Botanical Sciences 101 (2): 493-503. 2023
DOI: 10.17129/botsci.3188

Received: May 20, 2022, Accepted: October 24, 2022
On line first: February 14, 2023

Systematics / Sistemática

Preliminary report on the allelopathic potential of South American *Imperata* species (Poaceae: Andropogoneae)

Estudio preliminar sobre el potencial alelopático de las especies sudamericanas de *Imperata* (Poaceae: Andropogoneae)

Fernando Moro Cordobés[1]*, Ana M. Anton[1] and Lidia Raquel Scrivanti[1,2]

[1] CONICET-Universidad Nacional de Córdoba, Instituto Multidisciplinario de Biología Vegetal, Sistemática y Filogeografía de Plantas, Córdoba, Argentina.
[2] Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Córdoba, Argentina.
*Author for correspondence: fernandomorocordobes@gmail.com

Abstract

Background: A significant number of species of grasses (Poaceae) have allelopathic properties and two genera of Andropogoneae -*Cymbopogon* and *Bothriochloa*- are the main aromatic genera recognized in the family. The genus *Imperata* (Poaceae: Andropogoneae) is widely distributed, with several species being present around the world.

Questions and / or Hypotheses: This study assessed the allelopathic potential of some South American species of *Imperata* taking into account previous reports on *I. cylindrica*, which has been extensively studied due to its invasiveness and allelopathic potential.

Studied species / data description /Mathematical model: *I. brasiliensis*, *I. condensata*, *I. minutiflora*, and *I. tenuis*

Study site and dates: Greenhouse of the Instituto Multidisciplinario de Biología Vegetal, Sistemática y Filogeografía de Plantas, Córdoba, Argentina.

Methods: We obtain the aqueous extract from the studied species and we evaluated its effect on germination and root and shoot growth of lettuce, corn, and tomato.

Results: In bioassays, aqueous leaf extract of *I. brasiliensis*, *I. condensata*, *I. minutiflora*, and *I. tenuis* inhibited seed germination and root and shoot growth of lettuce (*Lactuca sativa*), tomato (*Solanum lycopersicum*), and maize (*Zea mays*). The extracts mainly affected root and shoot length, whereas the effect on seed germination was low.

Conclusions: The studied species may contain allelochemicals, which interfere with seed germination and seedling growth. Future research on the type of chemical compounds present in aqueous extracts may contribute to their use for agroecological purposes.

Key words: Allelopathy, aqueous extract, *Imperata*, seed germination, seedling growth.

Resumen

Antecedentes: Un número importante de especies de gramíneas (Poaceae) tienen propiedades alelopáticas y dos géneros de Andropogoneae -*Cymbopogon* y *Bothriochloa*- son los principales géneros aromáticos reconocidos en la familia. El género *Imperata* (Poaceae: Andropogoneae) está ampliamente distribuido con varias especies presentes en todo el mundo.

Preguntas y / o Hipótesis: En este estudio se evaluó el potencial alelopático de algunas especies sudamericanas de *Imperata* teniendo en cuenta los estudios realizados sobre *I. cylindrica*, la cual ha sido ampliamente estudiada debido a su cualidad de invasora y su potencial alelopático.

Especies de estudio / Descripción de datos / Modelo matemático: *I. brasiliensis*, *I. condensata*, *I. minutiflora* y *I. tenuis*.

Métodos: Obtuvimos el extracto acuoso de las especies estudiadas y evaluamos su efecto sobre la germinación y el crecimiento de raíces y brotes de lechuga, maíz y tomate.

Resultados: En los bioensayos, los extractos acuosos de las hojas de *I. brasiliensis*, *I. condensata*, *I. minutiflora* e *I. tenuis* inhibieron la germinación de las semillas y el crecimiento de las raíces y los brotes de la lechuga (*Lactuca sativa*), el tomate (*Solanum lycopersicum*) y el maíz (*Zea mays*). Los extractos afectaron principalmente a la longitud de las raíces y los brotes, mientras que el efecto sobre la germinación de las semillas fue débil.

Sitio y años de estudio: Invernadero del Instituto Multidisciplinario de Biología Vegetal, Sistemática y Filogeografía de Plantas, Córdoba, Argentina.

Conclusiones: Las especies estudiadas pueden contener aleloquímicos que interfieren en la germinación de las semillas y en el crecimiento de las plántulas. Futuras investigaciones sobre el tipo de compuestos químicos presentes en los extractos acuosos pueden contribuir a su uso con fines agroecológicos.

Palabras clave: Alelopatía, crecimiento de plántulas, extracto acuoso, *Imperata*, germinación de semillas.

Allelopathy can be studied from an ecological or applied approach. Allelopathy is considered a significant ecological factor in determining the structure, composition and dynamics of plant communities (Muller 1966, Ballester & Vieitez 1978, Rice 1984, Wardle *et al*. 1998, Inderjit & Duke 2003). One of the applied uses of allelopathy focuses on the interactions of cultivated species with another crop or weed, and the search of new bioactive compounds with herbicidal potential or as plant growth regulators (Reigosa *et al.* 2013, da Silva *et al*. 2017). There is great interest in the biological control of pests through the application of allelochemical compounds (Narwal 2010, Cheng & Cheng 2015, Jabran *et al*. 2015, Macías *et al*. 2019), because allelopathic compounds are considered safe and beneficial for the environment and human health (El-Kenany & El-Darier 2013). In addition, the selective pressure generated by the massive use of herbicides has led to the development of resistance in a large number of weeds (Cheng & Cheng 2015, Al-Samarai *et al.* 2018). Thus, there is a need to constantly search for new herbicidal compounds to avoid the resistance mechanisms of weeds (Gaines *et al*. 2020).

The family Poaceae has a significant number of species with allelopathic properties (Chou & Young 1975, Rietveld 1977, Bokhari 1978, Hussain *et al*. 1982, Li *et al*. 2005), with *Cymbopogon* Spreng. and *Bothriochloa* Kuntze (Poaceae: Andropogoneae) being the main aromatic genera known to date (Hussain *et al*. 1982, Kaul & Vats 1998, Scrivanti *et al*. 2009, 2011, Scrivanti 2010, Scrivanti & Anton 2019). The genus *Imperata* Cirillo (Poaceae: Andropogoneae) includes nine species distributed in tropical, subtropical, and temperate regions of both hemispheres (Gabel 1982). *Imperata cylindrica* has been widely studied for its invasive behavior and was reported as one of most damaging weeds, reducing biodiversity and causing losses in production of various crops globally (Jose *et al.* 2002, MacDonald 2004, Collins *et al.* 2007, Global Invasive Species Database 2021). Early in vitro and field studies demonstrated that aqueous extract of *I. cylindrica* inhibits the growth of some plants in vitro and on soil through leaching from rainfall and irrigation in field experiments. (Abdul-Wahab & Al Naib 1972, Eussen & Wirjahardja 1973, Eussen 1979, Eussen & Niemann 1981, Inderjit & Dakshini 1991). More recent studies have confirmed the presence of allelochemicals in rhizomes and aerial parts of *I. cylindrica*, and some authors have suggested their possible contribution to its invasion success (Inderjit & Dakshini 1991, Koger *et al*. 2004, Xuan *et al*. 2009, Cerdeira *et al*. 2012, Hagan *et al*. 2013, Suzuki *et al*. 2018). The production of allelochemicals by *I. cylindrica* has also been investigated in search of an alternative strategy to traditional herbicides for weed control. Aqueous extracts of *I. cylindrica* have shown an inhibitory effect on germination and development in different weed species, such as *Cynodon dactylon* (L.) Pers. and *Lolium multiflorum* Lam. (Koger *et al*. 2004), *Parthenium hysterophorus* L. (Anjum *et al*. 2016), and *Amaranthus spinosus* L. (Erida *et al*. 2019). Of the rest of *Imperata* species (*I. brasiliensis* Trin., *I. brevifolia* Vasey., *I. condensata* Steud., *I. conferta* (J. Presl) Ohwi, *I. cheesemanii* Hack., *I. contracta* (Humb. Bonpl. & Kunth) Hitchc., *I. minutiflora* Hack. and *I. tenuis* Hack.) allelopathic activity has only been demonstrated on *I. brasiliensis* Trin. as the aqueous extract of the whole plant inhibited germination and stem growth of *Oryza sativa* L. (Casini *et al*. 1998).

Most allelopathic or allelochemical compounds are intermediate molecules or products of secondary metabolism (Lotina-Hennsen *et al*. 2006). Evidence exists that ancestral members of a clade evolved the biosynthetic capacity to produce a similar secondary metabolite and bioactive properties (Wink 2003, Chon & Nelson 2010, Imatomi *et al*. 2013, Liu *et al*. 2017).

Considering the allelochemical biosynthesis pathway can be shared by all or some species of a plant genus, the species of *Imperata* may synthesize compounds with allelopathic activity like *I. cylindrica*.

Hence, this paper aims to carry out a first approach to the presence of allelopathic compounds in the South American species of *Imperata*. For this purpose, we tested the effect of leaf aqueous extract of *I. brasiliensis*, *I. condensata*, *I. minutiflora*, and *I. tenuis* on seed germination and early seedling growth of *Lactuca sativa*, *Zea mays*, and *Solanum Lycopersicum*. with rapid germination and high sensitivity.

Material and Methods

Plant material. Four *Imperata* species were studied: *I. brasiliensis, I. condensata, I. minutiflora*, and *I. tenuis*. Plants were collected from Argentina and Brazil (Table 1). Voucher specimens are deposited in the Museo Botánico de

Córdoba (CORD) herbarium. Plants were cultivated using pots in a greenhouse; fresh mature expanded leaves were collected to obtain aqueous extract. Seeds of three tested species –lettuce (*Lactuca sativa*), maize (*Zea mays*), and tomato (*Solanum lycopersicum*) were used for germination and seedling growth assays. Tested species selected are used as evaluation models due to their rapid germination and high sensitivity. *Lactuca sativa* is the most widely used in allelopathy bioassays (Carvalho *et al*. 2019, Tigre *et al*. 2012, Wang *et al*. 2016). The inhibitory or stimulatory effect on shoot and root growth and germination is considered an indirect measure of how allelochemicals affect other internal physiological processes in the plant (Macías *et al*. 2019).

Table 1. *Imperata* specimens collected from field and used in bioassays.

***Imperata* species**	**Collection number (CORD)**	**Location**	**Coordinates**
I. brasiliensis	Scrivanti 564	Formosa, Clorinda, Argentina	25° 36’ 6.761” S 57° 54’ 26.3” W
I. condensata	Scrivanti 566	San Luis, Villa Mercedes, Argentina	33° 36’ 43.1” S 65° 34’ 46.5” W
I. minutiflora	Scrivanti 568	Jujuy, San Salvador de Jujuy, Argentina	24° 9’ 43.72” S 65° 23’ 16.77” W
I. tenuis	Scrivanti 561	RGS, Dom Pedrito, Brazil	30° 52’ 45” S 54° 53’ 26” W

Aqueous extracts. In order to obtain the aqueous extracts, we used a method adapted from the one described by Scrivanti (Scrivanti 2010, Scrivanti *et al*. 2011, Scrivanti & Anton 2019, 2021). Five grams of fresh leaf blades from each *Imperata* plant were crushed with a blender. Each sample was placed in a tube containing 50 mL of deionized water. The mixture was kept in a refrigerator for 24 h; then it was stirred in a rotary shaker for 1 h and centrifuged at 1500 revolutions min^{-1} for 15 min. The supernatant was recovered and filtered using filter paper. This process was performed in duplicate to remove as much of the undesirable residue from the extract as possible. The supernatant was recovered and stored in a refrigerator until being used as a crude water-soluble extract (100%). Other test solutions (75, 50 and 25% v/v) were prepared by diluting stock solution with sterile distilled water. The extracts were stored at 4ºC.

Bioassay. To evaluate the allelopathic effects of aqueous leaf extracts, seeds of lettuce, maize, and tomato (25 seeds each) were placed in respective Petri dishes containing two layers of filter paper moistened with 5 mL of aqueous extracts. The control Petri dishes received 5 mL deionized water. The Petri dishes were kept in the greenhouse under homogeneous conditions of light (12 h) and mean temperature of 25°C during seed germination and seedling growth for three (Lettuce), four (Maize), and five (Tomato) days. The treatments were replicated five times in a completely randomized design, so we used fifty seeds per treatment. Tests were previously conducted to establish incubation times using seeds of the tested plants and distilled water; this procedure allowed us to determine the germination time and seedling growth period of each crop. After incubation, germinated seeds were counted and length of shoot and root was measured using ruler; measurement was taken in 10 randomly selected seedlings per treatment.

Percentage of inhibition of germination was calculated as follows (Scrivanti 2010, Scrivanti *et al*. 2011, Scrivanti & Anton 2019):

$$I(\%) = \left[1 - \left(\frac{G}{C}\right)\right] \times 100$$

Were, I: percentage of inhibition; G: average germination percentage in the treatment; C: average germination percentage in the control.

Germination percentages were analyzed using a Chi-square (χ^2) test to determine the existence of differences between treatments and control at a probability level of 0.05, using the R software (R Core Team 2022).

Percentage of shoot and root growth reduction was calculated as follows (Scrivanti 2010, Scrivanti *et al*. 2011, Scrivanti & Anton 2019):

$$I(\%) = \left[1 - \left(\frac{L}{C}\right)\right] \times 100$$

Where, I: percentage of inhibition; T: mean root or shoot length (mm) in the treatment; C: mean root or shoot length (mm) in the control.

Data from inhibition (%) of root and shoot length growth were subjected to an analysis of variance (ANOVA) followed by a posteriori test of multiple comparisons based on the false discovery rate (Benjamini & Hochberg 1995) to determine the existence of differences of the treatments with respect to the control and between treatments, at a probability level of 0.05, using the R software (R Core Team 2022).

Table 2. Mean inhibitory effects of aqueous leaf extracts of *Imperata* species on germination of lettuce, tomato, and maize. A statistically significant value denotes inhibition over control (* $P \leq 0.05$).

Imperata species	**Aqueous extract concentration**	**Test species**		
		Inhibition (%) over control		
		Lettuce	**Tomato**	**Maize**
I. brasiliensis	25 %	-9.2	26.9*	-3.3
	50 %	7.8	48.7*	-1.1
	75 %	7.8	47.4*	6.7
	100 %	18.4*	80.7*	8.9
I. condensata	25 %	6.5	0	6.7
	50 %	7.8	-1.2	-3.3
	75 %	14.4	10.2	-2.2
	100 %	31.5*	21.7*	3.3
I. minutiflora	25 %	5.2	1.2	-25
	50 %	-6.5	5.1	-18.4
	75 %	2.6	2.5	-27.6
	100 %	28.9*	2.5	-18.4
I. tenuis	25 %	-7.8	30.7*	-9.2
	50 %	1.3	51.2*	6.7
	75 %	6.5	56.4*	10.1
	100 %	26.3*	66.6*	5.6

Table 3. Mean inhibitory effects of aqueous leaf extracts of *Imperata* species on root and shoot growth of lettuce, tomato, and maize. A statistically significant value denotes inhibition over control (* $P \leq 0.05$). Different letters indicate significant differences among treatments within each test plant ($P \leq 0.05$).

Imperata species	Aqueous extract concentration	Test species: Inhibition (%) over control					
		Root lenght			Shoot lenght		
		Lettuce	Tomato	Maize	Lettuce	Tomato	Maize
I. brasiliensis	25%	3.8a	22.8a*	6.8a	-7.8a	-21.2a	9a
	50%	16b*	43.2b*	5.2a	-3.5ab	1.2ab	6.3a
	75%	22.6bc*	38.2b*	7.3a	7.1bc	7.2bc	10.7a
	100%	28.2c*	58.4b*	14.6a	19.1c*	40.5c*	22.3a*
I. condensata	25%	22.5a*	39.1a*	0.6a	-3.9a	-7.3a	14.1a*
	50%	26.4b*	32.5a*	2.3a	-2.3ab	3.6ab	11.5a
	75%	34.4c*	41.7a*	8.8a	7.1b	11.9ab	21.2ab*
	100%	33bc*	54.4b*	26.4b*	2.9a	19.2b	32.4b*
I. minutiflora	25%	6.9a	-5.1a	12.4a	-9.6ab	-66.5a*	18.1a*
	50%	7a	-9.7a	13.3a	-13.8b	-80.4a*	19.4a*
	75%	21.1b*	8.5ab	8.4a	0.4ac	-55a*	18.6a*
	100%	22.1b*	14.1b*	0.2a	5.4c	-49.6a*	18.9a*
I. tenuis	25%	19.1a*	43.6a*	19.8a*	8.5a	10.4a	20.2a*
	50%	19.1a*	54.6ab*	12.3a	-0.8b	27.3ab*	5.4a
	75%	37.7b*	63.8b*	9.4a	17.6c*	35.8b*	9.4a
	100%	41.6b*	66.6b*	23.3a*	20c*	47.9b*	18.4a*

Results

Seed germination. Aqueous leaf extract of *I. brasiliensis* and *I. tenuis* reduced germination of tomato at all tested concentrations (25, 50, 75, and 100 %) as compared to the control (Figure 1 and Table 2). Aqueous leaf extract of *I. minutiflora* reduced germination of lettuce at the highest (100 %) concentration (Figure 1 and Table 2). Aqueous leaf extract of *I. brasiliensis*, *I. condensata*, *I. minutiflora*, and *I. tenuis* reduced germination of lettuce at the highest (100 %) concentration as compared to the control (Figure 1 and Table 2). None of the aqueous extracts tested reduced germination of maize with respect to control.

Root and Shoot growth. Aqueous leaf extract of *I. brasiliensis* inhibited the growth of lettuce and tomato root at 50, 75, and 100 %, and at all concentrations, respectively, as compared to the control (Figure 2 and Table 3). The inhibition percentage was statistically different between 50 and 100 % concentrations for lettuce and between 25 % and the remaining concentrations for tomato (Figure 2 and Table 3). The aqueous leaf extract of *I. brasiliensis* did not produce a statistically significant reduction in the growth of the maize root as compared to the control at any concentration (Figure 2 and Table 3). Regarding shoot growth, the aqueous extract of *I. brasiliensis* inhibited the growth of all the test plants as compared to the control only at the highest concentration (100 %) (Figure 2 and Table 3).

Aqueous leaf extract of *I. condensata* inhibited the growth of lettuce and tomato root at all concentrations with respect to control, and maize root only at the highest concentration (Figure 2 and Table 3). The inhibition percentage was statistically different between 25 % and the remaining concentrations for lettuce, and between 100 % and the remaining concentrations for tomato (Figure 2 and Table 3). Regarding shoot growth, the aqueous extract of *I. condensata* inhibited maize growth at all concentrations compared to the control, with inhibition percentage being statistically different between 25-50 % and 100 % (Figure 2 and Table 3). The aqueous extract of *I. condensata* did not inhibit shoot growth of either lettuce or tomato (Figure 2 and Table 3).

Aqueous extract of *I. minutiflora* inhibited root growth of lettuce (at 75 and 100 %) and tomato (at 100 %) as compared to the control (Figure 2 and Table 3). The inhibition percentage was not statistically different between 75 and 100 % concentrations for lettuce (Figure 2 and Table 3). Regarding shoot growth, the aqueous extract of *I. minutiflora* inhibited the growth of maize at all concentrations as compared to the control, with no statistical differences among concentrations (Figure 2 and Table 3). Aqueous extract of *I. minutiflora* stimulated the growth of tomato shoot at all concentrations as compared to the control, with no statistical differences in inhibition percentage among concentrations (Figure 2 and Table 3).

The aqueous leaf extract of *I. tenuis* inhibited root growth of lettuce and tomato as compared to the control at all concentrations, and of maize at 25 and 100 % (Figure 2 and Table 3). The inhibition percentage was statistically different between 25-50 and 75-100 % concentrations for lettuce, and between 25 and 75-100 % concentrations for tomato (Figure 2 and Table 3). The inhibition percentage was not statistically different between the concentrations tested for maize (Figure 2 and Table 3). Regarding shoot growth, the aqueous extract of *I. tenuis* inhibited the growth of lettuce at 75 and 100 % concentrations, of tomato at 50, 75, and 100 %, and of maize at 25 and 100 %, with no statistical differences in inhibition percentage among concentrations (Figure 2 and Table 3).

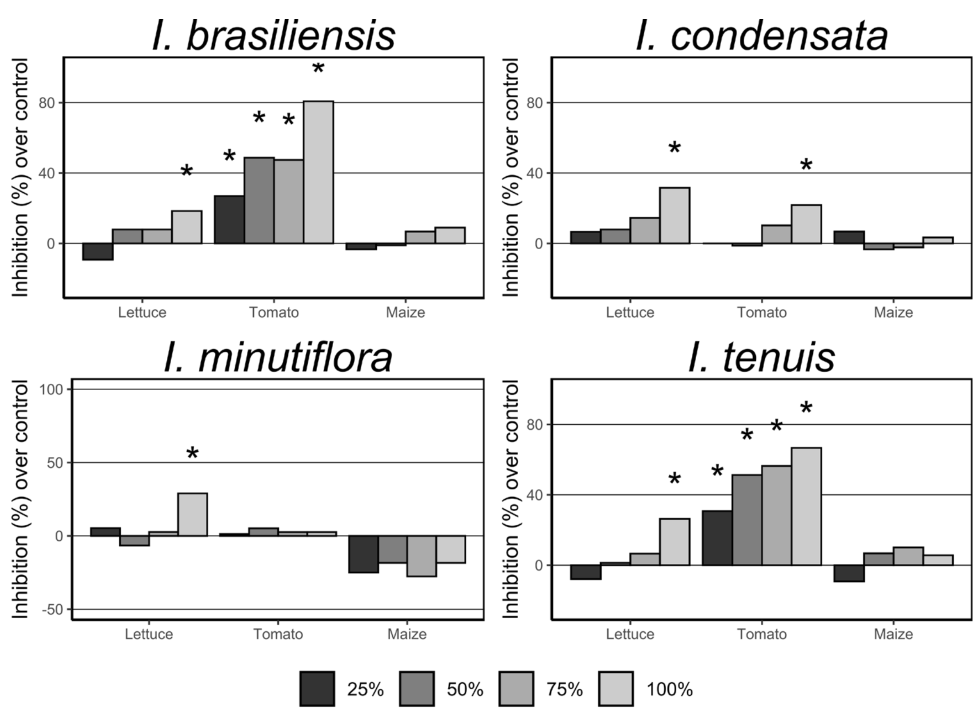

Figure 1. Mean inhibitory effects of aqueous leaf extracts of *Imperata* species on germination of lettuce, tomato, and maize. Symbol above the bars indicates values significantly less than the respective control ($P \leq 0.05$).

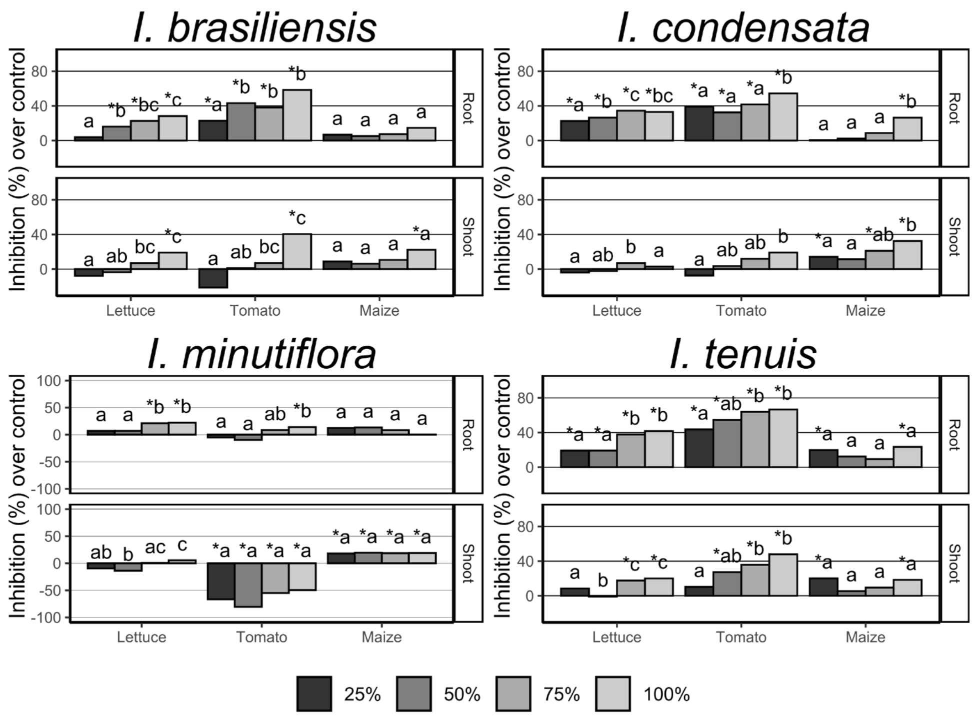

Figure 2. Mean inhibitory effects of aqueous leaf extracts of *Imperata* species on root and shoot growth of lettuce, tomato, and maize. Symbol above the bars indicates values significantly less than the respective control ($P \leq 0.05$). Different letters indicate significant differences among treatments within each test plant ($P \leq 0.05$).

Discussion

Bioassays are an initial and essential stage to determine allelopathic activity in plants. In this sense, in this work, the aqueous leaf extracts of South American *Imperata* taxa showed allelopathic effects on seed germination and seedling growth of maize, lettuce, and tomato. An interesting future approach would be the use of non-allelopathic plants as controls to verify that the procedures and methodologies are not creating artifacts. In general, the inhibitory effects of aqueous extracts of *Imperata* species were greater on root and shoot growth than on germination of the tested plants. The results obtained with aqueous extract of *I. brasiliensis* reinforce previous findings by Casini *et al*. (1998). The aqueous extract of *I. tenuis* exhibited the highest inhibitory activity on the tested plants, followed by the aqueous extracts of *I. brasiliensis*, *I. condensata*, and *I. minutiflora*. The concentration of the crude extract (100 %) is probably not found in nature, however using the crude extract allows us to make sure that if these plants produce allelopathic compounds we could detect some effect and also test a possible application as a herbicide. An interesting result is the growth stimulation of the shoot of tomato by the aqueous extract of *I. minutiflora*. The fact that allelopathic substances can produce inhibitory and stimulatory effects has already been reported and is currently being investigated for their agronomic use (Abbas *et al*. 2017). In general, the effects of the different concentrations did not differ in each treatment. However, when there were differences between the effects at the different concentrations, the degree of inhibition increased with the increasing extract concentration.

Studies on the production and release of allelopathic compounds by *I. cylindrica* have covered both the ecological and the agronomic aspects. Phenolic compounds and aldehydes were identified in the aqueous leaf extracts of *I. cylindrica* as responsible for the allelopathic activity, such as p- and o-coumaric acid, gentisic acid, vanillic acid, p-hydroxybenzoic acid, scopolin, scopoletin, chlorogenic, and isochlorogenic acid, vanillin and p-hydroxy-benzaldehyde (Abdul-Wahab & Al Naib 1972, Eussen & Wirjahardja 1973, Eussen 1979, Eussen & Niemann 1981). Inderjit

& Dakshini (1991) found that the phenolic fraction of the aqueous extracts of *I. cylindrica* was responsible for the phytotoxic activity and that the release of the compounds to the ground could be selective. Hussain & Abidi (1991) identified caffeic, p-coumaric, p-hydroxybenzoic, syringic, chlorogenic, and vanillic acids as responsible for the allelopathic effects generated by aqueous extracts and rain leachates. In addition, a great variety of chemical compounds with allelopathic activity have been found in aqueous root and rhizome extracts of *I. cylindrica*, including gallic acid, iso-Eugenol, ferulic acid, caffeic acid, 4-acetyl-2-methoxy phenol, 5-methoxy flavone, and 5,2'-dimethoxyflavone (Xuan *et al.* 2009, Hagan *et al.* 2013, Suzuki *et al.* 2018). The mixture of phenolic acids is the factor that contributes to the allelopathic effect, since each acid separately has a weak effect (Blum *et al.* 1985). Phenolic compounds can cause this inhibition through different mechanisms that affect vital physiological processes for plants such as nutrient absorption, cell elongation, photosynthesis, and respiration (Li *et al.* 2010). The biosynthetic pathways of phenolic compounds have been traced by natural selection throughout evolution between specific plant lineages, especially when these compounds perform specific advantageous functions (Li *et al*. 2010). Although the chemical composition of the aqueous extracts of South American taxa has not been studied, the phytotoxic activity observed in this work is likely due to the phenolic fraction, as has been demonstrated in *I. cylindrica*. Furthermore, the results showed differences in the effects on germination and seedling growth. Allelochemical composition and allelopathic effect are influenced by the historical biogeography of the species (Irimia *et al*. 2019). Considering that South American species of *Imperata* and *I. cylindrica* have different evolutionary histories (Cordobés *et al*. 2021), the observed differences in the effect of aqueous extracts could reflect the production of different compounds by each taxon. The results also show that the compounds produced by these plants may potentially be used as natural herbicides.

The results obtained are promising and provide the basis for future studies on the role of the production of allelopathic compounds in the South American *Imperata* taxa analyzed. The results also show that the compounds produced by these plants may potentially be used as natural herbicides. The characterization of the allelochemicals and their release and movement under field conditions are important guidelines for future research in the ecology of *Imperata* and potential agroecological uses.

Acknowledgements

This work was supported by grants from Agencia Nacional de Promoción Científica y Tecnológica (FONCYT) [PICT2014-1095]; Universidad Nacional de Córdoba (FCEFyN - SECyT - UNC) [Res. 266/18].

Literature cited

Abbas T, Nadeem MA, Tanveer A, Chauhan, BS. 2017. Can hormesis of plant-released phytotoxins be used to boost and sustain crop production? *Crop Protection* 93: 69-76. DOI: https://doi.org/10.1016/j.cropro.2016.11.020

Abdul-Wahab AS, Al Naib FAG. 1972. Inhibitional effects of *Imperata cylindrica* (L.) P.B. *Baghdad Univ Iraq Natur Hist Mus Bull* 5: 17-24

Al-Samarai GF, Mahdi WM, Al-Hilali BM. 2018. Reducing environmental pollution by chemical herbicides using natural plant derivatives- allelopathy effect. *Annals of Agricultural and Environmental Medicine* 25: 449-452. DOI: https://doi.org/10.26444/aaem/90888

Anjum T. Bajwa R, Javaid A. 2016. Biological control of *Parthenium* I: *effect* of *Imperata cylindrica* on distribution, germination and seedling growth of *Parthenium hysterophorus* L. *International Journal of Agriculture and Biology* 7: 448-450.

Ballester A, Vieitez AM. 1978. Estudio de potenciales alelopáticos en comunidades vegetales. *Anales Instituto Botánico Cavanilles* 34: 713-722.

Benjamini Y, Hochberg Y. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society* 57: 289-300. DOI: https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Blum U, Dalton BR, Shann JR. 1985. Effects of ferulic and p-coumaric acids in nutrient culture of cucumber leaf expansion as influenced by pH. *Journal of Chemical Ecology* 11: 1567-1582. DOI: https://doi.org/10.1007/BF01012202

Bokhari UG. 1978. Allelopathy among prairie grasses and its possible ecological significance. *Annals of Botany* 42: 127-136. DOI: https://doi.org/10.1093/oxfordjournals.aob.a085432

Carvalho MSS, Andrade-Vieira LF, dos Santos FE, Correa FF, Cardoso MdG, Vilela LR. 2019. Allelopathic potential and phytochemical screening of ethanolic extracts from five species of *Amaranthus* spp. in the plant model *Lactuca sativa*. *Scientia Horticulturae* 245: 90-98. DOI: https://doi.org/10.1016/j.scienta.2018.10.001

Casini P, Vecchio V, Tamantini I. 1998. Allelopathic interference of itchgrass and cogongrass: Germination and early development of rice. *Tropical Agriculture* 75: 445-451.

Cerdeira AL, Cantrell CL, Dayan FE, Byrd JD, Duke SO. 2012. Tabanone, a New Phytotoxic Constituent of Cogongrass (*Imperata cylindrica*). *Weed Science* 60: 212-218. DOI: https://doi.org/10.1614/WS-D-11-00160.1

Cheng F, Cheng Z. 2015. Research Progress on the use of Plant Allelopathy in Agriculture and the Physiological and Ecological Mechanisms of Allelopathy. *Frontiers in Plant Science* 6: 1020. DOI: https://doi.org/10.3389/fpls.2015.01020

Chon SU, Nelson CJ. 2010. Allelopathy in compositae plants. A review. *Agronomy for Sustainable Development* 30: 349-358. DOI: https://doi.org/10.1051/agro/2009027

Chou CH, Young CC. 1975. Phytotoxic substances in twelve subtropical grasses. *Journal of Chemical Ecology* ***1***: 183-193. DOI: https://doi.org/10.1007/BF00987867

Collins AR, Jose S, Daneshgar P, Ramsey CL. 2007. Elton's hypothesis revisited: An experimental test using cogongrass. *Biological Invasions* 9: 433-443. DOI: https://doi.org/10.1007/s10530-006-9050-4

Cordobés FM, Robbiati FO, Anton AM, Scrivanti LR. 2021. Phylogeny, evolution and ecological speciation analyses of *Imperata* (Poaceae: Andropogoneae) in the Neotropics. *Systematics and Biodiversity* 19: 526-543. DOI: https://doi.org/10.1080/14772000.2021.1887959

da Silva ER, Overbeck GE, Soares GLG. 2017. Something old, something new in allelopathy review: what grassland ecosystems tell us. *Chemoecology* 27: 217-231. DOI: https://doi.org/10.1007/s00049-017-0249-x

El-Kenany ET, El-Darier SM. 2013. Suppression effects of *Lantana camara* L. aqueous extracts on germination efficiency of *Phalaris minor* Retz. and *Sorghum bicolor* L. (Moench). *Journal of Taibah University for Science* 7: 64-71. DOI: https://doi.org/10.1016/j.jtusci.2013.04.004

Erida G, Saidi N, Hasanuddin, Syafruddin. 2019. Allelopathic Screening of Several Weed Species as Potential Bioherbicides. *IOP Conference Series: Earth and Environmental Science* 334. DOI: https://doi.org/10.1088/1755-1315/334/1/012034

Eussen JHH. 1979. Some competition experiments with alang-alang (*Imperata cylindrica* (L.) Beauv.) in replacement series. *Oecologia* 40: 351 356. DOI: https://doi.org/10.1007/BF00345330

Eussen, Jacques HH, Niemann GJ. 1981. Growth Inhibiting Substances from Leaves of *Imperata cylindrica* (L.) Beauv. *Zeitschrift Für Pflanzenphysiologie* 102: 263-266. DOI: https://doi.org/10.1016/S0044-328X(81)80229-2

Eussen JHH, Wirjahardja S. 1973. *Studies of an alang-alang (Imperata cylindrica (L.) Beauv.) vegetation*. Bogor, Indonesia: Regional Center for Tropical Biology Bogor.

Gabel ML. 1982. *A biosystematic study of the genus Imperata (Gramineae: Andropogoneae)*. PhD Thesis. Iowa State University. DOI: https://doi.org/10.31274/rtd-180813-5836

Gaines TA, Duke SO, Morran S, Rigon CAG, Tranel PJ, Anita Küpper, Dayan FE. 2020. Mechanisms of evolved herbicide resistance. *Journal of Biological Chemistry* 295: 10307-10330. DOI: https://doi.org/10.1074/jbc.REV120.013572

Global Invasive Species Database (http://www.issg.org/database). *Imperata cylindrica*

Hagan DL, Jose S, Lin CH. 2013. Allelopathic Exudates of Cogongrass (*Imperata cylindrica*): Implications for the Performance of Native Pine Savanna Plant Species in the Southeastern US. *Journal of Chemical Ecology* 39: 312-322. DOI: https://doi.org/10.1007/s10886-013-0241-z

Hussain F, Abidi N. 1991. Allelopathy exhibited by *Imperata cylindrica* (L.) P. Beauv. *Pakistan Journal of Botany* 23: 15-25. DOI: https://doi.org/citeulike-article-id:5726335

Hussain, Farrukh, Naqvi HH, Ilahi I. 1982. Interference exhibited by *Cenchrus ciliaris* L. and *Bothriochloa pertusa* (L.) A. Camus. *Bulletin of the Torrey Botanical Club* 109: 513-523. DOI: https://doi.org/10.2307/2996492

Imatomi M, Novaes P, Gualtieri SCJ. 2013. Interspecific variation in the allelopathic potential of the family Myrtaceae. *Acta Botanica Brasilica* 27: 54-61. DOI: https://doi.org/10.1590/S0102-33062013000100008

Inderjit, Dakshini KMM. 1991. Investigations on some aspects of chemical ecology of cogongrass, *Imperata cylindrica* (L.) Beauv. *Journal of Chemical Ecology* 17: 343-352. DOI: https://doi.org/10.1007/BF00994337

Inderjit, Duke SO. 2003. Ecophysiological aspects of allelopathy. *Planta* 217: 529-539. DOI: https://doi.org/10.1007/s00425-003-1054-z

Irimia RE, Lopes SMM, Sotes G, Cavieres LA, ErenÖ, Lortie CJ, Montesinos D. 2019. Biogeographic differences in the allelopathy of leaf surface extracts of an invasive weed. *Biological Invasions* 21: 3151-3168. DOI: https://doi.org/10.1007/s10530-019-02038-1

Jabran K, Mahajan G, Sardana V, Chauhan BS. 2015. Allelopathy for weed control in agricultural systems. *Crop Protection* 72: 57-65. DOI: https://doi.org/10.1016/j.cropro.2015.03.004

Jose S, Cox J, Miller DL, Shilling DG, Merritt S. 2002. Alien plant invasions: The story of cogongrass in Southeastern forest. *Journal of Forestry* 100: 41-44.

Kaul VK, Vats SK. 1998. Essential oil composition of *Bothriochloa pertusa* and phyletic relationship in aromatic grasses. *Biochemical Systematics and Ecology* 26: 347-356. DOI: https://doi.org/10.1016/S0305-1978(97)00103-8

Koger CH, Bryson CT, Byrd JrJD. 2004. Response of selected grass and broadleaf species to cogongrass (*Imperata cylindrica*) residues. *Weed Technology* 18: 353-357. DOI: https://doi.org/10.1614/WT-03-092R1

Li H, Huang J, Zhang X, Chen Y, Yang J, Hei L. 2005. Allelopathic effects of *Cymbopogon citratu* volatile and its chemical components. *Chinese Journal of Applied Ecology* 16: 763-767.

Li ZH, Wang Q, Ruan X, Pan C, De, Jiang DA. 2010. Phenolics and plant allelopathy. *Molecules* 15: 8933-8952. DOI: https://doi.org/10.3390/molecules15128933

Liu K, Abdullah AA, Huang M, Nishioka T, Altaf-Ul-Amin Md, Kanaya S. 2017. Novel Approach to Classify Plants Based on Metabolite-Content Similarity. *BioMed Research International* 2017: 12 pages. DOI: https://doi.org/10.1155/2017/5296729

Lotina-Hennsen B, King-Diaz B, Aguilar M, Hernandez Terrones M. 2006. Plant secondary metabolites. Targets and mechanisms of allelopathy. *In*: Reigosa M, Pedrol N, González L, eds *Allelopathy*. Dordrecht: Springer Netherlands, pp. 229-265. DOI: https://doi.org/10.1007/1-4020-4280-9_11

MacDonald GE. 2004. Cogongrass (*Imperata cylindrica*) - biology, ecology, and management. *Critical Reviews in Plant Sciences* 23: 367-380. DOI: https://doi.org/10.1080/07352680490505114

Macías FA, Mejías FJR, Molinillo JMG. 2019. Recent advances in allelopathy for weed control: from knowledge to applications. *Pest Management Science* 75: 2413-2436. DOI: https://doi.org/10.1002/ps.5355

Muller CH. 1966. The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition. *Bulletin of the Torrey Botanical Club* 93: 332. DOI: https://doi.org/10.2307/2483447

Narwal SS. 2010. Allelopathy in ecological sustainable organic agriculture. *Allelopathy Journal* 25: 537-564. DOI: https://doi.org/10.1007/1-4020-4280-9_24

R Core Team 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reigosa M, Gomes AS, Ferreira AG, Borghetti F. 2013. Allelopathic research in Brazil. Acta Botanica Brasilica 27: 629-646. DOI: https://doi.org/10.1590/S0102-33062013000400001

Rice EL. 1984. Natural Ecosystems: Allelopathy and Patterning of Vegetation. *Allelopathy*. DOI: https://doi.org/10.1016/b978-0-08-092539-4.50009-5

Rietveld WJ. 1977. Phytotoxic effects of bunchgrass residues on germination and initial root growth of yellow sweetclover. *Journal of Range Management* 30: 39-43. DOI: https://doi.org/10.2307/3897333

Scrivanti LR. 2010. Allelopathic potential of *Bothriochloa laguroides* var. laguroides (DC.) Herter (Poaceae: Andropogoneae). *Flora: Morphology, Distribution, Functional Ecology of Plants* 205: 302-305. DOI: https://doi.org/10.1016/j.flora.2009.12.005

Scrivanti LR, Anton AM. 2019. Allelopathic effect of endemic South American *Bothriochloa* species (Poaceae: Andropogoneae). *Journal of Essential Oil Research* 31: 247-254. DOI: https://doi.org/10.1080/10412905.2018.1563569

Scrivanti LR, Anton AM. 2021. Germination inhibitory activity of aqueous extracts of native grasses from South America. *Rodriguésia* 72 DOI: https://doi.org/10.1590/2175-7860202172028

Scrivanti LR, Anton AM, Zygadlo JA. 2009. Essential oil composition of *Bothriochloa* Kuntze (Poaceae) from South America and their chemotaxonomy. *Biochemical Systematics and Ecology* 37: 206-213. DOI: https://doi.org/10.1016/j.bse.2009.03.009

Scrivanti LR, Anton AM, Zygadlo JA. 2011. Allelopathic potential of South American *Bothriochloa* species (Poaceae: Andropogoneae). *Allelopathy Journal* 28: 189-200. DOI: http://dx.doi.org/10.1080/10412905.2018.1563569

Suzuki M, Tominaga T, Ohno O, Iwasaki A, Suenaga K, Kato-Noguchi H. 2018. Plant growth inhibitory activity and active substances with allelopathic potential of cogongrass (*Imperata cylindrica*) rhizome. *Weed Biology and Management* 18: 92-98. DOI: https://doi.org/10.1111/wbm.12144

Tigre RC, Silva NH, Santos MG, Honda NK, Falcão EPS, Pereira EC. 2012. Allelopathic and bioherbicidal potential of *Cladonia verticillaris* on the germination and growth of *Lactuca sativa*. *Ecotoxicology and Environmental Safety* 84: 125-132. DOI: https://doi.org/10.1016/J.ECOENV.2012.06.026

Wang C, Xiao H, Zhao L, Wang L, Zhang F, Shi Y, Du D. 2016. The allelopathic effects of invasive plant *Solidago canadensis* on seed germination and growth of *Lactuca sativa* enhanced by different types of acid deposition. *Ecotoxicology* 25: 555-562. DOI: https://doi.org/10.1007/s10646-016-1614-1

Wardle DA, Nilsson MC, Gallet C, Zackrisson O. 1998. An ecosystem-level perspective of allelopathy. *Biological Reviews* 73: 305-319. DOI: https://doi.org/10.1111/j.1469-185X.1998.tb00033.x

Wink M. 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. *Phytochemistry* 64: 3-19. DOI: https://doi.org/10.1016/S0031-9422(03)00300-5

Xuan TD, Toyama T, Fukuta M, Khanh TD, Tawata S. 2009. Chemical Interaction in the Invasiveness of Cogongrass (*Imperata cylindrica* (L.) Beauv. *Journal of Agricultural and Food Chemistry* 57: 9448-9453. DOI: https://doi.org/10.1021/jf902310j

---

Associate editor: Enrique Jurado

Author contributions: FMC, field work, design, experimentation, analysis, writing; AMA, field work, review, writing; LRS, review, writing.