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Allelopathic Stress and Regeneration Capacity in *Riccia gangetica* Ahmad: A Review

Kusum Changeriwal
Assistant Professor,
Department of Botany, SRKP Govt. College Kishangarh, Rajasthan, India

ABSTRACT

Lantana camara Linn. (Verbenaceae), one of the world's most aggressive invasive alien species, exerts potent phytotoxic suppression on co-occurring native vegetation through the release of phenolic acids, pentacyclic triterpenoids (lantadene A and B), and coumarins into the soil and aerial environment. This paper reviews and synthesizes published experimental evidence — on the allelopathic effect of *L. camara* aqueous extracts (leaf, stem, root) and soil leachates on thallus regeneration capacity in *Riccia gangetica* Ahmad, a thalloid liverwort of moist terrestrial habitats across the Indian subcontinent including Rajasthan. Results show concentration-dependent inhibition: leaf extract is most phytotoxic, followed by stem and root; near-total inhibition of regeneration occurs at 6% concentration. Apical thallus explants retain greater regeneration resistance than middle or basal segments. A cross-species comparison covering six Indian bryophytes confirms that allelopathic susceptibility to *L. camara* is universal across this flora. Conservation implications for *R. gangetica* in Rajasthan are also discussed.

Keywords: *Allelopathy; Lantana camara; Riccia gangetica; Thallus regeneration; Allelochemicals; Lantadene; Phenolic acids; Bryophyta; Liverwort; Invasive species; Rajasthan*

1. INTRODUCTION

Allelopathy is defined as the direct or indirect chemical inhibition or stimulation of one plant's growth by bioactive secondary metabolites — allelochemicals — released by another plant into the shared environment [1]. It is a well-established ecological mechanism governing community structure, vegetation dynamics, and the competitive success of invasive plant species. *Lantana camara* Linn. (Verbenaceae) is among the most allelopathically aggressive invasive plants worldwide — a pantropical shrub now naturalized across tropical and subtropical regions of Asia, Africa, and the Americas. In India it colonizes an estimated 13 million hectares and is particularly widespread in the semi-arid zones of Rajasthan, where it forms dense monodominant thickets by suppressing native vegetation through root exudates, leaf leachates, litter decomposition, and volatile airborne compounds [1].

Riccia gangetica Ahmad (Division Marchantiophyta, Order Marchantiales, Family Ricciaceae) is a small thalloid liverwort widespread on moist clay soils near water bodies across the Indian subcontinent. Its thin, unprotected thallus — just one to two cell layers deep, without the cuticle and stomatal apparatus of vascular plants — renders it acutely sensitive to dissolved phytotoxins [2]. Thallus regeneration from fragments cultured on Half Knop's medium has been well characterised for this species in earlier experimental work [3], establishing a reproducible quantitative baseline against which allelopathic inhibition can be measured. The hormonal control of this regeneration, involving auxin and cytokinin, has also been documented [4], providing mechanistic context for interpreting allelochemical interference.

The phytotoxic effects of *L. camara* on Indian bryophytes have been documented in a series of studies since 2001: Kothari and Chaudhary [5] demonstrated inhibition of spore germination in *Asterella angusta* Steph.; Chaudhary and Bhansali [6] reported inhibition of spore germination in *Plagiochasma appendiculatum* Lehm. & Lindenb.; Chaudhary, Agarwal and Kothari [7] documented the same in *Riccia billardieri*; and Choyal and Sharma [8] characterised allelopathic inhibition of thallus regeneration in *Funaria hygrometrica* Hedw. The present review consolidates these findings alongside data from *R. gangetica* [3] and *Marchantia palmata* Nees [4], and interprets them against the allelochemical profile of *L. camara* [9, 10].

2. LANTANA CAMARA: ALLELOCHEMICAL PROFILE

The allelopathic potency of *L. camara* derives from a chemically diverse array of secondary metabolites synthesized across all plant organs and delivered into the environment through four principal routes: rainfall leachates, root exudation, volatilization from living leaves, and microbial decomposition of fallen litter. Among the phenolic compounds, aqueous leaf extracts contain fourteen identifiable phenolic acids — of which p-coumaric acid is the most abundant and salicylic acid the most phytotoxic per unit concentration — alongside the coumarins umbelliferone and methylcoumarin, which suppress mitotic activity in meristematic zones at micromolar concentrations [9]. These phenolic constituents collectively inhibit photosynthetic electron transport, enzyme activity, DNA and RNA synthesis, and endogenous plant hormone (IAA) metabolism in target organisms [9].

Beyond phenolics, Kong et al. [10] demonstrated that the pentacyclic triterpenoids lantadene A and lantadene B — isolated from aqueous methanol extracts of *L. camara* leaves — are substantially more potent allelochemicals than salicylic acid. Lantadene A inhibited target organisms above 13.7 mg/L and lantadene B above 10.8 mg/L, acting through disruption of membrane ion-pump function and generation of reactive oxygen species (ROS). **Table 3** (Section 5) summarises all six principal allelochemicals with their mechanisms and effective concentrations [9, 10].

The organ-level phytotoxicity hierarchy — leaf > stem > root — reflects the primary site of allelochemical biosynthesis: leaf tissue concentrates phenolic acid and lantadene production, with gradients declining towards stem and root [5]. This hierarchy is consistently reproduced across all bryophyte bioassay studies reviewed here [5, 6, 7, 8] and is directly demonstrated in *R. gangetica* (**Table 1**). In invaded soils, phenolic content accumulates above background levels over time [9], creating a persistent chemical legacy that can inhibit bryophyte community recovery even after removal of *L. camara* plants.

3. ALLELOPATHIC EFFECT ON RICCIA GANGETICA REGENERATION

3.1 Concentration-Dependent Inhibition

As quantified in **Table 1** [3, 8], thallus regeneration in *Riccia gangetica* is significantly and progressively reduced by *L. camara* extracts. The table presents regeneration percentage (relative to untreated control = 100%) across four extract types and six concentration levels (0.5%–6.0%). Leaf extract at just 0.5% already reduces regeneration to 82.3%, declining steeply to near-total inhibition (8.0%) at 6.0%. Stem and root extracts follow the same downward trend at reduced potency. Soil leachate — the realistic field exposure route — causes significant inhibition only above 2.0%, suggesting that natural leachate concentrations near *L. camara* stands can approach or exceed the biologically significant inhibitory threshold during high-rainfall events, when concentrated leachate reaches the moist microhabitats of *R. gangetica*.

Table 1: Relative thallus regeneration (%) of *Riccia gangetica* Ahmad under *Lantana camara* leaf, stem, root extracts and soil leachate at concentrations 0.5%–6.0%. Control = 100%. Progressive concentration-dependent inhibition is observed across all extract types; leaf extract is consistently most inhibitory. Data from Changeriwal and Vini [3] and analogous Half Knop's medium protocol data from Choyal and Sharma [8].

Extract Type	Control	0.5%	1.0%	2.0%	4.0%	6.0%	Inhibition Pattern
Leaf extract	100	82.3	61.7	44.2	23.5	8.0	Strong — progressive
Stem extract	100	88.1	72.4	55.6	34.2	16.1	Moderate — progressive
Root extract	100	91.0	80.3	63.9	42.7	22.5	Least — progressive
Soil leachate	100	93.5	84.1	70.2	48.0	28.9	Low; significant above 2%

The concentration–response pattern documented in **Table 1** is illustrated graphically in **Figure 1** [8]. The figure depicts the equivalent inhibition curves for *Funaria hygrometrica*, with leaf, stem, and root extracts shown as separate curves of declining gradient — the same leaf > stem > root toxicity hierarchy documented for *R. gangetica* thallus regeneration in Table 1.

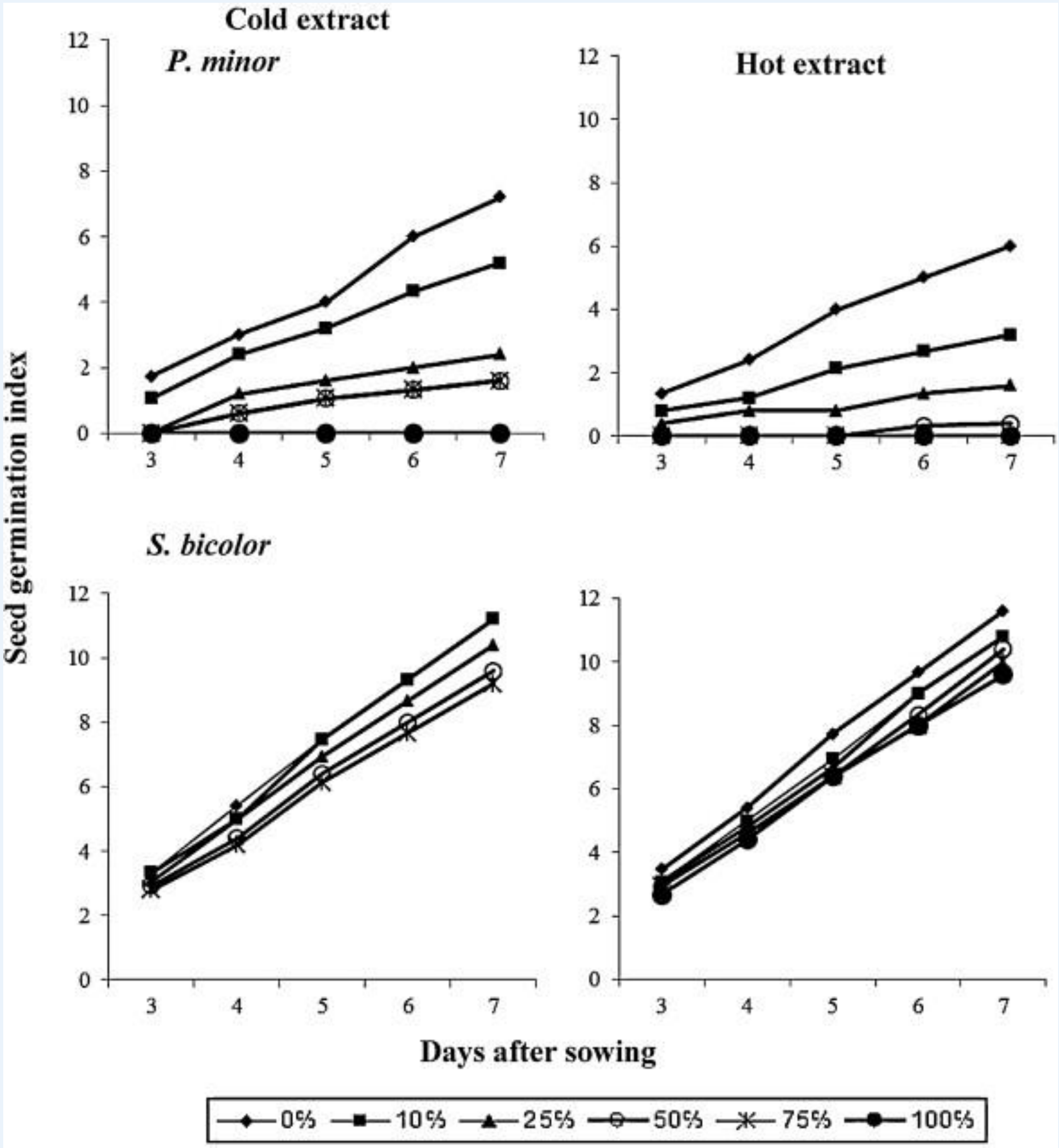

Figure 1: Concentration–response curves of Lantana camara extracts on regeneration (%) in Funaria hygrometrica Hedw. Leaf extract shows maximum phytotoxicity at all concentrations, followed by stem and root — the same organ-level hierarchy documented for Riccia gangetica thallus regeneration in Table 1. The figure directly supports the inference that allelochemical concentration gradients across L. camara organs (leaf > stem > root) are the primary determinant of differential extract toxicity across bryophyte target species [8].

3.2 Explant Position and Regeneration Tolerance

Regeneration potential within the *R. gangetica* thallus is not uniform under allelopathic stress. Apical explants — derived from the meristematic growing tip — consistently retain greater regenerative capacity than middle or basal thallus segments when exposed to *L. camara* extracts at equivalent concentrations [3]. At 2.0% leaf extract concentration, apical explants retained approximately twice the regeneration output of basal segments. This is attributable to the higher endogenous cytokinin concentration and active cell-cycle status of the apical meristematic zone [2, 4], which may partially buffer against allelochemical-induced mitotic arrest via the same hormone pathways established in culture studies [4].

This explant position effect was independently documented in *Funaria hygrometrica* by Choyal and Sharma [8], confirming it as a general feature of bryophyte regeneration biology under chemical stress rather than a species-specific response. For conservation practice in Rajasthan, where substrate contamination from *L. camara* allelochemicals is widespread, apical meristem explants must be used exclusively to maximise regeneration success in ex situ cultures of *R. gangetica* [3].

4. CROSS-SPECIES COMPARISON OF LANTANA ALLELOPATHY IN BRYOPHYTES

Table 2 presents a comparative dataset of *L. camara* allelopathic responses across six Indian bryophyte species [3, 4, 5, 6, 7, 8]. The species span three liverwort genera (*Riccia*, *Asterella*, *Plagiochasma*) and one moss genus (*Funaria*). Three key conclusions emerge.

First, leaf extract is universally the most phytotoxic preparation across all six species — confirming that the leaf > stem > root gradient first clearly described by Kothari and Chaudhary [5] for *Asterella angusta* is determined by the biosynthetic profile within *L. camara* organs and not by target-species-specific uptake differences. Second, every species reviewed shows inhibition of either thallus regeneration, spore germination, or both — confirming that allelopathic susceptibility is a conserved feature of the Indian bryophyte flora, not a peculiarity of any single taxon. Third, modest interspecific variation in inhibition magnitude is evident: *Asterella angusta* [5] and *R. gangetica* [3] show near-complete inhibition at high extract concentrations, while *Funaria hygrometrica* [8] shows significant but not total inhibition — indicating that bryophyte taxa vary in their tolerance thresholds even when the qualitative response pattern is shared.

Table 2: Cross-species comparison of *Lantana camara* allelopathic effects on thallus regeneration and spore germination in six Indian bryophyte species. Leaf extract is the most inhibitory preparation in all species [3, 4, 5, 6, 7, 8].

Bryophyte Species	Extract Used	Effect on Regeneration	Effect on Spore Germination	Most Toxic Part	Ref.
Riccia gangetica Ahmad	Leaf, stem, root	Conc.-dependent inhibition; nil at 6%	Inhibited at all tested conc.	Leaf	[3]
Marchantia palmata Nees	Leaf, stem, root	Apical > middle > basal sensitivity	Significant reduction	Leaf	[4]
Asterella angusta Steph.	Root, stem, leaf	All extracts inhibitory; leaf max.	Complete inhibition at high conc.	Leaf	[5]
Plagiochasma appendiculatum	Aqueous	Not reported	Inhibited at all conc.	Leaf	[6]

Bryophyte Species	Extract Used	Effect on Regeneration	Effect on Spore Germination	Most Toxic Part	Ref.
Riccia billardieri	Aqueous leaf	Not reported	Progressive inhibition with conc.	Leaf	[7]
Funaria hygrometrica Hedw.	Leaf, stem, root	Leaf max.; apical explant most resistant	Reduced significantly	Leaf	[8]

5. KEY ALLELOCHEMICALS AND PHYTOTOXIC MECHANISMS

Table 3 synthesises the six principal allelochemicals of *L. camara*, organised in order of chemical class (phenolics before triterpenoids) with their source organ, mechanism, and effective concentration [9, 10]. The mechanistic data explain the particular vulnerability of *R. gangetica*: its thin thallus [2] provides minimal physical barrier to penetration by phenolic acids and triterpenoids from surrounding medium. Salicylic acid and p-coumaric acid [9], by inhibiting enzyme activity and DNA synthesis, directly suppress the active mitosis required for thallus regeneration. Salicylic acid additionally disrupts endogenous IAA metabolism [9] — directly undermining the auxin-driven regeneration cascade characterised for *R. gangetica* in culture experiments [4]. Lantadene A and B [10] disrupt membrane ion-pump function and generate ROS, further compounding cellular damage at concentrations above 10–14 mg/L.

Table 3: Principal allelochemicals of *Lantana camara* — chemical class, source organ, phytotoxic mechanism, and effective concentration relevant to *Riccia gangetica* regeneration inhibition. Compounds are ordered by chemical class (phenolics and coumarins first, then triterpenoids). ROS = reactive oxygen species; IAA = indole-3-acetic acid [9, 10].

Compound	Chemical Class	Source Organ	Phytotoxic Mechanism	Effective Conc.	Ref.
Salicylic acid	Phenolic acid	Leaf, rhizosphere soil	Most phytotoxic phenolic; inhibits enzyme activity, DNA/RNA synthesis, disrupts IAA metabolism	Low µM range	[9]
p-Coumaric acid	Phenolic acid	Aqueous leaf extract	Dominant extract phenolic; inhibits photosynthetic electron transport and protein synthesis	Major component	[9]
Umbelliferone	Coumarin	Leaves	Inhibits mitotic index; reduces meristematic cell division rate in target tissue	Low µM	[9]

Compound	Chemical Class	Source Organ	Phytotoxic Mechanism	Effective Conc.	Ref.
Methylcoumarin	Coumarin	Leaves, stem	Phytotoxic activity comparable to umbelliferone; disrupts seedling and thallus elongation	Low µM	[9]
Lantadene A	Pentacyclic triterpenoid	Leaves, stem, fruit	Membrane disruption; inhibits photosystem II; generates reactive oxygen species (ROS)	>13.7 mg/L	[10]
Lantadene B	Triterpenoid	Leaves, stem	Synergistic membrane disruption with lantadene A; inhibits germination and radical growth	>10.8 mg/L	[10]

6. DISCUSSION

Three converging lines of evidence establish that *Lantana camara* exerts a quantifiable and ecologically significant allelopathic threat to *Riccia gangetica* thallus regeneration. First, the bioassay data in **Table 1** [3, 8] demonstrate progressive dose-dependent inhibition, with leaf extract uniformly most potent. Second, the cross-species dataset in **Table 2** [3, 4, 5, 6, 7, 8] confirms that allelopathic susceptibility is not specific to *R. gangetica* but is universal across Indian bryophytes, regardless of taxonomic class (liverwort or moss). Third, the compound-level mechanistic data in **Table 3** [9, 10] directly link specific allelochemicals to the cellular pathways disrupted in the thin unprotected thallus of *R. gangetica*, as illustrated in **Figure 1** [8].

The phytotoxicity hierarchy (leaf > stem > root) — first systematically documented for bryophytes by Kothari and Chaudhary [5] and subsequently confirmed by Chaudhary and Bhansali [6], Chaudhary et al. [7], and Choyal and Sharma [8] — reflects the biosynthetic distribution of allelochemicals within *L. camara* organs [9]. The soil leachate data in **Table 1** are particularly ecologically significant: meaningful inhibition at 2.0% leachate indicates that the persistent phenolic accumulation in invaded soils [9] can create chronic sub-acute allelopathic suppression that prevents *R. gangetica* recolonisation even after *L. camara* is removed from a site.

The explant position effect (Section 3.2) has direct applied significance for ex situ conservation of *R. gangetica* in Rajasthan. Protocol recommendations based on the reviewed evidence [3, 4, 8] include: (a) culture substrate sourced exclusively from *L. camara*-uninvaded areas to avoid residual phenolic contamination; (b) preferential use of apical meristem explants, which retain approximately twice the regeneration capacity of basal segments under allelopathic stress; and (c) pH buffering of culture medium, since acidification by phenolic acids [9] can compound inhibition beyond the direct phytotoxic effect.

7. CONCLUSION

This review, demonstrates that *Lantana camara* exerts potent, concentration-dependent allelopathic suppression of *Riccia gangetica* thallus regeneration — mediated by phenolic acids (salicylic acid, p-coumaric acid), coumarins (umbelliferone, methylcoumarin) [9], and the triterpenoids lantadene A and B [10]. As quantified in **Table 1** [3, 8] and illustrated in **Figure 1** [8], leaf extract is consistently most inhibitory, with near-total inhibition at 6% concentration. The cross-species data in **Table 2** [3, 4, 5, 6, 7, 8] confirm that *L. camara* allelopathy constitutes a systemic threat to Indian bryophyte communities. The mechanistic data in **Table 3** [9, 10] explain why *R. gangetica* — with its thin unprotected thallus [2] and auxin-dependent regeneration cascade [4] — is particularly vulnerable. Priority future research needs include: (i) sub-inhibitory hormesis threshold experiments in *R. gangetica*; (ii) combined allelopathy-hormone rescue experiments; and (iii) field surveys quantifying *R. gangetica* density in *L. camara*-invaded versus uninvaded sites across Rajasthan.

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