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REVIEW ARTICLE

Allelopathy in Poaceae species present in Brazil. A review

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Abstract

Allelopathy is an important ecological mechanism in natural and managed ecosystems. Its study is critical to understand natural plant behaviors, to isolate allelochemicals with herbicide potential, and to use the allelopathic genes in transgenic studies. Poaceae is an ecologically dominant plant family and it is economically important worldwide because its chemical diversity represents an important source to discover new molecules. From this viewpoint, Brazil is an interesting place to study, encompassing 197 genera of the Poaceae family, many of them being dominant in various biomes and some being native to Brazil. Here, we review the literature describing allelopathic activities involving grasses of the Poaceae family. We evaluate the experimental conditions used in these studies, we identify the allelochemicals involved, and, finally, we assess the applicability of allelopathy. Our main findings are (1) among the 47 Brazilian species studied for their allelopathic effects, only *Bothriochloa barbinodis*, *Bothriochloa laguroides*, *Paspalum notatum*, and *Paspalum urvillei* are native to Brazil; (2) 51% of the reviewed studies prepared extracts from the leaves and used lettuce as the target plant; and (3) 64% of the papers identified allelochemicals, of which 67% were phenolic acids. This first bibliographical survey on allelopathy in Poaceae species present in Brazil shows that less than 3% of the Brazilian species have been studied, suggesting it is an incipient research subject. Since this plant family is a valuable source of unknown natural products, refining such studies should contribute to a better understanding of the ecosystem relationships. Identification and isolation of grass allelochemicals should promote environmentally safer compounds with bioherbicide properties, in sustainable agriculture.

Keywords Allelochemicals · Bioprospecting · Grasses · Native resources

Contents

1 Introduction

The influence of some plant species on the growth of others in their vicinity remained an unexplained phenomenon (Rodrigues et al. 1992) until Theophrastus (300 B.C.) conceptualized it as allelopathy (Reigosa et al. 2013). In 1974, Elroy L. Rice defined allelopathy as the effect of one plant on another via the release of chemical compounds into the environment (Rice 1984). Currently, the most accepted concept of allelopathy is as "any process involving secondary metabolites produced by plants, algae, bacteria, and fungi that influence the growth and development of agriculture and biological systems" (Ias 1996).

Allelopathy is an important ecological mechanism in the natural and managed ecosystems. It is a phenomenon that influences the primary and secondary plant succession, encompassing all successional stages (Reigosa et al. 1999); the structure and composition of plant communities and the dynamics between different formations (Rizvi et al. 1992); the dominance of certain plant species that affect the local biodiversity (Reigosa et al. 1999); and agriculture, which is the target of most studies (Chou 1989). Considering the importance

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of allelopathy, several studies have been conducted on the subject, a great majority of which focused on species of economic interest. Allelopathic studies in Brazil also focused on agroecosystems, especially with cultivated and weedy plants. On the other hand, considering the territorial extent and the diversity of the Brazilian flora, studies on the allelopathic potential of native species are scarce (Ferreira et al. 1992).

The Poaceae family is ecologically the most dominant and economically the most important family in the world (Heywood 1978), with approximately 793 genera and 8,000–9,000 species (Sánchez-Moreiras et al. 2004). In Brazil, this family is represented by 197 genera and 1,368 species, many of which are native and dominant in several Brazilian biomes. However, despite the representativeness of this family, the knowledge about allelopathy and the allelochemicals present in these species is limited (Fig. 1).

In order to investigate works related to the allelopathic potential of Poaceae species present in Brazil, research literature were searched in the databases of Science Direct, the Portal of Periodicals of Capes (Coordination for the Improvement of Higher Education Personnel), and the Academic Google. For the search purpose, the following keywords were used: "allelopathy," "allelochemicals," "phytochemistry," "chemical compounds," and "bioprospecting," besides the genera of Poaceae species present in Brazil, as described by Boldrini et al. (2010) and Pillar et al. (2009).

2 Poaceae genera native to Brazil with allelopathic effect

A total of 44 papers referring to 47 species were found for works related to the allelopathic effect of grasses present in Brazil (Table 1). Of these, 31 species occur in Brazil, but only four are native to the country, which include *Bothriochloa barbinodis*, *Bothriochloa laguroides*, *Paspalum notatum*, and *Paspalum urvillei*. The fact that only 2.56% of the Brazilian species have been studied in terms of their allelopathic potential shows that this area is still incipient for the Poaceae, especially, for the species native to the country.

Despite the popular belief of several authors that scientific studies on allelopathy has been successful in recent years (Reigosa et al. 2013), most studies so far refer to the interaction between crops and weeds and only few to the grasses native to Brazil.

Among the genera studied, *Bothriochloa* stands out as the most studied in relation to the allelopathic effect of its species, for which seven works were found (Table 1). Allelopathy in species of this genus is attributed to the production and release of essential oils and richness in sesquiterpenes and monoterpenes (Scrivanti 2010).

3 Experimental conditions

3.1 Plant organs used to prepare extracts

We found that most of the studies have investigated the allelopathic properties of the leaves of the Poaceae species. Only a small minority investigated seeds, inflorescences, and pollen (Fig. 2). These data are in agreement with those reported by Reigosa et al. (2013), who investigated the works of allelopathy in Brazil. According to them, the preference for leaves may reflect the fact that it is certainly easier to collect leaves than other parts and that leaves represent a large part of the

Fig. 1 Grasses with allelopathic effect, native to Brazil. **a** *Bothriochloa laguroides*. **b** *Paspalum urvillei*. Photos from University of Passo Fundo, Passo Fundo, RS, Brazil

Table 1 General characteristics of allelopathic works conducted with grasses present in Brazil

Species	Plant organ	Target species	Effect	Reference
Aristida junciformis	Leaves and roots	*Lactuca sativa*	Germination, root and shoot length	Ghebrehiwot et al. (2014)
Arundo donax[a]	Leaves	*Lens culinaris*	Germination and initial growth	Abu-Romman and Ammari (2015)
Avena fatua[a]	Whole plant	*Triticum aestivum*	Germination, root and shoot length	Ahmad et al. (2014)
Axonopus compressus[a]	Leaves	*Asystasia gangetica*, *Pennisetum polystachion*	Hypocotyl and shoot length, mean germination time	Samedani et al. (2013)
Brachiaria brizantha[a]	Seeds, shoot, and roots	*Desmodium adscendens*, *Sida rhombifolia*, *Vernonia polyanthes*, *Stylosanthes guianensis*, *Lepidium sativum*, *Lactuca sativa*, *Phleum pratense*, *Lolium multiflorum*	Germination, root and shoot length	Souza Filho et al. (1997); Carvalho et al. (1993); Kato-Noguchi et al. (2014)
Brachiaria decumbens[a]	Seeds, shoot, and roots	*Desmodium adscendens*, *Sida rhombifolia*, *Vernonia polyanthes*	Germination and root length	Souza Filho et al. (1997)
Brachiaria humidicola[a]	Seeds, shoot, and roots	*Desmodium adscendens*, *Sida rhombifolia*, *Vernonia polyanthes*	Germination and root length	Souza Filho et al. (1997)
Bothriochloa barbinodis[b]	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root and shoot length	Scrivanti et al. (2011)
Bothriochloa edwardsiana	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root and shoot length	Scrivanti et al. (2011)
Bothriochloa laguroides[b]	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root, and shoot length	Scrivanti (2010)
Bothriochloa perforata	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root and shoot length	Scrivanti et al. (2011)
Bothriochloa pertusa[a]	Inflorescence, roots, stem, and leaves	*Pennisetum americanum*, *Setaria italica*, *Lactuca sativa*	Germination, root and shoot length	Hussain et al. (2010)
Bothriochloa saccharoides[a]	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root and shoot length	Scrivanti et al. (2011)
Bothriochloa springfieldii	Roots, stem, and leaves	*Lactuca sativa*, *Zea mays*, *Eragrostis curvula*, *Paspalum guenoarum*	Germination, root and shoot length	Scrivanti et al. (2011)
Cenchrus ciliaris[a]	Inflorescence, roots, stem, and leaves	*Pennisetum americanum*, *Setaria italica*, *Lactuca sativa*	Germination, root length	Hussain et al. (2010)
Cenchrus echinatus[a]	Shoot and roots	*Panicum maximum*, *Amaranthus hypochondriacus*, *Physalis ixocarpa*, *Trifolium alexandrinum*, *Lolium perenne*	Germination, root and shoot length	Nascimento et al. (2009)
Chloris gayana[a]	Leaves	*Lactuca sativa*	Germination	Chou and Young (1975)
Cynodon dactylon[a]	Shoot, roots, stem, and leaves	*Ocimum basilicum*, *Portulaca oleracea*, *Triticum aestivum*, *Phaseolus vulgaris*, *Pisum sativum*, *Vicia faba*, *Thymus vulgaris*, *Melissa officinalis*, *Mentha spicata*, *Avena fatua*, *Sorghum halepense*, *Oryza sativa*, *Zea mays*	Length and weight of coleoptile and root germination, dry and fresh weight	Golpavar et al. (2015); Mahmoodzadeh and Mahmoodzadeh (2013); Mahmoodzadeh and Mahmoodzadeh (2014); Novo et al. (2009)
Dactylis glomerata	Shoot	*Phleum subulatum*	Germination, root and shoot length	Scognamiglio et al. (2012)
Danthonia richardsonii	Leaves and stem	*Trifolium subterraneum*	Germination	Slater et al. (1996)
Digitaria decumbens[a]	Leaves	*Lactuca sativa*	Germination	Chou and Young (1975)
Festuca arundinacea[a]	Shoot	*Lactuca sativa*	Germination and hypocotyl length	Bertoldi et al. (2012)
Festuca paniculata	Leaves	*Bromus erectus*, *Raphanus sativus*, *Lactuca sativa*, *Centaurea uniflora*, *Dactylis glomerata*	Germination, dry mass of leaf and root	Mold (2005)
Festuca rubra	Shoot	*Dactyilis glomerata*, *Lolium perenne*, *Poa pratensis*	Protein content	Bostan et al. (2013)
Hordeum spontaneum[a]	Shoot and seeds	*Triticum aestivum*		Hamidi et al. (2006)

Table 1 (continued)

Species	Plant organ	Target species	Effect	Reference
			Germination, dry and fresh mass of root and shoot	
Hordeum vulgare[a]	Leaves	*Brassica juncea*, *Setaria viridis*	Germination, root and shoot length	Asghari and Tewari (2007)
Imperata cylindrica[a]	Shoot, leaves, and roots	*Andropogon arctatus*, *Aristida stricta*, *Lyonia ferruginea*, *Pinus elliottii*, *Echinochloa crus-galli*, *Cynodon dactylon*	Shoot weight, germination, root and coleoptile length	Hagan et al. (2013); Koger and Bryson (2004)
Lolium rigidum[a]	Shoot, leaves, and roots	*Triticum aestivum*, *Lolium multiflorum*, *Dactylis glomerata*, *Medicago sativa*	Root and shoot length	Amini et al. (2009); Emeterio et al. (2004)
Melinis minutiflora[a]	Leaves	*Lactuca sativa*	Germination	Bomediano et al. (2013)
Merostachys multiramea[a]	Leaves	*Araucaria angustifolia*	Germination	Fernandes et al. (2007)
Merostachys pluriflora[a]	Leaves, stem, and rhizome	*Lycopersicum esculentum*, *Oryza sativa*	Germination and root and hypocotyl growth	Faria and Guaratini (2011)
Miscanthus transmorrisonensis	Leaves, stem, and roots	*Lactuca sativa*, *Brassica oleracea*, *Festuca arundinacea*, *Lolium perenne*	Germination and root and hypocotyl growth	Chou and Lee (1991); Ma et al. (2014)
Oryza sativa[a]	Shoot, glumes, and exocarp	*Echinochloa crus-galli*, *Lactuca sativa*, *Triticum aestivum*, *Oryza sativa*	Germination, dry mass	Jung et al. (2004)
Panicum maximum[a]	Shoot, leaves, and roots	*Lactuca sativa*, *Leucaena leucocephala*, *Cajanus cajan e Sesbania sesban*, *Amaranthus viridis*	Germination, germination speed index, root length, leaves chlorosis and necrosis	Chou and Young (1975); De Almeida et al. (2000); Santos et al. (2002)
Panicum virgatum[a]	Shoot and roots	*Lolium perenne*, *Medicago sativa*	Germination, root and coleoptile length	Shui et al. (2010)
Paspalum notatum[b]	Leaves, stem, and roots	*Medicago sativa*	Germination and seedling growth	Martin and Smith (1994)
Paspalum urvillei[b]	Leaves	*Cucumis sativus*, *Solanum lycopersicum*	dry mass, leaves number	Ishimine et al. (1987)
Pennisetum purpureum[a]	Leaves, shoot	*Cyperus iria*, *Hedyotis verticillata*, *Leptochloa chinensis*	Germination, root and shoot length, fresh mass	Tan et al. (2011); Zain et al. (2013)
Phleum pratense[a]	Pollen	*Agropyron repens*, *Bromus inermis*, *Danthonia compressa*, *Poa compressa*	Germination	Murphy and Aarssen (1995)
Phyllostachys edulis[a]	Shoot	*Castanopsis sclerophylla*, *Cyclobalanopsis glaunca*	Germination, root length	Bai et al. (2013)
Poa pratensis[a]	Leaves	*Lolium perenne*, *Dactylis glomerata*, *Festuca rubra*	Root and coleoptile length	Bostan et al. (2010)
Saccharum spontaneum[a]	Leaves, stem	*Lactuca sativa*	Germination	Tantiado and Saylo (2012)
Setaria faberi	Leaves, stem, and roots	*Medicago sativa*	Germination and seedling growth	Martin and Smith (1994)
Setaria glauca	Leaves, stem, and roots	*Medicago sativa*	Germination and seedling growth	Martin and Smith (1994)
Setaria viridis[a]	Leaves, stem, and roots	*Medicago sativa*	Germination and seedling growth	Martin and Smith (1994)
Vulpia bromoides	Shoot	*Triticum aestivum*	Germination, coleoptile length and seminal roots	An et al. (1996)
Vulpia myuros[a]	Shoot	*Triticum aestivum*	Germination, coleoptile length and seminal roots	An et al. (1996)

[a] Species present in Brazil

[b] Species native to Brazil

litter produced by the vegetation biomass that directly impacts the growth of the seedling.

The leaves are considered to be the most metabolically active organ of a plant and, therefore, it is reasonable that they present greater diversity of allelochemicals and, consequently, greater allelopathic effect (Ribeiro et al. 2009). However, it is known that allelochemicals can be produced in different organs of a plant, including the stems, roots, flowers, and seeds (Parvez et al. 2003; Weston and Duke 2003), with varying concentrations from one organ to another (Hong et al. 2004). However, for grasses, the evidence indicates that the aerial part, followed by the roots and seeds, are the main sources of potentially allelopathic substances (Souza Filho 1995).

In seed allelopathy, it is worth considering that the seeds of several forage grass that contain phytotoxic compounds may inhibit the germination of other seeds in their vicinity, compromising the germination and establishment of one or more species in the mixture, which in turn compromises the performance of the pasture (Souza Filho and Alves 1998).

3.2 Target species

The effect of grass extracts was tested in different target species, including lettuce (*Lactuca sativa*) (Table 2), followed by cultivated species such as maize (*Zea mays*), wheat (*Triticum aestivum*), and alfalfa (*Medicago sativa*). Lettuce is considered as a bioindicator plant and has been used in several allelopathy researches because it presents with rapid germination and uniform initial growth, which are desirable attributes for experiments that compare the effects of different treatments (Reigosa et al. 2013).

Most of the past studies have evaluated the allelopathic effect of grasses on cultivated species, followed by native, forages, and invasive plants (Fig. 3). In the ecological context, once the allelopathy of a species is verified, this effect can be tested in species that live together in the field, as only then can the applicability of allelopathy and the interaction with neighboring plants be inferred. As pastures are constituted of several types of grasses, it is interesting to examine the allelopathic effect in other forage plants or in weeds.

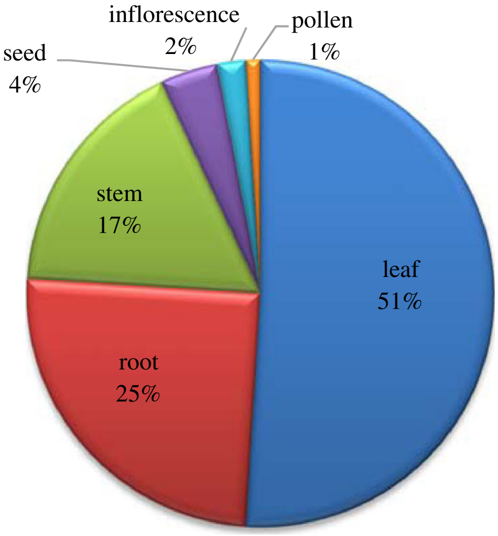

Fig. 2 Plant organs used for the preparation of extracts in allelopathy studies of Poaceae species present in Brazil

Table 2 Target species used in allelopathy studies of Poaceae species present in Brazil

Target species	Number	Percent
Lactuca sativa	19	15.08
Triticum aestivum	7	5.56
Zea mays	7	5.56
Medicago sativa	6	4.76
Eragrostis curvula	6	4.76
Paspalum guenoarum	6	4.76
Lolium perene	5	3.97
Oryza sativa	3	2.38
Vernonia polyanthes	3	2.38
Sida rhombifolia	3	2.38
Desmodium adscendens	3	2.38
Others (with fewer than 5 mentions)	58	46.03

3.3 Evaluation of allelopathic effect

The most common physiological parameters used to identify the allelopathic effects of grasses were germination (41.35%), followed by the root length (27.89%) and shoot length (15.38%) (Table 3). Although germination is largely considered to be less sensitive to the presence of allelochemicals (Oliveira et al. 2012), it is the most commonly used attribute in evaluations of allelopathy. As for the vegetative structures, the allelopathic effect is most observed in the root system (Yamagushi et al. 2011). However, the allelopathic effect is often not evident in the germination process or during the initial growth of the seedlings; therefore, the evaluation of the appearance of abnormalities becomes a valuable tool to

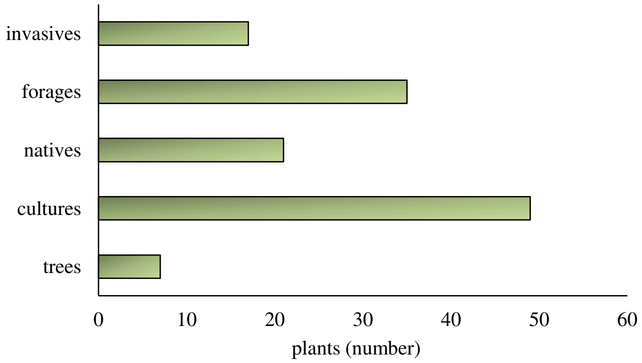

Fig. 3 Classification according to the use of target species in Poaceae allelopathy bioassays

Table 3 Most commonly reported physiological effects in allelopathic studies conducted with Poaceae species present in Brazil

Effects	Number	Percent
Germination	43	41.35
Root length	29	27.89
Shoot length	16	15.38
Hypocotyl length	4	3.85
Coleoptile length	5	4.81
Dry mass of leave and root	6	5.77
Abnormalities (chlorosis and necrosis)	1	0.96

study allelopathy (Ferreira and Aquila 2000). However, of all the studies evaluated, only 0.96% studies analyzed the presence of abnormalities in the target species, which may have underestimated the allelopathic effect of the tested plants.

Most of the research reported so far has been conducted under laboratory conditions or under controlled conditions. Although such studies are important for isolating variables and identifying the true factors involved in plant interactions, there is a need for further studies to describe the allelopathic properties of plants under natural conditions.

Based on this requirement, the type of research on allelopathy can be divided into two main categories: (i) the one that follows the concepts of an ecological approach, corresponding to studies on phenomena occurring in natural ecosystems (allelopathy sensu stricto) and (ii) the other one that follows the criteria and commercial and economic interests corresponding to studies based on interactions between cultivated species that do not occur naturally in the same habitat (applied allelopathy). In the first category, preliminary or complementary laboratory studies could replicate, under controlled conditions, the expected effects of rain or dew on substance leaching, mimicking the events in natural environment. In fact, the species under study should coexist in the same habitat (Reigosa et al. 2013).

Due to the complexity of this kind of study, only limited studies have successfully “completed the cycle” or, in other words, have shown the production of a specific metabolite by the allelopathic (donor) plant, its journey through the environment (soil, water, or atmosphere), its arrival at the target, and its influence on the affected (recipient) plant (Reigosa et al. 2013).

4 Allelochemicals in Poaceae genera native to Brazil

For the successful application of allelopathic properties of a plant, the identification of allelochemicals is required (Bhadoria 2011). In this bibliographical survey review, only thirty (30) papers were found on the identification of allelochemicals in 23 genera and thirty (30) species of Poaceae present in Brazil (Table 4). Among the species studied, 22 occur in Brazil and only one is native to this country, namely, *Merostachys riedeliana* (Table 4).

Chemicals that establish allelopathic influence are called allelochemicals and they are divided into classes, viz., water-soluble organic acids; simple unsaturated lactones; long-chain fatty acids and polyacetylenes; naphthoquinones, anthraquinones, and complex quinines; simple phenols; benzoic acid and derivatives; cinnamic acid derivatives; coumarins; flavonoids; condensed and hydrolysable tannins; terpenoids and steroids; amino acids and polypeptides; alkaloids and cyanohydrins; sulphides and glycosides; and purines and nucleosides (Rice 1984). Although allelochemicals may belong to any of these classes, they generally belong to the terpenoids (Llusià et al. 1996), phenolic compounds (Li et al. 2010), and alkaloids (Levitt and Lovett 1985), which are mainly responsible for allelopathy (Trezzi 2002; Taiz and Zeiger 2013).

The allelochemicals present in the Poaceae are diverse, ranging from phenols to quinones. The most clearly identified compounds of these can be broadly divided into four groups: phenolic acids, hydroxamic acids, alkaloids, and quinones (Sánchez-Moreiras et al. 2004). In this review, despite the great diversity of compounds (Table 4), the main allelochemicals were found to belong to the group of phenolic acids, flavonoids, alkaloids, and terpenoids, with a predominance of phenolic acids (67%) (Fig. 4) probably due to the methodological facility adopted to identify these compounds.

The plant that releases allelochemicals is known as the donor plant, whereas the plant that is influenced by the release of the allelochemicals is termed as the target plant or a recipient plant (Inderjit and Duke 2003). The release of the allelochemicals by the donor plant can happen through leaching, volatilization, and decomposition of the plant material or by release from the roots (Bhadoria 2011).

From the release process of the allelochemical by the donor plant to the effect in the recipient plant, several factors can influence the allelopathic activity. However, for the optimal use of allelopathy under field conditions, the influence of environmental factors needs to be investigated. In this context, the soil factor can be said to be the most important (Bhadoria 2011).

Understanding the effect of the relationships as well as the release form of the allelochemicals is crucial for designing alternatives for possible applications of these compounds. The first step is to know the potential of the species as well as to identify the compounds responsible for allelopathy. In this sense, a positive aspect observed in the last decades was that there was an increase both in the number of studies related to Brazilian Poaceae allelopathy and in those that isolated and identified allelochemicals from these species. In a review of allelopathy surveys conducted in Brazil, Reigosa et al. (2013)

Table 4 Allelochemicals in Poaceae species present in Brazil

Specie	Allelochemical	Reference
Andropogon nodosum	Syringic, vanillic, o-hydroxyphenyl acetic, ferulic, trans-p-coumaric, cis-p-coumaric, and o-coumaric acids	Chou and Young (1975)
Anthoxanthum odoratum	Coumarin	Yamamoto and Fugii (1997)
Arundo donax	Donaxine, donaxaridine, arundinine	Khuzhaev (2004)
Axonopus compressus	Alkaloids, saponins, tannins, flavonoids, terpenes	Bartholomew et al. (2013); Ogie-Odia et al. (2010)
Brachiaria brizantha	(6R,9R)-3-Oxo-α-ionol, (6R,9S)-3-oxo-α-ionol, 4-ketopinoresinol	Kato-Noguchi et al. (2014)
Brachiaria humidicola	p-Coumaric acid	Souza Filho et al. (2005)
Brachiaria mutica	Ferulic, 2,4-dihydroxybenzoic, vanillic, p-hydroxybenzoic, p-Hydroxyphenyl acetic, trans-p-coumaric, and cis-p-coumaric	Chou (1989); Chou and Young (1975)
Cenchrus ciliaris	Phenols, flavonoids, saponins, alkaloids	Kannan and Priyal (2015)
Chloris gayana	Ferulic, p-coumaric, syringic, vanillic, o-hydroxyphenyl acetic, p-hydroxyphenyl acetic, trans-p-coumaric, and cis-p-coumaric acids	Chou and Young (1975)
Cynodon dactylon	p-Coumaric, syringic, vanillic, o-hydroxyphenyl acetic, p-hydroxyphenyl acetic, trans-p-coumaric, and cis-p-coumaric acids; alkaloids; terpenoids; saponins; flavonoids; tannins	Chou and Young (1975); Abdullah et al. (2012)
Dactylis glomerata	Polygonocinol, 5-alkylresorcinols, 5-alkyl-2-methylresorcinols, 5-alkylresorcinol-3-methyl ethers, 5-eicosanoyl-2-methylresorcinol	Scognamiglio et al. (2012)
Digitaria decumbens	Ferulic, syringic, vanillic, p-hydroxyphenylacetic, trans-p-coumaric, and cis-p-coumaric acids	Chou and Young (1975)
Festuca arundinacea	E/Z-thesinine-O-40-α-rhamnoside, E/Z-thesinine, quercetin-3-O-xylosylglucoside, isorhamnetin 3-O-glucoside, quercetin 3-O-rutinoside, isorhamnetin 3-O-xylosylglucoside, kaempferol 3-O-rutinoside	Bertoldi et al. (2012)
Festuca paniculata	Caffeic and ferulic acids	Mold (2005)
Festuca rubra	N-Formyl loline, N-acetyl loline, ergovaline	Bostan et al. (2013)
Hemarthria altissima	Benzoic, phenylacetic, hydroxycinnamic, cinnamic, syringic, ferulic, and synaptic acids	Tang and Young (1982)
Hordeum vulgare	Gramine, hordenine, benzoic, caffeic, chlorogenic, m-coumaric, o-coumaric, p-coumaric, ferulic, synaptic, cinnamic, vanillic and gentisic acids, coumarin, apigenin, lutonarin, catechin, saponarin, cyanadin, isovitexin, heterodendrin, epidermin, sutherlandin, osmaronin, hordatine, DIBOA, butyronitrile	Hoult and Lovett (1993); Kremer and Ben-Hammouda (2009)
Imperata cylindrica	Gallic, caffeic, salicylic, synaptic, benzoic, cinnamic, ferulic, chlorogenic, linoleic, vanillic, p-coumaric, o-coumaric, gentisic, and p-hydroxybenzoic acids; emodin; resorcinol; 4-acethyl-2-methoxyphenol	Hagan et al. (2013); Xuan et al. (2009); Eussen and Niemann (1981)
Melinis minutiflora	1,8-Cineole, limonene, α-pinene	Mbuthia (1997)
Merostachys riedeliana[a]	p-Hydroxybenzoic, benzoic, benzeneacetic, 3,4-metylenedioxymandelic, salicylic, p-hydroxyphenylacetic, isovanillic, m-anisic, p-coumaric, protocatechuic, syringic, gallic, ferulic, m-coumaric, vanillylmandelic, and 4-metylmandelic acids; orientine; isovitexine	Torres et al. (2014)
Miscanthus sinensis	Caffeic, p-coumaric, and ferulic acids	Parveen et al. (2013)
Miscanthus sacchariflorus	Syringic, p-coumaric, ferulic, dihydroxybenzoic, and vanillic acids	Parveen et al. (2013)
Miscanthus transmorrisonensis	Caffeic, gallic, p-hydroxybenzoic, ferulic, m-hydroxybenzoic, and o-hydroxybenzoic acids; floridzine	Chou and Lee (1991)
Oryza sativa	Salicylic, p-coumaric, o-hydroxyphenyl acetic, syringic, ferulic, benzoic, p-hydroxybenzoic, octacosanoic, m-coumaric, and o-coumaric acids; hentriacontane; 1-tetratriacontanol; β-sitosterol; momilactone A; momilactone B; tricin; 3,7-dimethyl-n-octan-1-yl benzoate; β-sitosterol-3-O-β-D-glucoside; n-tritriacont-4,12-diene; n-pentacosane; stigmastanol-3beta-p-glyceroxydihydrocoumaroate; stigmastanol-3beta-p-butanoxydihydrocoumaroate; lanast-7; 9(11)-dien-3α,15α-diol-3α-D-glucofuranoside; 1-phenyl-2-hydroxy-3,7-dimethyl-11-aldehydictetradecane-2-β-D-glucopyranoside	Chung et al. (2015); Chung et al. (2006)
Panicum maximum	p-Hydroxyphenyl acetic, trans-p-coumaric, and cis-p-coumaric acids	Chou and Young (1975)
Setaria sphacelata	Ferulic, p-coumaric, syringic, vanillic, o-hydroxyphenyl acetic, and o-coumaric acids	Chou and Young (1975)
Setaria verticilllata	Alkaloids, flavonoids, saponins, tannins, terpenoides, phenols	Shivakoti et al. (2015)
Spartina alterniflora	Adipic acid, isohexyl methyl ester, hexadecanoic, dibutyl phthalato, and octadecanoic acids	Zheng et al. (2011)

Table 4 (continued)

Specie	Allelochemical	Reference
Sporobolus pyramidalis	Ferulic and p-coumaric acids	Rasmussen and Rice (1971)
Vulpia myuros	Salicylic, benzoic, protocatechuic, succinic, 3,4-dymetoxyphenol, syringic, hydrocaffeic, p-hydroxybenzoic, vanillic, p-hydroxyphenyl acetic, gentisic, p-coumaric, ferulic, and hydrocinamic acids; coniferyl alcohol; hydroquinone; catechol	An et al. (2001)

[a] Specie native to Brazil

reached the same conclusion, that is, the last two decades has witnessed a proliferation of studies on the allelopathic properties of species introduced or cultivated in Brazil. These authors reported an evident increase in the number of publications, attributing it to the growing interest not only in allelopathic interactions in natural ecosystems and agroecosystems but also in products that can be derived from allelochemicals, such as natural herbicides and growth regulators.

The studies referring to the simple allelopathic activity of Brazilian Poaceae outnumber those that identify the allelochemicals (Fig. 5) owing to the comparatively greater ease, practicality, and lower costs of operations involved. In addition, bioprospecting for secondary metabolites in plants requires prior knowledge of biochemistry and molecular signaling among organisms, making them lengthier and more difficult to execute.

Although the search was made only for grasses present in Brazil, few of the works found in the survey performed the researches in this country. With respect to the allelopathy experiments, only 20% of the studies were performed in Brazil and a smaller percent (2%) of the allelochemical studies were developed in the country. This observation indicates that allelopathy in Brazil is an area of recent knowledge with much scope to expand.

5 Allelopathy and its applicability

Considering that Brazilian Poaceae can be found mainly in natural fields and cultivated pastures, it should be emphasized that allelopathy may play two extremely important roles in the pasture areas: (1) act as a management tool and (2) act as a supplier of basic structures for the production of bioherbicides (Souza Filho and Alves 1998).

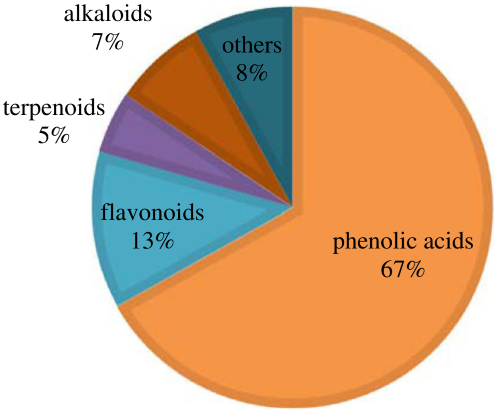

Fig. 4 Allelochemicals identified in Poaceae species present in Brazil

Bioherbicides are environmentally safe alternatives, sources of new mechanisms of action, and have a structural diversity that has been attracting the attention of companies and researchers. Although research in the field of allelopathy, which aims at the search for bioherbicides, is only a recent process, some examples of natural compounds with potential use for weed control has already been established. For instance, in the case of Poaceae, the products 2-benzoxazolinone (BOA) and 6-methoxy-2,3-benzoxazolinone (MBOA) can be highlighted (Macías et al. 2007). In addition, we highlight sorgoleone—a lipid benzoquinone exuded from sorghum roots (*Sorghum bicolor* L.)—that reduces weed growth through its action on the PSII (Hejl and Koster 2004) by inhibiting the enzyme H^+-ATPase in the roots. Sorgoleone affects the absorption of ions and the water balance of the plant, reducing its water absorption capacity (Soltys et al. 2013). It acts in a similar way to herbicides of the triazine class such as atrazine (Gniazdowska and Bogatek 2005).

On the other hand, allelopathy is important for the use of plants that control certain undesirable species (Resende et al. 2003). In this context, the identification of allelopathic forages and the knowledge of the mechanisms by which they exert their effects on the environment are of great importance as they provide a more adequate management of these plants in order to increase productivity and the persistence of pastures (Resende et al. 2003).

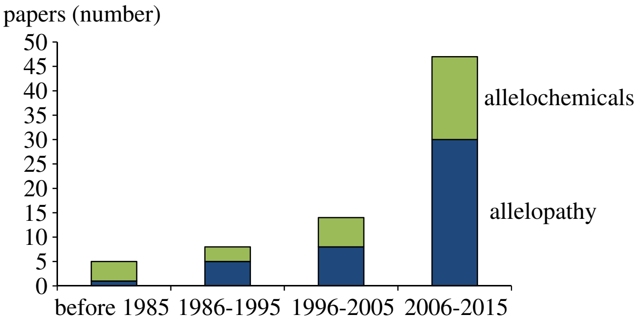

Fig. 5 The number of articles published quoting the terms associated with allelopathic studies from Poaceae species present in Brazil

The reductions affected by forage grasses on the germination and development of the weeds assume an important aspect from the ecological perspective, because, with the decrease in the germination of the seeds, a reduction in the number of undesirable plants in the area were noted, thus reducing the competition power of these plants for water, light, and nutrients. Moreover, with the reduction in the development of the root system, the weeds have reduced their aggressive capacity. As a consequence of these two aspects, there is a greater possibility of establishing denser stands of desirable plants in cultivated pasture areas (Souza Filho and Alves 1998).

In the last few years, some studies involving the analysis of allelopathic activity have been developed with different species of forage grasses (Souza Filho et al. 2005). Studies involving forage grasses *Brachiaria humidicola*, *Brachiaria decumbens*, and *Brachiaria brizantha* cv. Marandu showed potentially allelopathic effects on the desmodium pastures (*Desmodium adscendens*), arrowleaf sida (*Sida rhombifolia*), and assa-fish (*Vernonia polyanthes*) (Souza Filho et al. 1997). The use of cover crops for the control of weeds is one of the earliest examples of the economic use of allelopathy. In addition to the suppressive effect of weeds, mulching has important effects on soil conservation and the maintenance of soil moisture (Medeiros 1989).

Considering these points, allelopathy assumes an important aspect from the point of view of pasture management as it allows not only the identification of forage species that can exert a certain level of control of certain undesirable species but also the establishment of grasses and legumes that are not strongly allelopathic to each other and which can compose more balanced pastures, with extremely favorable effects on their productivity and longevity (Wardle 1987). The difficulty in managing these two groups of physiologically different plants is one of the factors that prevent the establishment of intercropped pastures in several places across Brazil. Therefore, before recommending consortia with known species, it would be advisable to evaluate the allelopathic potential of the species considered (Rodrigues et al. 1992), considering that the allelopathic potential of the grasses can compromise the persistence of a legume in a consortium (Souza Filho and Alves 1998).

Another important role that allelopathy may play in terms of pasture management strategies and other crops is the possibility of obtaining pest- and disease-resistant species of plants. This bias opens up from the perspective of genetic transfer—through the manipulation of DNA—of this ability of a plant without major agronomic interests to a forage species of great interest to livestock, in which this characteristic was absent. The current phase of global research presents with practically no results in this regard. However, given the importance of this line of research, it is essential that studies be conducted in this sense (Souza Filho and Alves 1998).

The main problem in allelopathy works is to probe this phenomenon. It often happens due to the difficulty in separating allelopathy from competition. According to Duke (2015), most articles that claim to demonstrate allelopathy do not prove that it occurs. They only demonstrate that a crude extract of a plant species suspected to be allelopathic, or one or more compounds from such a plant, are phytotoxic in unrealistic bioassays that maximize the effects of the phytotoxin. This can be a first step in the proof of allelopathy, but all plants produce compounds that are weakly phytotoxic in simple bioassays conducted in the absence of soil. A successful demonstration of an allelopathic interaction has three components: (1) an ecological component—a demonstration that it exists in nature; (2) a chemical component—isolation, identification, and characterization of allelochemicals involved; and (3) a physiological component—identification of the interference mechanism at the biochemical, physiological, cellular, and molecular level (Inderjit and Weston 2000). Besides the difficulty of proving allelopathy, the studies that have been developed do not have an adequate standard methodology, which makes it difficult to compare them.

6 Conclusion

The allelopathic properties of Poaceae species present in Brazil are poorly studied. Moreover, most of the species described in studies as belonging to the genera native to Brazil are not actually native to the country. Most of the reported work was performed only under laboratory conditions with leaf extracts, using lettuce as a target plant and by evaluating simple growth characters such as germination. The number of papers that identified or isolated allelochemicals in Poaceae is lower than those that simply tested the allelopathic effect. Among the species studied, the great majority of identified allelochemicals belong to a group of phenolic acids. A fewer number of studies identified compounds responsible for allelopathy, reflecting the complexity and costs of this type of study.

Despite the increase in the number of studies on allelopathy in recent years, the fact that only a minority of these works have been performed in Brazil is worrisome as the information about the chemical composition and biological properties of native Poaceae is limited. Allelopathy is important to explain interactions both in the composition of natural ecosystems and in the interaction between cultivated and invasive plants. Therefore, to understand this phenomenon and to identify allelochemicals, it is fundamental to understand the natural behavior of plants and managed pastures, besides bioprospecting for allelochemicals with potential herbicide value. In addition, there is a need for further genetic and molecular studies of allelopathic plants toward increasing their protection against competitors as well as to identify allelopathic genes that can be used in transgeny.

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