHY IN AGROECOSYSTEMS

In conventional agriculture crops are grown in fields well prepared by tillage, using mechanical methods to remove rocks, stones and weeds. In addition, fertilizers are applied to the poor nutrients soil and agrochemicals are used to control crops pests to get higher productivity. Modern agricultural specialists intend to modify the soil environment for better crop growth and good yield. The applied soil fertilizers or agrochemicals are expensive and might cause environmental pollution and deterioration. In long time tillage, the soil becomes infertile and crop yields decrease. The agriculture scientists have become aware of the importance of environmental stability, hence, the concept of sustainable agriculture has increasingly been recognized as an important matter in the managed ecosystems following the principles of agroecology (44).

The sixth International Scientific Conference of the International Federation of Organic Agriculture Movements (IFOAM) held in 1986 at UC Santa Cruz, the main themes were Agroecology and Sustainable agriculture (SA). Since then, SA has increasingly received attention. Especially, after the Earth Summit held in Rio de Janeiro in 1992, the conference established the Sustainable Development (SD), in which the SA becomes one of the most important goals. The research and practical achievements of SA have been brought over the world. The SA emphasized on making efficient use of internal farm resources and minimum use of off-farm purchased inputs. It minimizes the influence of agricultural practices beyond the farm boundaries. The SA is also known as organic, alternative, regenerative, biodynamic, intensive, low-input, or resource conserving (15,38), to achieve the goal of SA, extensive researches have been done by scientists all over the world. They worked on crop protection, crop systems and particularly paid attention to applied aspect of allelopathy in agriculture practices. For example, developing transgenic rice varieties to control the neighbouring weeds (89). Gliessman (42) concluded that allelopathy can play beneficial role in multiple cropping and cover cropping. Chou (16) reported the use of allelochemicals as naturally occurring bio-agrochemicals. Fujii (40) isolated potent allelochemicals from velvet bean (*Mucuna pruriens*) and hairy vetch (*Vicia villosa*) applying to farms to suppress the growth of weeds. In addition, cover crops can be used as a preventive method in integrated pest management. Malbrendt (68) applied allelopathy in management of plant-parasitic nematodes, using a green manure crop to reduce populations of nematodes. The crop rotations are one of important agricultural practices and are advantageous to crops (45).

2.1. Rice Allelopathy

2.1.1. Auto-intoxication

2.1.1.1. Auto-intoxication mechanism of rice (*Oryza sativa*) varieties: For over a century, the yield of rice (*Oryza sativa*) crop in the second crop (from July to November) in Taiwan has been reduced 25 % to 50 % as compared to first crop (February to July)

(114). The causes of yield reduction were investigated by a thematic research group, involving plant genetics, agronomist, soil scientist, plant pathologists and climatologist, etc. The senior author proposed that the reduction of rice yield in the second crop was thought to be caused by the phytotoxins released from the submerged rice residues in soil after decomposition via microorganisms. In Taiwan, the rice crop is grown in continuous monoculture, thus the soil accumulated a significant amount of phytotoxins, resulting in the suppressive effects on the growth of second rice crop at the tiller and panicle initiation stages (17,23). The responsible phytotoxins, namely, *p*-hydroxybenzoic, *o*-hydroxyphenylacetic, vanillic, *p*-coumaric, ferulic and syringic acids were found (19). This phenomenon was designated as “auto-intoxication” that occurs in many parts of the world, such as China, India, Japan, Korea, where the continuous monoculture was practised.

Later, Kato-Noguchi (54) found a diterpenoid, momilactone B, which caused allelopathic effects upon its own or on the neighboring plants (54,99). In addition, Li *et al.* (62) found (-)-loliolide, which elicited the production of momilactone B and tricin and the loliolide acts as a signaling chemical participating in the barnyard grass-rice allelopathy interactions (62).

Nevertheless, Olofsson *et al.* (79,80) indicated that the phenolic acids were unlikely primary allelochemicals in rice. Chou does not make a debate on this contradictory argument. However, Chou *et al.* (23) pointed out that rice residues submerged in the paddy soil were decomposed and continuously released phytotoxic phenolics which were accumulated in soil. The phenomena have also been found in wheat, sorghum, sugarcane and other crops in many parts of the world, particular in Asia. McCalla (71) is one of pioneers working on the phytotoxins released from the decomposition of crop residues through microorganisms in soil.

2.1.1.2. Auto-intoxication mechanism: Allelochemicals (cinnamic and ferulic acids), inhibited the protein synthesis and the enzymes (Ammonia-lyse, cellulase, petotytic enzymes, phenylalanine ammonia lyase, pepsin dehydrogenase, etc.) activities and can be regulated by plant metabolism via transcripton processes. As mentioned earlier, autotoxicity plays an important role in regulating rice yield and quality. To understand the molecular mechanism of action mode, a large-scale transcriptome analysis of rice root response to ferulic acid was conducted by Chi *et al.* (12a). They reported the molecular mechanisms of plants in response to ferulic acid, involving toxicity, detoxification and signaling machinery clearly showed the mechanisms of autotoxicity in rice plant. This work encouraged the investigators to further clarify the mechanism of auto-intoxication.

2.1.2. Rice varieties allelopathy as weed suppressor: Presumably, the rice mutants exhibit allelopathic potential, which suppresses the neighbouring weeds, such as barnyard grass and *Leersia hexandra* (24). A wild rice, *Oryza perennis* also exhibits high allelopathic potential, that can be used as a weed suppressor (22). Oka studied the mortality and adaptive mechanisms of *Oryza perennis* and wild rice species and found some varieties exhibit

allelopathic potential (77,78). Patni *et al.* (82) and Farroq *et al.* (37) suggested that allelopathic rice plants can be a useful tool for the integrated management of weeds in agroecosystems. Macias *et al.* (65) indicated that allelopathy is a natural alternative for weed control, suggesting that the in-depth investigation of genomics and proteomics should be focussed as emerging fields in allelopathy. In fact, Chou (16) indicated that the allelopathic compounds, such as phenolics, terpenoids and alkaloids, can be developed as naturally occurring herbicide that was later supported by Macias *et al.* (65). Furthermore, Qi *et al.* (92) indicated that allelochemicals from invasive *Wedelia* plants could be potentially developed into pesticide and anti-pathogen. Hegazy *et al.* (48) also reported that the *Anastatica hierochuntica* showed allelopathic and autotoxic effects on test plants, suggesting that the plant can also be used as weed suppressor.

Seal *et al.* (98) reported that 15 putative allelopathic compounds were isolated and identified from root exudates of both allelopathic and non-allelopathic rice varieties and their phytotoxicities were evaluated. Nevertheless, the research on “rice allelopathy” becomes very attractive to different discipline scientists, hence, literature is increasing. For examples, Ebana and Okuno (33) made an extensive review on *Rice Allelopathy* and evaluate the phytotoxicity of two rice varieties, PI312777 and Rexmont, showing weed suppressive effects in the field but the latter was less inhibitory. They also indicated that these two varieties might have different metabolism, resulting in the difference in the quantity and/ or quality of allelochemicals. Dilday *et al.* (31) assayed the allelopathic activity among rice germplasm collections of the USDA-ARS and found that the phytotoxicity varied with strains, indicating that the degree of toxicity was regulated by genetics. Song *et al.* (100) indicated that the PI312777 exhibited strong ability to suppress target weed, especially in low nutrient conditions, suggesting that the strong interaction of the gene function in the *de novo* synthesis of allelochemicals.

The inhibitory effects of 13 representative compounds isolated from allelopathic rice seedlings PI312777 on the growth of major weeds (*Echinochloa crus-galli*, *Cyperus difformis* and *Leptochloa chinensis*) was assayed and found that cyclohexene and urea derivatives exhibited significant inhibition on tested plants. Other compounds showed inhibition but varied with the concentration of each compound (59).

In conclusion, the frontier of *Rice Allelopathy* research should be conducted, using rice mutants of transgenic rice plants or weeds for naturally occurring herbicides (15,16).

2.2. Wheat Allelopathy

Wheat (*Triticum* spp.) is one of the most important crops for human food and has become a focus of allelopathic research in past decades. Haig (46) made a comprehensive review on allelopathy of wheat, which has been officially recognized by the Commission of European Communities and established a project “FATEAIIICHEM” (Fate and Toxicity of Allelochemicals) in relation to environment and consumer. Five objectives were focussed (Fomsgarrd, 2004) (see Ref. 46), these guidelines would be good reference for allelopathic researchers in the future. The allelochemicals found in wheat are phenolic acids [salicylic, vanillic gallic, ferulic, caffeic and *p*-coumaric acids (7,34,35,50)], their concentrations

ranged from 0.1 to 1.0 mM for phytotoxicity, indicating that the above concentration was too high to be used as herbicide. Recently, using MS/MS and GC/MS/MS techniques via trimethylsilyl derivatization, the sensitivity and selectivity was found to be great (46). Furthermore, the allelochemicals metabolites from wheat were completely degraded into DIMBOA in wheat crop soil and the degradation pattern varied with wheat cultivars. Phytotoxicity of aqueous extracts of harvested rye tissue correlated with the levels of DIBOA recorded, which varied with harvest date and the level was particularly high in the late harvest season (4,93). In 58 wheat accessions, 7-known phenolic acids were found in wheat tissues and these compounds were allelopathic to the growth of annual rye grass (4,113). Wallace and Elliott (102) isolated phytotoxins from anaerobically decomposing wheat straw, most of the phytotoxins were phenolics.

Macias *et al.* (66,67) did a series of allelopathy studies in Spain and isolated several new allelochemicals from *Pilocarpus goudotianus* and *Melilotus messanensis*. An enzymatic decarboxylation of coumaric acid may convert it to 4-hydroxystyrenes, which exhibited significant bioactivity. The allelopathy of durum wheat (*Triticum turgium* Durum) was used as a crop-breeding tool to develop varieties to improve the biological weed control (39). Furthermore, Blum *et al.* (6) indicated that allelopathic activity varied with development of soil extract bioassays in wheat-conventional and wheat-no-till soils.

2.3. Allelopathy in Other Crops

Chou and Young (21) evaluated the phytotoxicity of 12-subtropical grasses by aqueous extracts or leachates of the grasses and found that *Digitaria decumlers* (pangola grass) exhibited the highest phytotoxicity on tested species at low osmotic concentration of 10 mosmols. Pangola grass has been introduced to Taiwan as an important feed pasture for livestock for more than five decades, however, under continuous monoculture practice, the productivity of the grass declines due to certain degree of autotoxicity produced by the grass (18,63,81,85). Nevertheless, after field treatment of alternative pangola-alfalfa intercropping practice, decreased the autotoxicity and thus restored the productivity of grass (13). The autotoxic phenomenon was also found in other monoculture crops [sugar cane (109), asparagus (115), oats (53)]. In addition, alfalfa (*Medicago sativa*) contains saponin, showing allelopathic properties of anti-fungal and hemolytic activities. Young (115) demonstrated the mechanism of auto-intoxication of asparagus (*Asparagus officinalis*). Hartung *et al.* (47) further isolated phytotoxic compounds from asparagus and characterized the allelopathic activity. Lovett and Houlton (64) demonstrated allelopathy and self-defense in barley. Chou *et al.* (29) and Waller *et al.* (103) conducted experiments, showing allelochemicals activity of naturally occurring compounds from mungbean (*Vigna radiata*) plants and their surrounding soil. Indeed, there are many agronomic crops exhibiting allelopathic potential to act as self-defense or allelopathy as far as evolution is concerned.

2.4. Allelopathy Modified by Environmental Stresses

Plants are able to grow in different environmental stresses [temperature, soil pH, water stress, oxygen deficiency, poor drainage paddy soil, nutrient deficiency, heavy metal, light quality and quantity, etc.]. The growth performance of crops depends on their adaptive

mechanisms to these environmental factors. The quantity of allelochemicals can be regulated by the stressful environmental factors as mentioned above. However, the allelochemicals, such as short chain fatty acids, phenolic, flavonoids, terpenoid, or alkaloids, can be bounded or polymerized with soil humic acids and clay minerals to form organo-mineral complex, which may lose their phytotoxic activity. On the contrary, the compound-complex structure can be de-polymerized and converted to simple organic acids through microbial transformation, resulting in allelopathic activity (107,108). Hereinafter, we like to present several unique cases, concerning the plants growth under specific environmental stresses.

2.4.1. Allelopathy affected by water stresses: In good drained paddy field, the rice plants grow healthy and give high yield, while in the poor drainage field the yield is low. The yield reduction is due to the accumulation of phytotoxins released from the decomposition of rice residues in soil as mentioned before. The amount of phytotoxins were significantly higher in oxygen deficient soil, leading to autointoxication of *Oryza sativa* (17,25). Because of the phytotoxins accumulated in paddy soil, the soil redox potential tends to be lower, leading to low soil pH (26), resulting in auto-intoxication and reduced the rice yield in the second crop season. To get high rice yield, it is necessary to remove the phytotoxins by improving the drainage system or applying calcium salt or other minerals to neutralize phytotoxins in the paddy soil (15).

2.4.2. Allelopathy as affected by nutrients: Lehman and Rice (61) indicated that the chlorogenic acid and scopoletin contents are significantly affected under deficiencies of N, P and S. Chou and Chiou (17) reported that the ammonium-nitrogen fertilizer may overcome the phytotoxic effects of decomposing rice residues in soil. These findings agreed with that of Chandrasekaran and Yoshida (12), who concluded that some nutrients may chelate phytotoxins. Chou *et al.* (26) used enriched 30 % ¹⁵N-ammonium sulfate into a soil-straw mixture to study the soil N metabolism and found that phytotoxins were affected by the levels of nitrogen in soil. Without straw most of fertilizer N remained in the mineral form, indicating that straw enhanced the N immobilization only moderately. The gradual decrease in the proportion of fertilizer N in the mineral form was accompanied by a steady increase of organic N; however, accumulation of fertilizer N was found in the amino sugar or insoluble humin fraction. The findings concluded that the amount of phytotoxins released from rice residues may be regulated by doses of N fertilizers, to reduce the harmful effects of phytotoxins on plant growth.

2.4.3. Allelochemicals enhanced by nutrients deficiently stress: Waller and Nowacki (104) found that the amount of alkaloid production was significantly higher in poor nitrogen soil in Africa. This reflected that under nitrogen deficient stress condition plants released growth inhibitors, such as toxic alkaloid, caffeine and threobromine, rather than growth stimulator, such as kinetin (56,57). Einhellig (34) also made a comprehensive study on the interactive effects of allelochemicals and environmental stresses, indicating that the quantity of allelochemicals are significantly higher under the nutrients deficiency.

2.4.4. Allelochemicals enhanced by UV light and gamma radiation: The quantity of secondary metabolites, such as flavonoids, phenolics and alkaloids are significantly enhanced when plant grow under high intensity of UV light and gamma irradiation. Koeppel *et al* (58) demonstrated that the amount of scopoletin and caffeoylquinic acid of tobacco and sunflower plants grown in high-intensity UV irradiation area was significantly enhanced. Similarly, AlSaadawi *et al.* (1) indicated that *Ammaranthus retroflexus* plants placed under the increased doses, 500, 1000 and 1500 rad, of gamma radiation enhanced the allelopathic substances in root extracts and decaying residues, resulting in the suppression of seed germination and radicle growth of tested plants. Al-Saadawi *et al.* (1) further used gamma irradiation on *Sorghum bicolor* cultivars and showed that the allelopathic effect on tested weeds was noticeably high.

2.5. Allelopathy is Co-evolved or A Strategy for Plants in Stressful Environment

The subject of allelopathy in relation to evolution has little been discussed until very recently. This philosophic concept is difficult to be elucidated; however, it is important for ecologist to explore the case study. Bull *et al.* (9) recently proposed models for the directed evolution of bacterial allelopathy, using bacteriophage lysins, unfortunately, the models did not cover evolution of plant allelopathy. Uddin *et al.* (101) had elucidated the allelopathy and its co-evolutionary implications between native and non-native neighbours of invasive *Cynara cardunculus*. The results concluded that the allelochemicals induced by *C. cardunculus* exerted more suppressive effects on native than non-native plant that possibly linked to the coevolved tolerance of their environmental interactions. Unfortunately, the results were not clear enough to demonstrate the coevolution processes.

On the other hand, *Oryza sativa* survived in a poor drainage paddy field was thought to be an evolutionary strategy, allowing rice plants to self-thinning and save energy, to survive in poor environment. The common phenomena of autotoxicity of monocultural crops, such as mungbean, asparagus and sugarcane, perhaps take the same strategy for survival as far as coevolution is concerned. Chou (15) proposed an evolutionary scheme that the allelopathy plays an intermediate role of regulating biochemical metabolism favourable for plant inhibitors either affects the neighboring plant growth (narrow allelopathic effect) or affects itself (self-thinning by auto-intoxication) (15).

Recently, Meyer *et al.* (70) indicated that plant product, juglone, is a classic case of special metabolite known to mediate numerous plant biotic interactions, such as allelopathy. The compound involves in respiration and photosynthesis of quinone metabolism probably contribute to their important evolution. Blum *et al.* (7) tried to understand the allelopathic activity in conventional wheat and No tillage wheat soils, that developed a soil bioassay to study soil allelopathy (10).

The above findings strongly suggested that plants may adapt their growth in variable habitats particularly in stressful environment. Newman (76) pointed out that natural selection has specially favoured the development of allelopathic potential in plants. Recently, Marusa *et al.* (69) reported that a common weed, *Senna obtusifolia*, grown in subtropical and tropical region is able to germinate under adverse environmental conditions, indicating

that this species has efficient stress adaptation strategies. They found that shortly after germination the plant mitochondrial respiratory activity was active, leading to alcohol dehydrogenase (ADH), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (AP) and glutathione were noticeably found, indicating that the allelopathic compounds of the plant may actively promote enzyme activity as the survival strategy to adapt to variable environment.

2.5.1. Modification of allelochemicals effects through biochemical and physiological processes: Bi *et al.* (5) indicated that methyl jasmonate and methyl salicylate induced the allelopathic activity in rice plants grown in China. The compounds enhanced the allelopathic potential and led to accumulation of phenolics which may increase enzymatic activities and gene transcription of phenylalanine ammonia-lyase (PAL) and cinnamate 4-hydroxylase (C4H) in the phenylpropanoid pathway. This investigation found that the allelopathic rice plant, such as rice variety IAC165, is a putative allelopathy plant. The findings of PAL act as a positive regulator of rice allelopathic potential that are highly possible to be practically used in agroecosystems. Further study should be conducted on allelopathic potential of rice was regulated by various genes, including encode-transcription factors, such as MYB57 (36).

3. SUSTAINABLE AGRICULTURE

3.1. Allelopathy in Weeds and Pests Management

The mixture of allelopathic water extracts are more effective than the application of single plant extract, reflecting that the combination of different plant extracts may involve variety of chemicals, such as phenolic acids, flavonoids and /or terpenoids, resulting in additive toxic effects (88). Furthermore, *Agrostemin* is a natural agrochemical from the corn cockle (*Agrostemma githago* L.) and was applied as plant growth regulator and weed controller in eastern European countries (52). The allelopathic substances are often environmental friendly and are alternatively used as pesticide in agricultural pest management (37). The use of allelochemicals to control weeds, insects and pathogens do not lead to development of resistance in these organisms (49). Regarding the integrated management (IM) in agroecosystems, rice allelopathy can be useful for weed control and to improve crop yield. It is assumed that the allelopathic phenolics can solve various ecological problems especially in sustainable agriculture of forest, nature resource and environmental conservation.

Many examples have shown that allelopathic plants can be used as naturally occurring herbicide under variable field conditions, indicating that napropamide (a chiral acetamide herbicide) is commonly applied to control *Echinochloa cruz-galli* in maize crop (116). Regarding the integrated pest management (IMP), allelopathy is highly useful in crop production, based on chemical ecology in cereal-livestock farming system (55). Recently, Kong *et al.* (59) reviewed allelochemicals and signalling chemicals in plants, indicating that allelochemicals participate in the plants defence against microbial attack, herbivore

predation, and/or competition with other plants are noticeable in allelopathy. In addition, allelochemicals and signalling chemicals take place both in aboveground and belowground. They concluded that plant derived allelochemicals and signalling chemicals are important in agricultural pest management.

Malbrendt (68) successfully applied the allelopathy to control plant-parasitic nematode *Xiphinera americanum* by some crop rotations. Furthermore, Rusher and Hay (96) first demonstrated that induced allelopathy in a seaweed could reduce seaweed chemical defence against herbivores, but many seaweeds and terrestrial plants induced chemical defenses against competitors remains poorly understood.

3.1.1. Cover plants suppress weed growth: Many cover grasses exhibited allelopathic potential which can be applied on the farm to suppress the competitive weeds. The hairy vetch (*Vicia villosa*), one of the cover grasses, applied to the farm suppresses the weed growth (40). Another case is cover grass-orchard tree intercropping system, exhibiting allelopathic potential of cover grasses released allelochemicals to suppress the weeds growth underneath *Pyrus lindleyi* (15). The aqueous leachates of *Dactylis glomerata*, *Bromus catharticus*, *Lolium multiflorum* and *Eragrostis curvula*, suppress the weeds growth but do not affect the growth of *Pyrus* seedlings. Advancing cover cropping in temperate integrated weed management was conducted by Fujii *et al.* (40) reported that cover crops suppressed 70-75 % of weeds in volunteer crops, between the two crops during the seasons of fall to spring (40).

3.1.2. Allelopathy in cover grasses and orchard trees intercropping: In the past, orchard farmers often thought that the cover grasses might affect the growth of orchard trees, thus they often clean the weeds underneath the orchard trees. It is good to avoid the competitive interaction for water and nutrient uptake between weeds and tree; however, if we grow a cover grass instead of weed, the cover grass may benefit the growth of orchard trees. Chou (14) had conducted experiments in the Mei-Feng Highland Experimental Station, National Taiwan University. We selected 9-test cover plants [*Bromus catharticus* (Bc), *Dactylis glomerata* (Dg), *Eragrostis curvula* (Ec), *Lolium multiflorum* (Lm), *L. perenne* (Lp), *Paspalum notatum* (Pn), *P. dilatatum* (Pd), *Pennisetum clandestinum* (Pc) and *Triflorum repens* (Tr)] and prepared one aqueous leachate, to study their effects on the seedling growth of 10 cm tall *Pyrus lindleyi*. Aqueous leachate collected from soil without the aforementioned grasses was used as a control (14). The *Pyrus* seedling growth was stimulated by four cover grass leachates, such as Dg, Bc, Lm and Ec, whereas remaining leachates cause little inhibition in *Pyrus* seedlings (14). The findings concluded that the growth of orchard tree seedlings was stimulated by the selective cover grasses as mentioned. Thus, the selective cover grasses are good for orchard plant and the growth of cover grass is certainly good to prevent soil erosion in heavy rainfall areas.

3.1.3. Allelopathy in pasture-forest intercropping: Allelopathic interactions in a pasture-forest intercropping system were studied by Chou *et al* (28). In the forest plantation in Taiwan, *Cunninghamia lanceolata* (Chinese fir) is usually deforested every

30-years. After deforestation, the fir was replanted or regenerated, meanwhile, the field was cleared of fir litter and weeds and applied herbicides which deteriorated the environment. We introduced *Pennisetum clandestinum* grass in the deforested land, it suppressed the weeds growth and allowed the fir regeneration (28).

Moreover, another experiment was done in a pasture-hardwood forest intercropping by eight field treatments; planted with kikuyu grass and planted with *Cinnamomum camphora*, *Alnus formosana* and *Zelkova formosana* as described in the earlier section. The kikuyu grass decreased the growth of weeds one year after treatments, but had little effects on the seedling growth of three hardwood plants. The experiment indicated that the pasture-forest intercropping system is good for sustainable agriculture. We concluded that the three win-win strategies were successful and summarized as follows: (i) the kikuyu grass suppressed the weeds growth without application of synthetic herbicide, (ii) the kikuyu grass stimulated the growth of woody plants without applying fertilizers and (iii) the suppression of weed growth saved labour costs (27,28).

3.2. Allelopathy in Organic Farming

Schulz *et al.* (97) found benzoxazinoids in rye allelopathy was ideal case for weed control in organic farming. Exposure to benzoxazinoids (BOA) affects the transcriptome, proteome and metabolome patterns of seedlings, inhibits the germination and growth and induce death of sensitive tested species. Breeding of the weed resistance against benzoxazinoids and how allelopathic interaction are influenced by cultural practice, would provide the ways to include allelopathic rye varieties in organic cropping systems for weed control. Chou (16) described the role of allelopathy in sustainable agriculture by using allelochemicals from forest debris and allelopathic plant parts as naturally occurring bio-agrochemicals, which has been used in experimental farms. Puigi *et al.* (87) also indicated that allelochemicals released from *Eucalyptus globulus* leaves can be used as bioherbicide green manure for organic farming. Furthermore, Gliessman (44) pointed out the agricultural farming should base on the principles of agroecological concepts due to the complexity of agroecosystems that will be beneficial to sustainable agriculture.

3.3. Allelochemicals in Soils from Different Crop Systems

Cast *et al.* (11) studied the allelochemicals in soils from two tillage systems (non-tillage vs. conventional tillage) and found that the amount of allelochemicals was significantly lower in the conventional tillage than non-tillage. In addition, continuous single-cropping can cause soil sickness, imbalance of soil microorganisms or accumulation of toxins released from the root residues of crops and orchard trees (8,15,83,84,88,89,90). On the other hand, multiple cropping is an alternative cropping system, where one or more crops are grown simultaneously on the same land (42,43). This multiple cropping system is common component of agroecosystem management in many parts of the world (15,38,41,91). Amador and Gliessman (3) conducted a field trial to compare the biomass production of corn plants in polyculture with four densities in monoculture at two sites in Cardenas, Tabasco, Mexico. They found that the biomass production was the highest in all treatments of polyculture at a particular site. Nevertheless, the production was significantly

higher in intensive monoculture than in polyculture. This fact was possibly due to the complex ecological interactions in polyculture.

3.4. Plant Debris Use as Naturally Occurring Agrochemicals

Chou (16) attempted to use allelopathic plant parts, leaves, flowers, stems, litter or plant debris as source to make their aqueous extracts or to obtain the ground powder for naturally occurring agrochemicals. The allelopathic plants, namely *Acacia confusa*, *Alstonia scholaris*, *Leucanea leucocephala*, *Cryptomeria japonica*, *Phylostachy edulis*, *Litchi chinensis* and *Rhododendron formosanum* were used. The aqueous extracts of aforementioned plant parts and/ or plant powder were addressed or sprayed over the farm soil on lettuce, cabbage, to see the weeds response every two and four weeks after planting. The experiments were successful or failure, depending on the concentration of the extract and powder, or density of crops planting. The experimental findings indicated that the plant debris used as naturally occurring herbicide or fungicide are likely possible. There are several excellent examples being successfully used, such as *Agrostemin* in eastern European countries (52) and *Neem* plants in India (15). Such practices are beneficial to environment and human wellbeing in sustainable agriculture.

3.5. Allelopathy Benefits to Environment

Recently, the research findings indicated that the use of natural products of plant extracts from allelopathic plants are beneficial to environment without deterioration caused by use of synthetic herbicide or pesticides. For example, Al-Samarai *et al.* (2) indicated that the possibility of natural products of plant extracts can be used as herbicides for biological control to reduce environmental pollution. Worsham (112) indicated that allelopathic cover crops can reduce herbicide inputs that is a good example of benefit to environment. On the other hand, many sea weed and terrestrial plants induced chemical defences in response to herbivore but they defence also against competitors. Allelopathy still remains poorly understand, suggesting that chemical ecology of coral seaweed herbivore interactions can be greater ecological complexity that needs to be further studied (96). On the other hand, Castro-Castellon *et al.* (11) recently reported that the rhizofiltration plays an appreciable role on the removal of cyanobacters in a continuous flow system, reflecting the allelopathic effects on the growth of cyanobacters.

4. FRONTIERS OF ALLELOCHEMICALS RESEARCH

Allelochemicals are compounds released from living organisms, including plants, microorganisms and animals. These compounds act as chemical message between plant-plant, plant-microorganism, plant-insect and plant-animal. Recently, plant immunity is often being discussed that indicated does plant immunity present in crops or trees system. Pelissier *et al.* (86) initiated experiments to demonstrated that plants modify resistance to pests and pathogens between plants in their neighborhood by molecular exchanges aboveground and belowground, reflecting that the evidence is an example of plant immunity. An intriguing

relationship between allelopathy and immunity has not been fully developed and should merit further investigation.

The evidences are clear that allelochemicals performed functions not only to solve ecological problems in nature ecosystems, agroecosystems and are also beneficial to sustainable agriculture and human welfare. Therefore, we propose the following frontier of allelochemicals research:

- (i). It is needed to continuous investigation on the survey of allelopathic potential plants in managed ecosystems, including aquatic organisms. The allelochemicals in the allelopathic crops have to be isolated and structure needs to be identified precisely by advanced instruments, such as NMR and MS spectrophotometry. The newly identified compounds also need to be confirmed by bioassay and inhibition concentration of responsible compounds is expected as low as possible.
- (ii). To demonstrate the mechanism of allelopathic mode of action, the allelopathic pattern of crops need to be observed in field experiments, greenhouse experiments and lab. assays.
- (iii). The impacts of climate change on global ecosystem are increasingly important and the climate change might affect the quantity and quality of allelochemicals in managed ecosystems, particularly, some important crops should be emphasized.
- (iv). Studies on metabolomics of allelochemicals in various organisms need to be focussed to find out certain gene(s) that control the metabolic pathway(s). This will lead to get new transgenic organisms of crops which are healthy to human beings.
- (v). Allelochemicals can be used as naturally occurring herbicide, pesticides, fungicide and nematocides, etc. to apply in organic farming suitable for sustainable agriculture.
- (vi). Practical technologies for applying allelochemicals to farms are urgently needed to sustain environmental stability of agroecosystem.
- (vii). Plant immunity to pathogens via allelochemicals is a newly developed subject and can be further well developed in crops against pathogens.
- (viii). Allelochemicals are a multiple disciplinary subject that requires multidisciplinary training. It is strongly suggested to young students to take basic science courses (plant biology, molecular biology, microbiology, organic chemistry, soil sciences, ecology and earth sciences) to reinforce the scientific background. Particularly, the young students whose major in agriculture should pay more attention to the suggestion.
- (ix). A meta-analysis and statistical analysis are necessary to confirm the allelopathic effects of one species on another in particular to human health.

- (x). The advanced technologies via biochemistry, molecular biology and soil microbiology should be well developed, allowing the findings of allelopathic

research can benefit to human wellbeing to reach the Sustainable Development Goals.

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DECLARATION

We declare that all authors of this manuscript made a significant contribution, and we have not excluded any author that substantially contributed. We have followed the ethical norms established by our respective institutions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL APPROVAL

The authors declare that the study was carried out following scientific ethics and conduct. However, this study did not involve any use of animals, hence no ethical approval has been obtained from the concerned committee.

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