Bot. Bull. Acad. Sin. (1993) **34:** 211-221

(*Invited review paper*)

The role of allelopathy in the diversity of plant communities in Taiwan[1]

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Key words: Agroecology; Alkaloids; Allelopathy; Flavonoids; Phenolics; Phytotoxins; Plant communities; Plant diversity; Terpenoids.

Contents

Introduction

There is an increasing awareness of the importance of biological diversity, and concern about the loss of species and the resulting reduction in the genetic diversity of crops and wild species (Solbrig, 1991). The extinction of species is attributable primarily to the impact of human activities; only a small number of species extinctions are due to natural selection (Darwin, 1859). Both competition and allelopathy play important roles in determining the species composition

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[1]This paper was presented at the Symposium on Botany (December 7-11, 1992), in commemoration of the 30[th] anniversary of the

ous effect upon other plants that require the same factor. *Allelopathy* was coined by Molisch (1937) using two Greek words to mean the process in which a plant releases toxic chemicals to the environment and thereby has a detrimental effect upon other plants sharing the habitat (Muller, 1974). An *antibiotic* is a chemical produced by a microorganism and effective against other microorganisms. A *marasmin* is a chemical produced by a microorganism and effective against higher plants. *Phytonides* are chemicals produced by a plant that suppress the growth of microorganisms. A *koline* is a chemical produced by higher plants and effective against higher plants (Grummer, 1955).

In the early twentieth century, allelopathy research was focused on agricultural productivity (Bode, 1940; Borner, 1960; Evenari, 1949; Havis and Gilkeson, 1947; Patrick, 1955). Until the late 1960s, mention of allelopathy in texts on plant ecology referred primarily to contributions by Muller, who described a unique pattern of herb exclusion by adjacent chaparral vegetation, *Salvia leucophylla* (Muller, 1966). *S. leucophylla* releases toxic monoterpenoids, which suppress the growth of many nearby herbaceous plants, resulting in the formation of bare areas of inhibition and areas of normal growth. Muller and his students also contributed much to allelopathy research on several other chaparral shrubs (del Moral and Muller, 1969; McPherson and Muller, 1969; Cou and Muller, 1972; Gliessman and Muller, 1978) and suggested that allelopathy plays a significant role in the California fire cycle phenomenon of chaparral vegetation (Muller *et al.,* 1968). Muller concluded that the luxuriant growth of herbaceous plants in the a first growing season following a fire was due primarily to the denaturation of the allelopathic compounds from *Adenostoma fasciculatum.* The response of plants to the exudates of *Arctostaphylos glandulosa* var. *zacaensis* was less obvious, because a substantial amount of its phytotoxins was still present in the soil during the growing season after the fire (Chou and Muller, 1972; Chou, 1973). Rice and his students described a unique case study elucidating the allelopathic mechanism of old-field succession in Oklahoma (Rice, 1971, 1984). Allelopathic patterns are ubiquitous in cultivated and wild species of vegetation, from tropical rain-forest trees to desert shrubs (Chou, 1983, 1986, 1987; Muller, 1974; Rice, 1984; Waller, 1987).

Inasmuch as allelopathic research has been increasingly recognized by scientists in recent years, international symposia related to this topic have been held, resulting in the publication of several monographs (Chou and Waller, 1983; Putnam and Tang, 1986; Waller, 1987; Chou and Waller, 1989; ISCE, 1992). In the 20 years since the author returned to Taiwan, he and his co-workers have made extensive studies of allelopathy in the natural and agricultural ecosystems of subtropical and tropical regions of Asia (Chou and Young, 1975; Chou and Lin, 1976; Chou and Yang, 1982; Chou and Kuo, 1986; Chou *et al.,* 1987). This paper aims particularly to review findings on the role of allelopathy in the diversity of plant communities in Taiwan.

Allelochemicals as Regulators in Biodiversity

Secondary plant metabolites include a variety of compounds which when released from plants into the environment often attract or repel, nourish or poison other organisms. Theophrastus (372-285 BC), a disciple of Aristotle reported an example of the inhibitory effect of pigweed on alfalfa (Jelenic, 1987). Yang and Tang (1988) made an extensive review of plants used for pest control as described in *Shengnoon Ben Tsao Jing* in 25-220 A. D. in China. They found references to 267 plants containing pesticidal activity, many of them also exhibiting allelopathic potential. Lee, Shi-Jen (1518-1593 AD), a famous Chinese pharmacologist wrote a book on Chinese medicinal herbs, in which the specific toxic and remedial effects of their chemical constituents on organisms, particulary humans, were described. He also indicated that the plant constituents might play a role in plant-plant interaction and that the nature of the active compounds might be affected by habitat (Chou, 1989b). In 1832, De Candolle, a Swiss botanist, suggested that the soil sickness problem in agriculture might be due to exudates of crop plants (Rice, 1984). Later, Hoy and Stickney (1881) reported a deleterious effect by black walnut on the growth of plants nearby. Schreiner and Reed (1907, 1908) isolated soil organic acids released by plant roots that suppressed the growth of some crops. About a century after de Candolle's work, allelochemicals came into use as natural growth regulators, such as herbicides, fungicides, and pesticides, and their popularity is increasing (Chou and Waller, 1989).

Allelopathic chemicals are released into the environment by means of four ecological processes: volatilization, leaching, decomposition of plant residues in soil, and root exudation. Many secondary plant metabolites attracted scientists, particularly organic chemists, to the study of their structure, biosynthesis, and natural distribution, but not to that of function until Fraenkel (1959) and Whittaker and Feeny (1971) pointed out the important functions of secondary metabolites in plants and in ecosystems. Since then, secondary metabolites have no longer been regarded as metabolic waste. Waller and Nowacki (1975) noted that plants growing in nitrogen-poor soil produced high levels of alkaloids which are toxic to many organisms. In addition, Koeppe (1976) found that increased amounts of allelopathic substances were also produced when plants grew in phosphorus deficient soil. There is evidence that secondary plant metabolites are often stored in vacuoles or intercellular spaces when they are not being used. However, the compounds may be freely released to the cells or to the surface of leaves for defense, attraction, or as chemical signals. Even more, such compounds act as messages in plant-insect interaction, and have an important role in the mechanisms of plant adaptation and insect co-evolution (Ehrlich and Raven, 1965; Harborne, 1977). Whittaker and Feeny (1971) further stated that "chemical agents are of major significance in adaptation of species and orga-

survive two severe winters at the higher elevation. The growth performance and ecological adaptation of *M. transmorrisonensis* has resulted in excellent survival at low temperatures in Yushan National Park (Chou *et al.,* 1991). Both species developed relatively pure stands, and the allelopathic potentials were investigated (Chou and Chung, 1974; Chou and Lee, 1991).

Regarding the dominance of *Miscanthus floridulus* in fields, Chou and Chung (1974) found that about 30% of the canopy between the bunches of *Miscanthus* was free of any plants. The number of *M. floridulus* seedlings per square meter was 25.2, while the number was as low as 6.1 for *Lactuca* spp. and less than 2 for the remainding nine species, indicating a relatively low diversity in the *Miscanthus* stand. The leachate of leaves of *M. floridulus* caused significant inhibition of the growth of lettuce. The aqueous extract of leaves and soil from the *Miscanthus* area also showed phytotoxic effect. The phytotoxic substances responsible were identified; most of them were phenolic acids (Chou and Chung, 1974). It was concluded that the mechanism of dominance, in terms of low species diversity, was due primairly to the allelopathic effect.

On the other hand, in a Tatachia Anpu study site the relative frequency and relative coverage of *M. transmorrisonensis* was significantly higher than those of

Regarding other tropical and subtropical grasses in Taiwan, Chou and Young (1975) evaluated the phytotoxic nature of metabolites leached from 12 subtropical grasses and found that *Digitaria decumbens* (pangola grass) produced the highest phytotoxicity, leachates being active even at osmotic concentrations as low as 10 milliosmols. Liang *et al.* (1983) assayed 8 cultivars of pangola grass and found that the phytotoxicity of leachates varied with cultivar and habitat; *Digitaria decumbens* A254 and A24 having the highest phytotoxicity. Chou and Lee (1988) further compared the allelopathic potential of these two pangola grasses and two weed species, *Panicum repens* and *Imperata cylindrica.* They were treated with different levels of nitrogen fertilizer and were irrigated with leachates. The leachate of *Digitaria decumbens* A254 generally exhibited high phytotoxicity regardless of the levels of nitrogen fertilizer dressing. Chou (1989a) further confirmed that the leachate of *Digitaria decumbens* was toxic to the growth of the plant itself, due primarily to phytotoxic phenolic acids and some unidentified nitrogen-containing organic acids (Chou, 1977). The autotoxic effect could be responsible for the reduction in yield of pangola grasses observed for several years (usually 5 to 7) after planting in the Hengchun area (Chou, 1983).

Allelopathic Exclusion of Understory Species by Dominant Woody Species

Allelopathic Dominance of Woody Species in Northern Taiwan

Under the canopies of 25 dominant types of woody plants in northern Taiwan, particularly in the Taipei vicinity, there often are bare areas or a total lack of understory growth. The phenomenon was thought to be due to an allelopathic effect and experiments were conducted to test the allelopathy hypothesis. Chou and Chen (1976) concluded that the leachates and extracts of plant parts of some species, *Bauhinia purpurea, Bridelia balansae, Ficus gibbosa, F. retusa, F. vasculosa, Glochidion fortunei, Phyllostachys makinoi, Psidium* some, such as *Bambusa oldahamii, Phyllostachys edulis, Dendrocalamus densiflorius,* and *S. oldahamii*, that showed remarkably high phytotoxicity. This was confirmed by Chou and Yang (1982), who showed that the leachate of *P. edulis* (bamboo) contains significant amounts of allelopathic compounds that could depress the growth of understory weeds. Under the same edaphic and climatic conditions, however, weeds underneath *Cryptomeria japonica* (conifer) grew luxuriantly even though the light intensity was lower under the canopy of the conifer than under that of the bamboo. Light therefore was not a limiting factor in the regulation of the population dynamics of understory species beneath the bamboo plants, while allelopathy played an appreciable role therein.

Allelopathic Exclusion of Understory Plants by ***Leucaena leucocephala***

In addition to the aforementioned cases, there was an almost total lack of weed species under the canopy of *L. leucocephala* several years after the establishment of a *Leucaena* plantation. However, in the adjacent grassland control site the number and coverage of weed species were much higher, indicating that plant diversity was significantly depressed by *Leucaena.* Chou and Kuo (1986) demonstrated that the low diversity of plants at the *Leucaena* site in Kaoshu was due primarily to allelopathic effects. The leaf leachate of *L. leucocephala* suppressed the growth of the local weeds, *Ageratum conyzoides* and *Mimosa putica,* as well as that of lettuce, and that of the woody plants *Acacia confusa, Casuarina glauca.* and *Alnus formosana.* However, seedlings of *L. leucocephala* were not affected by the leachates or extracts, indicating that the allelopathic substances released from *L. leucocephala* were responsible for the low diversity of vegetation underneath *L. leucocephala.* The responsible allelopathic compounds were identified as minosine, pyridine-3,4-diol, and several phenolic acids (Chou and Kuo, 1986).

Allelopathic Inhibition of Weed Species by ***Delonix***

understory species was lower under *D. regia,* indicating suppression. A series of aqueous extracts of the leaves, flowers, and twigs of *D. regia* were bioassayed against [illegible] tested species to determine their phytotoxicity

and the results showed the highest level and inhibition by the extracts of the flowers. The aqueous extracts were also toxic to two local weeds, *Isachene nipponensis* and *Centella asiatica.* The allelopathic substances in the plant parts of *D. regia* were identified as 4-hydroxybenzoic, chlorogenic, 3,4-dihydroxybenzoic, gallic, 3,4-dihydroxycinnamic, 3,5-dinitrobenzoic, and *L*-azetidine-3-carboxylic acids, and 3,4-dihydroxybenzaldehyde (Chou and Leu, 1992).

The allelopathic substances released by the above-mentioned grasses and woody plants are water soluble; those that have been identified are phenolic acids, flavonoids, and alkaloids. Phenolic acids in particular, such as *p*-hydroxybenzoic, vanillic, *p*-coumaric, and ferulic acids, are ubiquitously distributed among many grasses. These compounds when released into the soil may accumulate in soil micelles or be fixed by humic acids, which play an important role in the regulation of plant growth. Water-soluble alakloids, such as mimosine, 3,4-pyridinediol, *L*-azetidine-3-carboxylic

ing greatly in life-history traits among its varieties (Oka and Morishima, 1967; Oka, 1976). *Leersia hexandra* Sw. is a perennial grass with short rhizomes, commonly found in marshy habitats in Taiwan and other

tropical Asian countries. It is a companion plant of *O. perennis* in about 40 percent of the habitats observed in India and Thailand (Morishima *et al.,* 1980).

Three small populations of *O. perennis* which were hybrid swarms with *O. sativa* (Oka and Chang, 1961) had existed in Taiwanese marshes along natural streams at Patu, Taoyuan Hsien, but they became extinct around 1975 ofter being displaced by *L. hexandra* (cf. Kiang *et al.,* 1979). An experimental introduction of this wild rice into a variety of denuded lowland habitats demonstrated that *L. hexandra* was a key species determining the successful regeneration of the wild rice, suggesting that the niches of *O. perennis* and *L. hexandra* overlap (Oka, 1984).

Adaptive Autotoxic Mechanism of Yield Reduction in Rice Plants

The author and his associates conducted a series of experiments to elucidate the mechanism of yield reduction. They demonstrated that when rice straw (even

(Chinese fir), a split plot treatment (litter removed, lit- [illegible] and litter retained and kikuyu grass planted) was instituted. Field experiments showed that fir litter left on the ground slightly suppressed the growth of weeds in the four months following deforestation, while kikuyu grass significantly suppressed the growth of weeds for more than four months. Neither fir litter nor kikuyu grass reduced the growth of fir seedlings. Bioassay of aqueous extracts of fresh fir leaves, fir litter, and kikuyu grass showed that the fresh leaves exhibited significant phytotoxicity, while litter and kikuyu grass were less toxic. Nine phytotoxic phenolics and many unidentified flavonoids were found in the plant materials (Chou *et al.*, 1987).

In addition to the above experiments, the allelopathic interaction between kikuyu grass and three hardwood forest species (*Alnus formosana, Cinnamomum camphora*, and *Zelkova formosana*) was also

Highland Experiment Station farm of National Tai- [illegible] itive and allelopathic natures of cover grasses, namely: *Bromus catharticus, Dactylis glomerata, Eragrotis curvula, Lolium multiflorum, L. perenne, Paspalum notatum, P. dilatatum, Pennisetum clandestinum*, and *Triflorum repens* (Chou, 1988). The soil leachate of each grass was used for watering pear seedlings (*Pyrus lindleyi*) of about 10 cm in height. Leachate collected from soil without grass was used as a control. Some *Pyrus* seedlings were planted in soil with fertilizer and some in soil without fertilizer. When they were grown in fertilized soil the growth of the *Pyrus* seedlings was stimulated by each of the leachates. When they were grown in soil without fertilizer their growth was stimulated by only four of the leachates (*D. glomerata, B. catharticus, L. multiflorum*, and *E. curvula*) (Chou, 1988). The remaining leachates, however, caused little inhibition of seedling growth. The effect of three cover

Effect of Nutrients on Production of Allelopathic Compounds

Wu and her co-workers (1976) conducted field experiments in the poorly drained paddy soil of Lotung in eastern Taiwan by applying ammonium sulfate, lime, and green manure to compare the phytotoxic effects of rice residues decomposing in the soil. The paddy soil treated with lime produced significantly higher yields than that treated otherwise. The increased rice yield was considered to be due simply to the conversion of phytotoxins into nontoxic substances. Chou and Chiou (1979) reported that ammonium sulfate fertilizer produced higher yields of rice than did nitrate-nitrogen fertilizer, indicating that the ammonium-nitrogen fertilizer may overcome the phytotoxic effects of decomposing rice residues in the soil. This agreed with the findings of Chandrasekaran and Yoshida (1973), who concluded that some nutrients may chelate the phytotoxins. Chou *et al.* (1981) incorporated 30% enriched ^{15}N-ammonium sulfate into a soil -straw mixture to study the behavior of soil phytotoxins as affected by the levels of nitrogen in soil. In the absence of straw, most of the fertilizer N remained in the mineral form. Straw enhanced N immobilization only moderately. The gradual decrease in the proportion of fertilizer N in the mineral form was accompanied by a steady increase of fertilizer N in the amino acid fraction of organic N. Little accumulation of fertilizer N in the amino sugar or insoluble humin fraction was found. These findings indicated that the amount of phytotoxic substances released from plant parts may be influenced by levels of nutrients leading to different degrees of phytotoxic effect on plant growth.

Dynamics of Allelopathic Compounds in Soil

Under natural conditions, allelopathic compounds released into soil may be quickly converted to a nontoxic form through abiotic or biotic processes. The phytotoxic phenolics rapidly bind with soil minerals and form so-called "organic-mineral complexes", part of the humic substances (Wang *et al.,* 1971, 1978, 1983). Formation of humic substances has long been recognized as a biological process (Wang *et al.,* 1986). However, many observations have showed the heterogeneous catalytic effect of clay minerals on the polymerization of phenolics (Scheffer *et al.,* 1959; Ziechmann, 1959; Kumada and Kato, 1970; Wang *et al.,* 1986). In particular, Wang *et al.* (1986) made an extensive study of the role of soil minerals in the abiotic polymerization of phenolic compounds and the formation of humic substances. They used suspension and plate methods (Wang *et al.,* 1983) to study the synthesis of humic substances and concluded that the polymerization of vicinal dihydric and trihydric phenolic compounds was accelerated in the presence of clay minerals. Polymer formation was not the only reaction taking place in the various systems, however; humic substances were formed by oxidation, by the formation of anions and radicals, as well as by polymerization. Decomposition and mineralization of the various intermediate products and even of humic substances may take place. Oxidative ring cleavage and the formation of low -molecular-weight products with acidic character are also possible. The relative importance of abiotic and biotic processes in the formation of humic substances may depend on soil parent materials, the nature of soil inorganic components, climatic and topographic conditions, plant cover, microbial population and activity, and land utilization practices. Chou (1987) further considered that the polymerization of phytotoxic phenolics by clay minerals is an important ecological phenomenon. The nature of polymerization and depolymerization of allelopathic compounds via humic acids needs to be throughly investigated to clarify the mechanism of soil organic-mineral complex formation. The natural organomineral complexes of humic acid may actually be a pool serving to detoxify allelopathic substances released from plants. Of course, the capacity of humic acid to function in this way depends totally upon the physicochemical nature of the soil as well as the degree of microbial activity in soil (Chou, 1989b).

Acknowledgements. The author is grateful to his former assistants and colleagues from the Taiwan Livestock Research Institute and the Hoshe Forest Experiment Station of National Taiwan University for their laboratory and field assistance. Acknowledgement is also due to Academia Sinica in Taipei, the National Science Council, and the Council of Agriculture of the Republic of China on Taiwan for financial support.

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