



Grasses as suitable targets for classical weed biological control

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Abstract Grasses are amongst the most abundant and environmentally damaging invasive weeds worldwide. Biological control is frequently employed as a sustainable and cost-effective management strategy for many weeds. However, grasses have not been actively pursued as targets for classical weed biological control due to a perceived lack of sufficiently specialised and damaging natural enemies to use as biological control agents. There are also concerns that the risk posed to economically important crop/pasture species and closely-related native species is too great to consider implementing biological control for inva-

sive grasses. In this paper, we review the literature and demonstrate that grasses can possess suitably host-specific and damaging natural enemies to warrant consideration as potential biological control agents. The risk of grass biological control is no greater than for other weedy taxa if practitioners follow appropriately rigorous risk assessments protocols.

Keywords Invasive grass · *Arundo donax* · *Phragmites australis* · *Tetramesa* · *Andropogon gayanus* · Host specificity

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Introduction

Grasses (Poaceae) are one of the most successful angiosperm families worldwide, consisting of ~ 11,000 species (Linder et al. 2017). They occupy a greater land area than any other vegetation type, covering one-third of the globe and contribute approximately 33% of global primary productivity (Tscharntke and Greiler 1995). Grasses have been deliberately translocated into many non-native regions across the globe (Cook and Dias 2006), making some of them amongst the most widespread and abundant weeds of natural and agricultural habitats worldwide (Daehler 1998; Pyšek et al. 2012). This is particularly notable for grasses of African origin that were introduced into the Americas and Australia, amongst other countries, in the 1900's, to improve the quality of pastures and forage for grazing livestock (Williams and Baruch 2000; Cook and Dias 2006; van Klinken and Friedel 2017). Approximately 2250 grass species (~ 22% of the world's grass species pool) have been introduced into Australia (Cook and Dias 2006; van Klinken and Friedel 2017). Many grasses were planted widely (providing ample propagule pressure), and in many instances, multiple agronomic lines were introduced during this period (increasing intra-specific genetic diversity) (Firn 2009), both of which are strong predictors of invasion success (Hui and Richardson 2017).

The Poaceae (4807 species) is second to only the Asteraceae (5094 species) in terms of the total number of weedy species per plant family worldwide (Randall 2017), including three of the world's top 100 invasive species, namely: *Arundo donax* L. (giant reed), *Imperata cylindrica* (P.) Beauv. (cogon grass) and *Spartina anglica* C.E. Hubbard (smooth cordgrass) (Lowe et al. 2000). Grasses are not only over-represented on inventories of invasive alien plants (Daehler 1998; Pyšek et al. 2012), but have a disproportionate impact on ecological functionality, biogeochemical cycles and human-kind (Linder et al. 2017). Indeed, grass invasions are associated with significant negative environmental and economic consequences. The negative impacts associated with invasive grasses have been thoroughly reviewed (e.g. D'Antonio and Vitousek 1992; Williams and Baruch 2000; Godfree et al. 2017), and include, but are not limited to: reducing native biodiversity, threatening native plant and wildlife populations, reducing grazing

and agricultural productivity, altering fire regimes and disrupting nutrient cycling and other ecological processes (see Fig. 1 for examples).

High-impact weeds, such as many invasive grasses, are traditionally the focus of management programmes, being targeted for active control interventions, usually in the form of mechanical, chemical and/or bioherbicide control (Lake and Minter 2018). While these control methods can be effective, they require follow-up applications, and thus, can be exorbitantly expensive (Quirion et al. 2018). Moreover, the mechanical and/or chemical control of many grasses is not feasible over the spatial scales required for their effective management (Grice et al. 2012). Due to the requirement of repeated herbicide-applications to provide control, many invasive grasses have evolved herbicide-resistance, rendering this control method ineffective (Powles and Yu 2010). Concerns over the non-target impacts of herbicidal applications and mechanical removal on native species also limits their use (Crone et al. 2009; Ray et al. 2018).

Classical weed biological control (hereafter 'biological control') is a cost-effective and sustainable management option for the control of many invasive plants (McFadyen 1998; Zachariades et al. 2017). To date, 468 biological control agent species have been intentionally released against a diverse suite of invasive plants and across an array of environmental conditions, consisting of 175 weed entities from 48 different families, the majority of which belong to the Asteraceae (44 species), Cactaceae (25 species) and the Fabaceae (23 species) (Winston et al. 2014; Schwarzländer et al. 2018). Globally, 115 target weed species (65.7% of all weeds targeted) are under some degree of control through the action of biological control agents (Schwarzländer et al. 2018).

Historically, very few invasive grasses have been targeted for biological control (Pemberton 1996; Schwarzländer et al. 2018). This may stem from the perception that grasses support an unspecialised and insufficiently damaging natural enemy community to exploit for potential biological control agents (Gill and Blacklow 1984; Evans 1991; Pemberton 2002), while the risk of non-target damage posed to economically valuable crops and/or native biodiversity, by introducing grass biological control agents, is considered too great to warrant implementing biological control (Wapshere 1990). Surveys for natural enemies performed on *I. cylindrica* and *Sorghum halepense* (L.)

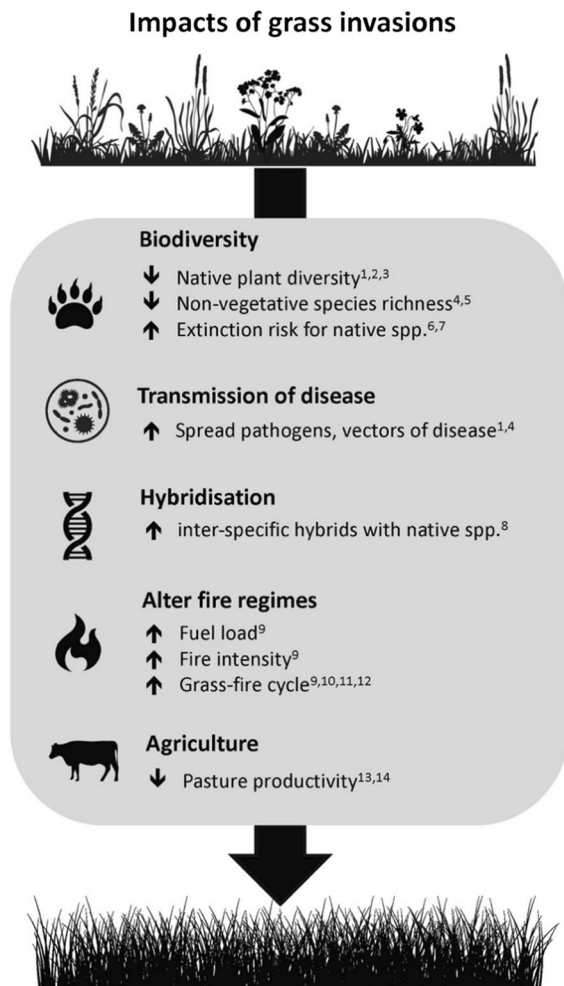


Fig. 1 Impacts associated with alien grass invasions, including examples from; ¹*Pennisetum setaceum* (D’Urso et al. 2017); ²*Brachiaria mutica* (Ferdinands et al. 2005); ³*Agropyron cristatum* (Heidinga and Wilson 2002); ⁴*Arundo donax* (Racelis et al. 2012; Moran et al. 2017); ⁵*Phragmites australis* (Benoit and Askins 1999); ⁶*Bromus inermis* (Williams and Crone 2007); ⁷*Cenchrus ciliaris* (Edwards et al. 2019); ⁸*Spartina alterniflora* (Ayres et al. 2004); ⁹*Andropogon gayanus* (Setterfield et al. 2010); ¹⁰*Melinis minutiflora* (D’Antonio and Vitousek 1992); ¹¹*Schizachyrium condensatu* (D’Antonio and Vitousek 1992); ¹²*Bromus tectorum* (D’Antonio and Vitousek 1992); ¹³*Eragrostis curvula* (Firn 2009); ¹⁴*Sporobolus* spp. (Witt and McConnachie 2004)

Pers. (Johnsongrass) in the 1970’s and 1980’s, which did not yield any suitable agents, reinforced the perception of grasses as poor targets for biological control (see Witt and McConnachie 2004).

Despite the largely negative stance on grass biological control in the literature, several authors

have suggested that the aforementioned arguments should not preclude the use of biological control for invasive grasses (Witt and McConnachie 2004; Overholt et al. 2016). To date, 23 invasive grasses worldwide have been investigated with regards to the potential for biological control using herbivorous arthropods and fungal pathogens (Table 1). Only *A. donax* (three agents) and *Spartina alterniflora* Loisel. (smooth cordgrass) (one agent) have had any biological control agents released against them (Table 1). Several of the remaining grasses, such as *Andropogon gayanus* Kunth. (gamba grass) and *Eragrostis curvula* (Schrad.) Nees. (African lovegrass), have not yet been subjected to a full-scale biological control programme, although preliminary surveys for potential agents are underway (S. Raghu and A. McConnachie pers. comm.).

Given the success of biological control for the management of other plant-life forms (Schwarzländer et al. 2018), and the relative unsuitability of traditional weed control methods for invasive grass management (e.g. mechanical and chemical control), practitioners may be missing an opportunity to control invasive grasses by avoiding biological control. A recent publication by Casagrande et al. (2018) argued that biological control of invasive grasses, and particularly *Phragmites australis* (Cav.) Trin. ex Steudel (common reed), is possible and that grass biological control should be utilised more often.

In this paper, we assess the suitability of biological control as a management option for invasive grasses. To do this, we asked: (1) are there sufficiently specialised, and (2) damaging natural enemies associated with grasses, to warrant pursuing biological control? Additionally, (3) are the risks of introducing biological control agents any greater for grasses than other weedy taxa? We then discuss which grasses may be suitable targets for biological control, and which natural enemies are most likely to satisfy the specificity and damage requirements imposed on candidate control agents.

We reviewed the literature by searching Google Scholar and CABI abstracts for examples of natural enemies associated with grasses that were host-specific and/or able to reduce host plant fitness (e.g. growth rate, reproductive output, density). We used various combinations of general keywords, such as ‘grass’ AND ‘natural enemy’, ‘herbivore’, ‘mite’, ‘fungal pathogen’; AND ‘host specific’, ‘host

Table 1 Summary and status of current and past biological control projects (listed alphabetically) considered for invasive grasses

Target weed (common name)	Country	Candidate agent			Key references
		Identity	Status	Control ^a	
<i>Andropogon gayanus</i> Kunth. (gamba grass)	Australia	–	Preliminary surveys underway	–	S. Raghu (pers. comm.)
<i>Arundo donax</i> L. (giant reed)	USA	Multiple potential candidates	–	–	Tracy and DeLoach (1998)
		<i>Tetramesa romana</i> Walker (Hymenoptera: Eurytomidae)	Already present; new genotypes of wasp from origin of invasive plant genotypes were released	Yes	Goolsby and Moran (2009); Goolsby et al. (2016); Marshall et al. (2018)
		<i>Rhizaspidiotus donacis</i> (Leonardi) (Hemiptera: Diaspididae)	Established, 2011	?	Goolsby et al. (2009a)
		<i>Lasioptera donacis</i> Coutin (Diptera: Cecidomyiidae)	Released, 2017	?	Goolsby et al. (2017)
	South Africa	<i>Tetramesa romana</i> Walker (Hymenoptera: Eurytomidae)	Already present	?	Angela Bownes (pers. comm.)
	<i>Rhizaspidiotus donacis</i> (Leonardi) (Hemiptera: Diaspididae)	Under evaluation	–	Angela Bownes (pers. comm.)	
<i>Avena fatua</i> L. (wild oats)	Australia	<i>Puccinia coronata</i> f.sp. <i>avenae</i> Corda (Uredinales)	Additional testing required	–	Johnston et al. (2000)
<i>Cortaderia jubata</i> (Lem.) Stapf (Purple Pampas grass)	New Zealand	<i>Ustilago quitensis</i> Lagerh. (Ustilaginales)	Under evaluation	–	Hayes (2015)
		<i>Saccharosydne subandina</i> Remes Lenicov and Rossi (Hemiptera: Delphacidae)	Under evaluation	–	Hayes (2015)
<i>Cortaderia selloana</i> (Schult. & Schult.f.) Asch. & Graebn. (Pampas grass)	New Zealand	<i>Ustilago quitensis</i> Lagerh. (Ustilaginales)	Under evaluation	–	Hayes (2015)
		<i>Saccharosydne subandina</i> Remes Lenicov and Rossi (Hemiptera: Delphacidae)	Under evaluation	–	Hayes (2015)
<i>Digitaria abyssinica</i> (A. Rich.) Stapf. (blue couch grass)	East Africa	Multiple potential candidates	–	–	Sileshi (1997)
<i>Echinochloa crus-galli</i> (L.) Beauv (barnyard grass)	Asia	Multiple potential candidates	–	–	Tosiah et al. (2009)
		<i>Emmalocera leucotaeniella</i> (Ragonot) (Lepidoptera: Pyralidae)	Additional testing required	–	Tosiah et al. (2009)
<i>Eragrostis curvula</i> (Schrad.) Nees. (African lovegrass)	Australia	–	Preliminary surveys underway	–	A. McConnachie (pers. comm.)
<i>Hymenachne amplexicaulis</i> (Rudge) Nees (West Indian marsh grass)	Australia	<i>Ischnodemus variegatus</i> (Signoret) (Hemiptera: Blissidae)	Pending approval	–	Diaz et al. (2009)

Table 1 continued

Target weed (common name)	Country	Candidate agent			Key references
		Identity	Status	Control ^a	
<i>Imperata cylindrica</i> (P.) Beauv. (cogongrass)	USA	Multiple potential candidates	–	–	van Loan et al. (2002); Overholt et al. (2016)
		<i>Acrapex azumai</i> Sugi (Lepidoptera: Noctuidae)	Additional testing required	–	Takasu et al. (2014)
		<i>Orseolia javanica</i> Kieffer & van Leeuwen-Reijnders (Diptera: Cecidomyiidae)	Additional testing required	–	Overholt et al. (2016)
<i>Megathyrus maximus</i> (= <i>Panicum maximum</i>) (Jacq.) B. K. Simon & S. W. L. Jacobs (Guineagrass)	USA	No suitable agents found	–	–	Simmonds (1972)
		Multiple potential candidates	Additional testing required	–	Mercadier et al. (2009); M. Cristofaro and J.A. Goolsby (pers. comm)
<i>Microstegium vimineum</i> (Trin.) A. Camus (Japanese stiltgrass)	USA	–	Too early to evaluate	–	Nestory (2016)
<i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth (Chilean needlegrass)	Australia	Multiple potential candidates	–	–	Briese and Evans (1998)
		<i>Uromyces pencanus</i> Arth. & Holw. (Uredinales)	Additional testing required	–	Anderson et al. (2017)
	New Zealand	<i>Uromyces pencanus</i> Arth. & Holw. (Uredinales)	Approved (pending export permits)	–	Anderson et al. (2017)
	South Africa	No suitable agents found	–	–	Wells (1977)
<i>Nassella trichotoma</i> (Nees) Hack. ex Arechav. (serrated tussock)	Australia	Multiple potential candidates	–	–	Briese and Evans (1998)
		No suitable agents found	–	–	Anderson et al. (2017)
	South Africa	No suitable agents found	–	–	Wells (1977)
<i>Panicum repens</i> L. (torpedograss)	USA	<i>Steneotarsonemus</i> (= <i>Parasteneotarsonemus panici</i>) (Mohanasundaram) (Acari: Tarsonemidae)	Additional testing required	–	Cuda et al. (2007)
<i>Phragmites australis</i> (Cav.) Trin. ex Steudel (common reed)	USA	Multiple potential candidates	–	–	Tewksbury et al. (2002)
		<i>Archanara geminipuncta</i> (Haworth) (Lepidoptera: Noctuidae)	Under evaluation	–	Blossey et al. (2018); Kiviat et al. (2019)
		<i>Archanara neurica</i> (Hübner) (Lepidoptera: Noctuidae)	Under evaluation	–	Blossey et al. (2018); Kiviat et al. (2019)
	<i>Platycephala platifrons</i> (Fabricius) (Diptera: Chloropidae)	Shelved—'second tier priority'	–	–	Häffiger et al. (2005)

Table 1 continued

Target weed (common name)	Country	Candidate agent			Key references
		Identity	Status	Control ^a	
<i>Rottboellia cochinchinensis</i> (Lour.) W.D. Clayton (itchgrass)	New World	<i>Sporisorium ophiuri</i> (P. Henn.) Vanky (Ustilaginales)	Additional testing required	–	Ellison and Evans (1995)
<i>Sorghum halepense</i> (L.) Pers. (Johnsongrass)	USA	No suitable agents found	–	–	Domenichini et al. (1989)
		Multiple potential candidates	–	–	Charudattan and deLoach (1988)
		<i>Bipolaris</i> spp. (Pleosporales)	Additional testing required	–	Winder and van Dyke (1990)
		<i>Sporisorium cruentum</i> (J.G. Kuhn) Vanky	Additional testing required	–	Gassó et al. (2017)
<i>Spartina alterniflora</i> Loisel. (smooth cordgrass)	USA	<i>Prokelisia marginata</i> (van Duzee) (Hemiptera: Delphacidae)	Established	?	Grevstad et al. (2003)
<i>Spartina anglica</i> C. E. Hubbard (English cordgrass)	USA	<i>Prokelisia marginata</i> (van Duzee) (Hemiptera: Delphacidae)	Additional testing required	–	Wu et al. (1999)
<i>Sporobolus natalensis</i> (Steud.) Dur. & Schinz (giant rat's tail grass)	Australia	<i>Tetramesa</i> sp. 1 (Hymenoptera: Eurytomidae)	Under evaluation	–	Witt and McConnachie (2004); G.F. Sutton (unpublished data)
		<i>Tetramesa</i> sp. 2 (Hymenoptera: Eurytomidae)	Under evaluation	–	G.F. Sutton (unpublished data)
		prob. <i>Bruchophagus</i> sp. (Hymenoptera: Eurytomidae)	Under evaluation	–	G.F. Sutton (unpublished data)
		<i>Ustilago sporoboli-indici</i> L. Ling (Ustilaginales)	Rejected; already present	?	Witt and McConnachie (2004); Yobo et al. (2009); Vitelli et al. (2017)
<i>Sporobolus pyramidalis</i> P. Beauv. (giant rat's tail grass)	Australia	<i>Tetramesa</i> sp. 1 (Hymenoptera: Eurytomidae)	Under evaluation	–	Witt and McConnachie (2004); G.F. Sutton (unpublished data)
		<i>Tetramesa</i> sp. 2 (Hymenoptera: Eurytomidae)	Under evaluation	–	G.F. Sutton (unpublished data)
		prob. <i>Bruchophagus</i> sp. (Hymenoptera: Eurytomidae)	Under evaluation	–	G.F. Sutton (unpublished data)
		<i>Ustilago sporoboli-indici</i> L. Ling (Ustilaginales)	Rejected; already present	?	Witt and McConnachie (2004); Yobo et al. (2009); Vitelli et al. (2017)

Table 1 continued

Target weed (common name)	Country	Candidate agent			Key references
		Identity	Status	Control ^a	
<i>Taeniatherum caput-medusae</i> (L.) Nevski (medusahead)	USA	Multiple potential candidates	Additional testing required	–	Widmer and Sforza (2004)
		<i>Fusarium arthrosporioides</i> Sherb. (Hypocreales)	Rejected	–	Widmer and Sforza (2004)
		<i>Aculodes altamurgiensis</i> de Lillo & Vidović (Acari: Eriophyidae)	Under evaluation	–	De Lillo et al. (2018)
		<i>Eurytoma</i> sp. (Hymenoptera: Eurytomidae)	Under evaluation	–	M. Cristofaro (pers. comm)

^aControl: Yes—effective biological control, ?—Too early to evaluate or unknown

specificity’, ‘monophagous’, ‘host range’, to search for relevant literature. We also used all the available literature on grass biological control projects to date that the authors have acquired over the years to extract examples directly from grasses that are either current or prior targets for biological control. Moreover, we searched for grey literature by using the above keyword combinations in a general Google search. We then manually checked the references of all seemingly relevant papers for additional material, and checked articles that cited each relevant paper for additional examples using the ‘cited by’ function in Google Scholar.

Grasses as suitable targets for biological control

Specificity of natural enemies

Most grasses lack the diversity and quantity of secondary chemical compounds (i.e. feeding deterrents, toxins, stimulants) typically found in dicotyledons, which are considered the primary drivers of herbivore specialisation (Ehrlich and Raven 1964; McNaughton et al. 1985; Moore and Johnson 2017; but see Kellogg 2015). Fewer than 0.2% of grasses produce alkaloids, while many other important secondary chemicals are almost entirely absent from grasses (McNaughton et al. 1985). Hence, grasses are

expected to harbour relatively unspecialised herbivore assemblages (Gill and Blacklow 1984; Wapshere 1990; Pemberton 2002). Biological control programmes require that at least one natural enemy demonstrates a sufficiently narrow host range to not pose any significant risk to economic crops and/or native biodiversity in the region of intended control. If grass-associated natural enemy assemblages are unspecialised, then it is expected that very few grasses may possess natural enemies that could serve as biological control agents.

Several invasive grass species that have been considered as possible targets for biological control possess at least one phytophagous insect, mite and/or fungal pathogen that could, or already has been, screened as a potential biological control agent (Table 1). Indeed, all 20 of the 23 invasive grasses listed in Table 1 that have been thoroughly surveyed for natural enemies in their native range have yielded candidate agents (i.e. not including *A. gyanus*, *E. curvula* and *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass); because only preliminary surveys for potential agents have been performed). The finding of candidate biological control agents on *I. cylindrica* and *S. halepense* is noteworthy as the lack of suitably host-specific herbivores recorded on these species during surveys in the early 1970’s and 1980’s was a significant contributing factor to the perception

that grasses are poor targets for biological control (see Witt and McConnachie 2004).

The finding of potentially host-specific natural enemies on grasses is in contrast to the prevailing opinion in the literature. This contradiction may arise due to the overemphasized role secondary chemicals play in promoting insect specialisation (Bernays and Graham 1988). Numerous alternative mechanisms have been proposed to explain insect host-range patterns, most notably: the acquisition of enemy-free space (Bernays and Graham 1988), host-plant life histories (Strong et al. 1984), and structural defences (e.g. trichomes and silica deposits) (Vicari and Bazely 1993). Structural defences are believed to play a significant role in promoting diversification and specialisation of grass-associated herbivores (McNaughton et al. 1985; Vicari and Bazely 1993; Moore and Johnson 2017).

Of the 171 herbivores found on *P. australis*, 66 (38.6%) are considered to be monophagous, while preliminary field surveys and ongoing host-specificity assessments, indicate that at least nine species show promise as biological control agents (Tewksbury et al. 2002; Häfliger et al. 2005, 2006; Blossey et al. 2018; Canavan et al. 2018). Three herbivores, the Arundo wasp *Tetramesa romana* Walker (Hymenoptera: Eurytomidae), the Arundo scale *Rhizaspidiotus donacis* (Leonardi) (Homoptera: Diaspididae), and the Arundo leaf sheath-miner *Lasioptera donacis* Coutin & Faivre-Amiot (Diptera: Cecidomyiidae) (Goolsby and Moran 2009; Goolsby et al. 2009a; 2017), have been identified as suitably host-specific and have been released as biological control agents on *A. donax* in the USA.

Surveys on several other important invasive grasses have yielded candidate biological control agents, albeit not yet approved for release, including herbivorous insects on *Cortaderia jubata* (Lem.) Stapf (Purple Pampas grass), *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn., *Digitaria abyssinica* (A. Rich.) Stapf. (blue couch grass), *Echinochloa crus-galli* (L.) Beauv (barnyard grass), *Hymenachne amplexicaulis* (Rudge) Nees (West Indian marsh grass), *I. cylindrica*, *Megathyrus maximus* (= *Panicum maximum*) (Jacq.) B.K. Simon & S.W.L. Jacobs (Guineagrass), *S. alterniflora*, *S. anglica*, *Sporobolus pyramidalis* P. Beauv. (giant rat's tail grass), *Sporobolus natalensis* (Steud.) Dur. & Schinz (giant rat's tail grass) and *Taeniatherum caput-medusae* (L.) Nevski

(medusahead). Moreover, several candidate biological control agents are phytophagous mites on *Panicum repens* L. (Torpedograss) and *T. caput-medusae*, and fungal pathogens on *Avena fatua* L. (wild oats), *C. jubata*, *C. selloana*, *E. crus-galli*, *Nassella trichotoma* (Nees) Hack. ex Arechav. (serrated tussock), *Nassella neesiana* (Trin. & Rupr.) Barkworth (Chilean needlegrass), *Rottboellia cochinchinensis* (Lour.) W.D. Clayton (itchgrass) and *S. halepense* (see Table 1 and references therein).

Several other grass species that have not been considered as biological control targets, but have been surveyed for natural enemies in their native range, possess an assemblage of phytophagous insects, mites and/or fungal pathogens, containing at least one potentially host-specific natural enemy. For example, *Aristida longiseta* Steud. (Fendler threeawn), *Calamagrostis epigejos* (L.) Roth (wood small-reed), *Ehrharta calycina* Sm. (perennial veldtgrass), *Leymus* (= *Elymus*) *cinereus* (Scribn. & Merr.) A. Löve (Great Basin wildrye), *Sporobolus cryptandrus* (Torr.) A. Gray (sand dropseed), *Sitanion hystrix* (Nutt.) J.G. (Smith bottlebrush squirreltail) and *Hesperostipa* (= *Stipa*) *comata* (Trin. and Rupr.) Barkworth (needle and thread) are all attacked by at least one natural enemy that could be tested as potential biological control agents (Spears and Barr 1985; Youtie et al. 1987; Dubbert et al. 1998; Piątek et al. 2015).

Damaging natural enemies

Only candidate agents that demonstrate the capacity to regulate host-plant populations should be considered for biological control (McEvoy and Coombs 1999; McClay and Balciunas 2005). Releasing control agents that do not inflict sufficient damage to negatively impact weed populations represents a significant waste of resources (McEvoy and Coombs 1999), and may increase the risk of indirect non-target impacts occurring by subsidising and disrupting native food webs (e.g. Pearson and Callaway 2003).

However, grasses are believed to be relatively tolerant to herbivory since they have evolved in the presence of grazing by large mammals and harvesting (Tscharntke and Greiler 1995). This tolerance is ascribed to the rapid regrowth potential of grasses from basal meristems and underground storage organs, and their extensive tillering ability (Coughenour 1985). Herbivores targeting above-ground

biomass, therefore, may not be able to cause enough damage to regulate grass populations.

Grasses also typically have a low essential nutrient content (Bernays and Barbehenn 1987), and the presence and abundance of such nutrients are typically positively correlated with insect performance and host choice (Scheirs et al. 2003). Moreover, grasses produce an array of structural defences that may deter herbivores and/or reduce palatability and digestibility (Bernays and Barbehenn 1987; Vicari and Bazely 1993), with silica being a particularly important grass anti-herbivore defence (McNaughton et al. 1985).

However, there are a number of host-specific pests that cause serious economic damage to grasses. For example, *Eragrostis tef* (Zucc.) Trotter., an introduced crop species in North America, suffered yield losses of over 70% due to the action of the stem-boring wasp *Eurytomocharis eragrostidis* (Howard) (Hymenoptera: Eurytomidae) (McDaniel and Boe 1990). *Tetramesa* spp. infestations caused significant reductions in seed weight, germination percentage and germination rate for four different grass species in Idaho, USA (Spears and Barr 1985). Furthermore, yield losses in cereal crops due to host-specific genetic entities of the herbivorous mite, *Aceria tosichella* Keifer (Wheat curl mite), can reach up to 30% (Harvey et al. 2002).

Laboratory-based impact assessments conducted for candidate grass biological control agents provide support for the damaging nature of grass-feeding insects. Two of the biological control agents released against *A. donax* in the USA, *T. romana* and *R. donacis*, were found to be damaging to the host plant under laboratory conditions (Goolsby et al. 2009b). Importantly, the damaging nature of *T. romana* has been corroborated by evidence from field sites along the Rio Grande River (Texas, USA) (Goolsby et al. 2016; Moran et al. 2017). The reduction in *A. donax* above-ground biomass along the Rio Grande River, associated with *T. romana* damage, is estimated to be saving up to 7400 megalitres of water per annum (valued at approximately US\$ 4.4 million) (Goolsby et al. 2016). However, Showler and Osbrink (2018) found that *T. romana* had minimal impact on *A. donax* in Kerr County (Texas), which is outside the Lower Rio Grande Basin. This contrasting report on the efficacy of *T. romana* may be explained by region-specific variation in heat unit accumulation (Marshall et al. 2018) and resulting fitness parameters of *T.*

romana between the Rio Grande Basin and other regions including Kerr County. Annual heat units for *T. romana* in Kerrville, Texas (Kerr County) for 2017 were 3671 as compared to 5513 in Brownsville, Texas (Rio Grande Basin). The field impact of *R. donacis* was evaluated in its native distribution. *Arundo donax* rhizomes infested with *R. donacis* weighed 46% less than rhizomes that were not attacked by the scale (Cortés et al. 2011). Seven years since *R. donacis* was released in the Lower Rio Grande Basin of Texas, USA in 2012, the scale has reduced above-ground shoot biomass by an additional 55% as compared to field plots with populations of only *T. romana* (Goolsby and Moran, pers. comm.).

Several natural enemies that have been screened as candidate agents for other grass invaders can have significant negative impacts on their respective host plants. Häfliger et al. (2006) demonstrated that the stem-boring moth *Archanara geminipuncta* (Haworth) (Lepidoptera: Noctuidae), a candidate agent for *P. australis*, reduced stem biomass by up to 65% under field conditions, and stem height (40%), stem biomass (50%) and the percentage of flowering stems (90%) in a common experimental garden. The impact of *A. geminipuncta* on *P. australis* in the USA is expected to reduce the competitive ability of the target weed, thus allowing the recovery of native wetland species (Häfliger et al. 2006). The shoot-galling fly, *Platycephala planifrons* (Fabricius) (Diptera: Chloropidae), which is a second choice candidate for the *P. australis* biological programme in the USA, reduces stem biomass by up to 70% (Häfliger et al. 2005).

The planthopper, *Prokelisia marginata* (van Duzee) (Hemiptera: Delphacidae) reduced *S. alterniflora* biomass by approximately 49% and plant height by approximately 15% in only three months using a field-cage experimental design (Grevstad et al. 2003). However, Daehler and Strong (1995), who suppressed similar densities of *P. marginata* using insecticide exclusion methods, found no appreciable impact of *P. marginata* on *S. alterniflora* productivity. We are not aware of any quantitative post-release evaluation of the *S. alterniflora* biological control programme.

The current lack of control agents that have been released for grasses and scarcity of adequate post-release evaluations limits the conclusions that can be drawn regarding the efficacy of grass-associated natural enemies as biological control agents.

However, the examples provided above demonstrate that not only can natural enemies of grasses be highly damaging, but they can also mitigate the negative environmental impacts associated with invasive grasses, which is the ultimate aim of biological control.

Risk of targeting grasses versus other weed taxa for biological control

An argument has been made that the risk posed to native biodiversity, valued ornamentals, and economic crops, by introducing grass biological control agents, is too great to consider implementation (Wapshere 1990; Pemberton 2002). While many programmes have successfully used oligophagous natural enemies to control a target weed, partly due to a lack of economically important close-relatives and native congeners in the weeds' introduced range (e.g. Paterson et al. 2011), the majority of biological control agents for invasive grasses will likely need to be strictly monophagous, or in extreme cases, demonstrate sub-specific affinities (Casagrande et al. 2018). This requirement will likely be imposed on many grass biological control programmes due to the close phylogenetic relationships between invasive grasses and economically important crops (cereals) and pasture/fodder species. For example, Wapshere (1990) regarded the potential for the biological control of invasive grasses in Australia (specifically *N. trichotoma*) to be limited due to the presence of closely-related valued pasture species (i.e. multiple native *Stipa* species).

Biological control programmes have been initiated against weeds that possess native congeners and/or closely-related economic crop species in their adventive range (e.g. *Senecio* spp. in Australia, McFadyen and Morin 2012), and in the case of the biological control programmes against *Solanum* spp. in South Africa, multiple sufficiently host-specific natural enemies have been released despite a high diversity of native congeners (Cowie et al. 2017). Practitioners conduct host-specificity testing to carefully evaluate the risk posed by candidate biological control agents to native biodiversity and economic crops in the area of intended introduction (Paynter et al. 2015; Hinz et al. 2019). Over the last 30 years, practitioners have developed the theory and practical applications of host-specificity testing to the point where the host

range of a candidate agent is reliably predictable from host-specificity testing (Paynter et al. 2015; Hinz et al. 2019). Host-range testing, and our ability to assess the safety of a potential biological control agent, should be no different for a candidate being screened against an invasive grass compared to other weed taxa. As such, targeting grasses with native congeners and/or economic crops in the adventive range should also be no different than that for biological control of other weed taxa with similar constraints.

Which natural enemies will be good candidate biological control agents?

The major constraint imposed on a new biological control programme is the availability of candidate biological control agents, which is ultimately determined by the host specificity and potential efficacy (i.e. estimated impact on target weed) of the natural enemy assemblage. Consumers that have a strong physiological dependency on the host plant are expected to demonstrate a greater degree of host specificity than less physiologically dependent consumers (Hardy and Cook 2010). This pattern emerges as the more strongly dependent the consumer is on the host plant, the more likely the consumer is to develop mechanisms to counter host plant defences and/or to be protected from predation and parasitism, thus selecting for greater host specificity (Raman 1993; Hardy and Cook 2010). For example, gall-inducing arthropods have a strong physiological interaction with their host plant, and thus are typically more specialised than their ectophagous counterparts (Cornell 1989). Moreover, gall-inducers feed on actively growing plant tissue where they usually initiate the formation of a nutrient sink and are typically highly damaging to the host plant (Raman 1993). For this reason, gall-formers are frequently sought as biological control agents, and are usually relatively effective at controlling the target weed (Muniappan and McFadyen 2005). Plant fungal pathogens too may be particularly well suited as biological control agents of grasses as they often have a strong physiological dependency on the host plant (Cummins 1971). In the following section we discuss taxa of likely potential biological control agents for grasses, in terms of their predicted specificity and mode of damage. These are certainly not the only agents available, but based on

past experience and literature on host-specificity and potential efficacy, these taxa are likely to be the best potential natural enemies.

Stem-galling wasps—*Tetramesa* (Hymenoptera: Eurytomidae)

Tetramesa Walker (Hymenoptera: Eurytomidae) is a cosmopolitan genus of 204 described species (Al-Barrak 2006), and numerous presently undescribed species (Canavan et al. 2018; G.F. Sutton, unpublished data). The larvae of *Tetramesa* are phytophagous, endophagous borers of cereals and other grasses (Poaceae) (Claridge 1961). Most *Tetramesa* have a narrow host range, with most species being recorded from a single genus of host plants (Claridge 1961).

Tetramesa romana has already been demonstrated to be sufficiently host-specific to gain approval for release for the biological control of *A. donax* in the USA (Goolsby and Moran 2009). Three undescribed species of *Tetramesa* are also being considered as candidate agents for the biological control of *S. pyramidalis* and *S. natalensis* in Australia, and *M. maximus* in the USA, due to their narrow field host range from phytophagous surveys conducted in their respective native ranges (G.F. Sutton and M. Cristofaro, unpublished data). Moreover, unidentified *Tetramesa* spp. are apparently monospecific to *Phragmites mauritianus* Kunth. (Canavan et al. 2018), and *A. longiseta*, *S. cryptandrus*, *S. hystrix* and *S. comata* (Spears and Baar 1985), although host-specificity testing is required to confirm this. The relative paucity of surveys of grass-feeding insects to date, and a lack of any taxonomic resolution for associated taxa, suggests that there are likely to be numerous undescribed *Tetramesa* spp. associated with grasses that could be investigated for their potential as biological control agents.

Tetramesa spp. can also have significant impacts on plant productivity, with several species being considered to be important cereal crop pests (Spears and Barr 1985). The biological control agent *T. romana* is proving to be a highly damaging and successful biological control agent of *A. donax* along the Rio Grande River, USA (Goolsby et al. 2016; Moran et al. 2017).

Eriophyid mites (Acari: Eriophyoidea)

Eriophyid mites are obligate herbivores (De Lillo et al. 2018). There are several genera that appear to have radiated amongst the Poaceae, including *Abacarus* (Laska et al. 2018) and *Aculodes* (De Lillo et al. 2018). Eriophyids have frequently been prioritised for the biological control of weeds due to their often restricted host ranges and damage caused to their host plants (Skoracka et al. 2010; Smith et al. 2010). Indeed, 14 species of eriophyids have been deployed as weed biological control agents to date (Winston et al. 2014).

Approximately 80% of phytophagous eriophyid mites are monophagous (Skoracka et al. 2010). Several of these monophagous species have been recorded on grass hosts. For example, an apparently host-specific mite, *Abacarus plumiger* Laska, Majer, Szydlo & Skoracka has been reported on *Bromus inermis* Leyss (smooth brome) (Laska et al. 2018), while the apparently monophagous mite, *A. altamurgiensis*, demonstrates potential as a biological control of *T. caput-medusae* (De Lillo et al. 2018). A currently unidentified eriophyid mite is likely to be host-specific to *P. mauritianus* Kunth in South Africa (Canavan et al. 2018). While these examples would require formal host range testing to be conducted to confirm their host specificity, there are undoubtedly phytophagous eriophyid mites that could serve as biological control agents of grasses.

Eriophyid mites can cause substantial damage to their host plants, by stunting vegetative growth and limiting plant reproductive output. Some eriophyid mites are important economic crop pests worldwide. For example, the wheat curl mite *Aceria tosichella* Keifer, is a significant pest of cereal crops, causing yield losses of up to 30% (Harvey et al. 2002). The damage caused by eriophyid mites has resulted in biological control practitioners giving mites high priority when prospecting for candidate biological control agents (Smith et al. 2010). Three phytophagous mites released as biological control agents that have had post-release evaluations studies conducted on them, albeit none on invasive grasses, have had a measurable impact on their host plant (Smith et al. 2010).

Shoot-galling flies (Diptera: Chloropidae)

Shoot-galling flies (Diptera: Chloropidae) are a largely phytophagous taxon that appears to have radiated within the Poaceae (Nartshuk 2014). Larvae of this group typically attack the vegetative parts of grasses. However, many species are associated with seeds, while several species are gall-formers on undifferentiated tissues (Nartshuk 2014). Species richness of shoot-galling flies can be relatively high on grasses, with at least ten species, being recorded on *P. australis* (Häfliger et al. 2005).

Shoot-galling flies often demonstrate a sufficiently narrow host range to warrant consideration as candidate biological control agents. For example, at least three shoot-flies are apparently host specific to *D. abyssinica* (Sileshi 1997). Shoot-galling flies can have a detrimental impact on the productivity of their host grasses, with several species being important economic crop pests (Nartshuk 2014). In a biological control context, Häfliger et al. (2005) demonstrated that *P. platifrons* had a significant impact on *P. australis* productivity, whereby attacked stems prematurely wilted and shoot biomass was 60–70% lower than for control stems. Moreover, shoots of *D. abyssinica* damaged by a complex of shoot-galling flies typically did not produce any seed, prompting Sileshi (1997) to propose that these species have promise as candidate biological control agents.

Fungal pathogens

The abundance and diversity of fungal pathogens on grasses and their typically strong physiological dependency on their host plant suggests that pathogens have potential as biological control agents of grasses. However, we are not aware of any fungal pathogens that have been released as control agents on grasses to date (Winston et al. 2014). Many fungal pathogens on grasses, especially smuts (Ustilaginales) and rusts (Uredinales), are known to exhibit a typically narrow host range (Vánky 2003; Le Gac et al. 2007). The rust fungus, *Uromyces pencanus* Arth. & Holw., has been approved for release against *N. neesiana* in New Zealand, and is awaiting release permits from Argentina (Anderson et al. 2017). Additional testing has been requested before *U. pencanus* will be considered for release in Australia, due to the fungus sporulating on two native Australian species during

host-specificity inoculation trials (Anderson et al. 2017). Several other fungal pathogens show promise with regards to displaying a narrow host range on invasive grasses, and that could potentially serve as biological control agents for *E. calycina*, *E. crus-galli*, *R. cochinchinensis* and *S. halepense* (Charudattan and deLoach 1988; Ellison and Evans 1995; Tosiah et al. 2009; Piątek et al. 2015).

Fungal pathogens can be particularly damaging to their host grasses. The head smut, *Sporisorium ophiuri* (P. Henn.) Vánky (Ustilaginales), a candidate biological control agent for *R. cochinchinensis* in Costa Rica, can reduce plant densities by 90% (Smith et al. 1997). The stem-rust fungus *Puccinia graminis* Pers. (Pucciniaceae) causes extensive damage to wheat crops across the globe, with yield reductions sometimes exceeding 50% (Leonard and Szabo 2005). Infection by *Ustilago cynodontis* (Pass.) Henn. stops seed production by the rhizomatous grass *Cynodon dactylon* (L.) Pers., while reducing plant growth rates, biomass accumulation and survival (García-Guzmán and Burdon 1997). These examples demonstrate that many fungal pathogens may be suitably damaging to grasses to warrant their consideration as biological control agents.

Discussion

Invasive grasses have traditionally been considered poor targets for biological control, due to a perceived lack of suitability host-specific and damaging natural enemies (Wapshere 1990; Evans 1991; Pemberton 1996). Moreover, an argument has been made that the risk posed by introduced biological control agents of weedy grasses to economically viable crop species (i.e. cereals) and closely related native species is too great to consider implementing this management option (Wapshere 1990). We reviewed the literature and demonstrated that not only do grasses possess specialised natural enemies that could serve as biological control agents, but that these candidate agents may be sufficiently damaging to provide effective control of a target weed. Host-specificity testing provides a scientifically rigorous and reliable assessment of the risk posed to important economic crops, ornamentals, and native plant species. As such, the risks associated with grass biological control are no greater than for other weedy taxa, given that

practitioners follow appropriately rigorous methods when assessing the specificity of candidate biological control agents.

We encourage biological control practitioners to consider grasses as suitable targets for biological control. As is the case for any taxonomic group of plants, biological control will not necessarily be a silver-bullet nor a one-size-fits-all option for management of invasive grasses. It is likely that many invasive grasses will not be suitable targets for biological control, owing to a lack of suitably host-specific and/or sufficiently damaging natural enemies. However, the likelihood of finding a suitably host-specific natural enemy may be similar for grasses, as for non-grass biological control targets. We advocate that biological control of grasses be considered on a case-by-case basis until any generalities emerge based on the evaluation of such programmes. Biological control could play an important role in the management of invasive grasses, but a greater ecological and evolutionary understanding of grass-consumer interactions is required to harness the full potential of this weed control strategy.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Research involving human participants and/or animals This paper does not contain any studies with human participants or animals performed by any of the authors.

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