



Soils and the conditional allelopathic effects of a tropical invader

Rajwant Kaur^a, Ragan M. Callaway^b, Inderjit^{a,*}^a Department of Environmental Studies, Centre for Environmental Management of Degraded Ecosystems (CEMDE), University of Delhi, Delhi 110007, India^b Division of Biological Sciences and the Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA

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ABSTRACT

Allelopathy may contribute to the formation of mono-dominant stands of exotic species, but the effects of allelochemicals can be highly conditional. We explored variation in the production of phenolics in leaves, accumulation of phenolics in soils, and the inhibitory effects of soils under an aggressive invader *Prosopis juliflora* across a range of invaded sites and potential mechanisms by which soils alter the effects of *P. juliflora* leaf litter. For eight sites in Northwest India we compared the concentration of total phenolics and the seedling growth of *Brassica campestris* in soils from beneath *P. juliflora* to that in soils collected away from *P. juliflora* canopies. We then explored these effects in detail in soils from two sites that differed substantially in texture by germinating seeds of *B. campestris* in these soils amended with *P. juliflora* macerated leaf leachate. Finally, we tested the effects of L-tryptophan in soils from these two sites on the seedling growth of *B. campestris*. Across all sites soil beneath *P. juliflora* contained higher levels of total phenolics and suppressed the growth of *B. campestris* than soil that was not under *P. juliflora*. We observed much variation among *P. juliflora*-invaded sites in the total phenolic levels of soils and the degree to which they suppressed *B. campestris* and the concentration of phenolics in soils significantly correlated with the root length of *B. campestris* when grown in these soils. Soil from two sites amended with *P. juliflora* macerated leachate suppressed seedling growth of *B. campestris*, with the effect being higher in sandy soil than sandy loam soil. In soil amended with leachate the strong suppression of *B. campestris* corresponded with much higher total phenolic and L-tryptophan concentrations. However, in other tests L-tryptophan did not affect *B. campestris*. Our results indicate that the allelopathic effects of *P. juliflora* can be highly conditional and that variation in soil texture might contribute to this conditionality.

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1. Introduction

Exploring variation in the ways that plants compete with or facilitate each other has improved our understanding of the relative importance of these interactions in plant communities (Brooker et al., 2005; Baumeister and Callaway, 2006; Thorpe et al., 2011). Allelopathy can provide competitive advantages to plants, but allelopathic interactions can be influenced by a range of ecosystem processes (Inderjit et al., 2011). For example, in natural conditions the availability and functioning of allelochemicals can be influenced by abiotic variation in soil texture and ion concentrations, and by the biotic communities present in soils (Inderjit et al., 2011; Metlen et al., 2013; Uesugi and Kessler, 2013). Taking the next step to explicitly quantify variation in the field and testing potential

mechanisms may yield important insight into the conditionality of allelopathy.

Allelopathy is suspected as a mechanism that contributes to the formation of mono-dominant stands by some exotic invaders (Callaway and Ridenour, 2004; Kaur et al., 2012a; Qin et al., 2013), thus invasive species provide good opportunities to explore conditionality in allelopathy. *Prosopis juliflora* is one of the world's most aggressive invasive species and occupies a very broad range of habitats. A native of Central America, northern South America and Caribbean islands, *P. juliflora* was introduced to the Indian sub-continent in 1877 (Pasiiecznik et al., 2001; Kaur et al., 2012a). It has now invaded a wide range of environments in India and at some sites strongly suppresses species diversity (Kaur, 2013). Kaur et al. (2012a) found that leaf litter from *P. juliflora* was highly inhibitory to a suite of species native to areas of northern India that have been invaded by *P. juliflora*. Furthermore, soil under *P. juliflora* canopies has been found to have higher levels of total phenolics than soil away from canopies, or in soil under *Prosopis cineraria*, a native

* Corresponding author. Tel.: +91 11 27667689.

E-mail address: inderjitdu@gmail.com (Inderjit).

congener (Kaur et al., 2012a). Phenolics are potential allelopathic agents (Inderjit, 1996; Inderjit et al., 2002). Depending upon the qualitative nature and quantitative availability of phenolics in the soil, phenolic compounds can directly affect the growth and establishment of plant species or act indirectly by influencing soil biological and chemical characteristics (Inderjit and Dakshini, 1994; Inderjit, 1996; Dalton, 1999). The phenolic-rich soil under *P. juliflora* has been found to suppress the growth of *Bambusa arundinacea* (Inderjit et al., 2008). Allelopathy may contribute to the abundance of *P. juliflora* because the invader (i) produces a large amount of phenolic-rich litter throughout the year (Goel et al., 1989; Jha and Mohapatra, 2010; Getachew et al., 2012); (ii) this litter has strong inhibitory effects on species native to India (Kaur et al., 2012a), (iii) *P. juliflora* can maintain far higher levels of phenolics in its sub-canopy soil compared to uninvaded soil (Inderjit et al., 2008), and (iv) *P. juliflora* releases experimentally tested allelochemicals such as L-tryptophan and several phenolics from its litter (Nakano et al., 2001, 2002, 2003, 2004).

Exotic plants invade a variety of habitats with significant variation in soil microorganisms, consumers, competition and soil chemistry, all of which influence the expression of allelopathy (Inderjit et al., 2011) and which might create substantial conditionality in allelopathic effects in nature. Soil texture has the potential to influence the availability of phenolic compounds because the carboxylic group of phenolics are often sorbed onto soil particles and organic matter. Inderjit and Bhowmik (2004) found that benzoic acid was sorbed in higher amounts onto soil with higher values of clay content, Ca²⁺ and organic matter than soil with relatively lower values. The adsorbed concentration of chemicals may have a positive relationship with concentrations in solution (Inderjit and Bhowmik, 2004). Soil microorganisms can also use phenolic compounds as carbon sources. Addition of labile carbon through plant leachates and litter causes microbial nutrient immobilization (for example, temporary nitrogen deficits) which may influence the allelopathic effects of phenolic compounds (Schmidt and Ley, 1999; Inderjit, 2001). Hydrocinnamic acid, for example, suppresses the growth of little bluestem grass (*Schizachyrium scoparium*) under low nitrogen conditions (Williamson et al., 1992). Inderjit and Weiner (2001) suggested that allelopathic activities of plant chemicals are greatly influenced by soil nutrient concentrations. We hypothesize that accumulation of phenolic compounds in soil at phytotoxic levels is influenced by physical, biological and or chemical characteristics of soil and their impact on plant growth could either be direct interference with the growth of plant seedlings or through altering soil characteristics particularly microbial activity and nitrogen, thus making allelopathy conditional. Thus, we explored conditionality in the allelopathic effects of *P. juliflora* by focussing on the following questions: 1) does the accumulation of phenolics and inhibitory effects of soils beneath *P. juliflora* vary among sites? 2) Does the concentration of phenolics in the leaves of *P. juliflora* vary among sites? 3) Do the inhibitory effects of *P. juliflora* litter vary between different soils? 4) Do specific soil characteristics correspond with variation in the effects of *P. juliflora* litter? 5) Do the levels of total phenolics or L-tryptophan, an allelochemical previously reported from *P. juliflora*, vary in soils treated with *P. juliflora* litter? and 6) Does L-tryptophan reduce target plant growth?

2. Materials and methods

2.1. Variation among sites

We hypothesized that soil legacy effects in terms of impact on plant growth are influenced by soil-mediated variation in the allelochemical pool. We collected soil beneath *P. juliflora* canopies

and soil from nearby open areas not invaded by *P. juliflora*. We chose eight sites spread over a ~2000 km area in the States of Delhi, Punjab, Rajasthan, Gujarat and Haryana. A detailed description of the geographic coordinates and description of the sites are in Table 1. In Delhi, the study area was part of open native scrub forest that had been heavily invaded by *P. juliflora*. The open area without *P. juliflora* was characterized by sparsely scattered native tree species including *Albizia lebbbeck*, and *Balanites roxburghii*, shrub species including *Grewia* sp., *Capparis sepiaria*, *Capparis decidua* and *Zizyphus nummularia*, and grasses including *Cenchrus ciliaris*, *Chrysopogon fulvus* and *Heteropogon* sp. (see Kaur et al., 2012a). In Punjab, a semiarid zone with a subtropical climate, the site was located outside Moti Bagh Beed Deer Park, Patiala where *P. juliflora* formed pure stands with a closed canopy. The open area sampled was ~500 m away from the *P. juliflora* stand and was grassland dominated by *Cynodon dactylon*, *Vernonia* sp., and *Sida* sp. In Rajasthan, we selected two sites, Rajasthan 1 and 2, which were located 3 km apart. In Rajasthan 1 and Rajasthan 2, *P. juliflora* occurred on the edges of agricultural fields. Open areas were ploughed agricultural fields situated 200 m away from the *P. juliflora* stands. These fields were previously cultivated with *Brassica campestris*. In Gujarat, two sites were located along roadsides, which were 3 km apart. Open areas were located outside of the *P. juliflora* thickets in adjacent ploughed agricultural fields. In Haryana, two sites, Haryana 1 and Haryana 2 were located along the roadsides within a stretch of 500 m. The open area was native grassland with a few scattered tree and shrub species including *Acacia senegal*, *Ehretia laevis*, *Grewia* sp., *C. decidua*, *C. sepiaria*, *Carissa spinarum* and *Murraya paniculata*.

Six trees of *P. juliflora* were sampled at each site. Soil was collected below *P. juliflora* canopies within 1 m of the trunk at a depth of 0–30 cm. Field-collected soil was sieved to remove stones and roots and then used to fill pots. For each of the eight sites, soil collected from each of the open samples ($n = 6$) or below the *P. juliflora* canopy ($n = 6$) was placed in six 70 mL pots, for a total of 72 pots per site. In each pot, 10 seeds of *B. campestris*, a common crop species in northwest India, were sown. Pots were irrigated with 5–15 mL distilled water per day and seedlings were harvested seven days after seed sowing and their root length was measured. The impact of ecosystem processes (microbial degradation and metal oxidation) on the availability and fate of allelochemicals generally occur at very small scale, seconds to hours (Inderjit et al., 2011). We measured root length which is more sensitive to allelochemicals than shoot length, and therefore is a preferred bioassay parameter in allelopathy bioassays (Inderjit and Nilsen, 2003; Bertin et al., 2007; Heidarzade et al., 2012).

Soil texture was determined by using the Bouyoucos hydrometer method (Bouyoucos, 1962) at the Soil Testing Laboratory, Division of Soil Science and Agricultural Chemistry, Indian Agricultural Research Institute, New Delhi. Soil taxonomy was determined by using soil taxonomic information at various sites from soil resource maps available at National Bureau of Soil Science & Land use planning, ICAR, New Delhi.

Five grams of soil that had been collected from underneath *P. juliflora* canopies and from open areas from each of the sites were soaked in 25 mL distilled water to quantify total phenolics using Folin Ciocalteu's reagent, which is used to quantify the variation in the concentration of phenolics (Box, 1983). We also determined the total phenolic content of macerated leachate of *P. juliflora* leaves collected from our field sites with the exception of Rajasthan 1 and Haryana 1. We soaked 200 mg *P. juliflora* leaves in 10 mL water for 6 h followed by filtration through Whatman # 42 filter paper. Total phenolic concentrations of the leaf leachate were determined as described above.

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