

Pollen Allelopathy

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(Received in revised form: February 1, 2024)

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ABSTRACT

Pollen allelopathy positively or negatively influences the fertilization of plants and has great significance from ecological perspectives. The release of allelochemicals from foreign pollen grains on the stigmatic surface obstructs the processes of fertilisation, seed establishment, tube formation, stigma receptivity, and pollen germination. So far, pollen allelopathy has received little attention and still a growing topic of ecological studies. Therefore, a literature review was undertaken to provide the valuable information regarding the ecological and reproductive implications of pollen allelopathy, heterospecific pollen transfer mechanisms of allelopathic anemophilous and entomophilous plants, and to shed light on the biochemistry and mode of action of allelochemicals. The majority of entomophilous plants share pollinators within communities, and heterospecific pollen transfer by both anemophilous and entomophilous plants causes a reduction in their reproductive success, like pollen germination, tube development, ovule maturation and seed set. For detailed study of pollen allelopathy, a few factors should be considered like metrological parameters, distance travelled by pollen, pollen viability, and stigma receptivity during foreign pollen deposition. A thorough understanding of the biochemical and enzymatic processes that occur after foreign pollen is deposited on the native stigma will open up new perspectives on plant reproduction. Pollen allelochemicals, which have important significance as biocontrol agents for the maintenance of agroecosystems, need to be identified and characterised. The ecological aspects of pollen allelopathy may be well understood with the help of field studies.

Keywords : Foreign pollen, hetero specific pollen transfer, pollen allelochemicals, pollen germination, seed set.

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1. INTRODUCTION

‘Allelopathy’ is defined as the release of chemical compounds by plants that positively or negatively influence the neighbouring population through different physiological processes i.e., root exudation, leaching, decomposition, volatilization etc. (37). Allelochemicals are present in different plant parts like leaves, roots, stems, rhizomes, and litter (37,38). Allelochemicals are secondary metabolites that include phenols, derivatives of benzoic and cinnamic acids, alkaloids, terpenes, sugars, glycosides, and amino acids. Their action mode may include an inhibition of root or seedling growth, a decrease in photosynthesis or chlorophyll content and an inhibition of cell division (37,38). A detailed knowledge of plant-to-plant allelopathic interactions in ecosystems may have many implications and applications to develop new, ecologically safe biological control strategies for sustainable agriculture. Studies to manipulate allelopathy in crops to control weeds have increased recently, but pollen allelopathy with its ecological implications is still needed for further research.

2. SIGNIFICANCE OF POLLEN ALLELOPATHY

The term ‘Pollen allelopathy’ is defined as the release of allelochemicals from pollen grains that inhibit or stimulate pollen germination (29,30) pollen tube growth and stigma receptivity (46), mitotic activity (35), ovule development (52) and seedling development (3). Roshchina (41) described the phenomenon, which includes the release of signalling chemical compounds (allelochemicals) from the donor cell (pollen) and specific signals for the germination of pollen grains recognized by the acceptor (stigma). The specific signals are an important factor for the pollen germination on the stigmatic surface. Allelopathic pollens are a major threat to anemophilous crops as they require a large number of pollen grains for fertilization. The effect of allelopathic pollen results in the loss of genetic variation in plants, which affects their reproductive ability and adaptability to new environmental challenges (29,30).

(i). Anemophily: Wind pollination is a type of pollination in which pollen grains are delivered through the wind. Most of the grasses and all the gymnosperms generally disperse their pollen into ambient air for their pollination. According to Linder (17) 10 % of angiosperm species rely on wind pollination. The anemophilous plants showed some common characteristics, such as small, unisexual flowers, open anther, pollen production, dry and smooth-walled pollen that generally facilitate wind pollination (14,17,18).

(ii). Entomophily or insect pollination: In this pollination an insect can transfer the pollen grains from the anther to the stigma of a flower and the fertilized ovule produce seeds. Flowers that are pollinated by insects generally showing characteristics, such as bright colour, sugar-rich nectar, and sticky pollen grains. Most of the angiosperms are pollinated by animals, and 87.5 % of the angiosperms have benefited from biotic pollination (34). Mostly, bees, butterflies, moths, flies, ants, wasps, beetles etc., are the most common pollinating insects.

Pollen allelopathy also plays an important role that influence sexual reproduction. There is little evidence of inhibition or stimulation of pollen germination by one or more

mixed plant species. Such interactions of pollen grains from different individuals influence the fruit and seed sets of many plants; however, releases of allelochemicals after the deposition of pollen grains on the stigmatic surface of heterospecific plants affect the reproductive success of the recipient plants. Sukhada and Jayachandra suggested that the toxicity of pollen allelochemicals may vary depending on the allelopathic nature of plants. Allelopathic pollen grains of weeds are a serious threat to crops and especially if both are anemophilous in nature (46,47). The utilization of plants with the allelopathic potential to control weed infestations provides an effective, cost-efficient, and eco-friendly alternative to commercial herbicides and mechanical weed management (2). The recommendations given in this review are meant to guide future investigations into finding and highlighting the basic elements influencing the pollen allelopathy of both entomophilous and anemophilous plants. This review is also helpful to understand the heterospecific pollen transfer mechanisms between the donor and recipient plants, which lead to the failure of reproductive success.

3. MECHANISM OF POLLEN ALLELOPATHY

Pollen allelopathy played a significant role as a mechanism of competition through heterospecific pollen transfer, which directly impedes the sexual reproduction of neighbouring plants. The heterospecific pollen transfer is another important factor for the study of pollen allelopathy. Many invasive plants compete with native plants to assure their reproductive success, and during the process, they share their pollinators. In entomophilous plants, pollinators play a vital role in transferring the pollen grains from species to species, while in anemophilous plants, pollen grains can disperse with the help of winds. Several studies have reported that invasive plants have a negative effect on the reproductive success of native plants (48,51). Pollinator sharing might be a result of competition in pollination, which leads to pollen contamination and reduces the fruit and seed set (6). Most of the invasive plants interact with the native plants via generalist pollinators. Various factors like abundance, behaviour of pollinators, blooming pattern, shared pollinators and breeding systems of native and invasive plant communities influenced the study. Most of the studies determined the effects of pollen grains from invasive plants on the reproductive success of native plant by hand pollination or by detecting heterospecific pollen transfer from invasive plants on native plants stigma (8,36). Generally, the allelopathic nature of pollen grains of invasive plants reduces the productivity of native plants.

4. POLLEN ALLELOPATHY IN DIFFERENT PLANT TYPES

Pollen allelopathy plays an important role as a mechanism of 'competition through interspecific pollen transfer' and this may occur through direct inhibitory effects on the reproduction of neighbours. This review focuses on the heterospecific pollen transport mechanisms of entomophilous and anemophilous plants.

4.1. Entomophilous Plants

Generally, pollen grains germinate on the stigma and resulted in pollen tubes growth through the stigma and style; ultimately, pollen tubes enter the ovary. During the pollen-pistil interactions, the pistil screens pollen grains, and heterospecific pollen grains are

inhibited at the level of pollen germination or pollen tube development in the style (44). The stigmatic surface of a plant not only maintains the proper conditions for pollen germination but also inhibits foreign pollen germination. But in some cases, it was also observed that pollen grains germinated in crosses of closely related species. The interactions between pollen and the stigma of other species are similarly related to the interactions between self-incompatible and self-fertile plant species.

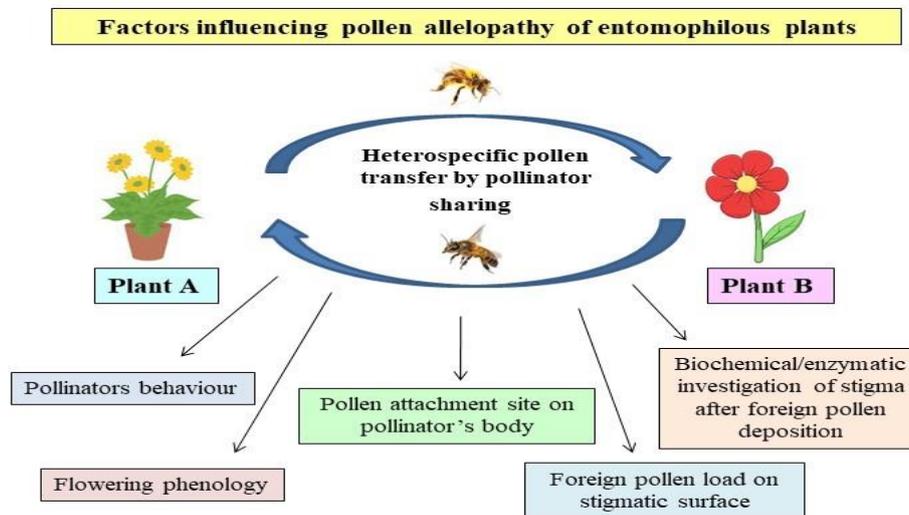


Figure 1. Factors influencing pollen allelopathy of entomophilous plants.

Less attractive plant species like *Viola* in Britain, are mostly visited by insects and always carry and deposit some foreign pollen on the stigma from highly attractive plant species like *Taraxacum* and *Endymion* (7). However, specialized pollinator services may reduce the chances of mixing the native and foreign pollen grains on the stigma. Most of the plant species that share their pollinators generally suffer from heterospecific pollen deposition, and severe challenges may occur because of pollen allelopathy. The heterospecific pollen deposition also influences the vegetation dynamics of a particular area. Etter *et al.* (12) reported that 96% of total flower visitors of buckwheat (*Eriogonum arborescens*) which is endemic to Santa Cruz Island, carried non-native fennel (*Foeniculum vulgare*) pollen grains and 72% of visitors of fennel flowers carried buckwheat pollen grains. The research is required to answer the question regarding the allelopathic nature of invasive fennel pollen grains and whether it reduces the reproductive success of buckwheat or not. Loughnan *et al.* (19) reported that pollen grains of the invasive plant species *Taraxacum officinale* reduced the seed set of common wild flowers of Montane *Erysimum capitatum* (Brassicaceae) and *Erythronium grandiflorum* (Liliaceae). On the other hand, Jones (16) reported that the pollen grains of *Taraxacum officinale* might not affect the seed set of *Delphinium nuttallianum*. Detailed field studies are required to understand the positive or negative role of the co-flowering taxa in relation to pollen allelopathy. A list of pollen allelopathic interactions between entomophilous donor and recipient plants is presented in Table 1.

Table 1. Effects of entomophilous donor species on recipient plants.

Donor Plants	Recipient plants	References
Pollen germination		
<i>Acacia dealbata</i> Link	<i>Hippeastrum hybridum</i> Hort.	43
<i>Achillea millefolium</i> L.	<i>Philadelphus grandiflorus</i> Willd.	
<i>Alstroemeria aurantiaca</i> D.Don	<i>Hippeastrum hybridum</i> Hort.	
<i>Anthriscus sylvestris</i> (L.) Hoffm.	<i>Philadelphus grandiflorus</i> Willd.	
<i>Barbarea vulgaris</i> W.T.Aiton	<i>Philadelphus grandiflorus</i> Willd.	
<i>Calendula officinalis</i> L.	<i>Oenothera biennis</i> L.	
<i>Calendula officinalis</i> L.	<i>Plantago major</i> L.	
<i>Centaurea jacea</i> L.	<i>Knautia arvensis</i> (L.) Coult.	
<i>Echinopsis bridgesii</i> Salm-Dyck	<i>Hippeastrum hybridum</i> Hort.	
<i>Helianthus exilis</i> A.Gray	<i>Mimulus guttatus</i> DC.	4
<i>Hieracium pratense</i> Tausch	<i>Achillea millefolium</i> L.	26
	<i>Cirsium arvense</i> (L.) Scop.	
	<i>Sonchus arvensis</i> L., <i>Sonchus oleraceus</i> L.	
<i>Hieracium aurantiacum</i> L. <i>H. floribundum</i> Wimm. & Grab. <i>H. pratense</i> Tausch	<i>Lotus corniculatus</i> L.	31
	<i>Medicago sativa</i> L.	
	<i>Trifolium hybridum</i> L.	
	<i>T. pratense</i> L., <i>T. repens</i> L., <i>Vicia cracca</i> L.	
<i>Knautia arvensis</i> (L.) Coult.	<i>Philadelphus grandiflorus</i> Willd.	43
<i>Matricaria chamomilla</i> L.	<i>Oenothera biennis</i> L.	
<i>Petunia hybrida</i> (Hook.) Regel	<i>Hippeastrum hybridum</i> Hort.	
<i>Ranunculus acer</i> L.	<i>Philadelphus grandiflorus</i> Willd.	
<i>Solidago virgaurea</i> L.	<i>Knautia arvensis</i> (L.) Coult.	
<i>Tagetes patula</i> L.	<i>Knautia arvensis</i> (L.) Coult.	
<i>Zephyranthes grandiflora</i> Lindl.	<i>Hippeastrum hybridum</i> Hort.	
Pollen tube growth		
<i>Helianthus exilis</i> A.Gray	<i>Mimulus guttatus</i> DC.	4
<i>Streptanthus polygaloides</i> A.Gray	<i>Mimulus guttatus</i> DC.	53
<i>Tamoneacur assavica</i> (L.) Pers.	<i>Cuphea gaumeri</i> Koehne	10
<i>Taraxacum officinale</i> F.H.Wigg.	<i>Taraxacum longe-appendiculatum</i> Nakai	33
Ovule development		
<i>Hieracium floribundum</i> Wimm.	<i>Diervilla lonicera</i> Mill.	52
Fruit Set		
<i>Echium vulgare</i> L.	<i>Phacelia secunda</i> J.M.Gmel.	9
	<i>Stachys albicaulis</i> Lindl.	
<i>Securigera varia</i> (L.) Lassen	<i>Tradescantia ohiensis</i> Raf.	21
Seed set		
<i>Impatiens glandulifera</i> Royle	<i>Lythrum salicaria</i> L.	51
<i>Lythrum salicaria</i> L.	<i>Decodon verticillatus</i> (L.) Elliott	11
	<i>Mimulus ringens</i> L.	13
	<i>Lythrum alatum</i> Pursh	8
<i>Securigera varia</i> (L.) Lassen	<i>Tradescantia ohiensis</i> Raf.	21
<i>Streptanthus polygaloides</i> A. Gray	<i>Mimulus guttatus</i> DC.	53
<i>Taraxacum officinale</i> F.H.Wigg.	<i>Erythronium grandiflorum</i> Pursh	19
	<i>Erysimum capitatum</i> (Douglas) Greene	
	<i>Taraxacum japonicum</i> Koidz.	
<i>Veronica persica</i> Poir.	<i>Veronica politalilacina</i> (T.Yamaz.)	20
<i>Impatiens glandulifera</i> Royle	<i>Lythrum salicaria</i> L.	49

4.2. Anemophilous Plants

The methods of assessment for pollen allelopathy in anemophilous plants are the same as in entomophilous plants (25). In field studies, there is a lack of evidence that pollen grains are successfully deposited on the foreign stigma naturally. Mainly, the experiments are carried out based on hand pollination for the evaluation of the pollen allelopathy of a particular plant. Generally, pollen grains of anemophilous plants are smooth-walled and light-weighted; thus, they can disperse or sustain a long distance in the ambient air, and they are deposited on the stigma.

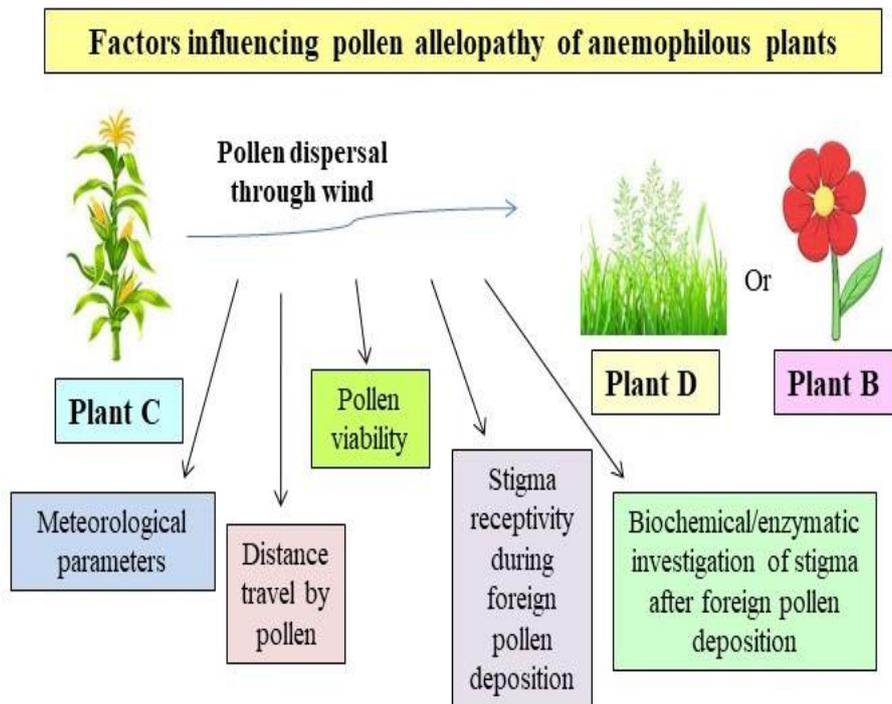


Figure 2. Factors influencing pollen allelopathy of anemophilous plants.

The pollen allelopathic nature of anemophilous *Phelum pratense* reduced the seed set of *Danthonia spicata* and *Danthonia compressa*, while the cleistogamous flowers of *Danthonia spicata* and *Danthonia compressa* remained unaffected (25). *Danthonia* sp. undergoes self-fertilization due to the long exposure to allelopathic pollen grains of *P. pratense*. Due to self-fertilization, the genetic variations reduced the fitness of offspring. Murphy reported that offspring might have a more adaptive ability to the habitat for managing pollen allelopathy of such invasive plants (25,26). The alteration of different phenological events in flowers might be a vital strategy for plants to avoid or escape pollen allelopathy (24).

Table 2. Effects of anemophilous donor species on recipient plants.

Donor Plants	Recipient plants	References
Pollen germination		
<i>Artemisia absinthium</i> L.	<i>Knautia arvensis</i> (L.) Coult. <i>Philadelphus grandiflorus</i> Willd.	43
<i>Artemisia vulgaris</i> L.	<i>Knautia arvensis</i> (L.) Coult.	
<i>Chenopodium album</i> L.	<i>Philadelphus grandiflorus</i> Willd.	
<i>Cyperus papyrus</i> L.	<i>Hippeastrum hybridum</i> Hort.	
<i>Dactylis glomerata</i> L.	<i>Philadelphus grandiflorus</i> Willd.	
<i>Parthenium hysterophorus</i> L.	<i>Catharanthus roseus</i> (L.) G. Don	46
	<i>Crotalaria pallida</i> Aiton	
	<i>Desmodium heterocarpon</i> (L.) DC.	
	<i>Indigofera spicata</i> Forssk.	
	<i>Lycopersicon esculentum</i> Mill.	
	<i>Phaseolus vulgaris</i> L.	
<i>Phleum pratense</i> L.	<i>Solanum melongena</i> L.	28,30
	<i>Agrostis stolonifera</i> L.	
	<i>Agropyron repens</i> (L.) P. Beauv.	
	<i>Ambrosia artemisiifolia</i> L.	
	<i>Aster ericoides</i> L.	
	<i>Aster dumosus</i> L.	
	<i>Bromus inermis</i> Leyss.	
	<i>Cirsium arvense</i> (L.) Scop.	
	<i>Danthonia compressa</i> Austin	
	<i>Elymus repens</i> (L.) Gould	
	<i>Euphrasia officinalis</i> L.	
	<i>Solidago rugosa</i> Mill.	
	<i>Melilotus alba</i> Medik.	
	<i>Poa compressa</i> L.	
<i>Vicia cracca</i> L.		
<i>Pinus sylvestris</i> L.	<i>Hippeastrum hybridum</i> Hort.	43
<i>Plantago major</i> L.	<i>Knautia arvensis</i> (L.) Coult.	
<i>Salix caprea</i> L.	<i>Hippeastrum hybridum</i> Hort.	
Pollen tube growth		
<i>Parthenium hysterophorus</i> L.	<i>Catharanthus roseus</i> (L.) G. Don	46
	<i>Crotalaria pallida</i> Aiton	
	<i>Desmodium heterocarpon</i> (L.) DC.	
	<i>Indigofera spicata</i> Forssk.	
	<i>Lycopersicon esculentum</i> Mill.	
	<i>Phaseolus vulgaris</i> L.	
<i>Zea mays</i> L.	<i>Solanum melongena</i> L.	5
Fruit and seed production		
<i>Euphorbia esula</i> L.	<i>Linum rigidum</i> Torr. & A. Gray	22
Growth, respiration, cellular division		
<i>Zea mays</i> L.	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	35
Radicle length		
<i>Zea mays</i> L.	<i>Amaranthus leucocarpus</i> S. Watson	3
	<i>Echinochloa crus-galli</i> (L.) P. Beauv.	
	<i>Bidens Pilosa</i> L.	15
	<i>Cassia jalapensis</i> (Britton) Lundell	
	<i>Rumex crispus</i> L.	
Chlorophyll content		
<i>Parthenium hysterophorus</i> L.	<i>Catharanthus roseus</i> (L.) G. Don	46
	<i>Crotalaria pallida</i> Aiton	
	<i>Desmodium heterocarpon</i> (L.) DC.	
	<i>Indigofera spicata</i> Forssk.	
	<i>Lycopersicon esculentum</i> Mill.	
	<i>Phaseolus vulgaris</i> L.	
	<i>Solanum melongena</i> L.	

5. POLLEN ALLELOCHEMICALS

5.1. Identification and modes of action

Most of the allelochemicals are isolated from the different plant parts e.g., leaves, stems, roots, and flowers, but there is little information about the identification of pollen allelochemicals. The physiological and biochemical processes of pollen allelochemicals are still not well established. Anaya *et al.* (3) reported that the phenolic compound phenylacetic acid (PAA) from *Zea mays* var. *chalquiñocónico* altered the pollen membrane permeability by uncoupling mitochondrial oxidative phosphorylation. PAA is found in many plant species and is not a unique pollen allelochemical. According to Murphy, more than 20 allelochemicals are identified from allelopathic potent plants (*Artemisia vulgaris*, *Betula verrucosa*, *Gaillardia* spp., *Ledum* spp., *Urtica dioica*), and also suggested that the allelochemicals act as free radicals that alter the permeability of membranes via oxidation-induced changes of enzymes or glycoproteins present in the cell wall and membrane (27). Further research must be required to identify the chemical structure and Physico-chemical nature of pollen allelochemicals. The allelochemicals penetrated the stigma and damaged or hampered the receptivity of the stigmatic region (23,24,25,35). It was well established that mainly allelochemicals inhibited pollen germination and pollen tube growth. The identification and isolation of pollen allelochemicals are laborious processes because of the dehydration nature of pollen grains and the isolation of allelochemicals is required prior to pollen dehydration (25). Sukhada and Jayachandra (46) reported a few pollen allelochemicals like one terpenoid (e.g., parthenin) and three phenolics (e.g., caffeic acid, chlorogenic acid and vanillic acid) which are identified from *Parthenium hysterophorus* (Table 3 and Figure 3).

Table 3. Allelopathic plants containing the pollen allelochemicals.

Plant species	Allelochemical	Chemical formula	Chemical group	Ref
<i>Betula verrucosa</i> Ehrh.	Azulene	C ₁₀ H ₈	Aromatic hydrocarbon	42
<i>Clivia</i> sp. Lindl.	Carotenoid	C ₄₀ H ₆₄	Tetraterpenoids	45
<i>Dactylis glomerata</i> L.	beta-carotene	C ₄₀ H ₅₆	Isoprenoids	
<i>Geranium pratense</i> L.	Anthocyanin	C ₁₅ H ₁₁ O ⁺	Flavonoid	
<i>Hibiscus rosa-sinensis</i> L.	Anthocyanin	C ₁₅ H ₁₁ O ⁺	Flavonoid	
<i>Parthenium hysterophorus</i> L.	Caffeic acid Chlorogenic acid Vanillic acid Ferulic acid Parthenin Fumaric acid	C ₉ H ₈ O ₄ C ₁₆ H ₁₈ O ₉ C ₈ H ₈ O ₄ C ₁₀ H ₁₀ O ₄ C ₁₅ H ₁₈ O ₄ C ₄ H ₄ O ₄	Phenolics Phenolics Phenolics Phenolics Sesquiterpene lactone Organic acid	46
<i>Petunia hybrida</i> (Hook.) Regel	Petunidin	C ₁₆ H ₁₃ O ₇ ⁺ (Cl ⁻)	Flavonoid	45
<i>Pinus sylvestris</i> L.	Azulene	C ₁₀ H ₈	Aromatic hydrocarbon	40
<i>Tulipa hybrida</i> L.	Anthocyanin	C ₁₅ H ₁₁ O ⁺	Flavonoid	45
<i>Zea mays</i> L.	Phenylacetic acid	C ₈ H ₈ O ₂	Organic compound	3

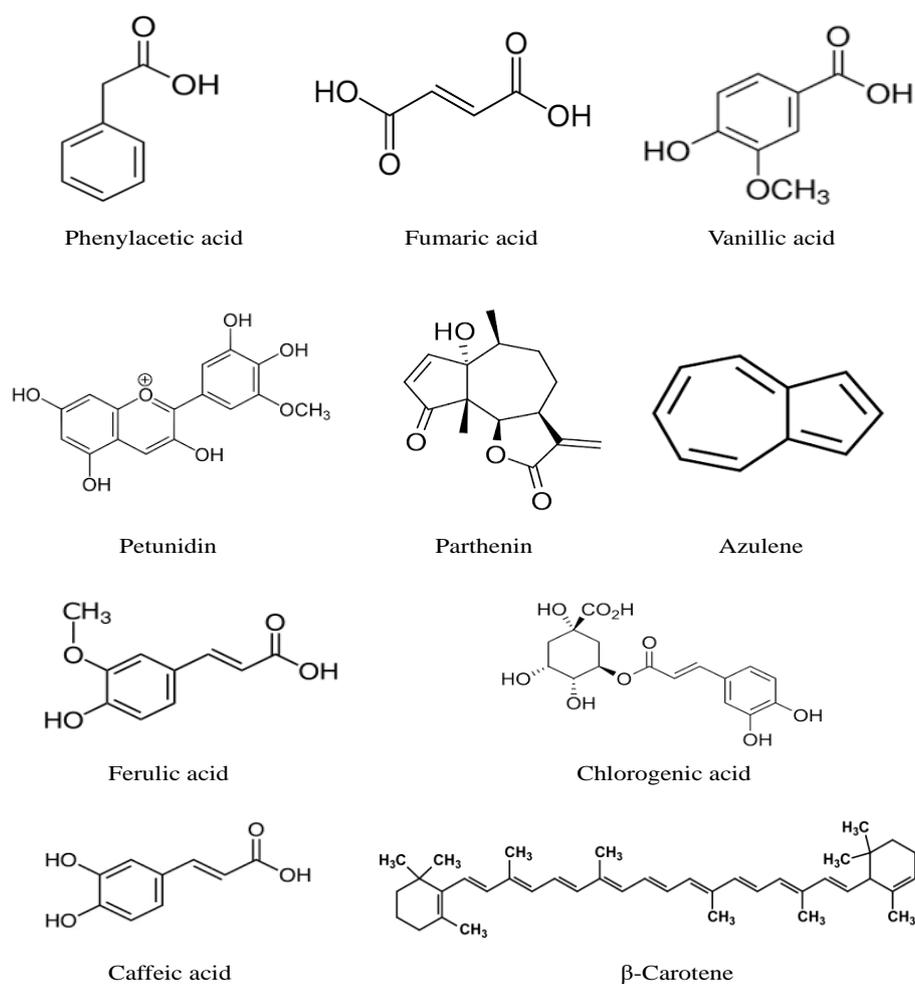


Figure 3. Molecular structure of some identified pollen allelochemicals.

5.2. Biochemistry of pollen allelochemicals

The biochemistry of pollen allelochemicals is studied using 'microspectrofluorometry' which sheds more light on pollen allelopathy (39,41). Roshchina (41) classified the pollen allelochemicals into groups as nitrogen-containing compounds (e.g., acetylcholine, histamine, serotonin, dopamine and noradrenaline); phenolics (e.g., quercetin, rutin, kaempferol, gallic acid, vanillic acid and benzoic acid); terpenoids (e.g., citral, linalool, cymol, azulene, desacetylulnicine, inulicine, ledol, artemisinin,

grosshemine, gaillardin, austricine and parthenin) and polyacetylenes (capilline). It was reported that terpenoids could stimulate or inhibit pollen germination depending on their concentrations. Through the chemosignalling process, the terpenoid compounds bind to the receptors of the plasmalemma, leads to an allelopathic effect on pollen germination and pollen tube growth (41). The allelopathic nature of pollen allelochemicals showed a concentration-dependent phenomenon. Akula and Mukherjee (1) reported that some neurotransmitters can regulate pollen allelopathy and help in recognition processes. It plays a vital role in the pollen-stigma recognition process during cross-pollinations signalling events (41). Further extensive research is needed to reveal the possible pathways and mechanisms of neuroamines in pollen biology in relation to pollen allelopathy.

5.3. Case studies

It was found that the chlorophyll content of the leaf surfaces of *Desmodium heterocarpon* and *Crotalaria pallida* was decreased by the deposition of allelopathic pollen of *Parthenium hysterophorus* (46). The pollen grains of *Zea mays* also reduced the root length of different plant species like *Rumex crispus*, *Bidens pilosa*, *Cassia jalapensis* (15). The allelochemicals of pollen grains damaged leaf chlorophyll and also decreased root length, which reflects that pollen allelochemicals may not only impede pollen tube development and ovule formation but also affect many tissues of plants. Therefore, invasive weeds like *Parthenium hysterophorus* should be taken into serious consideration for proper management. The pollen grains of anemophilous *Zea mays* are smooth-walled and light-weighted as they sustain themselves in the ambient air more than the pollen grains of entomophilous plants. The intercropping systems of *Zea mays* may hamper the production of other crops as they produce a large number of allelopathic pollen grains. The up-to-date reported research in the arena of pollen allelopathy is presented in Table 1, 2 which can provide details regarding the donor and recipient plants, and the parameters that were used during the study to prove the pollen allelopathy phenomenon, and the identified pollen allelochemicals (Table 3).

The autotoxicity of pollen allelochemicals has not been studied yet, and their mechanisms of action need to be addressed. In functional allelopathy, soil microbes play a key role in modifying the allelochemicals by detoxification or the extracellular enzymes bind with the allelochemicals and produce more toxic for other plants (38). The concept of functional allelopathy is less considered from a pollen allelopathy perspective. Microbial colonization on the stigmatic surface may also be an important factor; thus, microbial interactions on the stigma with respect to pollen allelochemicals must be considered during the evaluation.

6. FUTURE RESEARCH DIRECTIONS

Most of the research carried out is based on the pollen allelopathy in anemophilous plants, while a majority of entomophilous plants share their pollinators with co-flowering plants. In the process of pollination, pollinators significantly carried lots of pollen grains in their body parts, and during their visit from one flower to another, they deposited a significant number of pollen grains on the stigmatic surface. However, there is limited evidence of entomophilous plants that showed allelopathic effects caused by pollen and which lead to the reduction of seed set in the other plants. Field investigations of pollen

allelopathic interactions of entomophilous plants require careful consideration of some crucial aspects (Figure 1). Factors like pollinators' behaviour during their visits to heterospecific plants and pollen attachment sites to the body parts where pollen gets adhered might have a significant role in understanding pollen allelopathy. It must be taken into consideration whether the attached foreign pollen grains on the pollinator's body successfully get touched or deposited into the recipient's stigma or not. Different flowering phenological events like flower opening, pollen viability and stigma receptivity are also to be considered, as these factors influence pollen allelopathy. The investigation of foreign pollen load on the recipient stigmatic surface also played a vital role in considering the total number of pollen grains that caused pollen allelopathic effects on the recipient stigma. A detailed molecular, biochemical, and enzymatic investigation is required for understanding the mode of action of pollen allelochemicals.

6.1. Possible implications of pollen allelopathy: Ecological and agricultural

Long-term field experiments are also required for pollen allelopathic studies to understand the ecological impacts of anemophilous plants on native and invasive flora. Physiological and biochemical approaches are still unclear and require study on this particular aspect. A list of pollen allelopathic interactions between anemophilous donors and recipient plants is presented in Table 2. Some important factors must be considered during the study of the pollen allelopathic effect of anemophilous plants that are affecting the pollen allelopathic study (Figure 2). Meteorological parameters such as rainfall, humidity, and temperature can affect the distance travelled by pollen grains. So, the meteorological parameters must be included during the field study of the pollen allelopathic effect of anemophilous plants.

In natural ecosystems, pollination is required for reproductive success and thus pollinator sharing is a common strategy for plants. Therefore, pollen deposition from native to foreign stigma leads to impediments to the reproductive success of plants. It was observed that several invasive species shared their pollinators with the native plants and the allelopathic potentiality of pollen grains increased the chances of plant reproductive failure. Pollen allelopathy could be utilized for weed management in crop fields that reduce reproductive ability. Invasive plants with pollen allelopathic nature are serious threats to crops, especially if both are wind-pollinated species. The broad aspect of pollen allelopathy may be an effective biological control method for weed management on croplands. The phenomenon not only reduces the reproductive success of weeds but also hampers their genetic variation for adaptability to new environmental challenges. The pollen allelopathy approach might be helpful to combat some serious invasive weeds like *Parthenium hysterophorus* and *Lantana camara*. The study also shed light on the basis of the experimental tests for the potential impacts of allelopathic pollen grains on weed management. The heterospecific competition through pollen allelopathy must be considered to understand its impact on the ecosystem. Research in pollen allelopathy is required for understanding the community ecology and evolutionary perspectives of plants. However, much more research is required to fully understand the physiology and biochemistry of pollen allelopathy. Since pollen allelopathy's ecological importance has been proven, this type of research will probably pick up steam during the next few years.

7. CONCLUSIONS

The pollen allelopathy of anemophilous and entomophilous plants interactions affect plant reproduction and the ecology of the landscape. Rather than relying just on hand-pollination techniques to assess a plant's allelopathic character, factors like biochemical and enzymatic processes also need to be considered for a more comprehensive understanding of the phenomenon of allelopathy. A few studies were conducted regarding the pollen allelochemicals and there is a great possibility to identify new allelochemicals that might be important biocontrol agents for the agroecosystem. Additionally, this work offers insightful information for further research in pollen allelopathy.

ACKNOWLEDGMENTS

The authors are thankful to the UGC Non-NET fellowship for financial assistance and the Department of Botany (DST-FIST & UGC-SAP, DRS), Visva-Bharati, for providing necessary laboratory facilities.

DECLARATION

We declare that all authors of this Ms. have made substantial contributions. We have not excluded any author that substantially contributed to this Ms. We have followed our ethical norms established by our respective institutions.

CONFLICT OF INTEREST

The authors announce that they have no conflict of interest.

ETHICAL APPROVAL

The authors declare that the study was carried out following scientific ethics and conduct.

8. REFERENCES

1. Akula, R. and Mukherjee, S. (2020). New insights on neurotransmitters signaling mechanisms in plants. *Plant Signaling and Behavior* **15**: p.1737450.
2. Alsharekh, A., El-Sheikh, M.A., Alatar, A.A. and Abdel-Salam, E.M. (2022). Natural control of weed invasions in hyper-arid arable farms: allelopathic potential effect of *Conocarpus erectus* against common weeds and vegetables. *Agronomy* **12**: 703.
3. Anaya, A.L., Hernandez-Bautista, B.E., Jimenez-Estrada, M. and Velasco-Ibarra, L. (1992). Phenylacetic acid as a phytotoxic compound of corn pollen. *Journal of Chemical Ecology* **18**: 897-905.
4. Arceo-Gómez, G. and Ashman, T.L. (2011). hetero specific pollen deposition: does diversity alter the consequences? *New Phytologist* **192**: 738-746.
5. Arceo-Gómez, G., Jameel, M.I. and Ashman, T.L. (2018). Effects of hetero specific pollen from a wind-pollinated and pesticide-treated plant on reproductive success of an insect-pollinated species. *American Journal of Botany* **105**: 836-841.
6. Ashman, T.L. and Arceo-Gómez, G. (2013). Toward a predictive understanding of the fitness costs of hetero specific pollen receipt and its importance in co-flowering communities. *American Journal of Botany* **100**: 1061-1070.
7. Beattie, A.J. (1971). Pollination mechanisms in *Viola*. *New Phytologist* **70**: 343-360.
8. Brown, B.J., Mitchell, R.J. and Graham, S.A. (2002). Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* **83**: 2328-2336.
9. Carvalloa, G.O. and Medel, R. (2016). hetero specific pollen transfer from an exotic plant to native plants: assessing reproductive consequences in an Andean grassland. *Plant Ecology and Diversity* **9**: 151-157.

10. Celaya, I.N., Arceo-Gomez, G., Alonso, C. and Parra-Tabla, V. (2015). Negative effects of hetero specific pollen receipt vary with abiotic conditions: ecological and evolutionary implications. *Annals of Botany* **116**: 789-795.
11. Da Silva, E.M. and Sargent, R.D. (2011). The effect of invasive *Lythrum salicaria* pollen deposition on seed set in the native species *Decodon verticillatus*. *Botany* **89**: 141-146.
12. Etter, K.J., Junquera, G., Horvet-French, J., Alarcon, R., Hung, K.L. and Holway, D.A. (2022). Interspecific pollen transport between non-native fennel and an island endemic buckwheat: Assessment of the magnet effect. *Biological Invasions* **24**: 139-155.
13. Flanagan, R.J., Mitchell, R.J., Knutowski, D. and Karron, J.D. (2009). Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *American Journal of Botany* **96**: 809-815.
14. Friedman, J. and Barrett, S.C.H. (2008). A phylogenetic analysis of the evolution of wind pollination in the angiosperms. *International Journal of Plant Sciences* **169**:49-58.
15. Jimenez, J.J., Schultz, K., Anaya, A.L., Hernandez, J. and Espejo, O. (1983). Allelopathic potential of corn pollen. *Journal of Chemical Ecology* **9**: 1011-1025.
16. Jones, K. (2004). Do dandelion flowers influence seed set of a native plant (*Delphinium nuttallianum*) in subalpine meadows? *The American Midland Naturalist* **151**: 201-205.
17. Linder, H.P. (1998). Morphology and the evolution of wind pollination. In: *Reproductive Biology in Systematics, Conservation and Economic Botany* (Eds., S.J., Owens and P.J. Rudall). Kew: Royal Botanic Gardens, pp. 123-135.
18. Linder, P.H. and Midgley, J. (1996). Anemophilous plants select pollen from their own species from the air. *Oecologia* **108**: 85-87.
19. Loughnan, D., Thomson, J.D., Ogilvie, J.E. and Gilbert, B. (2014). *Taraxacum officinale* pollen depresses seed set of montane wildflowers through pollen allelopathy. *Journal of Pollination Ecology* **13**: 146-150.
20. Matsumoto, T., Takakura, K.I. and Nishida, T. (2010). Alien pollen grains interfere with the reproductive success of native congener. *Biological Invasions* **12**: 1617-1626.
21. Molano-Flores, B. (2014). An invasive plant species decreases native plant reproductive success. *Natural Areas Journal* **34**: 465-469.
22. Montgomery, B.R. and Caleb, W.P. (2015). Breeding system of *Linum rigidum* and effect of hetero specific pollen from introduced *Euphorbia esula*. *Journal of Pollination Ecology* **16**: 101-107.
23. Murphy, S.D. (1992). The determination of the allelopathic potential of pollen and nectar. In: *Modern Methods of Plant Analysis* (Eds., H.F. Linskens and J.F. Jackson) pp. 333-357. Springer-Verlag, New York.
24. Murphy, S.D. (1999). Pollen allelopathy. In: *Principles and Practices in Plant Ecology: Allelochemical Interactions* (Eds., Inderjit, K.M.M. Dakshini and C.L.Foy) pp. 129-148. CRC Press, Florida.
25. Murphy, S.D. (2000). Field testing for pollen allelopathy: A review. *Journal of Chemical Ecology* **26**: 2155-2172.
26. Murphy, S.D. (2001). The role of pollen allelopathy in weed ecology. *Weed Technology* **15**: 867-872.
27. Murphy, S.D. (2002). Biochemical and physiological aspects of pollen allelopathy. In: *Chemical Ecology of Plants: Allelopathy in Aquatic and Terrestrial Ecosystems* (Eds., A.U. Mallik and Inderjit) pp. 245-260. Springer, Basel.
28. Murphy, S.D. and Aarssen, L.W. (1989). Pollen allelopathy among sympatric grassland species: *In-vitro* evidence in *Phleum pratense* L. *New Phytologist* **112**: 295-305.
29. Murphy, S.D. and Aarssen, L.W. (1995a). Allelopathic pollen extract from *Phleum pratense* L. (Poaceae) reduces seed set in sympatric species. *International Journal of Plant Sciences* **156**: 435-444.
30. Murphy, S.D. and Aarssen, L.W. (1995b). Allelopathic pollen extract from *Phleum pratense* L. (Poaceae) reduces germination, *in vitro*, of pollen in sympatric species. *International Journal of Plant Sciences* **156**: 425-434.
31. Murphy, S.D. and Aarssen, L.W. (1995c). *In-vitro* allelopathic effects of pollen from three *Hieracium* species (Asteraceae) and pollen transfer to sympatric Fabaceae. *American Journal of Botany* **82**: 37-45.
32. Murphy, S.D. and Aarssen, L.W. (1996). Cleistogamy limits reduction in seed set in *Danthonia compressa* (Poaceae) by allelopathic pollen of *Phleum pratense* (Poaceae). *Ecoscience* **3**: 205-210.
33. Nishida, S., Kanaoka, M.M., Hashimoto, K., Takakura, K.I. and Nishida, T. (2014). Pollen-pistil interactions in reproductive interference: Comparisons of hetero specific pollen tube growth from alien species between two native *Taraxacum* species. *Functional Ecology* **28**: 450-457.
34. Ollerton, J. (2017). Pollinator diversity: Distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics* **48**: 353-376.

35. Ortega, R.C., Anaya, A.L. and Ramos, L. (1988). Effects of allelopathic compounds of corn pollen on respiration and cell division of watermelon. *Journal of Chemical Ecology* **14**: 71-86.
36. Powell, K.I., Krakos, K.N. and Knight, T.M. (2011). Comparing the reproductive success and pollination biology of an invasive plant to its rare and common native congeners: A case study in the genus *Cirsium* (Asteraceae). *Biological Invasions* **13**: 905-917.
37. Rice, E.L. (1984). *Allelopathy*. pp. 1-368. Academic Press, New York.
38. Rizvi, S.J.H. and Rizvi, V. (1992). *Allelopathy: Basic and Applied Aspects*. pp. 1-480. Springer, Chapman and Hall, London.
39. Roshchina, V.V. and Melnikova, E.V. (1996). Microspectrofluorometry: A new technique to study pollen allelopathy. *Allelopathy Journal* **3**: 51-58.
40. Roshchina, V.V. (1999). Mechanisms of cell-cell communication. In: *Allelopathy update* (Ed., S.S. Narwal) pp. 3-25. Science publishers, Enfield, New Hampshire.
41. Roshchina, V.V. (2001). Molecular-cellular mechanisms in pollen allelopathy. *Allelopathy Journal* **8**: 11-28.
42. Roshchina, V.V. (2008). *Fluorescing World of Plant Secreting Cells*. pp. 1-356. Science publishers, Enfield, Jersey (USA).
43. Roshchina, V.V., Yashina, A.V., Yashin, V.A. and Prizova, N.K. (2009). Models to study pollen allelopathy. *Allelopathy Journal* **23**: 3-24.
44. Shivanna, K.R., Tandon, R. (2020). Developmental biology of dispersed pollen grains. *The International Journal of Development Biology* **64**: 7-19.
45. Stanley, R.G., Linskens, H.F. (1974). *Pollen: Biology, Biochemistry and Managements*. pp. 1-258. Springer, Berlin.
46. Sukhada, K.D. and Jayachandra. (1980a). Allelopathic effects of *Parthenium hysterophorus* L. *Plant and Soil* **55**: 67-75.
47. Sukhada, K.D. and Jayachandra. (1980b). Pollen allelopathy-a new phenomenon. *New Phytologist* **84**: 739-746.
48. Sun, S.G., Montgomery, B.R. and Li, B. (2013). Contrasting effects of plant invasion on pollination of two native species with similar morphologies. *Biological Invasions* **15**: 2165-2177.
49. Takakura, K.I. (2013). Two-Way but asymmetrical reproductive interference between an invasive *Veronica* species and a native congener. *American Journal of Plant Science* **4**: 535-542.
50. Takemori, A., Naiki, A., Takakura, K.L., Kanaoka, M.M. and Nishida, S. (2019). Comparison of mechanisms of reproductive interference in *Taraxacum*. *Annals of Botany* **123**: 1017-1027.
51. Thijs, K.W., Brys, R., Verboven, H.A.F. and Hermy, M. (2012). The influence of an invasive plant species on the pollination success and reproductive output of three riparian plant species. *Biological Invasions* **14**: 355-365.
52. Thomson, J.D., Andrews, B.J. and Plowright, R.C. (1982). The effect of a foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytologist* **90**: 777-783.
53. Wipf, H.M., Meindl, G.A. and Ashman, T.L. (2016). A first test of elemental allelopathy via hetero specific pollen receipt. *American Journal of Botany* **103**: 514-521.

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Allelopathy Journal remains neutral with regard to jurisdictional claims in published Maps and Institutional Affiliations.