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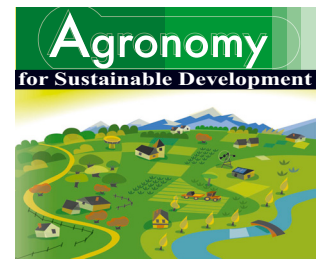
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Review article

Allelopathy in Compositae plants. A review

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Abstract – Allelopathy plays an major role in agricultural management such as weed control, crop protection, and crop re-establishment. Compositae plants have potent allelopathic activity, and the activity is confirmed through (a) bioassays with aqueous or various solvent extracts and residues, (b) fractionation, identification, and quantification of causative allelochemicals, and (c) mechanism studies on the allelochemicals. Most assessments of allelopathy involve bioassays of plant or soil extracts, leachates, fractions, and residues based on seed germination and seedling growth in laboratory and greenhouse experiments. Plant growth may be stimulated below the allelopathic threshold, but severe growth reductions may be observed above the threshold concentration depending upon the sensitivity of the receiving species. Generally germination is less sensitive than is seedling growth, especially root growth. Some approaches showed that field soil collected under donor plants significantly reduced or somewhat promoted growth of the test plants. Petri-dish bioassays with methanol extracts or fractions and causative phenolic allelochemicals showed significant phytotoxic activities in concentration-dependent manner. Delayed seed germination and slow root growth due to the extracts could be confounded with osmotic effects on rate of imbibition, delayed initiation of germination, and especially cell elongation; the main factor that affects root growth before and after the tip penetrates the seed coat. Light and electron microscopic approaches extract evaluation at the ultrastructural level have been precisely investigated. Many Compositae plants have allelopathic potentials, and the activities and types and amount of causative compounds differ depending on the plant species. The incorporation of allelopathic substances into agricultural management may reduce the use of pesticides and lessen environmental deterioration.

allelopathy / Compositae plants / eco-friendly weed control / bioassay / extracts / fractions / residues / water-soluble / activation mechanism / phenol compounds

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1. INTRODUCTION

Allelopathy was defined by Molisch (1937) as a chemical interaction between plants or sometimes between microbes and higher plants that includes stimulatory as well as inhibitory influences. Later it was defined as any direct or indirect, harmful or beneficial effect of one plant as a donor plant on another as a recipient plant through the production of chemical compounds that escape into the environment (Rice, 1984). When a plant produces allelopathic compounds that are detrimental to establishment of new seedlings of the same species, the effect is called autotoxicity which is a specialized intraspecific form of allelopathy. Allelopathy and autotoxicity can play significant roles under both natural and manipulated ecosystems (Rice, 1984), mainly by adversely affecting seed germination and seedling growth. Allelopathic interactions among plants have been observed for centuries even though few specific allelochemicals have been identified.

Allelopathy plays a key role in weed control, crop protection, and crop re-establishment. Suitable manipulation of allelopathy towards improvement of crop productivity and environmental protection through eco-friendly control of weeds, pests, crop diseases, conservation of nitrogen in crop land, and synthesis of novel agrochemicals based on natural products have gained prominent attention of scientists engaged in allelopathic research. The allelochemicals can affect physiological functions like respiration, photosynthesis and ion uptake. More recently, however, scientific attention has also been drawn to exploit the positive significant roles of allelopathy and what role this phenomenon can play in enhancing crop productivity.

A serious problem of modern agriculture is crop loss caused by weeds. Worldwide, weeds alone cause a 10% loss of agriculture production (Altieri and Liebman, 1988). Yet, allelopathic principles of crops can be used as an alternative mean of weed control based on natural products. Although allelopathy is often considered a problem for agriculture, there is now considerable evidence to suggest that it might be exploited to help manage weed problems in a variety of agroecosystems. In agroecosystems, several weeds, crops, agroforestry trees and fruit trees have been shown to exert allelopathic influence on associated or subsequent crops, thus, affecting their germination and growth adversely (Kohli et al., 1993). Most allelopathic evidence has been associated with the effect of weeds on crops and crops on crops, and crops on weeds. Of these, an important economical potential of allelopathy may be the ability of crops to suppress weeds. Allelopathic weeds also can affect crops by a number of ways like delaying or preventing seed germination and reducing seedling growth. Approaches that have already been explored are selection for allelopathic types within the germplasm of crops, use of allelopathic rotational or companion plants in cropping systems, and biosynthesis of useful natural herbicides from higher plants and microorganisms.

Alternatives to synthetic chemical herbicides need to be developed, especially for organic or eco-friendly farming operations, landscape management systems, home gardens, and

for situations where public policies mandate reduced pesticide use. Most studies on allelopathy have focused on interference and allelopathic effects of several important weeds on crop yields. Several weeds have been shown to have allelopathic potentials and others are suspected to have allelopathic potential in agro-ecosystems (Rice, 1984). Plant seedlings of various crops possess allelopathic potential or weed-suppressing activity, including cucumber (*Cucumis sativus* L.) (Putnam and Duke, 1974), oat (*Avena spp.*) (Fay and Duke, 1977) and rice (*Oryza sativa* L.) (Dilday et al., 1994; Olofsdotter and Navarez, 1996). A total of 538 accessions of cultivated and wild cucumber were screened in pot and field tests with several accessions causing inhibited growth of *Brassica hirta* and *Panicum miliaceum* (Putnam and Duke, 1974). Out of more than 3000 accessions of oat, several exuded a large amount of an allelochemical, scopoletin (Fay and Duke, 1977). Also oat suppressed the growth of *Erysimum cheiranthoides* in both laboratory and field tests due at least in part to an allelopathic mechanism (Markova, 1972).

Improving the competitive ability of crops also reduces dependency on herbicides. However, attempts to increase competitive ability while maintaining productivity have had limited success and no crop cultivar has been released with superior competing ability as a marketing argument. In crop competition including allelopathy, the importance of chemical interference has often been discussed (Rice, 1995). The incorporation of an allelopathic character into a crop cultivar could provide the plant with a means of gaining a competitive advantage over certain important weeds (Putnam and Duke, 1974). Wu et al. (1999) suggested that genetically improving crops with allelopathic potential and the allelopathy can play an important role in future weed management.

2. ALLELOPATHIC COMPOSITAE PLANTS

Twelve weed families include 68% of the 200 species that are the most important world weeds. Of them, Compositae plants account for 16% of the world's worst weeds are included (Holm, 1978). Allelopathy in weeds has been found in a number of plants employing various laboratory assays. Some of previous studies on allelopathic effects of weeds have been several Compositae plant species such as *Artemisia*, *Cirsium*, *Lactuca* and *Xanthium* species.

Inam et al. (1987) reported that aqueous extracts of *Xanthium strumarium* from different plant parts reduce germination, early growth and dry weight of *Brassica campestris*, *Lactuca sativa*, and *Pennisetum americanum*. *Parthenium hysterophorus* is also known to be very allelopathic to wheat (Kanchan and Jayachandra, 1979), soybean, and corn (Mersie and Singh, 1978). Extracts and residues of these plants significantly reduced germination and root and shoot dry weight of the test plants. Bendall (1975) studied water and ethanol extracts and residues in soil and concluded that an allelopathic mechanism might be involved in the exclusion of some annual thistle (*Carduus crispus* L.), pasture, and crop species in areas infested with *Cirsium arvense* (L.) Scop. *C. arvense* litter

Table I. Effects of aqueous extracts from several *Compositae* plants on alfalfa root length (mm) 6 days after seeding. Root length of untreated control was 34.6 mm. Adapted from Chon et al. (2003a).

Plant species	Extract concentration, g L ⁻¹			
	10	20	30	40
<i>Bidens frondosa</i>	44.3 (128)	39.7 (115)	31.4 (91)	7.1 (20)
<i>Breea segetum</i>	42.1 (122)	43.7 (126)	28.2 (81)	8.8 (25)
<i>Chrysanthemum indicum</i>	41.2 (119)	45.9 (133)	35.3 (102)	26.5 (76)
<i>Youngia sonchifolia</i>	43.5 (126)	40.1 (116)	36.5 (105)	27.4 (79)
<i>Eclipta prostrata</i>	28.9 (84)	19.5 (56)	4.1 (12)	1.7 (5)
<i>Cirsium japonicum</i>	31.5 (91)	22.0 (63)	7.6 (22)	0.0 (0)
<i>Xanthium occidentale</i>	33.3 (96)	2.9 (8)	0.0 (0)	0.0 (0)
<i>Lactuca sativa</i>	34.3 (99)	0.2 (1)	0.0 (0)	0.0 (0)

* Values in parentheses represent % of control.

reduced the growth of *Amaranthus retroflexus* L. and *Setaria viridis* L. more than that of cucumber (*Cucumis sativus* L.) or barley (*Hordeum vulgare* L.) in their greenhouse experiments (Stachon and Zimdal, 1980). In a field experiment, high densities of *C. arvense* reduced the incidence of annual weeds growing in the same vicinity of *C. arvense* (Stachon and Zimdal, 1980). More recently, Chon et al. (2003a) reported that aqueous leaf extracts from 16 Compositae plant species were bioassayed against alfalfa (*Medicago sativa*) to evaluate their allelopathic effects, and the results show the highest inhibition in the extracts from *C. japonicum*, *L. sativa*, and *X. occidentale*, all showing significant inhibition of seed germination and growth of alfalfa.

Einhellig (1986) noted that biological activity of allelochemicals, including the autotoxic factors in alfalfa, was concentration dependent with a response threshold. Plant growth may be stimulated below the threshold, with mild to severe growth reductions observed above the threshold; each depending on the sensitivity of the receiving species, the plant process affected and the existing environmental conditions. Many instances of stimulation effects of microorganisms on other organisms and of plants on microorganisms have been reported. Rice (1986) demonstrated growth stimulatory effects of volatile compounds, decaying leaves and root exudates of parasitic and non-parasitic plants on several other species. He showed that decaying ground ivy leaves stimulated seedling growth of downy brome and radish. Chon et al. (2003a) evaluated aqueous extracts of 16 Compositae plants and found *Lactuca sativa*, *Xanthium occidentale* and *Cirsium japonicum* showed the highest inhibition on alfalfa (*Medicago sativa*) seedlings. Conversely, extracts of *Chrysanthemum indicum*, *Youngia sonchifolia*, *Bidens frondosa*, and *Breea segeta* at concentrations below 20 g dry matter L⁻¹ increased root length of alfalfa by 13–33%. In another study, alfalfa root growth was stimulated by very low concentrations from alfalfa leaf extracts (Chon et al., 2000). Our findings, however, indicated that this stimulatory effect for a reputed autotoxic chemical was less than those reported by Einhellig (1986) and Rice (1986) who evaluated stimulatory effects of allelochemicals. Chon et al. (2003a) reported that stimulatory as well as inhibitory effects of Compositae plant species were exhibited (Tab. I).

2.1. *Artemisia* sp.

The genus *Artemisia* comprises over 400 species of perennial herbs and shrubs which are widely distributed throughout Europe, Asia, North America and South Africa (Stairs, 1986) and the plants are considered weeds in many part of the world. Many weeds are ecologically important and contain bioactive compounds such as allelopathic and antifungal constituents in order to survive in ecosystem (Meepagala et al., 2003). Allelopathic constituents are cause of the symptom of the non-growth or growth retardation of neighbouring plant. The phenomena have been found in the ethereal oils and alkaloid absinthium excreted from *Artemisia absinthium* (Funke, 1943), natural and artificial rain drip from *Artemisia californica* (Halligan, 1976), aqueous extract and volatile substances of *Artemisia princeps* var. *orientalis* (Yun, 1991) and aqueous extract of *Artemisia campestris* ssp. *Caudate* (Yun and Maun, 1997). And the genus *Artemisia* is rich sources of biologically active natural products (Tan et al., 1998). Approximately 30 *Artemisia* species grown in Korea have been used in traditional Korean medicine. Of them *Artemisia princeps* var. *orientalis* is widely used as medicinal herb and is known as a strong weed, it is a Korean custom to uproot the plant in old tomb area because its water-soluble allelochemicals retard turf growth.

Kil and Yun (1992) reported that aqueous extracts from mature leaf, stem, and root of *Artemisia princeps* var. *orientalis* caused significant inhibition in germination and decreased seedling elongation of receptor plants, whereas germination of some species was not inhibited by extracts of stem and root. Dry weight growth was slightly increased at lower concentrations of the extract, whereas it was proportionally inhibited at higher concentrations. Kil et al. (1992) also reported, an in vitro study, that aqueous extract of *A. princeps* var. *orientalis* caused some reduction in concentration, induction, and growth of callus, although they looked normal, whereas the explants of most receptor plants did not develop callus at higher concentration. They also found that lettuce and *Eclipta prostrata* were the most sensitive species, and even *A. princeps* var. *orientalis* was affected by its own extracts. Yun and Kil (1992) reported differential phytotoxicity of residues of *A. princeps* var. *orientalis* using various plants as test species in their field

and laboratory studies. In seedling growth tests with abandoned field soils (control) and soil underneath the *Artemisia* plant, the elongation and dry weight of seedlings grown in the soil from under the *Artemisia* plants were severely inhibited, thereby suggesting that certain growth inhibitors were released from the *Artemisia* plant and the inhibitor remained in the soil.

2.2. *Cirsium* sp.

Common thistle (*Cirsium japonicum*) is a noxious perennial weed which causes serious yield losses in spring sown small grains row crops, and pastures (Hodgson, 1963, 1968). Growth and germination of wheat (*Triticum aestivum* L.) and flax (*Linum usitatissimum* L.) were inhibited by aqueous extracts of Canada thistle (*Cirsium arvense* Scop.) roots and shoots (Helgeson and Konzak, 1950). Bendall (1975) studied water and ethanol extracts and residues in soil, and concluded that an allelopathic mechanism might be involved in the exclusion of some annual thistle, pasture, and crop species from Canada thistle areas. Stachon and Zimdahl (1980) in their greenhouse experiments found that Canada thistle litter reduced the growth of redroot pigweed (*Amaranthus retroflexus* L.) and green foxtail (*Setaria viridis* L.) more than that of cucumber (*Cucumis sativus* L.) or barley (*Hordeum vulgare* L.). Chon et al. (2003a) reported that the aqueous leaf extracts of 16 Compositae plant species, including common thistle, significantly inhibited hypocotyls and root lengths of alfalfa. In their earlier study, *trans*-cinnamic acid was found as the greatest amount at ethyl acetate fraction from methanol extracts of common thistle plant.

Chon (2004a) assayed phytotoxic effects of a series of aqueous extracts from leaves, stems, roots and flowers of common thistle (*Cirsium pendulum* Fisch.) against alfalfa (*Medicago sativa*) seedlings. The results showed highest inhibition in the extracts from flowers and leaves, and followed by stems, and roots. He found also that hexane and ethylacetate fractions of common thistle reduced alfalfa root growth more than did butanol and water fractions. Incorporation into soil with the leaf residues at 100 g kg⁻¹ inhibited shoot fresh weights of barnyardgrass and eclipta (*Eclipta prostrata*) by 88 and 58%, respectively, showing higher sensitivity in grass species.

2.3. *Lactuca* sp.

Lettuce (*Lactuca sativa*) is an annual herbaceous plant of Compositae, one of the largest and most diverse families of flowering plants. Major weeds including barnyard grass (*Echinochloa colonum*), common purslane (*Portulaca oleracea*), smooth pigweed (*Amaranthus hybridus*), shepherd's purse (*Capsella bursa-pastoris*) and common lambsquarters (*Chenopodium album*) are known to interfere with lettuce (Haar and Fennimore, 2003; Santos et al., 2003; Fennimore and Umeda, 2003).

Chon et al. (2005) showed phytotoxic effects of aqueous or methanol extracts and residues from leaves of lettuce cul-

vars on alfalfa seed germination. Methanol extracts from hexane fraction of lettuce plants showed the most inhibition on alfalfa root growth and followed by ethylacetate, butanol and water fractions. Incorporation with leaf residues of 100 g kg⁻¹ into soil significantly inhibited shoot- and root fresh weights of barnyard grass by 79 and 88%, respectively. Also, Chon et al. (2005) reported major allelopathic substances by means of HPLC were identified as coumarin, *trans*-cinnamic acid, *o*-coumaric acid, *p*-coumaric acid and chlorogenic acid. Of them *p*-coumaric acid was found as the greatest amount (8.9 mg 100 g⁻¹) in the EtOAc fraction. Hexane and EtOAc fractions of lettuce reduced alfalfa root growth more than did BuOH and water fractions.

2.4. *Xanthium* sp.

Xanthium species is one of the most competitive weeds in crop fields as well as wastelands. Inam et al. (1987) found that aqueous extracts of *Xanthium strumarium* from different plant parts reduce germination, early growth and dry weight of *Brassica compestris*, *Lactuca sativa*, and *Pennisetum americanum*. Especially, *Parthenium hysterophours* is known to be very allelopathic to wheat (Kanchan and Jayachandra, 1979), soybean, and corn (Mersie and Singh, 1978). Their extracts and residues significantly reduced germination and shoot and root dry weight of the test plants.

Chon (2004b) reported that aqueous extracts from *X. occidentale* completely inhibited the hypocotyl and root growth of alfalfa. Early seedling growth of both alfalfa barley (*Hordeum vulgare* L.), soybean (*Glycine max* L.), and barnyard grass (*Echinochloa crus-galli*) was significantly reduced by methanol extracts. By means of high-performance liquid chromatography, chlorogenic acid and *trans*-cinnamic acid were quantified as the highest amounts from water and ethylacetate fractions, respectively. Butanol and ethylacetate fractions of *X. occidentale* reduced alfalfa root growth more than did hexane and water fractions.

3. FROM PETRI-DISH BIOASSAYS TO FIELD TRIALS

3.1. Bioassays in Petri-Dish

Most assessments of allelopathy, especially in early stages, involve bioassays of plant or soil extracts based on seed germination and seedling growth. A reliable bioassay that is sensitive is needed for more in-depth studies of the growth mechanisms involved and for developing initial analytical procedures to determine the chemical (s) responsible. Generally germination is less sensitive to the allelopathic chemical than is seedling growth, especially root growth (Miller, 1996). Although many laboratory bioassays have proposed to demonstrate allelopathy, concerns have been raised that most of them have little relevance in terms of explaining behavior in the field (Connell, 1990; Inderjit and Olofsdotter, 1998; Inderjit and Dakshini, 1995, 1999).

It is a complex phenomenon involving a variety of inter-relationships among plants. Virtually all plant parts such as leaves (Kumari and Kohli, 1987), roots (Horsley, 1977), pollen (Cruz-Ortega et al., 1988), trichomes (Bansal, 1990), bark (Kohli, 1990) and seeds and fruits (Fredman et al., 1982) have allelopathic potential. It is generally accepted that water extracts of top growth (especially leaves) produce more allelopathy for seedlings than those from roots and crowns of alfalfa (*Medicago sativa* L.) (Miller, 1996), and that shoot extract from the reproductive stage was more inhibitory than from the vegetative stage under laboratory conditions (Chung and Miller, 1995a; Hegde and Miller, 1992a). Chung and Miller (1995a) ranked autotoxic effects of water extracts of plant parts of alfalfa as leaf (greatest), seed, root, flower, and stem (least). Chou and Leu (1992) reported that extracts from flowers of *Delonix regia* (BOJ) RAF exhibited highest inhibition against three test plants, alfalfa, lettuce (*Lactuca sativa*), and Chinese cabbage (*Brassica chinensis*). Chon (2004a) reported that phytotoxic effects of a series of aqueous extracts from leaves, stems, roots and flowers of common thistle (*Cirsium pendulum* Fisch.) on alfalfa (*Medicago sativa*) seedlings showed highest inhibition in the extracts from flowers and leaves, and followed by stems, and roots (Fig. 1).

3.2. Morphological responses

Some plant genotypes are likely to escape the allelopathic chemical (s) by being hypersensitive. In this regard the root tip may actually be strongly affected by allelochemical (s) and have its growth rate nearly stopped. But if the seedling quickly enables to produce several secondary roots, the number of apices per soil volume increases at higher position in soil profile. A study demonstrated microscopically that alfalfa extract reduced both root growth and root hair density of alfalfa (Hegde and Miller, 1992b). Stimulation of lateral root growth to the detriment of the primary root also suggests disruption of hormonal balance (Dayan et al., 2000). Anatomical responses of tissue cells upon water-soluble substances or allelochemicals need to be elucidated. The morphology of seedlings grown in the presence of a phytotoxin may also yield important information. Stimulation of lateral root growth to the detriment of the primary root also suggests disruption of hormonal balance (Dayan et al., 2000). Benzoic and cinnamic acids-treated soybean plants showed fewer lateral roots and tended to grow more horizontally compared to the untreated plants. Their lateral roots were stunted and less flexible (Baziramakenga et al., 1994).

Not many microscopic approaches at ultrastructural level have been conducted on allelopathic effects of extracts or allelochemicals. Chon et al. (2002) suggested that the root systems, especially root tips of alfalfa, were stunted and swollen by the aqueous alfalfa leaf extracts at 30 g L⁻¹ and coumarin at 10⁻³ M. Duke et al. (1987) discovered artemisinin, a constituent of annual wormwood (*Artemisia annua*), marginally increased the mitotic index of lettuce root tips at 33 μM. At the ultrastructural level by means of electron microscopic study, however, chromosomes were less condensed during mitosis

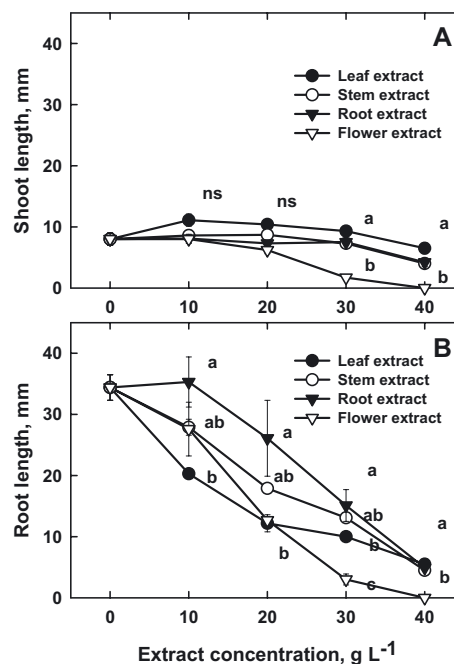


Figure 1. Effects of *Cirsium japonicum* leaf, stem, root and flower extracts on shoot (A) and root lengths (B) of alfalfa as affected by different concentrations. Within an extract concentration, means followed by the same letter are not significantly different at $P < 0.05$. Each bar represents standard error of the mean. Adapted from Chon et al. (2003a).

in artemisinin-treated than control meristematic cells. Liu and Lovett (1993) demonstrated that barley allelochemicals, hordenine and gramine affected damage of cell walls, increase in both size and number of vacuoles, autophagy, and disorganization of organelles. More recently, a study on allelopathic interference of benzoic acid against mustard (*Brassica juncea* L.) seedling growth showed irregular shaped cells arranged in a disorganized manner and disruption of cell organelles at cellular level (Kaur et al., 2005). Their result indicates that damage to the mustard root at cellular level was clearly evidenced by the changes in cell morphology and internal organization.

3.3. Residue incorporation in soil

Generally, residue inhibition of seedling growth was enhanced if crop residue was incorporated before planting, drastically reduced if residue remained on the surface (Cochran et al., 1980; Elliott et al., 1981). Crop residue toxicity to winter wheat seedlings was likely caused by either an allelopathic compound or N immobilization due to increased microbial populations. The allelopathic compound was either a water-soluble compound leached from residue or a compound produced during microbial decomposition of plant residue (Cochran et al., 1980; Elliott et al., 1981). Another study (Kadioglu, 2000) showed that the inhibitory effect of ground hearleaf cocklebur (*Xanthium strumarium* L.)

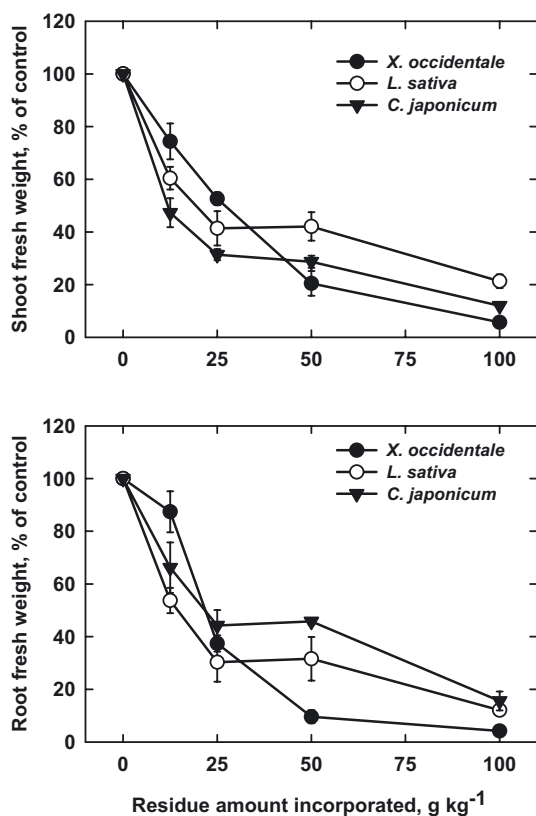


Figure 2. Effects of incorporation with dried leaf material of *Xanthium occidentale*, *Lactuca sativa*, and *Cirsium japonicum* on shoot (A) and root (B) fresh weight of barnyard grass 15 days after seeding or treatment. Material was incorporated by mixing with soils. After incorporation, barnyard grass was seeded and immediately sub-irrigated. Shoot and root fresh weights were measured 15 days later. Adapted from Chon and Kim (2005).

on *Amaranthus retroflexus*, *Amaranthus sterilis*, and *Conium maculatum*. Chon and Kim (2005) reported that the effect of residue incorporation with *Xanthium occidentale* plant samples into soil on seedling growth of barnyard grass was examined in the greenhouse, and results showed that the leaf residues at 100 g kg⁻¹ inhibited shoot and root dry weights of test plants by 70–90% (Fig. 2).

3.4. Field experiments

A field research described that the early stage of grassland succession in Korea would be composed of *Plantago asiatica*, *Artemisia princeps* var. *orientalis*, *Oenothera odorata*, and *Zoysia japonica* was inhibited greatly by the *Artemisia* extracts. These contrasting views could result from differences between laboratory work and field observations (Park, 1966). Yun and Kil (1992) reported that field soil collected under the *Artemisia* plants significantly reduced or somewhat promoted growth of the test plants. These results are in agreement or disagreement with following results: soil collected from some plant fields exhibited phytotoxicity by reducing growth (Al-Naib and Rice, 1971; AlSaadawi and AlRubeaa, 1985;

Inam et al., 1989) and soil from below some test plants did not inhibit germination and growth of the test species (Fadayomi and Oyebeade, 1984; Goel and Sareen, 1986).

4. DISCOVERY OF CAUSATIVE ALLELOCHEMICALS

4.1. Compounds involved

Most important approach on allelopathy is to successfully isolate, identify, and quantify causative allelochemicals that present in plants or soils. It is essential that potential allelopathic compounds can also relate to the levels originally in the whole extracts. Natural products identified as allelopathic agents have been classed into the following (a) toxic gases, (b) organic acids from Krebs cycle and aldehydes, (c) aromatic acids, (d) simple unsaturated lactones, (e) coumarins, (f) quinones, (g) flavonoids, (h) tannins, (i) alkaloids, and (j) terpenoids and steroids, etc. Although many of these compounds are secondary products of plant metabolism, several are degradation products that occur in the presence of microbial enzymes. Several biosynthetic pathways lead to production of the various categories of allelopathic agents. The inhibitors usually arise through either the acetate or through the shikimic acid pathway. Several types of inhibitors, which originated from amino acids, come through the acetate pathway. Most of compounds that cause allelopathy were derived from amino acids, via the shikimic acid pathway (Rice, 1984).

The source of the active agents may be living plants, litter, detritus, leachates, soil bacteria and fungi, mycorrhizal fungi, root exudates, the atmosphere, water, air-borne particles, or pathogenic organisms. Many organisms may be involved simultaneously in a particular interaction. Compounds isolated from plants or their leachates often do not reproduce the observed allelopathic effects without the associated factors. In many instances, these plant-derived compounds are modified by oxidation, reduction, photochemical activation (Fischer et al., 1994), detoxification, or biochemical activation by bacteria and fungi. Bioactive molecules may leave the system by being adsorbed onto inorganic particles or organic matter in the soil, or leached from the system.

4.2. Identification and quantification

Causative allelochemicals reported from Compositae plant species have not been identified sufficient. Identifying and quantifying the causative allelochemicals in plant and associated environments are the most important approaches for allelopathy study. Phenolic acids in the literature on allelopathy are often mentioned as putative allelochemicals and are perhaps the most commonly investigated compounds among potential allelochemicals. They are found in a wide range of soils or plants, and their phytotoxic potential against various plants has been demonstrated under controlled conditions. Phytotoxicity-based extraction and fractionation were employed to separate allelochemicals contained in each plant extracts. Chon et al. (2003a) reported that by means of

Table II. Quantitative determination using HPLC on concentration of some phenolic compounds present in leaves of *Xanthium occidentale* (Chon et al., 2003a).

Compound	Fractions				Total
	Hexane	EtOAc	BuOH	Water	
	- mg 100 g ⁻¹ -				
Coumarin	0.14	2.07	2.02	0.19	4.41
<i>trans</i> -cinnamic acid	8.39	20.16	4.20	0.2	32.95
<i>p</i> -coumaric acid	nd	0.24	nd	nd	nd
Chlorogenic acid	2.24	0.24	3.59	33.33	39.40
Total	10.77	22.67	9.81	33.54	76.76

^a nd: none detected.

high-performance liquid chromatography (HPLC) analysis, the responsible causative allelopathic substances present in *L. sativa*, *X. occidentale*, and *C. japonicum* were isolated from various fractions and identified as coumarin, *trans*-cinnamic acid, *o*-coumaric acid, *p*-coumaric acid, and chlorogenic acid.

4.3. Fractionation and bioassay of each solvent fractions

Methanol extracts from ground plant samples are used for the following bioassay and fractionation. Generally, for instance, crude methanol extracts are diluted with distilled water and hexane to collect hexane fraction using a separating funnel. After hexane collection, the distilled water fractions are added with ethylacetate to obtain ethylacetate fraction in the same way. The same procedure is used in preparing other solvent fractions. The fractions are taken to dryness on a rotary evaporator at 40–50 °C, and transferred into vacuum freeze dryer to obtain dry matters and used for quantification and bioassay. The dried samples concentrated from fractions are again dissolved in MeOH to use for bioassay (Chon et al., 2003a). Each of these fraction solutions are pipetted in a 9-cm plastic Petri dish lined with one Whatman No. 1 filter paper and evaporated to dryness for 24 h at 24 °C. For the control, 4 mL of methanol is applied to Petri dishes. After evaporation, distilled water is added onto the filter paper and then seeds of test plant are placed on the paper and grown for 6 days. Chon et al. (2003a) reported that these major phenolic compounds present in Compositae species were total phenol compounds of all fractions in *C. japonicum*, *L. sativa*, and *X. occidentale* by 60.3, 18.5, and 84.4 mg 100 g⁻¹, respectively. They reported also, through the bioassay procedure, *X. occidentale* which had the highest total concentration, showed the most inhibitory effect on test plants in Compositae plant species (Tab. II).

4.4. Phytotoxicity of major causative allelopathic compounds

Chon et al. (2003a) reported that among 10 phenolic compounds assayed for their phytotoxicity on root growth of alfalfa, coumarin, *trans*-cinnamic acid and *o*-coumaric acid were most inhibitory. Especially, coumarin at 10⁻³ M significantly inhibited root growth of alfalfa. Methanol extracts from

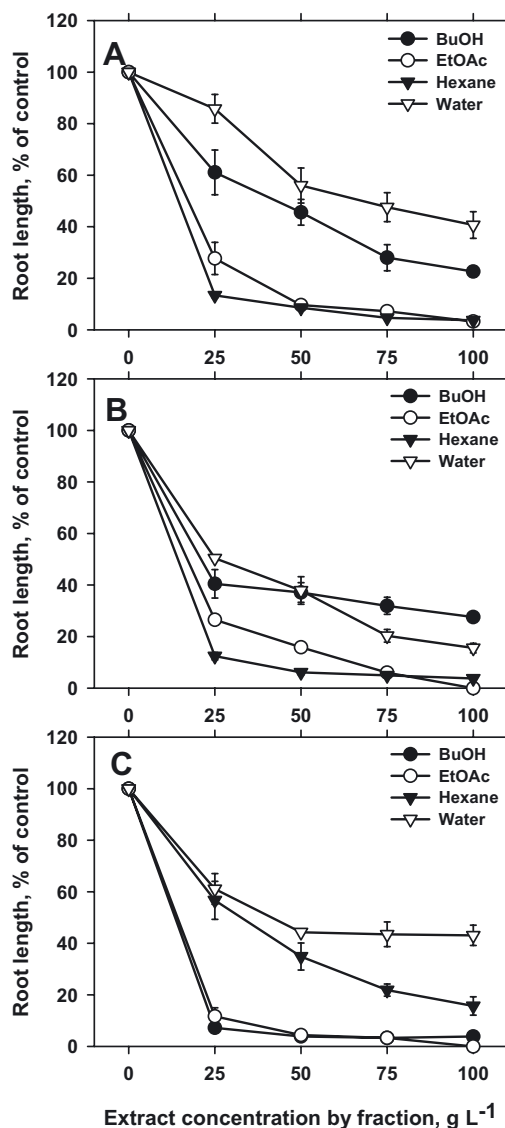


Figure 3. Effects of various fractions from methanol extracts of *Cirsiium japonicum* (A), *Lactuca sativa* (B), and *Xanthium occidentale* (C) on alfalfa root length 6 days after seeding. Adapted from Chon et al. (2002).

BuOH, EtOAc, hexane, and water fractions were also assayed to confirm their phytotoxic effects. The results showed that methanol extracts of *X. occidentale* were most inhibitory on root growth of alfalfa, and that methanol extracts from BuOH and EtOAc fractions of *X. occidentale* reduced alfalfa root growth more than did those from hexane and water fractions. Methanol extracts from hexane and EtOAc fractions of *L. sativa* and *C. japonicum* reduced alfalfa root growth more than did those of BuOH and water fractions. Especially, methanol extracts from hexane and EtOAc fractions at 50 g L⁻¹ reduced root growth by each 85%, while treatment at same concentration of BuOH and water fractions reduced root growth by 40 and 15%, respectively (Fig. 3).

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