Lichen Allelopathy: An Agricultural Prospect

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DOI: 10.18811/ijpen.v6i01.01

ABSTRACT

Allelopathy is a common biological miracle by which one organism produces biochemicals that affect the growth, existence, development, and reproduction of other organisms. These biochemicals are known as allelochemicals and have advantageous, as well as, harmful effects on target organisms. Lichens produce over a thousand different extracellular biochemical terms as secondary metabolites. The lichen secondary metabolites may show either positive effects, such as, in weed control, crop protection, or crop re-establishment or negative effects, e.g., autotoxicity, biological invasion, competition, deterioration, and eutrophic soil sickness. However, several lichen secondary metabolites can potentially be used as growth regulators, insecticidal, and antimicrobial since dated back. Here, we discuss the application of lichen allelopathy in various agricultural prospects in the near future.

Keywords: Agricultural practices, Competition, Natural biocides, Secondary metabolites.

International Journal of Plant and Environment (2020);

ISSN: 2454-1117 (Print), 2455-202X (Online)

INTRODUCTION

The term allelopathy was first time coined by Molisch (1937), to indicate all of the effects that directly and indirectly result from biochemical substances transferred from one plant to another. Later on, the term was refined by Rice (1984) as "any direct or indirect harmful or beneficial effect by one plant (including microorganisms) on another through the production of chemical compounds that escape into the environment." In the year 1996, the International Allelopathy Society (IAS) extended its definition of allelopathy as any process involving secondary metabolites produced by plants, microorganisms, and fungi that influence the growth and development of agricultural, as well as, biological systems.

Allelopathy is also considered as a sub-discipline of chemical ecology which concerned with the effects of chemicals produced by plants or microorganisms on the growth, development, and distribution of other plants and microorganisms in natural communities, agricultural, as well as, biological systems (Einhellig, 1995; Kohli *et al.*, 1997). The allelochemicals, which are non-nutritive substances mainly produced as secondary metabolites or decomposition products of microbes, are the active media of allelopathy.

Allelochemicals consist of various chemical families and are classified into different categories based on chemical similarity. The water-soluble organic acids, straight-chain alcohols, aliphatic aldehydes, and ketones; simple unsaturated lactones; long chain fatty acids and polyacetylenes; benzoquinone, anthraquinone and complex quinones; simple phenols, benzoic acid and its derivatives; cinnamic acid and its derivatives; coumarin; flavonoids; tannins; terpenoids and steroids; amino acids and peptides; alkaloids and cyanohydrins; sulfide and glucosinolates; purines and nucleosides. Plant growth regulators, including salicylic acid, gibberellic acid, and ethylene, are also considered to be allelochemicals. The rapid progress of nanotechnology in recent years has made it possible to isolate and identify even minute amounts of allelochemicals and to perform sophisticated structural analyses of these molecules (Rice, 1984).

A large number of studies are available in respect to allelopathic effect of higher plants and microbes, but in

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How to cite this article: Bajpai, R. and Upreti, D.K. (2020). Lichen Allelopathy: An Agricultural Prospect. International Journal of Plant and Environment 6(1):1-8.

Source of support: Nil Conflict of interest: None

Submitted: 25/08/2019 Accepted: 25/01/2020 Published: 31/01/2020

context to lichens, such studies are meager. The lichens are symbiotic organisms consisting of a fungus (mycobiont) and photosynthetic partner (photobiont), which can be either green algae or cyanobacteria. Lichens are the dominant component of the vegetation in approximately 8% of terrestrial ecosystems and are able to survive in environment subject to extremes of temperature, desiccation, and nutrient status (Ahmadijan, 1993).

The ecological success of symbioses forming, lichens may produce organic compounds called secondary metabolites. The lichen secondary metabolites are produced by the fungal partner, and their presence is mostly restricted to the lichens themselves (Hauck *et al.*, 2009). Lichen secondary metabolites (mostly depsides and depsidones) are deposited on the surface of hyphae, as well as, lichen algae, and typically constituting 0.1 to 5% (w/w) of thallus dry weight (Fahselt, 1994). However, more than 1,000 secondary metabolites are known to occur in lichens, but only approximately 7% of them have also been discovered in other organisms, for example, in non-lichenized fungi or even in higher plants (Bačkor *et al.*, 2013; Beckett and Minibayeva, 2013).

There are many evidences that specialized metabolites in lichens are synthesized in response to environmental stress. Lichen metabolites are considered as protective agents against oxidative damage by free radicals produced in response to different stress factors including high light intensity, herbicides, SO₂ or heavy metals, metalloid, and PoPs (Białońska and Dayan,

2005; Caviglia *et al.*, 2001; Shukla *et al.*, 2014). Additionally, it is suggested that lichen secondary metabolites control the uptake of pollutants from the environment like parietin may protect against Cd toxicity in *Xanthoria parietina* (Kalinowska *et al.*, 2015) or usnic acid acts as an antioxidant in *Parmelia soredians* (Caviglia *et al.*, 2001). Additionally, Białońska and Dayan (2005) suggested that physodic acid plays a role in the detoxification of heavy metals in *Hypogymnia physodes*.

The secondary metabolites of lichens are well known for their biological and ecological roles confirmed experimentally include mostly antimicrobial activity, antiherbivory, chelating of heavy metals, and light screening (Latkowska *et al.*, 2006; Hauck *et al.*, 2009; Solhaug *et al.*, 2009; Bačkor *et al.*, 2013; Canava *et al.*, 2020) but their role in agricultural are slightly known. Despite several evidences about the interaction between lichen secondary metabolites are available but agricultural prospect in lichens are not available. In the present communications, we have summarized the role of lichen secondary metabolites in terms of future directional agricultural research.

LICHENS AND LAND PLANTS INTERACTION

Lichen secondary metabolites, secreted by mycobionts and tolerated by photobionts through exclusion or detoxification mechanisms (Takahagi *et al.*, 2008), determine allelopathic effects on bryophytes and vascular plants which have been extensively examined both focusing on the inhibition of spore/ seed germination, and subordinately of other growth stages (Lawrey, 1984). Researches have dealt both with the effects of terricolous lichen metabolites on plants, to explain the competition for soil surfaces, and with the effects of corticolous lichens on the health of their phorophytes. As in the case of plant-plant interactions (Inderjit *et al.*, 2005), lichen allelopathic interferences have mainly been observed *in vitro* only.

Certain secondary metabolites of lichens appear to have allelopathic effects on vascular plants (Lechowski *et al.*, 2006), as well as, on the algal partner of lichens (Bačkor *et al.*, 2013). All the lichen secondary metabolites that have been discovered to date, phytotoxic effects to lichen photobionts have, thus far, only been confirmed after application of usnic acid and atranorin. Both the metabolites show phytotoxicity in terms of growth inhibition, inhibition of chlorophyll a fluorescence (FV/ FM), decrease of plant viability, and induction of oxidative stress in the plant cells (Bačkor *et al.*, 2010).

Besides, the effects of evernic acid injected by *Evernia prunastri* into living tissues of its phorophytes, usnic acid displays a multidirectional toxic effect on both the photosynthetic and respiratory pathways, and also on the transpiration and phytohormonal regulation of plant growth (Legaz *et al.*, 2004; Latkowska *et al.*, 2006). Plants cultivated with usnic acid (20 or 30μ M) have demonstrated lower photosynthetic (about -40%) and respiratory (down to -80%) activities than the controls and displayed a reduction in their chlorophyll and carotenoid contents (Vavasseur *et al.*, 1991; Latkowska *et al.*, 2006).

The hyphal penetration of lichen *E. prunastri* within the xylem vessels of oaks determines defoliation and a decrease in the vigor of colonized plants as a result of the mycobiont release of secondary metabolites, which are translocated with the xylem sap and induce allelopathic processes (Legaz *et al.* 2004).

Evernic acid, which is secreted by *E. prunastri* together with atranorin, chloroatranorin, and usnic acid, has caused changes in the internal organization of isolated chloroplasts of spinach and oak (*Quercus rotundifolia*) during *in vitro* tests at 35.5 mM, these changes include lowering of the number of grana per chloroplast section, of thylakoids per grana, and of the height of grana stacks (Ascaso and Rapsch, 1986). Evernic acid has been shown, *in vitro*, to induce the reduction of the total chlorophylls, chlorophyll a and b in spinach, and oak chloroplasts (Ascaso and Rapsch, 1986; Bouaid and Vicente, 1998). In a mixture with usnic acid, atranorin, and chloroatranorin, resulting in the formation of paracrystalline structures and other morphological alterations in the chloroplasts (Ascaso *et al.*, 1983).

On the other hand, the accumulation of evernic acid in the apical zones of branches without leaves and the buds of oaks and birches indicates an acropetal translocation of this chemical (Monso´ *et al.*, 1993), which inhibits bud differentiation and retards leaf initiation by affecting oxidative phosphorylation and induces a respiratory depletion (Legaz *et al.*, 1988). The parallel accumulation of usnic acid in the buds further decreases leaf growth, as this lichen metabolite conjugates auxin through an esterification reaction (Legaz *et al.*, 2004). Evidence of hyphal penetration within the bark and the secretion of allelopathic metabolites make. Thus, *E. prunastri* a lichen species that certainly has a harmful effect on trees. Similar processes may also explain the negative effect on tea plants of corticolous lichens, which suppress the growth of adventitious shoots (Asahina and Kurokawa, 1952).

Water extracts of terricolous lichen Cladonia species and the Peltigera canina, have been shown, in vitro, to reduce the seed germination of several vascular plants, including Pinus sylvestris and angiosperms, trees, and shrubs and grasses (Sedia and Ehrenfeld, 2003). Growth parameters like root elongation, are even more sensitive to allelopathic effects than seed germination (Peres et al., 2009). The chemical structure, i.e., the number and length of alkyl groups bonded to the benzene rings and to phenolic oxygen, is important in terms of activity (Peres et al., 2009). The different effects of lecanoric acid (from Parmotrema tinctorum) and its orsellinate derivatives on the germination and growth of Lactuca sativa and Allium cepa (strongly affected) have highlighted that the allelopathic action of certain metabolites, which can vary to a great extent between different plant species, as well as, grasses (Peres et al., 2009) (Figs 1A and B).

LICHENS AND BRYOPHYTES INTERACTION

The allelopathic effect of lichens on bryophytes has been inferred from *in vitro* experiments that have assayed spores of different moss species with terricolous lichen metabolites at different concentrations. Compounds extracted from *Cladonia* species, such as, usnic and fumarprotocetraric acid, inhibit spore germination of several moss species to various extents (Glime, 2007). In most cases, the toxic effect on *Funaria hygrometrica* spores is exerted at concentrations of 2.7 to 10^{-3} M and, in some cases, 2.7 to 10^{-4} M, by reducing present germination, and sporeling growth, the relative toxicity of the different compounds depends on the pH, with vulpinic acid being the most toxic over all the pH tested (Gardner and Mueller, 1981).



Fig. 1: Lichen show there invasion A. Physcia sp., with grasses; B. Cladonia sp., with grasses; C. Phaeophyscia sp., with mosses; D. Cladonia sp., restrict the growth of cyanolichen

O-methylated compounds, such as, evernic and squamatic acids, strongly inhibit the spore germination of several mosses (Lawrey, 1977). Though, O-methylated stictic acid has been shown to be poorly effective in spore inhibition in Figs 1C and D (Gardner and Mueller, 1981).

The secondary metabolites may contribute, together with the modification of microclimatic conditions, to the detrimental effects which, in some cases, characterize lichens that overgrow bryophyte. On the other hand, it is worth noting that some lichen metabolites extracted from *Cladonia foliacea* (arabitol and mannitol) exert a stimulating effect on moss growth. This may also explain the increasing development of gametophytes cultured with *C. foliacea* thalli from the third week to 2, 3 months, following an initial inhibition, during the first two weeks, associated with cytological alterations (granular appearance of cytoplasm and changes in chloroplast shape) (Giordano *et al.*, 1999).

LICHEN AND LICHEN INTERACTION

The lichen symbiosis is unusual in that it often dominates communities in extremely harsh environments, where vascular plants may be excluded. In these environments, lichens experience extravagances of temperature, moisture supply, and low availability of nutrients (Grime, 1979).

In the case of saxicolous lichens, secondary metabolites determine

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deterioration through ion leaching from minerals, are involved in the relationship of muscicolous, corticolous, and terricolous lichens with plants, as both growth substrates and neighbors on soil, causing allelopathic interferences (Legaz *et al.*, 2004; Lawrey, 2009). Enzymatic processes are involved in hyphal adhesion on, and penetrations within plant tissues, as well as, they have been recently suggested to explain carbonate dissolution by endolithic lichens (Laufer *et al.*, 2006; Tretiach *et al.*, 2008).

The importance of lichen chemistry and allelopathic effects in lichen competition is controversial in the past. But in recent years, several studies inferred that the metabolites leached from the thallus may suppress neighboring lichens mosses and land plants (Lawrey, 1995). Most evidence for allelopathy in lichen communities is based on observational studies, and few experiments have been carried out.

Whiton and Lawrey (1984) have demonstrated inhibitory effects of lichen compounds on spore germination of the lichen Caloplaca citrina (Hoffm.) Th. Fr. was inhibited by vulpinic, evernic, and atranoric acids while Graphis scripta (L.) Ach. was severely inhibited by vulpinic and evernic acids, but unaffected by atranorin. However, the phenolic defense compound lecanoric acid may prevent the growth of the symbiotic fungus Nectria parmeliae (Berk & Curtis) Hawksw. In addition, Hilmo (1994) and Glenn et al. (1995) reported that the presence of usnic acid and other secondary compounds, which may reduce grazing by microarthropods. The lichens colonize a substratum; they grow radially, and ultimately, the margins of thalli come into contact with each other (Figs 2A and B). The processes that occur when two thalli meet where one species will outcompete the other either by overgrowth or by the production of allelochemicals.

Additionally, there was evidence that *X. parietina* (L.) Th. Fr., reproduces sexually, which parasitizes the algal symbiont of *Physcia* species in an effort to promote its dispersal, and

such competition later or sooner effectively removes *Physcia* species from substrata colonized by *X. parietina* (Ott, 1987) (Figs 2C to F). It is earlier evidenced that lichen secondary metabolites, like atranorin, evernic, lecanoric, paretin, squamatic, stictic, usnic, and vulpinic acid show allelopathic effects (Bačkor *et al.*, 2010; Legaz *et al.*, 2004; Latkowska *et al.*, 2006). In the Indian context, several metabolites are common in different lichen species, can be used as allelochemicals (Table 1).

LICHENS AND SOIL INTERACTION

Lichens are known to trap seeds of the different organisms (Sedia and Ehrenfeld, 2003). The fruticose saxicolous lichen has even been shown to increase seed germination, growth, and the survival of Dudleya plants (Crassulaceae) by increasing water availability, offering a nutrient-enriched seedbed, and protection from herbivores (Riefner and Bowler, 1995). Some epiphytic lichens (Parmotrema tinctorum, with lecanoric acid, and P. rigidum) speed up the colonization by epiphytic Tillandsia (Bromeliaceae) on its most common host Quercus virginiana and increase the number of seeds that adhere to the trunk of other unusual host trees (Callaway et al., 2001). However, in most cases, vascular plants have rarely been observed to massively overgrow terricolous lichen carpets and in many cases are absent from the vicinity of lichen patches, suggesting some adaptive strategies of the symbiotic slow-growing organisms against their higher-biomass producing competitors (Sedia and Ehrenfeld, 2005; Lawrey, 2009). In this context, a physical inhibition of seedling establishment by Cladonia rangiferina was described long ago: the expansion of thalli, driven by morning dew, pulls the seedlings completely out of the ground, breaking their root connection, and preventing their establishment (Allen, 1929).

S. No.	Secondary metabolites	Molecular formula	Lichen genera
1.	Atranorin	C ₁₉ H ₁₈ O ₈	Hypogymnia, Lecanora, Hypotrachyna, Acroscyphus, Cetrelia, Lepraria, Parmelia, Stereocaulon, Heterodermia, Parmotrema, Cladonia, Pseudoevernia, Menegazzia, Phyllopsora, Buellia, Dirinaria, Bulbothrix, Physcia, Rinodina
2.	Barbatic acid	$C_{19}H_{20}O_7$	Some species of Hypotrachyana, Hypogymnia, Remototrachyna, Cladonia, Cladia, Usnea, Diabaeis
3.	Evernic acid	1C ₁₇ H ₁₆ O ₇	Evernia, Ramalina, Usnea
4.	Fumarprotocetraric acid	$C_{22}H_{16}O_{12}$	Member of lichen family Cladoniaceae, Bryoria, Cetraria, Cetreliopsis, Lerpraria, Usnea, Melenelia, Nephromopsis
5.	Gyrophoric acid	C ₂₄ H ₂₀ O ₁₀	Some species of Acroscyphus, Peltigera, Xanthoparmelia, Lobaria, Herpothallon, Cryptothecia, Diploschistes, Sticta, Lobaria, Acarospora, Caloplaca, Remotrachyna, Nephroma, Parmotrema, Umbilicaria, Melenelia
6.	Lecanoric acid	C ₁₆ H ₁₄ O ₇	Member of lichen family Lecanoraceae, Herpothallon, Lepraria, Ochrolechia, Diploschistes, Parmelia, Acarospora, Cryptothecia, Parmotrema, Melanelixia, Flavopunctelia, Lecidea, Pertusaria, Melanelia, Melanohalea, Punctelia
7.	Parietin	C ₁₆ H ₁₂ O ₅	Member of lichen family Teloschistaceae
8.	Squamatic acid	C ₁₉ H ₁₈ O ₉	Some member of lichen family Cladoniaceae
9.	Stictic acid	C ₁₉ H ₁₄ O ₉	Member of lichen family Physciaceae, Parmeliaceae, Pertusaria, Lecanora, Lepraria, Cladonia, Usnea, Stereocaulon, Lobaria, Diorygma, Graphis, Herpothallon, Rhizocarpon, Hemithecium, Buellia
10.	Usnic acid	C ₁₈ H ₁₆ O ₇	Usnea, Lecanora, Cladonia, Allocetraria, Xanthoparmelia, Hypogymnia, Nephromopsis, Canoparmelia, Parmotrema, Lepraria, Ramalina
11.	Vulpinic acid	C ₁₉ H ₁₄ O ₅	Sulcaria, Vulpicida, Chrysothrix, Chaenotheca

Table 1: Some common lichens metabolites and their respective lichen taxa



Fig. 2: Lichen show there invasion **A.** *Rhizocarpon* restrict the growth of *Physcia*; **B.** *Physcia* with *Lecanora* sp; **C.** *Physcia* with *Calplaca* sp; **D.** *Lecanora* with *Caloplaca* sp; **E.** *Porpidia* with *Diploschistes* sp; **F.** *Xanthoria* with *Physcia*

TERRICOLOUS LICHENS AND MYCORRHIZAL FUNGI INTERACTION

The effect of lichen mats on seedling growth has also repeatedly been correlated to the allelopathic effect of lichen metabolites on mycorrhizal fungi, which support plant nourishment (Kytöviita and Stark, 2009). Water extracts from terricolous lichens, Cladonia, Cetraria islandica, and Stereocaulon paschale, inhibit the growth of an extensive set of mycorrhizal fungi in pure cultures: mycorrhiza formation and phosphorous absorption by pine and spruce seedlings are reduced to various degrees, depending on the mycorrhizal fungus species, and the different lichen extracts (Brown and Mikola, 1974). The results obtained with purified compounds of usnic acid inhibits the growth of Pisolithus, tinctorius (Goldner et al., 1986). The growth of Pinus banksiana and Picea glauca transplants and seedlings also reduces the following mulching with C. rangiferina or C. alpestris, and the phosphorous accumulation by the plants decreases (Fisher, 1979). The other metabolites that have been investigated for their phytotoxic mode of action, such as, barbatic, lecanoric (depsides), and gyrophoric acid (tridepside) have been shown to interrupt the photosynthetic electron transport by binding the secondary quinone acceptor (barbatic acid on tobacco cells) (Takahagi et al., 2006), by inhibiting the electron transfer between P680 and QA on the reducing side of PSII (gyrophoric acid on spinach chloroplasts) or by acting at the water-splitting enzyme level (lecanoric acid on spinach chloroplasts) (Rojas et al., 2000). Other depsides, like atranorin and nephroarctin, have not shown any inhibitory activity, while evernic acid and sphaeosporin have shown a strong inhibition activity, which is limited to the reducing and oxidizing side of P680 (Endo et al., 1998 and Stark et al., 2007). The lichen-derived anthraquinones, such as, emodin and rhodocladonic acid, have been shown to cause malformation and to determine bleaching in grasses, the former inhibiting the PSII in thylakoids isolated from spinach and corn (Romagni et al., 2004).

FUTURE RESEARCH DIRECTIONS

Lichen allelochemicals mainly consist of secondary metabolites that are released into the environment through natural pathways, such as, volatilization, leaching, residue decomposition, and/or exudation. The interactions, such as, synergy, antagonism, and incremental effects between different allelochemicals should be evaluated because one allelochemical may not show allelopathic activity as a single component in a certain situation, but might increase allelopathy in association with other allelochemicals (Albuquerque *et al.*, 2010).

The type and amount of allelochemicals released into the environment depend on the combined effects of the organism itself and environmental factors (Albuquerque *et al.*, 2010). The organism factors include the genera, species, growth form, communities, and various functional traits may be responsible for production of diverse secondary metabolites (Leao *et al.*, 2012; lannucci *et al.*, 2013). The organism from the same environment or with close taxonomic proximity does not necessarily display similar production of secondary metabolites, and they may, therefore, not secrete the same quantity and quality of allelochemicals or have similar allelopathic effects (Hagan *et al.*, 2013; Imatomi *et al.*, 2013). Whereas, the environmental factors, include both abiotic factors (irradiation, temperature, nutrient limitation, moisture, and pH) and biotic factors involving plant competition, diseases, insects, animal invasion, and receptor feedback regulation (Anaya, 1999). It has been noted that a stress environment can increase the release of allelochemicals from allelopathic plants (Albuquerque *et al.*, 2010).

In the recent past, scientific attention has also been drawn to exploit the positive significant roles of allelochemicals, in enhancing crop productivity. The remarkable scope of allelopathy towards weed and pest management, apart from nitrogen management, and synthesis of novel agrochemicals based on natural product chemistry. The use of natural products of plant or microbial origin as pesticide/herbicides has gained much attention from the scientists as they offer many advantages over synthetic chemicals.

Due to the different sensitivities of different receptors to the same allelochemical and the various allelopathic activities of different allelochemicals, it needs further study in the field of allelochemical research. On the other hand, little is known about the transportation and biodegradation of allelochemicals in soil or of allelopathic species; the establishment of practical ways of using allelochemicals in the field should be the focus of future investigations. The lichen researches have meticulously demonstrated that allelopathy has good application potential in agricultural areas in development of natural herbicide, pesticides, and crop improvement. The structure and mode of action of many allelochemicals have been deeply revealed in recent years, and this has laid a good foundation for the new studies, where lichens allelochemicals are used to obtain the basic structures or templates for developing new natural products. The studies on lichens inter/intra interactions may also play a significant role in the near future for agroforestry programs of the country.

CONCLUSION

Allelopathy has been known and used in agriculture since ancient times; however, its recognition and use in modern agriculture are very limited. Allelopathy plays an important role in investigations of appropriate farming systems, as well as, in the control of weeds, diseases and insects, the alleviation of continuous cropping problems, and allelopathic cultivar breeding. Furthermore, allelochemicals can act as environmentally friendly herbicides, fungicides, insecticides, and plant growth regulators, and can have great value in sustainable agriculture.

The *in vitro* studies highlight the possibility of lichen secondary metabolites, such as, usnic, lecanoric, stictic, fumerprotocetraric, evernic acid, and other metabolites extracted from lichens, which are multi directionally affecting plant metabolism such as, photosynthesis, respiration, transpiration, and hormonal regulation. The information may further support the recent suggestion of using lichen compounds, as herbicides and insecticides, and crop improvement will definitely open an avenue for further researches.

The lichen perspective should also be revisited with evidence of lichen allelopathy against plants, and their mycorrhizal partners have been poorly supported by recent research in natural settings that need to be more emphasized. With increasing emphasis on organic agriculture and environmental protection, the cumulative attention has been paid to allelopathy research with physiological and ecological mechanisms of allelopathy along with molecular mechanisms and nanotechnologies association. It is clear that lichen allelopathy warrants further research for widespread application in agricultural prospects worldwide in the near future.

ACKNOWLEDGEMENTS

Authors are thankful to the Director, CSIR-National Botanical Research Institute, Lucknow, for continuing support and encouragement. Rajesh Bajpai would like to thank the Council of Scientific and Industrial Research, New Delhi, for the award of the scientist pool fellowship (8909-A).

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