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REVIEW

Allelochemicals in the Invasive Success of Specific Alien Plant Species

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ABSTRACT: This review investigates the allelopathic characteristics of seven highly invasive plant species: *Lantana camara*, *Reynoutria japonica*, *Leucaena leucocephala*, *Bidens pilosa*, *Tithonia diversifolia*, *Arundo donax*, and *Pueraria montana* var. *lobata*. A thorough literature search was conducted using five databases. These plants employ allelopathy, releasing specific chemicals called allelochemicals that suppress the germination and growth of neighboring vegetation. Each species produces a distinct profile of allelochemicals, including cinnamic acid derivatives, benzoic acid derivatives, monoterpenes, sesquiterpenes, sesquiterpene lactones, pentacyclic triterpenoids, flavonoids, a non-protein amino acid, indole alkaloids, and anthraquinones. These allelochemicals are released into the environment through their roots, leaves, and decaying matter, giving the plants a competitive edge over native flora. This chemical suppression enables the plants to rapidly colonize and adapt to local habitats, indicating that allelopathy may contribute to their invasive success.

KEYWORDS: Allelopathy; competition; decomposition; exudation; growth inhibition; phytotoxicity; rhizosphere; volatile

1 Introduction

The plant invasion process comprises introduction, naturalization, and invasion phases. During the introduction phase, species are transported beyond their native range through intentional or accidental human activity. The naturalization phase involves environmental adaptation and successful reproduction. The invasion phase involves rapid population proliferation and geographic expansion [1–3]. During this process, species encounter environmental constraints that impede the establishment of self-sustaining populations and expansion [4–6]. Through environmental filtering, only a fraction of introduced species successfully become naturalized, and an even smaller subset becomes invasive [4–6]. The success of an invasion depends on several key factors, including the presence of empty niches, life history traits, and interactions with other organisms. Life history traits include the ability to adapt to climatic and edaphic conditions through phenotypic plasticity, along with successful growth and reproduction, and interactions with other organisms. These interactions include forming symbiotic relationships with microorganisms, defending against natural enemies, such as pathogens and herbivores, and competing with native plant communities [7–10]. Studies indicate that many invasive plants thrive due to their high adaptability, rapid growth, and prolific reproduction. These plants often form symbiotic relationships with soil microorganisms, including endophytes, arbuscular mycorrhizal fungi, and rhizobia. These plants have strong defenses against natural enemies and use allelopathy against native plant communities [11–13].

Allelopathy is the biological process by which host plants release chemicals called allelochemicals that affect the germination and growth of neighboring plants. Host plants synthesize and store these

allelochemicals within their tissues [14–16]. Depending on the conditions, these allelochemicals are released into the environment, including the rhizosphere, through root exudation, volatilization, and the degradation of plant residues in the soil [14–16]. This process gives host plants a competitive advantage by suppressing the germination and growth of neighboring vegetation. Plants compete intensely with neighboring vegetation for limited environmental niches and resources, including sunlight, nutrients, and moisture. A superior competitive advantage increases the likelihood of survival [17–19].

Allelochemicals are released into the environment, but identifying them is highly challenging due to their low concentration caused by adsorption into soil and degradation by microorganisms, oxidation, and photolysis. However, suitable solvents can be used to isolate allelochemicals stored in plant tissues. Many allelochemicals have been isolated and identified in the tissues of invasive plant species. These species use allelopathy to suppress competitive plants and secure a larger share of vital resources [20–22]. This review examines the allelopathic properties of seven notorious invasive plant species: *Lantana camara*, *Reynoutria japonica*, *Leucaena leucocephala*, *Bidens pilosa*, *Tithonia diversifolia*, *Arundo donax*, and *Pueraria montana* var. *lobata*. The primary objective is to clarify the mechanisms behind plant invasion, focusing on the role of allelopathy.

2 Methods

A thorough literature search was conducted using the Scopus, PubMed, Biological Abstracts, ScienceDirect, and Google Scholar databases. The search focused on terms related to invasive plant species, allelopathy, allelopathic substance, allelochemical, decomposition, exudation, inhibition, phytotoxicity, rhizosphere, and volatilization. A total of 284 publications were identified, comprising 57 for *L. camara*, 42 for *R. japonica*, 72 for *L. leucocephala*, 34 for *B. pilosa*, 29 for *T. diversifolia*, 27 for *A. donax*, and 23 for *P. montana* var. *lobata*. Every effort was made to include all relevant research papers in the analysis. To ensure broad coverage, no restriction was placed on the search period; however, a total of 41 studies were excluded due to a lack of clear methodologies, statistical analysis or because they were non-English papers without English abstracts. We included allelochemicals found in these species, but excluded compounds for which allelopathic activity in the respective species was not confirmed.

3 Allelopathy and Allelochemicals of *Lantana camara*

Lantana camara L. is a sprawling, perennial shrub in the Verbenaceae family. It is commonly known as lantana or shrub verbena. It can grow up to 4 m tall and form monospecific stands in various habitats, including forest edges, sparse forests, grasslands, coastal plains, and riparian zones. It also grows in disturbed areas, such as agricultural fields, orchards, forestry plantations, railroad tracks, roadsides, and abandoned land [23–27]. Originally from Mexico and tropical America, this plant was widely introduced for ornamental purposes. It has since become highly invasive, spreading across warm temperate, subtropical, and tropical regions in North and South America, Europe, Asia, Africa, and Oceania [23–26,28–31]. A random forest analysis indicated that *L. camara* is present in 114 countries. Areas between latitudes 35° N and 35° S exhibit a high invasion risk and include an additional 27 countries [32]. *Lantana camara* has been reported to have significant negative impacts on agriculture and natural ecosystems [27,33,34]. The International Union for Conservation of Nature and Natural Resources has listed it among the world's 100 worst alien invasive species [35] (Fig. 1).

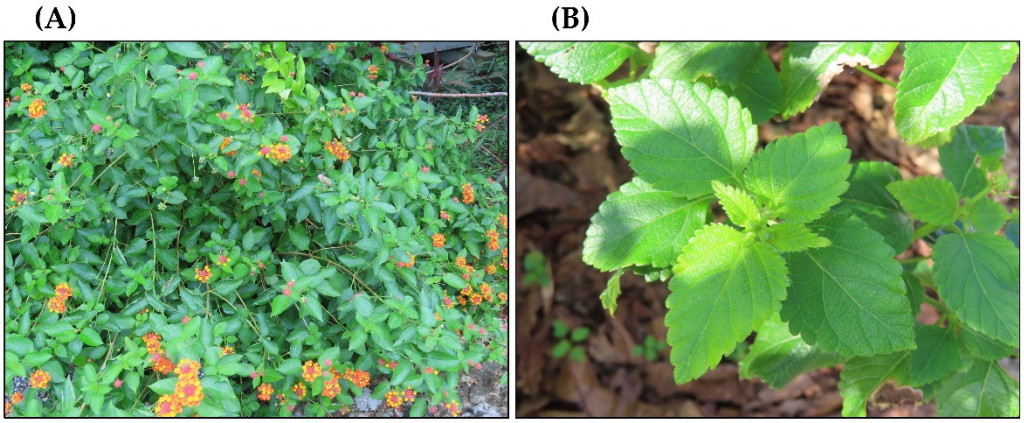

Figure 1: *Lantana camara.* (**A**): its monospecific stand. (**B**): its opposite leaves.

The rhizosphere soil of *L. camara* inhibited the germination and/or growth of *Albizia lebbeck*, *Achyranthes aspera*, *Cicer arietinum*, *Avena sativa*, *Triticum aestivum*, and *Hordeum vulgare* [36,37]. Residues from the shoots, leaves, and roots of *L. camara* also inhibited the growth of *Bidens bipinnata*, *B. pilosa*, *Urena lobata*, and *Morrenia odorata* [38,39]. A mixture of sand and chopped *L. camara* shoots inhibited the growth of *Abutilon theophrasti*, *Lepidium virginicum*, and *T. aestivum* [40]. Leachates from *L. camara* roots inhibited the germination of *T. aestivum* [41,42], and the growth of *Cucurbita pepo*, *Lycopersicon esculentum*, and *Phaseolus vulgaris* [43]. Leachates from *L. camara* leaves also inhibited the germination and growth of *Mimosa pudica* [44]. Additionally, soaking water from *L. camara* shoots was toxic to *Eichhornia crassipes*, ultimately killing it [45,46]. These findings suggest that *L. camara* contains allelochemicals that are released into rhizosphere soil through plant decomposition and leaching from plant parts by water.

Three cinnamic acid derivatives, including *p*-coumaric acid (**1**), caffeic acid (**2**), ferulic acid (**3**), and six benzoic acid derivatives, including salicylic acid (**5**), *p*-hydroxybenzoic acid (**6**), gentisic acid (**7**), α-resorcylic acid (**8**), β-resorcylic acid (**9**), and vanillic acid (**12**), were identified in the aqueous leaf extracts of *L. camara* [47] (Fig. 2). Cinnamic acid derivatives are synthesized from phenylalanine through the phenylpropanoid pathway in the cytoplasm of plant cells. The first intermediate in this pathway is cinnamic acid. The enzyme cinnamate 4-hydroxylase converts cinnamic acid into *p*-coumaric acid, which is then enzymatically converted into caffeic acid and ferulic acid [48–51]. Benzoic acid is produced from cinnamic acid via either a peroxisomal β-oxidative pathway or a mitochondrial non-β-oxidative pathway. Benzoic acid derivatives are typically synthesized by altering the aromatic ring or transforming functional groups on the existing benzoic acid skeleton [52].

These cinnamic acid and benzoic acid derivatives have been identified in various plant extracts [53,54]. Their involvement in plant allelopathy and modes of action have been investigated in many other plant species [55–57]. These compounds modify the protein and lipid profiles of the plasma membranes of target plant cells [52,56]. Consequently, the transmembrane electrochemical potential dissipates, leading to depolarization of the plasma membrane. This depolarization triggers indiscriminate leakage of various ions, including magnesium, potassium, phosphate, and nitrate, and alters cellular water homeostasis. These compounds also impair various enzymes involved in photosynthesis, protein synthesis, phytohormone synthesis, and secondary metabolism. Ultimately, this retards the proliferation and normal growth of plant cells [57–59]. Thus, the presence of these compounds in *L. camara* can alter the structural integrity of plasma membranes, disrupt the transmembrane electrochemical balance, and inhibit key metabolic enzymes in target plants.

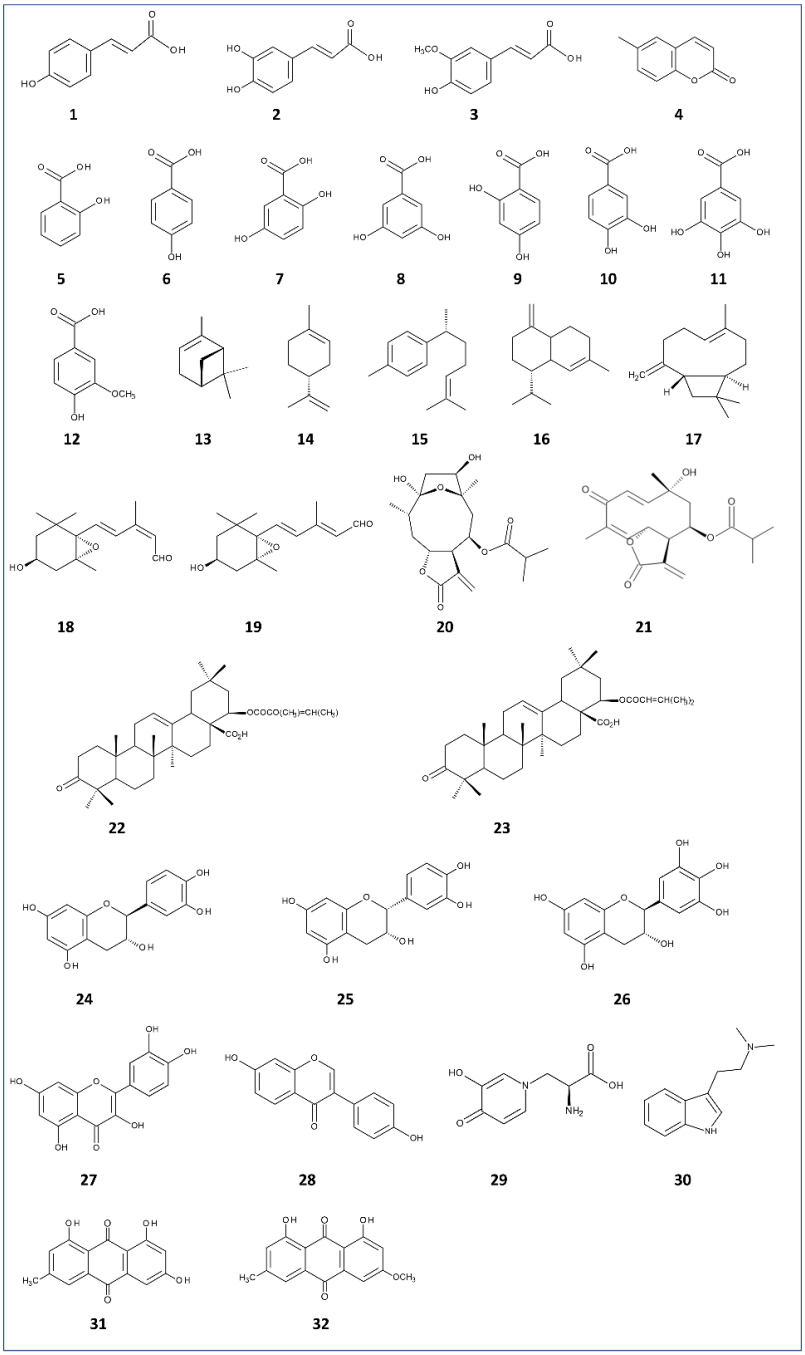

Figure 2: Allelochemicals identified in the invasive plants. Cinnamic acid derivatives; **1**: *p*-coumaric acid, **2**: caffeic acid, **3**: ferulic acid, **4**: methyl coumarin. Benzoic acid derivatives; **5**: salicylic acid, **6**: *p*-hydroxybenzoic acid, **7**: gentisic acid, **8**: α-resorcylic acid, **9**: β-resorcylic acid, **10**: protocatechuic acid. **11**: gallic acid, **12**: vanillic acid. Monoterpenes; **13**: α-pinene, **14**: limonene. Sesquiterpenes; **15**: α-curcumene, **16**: γ-muurolene, **17**: β-caryophyllene, **18**: *cis,trans*-xanthoxin, **19**: *trans,trans*-xanthoxin. Sesquiterpene lactones; **20**: tagitinin A, **21**: tagitinin C. Pentacyclic triterpenoids; **22**: lantadene A, **23**: lantadene B. Flavonoids; **24**: catechin, **25**: epicatechin, **26**: gallocatechin, **27**: quercetin, **28**: daidzein. Non-protein amino acid; **29**: mimosine. Indole alkaloid; **30**: gramine. Anthraquinones; **31**: emodin, **32**: physcion.

Research demonstrates that the essential oil from *L. camara* leaves suppresses the growth of *Portulaca oleracea*. This effect is primarily caused by three sesquiterpenes: α-curcumene (**15**), γ-muurolene (**16**), and β-caryophyllene (**17**) [60–62] (Fig. 2). As volatile agents, β-caryophyllene and α-humulene induce membrane damage in target plants, resulting in electrolyte leakage [63,64]. Additionally, β-caryophyllene has been reported to induce oxidative stress [65], and disrupt photosynthesis and water potential in target plants [66–68].

Two pentacyclic triterpenoids, lantadene A (**22**) and lantadene B (**23**) (Fig. 2), were identified in the leaves and rhizosphere soil of *L. camara*. Both compounds inhibited the growth of *Eichhornia crassipes* [69]. Lantadene A and lantadene B have been reported to act as defensive compounds against herbivores, causing cholestasis, hepatic necrosis, nephrosis, and jaundice [70]. However, the modes of action of lantadene A and lantadene B in allelopathy remain unknown.

These findings suggest that *L. camara* exhibits allelopathic properties by releasing allelochemicals, including cinnamic acid and benzoic acid derivatives, sesquiterpenes, and pentacyclic triterpenoids, into the rhizosphere and atmosphere through decomposition, leaching, and volatilization.

4 Allelopathy and Allelochemicals of *Reynoutria japonica*

Reynoutria japonica Houtt. (syn. *Polygonum cuspidatum* Siebold & Zucc.; *Fallopia japonica* (Houtt.) Ronse Decr.), is a bushy, perennial herb belonging to the Polygonaceae family. It is commonly known as Asian knotweed or Japanese knotweed and grows up to 3 m in height [71–73]. It branches well and forms monospecific stands [74]. The species is found in areas altered by human activity, including riverbanks, grasslands, pastures, forest margins, agricultural fields, roadsides, and other disturbed areas [74–76]. Originally from East Asia, it was widely introduced as an ornamental plant. This invasive species has spread to temperate regions of South Asia, North America, and Europe. It threatens native plant communities in these areas [73,74,77–79]. It has been listed among the world's 100 worst invasive alien species [35] (Fig. 3).

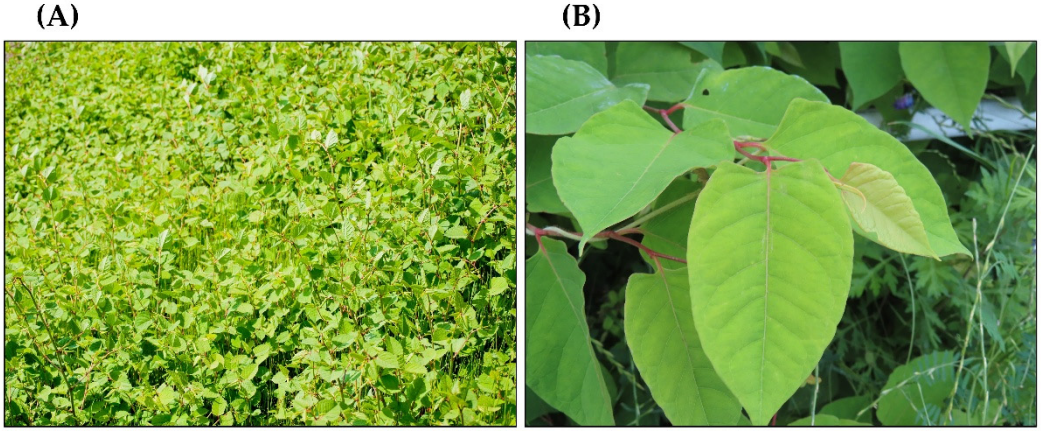

Figure 3: *Reynoutria japonica*. (**A**): its monospecific stand. (**B**): its alternate leaves.

Allelopathic property of *R. japonica* was confirmed using a donor-receiver bioassay. Test plants (*Salix atrocinerea*, *S. viminalis*, and *Populus nigra*) were irrigated with a mixture of nutrient solution and drain solution from *R. japonica*, and grown for four months. The growth of all the test plants was suppressed by the mixture solution [80]. The irrigated solution contained nutrients. Therefore, the inhibition may have been caused by allelochemicals in the drain solution from *R. japonica*. Considering this bioassay method, these allelochemicals may also be released through root exudation from *R. japonica*.

Reynoutria japonica is a perennial, but its above-ground parts die back in the winter [73]. These parts decay to form a litter layer. During the decomposition process, secondary metabolites are released into the rhizosphere soil where they act as allelochemicals [81–83]. Soil mixed with *R. japonica* leaves inhibited the germination of *Brassica napus* and *Sinapis alba* [84]. Soaking water from the senescent above-ground parts of *R. japonica* suppressed the germination of *Triticum aestivum* and *Sinapis arvensis* [85], suggesting that the water leachates contain allelochemicals. Aqueous extracts from the above-ground parts of *R. japonica* suppressed the germination of *Calamagrostis epigejos*, *Urtica dioica*, and *Lactuca sativa* [86], and the growth of *Helianthus annuus*, *Avena sativa*, and *Brassica napus* [87]. These findings suggest that *R. japonica* may contain allelochemicals that are released into the rhizosphere through decomposition and leaching.

Two flavonoids, catechin (**24**) and epicatechin (**25**) (Fig. 2), were identified in the roots and shoots of *R. japonica* [88–90]. These compounds have been found in various plants and are linked to allelopathic interactions [91–94]. Flavonoids regulate plant physiology by controlling auxin transport, driving shoot and root morphogenesis, and balancing reactive oxygen species. In allelopathic interactions, flavonoids significantly alter target root growth by suppressing ATP synthesis and interfering auxin pathways [95]. Plants also release certain flavonoids into the rhizosphere to modulate microbial dynamics [96]. The application of catechin and epicatechin initiated programmed cell death, which expanded from the root periphery to the stele. This propagation is likely driven by a calcium wave elicited by reactive oxygen species that disturbs ionic homeostasis and leads to cellular acidification [97–99].

Two anthraquinones, emodin (**31**) and physcion (**32**) (Fig. 2), were identified in the rhizosphere soil of *R. japonica* at concentrations of 55 and 30 mg per kg of dry soil, respectively. These compounds inhibited the growth of *Lactuca sativa*, *Phleum pratense*, and *Amaranthus* spp. at concentrations greater than 50–100 ppm in a laboratory setting [100]. While the pharmacological properties of these compounds are well-established, the mechanisms underlying their allelopathic effects remain unclear [101,102]. Furthermore, the activity of these compounds should be evaluated under field conditions with native plant species.

Reynoutria japonica is allelopathic and produces allelochemicals, such as catechin, epicatechin, emodin and physcion. These allelochemicals are released into the rhizosphere soil through decomposition, leaching, and root exudation.

5 Allelopathy and Allelochemicals of *Leucaena leucocephala*

Leucaena leucocephala (Lam.) de Wit is a small tree in the Fabaceae family. It is commonly known as white lead tree. It grows to a height of 3–20 m and has high biomass production. It reaches reproductive maturity within 4–12 months after germination and produces numerous viable seeds [103–107]. Originally from Mexico and Central America, it has been introduced to many subtropical and tropical regions for paper pulp and biochar production [108,109]. It is also used as a shade tree [110,111], as livestock fodder [112], and for erosion control [113–115]. However, *L. leucocephala* can easily spread to unintended areas. It forms monospecific stands in riparian zones, grasslands, forest edges, hillsides, and disturbed areas, including agricultural fields, abandoned land, and roadsides [116–118]. This species has spread to over 130 countries in warm temperate, subtropical, and tropical regions of South America, Southern Europe, South and East Asia, Africa, Australia, and the islands in the Caribbean, Indian, and Pacific Oceans [103–105,116]. *Leucaena leucocephala* negatively impacts native *plant communities by reducing abundance and richness* in infested areas [119,120]. Consequently, it is classified among the world's 100 worst invasive alien species [35] (Fig. 4).

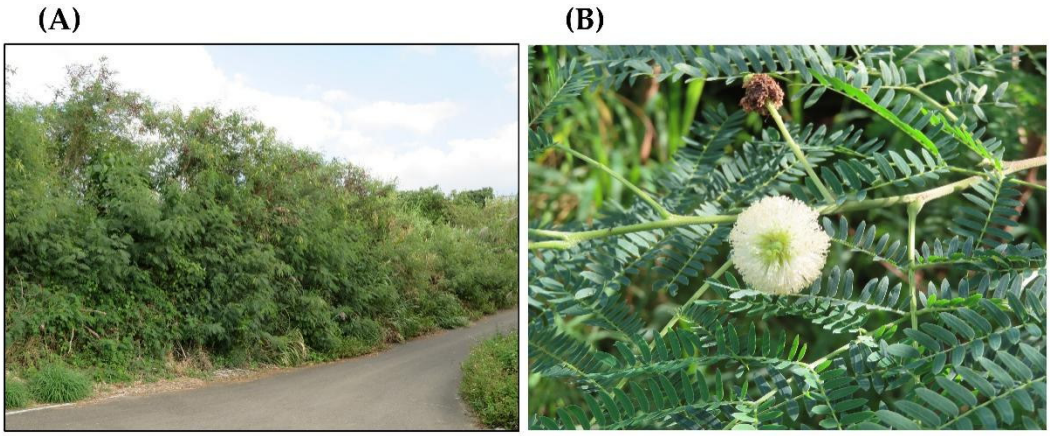

Figure 4: *Leucaena leucocephala*. (**A**): its monospecific stand along roadside. (**B**): its capitulum and alternate, bipinnate leaves.

Under controlled field conditions, the presence of *L. leucocephala* was observed to stunt the growth and survival of the woody plant species, *Erythrina velutina* [120]. Since typical resource competition was ruled out in the experimental setup, the finding suggests that allelopathy limits the growth and survival of *E. velutina*.

Soil samples taken beneath the *L. leucocephala* canopy and its leaf litter extracts significantly reduced the germination and early growth of *Tridax procumbens*, *Emilia sonchifolia*, and *Ageratum conyzoides* [121,122]. Incorporating its leaves and decomposed leaf litter into the soil inhibited the seedling growth of several tree species, including *Albizia procera*, *Liquidambar formosana*, *Mimosa pudica*, *Acacia confusa*, *Casuarina glauca*, and *Alnus formosana* [121,123]. Root exudates from *L. leucocephala* also inhibited the germination and growth of *T. procumbens*, *E. sonchifolia*, and *A. conyzoides* [122]. These findings suggest that allelochemicals likely enter the rhizosphere soil through root exudation and litter decomposition. Additionally, aqueous extracts from the aerial parts of *L. leucocephala* inhibited the growth of *Bidens pilosa*, *Amaranthus hybridus*, *T. procumbens*, *E. sonchifolia*, and *A. conyzoides* in both laboratory and greenhouse settings [124–126]. Thus, these extracts may contain allelochemicals.

Mimosine (**29**) (Fig. 2), a non-protein amino acid, is recognized as an allelochemical in *L. leucocephala* due to its ability to suppress the growth of various plants [121,127,128]. At a concentration of 100 ppm, mimosine suppressed the growth of *Mimosa pudica, Bidens pilosa*, *Lolium multiflorum*, *Brassica rapa*, and *Phaseolus vulgaris* by 31–93% for their shoots and 40–95% for their roots, respectively [129]. Mimosine also suppressed the growth of the shoots and roots of *Sesbania herbacea* and *Senna obtusifolia* [130], and *T. procumbens*, *E. sonchifolia*, and *A. conyzoides* [131]. Mimosine inhibits plant growth by disrupting cell division. This is evidenced by its suppression of rooting in *Allium cepa* [132], cell arrest between the G_1 and S phases in *Petunia hybrida* protoplasts [133], and its effect on the phytoplankton *Rhodomonas salina* [134]. However, exogenously applied mimosine has been reported not to significantly inhibit the growth of *L. leucocephala* [129]. *Leucaena leucocephala* contains mimosinase, an enzyme responsible for mimosine degradation, which exhibits significantly high gene expression [135–137]. Consequently, mimosinase-driven degradation of mimosine could mitigate its toxicity to the host plant.

Aqueous extracts of *L. leucocephala* aerial parts stimulated the activity of peroxidase in *Zea mays* roots [126]. Similarly, its aqueous leaf extracts induced the activity of key antioxidant enzymes, ascorbate peroxidase and catalase, in *Eichhornia crassipes* leaves, while promoting electrolyte leakage from cell membranes [138]. These enzymes are known to be upregulated in plants subjected to oxidative stress. Oxidative stress alters the physiological and structural processes of plant cells, particularly those of the

plasma membrane [139–143]. Mimosine triggered necrotic cell death and caused structural damage to cytoplasmic organelles in the root meristem of *Allium cepa*. Mimosine also increased superoxide dismutase and catalase activities, as well as malondialdehyde levels in root cells [132], suggesting that it may induce oxidative stress in root cells. This results in abnormal cytoplasmic organelles and necrosis [144–146]. Consequently, mimosine can trigger oxidative stress in target plants, disrupting their physiology and cellular structures.

Mimosine is highly concentrated throughout *L. leucocephala* plants. On a dry-weight basis, concentrations ranged from 2.4–13.6% (mature seeds), 0.47–8.6% (leaves), 1.2–2.7% (flowers), 0.15–0.68% (stems), and 0.16–0.66% (roots) [129,147,148]. Mimosine levels increased during germination and seedling development. Levels started at 3.9% in seeds and increased to 6.9% in six-day-old seedlings. Levels then reached 15.2% in two-week-old seedlings [148,149]. This progressive accumulation provides clear evidence that mimosine is synthesized *de novo* during these early developmental stages. In *L. leucocephala*, mimosine is synthesized by mimosine synthase from 3-hydroxy-4-pyridone and *O*-acetyl-L-serine [150,151]. *O*-acetyl-L-serine is catalyzed by serine acetyltransferase from serine and acetyl-CoA [150–153]. However, the biosynthesis pathway of 3-hydroxy-4-pyridone in *L. leucocephala* remains unknown.

Seedlings of *L. leucocephala* secreted mimosine into the growth medium at a daily rate of 1–5 μg per g of dry plant weight [154]. Mimosine accumulated in the soil at a concentration of 7.4 μg per g of dry soil weight [155]. These findings suggest that *L. leucocephala* releases mimosine into its rhizosphere soil. As previously mentioned, *L. leucocephala* tissues are rich in mimosine. It is also likely released into the soil through the decomposition of plant residues, resulting in its buildup. However, the concentration of mimosine in the soil, along with its specific activity, may not fully explain the allelopathic activity of *L. leucocephala*. Therefore, other compounds may be involved in the allelopathy of *L. leucocephala*.

The application of jasmonic acid and ethylene promotes mimosine biosynthesis in *L. leucocephala* seedlings [156]. Salicylic acid, UV irradiation, physical wounding, and sodium chloride (NaCl) stress also increase mimosine accumulation in these seedlings [148,156,157]. Jasmonic acid, ethylene, and salicylic acid are plant hormones that act as stress signaling molecules, triggering the transcription of stress-responsive genes [158–162]. These findings suggest that stress signaling molecules and environmental stressors, such as UV irradiation, physical wounding, and NaCl, may promote mimosine synthesis in *L. leucocephala*. Therefore, stress conditions caused by competition with neighboring plants may also increase the production of mimosine, enhancing the allelopathic activity and competitive ability of *L. leucocephala* against these plant species.

Gallocatechin (**26**) (Fig. 2), a flavonoid and the primary active agent in the methanol extracts of *L. leucocephala* roots, has been shown to suppress soil nitrification [163]. Nitrification is an essential mechanism that drives nitrogen cycling in ecosystems [164,165]. The exact mechanism is unclear, but gallocatechin from *L. leucocephala* may interfere with nitrification by inhibiting bacterial activity. Reduced nitrification decreases soil nitrate levels, thereby suppressing the growth of neighboring vegetation. Conversely, *L. leucocephala* stands have been shown to enrich soil nitrogen pools through symbiotic nitrogen fixation [166,167]. Future studies should assess the amount of available nitrogen in the soil under the *L. leucocephala* canopy.

Three cinnamic acid derivatives, such as *p*-coumaric acid (**1**), caffeic acid (**2**), and ferulic acid (**3**), and four benzoic acid derivatives, such as *p*-hydroxybenzoic acid (**6**), protocatechuic acid (**10**), gallic acid (**11**), and vanillic acid (**12**) (Fig. 2), have been identified in *L. leucocephala* leaves [121]. As described in the section on *L. camara*, these compounds function as allelochemicals.

A review of the literature revealed that *L. leucocephala* exhibits allelopathic effects due to the presence of allelochemicals, including mimosine, gallocatechin, and cinnamic acid and benzoic acid derivatives. The

plant releases mimosine into rhizosphere soil through root exudation. Additionally, the decomposition of its plant residues contributes to its accumulation in the soil. Gallocatechin suppresses nitrification in soil. Cinnamic acid and benzoic acid derivatives suppress the growth of neighboring plants. Consequently, *L. leucocephala* outcompetes other species for resources, which boosts its growth and population size.

6 Allelopathy and Allelochemicals of *Bidens pilosa*

Bidens pilosa L. is an annual herb in the Asteraceae family. It grows to a height of 20–180 cm and forms thick, monospecific stands [168–172]. It can grow in various habitats, including secondary forests, forest edges, grasslands, wetlands, streams, coastal areas, agricultural fields, pastures, railway lines, and roadsides [168–170,173,174]. Originally from subtropical and tropical America, this plant was widely introduced for ornamental purposes. Since then, it has become highly invasive, spreading across warm temperate, subtropical and tropical regions in Europe, Asia, North and South America, Australia, and Africa. *Bidens pilosa* has significant negative impacts on agriculture and natural ecosystems [169–176]. It is listed as an invasive plant that threatens the environment in over 40 countries [169,170,173–175] (Fig. 5).

The growth of *Cyperus rotundus* was inhibited by field soils obtained under *B. pilosa* stands [177], suggesting the presence of allelochemicals in the soil. Incorporating the chopped leaves and above-ground parts of *B. pilosa* into the soil inhibited the germination and growth of several spontaneous weed species and *C. rotundus* under field and greenhouse conditions [177–179]. Root exudates from *B. pilosa* suppressed the growth of *Leucaena leucocephala*, *Echinochloa crus-galli*, and several crop species, including *Medicago sativa*, *Lactuca sativa*, *Oryza sativa*, *Zea mays*, and *Sorghum bicolor* [180,181]. Its root exudates also inhibited the spore germination, growth, and photosynthesis of the fern *Pteris multifida* [182,183]. However, adding activated carbon to the soil significantly reduced growth inhibition [177]. Activated carbon can absorb various compounds, including allelochemicals, which renders them ineffective [184,185]. These findings suggest that allelochemicals are released into the soil from *B. pilosa* through root exudation and plant decomposition. Additionally, aqueous extracts from various parts of *B. pilosa*, such as the stems, leaves, and roots inhibited the germination and growth of several weeds, including *Amarantus dubius* [186], *Ageratum conyzoides* [187], *E. crus-galli*, *E. coloa*, *Ludwigia chinensis*, *L. hyssopifolia*, *Sphenoclea zaylania*, *Cyperus iria*, *Fimbristylis dichotoma*, and *Fimbristylis milacea* [179,188]. These results suggest that the allelochemicals in *B. pilosa* are extractable.

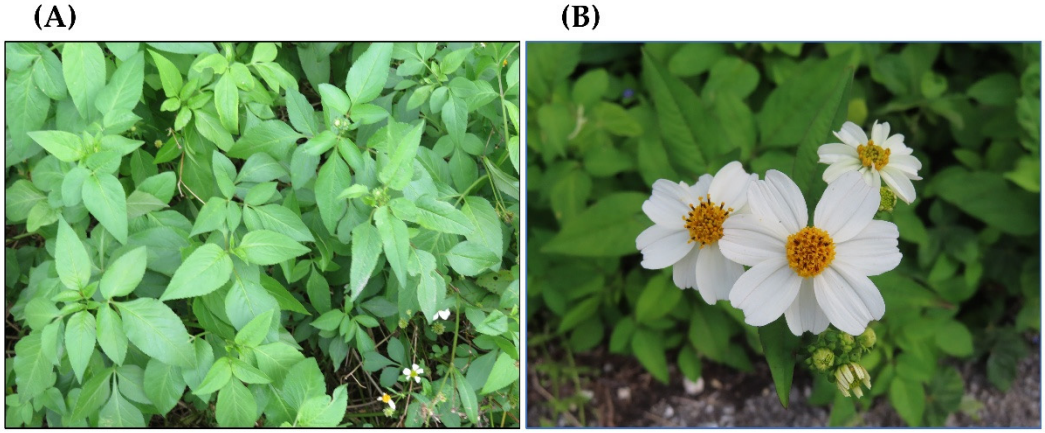

Figure 5: *Bidens pilosa*. (**A**): its monospecific stand. (**B**): its capitula.

Cinnamic acid derivatives, *p*-coumaric acid (**1**), caffeic acid (**2**), and ferulic acid (**3**), and benzoic acid derivatives, salicylic acid (**5**), *p*-hydroxybenzoic acid (**6**), and vanillic acid (**12**) were identified in the boiling water extracts of the stems, leaves, and roots of *B. pilosa* [189]. A flavonoid, quercetin (**27**) (Fig. 2), was identified from *B. pilosa* leaf extracts [190]. Quercetin inhibits growth and mitochondrial function in several plant species as an allelochemical [191,192]. Several monoterpenes were identified in the essential oil of *B. pilosa* [193]. Among these monoterpenes, α-pinene (**13**) and limonene (**14**) were reported to exhibit allelopathic activity as volatile agents [194]. These monoterpenes reduce chlorophyll levels and cellular respiration in target plants, indicating that they disrupt photosynthesis and energy metabolism [195,196].

Bidens pilosa is allelopathic, releasing allelochemicals, such as cinnamic acid and benzoic acid derivatives, quercetin, α-pinene, and limonene into the rhizosphere and atmosphere through decomposition, leaching, and volatilization. These allelochemicals may contribute to *B. pilosa* infestation by suppressing the germination and growth of neighboring plant species within its introduced ranges.

7 Allelopathy and Allelochemicals of *Tithonia diversifolia*

Tithonia diversifolia (Hemsl.) A. Gray is a bushy, perennial herb belonging to the Asteraceae family. It is commonly known as Mexican sunflower, Nitobe chrysanthemum, or tree marigold. It can grow up to 4 m in height and branches well. It often forms high-density, monospecific stands of 8–20 plants/m^2 in grasslands, forest edges, riverbanks, and other disturbed areas, including pastures, agricultural fields, abandoned places, and roadsides [197–203]. Originally from Mexico and Central America, it was introduced for landscaping, green manure, and as an incidental contaminant in agricultural seeds [203,204]. This highly invasive species has spread across warm temperate, subtropical, and tropical regions globally, including South America, Southeast Asia, Africa, Australia, and various islands in the Indian and Pacific Oceans [197–203]. *Tithonia diversifolia* infestation negatively impacts the abundance and diversity of native plant communities [198–201,204,205] (Fig. 6).

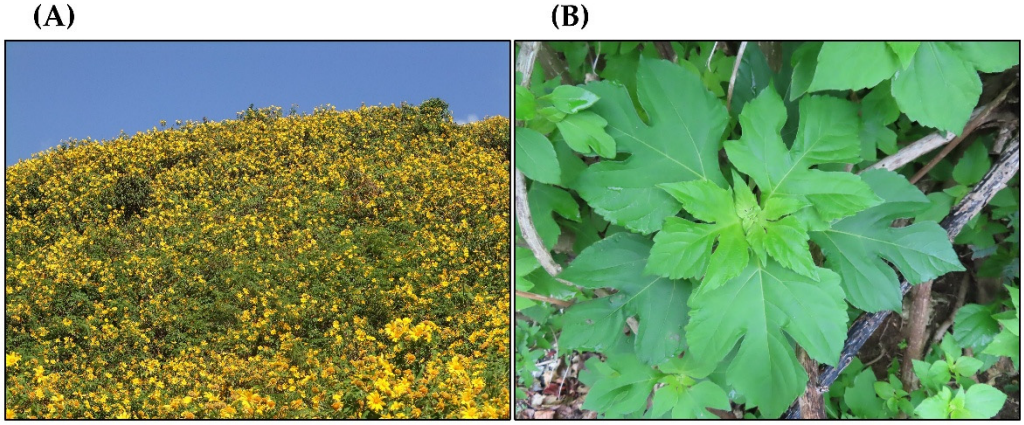

Figure 6: *Tithonia diversifolia*. (**A**): its monospecific stand. (**B**): its alternate lobe leaves.

Field soil obtained from under *T. diversifolia* stands inhibited the germination of *Bidens pilosa*, *Euphorbia heterophylla*, *Acanthospermum hispidum*, *Pennisetum polysachyum*, and *Panicum maximum* [206] and the growth of *Amaranthus viridis*, *Cyperus iria*, and *Digitaria ciliaris* [207]. Aqueous extracts of *T. diversifolia* soil also inhibited the growth of *A. viridis*, *C. iria*, and *D. ciliaris* [208]. Soil mixed with *T. diversifolia* leaves suppressed the germination and growth of *Abelmoschus esculentus* [209]. Root exudates from *T.*

diversifolia suppressed the germination and growth of *Amaranthus dubius* [210]. These findings suggest that *T. diversifolia* releases allelochemicals into the soil through root exudation and decomposition.

Aqueous extracts of *T. diversifolia* shoots have been shown to inhibit the germination and growth of *Tridax procumbens* [211], *Amaranthus cruentus* [212], and *B. pilosa* [213]. These extracts have also been found to hinder the growth and leaf development of the woody plants; *Monodora tenuifolia*, *Dialium guineense*, and *Hildegardia barteri*, under field conditions [214]. Aqueous methanol extracts of *T. diversifolia* leaves inhibited the growth of *Phleum pratense*, *Lolium multiflorum*, and *Echinochloa crus-galli* [215]. These findings suggest that allelochemicals in *T. diversifolia* can be extracted from its shoots and leaves using water or methanol.

To identify allelochemicals in *T. diversifolia*, the leaves were extracted with an aqueous methanol and subjected to a bioassay-guided separation process. The allelopathic activity of each chromatography fraction was determined during this process. The most active fraction the proceeded to the next chromatographic step. This process resulted in the isolation of a sesquiterpene lactone, tagitinin C, which inhibited the growth of *P. pratense*, *L. multiflorum*, and *E. crus-galli*. These test plants required 0.35–0.83 mM of tagitinin C to inhibit growth by 50% [215]. Tagitinin A (**20**) and tagitinin C (**21**) (Fig. 2) were identified as primary sesquiterpene lactones in *T. diversifolia*. These compounds inhibited the growth of *Lactuca sativa*, *Lepidium sativum*, *Solanum lycopersicum*, and *Allium cepa* in a concentration-dependent manner [216,217]. Tagitinins, especially tagitinin C, disrupt cell division and induce programmed cell death in several cancer cell lines [218,219]. However, the mode of action of tagitinins on plants remains unclear.

Tithonia diversifolia releases allelochemicals into the soil under its stands through root exudation and decomposition. Two sesquiterpenes, tagitinin A and tagitinin C, have been identified in *T. diversifolia* as allelochemicals. These allelochemicals give *T. diversifolia* a competitive advantage as an invasive plant species. However, it is unclear whether *T. diversifolia* produces other allelochemicals.

8 Allelopathy and Allelochemicals of *Arundo donax*

Arundo donax L. is a perennial grass in the Poaceae family that resembles bamboo. It is commonly known as giant cane or giant reed. Originally from the Middle East and East Asia [220–223], this species has been cultivated in the Mediterranean region since ancient times for woodwind reeds and various household and construction items [224,225]. However, genetic analyses have identified it as an invasive archaeophyte in the Mediterranean region [226–228]. The species grows in large, monospecific stands in riparian zones including floodplains, riverbanks, and streams. It can switch from aerobic respiration to alternate anaerobic respiration. This process produces supplemental energy [229–233]. It also grows on hillsides, in agricultural fields, and along roadsides [224,225]. This invasive species has spread to over 100 countries in warm temperate, subtropical, and tropical regions across Europe, North and South America, Oceania, and Africa. It threatens native plant communities in these areas [231–233]. Due to the severe threat it poses to native plant ecosystems, this species is included on the list of the world's 100 worst invasive alien species [35] (Fig. 7).

The allelopathic properties of *A. donax* have been determined in its various extracts. Aqueous extracts of its leaves and/or rhizomes have been shown to inhibit the growth of the crop plant *Lens culinaris*, the forage grass *Megathyrsus maximus*, and the woody plants *Guazuma ulmifolia*, *Handroanthus impetiginosus*, *Eriotheca pubescens*, *Parkia platycephala*, and *Pseudobombax tomentosum* [234,235].

An indole alkaloid, gramine (**30**) (Fig. 2), has been identified in methanol extracts of *A. donax* as an inhibitory substance against the growth of the flagellated alga, *Prymnesium parvum* [236]. Gramine has been identified in several other plant species and has been reported to act as a defensive compound

against insect herbivores and fungal pathogens [237]. Various alkaloids, including bufotenidine and 2,2,4,4-tetramethyl-*N*,*N*-bis(2,6-dimethylphenyl)-cyclobutane-1,3-diamine, have also been identified in *A. donax*. These compounds also act as defense mechanisms against insect herbivores and fungal pathogens [238,239]. As described above, *A. donax* exhibits allelopathic effects against crops, a forage grass, and woody plants. However, the specific allelochemicals responsible for inhibiting terrestrial plants have not yet been identified. Therefore, identifying these allelochemicals is crucial to understanding its allelopathic mechanisms.

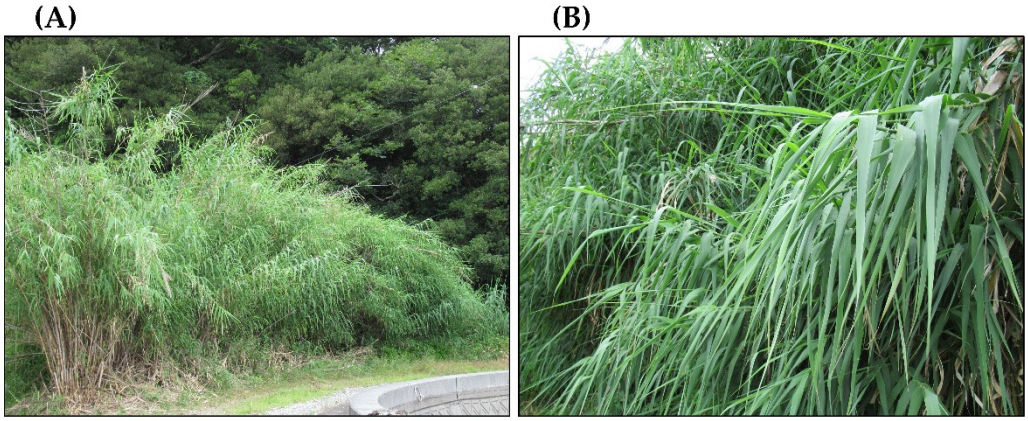

Figure 7: *Arundo donax*. (**A**): its monospecific stand. (**B**): its distichous phyllotaxis leaves.

9 Allelopathy and Allelochemicals of *Pueraria montana* var. *lobata*

Pueraria montana var. *lobata* (Willd.) Maesen & S.M.Almeida ex Sanjappa & Predeep (hereafter, *Pueraria montana*) is a perennial vine in the Fabaceae family. It is commonly known as kudzu vine or East Asian arrowroot. It can exceed 20 m in length, branch extensively, and overgrow other vegetation [240–244]. This highly adaptable species is commonly found in shrubby terrain, slopes, ecotones, riparian zones, transportation corridors, agricultural fields, and various disturbed ecosystems [241–245]. Originally from East Asia, it was widely introduced for ornamental purposes, soil erosion control, manufacturing, and as a high-nitrogen forage [246–248]. This invasive species has spread to temperate and subtropical regions in Europe, South Asia, Oceania, North and South America, and Africa. It threatens native plant communities in these areas [240–242,244,249]. Due to its negative impact on native plant communities, it has been listed among the world's 100 worst invasive alien species [35] (Fig. 8).

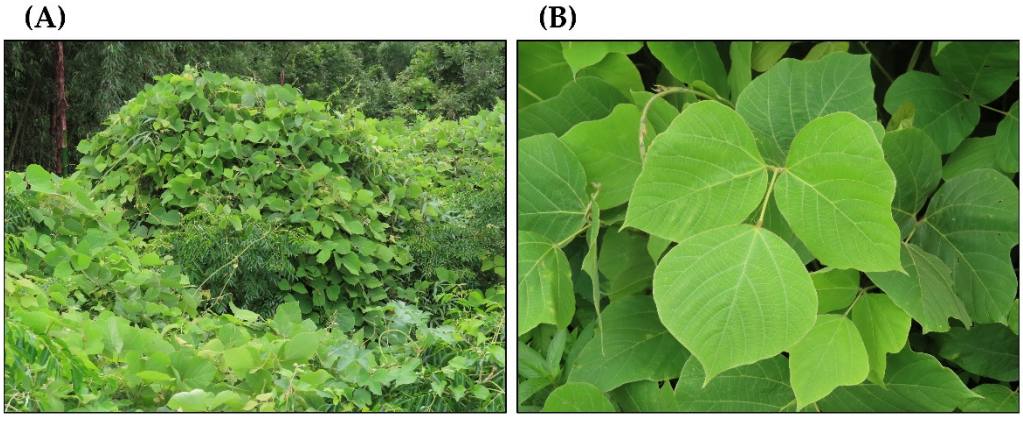

Figure 8: *Pueraria montana* var. *lobata*. (**A**): claiming on the other vegetation. (**B**): its trifoliate leaves.

The rhizosphere soil of *P. montana* inhibited the growth of *Lolium perenne* and *Raphanus sativa*. Soil mixed with aqueous extracts of *P. montana* residue also inhibited the germination of *L. perenne* and *Bidens pilosa* [250,251]. A mixture of sand and leaf powder of *P. montana* inhibited the germination and growth of *Phleum pratense* and *Lolium multiflorum* [252]. Two sesquiterpenes, *cis,trans*-Xanthoxin (**18**) and *trans,trans*-xanthoxin (**19**) (Fig. 2), have been identified as allelochemicals in *P. montana* leaves [253]. *cis,trans*-Xanthoxin has been reported to metabolize into the plant hormone, abscisic acid, in cell-free systems and in some plants. However, this has not been observed for *trans,trans*-xanthoxin [254–256]. *cis,trans*-Xanthoxin and *trans,trans*-xanthoxin have been reported to inhibit the growth of several plant species [257,258], suggesting that both xanthoxins may act as allelochemicals. *p*-Coumaric acid (**1**) and caffeic acid (**2**) (Fig. 2) have been identified in *P. montana* roots [259]. As described in the section on *L. camara*, caffeic acid and *p*-coumaric acid have been reported to act as allelochemicals [260].

The growth of *Lactuca sativa* protoplasts was significantly suppressed by incubation with *P. montana* protoplasts [260]. Daidzein (**28**) (Fig. 2), the primary flavonoid found in *P. montana* leaves, disrupts cell division and cell wall formation in *L. sativa* protoplasts [260,261]. Therefore, daidzein from *P. montana* suppresses the growth of *L. sativa* protoplasts.

Pueraria montana exhibits allelopathic properties by exuding allelochemicals, including xanthoxins, daidzein and cinnamic acid derivatives. These compounds are released into its rhizosphere soil through decomposition. These allelochemicals may contribute to the invasive nature of *P. montana*.

10 Discussion

Alien plants must engage in competition with native plant species for limited ecological niches and essential resources: sunlight, nutrients, and moisture. An elevated competitive edge improves their chances of survival [8–11]. Allelopathy confers a significant competitive advantage in interspecific interactions [15–20]. To study the invasiveness of plants through the lens of allelopathic strategies, we examined seven prominent invasive species: *L. camara* (Verbenaceae), *R. japonica* (Polygonaceae), *L. leucocephala* (Fabaceae), *B. pilosa* (Asteraceae), *T. diversifolia* (Asteraceae), *A. donax* (Poaceae), and *P. montana* var. *lobata* (Fabaceae). Each plant species produces a unique set of allelochemicals, including cinnamic acid derivatives, benzoic acid derivatives, monoterpenes, sesquiterpenes, sesquiterpene lactones, pentacyclic triterpenoids, flavonoids, a non-protein amino acid, indole alkaloids, and anthraquinones (Table 1).

These allelochemicals demonstrate allelopathic capabilities and enter the surrounding environment, including the rhizosphere, through root exudation, decomposition, leaching, and volatilization. Cinnamic acid and benzoic acid derivatives alter the protein and lipid profiles of the plasma membranes of target plant cells [52,56] and impair enzymes involved in photosynthesis, protein synthesis, phytohormone synthesis, and secondary metabolism [57–59]. Sesquiterpenes, such as α-curcumene, γ-muurolene, and β-caryophyllene, cause electrolyte leakage in cell membranes [63,64], and disrupt photosynthesis and water potential in target plants [66–68]. Flavonoids significantly alter target root growth by suppressing ATP synthesis and interfering with auxin pathways [95]. Among flavonoids, catechin and epicatechin initiate programmed cell death [97–99] and gallocatechin suppresses soil nitrification [163]. Monoterpenes, such as α-pinene and limonene reduce chlorophyll levels and cellular respiration in target plants, indicating that they disrupt photosynthesis and energy metabolism [195,196]. Mimosine inhibits plant growth by disrupting cell division between the G_1 and S phases [133] (Table 1).

Table 1: Allelochemicals identified in invasive plant species and their release routes and concentrations in soil.

Species (Family)	Native Range	Identified Allelochemicals (Compound No. in Fig. 2)	Release Routes	Allelochemicalsi n Soil
Lantana camara (Verbenaceae)	Mexico, tropical America	Cinnamic acid derivatives; *p*-coumaric acid (1), caffeic acid (2), ferulic acid (3). Benzoic acid derivatives; salicylic acid (5), *p*-hydroxybenzoic acid (6), gentisic acid (7), α-resorcylic acid (8), β-resorcylic acid (9), vanillic acid (12). Sesquiterpenes; α-curcumene (15), γ-muurolene (16), β-caryophyllene (17).	Decomposition, leaching, volatilization.	Not available
Reynoutria japonica (Polygonaceae)	East Asia	Pentacyclic triterpenoids; lantadene A (22), lantadene B (23). Flavonoids; catechin (24), epicatechin (25). Anthraquinones; emodin (31), physcion (32).	Decomposition, leaching, root exudation.	Emodin: 55 mg/kg dry soil. Physcion: 30 mg/kg dry soil.
Leucaena leucocephala (Fabaceae)	Mexico, Central America	Cinnamic acid derivatives; *p*-coumaric acid (1), caffeic acid (2), ferulic acid (3). Benzoic acid derivatives; *p*-hydroxybenzoic acid (6), protocatechuic acid (10), gallic acid (11), vanillic acid (12). Flavonoid; gallocatechin (26). Non-protein amino acid; mimosine (29).	Decomposition, root exudation.	Mimosine: 7.4 μg/g dry soil. Its root exudation: 1–5 μg/g dry plant/day.
Bidens pilosa (Asteraceae)	Sub- & tropical America	Cinnamic acid derivatives; *p*-coumaric acid (1), caffeic acid (2), ferulic acid (3). Benzoic acid derivatives; salicylic acid (5), *p*-hydroxybenzoic acid (6), vanillic acid (12). Monoterpenes; α-pinene (13), limonene (14). Flavonoid; quercetin (27).	Decomposition, leaching, volatilization.	Not available
Tithonia diversifolia (Asteraceae)	Mexico, Central America	Sesquiterpene lactones; tagitinin A (20), tagitinin C (21).	Decomposition, root exudation.	Not available
Arundo donax (Poaceae)	Middle East, East Asia	Indole alkaloid; gramine (30). Allelochemicals against terrestrial plants have not yet been identified.	Not available	Not available
Pueraria montana var. *lobata* (Fabaceae)	East Asia	Cinnamic acid derivatives; *p*-coumaric acid (1), caffeic acid (2). Sesquiterpenes; *cis,trans*-xanthoxin (18), *trans,trans*-xanthoxin (19). Flavonoid; daidzein (28).	Decomposition	Not available

Allelochemicals cannot stunt the growth of target plants unless they are released into the environment, including the rhizosphere, and reach certain concentrations [262–265]. Otherwise, these allelochemicals are unable to suppress the germination and growth of target plants in a natural environment [266–268]. Many allelochemicals have been isolated and identified in the tissues of invasive plant species. The exact release rates and concentrations of most of these allelochemicals in ecosystems remain unclear. The concentrations in the soil were determined to be 55 and 30 mg per kg of dry soil for emodin and physcion, respectively [100], and 7.4 μg per g of dry soil weight for mimosine [155]. However, the allelopathic activity of emodin and physcion was determined only under laboratory conditions (Table 1). Considering the inhibitory activity, mimosine alone cannot explain the allelopathic activity of *L. leucocephala*. Additionally, allelochemicals are often only tested for their effects on the germination and growth of crop plants in a laboratory setting rather than in a field setting with native plant species. To fully understand allelopathic interactions between invasive and native plant species in introduced ecosystems, future research must investigate the release rates and concentrations of allelochemicals in the environment, including the rhizosphere, as well as the fate of these chemicals in the environment. Allelopathy refers to the chemical interactions through a donor plant species affects the germination and growth of neighboring plants. Many allelopathy studies, however, have not adequately addressed competition for resources in their experimental designs. Because competitive interactions also affect the germination and growth of neighboring plants [269–271], future research must strictly distinguish the effects of chemical interactions from resource competition in both laboratory and field studies.

Additionally, high extract concentrations alter the osmotic potential and pH of the bioassay solutions, thus, plant extract bioassays conducted at high concentrations often carry potentially confounding osmotic and pH effects that can independently suppress growth. However, separating controls (such as activated carbon or osmotic adjustments) have been reported in only a minority of the cited studies [184,185]. Furthermore, a clear dose-response structure is largely absent across the literature, with tagitinin C being the sole compound for which an IC_{50} value is provided [215]. Consequently, there is currently no established threshold against which field concentrations can be reliably evaluated to confirm actual chemical interference in natural ecosystems.

Phytochemical analyses and pharmacological studies have revealed that these invasive plant species contain various secondary metabolites, including terpenoids, benzenoids, flavonoids, polyphenols, steroids, alkaloids, and quinones. Many of these compounds are responsible for their diverse pharmacological properties, including anti-inflammatory, anticarcinogenic, antiviral, antidiabetic, and antipyretic activities [272–277]. While the majority of these compounds have not yet been linked to the allelopathy of the respective species, some may play a role in this chemical interference.

The novel weapon hypothesis, states that alien plants gain a competitive advantage in new environments because their allelochemicals suppress native species more effectively than in their home environments. Plants in their home environments often develop tolerance to local allelochemicals through long-term coevolution. However, native species in newly invaded ecosystems lack this historical exposure. Consequently, they miss the opportunity to acquire these defensive traits, leaving them highly vulnerable to these allelochemicals [278–280]. The invasive plant species discussed in this review may gain a competitive advantage in their introduced environments by releasing allelochemicals that suppress the germination and growth of competing plant species. However, it is necessary to evaluate the activity of these allelochemicals in both the native and introduced ranges of these invasive plants.

11 Conclusion

All invasive species exhibit significant allelopathic capabilities and produce unique sets of allelochemicals, which include cinnamic acid derivatives, benzoic acid derivatives, monoterpenes, sesquiterpenes, sesquiterpene lactones, pentacyclic triterpenoids, flavonoids, a non-protein amino acid, indole alkaloids, and anthraquinones. These compounds can be released into the surrounding environment, including the rhizosphere, through root exudation, decomposition, leaching, and volatilization. Through this process, these invasive plant species may gain a competitive advantage over native vegetation in their introduced ranges, allowing them to propagate and adapt to non-native ecosystems. However, soil concentrations have only been determined for emodin and physcion (from *R. japonica*) and mimosine (from *L. leucocephala*). The concentrations of other allelochemicals must be determined to evaluate their specific contributions to plant invasion mechanisms.

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