

REVIEW

Allelopathy in Solanaceae plants

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Abstract

Solanaceae plants have strong allelopathic potential, and therefore the action is confirmed through: a) bioassays with liquid or various solvent extracts and residues, b) fractionation, identification, and quantification of causative allelochemicals. Most assessments of allelopathy involve bioassays of plant or soil extracts, leachates, fractions, and residues which support seed germination and seedling growth in laboratory and greenhouse experiments. Plant growth is also stimulated below the allelopathic threshold, however severe growth reductions may be observed above the threshold concentration depending on the sensitivity of the receiving species. Generally, seedling growth is more sensitive than germination, particularly root growth. Some approaches showed that field soil collected beneath donor plants significantly reduced or somewhat promoted the growth of the recipients plants. Petri dish bioassays with aqueous extracts of different parts of donor plants showed considerable phytotoxic activities in a concentration-dependent manner with leaf aqueous extracts being most dominant. Delayed seed germination and slow root growth attributable to the extracts may be baffled with diffusion effects on the rate of imbibition, delayed initiation of germination, and particularly cell elongation; the main factor that is responsible for affecting root growth before and after the tip penetrates the testa. Light and electron microscopy extract analysis at the ultrastructural level are correctly investigated. Several Solanaceae plants have allelopathic potential, and therefore the activities, kinds and quantity of allelopathic compounds differ depending on the plant species. The incorporation of allelopathic substances into agricultural management might scale back the development of pesticides and reduce environmental deterioration.

Key words: allelopathy, allelochemicals, bioassay, extracts, fractions, residues, Solanaceae

Introduction

The term “allelopathy” was first used by Molisch (1937) to describe direct or indirect chemical interaction between plants that results from the transfer of biochemical substances from one plant to another. During the 1970s the study of allelopathy increased significantly and has experienced tremendous development since the mid of 1990s, becoming an important topic in agriculture, chemical ecology, botany, soil science, environment and other areas of research. The believed targets of allelochemicals in the plant kingdom range from algae and fungi to various microbes. Allelopathy usually is interspecific however, it is called autotoxicity if intraspecific i.e. when a donor plant

produces allelopathic compounds that are harmful to the development of new plantlets of the same species. Rice (2012) suggested that autotoxicity and allelopathy can perform significant roles under both natural and manipulated ecosystems, largely by being detrimental to seed germination and seedling development. Although allelopathic interactions between plants have been known for decades, even centuries, only a few allelochemicals have been recognized.

Allelopathy plays a key role in weed management, crop protection, and crop restoration. Scientists engaged in allelopathic analysis focus on appropriate manipulation of allelopathy to advance of crop

productivity and environmental protection through the eco-friendly management of weeds, pests, crop diseases, conservation of nutrients in crop land, and synthesis of fresh agrochemicals supported on natural products. Allelochemicals affect physiological functions like respiration, biosynthesis and mineral uptake. More recently, however scientific attention has also concentrated on taking advantage of the significant positive roles of allelopathy and what roles these interactions play in enhancing crop productivity. A serious drawback of contemporary agriculture is crop loss caused by weeds. Worldwide, weeds alone cause the tenth greatest loss of agriculture production (Altieri and Liebman 1988). Yet, allelopathic principles of crops are utilized as alternate means of weed management based on natural products. Although allelopathy is usually thought of as being a strain on agriculture, there is currently sizeable proof to recommend that it be exploited to assist weed management issues in agroecosystems.

Allelopathic Solanaceae plants

Twelve weed families embody 68 of the 200 species that are the foremost vital world weeds (Holm 1978). Solanaceae accounts for 102 genera and nearly 2,500 species throughout the globe. However, they are the most abundant and cosmopolitan in tropical regions of Latin America, where nearly 40 genera are endemic. Only a few members are found in temperate regions, and approximately 50 species only are present in the United States and Canada collectively. Nearly half of all the species are present in the genus *Solanum*, which also contains all the wild species of potatoes found in the Western Hemisphere. The toxic alkaloids present in certain species of the family have given it its vernacular name of “nightshade”. Solanaceae includes several plants of considerable economic importance as vegetables and drug plants. However, some of these occur in nature as weeds as well. Allelopathy in weeds has been found in a great variety of plants using numerous laboratory assays. Some of the previous studies on the allelopathic effects of the nightshade family include genera like: *Withania*, *Solanum*, *Iochroma*, *Nicotiana* and *Datura*. Potato (*Solanum tuberosum* L.), pepper (*Capsicum annum* L.), tobacco (*Nicotiana* species), eggplant (*Solanum melongena* L.), tomato (*Lycopersicon esculentum* Mill.) and jimsonweed (*Datura stramonium* L.). These are all members of the Solanaceae family, and are rich sources of sesquiterpenoid phytoalexins (Elakovich 1987). Allelopathic sesquiterpenoids have been implicated in a limited number of investigations. Javaid *et al.* (2011) reported that shoot and root aqueous extracts of

Withania somnifera L. inhibited germination and reduced both growth parameters and dry biomass of the noxious weed *Parthenium hysterophorus* L. Bosch *et al.* (2004) showed that leaf leachates of woolly nightshade (*Solanum mauritianum* Scop.) reduced germination percentages in *Hebe stricta* Benth. in a concentration dependent manner. Morais *et al.* (2013) displayed that ethanol extract and fractions obtained from ripe fruits of *S. lycocarpum* A. showed allelopathic potential, particularly on the growth of onion radicles; the dichloromethane and hydroethanolic fractions showed inhibitory activity on the growth of hypocotyls and radicles of lettuce. *Iochroma austral* extract reduced growth of the weed radicles: *Sorghum halepense* L. and *Chenopodium album* L. (Vacarini and Bonetto 2000). The same researchers also concluded that the extract had selective herbicidal activity against weed species. Lovett *et al.* (1981) spotted allelopathic effects of different concentrations of aqueous leachate of *D. stramonium* seeds and leaves on seed germination and radicle elongation of *Linum usitatissimum* L. Fujii *et al.* (2003) screened leaf litter of *Nicotiana tabacum* L., *Datura suaveolens* Wild. and *Lycium chinense* Mill. for potential allelopathic traits. Singh *et al.* (2009) observed that the allelochemicals present in the aqueous leachate of *N. plumbaginifolia* Viv. delayed germination, reduced seedling growth and the macromolecule content of *Zea mays* L. *Nicotiana glauca* Gr. root extract had a negative effect on root dry weight and root to shoot ratio of *Juniperus procera* Hochst. ex Endl. seedlings (Alshahrani 2008).

Solanum spp.

The genus *Solanum* is massive, cosmopolitan in distribution and includes two food crops of great economic importance, the potato and the tomato. It conjointly includes the nightshades and horse nettles, as well as various plants cultivated for their decorative flowers and fruit. *Solanum* species show a wide range of growth habits, like annuals and perennials, vines, shrubs, subshrubs, and little trees. Many previously independent genera like *Lycopersicon* and *Cyphomandra* are now contained within *Solanum* as subgenera or sections. Therefore, the genus at present contains roughly 1,500–2,000 species and the plants are found in many parts of the world. Many weeds are ecologically important and contain bioactive compounds such as allelopathic and antifungal constituents in order to survive in the ecosystem. Allelopathic constituents are the cause of the non-growth or growth retardation of the neighbouring plant. The phenomena have been found in the two biologically active glycoalkaloids, solasonine and solamargine excreted from the ripe fruit of *Solanum incanum* L. by a combination of two countercurrent chromatographic steps: rotation

locular countercurrent chromatography (RLCC) and droplet countercurrent chromatography (DCCC) (Fukuhara and Kubo 1991) that inhibited the growth of lettuce seedlings (Table 1). Bioassay-guided fractionation of the methanol extract of the root bark of *S. arundo* Matt. led to the isolation of a steroidal glycoalkaloid, designated arudonine which negatively affected the development of lettuce sprouts (Fukuhara and Kubo 2004). Debnath *et al.* (2016) witnessed that the aqueous leaf and flower extracts of invasive weed *S. sisymbriifolium* Lam. suppressed the germination and seedling growth of the four selected crop species at different concentrations tested in the laboratory (Table 2). Girija and Gowri (2008) determined the allelopathic potential of *S. nigrum* L. on *Pisum sativum* L., *Eleusine coracana* L. and *Trigonella foenum* L.; the presence of secondary metabolites (Table 3) in leaf and fruit extracts suppressed the germination, radicle length and total protein content of test plants.

***Withania* spp.**

The genus *Withania* belongs to flowering plants within the potato family Solanaceae. It is enriched with 23 species that are native to western and southern landscapes of Asia, North Africa, southern Europe, the Mediterranean, and the Canary Islands. It contains two economically important species; *W. somnifera* (Ashwagandha) and *W. coagulans* Dunal. (Ashutosh

booti) which are traditionally cultivated in many parts of the world for their healthful uses. Numerous medicinal values of *W. somnifera* have been reported and its allelopathic potential has also been declared by many researchers (Jabran *et al.* 2010; Javaid *et al.* 2011; Chandra *et al.* 2012; Khaliq *et al.* 2013; Sharma *et al.* 2017). The hydroalcoholic extract of ashwagandha mainly at higher concentrations demonstrated promising allelopathic properties by significantly affecting seed germination and radicle elongation of both *Cicer arietinum* L. and *Triticum aestivum* L. in a concentration dependent manner. *Triticum aestivum* was found to be more sensitive than *C. arietinum* (Chandra *et al.* 2012).

***Nicotiana* spp.**

The genus *Nicotiana* represents herbaceous plants and shrubs of the family Solanaceae, that is native to America, Australia, southwest Africa and the South Pacific. *Nicotiana tabacum* is cultivated universally for the production of tobacco leaves for cigarettes and other tobacco related products. Many species of *Nicotiana* are grown as ornamental plants such as *N. sylvestris*, *N. alata* and *N. langsdorffii*, often under the label of 'flowering Tobacco'. However, many species of the said genus are capable of suppressing the growth of plants that grow in their vicinity. Singh *et al.* (2009) presented the adverse effects of aqueous leachate of *N. plumbaginifolia* on amylase and nitrate reductase activity;

Table 1. Inhibitory effect of two steroid glycoalkaloids at various concentrations on lettuce roots after 6 days (Fukuhara and Kubo 1991)

Glycoalkaloids	Concentration [ppm]							
	0	1.0	2.5	5.0	7.5	10	100	250
Solamargine	0	21.8	25.8	34.1	22.2	28.0	95.3	95.32
Solasonine	0	27.3	23.4	35.1	29.1	29.4	95.3*	95.3*

*Inhibition % = $(C-X)/C \times 100$ ($p < 0.5$)

C = the average root length of 20 control lettuce seedlings

X = the average root length of 20 seedlings treated with the alkaloid at each concentration

Table 2. Inhibition (%) of seed germination of four common crops treated with aqueous leaf and flower extracts of *Solanum sisymbriifolium* (Debnath *et al.* 2016)

Concentration [%]	Inhibition [%]							
	<i>Vigna radiata</i>		<i>Amaranthus mangostanus</i>		<i>Oryza sativa</i>		<i>Brassica campestris</i>	
	F	L	F	L	F	L	F	L
Control	0	0	0	0	0	0	0	0
0.5	7.8	4.8	5.6	13.6	6.4	0.8	5.6	8.8
1	13.2	15.2	21.6	19.2	10.4	1.6	20.8	22.4
2	65.6	24.8	88.8	28.8	16.8	1.67	1.2	27.2
4	100.0	48.8	100.0	88.8	88.8	9.6	100.0	56.8
8	100.0	53.8	100.0	99.0	100.0	95.0	100.0	100.0
IC ₅₀	2.75	6.25	2.51	3.1	3.38	5.34	2.51	3.91

L = leaf; F = flower; IC₅₀ = half maximal inhibitory concentration

Table 3. Phytochemical analysis of leaf and fruit extracts of *Solanum nigrum* (Girija and Gowri 2008)

Serial no.	Secondary metabolites	Leaf extract	Fruit extract
1	Tannin	+	+
2	Phlobatannin	-	-
3	Saponin	-	+
4	Flavonoids	-	-
5	Steroid	-	-
6	Terpenoids	+	+
7	Anthraquinone	-	-
8	Cardiac glycosides	+	+
9	Phytosterols	+	+
10	Carbohydrates	-	-
11	Phenol	-	-
12	Alkaloid	+	+

"+" - present; "-" - absent

sugar, protein, chlorophyll and starch contents of germinated seeds of maize (*Z. mays*). *Nicotiana glauca* leaves and root extracts decreased seedling shoot dry weight of juniper with increasing extract concentrations for both leaf and root (Alshahrani 2008). Powder and aqueous extracts of *N. tabacum* showed a significant inhibitory effect on germination, seedling length and dry biomass (Table 4) of redroot pigweed plants (*Amaranthus retroflexus* L.) both under laboratory as well as greenhouse conditions (Nekonam *et al.* 2014).

***Datura* spp.**

Today, experts classify only nine species of *Datura* (Preissel and Preissel 2002) belonging to the family Solanaceae. They are commonly known as daturas, but also known as devil's trumpets, moonflowers and jimsonweed. The precise and natural distribution of the said genus is uncertain, however, it is most likely restricted to the United States, Mexico, southern Canada and Tunisia in Africa, where the highest species diversity occurs. All species of *Datura* are poisonous, especially their seeds and flowers. Laboratory and

greenhouse experiments carried out by Pacanoski *et al.* (2014) showed that the aqueous leachates of *Datura stramonium* L. root and shoot did not produce any significant effect on germination and shoot length of maize, but root length was significantly reduced. Ramona *et al.* (2016) revealed that the highest quantity of tropane alkaloids is found in the extract from jimsonweed leaves, the lowest quantities of hyoscyamine and scopolamine were found in the root. *Datura stramonium* also displays its inhibitory action on the growth and survival of various grass and legume species (Elisante and Ndakidemi 2014). The study conducted by Elisante *et al.* (2013) concluded that aqueous seed and leaf extract of *D. stramonium* have allelopathic effects on leaf chlorophyll content, root and shoot length, fresh and dry weight of grass (*Cenchrus ciliaris* L.) and legume (*Notonia wightii* Am.) species. Aqueous extracts from *D. stramonium* are adequate when *Sorghum halepense* L. causes damage (Butnariu 2012).

From Petri dish bioassays to residue incorporation

Bioassays in Petri dishes

Most evaluations of allelopathy, particularly in primary stages, encompass bioassays of plant or soil extracts that rely on seed germination and seedling growth. A more dependable bioassay is needed for the detailed study of the growth mechanisms involved and for constructing initial analytical measures to determine the chemical(s) responsible. Usually, germination is less sensitive to the allelopathic chemicals than is seedling growth, particularly root growth (Miller 1996). Although many laboratory bioassays have been anticipated to demonstrate allelopathy, apprehensions have been raised that most of them have little applicability in terms of enlightening behaviour in the field (Connell 1990; Dakshini 1995; Inderjit and Olofsdotter 1998). It is a complex phenomenon involving a variety of inter-relationships between plants. Virtually all plant parts such as leaves (Kumari and Kohli 1987), roots (Horsley

Table 4. Effects of *Nicotiana tabacum* extracts on pigweed germination, germination rate, seedling length, and dry weight (Nekonam *et al.* 2014)

Concentration [g · l ⁻¹]	Germination [%]	Germination rate	Seedling length [cm]	Dry weight [g]
0	56.00	42.42	2.49	0.53
2.5	1.33 (97.6)	1.04 (97.5)	0.33 (86.7)	0.04 (92.5)
5.0	0.00 (100)	0.00 (100)	0.00 (100)	0.00 (100)
7.5	0.00 (100)	0.00 (100)	0.00 (100)	0.00 (100)
10.0	0.00 (100)	0.00 (100)	0.00 (100)	0.00 (100)

Numbers in parentheses are the inhibition percentages [%] compared with the control

1977), pollen (Cruz-Ortega *et al.* 1988), trichomes (Bansal 1990), seeds and fruits (Friedman *et al.* 1982) have allelopathic potential. It is generally acknowledged that water extracts of leaves exhibit more allelopathy for seedlings than those from the flowers of *Solanum sisymbriifolium* Lam. (Debnath *et al.* 2016) and has high allelopathic potential on *Vigna radiata* L., *Amaranthus mangostanus* L., *Brassica campestris* L., whereas it is less effective on *Oryza sativa* L. The leachates extracted at the flowering stage from *N. plumbaginifolia* produced the highest inhibition on the growth and biochemical parameters of sunflower seedlings and was concentration dependent (Singh *et al.* 2015). Solomon (1983) ranked auto toxic effects of plant parts of horse-nettle (*Solanum carolinense* L.), with the leaf at the top.

Morphological responses

A few plant genotypes are expected to avoid the allelochemical(s) by being hypersensitive. In this regard, the root tip may actually be intensely affected by plant chemical(s) and have its growth rate almost stopped. However, if the seedling quickly produces many secondary roots, the number of apices per soil volume increases at a higher position in the soil profile. A study by Jeronimo *et al.* (2005) demonstrated microscopically that an aqueous leaf extract of *S. lycocarpum* at 1% significantly reduced root growth and inhibited root hair and lateral root differentiation in sesame (*Sesamum indicum* L.) saplings (Table 5). Anatomical responses of tissue cells to water-soluble substances or allelochemicals need to be interpreted. The morphology of seedlings grown in the presence of a phytotoxic extract may also yield essential information. Soybean plants treated with benzoic and cinnamic acids displayed fewer lateral roots, grew more horizontally and were stunted and rigid (Baziramakenga *et al.* 1994). Little research has been conducted at the ultrastructural level that could elucidate the allelopathic effects of extracts or allelochemicals. Recently, an experiment on allelopathic interference of benzoic acid against mustard seedling growth recognized irregularities in cell forms being arranged in a disorganized manner

and destruction of cell organelles at the cellular level (Kaur and Kaushik 2005). This indicates that damage to the mustard root at the cellular level was undoubtedly caused by transformations in cell morphology and internal organization.

Residue incorporation in soil

Generally, residue inhibition of seedling growth was increased if crop residue was incorporated before planting. It was severely reduced if residue stayed on the surface (Cochran *et al.* 1980; Elliott *et al.* 1981). Crop residue phytotoxicity to winter wheat seedlings was probably caused either by an allelopathic compound or N immobilization because of exaggerated microbial populations. The allelopathic compound was either a water-soluble compound leached from residue or a compound created throughout microbial decomposition of plant residue (Cochran *et al.* 1980; Elliott *et al.* 1981). Another study (Javaid *et al.* 2011) showed that crushed shoots of *W. somnifera* when incorporated in the soil at 1–5% w/w, significantly reduced seed germination by 43–89% of *Parthenium hysterophorus* L. seeds.

Practical use of the allelopathy phenomenon of the Solanaceae family

Organic alternatives of weed control are gaining increased attention in agriculture because of growing concerns of environmental pollution caused by the usage of pesticides, chemical herbicides and their buildup in the soils. Several species of Solanaceae as mentioned above offer the potential for bio control of weeds through the production and discharge of allelochemicals from their leaves, stems, roots, flowers, bark and seeds. There are several examples of allelochemicals as herbicides (Duke and Lydon 1987; Anaya-Lang 1989). Allelopathic elements have the potential to act as stimulants as well as suppressants. Wise exploitation

Table 5. Effect of *Solanum lycocarpum* aqueous leaf extracts on the growth of shoots and roots and on root differentiation of *Sesamum indicum* (Jeronimo *et al.* 2005)

Treatment with leaf extract [%]	Shoot length [cm]		Root length [cm]		Lateral roots	Root hairs
	2 days after treatment	5 days after treatment	2 days after treatment	5 days after treatment		
Control	0.77(0.20) a	1.72(0.41) a	1.88(0.49) a	5.42(1.60) a	++++	+++++
1	0.57(0.22) b	1.41(0.42) a	0.68(0.27) b	1.55(0.71) b	+++	+++
3	0.52(0.22) b	0.73(0.48) b	0.37(0.25) b	0.25(0.31) c	++	+

Standard deviations are in parentheses; “+, ++, +++, ++++” – relative quantity with respect to the control; data followed by the same letters are not significantly different and with different letters show the significant difference

of both of these abilities can contribute positively to agriculture. Allelochemicals identified and separated from Solanaceae plants can be employed as natural weedicides. Allelopathy at present is a challenge and provides a rich source of allelochemicals.

Identification and quantification of causative allelochemicals

The key to successful understanding of allelopathic mechanisms is to separate, recognize, and enumerate causative allelochemicals that are present in different plant parts or soils. It can also relate potential allelopathic compounds to the levels originally present in the whole extracts of the plant part under consideration. Natural products identified with allelopathic properties have been categorized into the following groups: a) cytotoxic gases, b) organic acids from the tricarboxylic acid 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. Though various compounds mentioned above are secondary metabolites of physiological processes, many are decomposition products as a result of the presence of microbial enzymes. Several biosynthetic pathways cause the production of the various classes of allelopathic agents. Generally, inhibitory compounds originate either from the acetate or from the shikimic acid pathways. Most of the inhibitors that evolve from amino acids come through the acetate pathway. Most of the compounds that cause allelopathy are basically derived from amino acids, via the shikimic acid pathway (Rice 2012). The source of the active agents may be living plants, litter, detritus, leachates, soil bacteria and fungi, mycorrhizal fungi, root exudates, the atmosphere, water, airborne particles, or pathogenic organisms. Several organisms may also be involved at the same time during an explicit interaction. Very often the compounds that are derived from plants or their extracts do not produce the detected allelopathic effects without the associated factors. In various cases, these plant-derived compounds are further modified by oxidation, reduction, photochemical activation (Fischer *et al.* 1994), detoxification, or biochemical activation by microbes. Bioactive molecules released may enter the neighbouring plants by being adsorbed onto inorganic particles or organic matter in the soil, thereafter absorbed by roots.

Causative allelochemicals present in Solanaceae plant species have not been identified sufficiently. Identifying and quantifying the causative allelochemicals in plants and associated environments are the most important elements of 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 extract. Girija and Gowri (2008) reported the presence of various secondary metabolites by means of phytochemical analysis (Table 3). The alkaloid profile of the petioles of most *Datura* species was dominated by hyoscyamine, scopolamine and an alkaloid provisionally identified as meteloidine by HPLC comparison with reference material (Parr *et al.* 1990).

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