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Biology of the invasive species *Eragrostis plana* in Southern Brazil: What have we learned and how may this help us manage it?

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Abstract

Since its accidental introduction in 1951, the South African species *Eragrostis plana* has invaded a large part of the Pampa biome in South America, a highly diverse grassland ecosystem that has coexisted with livestock since its introduction at the beginning of the 17th century. *E. plana*, a perennial tussock grass with a deep and abundant root system, is resistant to frost and cattle grazing, and a successful competitor for environmental resources. The species is diploid, C4 dispersed endozoochorically, and flowers in late spring and early summer, with optimal germination occurring at 35°C and viability up to 39–40°C. It is allelopathic because it produces several phenols and alkaloids. Extreme soil disturbance or intense grazing favours initial invasion. Nonetheless, grazing exclusion enhances *E. plana* competition and affects the grassland community and diversity. *E. plana* is highly tolerant to interspecific competition, especially with grasses exhibiting a similar growth habit. Under water stress, it responds faster by increasing its root system by 66% more than native grass. Moreover, antioxidant system activity increases, and the species recovers quickly through osmolyte production. In non-invaded fields, avoiding soil disturbance and intensive grazing are key strategies to preserving Biome Pampa. Nonetheless, in fields where the invasion has already occurred, grazing must be maintained, cattle quarantined practiced, along with strategies that reduce cover and prevent the spread of *E. plana*. Liming and fertilising native grasslands improve their potential to compete with *E. plana*. The wiper applicator, a device that allows glyphosate herbicide application selectively to *E. plana*, is an important component of the integrated weed management system, especially with very severe infestations. Establishing strategies to contain or manage *E. plana* should be a priority to preserve the biodiversity of the Pampa. In the future, innovative options could also help prevent new invasions.

KEYWORDS
allelopathy, biotechnology, grassland, invasive weed, rangeland, weed ecology, weed management

1 | INTRODUCTION

Invasion of the Pampa is the main consequence of the *Eragrostis plana* (South African lovegrass) introduction in South America. The biome, which stretches across Southern Brazil, Uruguay, Northeast Argentina, and part of Paraguay, covers 500 000 km^2 (Pallarés et al., 2005). In Southern Brazil, the Pampa comprises about 63% of Rio Grande do Sul (RS) state, and grassland is the predominant vegetation (Cordeiro & Hasenack, 2009). Grasslands are essential for livestock exploitation, representing about 90% of the food source of cattle and sheep (Nabinger et al., 2009). Cattle were first introduced east of the Uruguay River in the 17th century, and then feral cattle spread rapidly over a large area towards Southern Brazil (Cordeiro & Hasenack, 2009). Conserving high species diversity is essential for biome and livestock production. Thus, sustainable grazing is necessary to maintain grassland diversity, preserve the soil, and prevent *E. plana* expansion.

Once *E. plana* has invaded a grassland, the consequences for livestock production are unavoidable. The average annual live weight beef production in RS in *E. plana*-infested areas can vary from 45 to 70 kg per hectare (Nabinger et al., 2009); this can be increased to 410 kg ha^{-1} per year through good management—for example, adjusting the number of grazing animals per area, fertilising fields, and controlling weeds (Perez, 2015). In 2009, it was estimated that 1000 000 ha of the biome was invaded by *E. plana* (Medeiros et al., 2009). Many more areas have likely been compromised, some covered with more than 90% *E. plana* compared to the native species (Pérez, personal communication, November 2015). The effect of grazing to attenuate invasion is insignificant since animals prefer short-statured native species in Southern Brazil; however, when grazing is suppressed in already invaded land, *E. plana* proliferation increases, as will be explained later.

South African lovegrass (*E. plana*), a C4 grass native to South Africa (Pyšek et al., 2020), is an aggressive and phytotoxic invasive species in South America, densely propagated in native Pampa grasslands (Figure 1). *E. plana* entered Brazil accidentally mixed with forage seeds imported from Africa. As suggested by Reis and De Oliveira (1978), although still unclear, the species may have entered on

FIGURE 1 Rangeland invasion of *Eragrostis plana* in Bagé, RS, Southern Brazil. Photograph: Fabiane Lamego.


SUPLEMENTO RURAL 7

Capim Annoni S 2
uma revolução em forrageiras

Aproveite a Feira do Terneiro
e venha conhecer
de 24 a 26 de Maio
a demonstração
com "CAPIM ANNONI S 2"
na Cabanha da Lagoa — Carazinho

FIGURE 2 Brochure promoting South African lovegrass as forage in Brazil (Extract from the rural supplement of the newspaper Correio do Povo, RS, 1978). Photograph: Diana Zabala-Pardo.

FIGURE 3 *Eragrostis plana* morphology. (A) Flattened basal leaves, (B) ciliated ligule (C) fasciculated root (D), plant growing at the roadside (E) and (F) panicles with spikelets. Photographs: Diana Zabala and Julia Nachtigall.

imported *Chloris gayana* Kunth and *Eragrostis curvula* (Schrad.) Nees seeds. According to these authors, in 1951, a commercial group started to grow and market *E. plana* seeds under the common name of "capim-annoni" as an excellent and revolutionary forage (Figure 2).

The features used to promote *E. plana* as a forage make it a thriving invader. These plants are tolerant to drought and grazing, efficient at capturing resources even in degraded soils (Medeiros & Focht, 2007), the roots are dense and highly developed (Reis Leite, 1993, Figure 3), and the tussocks are difficult to eliminate by mechanical cutting or uprooting in clay soils, due to its hardy tissues. Livestock avoid the invasive weed allowing it to grow and spread. *E. plana* has low nutritional quality and leaf consumption causes teeth loss (Reis Leite, 1993). Seeds that have passed through the digestive tract of animals are still viable (Reimche et al., 2022; Reis & De Oliveira, 1978). In 1979, the Ministry of Agriculture of Brazil prohibited the commercialization, transport, import, and export of the species. Since then, research on *E. plana* in Brazil and Uruguay, the most affected countries, has focused on understanding the biology and ecology of this species, its anatomy, distribution, competitiveness with native grasses, growth, development, germination potential, seed longevity, light, temperature, and osmotic potential response and allelopathy, in order to find management tools.

This review aims to compile the current knowledge of *E. plana* since its unintentional introduction in Southern Brazil, and how we can use it for integrated management of the species to prevent the impact of livestock and biodiversity losses in the Pampa. Future management perspectives are also discussed.

2 | ORIGIN AND INVASION

Eragrostis plana is native to the African steppes, ranked as an invasive species in 10 regions worldwide, and particularly problematic in South America (Pyšek et al., 2020). The genus *Eragrostis* has two diversity centres, Africa with around 150 species and the Americas with 135. North America has 43, Central America 25, and South America 67 native and 21 exotic species. Brazil has the largest number of *Eragrostis* taxa in South America (53), including 38 native, seven endemic, and 15 brought from Europe, Africa, and North America (Boechat & Longhi-Wagne, 2000). A recent study presenting a global perspective on genome size variation and evolution in the genus *Eragrostis* indicates that the variation detected allows the species to spread worldwide (Hutang et al., 2023).

Once *E. plana* entered Brazil, it spread rapidly. Cattle only graze on the plant when it is young or selectively on panicles, the most palatable part of the adult plant (Reis Leite, 1993), but if other species are available, they reject it. By 2012, *E. plana* occupied 23% of natural grasslands in southern Brazil, which covers about 5 million hectares (Focht & De Medeiros, 2012), meaning that about 1150 000 hectares were invaded by the species. In this region, *E. plana* is widely spread mainly along roadsides and in the natural grassland (Medeiros & Focht, 2007). It also occurs to a lesser extent in other Brazilian states such as Santa Catarina, Paraná, São Paulo, Mato Grosso, Mato Grosso do Sul, Bahia, Tocantins, and Pará, in addition to the Federal District (Medeiros et al., 2009), Uruguay and Argentina (Barbosa et al., 2013).

Eragrostis plana invasion is controlled by abiotic factors such as water deficit, road density, climate, and land use, and biotic factors in terms of its interaction with native species in the host community (Guido et al., 2016; Guido et al., 2019). Grassland disturbances, such as soil scarification and heavy grazing, facilitate *E. plana* invasion (Baggio et al., 2018). Evaluating different degrees of grassland invasion in the Brazilian Pampa established that *E. plana* affects species richness in the plant community. The most affected species group shares a similar niche with *E. plana* (Dresseno et al., 2018), which influences the composition, structure, diversity, and forage quality of native grasses (Medeiros et al., 2009).

Human intervention and grazing support invasion by *E. plana*, and its rejection by cattle favours its spread. Grazing has been practiced since the 17th century; as such, plant species have co-evolved in response to grazing, exhibiting adaptations such as meristem protection and high regrowth capacity (Baggio et al., 2018). A community invaded by *E. plana* increases leaf hardness, which means less consumable forage for cattle (Guido et al., 2021). This causes overgrazing of native species, thereby promoting *E. plana* invasion. However, grazing exclusion leads to changes in community composition and decreased diversity (Baggio et al., 2018). Removing livestock from this ecosystem is not advisable, because it would alter community diversity and resistance to invasion. Thus, practices such as rotational or continuous grazing would ensure community composition (Baggio et al., 2018). Previously investigated mechanical, manual, or chemical removal strategies are unable to eradicate the weed. In addition, even when the invasive species was controlled, original community recovery was not possible, at least during the 3 years of a study, which implies that community recovery would require more time or restoration strategies (Guido & Pillar, 2017).

3 | BIOLOGY

3.1 | Life cycle, botany, and anatomy

Like most invasive species, *E. plana* has a high reproductive and propagation capacity. The baseline chromosome count for *Eragrostis* is $x = 10$ chromosomes (Streetman, 1963). Polyploidy is common within the genus (69% are polyploid), where *E. curvula*, one of the most widely studied species, contains ploidy levels from 2× to 8× (Garbus et al., 2019; Ingram & Oyle, 2003). According to cytometric analyses, *E. plana* is diploid (Caratti, 2019). The chromosomal counts of two *E. plana* populations confirm a somatic number of $2n = 20$ (Pastori et al., 2009). Field observations and research findings indicate that *E. plana* is preferentially an allogamous species, and a study investigating the transgenerational effect of stress on the weed also considered it allogamous (Fipke et al., 2022). Flowering (Figure 3) occurs in late spring or summer until the first frosts. The seeds (caryopses, Figure 4) are formed in mid-December, a period of increased production, until March (Reis Leite, 1993). A single plant can produce around 64–90 tillers and 30–68 panicles per year (Caratti, 2019). A single panicle contains 146 spikelets (Coelho, 1983) and 1250–1800 seeds, meaning that one plant can produce 37 000–111 000 seeds (Caratti, 2019). Accordingly, in a field with 40 plants m^{-2}, 11 of which are in bloom, each with 12 panicles, will result in 132 panicles m^{-2}, that is, 1142 857 056 seeds ha^{-1} (Coelho, 1983).

C4 plants are highly productive at high temperatures and low relative humidity. *Eragrostis plana* leaves are amphistomatic with paracytic stomata (Favaretto, Santos, et al., 2015). Cell wall thickening and lignification in the genus *Eragrostis* results in high tensile strength and greater tolerance to drought and mechanical damage (Balsamo et al., 2006). Leaves have a Kranz structure (Figure 5A) and two sizes of collateral vascular bundles (Favaretto, Santos, et al., 2015). Roots have a parenchymatic pith with starch storage cells (Favaretto, Santos, et al., 2015), and aerenchym extension (Caratti, 2019; Favaretto, Santos, et al., 2015).

3.2 | Seed biology

Eragrostis plana seeds exhibit high germination rates, germination speed, survival rates, and biomass per individual (Roitman et al., 2022). After 24 h at 25°C, constant humidity, and a 12 h photoperiod, 73.3% of the seeds germinated (Guido et al., 2017). Although the ideal germination temperature is 35°C (Bittencourt et al., 2017; Maldaner et al., 2019), the species can germinate between 12.3 and 40°C (Bittencourt et al., 2017; Caratti, 2019). The secondary dormancy of *E. plana* seeds can be broken by cold (Medeiros et al., 2014). Light is a favourable condition, albeit not required for germination (Caratti, 2019). Indeed, E. *plana* germination is difficult when buried more than 3 cm deep (Caratti, 2019), and when placed on the soil surface, the emergence rate was 87% (Bittencourt et al., 2017). Burial depth is directly associated with physical and physiological seed integrity, and viable seeds were collected up to 20 cm deep within 2.5 years of burial (Medeiros et al., 2014). Germination, which is closely related to water potential, could vary from 0 to 98% when potential varies from −1.2 to 0 MPa (Bittencourt et al., 2017). Germination is also possible after periods of water restriction, which means resiliency to desiccation (Bittencourt et al., 2017). *E. plana* seed dispersion occurs mainly by endozoochory (Lisboa et al., 2009; Reimche et al., 2022; Schaedler et al., 2021). A high proportion of seeds consumed by cattle are excreted, but only a fraction are still viable. Digestion is the main cause of the disappearance and loss of germinative power (Lisboa et al., 2009). A seven-day quarantine is sufficient to clean the cattle digestive tract (Lisboa et al., 2009).

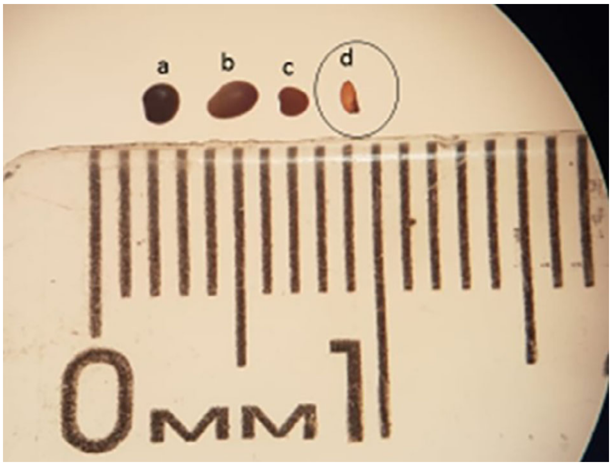

FIGURE 4 *Eragrostis plana* seeds (d) compared with forage seeds. (A) *Lotus corniculatus* L., (B) *Trifolium pratense* L., (C) *Trifolium repens* L. *E. plana* seed size: width 0.66 mm and length 1.33 mm. Photograph: Miriany Bonfada.

4 | IMPACTS ON NATURAL GRASSLANDS

4.1 | Overall impact

The *E. plana* invasion of Brazilian grasslands threatens Pampa diversity and the livestock economy of RS. Brazil is the largest beef exporter in the world, with about 12 million cattle in RS alone (Nespro, 2023). In the Brazilian Pampa, grasslands are the dominant ecosystem, and grasses the dominant species group (Vasconcelos et al., 2018). These native ecosystems, with their high diversity and species richness (Boldrini et al., 2009), have provided ecosystem services to society, mainly through cattle production (Overbeck et al., 2007). Livestock farming and species co-evolution due to grazing, shape the current plant community (Baggio et al., 2018; Overbeck et al., 2007). However, the *E. plana* invasion has changed the landscape, threatening ecosystem diversity and livestock in Southern Brazil. *E. plana* has reduced the total richness of the

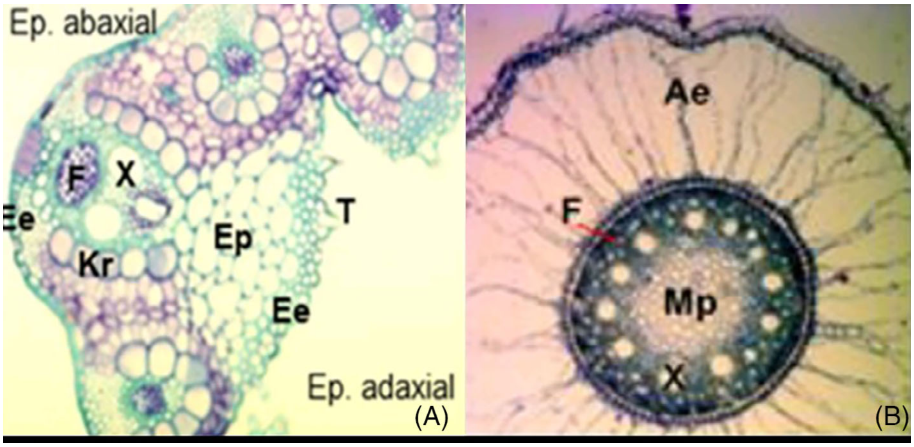

FIGURE 5 Cross section of the leaf (A) and root (B) of *Eragrostis plana*. Ep. Abaxial (abaxial epidermis); Ep. Adaxial (adaxial epidermis); F (phloem); X (xylem); Ee (sclerenchyma extension); Kr (Kranz anatomy); Ep (parenchymatic extension); T (trichomes), Ae (aerenchyma); Mp (parenchymal cord), under 20× objective lens. Adapted from Caratti (2019).

Pampa, grass species being the most affected (Dresseno et al., 2018). Between 1985 and 2019, the economic cost of invasive species to Brazil was 105.53 billion dollars, 98.9% attributed to damages and losses and 1.1% to management investment (prevention, control, or eradication) (Adelino et al., 2021), and *E. plana* accounted for 109.43 million dollars. Without *E. plana* management, it would cover 90% of native grassland (Perez, 2015).

4.2 | Interference through competition

Eragrostis plana is a successful species competing for resources (water, nutrients, and light). Stressful conditions such as drought or other resource-limiting scenarios might favour the invasion process (Guido et al., 2016). Competitiveness would be linked to its centre of origin since African soils are low in nitrogen (N). Plants that grow in these soils develop N-capture abilities in degraded soils, such as grassland soils in Brazil. These plants produce very dense tillers with erect culms, and reduced leaf area, traits present in *E. plana* (Medeiros & Focht, 2007). Low water availability would have positive effects on *E. plana* cover. Guido et al. (2016) propose that water stress provides temporal heterogeneity of resource availability, opening a window for invasive species to colonise. Indeed, the global aridity index is directly related to the *E. plana* invasion in the Pampa. Although this biome has well-distributed rainfall regimes, prolonged drought periods have occurred in recent decades, mainly in the southwest of RS (Leivas et al., 2006). Water deficit tolerance enables *E. plana* to over-compete with other weeds. When subjected to water deficit at different developmental stages, *E. plana* is mainly affected at the initial stages. Tillering is the stage most tolerant to water deficit, measured in terms of stomatal conductance and relative leaf water content (Bastiani et al., 2024). The root system is deep (up to 40 cm) and highly developed (Abichequer et al., 2009; Reis Leite, 1993), and under water stress, dry mass allocation to the root increases (Bastiani et al., 2024). This species can increase antioxidant system activity even under moderate stress, preventing reactive oxygen species accumulation, and, as stress abates, the plant rapidly induces osmolyte production to recover (Bastiani et al., 2024).

Studies that compare the growth of an invasive species in competition with coexisting native species make it possible to establish the real impact of an invader (Dresseno et al., 2018). In competition with the native grass *Paspalum notatum* Flüggé, *E. plana* responds faster to water stress (Bastiani et al., 2024). *E. plana* in the field develops an extensive root system, up to 66% larger than in native species (Abichequer et al., 2006). In a similar study, the interspecific and intraspecific competition of *E. plana* was evaluated (Guido et al., 2019) in relation to the native species *Aristida laevis*, *E. neesii*, and *P. notatum*. The type of neighbouring species determined the response to competition. For *E. plana*, intraspecific competition was larger than its interspecific counterpart. *Eragrostis plana* affected the native species negatively, and its growth was positively or neutrally stimulated in interspecific competition conditions, implying high tolerance to competition.

4.3 | Interference through allelopathy

Allelopathy may be one of the key traits of *E. plana's* success as an invader in Southern Brazil (Coelho, 1983; Favaretto, Chini, et al., 2015; Ferreira et al., 2008; Medeiros & Focht, 2007). Early studies showed that extracts and decomposing plant remains caused a significant decrease in the germination of *P. notatum*, *Setaria sphacelata*, *Trifolium repens*, and *Lolium multiflorum* (Ferreira et al., 2008; Coelho, 1983), forage used by producers in Southern Brazil, where *E. plana* occurs. *E. plana* crude extracts affected the development of the radicle and shoot of the cultivated species lucerne (*Medicago sativa*) and wheat (*Triticum aestivum*) (Bittencourt, Trezzi, Teixeira, et al., 2018). This led to the study of the active compounds involved in the allelopathic potential of *E. plana*. In the histological sections of the leaves and roots, phenols and alkaloids associated with their allelopathic effect have been identified (Favaretto, Chini, et al., 2015). High-performance liquid chromatography confirmed the presence of alkaloids, flavonoids, and saponins in the leaves, roots, and rhizosphere (Bittencourt, Trezzi, Teixeira, et al., 2018; Favaretto, Chini, et al., 2015). These compounds included caffeic, coumaric, ferulic, gallic and vanillic acid, catechin, epicatechin, resveratrol, and rutin in amounts that vary according to organ and soil profile depth (Bittencourt, Trezzi, Teixeira, et al., 2018; Favaretto, Chini, et al., 2015). Catechin, epicatechin, and ferulic acid are found in high concentrations on the soil surface where *E. plana* grows, being released by the decomposing tissues, while coumaric acid is found deeper in the soil, indicating that in addition to being decomposition products, they are also released by the root system (Bittencourt, Trezzi, Da Silva Bonome, et al., 2018).

Additional work seeking to isolate the compounds responsible for *E. plana* allelopathy resulted in eight neocassane diterpenoids (Favaretto et al., 2019; Klein Hendges et al., 2020). Three of these, isolated from *E. plana* roots, were phytotoxic in *Ipomoea grandifolia* (Dammer) O'Donnell and *Euphorbia heterophylla* L. In addition, the three compounds together inhibit weed growth (*Lemna paucicostata* L.) and one exhibited fungicidal activity against *Colletotrichum fragariae*, *C. acutatum*, and *C. gloeosporioides* (Favaretto et al., 2019). Of the five remaining terpenes, one demonstrated powerful phytotoxic activity on the growth of *I. grandifolia* roots and *E. heterophylla* shoots. Likewise, another compound reduced the germination index of *E. heterophylla* even more effectively than the glyphosate herbicide (Klein Hendges et al., 2020). Moreover, allelopathic potential increases with nitrogen fertilisation, and phenolic compound concentration increases in the reproductive stage (Cecchin et al., 2017). In addition, allelopathic compounds have an autotoxic effect on *E. plana*, reducing germination and growth in the early development stages, which could potentially control the species (Favaretto et al., 2017).

5 | INVASION MANAGEMENT

Native grasslands provide ecosystem services to society, livestock farming being one of the main economic activities in the Brazilian

Pampa. Indeed, grazing is considered the main factor in maintaining the ecological properties and physiognomic characteristics of grasslands (Overbeck et al., 2007). Thus, livestock production and ecosystem conservation are key factors in *E. plana* management. Prevention is essential, safeguarding against invasion in new areas by avoiding soil disturbance such as scarification or intense grazing (Baggio et al., 2018). Livestock should be quarantined before entering non-infested grasslands. In areas where *E. plana* is already present, grazing exclusion is not an option, since this decreases species richness and affects community composition (Baggio et al., 2018). As such, promoting the growth and development of native grasses is recommended. In addition, in highly infested areas, reduced *E. plana* cover strategies, such as physical or mechanical removal and chemical control under technical supervision, have already been implemented. These are described below.

5.1 | Cultural management

In grasslands used for livestock production, practices that promote vigorous and dense native grass growth prevent *E. plana* invasion. In rotational grazing systems, when native grasses were kept around 10 cm high, resources were scarce for *E. plana* establishment (Faleiro et al., 2021). In addition, fertilisation confers competitive advantage to grasslands over *E. plana*. The biome is composed of summer grasses with high biomass production at high temperatures (spring/summer), albeit with low quality (Schaefer et al., 2009). Introducing other grasses without replacing their natural counterparts improves protein levels and forest digestibility in the agroecosystem, increasing potential yields and lowering production costs (Barcellos & Villela, 1994; Maraschin, 1997). Introducing *Arachis pintoi* and adding phosphate and potassium fertilisers to a native grassland enhanced biomass production (Schaefer et al., 2009). In addition, applying 200 kg of N ha^{-1}, 190 kg ha^{-1} of P_2O_5, and 140 kg ha^{-1} of K_2O contributed to enhancing Pangola grass (*Digitaria eriantha*) growth and reducing *E. plana* growth, promoting a higher control index (Faleiro et al., 2021). In another study, liming and fertilisation, as recommended for pastures in Southern Brazil, favoured native grass and stunted *E. plana* growth, promoting higher native grass species height, resulting in ground shading and reducing invasive species growth (Abichequer et al., 2022). In areas outside native grasslands, where the invasive species also occurs, growing forage in winter followed by a crop (soybean, rice) in summer, reduced *E. plana* expansion, as shown in a soil seed bank assessment (Lamego et al., 2020). After 6 years, few seedlings emerged from the soil collected at a depth of 0–5 cm when compared with an infested area without *E. plana* management. Crop rotation is an alternative to cultivated pasture, but not recommended in the Pampa because conserving native grassland is the primary objective (Reis & Coelho, 2000).

5.2 | Physical and mechanical control

Defoliation and depletion of root resources reduce *E. plana* growth. An extensive and deep root system is critical to *E. plana* competition because it helps access water and nutrients (Abichequer et al., 2009). *E. plana* roots have greater resource allocation when compared to those of other grasses. Although severe defoliation affects shoot growth, it does not affect the roots. Cutting plants 5 cm from the ground in the early stages reduces the size and yield of *E. plana* (Scheffer-Basso et al., 2012). These data suggest that early mowing of the weed, a few centimetres above ground level, could reduce weed growth. However, for this to be effective, it should be repeated often enough to deplete the root reserve (Favaretto, Santos, et al., 2015). Other mechanical methods such as ploughing decrease the number of *E. plana* plants but increase the bare soil area. The weed itself, which has a large seed bank, and other weed species can quickly take advantage of this situation, thereby compromising the preservation of native grass species (Faleiro et al., 2022).

Although prohibited in RS, controlled burning was evaluated as a weed control method. The results showed that, as an isolated strategy, it did not reduce *E. plana* density, but reduced the exposed soil area (Faleiro et al., 2022). However, when burning occurred 7 days before pre-emergent herbicide application in an experimental study, it facilitated herbicide disposal in the soil, improving weed control (Goulart et al., 2009). Nevertheless, burning is not recommended because it affects the native species development and could cause more damage to native plants than to *E. plana* itself (Faleiro et al., 2022).

5.3 | Chemical control

Studies have evaluated glyphosate for *E. plana* control (Bastiani et al., 2021; Caratti et al., 2022; Faleiro et al., 2022). In plants with four tillers, 1080 g ae ha^{-1} of glyphosate controlled over 90% (Faleiro et al., 2021), and at the 2–3 tiller stage, 700 g ae was enough to control it (Caratti et al., 2022). Bastiani et al. (2021) found that the potassium salt in glyphosate had the fastest activity in different *E. plana* growth stages, but panicle initiation was the most vulnerable, and adding ammonium sulphate to the herbicide mix tank increased the control of drought-stressed plants. According to Merotto et al. (2022), glyphosate diammonium salt, applied with a wiper applicator (8–40 L ha^{-1} volume application), was the most effective formulation when applied in summer at 1440 g ae ha^{-1}.

Other post-emerging herbicides inhibiting acetyl-CoA carboxylase and acetolactate synthase have been tested; however, they are not as effective as glyphosate. With cyhalofop-butyl (315 g active ingredient (ai) ha^{-1}), between 16% and 70% weed inhibition was achieved depending on water and light availability, while with sethoxydim values ranged from 75% to 87%. However, in the same study, close to 100% weed inhibition was obtained under all conditions with a glyphosate dose of 1080 g ae ha^{-1} (Faleiro et al., 2021). Fluazifop-p-butyl has also been evaluated at 187.5 g ai ha^{-1}, but only 20% inhibition was achieved. However, in association with glyphosate (1440 g ae ha^{-1}), it was 99%, in contrast to the 73% obtained with glyphosate alone (Caratti et al., 2018). In addition, Fipke et al. (2022) showed that the amount of quizalofop-p-ethyl required to cause 50% damage to

FIGURE 6 Selective glyphosate wiper applicator (Campo Limpo®) for *Eragrostis plana* control (Perez, 2015).

plants (ED_{50}) is 10.3 g ha^{-1}. For imazethapyr (184 g ai ha^{-1}) inhibition ranged between 34% and 80%. Finally, when glyphosate (700 g ae ha^{-1}) is applied with fluazifop-butyl (47 g ai ha^{-1}), root translocation increases, thereby preventing rapid regrowth (Caratti et al., 2022).

Pre-emergent herbicides (alachlor, ametrine, atrazine, clomazone, diuron, flumioxazin, imazaquin, mesotrione, metribuzin, oxadiazon, S-metolachlor, sulfentrazone, terbuthylazine, and trifluralin) were evaluated in *E. plana* control (Goulart et al., 2009). Although all the herbicides were efficient in controlling weeds in the greenhouse, many of them perennial species, in the field, the heterogeneous development stages meant there was no satisfactory control. Nonetheless, mowing or burning before herbicide application improved efficiency.

As shown above, some herbicides can potentially control *E. plana*, glyphosate being the most effective. However, in Pampa grasslands, herbicide spraying is not indicated or permitted, given the possible damage to the native species and the biome. One option developed for heavily infested areas is a machine called Campo Limpo® (Bastiani et al., 2021), developed by Embrapa. The herbicide is applied selectively, by direct contact only with the leaves, using ropes moistened with herbicide through a wiper applicator (Figure 6). With this system, as many as 80% or more can be controlled without damaging native grass (Perez, 2015). Grassland should be grazed before machine use to create a difference in plant height since *E. plana* rejected by the animals will be taller than native species, which are grazed preferentially. Technical support from the Brazilian Agricultural Research Corporation (Embrapa) teaches farmers how to use the machine properly, without damaging the grassland (Pérez, 2010; Perez, 2015; Faleiro et al., 2022; Merotto et al., 2022).

5.4 | Integrated *E. plana* management

E. plana management is complex and requires integrating biological and ecological knowledge of the species and tools developed to date. Prevention is essential and recognising and distinguishing it from native grasses is critical. This would allow the removal of any plant before it establishes itself or spreads from roadsides or pasture margins to weed-free fields, thereby avoiding re-infestation. In addition, any machinery entering pastures must be clean and free of contaminating seeds, and cattle must be quarantined for a minimum of 7 days.

The previously mentioned management practices should be used jointly as part of an integrated weed management system. Faleiro et al. (2021) explored the integrated use of practices such as liming, fertilisation, forage crops, and herbicides. The herbicides tested were clethodim and the four formulations of glyphosate listed above. Crops were elephant grass (*Pennisetum purpureum*), pangola grass (*Digitaria eriantha*), foraging peanut (*Arachis pintoi*), and birdfoot clover (*Lotus corniculatus*). Physical and mechanical practices such as mowing, burning, and soil inversion were also evaluated. The authors concluded that isolated physical-mechanical management practices are not efficient; however, integrated methods such as liming, fertilisation, and the use of glyphosate together with the integration of Pangola grass (*Digitaria eriantha*) without removing native grasses, produced the best results.

Embrapa suggests four *E. plana* management strategies in invaded grasslands: (1) weed control based on the wiper applicator (glyphosate); (2) pasture fertilisation (based on soil analysis); (3) grass sowing (introduced in areas with high *E. plana* infestation without removing natural grasses); and (4) quantity control of animal grazing (Perez, 2015). Grazing exclusion is not viable in invaded grassland, but in *E. plana*-free areas, soil disturbance, and intensive grazing should be avoided.

6 | CHALLENGE AND FUTURE PERSPECTIVES

The study of *E. plana* as invasive species is more recent than that of other weeds. In Brazil, research has concentrated on the botanical, anatomical, phytosociological, physiological, and biochemical aspects. Genomics and transcriptomics data could increase understanding of *E. plana* invasiveness, biology, and ecology. A study based on next-generation sequencing tools is underway (Lamego et al., 2022). In the first phase, 53 million reading pairs were generated, describing 369 Mb of the genome (Illumina). Transcriptomics is still ongoing.

Finally, in pursuit of tools beyond classic management methods, Embrapa is conducting collaborative research on RNAi technology with other organisations (Zabala-Pardo et al., 2022). The focus of this approach is to avoid seed production and dissemination. RNAi technology has been implemented in pest and disease management (Dias et al., 2020; Mcloughlin et al., 2018); however, this technique is still incipient in weed science, as are many bioinformatics tools in this area, which delays progress. RNA interference (RNAi) is a biological process in which RNA molecules are involved in sequence-specific suppression of gene expression by double-stranded RNA, through translational or transcriptional repression (Zabala-Pardo et al., 2022).

RNAi in pest and disease management has made progress using large double-stranded RNAs (> 26 nucleotides)—dsRNAs. However, dsRNAs are not suitable for weed management. Once present in the cell, dsRNAs may result in different-sized siRNAs, making it difficult to predict potential targets. Using siRNAs, which are more specific, may induce effects as a function of their size. The 21-nucleotide (nt) siRNAs induce post-transcriptional gene silencing (PTGS), 22-nt siRNAs produce PTGS and secondary siRNAs, and 24-nt siRNAs are involved in DNA methylation or RNA-directed DNA methylation (RdDM) (Dalakouras & Papadopoulou, 2020; Erdmann & Picard, 2020). For weed management, the ideal situation would be to have accurate molecules with maximum effect, that is, siRNAs being systemic and inducing secondary silence. Furthermore, siRNAs could guarantee crop or forage selectivity (no off-target effects), leading to a new weed management era.

Rice was used as a model plant, and siRNAs that silenced the *phytoene desaturase* gene in rice seedlings were designed and tested (Zabala-Pardo, 2023). Based on these results and advances in *E. plana* transcriptome, ongoing research is being conducted on the siRNAs designed to silence genes or transcription factor genes on *E. plana*, usually regulated by microRNAs and related to flowering and transition to the reproductive stage. This strategy can help avoid/reduce seed dispersal.

7 | CONCLUSIONS

Eragrostis plana, an aggressive C4 plant introduced in Brazil in the 1950s, has already invaded more than one million hectares in the Pampa. In non-intervened Pampa areas, *E. plana* invasion and cattle grazing must be avoided. In areas where grazing has occurred for decades, using *E. plana* as forage favoured its invasion. The ecological attributes of *E. plana* and its rejection by cattle make it difficult to contain and control effectively. The strategies to control *E. plana* presented here are efficient when used together. However, grassland recovery (weed-free) takes time and requires livestock farmers to persist with a weed management programme, which does not usually occur. The future of the Pampa and livestock production based on natural grasslands are threatened and need to be taken seriously by farmers and society. Quarantining livestock should be prioritised to prevent *E. plana* seed dissemination. New strategies such as those based on RNAi will hopefully be available as well as complementary tools, aimed at preserving the biome's biodiversity.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data included in article/supplementary material/referenced in article.

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