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Allelochemicals and their role in defense response to highly invasive plants in tropical forests in India: A review

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Abstract
Plant invasion is an alarming concern in the tropical eco-climate, and creates an opportunistic advantage to mimic non-native climate conditions abruptly. Invasive plants possess a few marker allelochemicals that culminate in them for biological invasions to the non-native environment. The defense regulation of invasive plants mediated by the secretion of allelochemicals and interaction with peripheral native communities is fascinating to understand their successful establishment. Phyto and rhizo-secretions of allelopathic invaders and their antagonistic interaction with local plant communities navigate the entire process of native-invasive severance leading to causalities to regional flora of its vicinity betraying habitat and nutrient partitioning.

The Indian subcontinent is a widespread hub of most of the dominant invasive plant species. Out of about 40% of alien plants occupying 8.5% of total vascular flora in India, invasive species are represented by 25% species out of the total species. The alleviated effects of allelochemicals secreted by some of the most obnoxious invasive species and their pervasive role in the native flora of India have been reviewed in this context.

Keywords: invasive, allelochemicals, allelopathy, defense response, alien flora, obnoxious

Introduction

Invasive alien plant species (IAPS) are non-native to a particular eco-climate and are introduced intentionally or accidentally regulated by a multitude of factors including human-aided and other ecological influences. Invasion of non-native alien plants is a major concern for the global ecosystem, the consequences of which lead to deleterious effects on the habitat of naturally occurring species [1, 2]. The widespread expansion of invasive plant propagules causes the extinction of native species by modification of ecosystem functioning. The high-priority invasion has a deleterious effect on the native plant composition, abundance, and diversity of tropical and sub-tropical ecosystems [3–5]. The major contributing factor to the successful invasion of non-native plants is phenotypic and genetic plasticity and increased vigor for resource acquisition competing with native plants. Such species release a wide array of allelopathic compounds that inhibit/suppress neighboring plant communities [6].

Allelopathy is a biological term used to designate a group of biochemicals released by different parts of the plant body including leaves, stems, roots, flowers, fruits, pollens, etc. The term is derived from a combination of two Greek words allelo and pathy (meaning mutual suffering). The chemical interaction of released biochemicals or allelochemicals hinders many physiological processes in plants *viz*. seed germination, seedling growth and survival, reproduction, photosynthesis, respiration, transpiration, protein synthesis and enzyme activity in plants [7]. Apart from physiological hindrances the allelopathic biochemical also influence the distribution, abundance, and establishment of plant species in their native or introduced landmass.

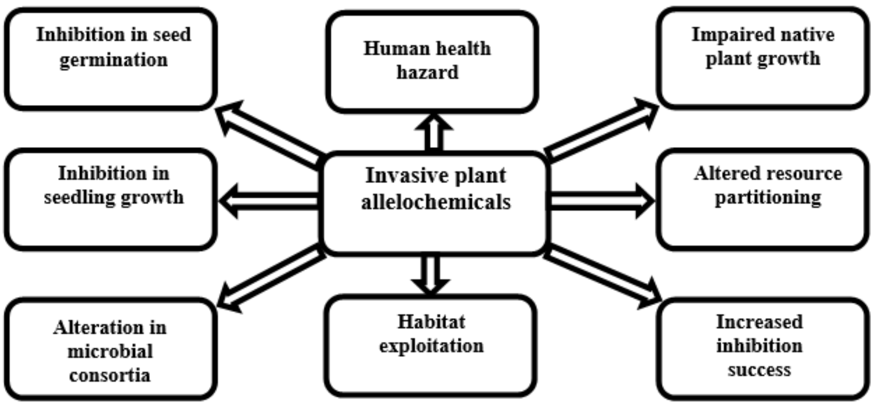

Fig 1: Multifarious effects of invasive plant allelochemicals on native plant communities

Allelochemicals are secondary metabolites that assemble as a byproduct during intermediate metabolism in plants. These are present in vegetative (roots, stems, leaves, rhizomes) and reproductive (flower, inflorescence, fruits, and seeds) parts of plants and released into their vicinity through the aerial and below-ground parts [8, 9]. The phytotoxic allelochemicals negatively impact vital physiological processes of nearby plants including germination and growth, pollination, photosynthesis, respiration, membrane damage, and DNA and protein damage [10–13]. Allelopathy is an alarming invasion mechanism for plants that acts as a weapon for direct or indirect interaction with native plant species. Recently Kalisz *et al*. (2020) investigated the allelopathic effects of 51.4% of invasive plants from a dataset of 524 known species [6].

Invasive noxious weeds of pantropical distribution are mostly allelopathic to wide groups of native plant species. The diverse group of phytochemicals released by them is a detriment to the growth and survival of native plants. Their easy mode of pollination and non-palatability contribute significantly contribute to the dominance in invasion land. Similarly, abundant seed production, fast-growing and spreading, and the broad range of adaptation tremendously contribute to the successful establishment of non-native habitats. *Parthenium hysterophorus*, *Ageratina adenophora*, *Lantana camara* secrete a broad range of highly phytotoxic allelochemicals that inhibit plant growth by perturbation of microbial consortia and soil physio-chemical properties [14, 15]. Allelopathic effects of such noxious species were reported in many crops including *Zea mays*, *Eragrostis* Sp., and *Eleusine coracana* [16]. Various researchers reviewed the allelopathic effects of invasive plants that culminate the native plant communities [17, 18].

Allelopathy of invasive plants: Allelopathy is a biological phenomenon commonly used to designate a class of biochemical compounds secreted by plants during their life processes. Allelochemicals released by plants or biological invaders have shown both stimulatory and detrimental roles in many physiological processes including growth, seed germination, reproduction, and overall development [7, 19, 20]. Allelopathy has been regarded as an important factor in the biological invasion of non-native habitats. The causalities caused by allelopathy are more serious if the native plants fail to co-evolve with the invaders [21]. Allelopathic interaction is an emerging topic of research to decipher the role of allelochemicals in regulating plant communities and their abundances. The subject receives higher attention to acknowledge the role of the invasive plant in recent times [22]. Zhu *et al*. (2011) have reported that soil microbiota plays a crucial role in negating the allelopathic effects of invasive plants. This research group experimentally demonstrated that *Eupatorium adenophorum* Spreng. a high-priority invasive species of China could reduce allelopathic effects in the presence of natural soil microbial communities.

The phytotoxins secreted by invasive plants are always detrimental to native plant species [23]. These allelochemicals are reported to inhibit seed germination and seedling growth in a multitude of plant species [23, 24]. A class of terpenes isolated from *Eupatorium adenophorum* was reported to inhibit seed germination in *Arabidopsis* [25]. *Mikania micrantha* H.B.K., an obnoxious weed to the Indian subcontinent has been reported to occur in more than 79 allelochemicals including phenolics, alkaloids, flavonoids and terpenes. The aqueous extracts of leaf and sesquiterpenes were inhibitory to the seedling establishment in a multitude of plants [26, 27]. Allelopathic properties of *Ipomoea carnea* Jacq., a wetland invader established in seed germination and seedling growth [28–30]. *Prosopis juliflora* (Swarz) DC has wider ecological adaptability in arid and semi-arid regions of the world and is commonly found in riparian belts of the Indian subcontinent. The leaf leachates predominantly contain higher concentrations of total phenolics and L-tryptophan which designates the allelopathic properties of the plant [3]. The allelopathic effects of the plant extracts in seed germination and seedling establishment were reported in a diverse group of plant species [31, 32]. The plant was reported to cause detrimental influences on seedling growth with increased seedling mortality in the vast majority of woody plant species [33]. *Eichornia crassipes* (Mart.) Solms is an obnoxious aquatic weed of water bodies in India with potential phytotoxic effects. The leaf extracts were reported to use as a biocontrol agent against *Mimosa pigra* and *Vigna radiata* [34]. Extensive dense mats grown in no more time can diminish dissolved oxygen in water bodies. More plant biomass production directly impacts more production of allelochemicals for biological invasion.

Impact of allelochemicals on soil: Invasive plants have myriad influences on soil chemistry that culminate in the ecosystem structure of the native plant communities. Root and litter exudates of invasive plants have an impact on the soil nutrient pool [35]. A high-priority invasive plant from Mexico, *Ageratina adenophora*, has acquired leaves that can break down in the soil more quickly than those of the native species. Corresponding to its native range, the plant acquired 13% more leaf nitrogen for photosynthesis which indicates an enhanced growth phenotype in the invasion land [36]. An invasive species may possess an allelochemical that is novel to an invaded community and may play a pertinent role as an emerging invader as suggested by the "novel weapon hypothesis" ultimately affecting the soil biogeography.

Table 1: High-priority invasive plant species that have an alarming impact on the forest ecosystems in India

Species	Family	Native range	Habit
Parthenium hysterophorus L.	Asteraceae	Tropical America	Terrestrial obnoxious herb
Ageratum conyzoides L.	Asteraceae	South America	Annual, herb
Eupatorium adenophorum (Spreng.) King & H.Rob.	Asteraceae	Mexico, Costa Rica, and South America	Perennial herb
Lantana camara L.	Verbenaceae	Tropical and Subtropical America	Perennial herb
Ipomoea carnea Jacq.	Convolvulaceae	Tropical America	Perennial herb
Mikania micrantha H.B.K.	Asteraceae	Neotropical origin	Perennial herbaceous vine
Prosopis juliflora (Swarz) DC	Fabaceae	Caribbean, Central and northern South America	Evergreen tree/bush, terrestrial
Eichornia crassipes (Mart.) Solms	Pontederiaceae	South America	Obnoxious aquatic weed

Allelochemicals as a potential source of herbicide

Herbicides are a popular source of biocontrol agents in agricultural fields. With the extent of herbicide application in global agriculture, some of the weeds are persistent to the effects of herbicides. As a consequence, novel technologies are employed for effective weed management. The application of allelochemicals has been an emerging weapon in the management practices of herbicides. Various allelochemicals have been isolated and employed as bioherbicides for a diverse group of plant species [37]. Allelochemicals have no residual toxic effects and are an effective method for sustainable agricultural production. Mulching i.e. use of allelopathic plant residue as ground cover can reduce weed growth, and enhance soil organic matter and fertility. The phytotoxic effects as revealed by metabolomic analysis of *Eupatorium adenophorum* extracts have impaired the metabolism of *Arabidopsis thaliana* [38]. The findings of this research may unfurl the potential allelopathic impacts of such obnoxious invasive plants as a novel strategy for bioherbicide. Herbicides are also deployed as biocontrol agents for a wide range of invasive plant species. However, they may affect soil microbial communities, that indirectly alter nodulation bacteria and mycorrhizal associations [39, 40].

Table 2: Major phytochemicals released by nuisance invasive plants (Modified after Das *et al*. 2021 [41]).

Invasive plant species	Phytochemicals group	Major chemical entities found to be associated with phytochemicals activities	Reference
Parthenium sp.	Essential oils	α-Pinene, Camphene, Sabinene, α-Phelandrene, trans-β-Ocimene, Borneol acetate, β-Caryophylene, Germacrene D	[42]
	Phenolic compound	caffeic, p-coumaric, gallic, p-hydroxybenzoic, anisic, vanillic and Ferulic acid, Gallic acid	[43]
	Sequineterpine lactone	Parthenin, coronopilin, hymenin	[44]
Lantana sp.	Essential oils	p-cymene, a-phellandrene, a-pinene, diterpene, c-terpinene, caryophyllene, cardinene, cineole, linalool, geraniol, a-terpinol, citral, phellandral	[45,46]
	Phenolic compound	Protocatechuic acid, Gentisic acid, p-hydroxybenzoic acid, Vanillic acid, Caffeic acid, Syringic acid, Vanillin, p-coumaric acid, m -coumaric acid, Ferulic acid, Salicylic acid, o -coumaric acid, t-cinnamic acid, Methyl coumarin	[47]
	Terpenoids	Lantadene A and B	[48]
Ageratum sp.	Essential oils	Precocene I and II, b-caryophyllene, a-bisabolene, a-cubebene, a-farnesene, b-farnesene, b-cubebene, germacrene, eupatoriochromene, fenchyl acetate, sesquiterpene hydrocarbon, nerolidal, caryophyllene oxide, bornyl formate, b-gurijunene, copane, camphene, b-elemene, methanezulene, tricycoundecane, a-muurolene, demethoxyencecalin, audorenececalinol, p-coumarin	[42]
	Phenolic compound	Gallic acid, Coumalic acid, Protocatechuic acid, Catechin, p-Hydroxybenzoic acid, p-Coumaric acid, Sinapic acid, Benzoic acid	[12]
Eupatorium adenophorum Spreng.	Phenolic compound	7-hydroxy-8,9-dehydrothymol 9-O-transferulate; 7-hydroxythymol 9-O-trans-ferulate; 7,8-dihydroxythymol 9-O-trans-ferulate; 7,8-dihydroxythymol 9-O-cis-ferulate; methyl (7R)-3-deoxy-4,5-epoxy-D-manno-2-octulosonate 8-O-trans-p-coumarate; methyl (7R)-3-deoxy-4,5-epoxy-D-manno-2-octulosonate 8-O-cis-p-coumarate; and o-coumaric acid	[49,50]
	Quinic acid derivatives	(5-O-trans-o-coumaroylquinic acid methyl ester; chlorogenic acid methyl ester; macranthoin F and macranthoin G	[51]
	thymol derivatives	7,9-diisobutyryloxy-8-ethoxythymol; 7-acetoxy-8-methoxy-9-isobutyryloxythymol and 7,9-di-isobutyryloxy-8-methoxythymol; 9-oxoageraphorone; (−)-isochaminic acid and (1α,6α)- 10-hydroxycar-3-ene-2-one	[52]
Mikania micrantha H.B.K.	Terpenes	deoxymikanolide, dihydromikanolide, and 2,3-epoxy-1-hydroxy-4,9-germacradiene-12,8:15,6-diolide	[27]
	Phenolics	Vanillic acid, Caffeic acid, Resorcinol, p-Hydroxybenzaldehyde, 3,4-Di-o-caffeoylquinic acid n-butyl ester, 3,5-Di-o-caffeoylquinic acid n-butyl ester	[53,54]
	Flavonoids	Eupalitin, Eupafolin, Luteolin, Mikanin	[54]
Ipomoea carnea Jacq.	Alkaloids	Swansonine, Calystegine	[55,56]
	Terpenes	tau-cadinol, α-cadinol, spathulenol, caryophyllene oxide	[57]
Prosopis juliflora (Swarz) DC	Flavonoids	Schaftoside, vitexin, Isovitexin, vicenin II, Isoschaftoside	[58]
	Alkaloids	Juliflorine, Julifloricine, Juliflorídine, Juliprosinene, Juliprosine, Juliprosopine, Mesquitol, Seco-juliprosopinal,	[59,60]
Eichornia crassipes (Mart.) Solms	Phenolic compound	Pyrogallol, resorcinol, 4-methylresorcinol, catechol, 2-methylresorcinol, p-hydroxybenzoic, Gentisic, chlorogenic, caffeic, p-coumaric, ferulic, vanillic, syringic, gallic, protocatechuic, salicylic acids.	[61]
	Flavonoids	Gossypetin, luteolin, tricin, apigenin, azaleatin, chrysoeriol, kaempferol, orientin, quercetin, isovitexin, naringenin, myricetin, rutin	[61]
	Terpenoids	Phytol, Squalene, camarolide	[61]
	Alkaloids	Tomatine, cytisine, Quinine, thebaine, codeine, nicotine, 1H-pyrrole,1-phenyl, pipradrol, pipradrol	[61–63]

Conclusion

Allelochemicals from a wide range of plant species have been identified to date. Their potential application as bioherbicides, agents for stress mitigation, and disease and paste management has been realized in recent times. Their inhibitory properties as volatile oils, leaf leachates, root exudates, and mulches have been investigated. However, there lies tremendous scope in deciphering the intricate mechanisms behind their mode of action, concentration, and role of microbial consortia in the ameliorations of allelopathy. The physiological and ecological role of allelochemicals in developing environment-friendly herbicides, and insect repellants have been in the limelight of research in current times. The role of allelopathy in the field of invasion ecology could underpin the causalities of biotic interferences caused during the secretion of bioactive compounds by invasive plants. Allelochemicals are novel weapons or enemy-established strategies to suppress the habitat and distribution of native plant species. Furthermore, a consensus of invasive plants could be realized as new non-indigenous species to understand anthropogenic disturbances as an ecological indicator.

Conflict of interests: Not applicable

Author contribution: M.D. and L.G. conceived the idea; M.D., N.I., M.N., C.R.B., H.J.K., and L.G. analyzed the data; M.D. wrote the manuscript; M.D., C.R.B., H.J.K., and L.G. critically reviewed the manuscript; All the authors approved the final version.

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