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Chemical Ecology and Allelopathic Nature of *Lantana camara* L.: Role of Secondary Metabolites in Plant Invasion Biology

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Abstract

Lantana camara L. is a flowering shrub native to tropical America, but today it has spread widely in many parts of the world as an invasive plant. One important reason behind its successful spread is the presence of many secondary metabolites and other bioactive compounds. These chemicals help the plant survive under different environmental conditions and protect it from insects, microbes, and grazing animals. The article provides an overview of the chemical ecology, allelopathic potential, and localization of important phytochemicals across various plant parts. *L. camara* contains several phytochemicals such as triterpenes, sesquiterpenes, monoterpenes, flavonoids, phenolic acids, and alkaloids. Together, these compounds help the plant compete strongly with nearby vegetation. In many studies, extracts and residues from leaves, roots, flowers, stems, fruits, and even rhizosphere soil showed inhibitory effects on seed germination and seedling growth of many monocot and dicot plants. Different plant parts contain different types of metabolites, and this variation may help the plant adapt easily to changing environmental conditions. The allelopathic nature of *L. camara* is considered one of the major reasons for its ecological dominance in invaded areas. At the same time, some of these compounds also show useful medicinal and biocontrol potential. Therefore, understanding the phytochemistry and ecological effects of this plant may help in better ecosystem management and future utilization of its bioactive compounds.

Keywords: *Lantana camara*, Secondary metabolites, Allelopathy, Phytochemicals, Invasive plant ecology, Chemical interactions.

1. Introduction

Lantana camara L. is commonly known as wild sage or red sage and a member of the family Verbenaceae. It is a perennial shrub and usually grows about 1–4 m tall. The plant forms dense bushes in open areas. Leaves are opposite, hairy having serrated margins with long petioles. Flowers are small and colorful and grow in clusters near the leaf axils. Under suitable conditions, flowering occurs throughout the year. The fruits are small round drupe, and each fruit generally contains 1–2 seeds¹⁻⁴. Being native to tropical America, it is recognized among the world's ten most noxious weeds, was introduced into the Indian subcontinent in the early nineteenth century⁵. Over time, it has become a major ecological threat, adversely affecting both native plant and animal communities (Fig. 1). The species produces toxic compounds such as Lantadene A, which can be harmful to grazing animals, and releases allelopathic chemicals that inhibit the growth of surrounding vegetation, thereby altering the natural balance of ecosystems⁶.





Figure 1. Taxonomic position with representative images of *Lantana camara* depicting its morphological characteristics and occurrence in natural field conditions.

1.1 Secondary metabolites (Bioactive Phytochemicals) of *Lantana camara* and Their Ecological Functions

Lantana camara accumulates a chemically diverse suite of secondary metabolites - principally pentacyclic triterpenoids, sesquiterpenes and other volatile terpenoids (essential-oil constituents), flavonoids and phenolic glycosides, alkaloids, saponins, steroids and tannins. These compounds are differentially localized in the plant's organs (leaves, flowers, stems, fruits, roots) and together underlie the species' medicinal uses, herbivore toxicity,

antimicrobial activity and strong allelopathic potential that promotes its invasiveness.

In other words, *L. camara* is a chemically rich invasive shrub that produces an extensive variety of secondary metabolites, which are primarily responsible for its ecological adaptability, allelopathic potential, and toxic effects on different organisms. These bioactive compounds belong to diverse phytochemical classes such as triterpenes, sesquiterpenes, monoterpenes, aromatic compounds, phenolic acids, phenolic aldehydes, phenylpropanoids, flavonoids, alcohols, and fatty acids. Each group contributes

uniquely to the plant's physiological defense mechanisms, ecological competitiveness, and invasiveness. These metabolites have been shown to affect mammals, insects, nematodes, fungi, bacteria, and competing plants⁷⁻²⁶.

The most dominant category is the triterpenes, which include compounds such as Lantadene A, Reduced Lantadene A, Lantadene B, Reduced Lantadene B, Lantadene C, Lantadene D, Icterogenin, Oleanonic acid, Lantanolic acid, Lantoic acid, Pomolic acid, Ursolic acid, Camarinin, Camarin, and Lantacin. Among the various compounds found in *Lantana camara*, Lantadene A is noted as one of the more toxic compounds. The molecule impacts mammals, insects and nematodes, and may also lead to liver damage and photosensitivity in grazing animals. According to previous works^{8-10, 20, 23}. Lantadene B disturbs wild animals and insects by disturbing normal cellular activities. Forms of Reduced Lantadene A and Reduced Lantadene B are also toxic but with lesser effect^{7,9,23}. Other compounds, like Lantadene C, D, and Icterogenin, exhibit potent biological activity against microorganisms and animals^{9,10}. Other compounds such as Lantadene C, Lantadene D, and Icterogenin also show strong biological activity against microorganisms and animals⁸.

Some triterpenes like Oleanonic acid, Lantanolic acid, Lantoic acid, Pomolic acid, and Ursolic acid have antimicrobial, antifungal, and insecticidal properties^{8,16,19}. These compounds help the plant protect itself from microbes and herbivores. Camarinin, Camarin, and Lantacin also show strong allelopathic effects and reduce the germination and growth of nearby plants^{16, 17}. Because of this, *L. camara* can spread easily and dominate surrounding vegetation.

The plant also contains many sesquiterpenes such as β -Caryophyllene, β -Humulene, Isoledene, α -Copaene, Farnesol, Germacrene-D, β -Curcumene, and γ -Muurolene. These compounds protect insects, fungi, and

nematodes. β -Caryophyllene is one of the important compounds and shows activity against insects and other harmful organisms^{11, 13, 14, 20, 24}. β -Humulene acts as an insect repellent, while Isoledene and α -Copaene affect insect feeding and egg laying^{13, 15}. Germacrene-D and β -Curcumene also possess antifungal and antibacterial properties^{20, 21, 24}.

Monoterpenes like Thymol and Loliolide are also present in *Lantana camara*. Thymol helps in controlling bacteria and fungi, whereas Loliolide is associated with allelopathic activity and suppresses the growth of nearby plants^{14, 22}.

Apart from terpenoids, the plant contains aromatic compounds and phenolics such as Methylcoumarin and Umbelliferone which show antioxidant and antimicrobial activity²⁵. Phenolic acids including Salicylic acid, Gentisic acid, Vanillic acid, and p-Hydroxybenzoic acid are also found in the plant. These compounds help the plant in stress tolerance and defence responses²⁵. Some phenolic compounds like Vanillin, Caffeic acid, p-Coumaric acid, and Ferulic acid also play important roles in antioxidant, antimicrobial, and allelopathic activities²⁵. Flavonoids such as Quercetin and Vitexin are important for reducing oxidative damage in plant cells. Characterized by their strong antioxidant activity, Quercetin and Vitexin also exhibit antimicrobial and anti-inflammatory properties^{25, 26}.

Cis-3-hexenol and other substances contribute to plant odor and insect repellent activity¹². Fatty acids (Hexadecanoic acid; Eicosapentaenoic acid) assist in membrane stability, energy storage, and defense signalling^{13, 22}.

The considerable abundance of secondary metabolites in *Lantana camara* has some important functions in its survival and invasiveness. By secreting these compounds plants can block the growth of other nearby plants. The plant is widely studied in the allelopathy, chemical ecology and pharmacology fields due to these properties (Fig. 2).

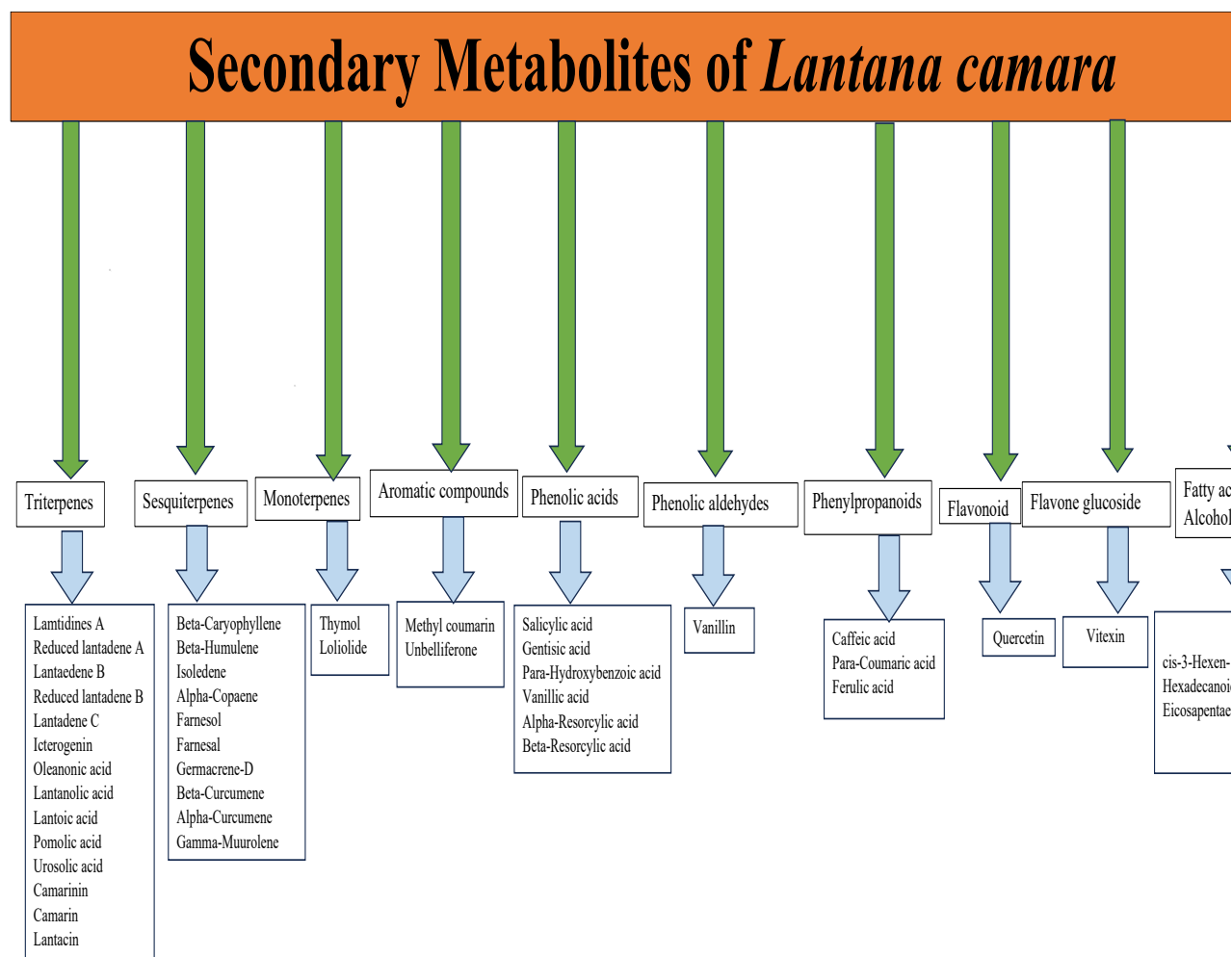


Figure 2. Chemical diversity of *Lantana camara* and major classes of secondary metabolites involved in defense, allelopathy and ecological adaptability.

1.2 Distribution of Allelochemicals in Plant Tissues

Research on the varied parts of the plant *L. camara* shows the plant has many secondary metabolites that have important biological activities. These organic compounds vary creatively in plant parts such as stem, leaves, root, flower or fruit. Most of the researchers have identified several chemical groups in the plant such as monoterpenes, sesquiterpenes, triterpenes, alkaloids, flavonoids, tannins, steroids, phenolic, essential oils, quinones, and saponins. These substances assist the plant in adapting to various environmental conditions and defend it against insects, diseases, and other stress factors²⁷.

Phytochemical investigations have also revealed that all the parts of the *L. camara* plant have allelochemicals. Bioactive compounds belonging

to different chemical classes occur in different parts of the plant including leaves, stems, roots, flowers, fruits and inflorescences. The spread of these compounds across the various tissues is probably crucial for the plant's allelopathic property and ecological adaptability.

The whole plant contains the characteristic triterpenoids lantadene A and lantadene B, which are considered the key bioactive and allelopathic compounds of *Lantana camara*²⁸.

The leaves exhibit a particularly complex phytochemical constitution. They are rich in lantadene A, lantadene B, lantanilic acid, icterogenin, and 4',5-dihydroxy-3,7-dimethoxyflavone-4'-O- β -D-glucopyranoside.

Other compounds such as stearoyl glucoside urs-12-en-3 β -ol-28-oic acid and 3 β -D-glucopyranosyl-4'-octadecanoate are also present. The leaf essential oils primarily comprise

germacrene D (19.8%), E-caryophyllene (19.7%), bicyclogermacrene (11.7%), and α -humulene (9.3%), alongside α -copaene, epi- α -muurolol, α -muurolene, germacrene-A, cubebol, germacrene-D-4-ol, davanone, phytol, globulol, δ -cadinene, tetradecane, β -elemene, β -gurjunene, and β -E-farnesene. Additionally, the leaves contain hexadecanoic acid, phytol, caryophyllene oxide, 9,12,15-octadecatrienoic acid, and its methyl ester, together with various other terpenoids such as α -thujene, 3-carene, β -phellandrene, limonene, β -cymene, eucalyptol, geranyl formate, α - and β -copaene, α - and β -elemene, δ -selinene, α -muurolene, caryophyllene oxide, espatulenol, intermedeol, humulene epoxide 2, and β -bisabolene. In addition to these volatiles, the leaves also exhibit the presence of alkaloids, flavonoids, phenols, steroids, cardiac glycosides, and carbohydrates. Several polyphenolic and terpenoid derivatives such as resveratrol dimer, iso-humolones, oleuropein glucoside, quercetin-3-O-glycoside, myricetin, oleuropein, 12-deoxy-16-hydroxy-phorbol, aloeresin A, humulones, ursolic acid, viniferin, epicatechin, oleanolic acid, 5-hydroxy-3,4,7-trimethoxy-flavanone, apigenin-6,8-di-C- β -D-glucoside, procyanidin A2, caffeoyl-O-hexoside, tanshinone IIA, and phillyrin have also been identified. Leaf extracts are therefore dominated by terpenoids, flavonoids, iridoid glycosides, phenolic acids, and their derivatives, along with compounds such as 13-docosenamide, α -hydroxyisocaproic acid, cyclo(L-prolyl-L-valine), and 2,5-piperazinedione. Further constituents include dodecanal, oxirane, tetradecyl, cholestan-3-ol, 2-methylene-, (3 α ,5 α), 1-dodecanamine, n,n-dimethyl, 1-chlorooctadecane, 9-octadecenoic acid (Z)-methyl ester, humulene, 1,6,10-dodecatrien-3-ol, 3,7,11-trimethyl-(E), eudesma-4(15),7-dien-1 α -ol, benzene (chloromethyl), 2-methyleneborexane, 7-(trifluoromethyl)naphthalen-1-ol, 1-chloroundecane, benzyl-(4-methylbenzyl)amine, and 1-(N-benzyl-N-methylamino)-4-methoxybutan-2-one^{21, 28-38}.

The essential oils of *Lantana* also contain high proportions of caryophyllene, humulene,

sabinene, α -pinene, β -myrcene, β -pinene, p-cymene, α -terpineol, β -cubebene, γ -muurolene, bicyclogermacrene, germacrene D, E-nerolidol, cubebol, caryophyllene oxide, isoaromadendrene epoxide, β -bisabolene, spathulenol, davanone, viridiflorol, β -eudesmene, δ -cadinene, copaene, eucalyptol, cis-sabinene hydrate, borneol, trans- β -ocimene, and D-limonene, demonstrating the chemical diversity and ecological significance of these volatiles^{21, 28-38}.

The aerial parts are predominantly composed of triterpenoids such as ursethoxy acid, camaryolic acid, methylcamaralate, camangeloyl acid, and β -sitosterol-3-O- β -D-glucopyranoside, as well as octadecanoic, docosanoic, and palmitic acids, together with camaric acid and lantanolic acid. Other identified triterpenes include lantanoic acid, camaranoic acid, lantic acid, camarinic acid, camangeloyl acid, camarinin, oleanonic acid, and ursonic acid. Additional compounds such as camarolic acid, lantrigloylic acid, 28-norolean-12,17-diene triterpene lantigdienone, lancamarinic acid, and lancamarinin have also been detected, highlighting the structural diversity of the plant's secondary metabolites^{17, 39-43}.

The inflorescences contain abundant volatile sesquiterpenes such as bicyclosesquiphellandrene, E- β -farnesene, E- β -caryophyllene, γ -muurolene, γ -curcumene, α -zingiberene, α -gurjunene, γ -amorphene, α -muurolene, sesquithujene, α -trans-bergamotene, and trans-cadina-1,4-diene⁴⁴.

The flowers of *Lantana camara* show the presence of luteolin 7-O- β -galacturonyl-(2 $\rightarrow$ 1)-O- β -galacturonide, α -pinene, sabinene, linalool, thymol, E- β -caryophyllene, E- β -farnesene, α -humulene, γ -muurolene, bicyclogermacrene (E,E), α -muurolene, and isospathulenol, along with several phenolic acid derivatives, phenylethanoid glycosides, and flavonoids. Other major flower volatiles include bicyclogermacrene, (+)-epi-bicyclosesquiphellandrene, γ -elemene, α -muurolene, α -humulene, α -trans-bergamotene, α -phellandrene, and (-)- β -caryophyllene^{14, 45-47}.

The fruits are enriched with trans- β -caryophyllene, sabinene, eucalyptol, α -humulene,

bicyclogermacrene, germacrene D, and trans-nerolidol, while the stems contain sabinene, linalool, neral, geranial, thymol, E- β -caryophyllene, E- β -farnesene, α -humulene, γ -muurolene, germacrene (E, E), α -muurolene, and isospathulenol^{14, 28}.

A combined extract of leaves and flowers has been reported to contain 3,7,11,15-tetramethylhexadec-2-en-1-ol (14.72%), methylhexopyranoside (13.83%), linolenic acid (12.70%), 3-deoxy-D-mannonic acid (7.97%), palmitic acid (6.99%), tiglic acid (6.47%), 2,3-dihydrobenzofuran (6.25%), tert-butyl phenyl carbonate (4.18%), 2,6-dimethoxyphenol (3.55%), and 9,12-octadecadienoic acid (2.23%)²².

1.3 Allelopathic Activities of *Lantana camara* Extracts and Residues

Many studies have shown that *L. camara* has strong allelopathic activity. Different parts of the plant such as leaves, stems, roots, flowers, fruits, and even surrounding soil release chemicals that affect nearby plants. These allelochemicals are released through leaf extracts, root extracts, leachates, plant residues, and decomposed plant material. Because of this, the growth and development of many plant species get affected. Leaf extract of *L. camara* has shown strong inhibitory effects on *Lactuca sativa* (lettuce). It reduces seed germination and affects normal cell development. Researchers observed increased production of reactive oxygen species (ROS), which damages plant cells and membranes⁴⁸. Similar effects were also seen in *Eichhornia crassipes* (water hyacinth). In this plant, leaf extracts disturbed leaf bud formation, increased catalase and SOD enzyme activity, and caused accumulation of hydrogen peroxide and membrane damage⁴⁹.

Lantana camara was also reported to have an allelopathic effect on many crops. Leaf extracts reduced seed germination and seedling growth in crops like *Brassica juncea*, *Cucumis sativus*, *Phaseolus mungo*, *Raphanus sativus*, *Vigna unguiculata*, and *Cicer arietinum*⁵⁰. The root and shoot growth of *Centroma pubescens* and *Vigna radiata* showed

similar inhibitions^{51, 52}. The extracts of *Lantana* also influenced regeneration in the moss *Funaria hygrometrica*⁶⁰. This shows that the plant can influence lower plant groups too.

The inhibitory effect was greater with the application of stem and leaf extracts. In both its germination and seedling growth were reduced⁵⁹. Extracts made from the leaves, stems and roots also inhibited germination as well as biomass of *Cicer arietinum*, *Phaseolus mungo* and *Lens esculenta*^{53, 56}. The early growth in *Eruca sativa* is affected by flower extracts. A similar study illustrated that combined extracts of flowers, fruits and leaves were able to reduce the germination of seed and seedling elongation in *Raphanus sativus* and *Lactuca sativa*^{56, 57}.

Inhibitory effects were also shown by leachates released from shoots and flowers of *L. camara*. Forms of leachates including salts and metallic salts may enter through rains and dew to soils and vegetations nearby. It was reported that growth inhibition was noticed in *Eichhornia crassipes*. *Mimosa pudica* leaf leachates also modified the levels of carbohydrates, proteins, and nuclear acids. The activities of catalase, dehydrogenase, and peroxidase enzymes were altered^{60, 61}.

Root leachates of *L. camara* negatively affected the growth of *Triticum aestivum*. Germination and protein synthesis were reduced in treated plants^{62, 63}. Fruit and leaf leachates also inhibited the growth of *Pennisetum americanum*, *Setaria italica*, and *Lactuca sativa*⁶⁴. This suggests that almost all parts of the plant contribute allelopathic chemicals to the surrounding environment.

Plant residues and decomposed litter of *Lantana camara* also show strong phytotoxic effects. When plant residues were mixed in soil, growth reduction was observed in *Triticum aestivum*, *Zea mays*, *Glycine max*, *Lepidium virginicum*, and *Abutilon theophrasti*⁶⁷. Decomposed root and shoot material also inhibited plant growth [66]. Leaf litter of *Lantana* suppressed seed germination and seedling development in plants like *Raphanus sativus*, *Lactuca sativa*, *Bidens pilosa*, *Bidens bipinnata*, and *Urena lobata*⁶⁷.

Rhizosphere soil collected from *Lantana*-dominated areas also showed phytotoxic effects. Growth inhibition was reported in *Achyranthes aspera* and *Albizia lebbek*. Seed germination was reduced in *Avena sativa*, *Cicer arietinum*, *Hordeum vulgare*, and *Triticum aestivum*^{25,59-69}.

Overall, *L. camara* affects nearby plants in many ways. Its extracts, leachates, residues, and rhizosphere soil all contribute to allelopathic activity. The plant can suppress both monocot

and dicot species, including many crops and weeds. This strong allelopathic nature is considered one of the important reasons behind the invasive success and ecological dominance of *L. camara* in different environments.

The proposed mechanism of allelochemicals of *Lantana camara* in influencing the neighboring plants by inducing oxidative and physiological disturbances is summarized in Figure 3.

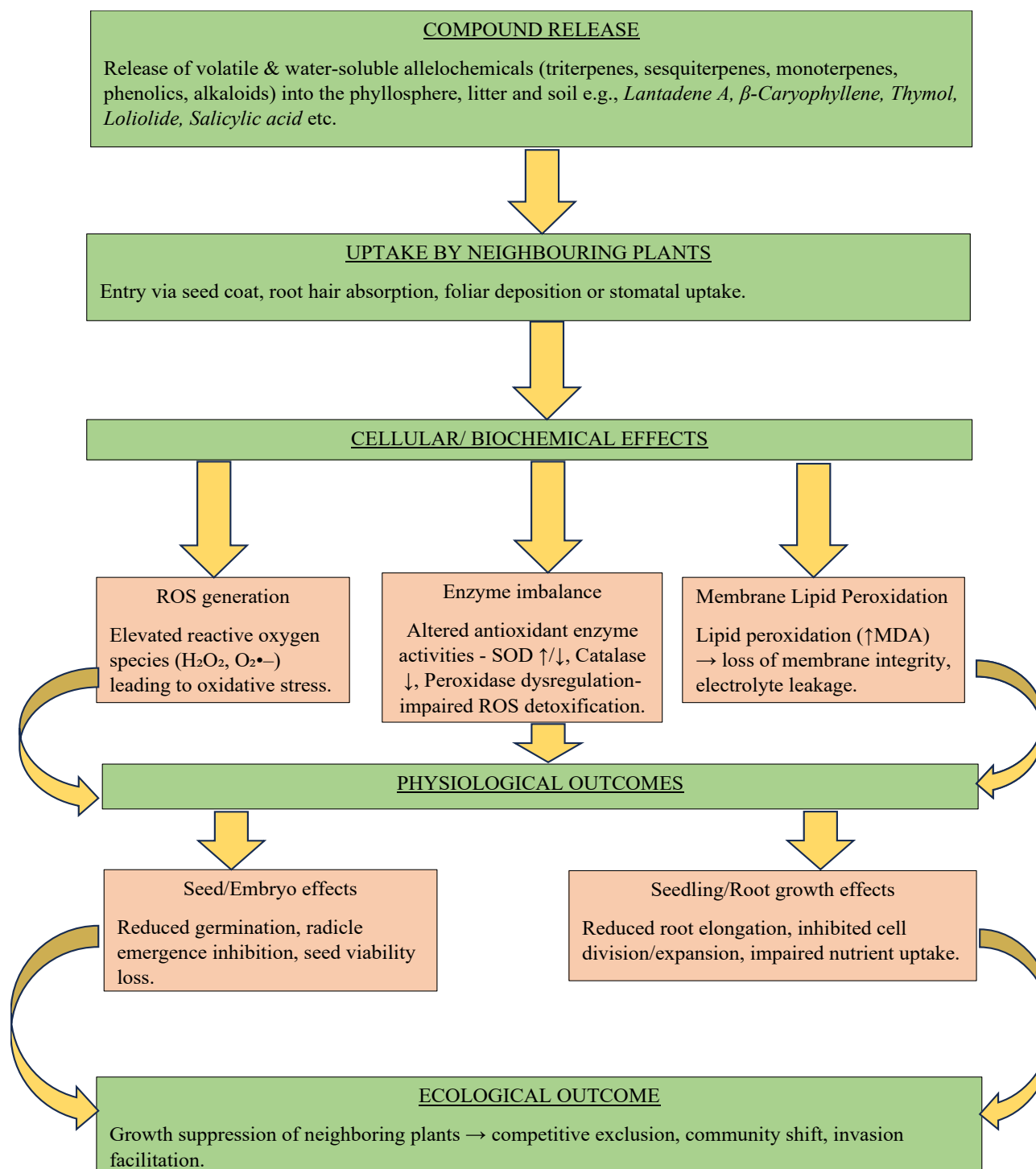


Figure 3. Allelopathic mechanism of *Lantana camara* showing the role of ROS (Reactive Oxygen Species), SOD (Superoxide dismutase) enzyme, and MDA (Malondialdehyde) in inhibition of seed germination and plant growth.

2. Conclusion

Overall, *Lantana camara* is a good example of how a plant can become highly invasive because of its strong chemical nature. Chemical composition analysis revealed secondary metabolites like flavonoids, phenolic acids, triterpenes, and more. These compounds assist the plant in defending itself against insects, microbes, diseases and neighboring plants. Various chemical components are produced in different parts of the plant, which help them to survive under different conditions.

Extracts, residues, and rhizosphere soil of *Lantana camara* have been shown in many studies to inhibit the germination and growth of surrounding vegetation. Due to the production of bioactive chemicals that inhibit the growth of other plants, the plant can quickly spread outwards and dominate space. Wild plants and cultivated crops are affected.

Simultaneously, these bioactive compounds also have scientific importance. Certain compounds exhibit antimicrobial, antioxidant and medicinal properties. In spite of being a harmful invasive weed, in the future, *Lantana camara* may become useful for medicine, agriculture, and biocontrol research. According to scientists, further studies on the chemical ecology and phytochemistry of the species may yield a greater understanding of the plant and its compounds, and their possible advantages.

3. Prospects

There is still a need for more studies to ascertain the allelopathic mechanism of *Lantana camara*. It is recommended that future studies focus on impacts of different allelochemicals on plant cells and other biochemical activities. ROS (Reactive Oxygen Species), the imbalance of enzymes, and stress-induced changes in target plants can be focus areas. Researchers may also study how these substances affect gene expression, as well as plant metabolism.

L. camara may be helpful in weed management due to its allelochemicals. The separation of these substances may aid in the creation of herbicides that are not hazardous to the natural

environment. Natural substances can replace synthetic chemicals and help restore our ecosystem and control invasive weeds from spreading.

Various compounds discovered in *L. camara* also exhibit medicinal potential. Anticancer activity is shown by triterpenoids and flavonoids of *Ganoderma*. There is a requirement of various studies to know their toxicity, bioavailability and medicinal values. Some of these compounds may find use in pharmaceutical research and drug discovery in future.

Contemporary approaches like genomics, transcriptomics, and metabolomics can also assist in studying the biosynthesis of crucial allelochemicals in *Lantana camara*. Investigating intermediates and secondary metabolites could reveal their metabolic pathways and potential applications.

Climate Change could have an impact on the invasiveness of *L. camara*. Secondary metabolite production and allelopathic activity can be affected by environmental stress conditions like drought, temperature changes and pollution. As a result, upcoming climate change and invasion biology studies will improve the prediction and management of the spread of this invasive plant.

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Authors' Contribution

Khushnuma Naz conducted the literature survey, analyzed the collected information, and prepared the manuscript draft. **Pramila Pandey**, as the corresponding author, provided guidance, supervision, and critical revisions throughout the manuscript preparation process. **Sujeet Gaur** carried out the final editing of the manuscript. **Surendra Pratap Singh** and **Narendra Shankar Pandey** provided overall supervision and academic support during the study.

Conflict of Interest

The authors declare that there is no conflict of interest related to this review work.

Data Availability Statement

The material for this review paper is prepared from already published research papers and scientific articles. The data consulted in this research is taken from the mentioned references. The current study did not include any new experimental work or data analysis.

Use of AI Statement

The author(s) utilized Gemini (developed by Google) and Grammarly during the writing process to enhance language clarity, correct spelling, and grammatical errors, and ensure appropriate formatting in alignment with *PhytoTalks* journal specifications. These tools were used strictly for language refinement and editing; no original scientific content or data interpretation was generated by the AI. The final manuscript was thoroughly reviewed and approved by the author(s), who remain fully accountable for its contents.

Ethical Approval

Ethical approval was not required for this study.

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