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REVIEW

Biocontrol of weedy *Sporobolus* grasses in Australia using fungal pathogens

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Abstract In Australia there are five weedy *Sporobolus* grass (WSG) species that heavily impact agricultural industries and native biodiversity. WSG have been the subject of several efforts to find host-specific pathogens with potential for classical and inundative biocontrol. Most of these studies are only discussed in unpublished reports or theses, so in this paper we synthesise the available peer-reviewed and 'grey' literature that discuss classical, augmentative and inundative biocontrol of WSG in Australia using fungal pathogens. We consider the hundreds of fungal pathogens previously isolated from *Sporobolus* hosts on an international and national scale. Of the pathogens investigated for WSG biocontrol previously, the only promising classical biocontrol agent was a smut fungus (*Ustilago sporoboli-indici*) from South Africa that is now present in Queensland and New South Wales, Australia. Its method of introduction to Australia is unknown. We hence discuss the history and potential for augmentative biocontrol of WSG using *U. sporoboli-indici.* Next, we summarise inundative biocontrol efforts. Several ascomycetes isolated from Australian WSG populations have been tested in this regard, including species of *Nigrospora*, *Fusarium*, *Curvularia*, *Microdochium*, *Pestalotiopsis*, and *Neopestalotiopsis*. However, a lack of host-specificity or efficacy subsequently precluded their further development, and potential improvements on those inundative biocontrol studies are discussed. Finally, we discuss a collection of endemic fungal taxa isolated from diseased *Sporobolus* in Australia, which are currently undergoing virulence, pathogenicity, and host-specificity screening as potential inundative biocontrol agents for WSG. Our intention is that the lessons learned from previous studies and summarised herein, will support ongoing development of WSG biocontrol agents in Australia, and more broadly, weed biocontrol using plant pathogens anywhere in the world.

Keywords Augmentative biological control · Classical biological control · Endophyte · Rats tail grass · Inundative biocontrol · Invasive grass · Poaceae · Review · Mycoherbicide

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Introduction

There are five species of *Sporobolus* grasses, collectively known as the rat's tail grasses or weedy *Sporobolus* grasses (WSG), that are highly invasive in Australia. These species are native in various regions across the globe (Fig. 1 a-e): *Sporobolus natalensis* (Steud.) Dur. & Schinz in central and southern Africa; *S. pyramidalis* P.Beauv in sub-Saharan Africa and the Arabian Peninsula; *S. fertilis* (Steud.) W.D. Clayton in the Indian sub-continent and eastern Asia; *S. africanus* (Poir.) Robyns & Tourn. in southern and eastern Africa as well as parts of Western Africa; and *S. jacquemontii* Kunth from Mexico, Central America, and tropical South America (Biosecurity Queensland 2016). Despite their diverse origins, the WSG are morphologically plastic, and sometimes appear similar to each other either within a locality or across vast distances (Shrestha et al. 2005). This morphological similarity of WSG negatively affects identification in the field and the laboratory.

Five native *Sporobolus* species (*S. blakei* De Nardi ex B.K. Simon, *S. creber* De Nardi, *S. elongatus* R.Br., *S. laxus* B.K. Simon and *S. sessilis* B.K. Simon) are endemic to Australia and belong to the same phylogenetic clade (Clade A, the *indicus*

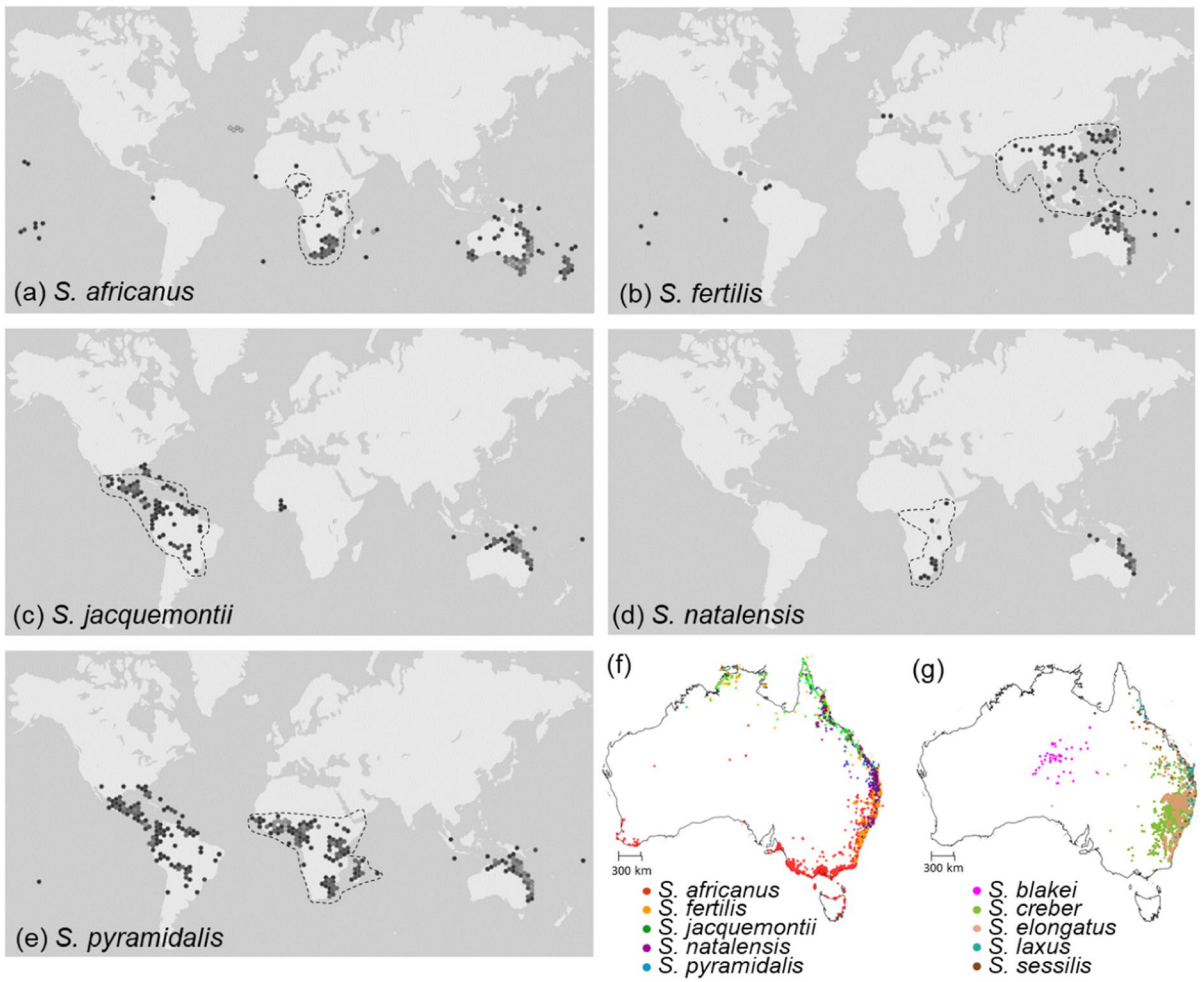

Fig. 1 Global occurrence records of weedy *Sporobolus* grasses (WSGs) (**a**) to (**e**) from 1981 to 2019 (GBIF Secretariat 2019). The approximate native range of each species is indicated with a dashed-line polygon (Biosecurity Queensland 2016). Maps (**f**) and (**g**) show the submitted occurrence records of WSGs (f) and native "clade A" *Sporobolus* grasses (**g**) in Australia from 1980 to 2021 (Atlas of Living Australia 2021)

complex) as the five WSG (Simon and Jacobs 1999; Peterson et al. 2014). A further 14 Australian native *Sporobolus* species are classified outside the *indicus* complex. Two of these (*S. disjunctus* R. Mills ex B.K. Simon and *S. partimpatens* R. Mills ex B.K. Simon) are considered rare and one (*S. pamelae* B.K. Simon) is listed as endangered in the Queensland Nature Conservation Act 1992 (Simon 1993; Simon and Jacobs 1999). Of note, the physical appearance of *S. africanus* and *S. fertilis* is sometimes like that of the close relative *S. elongatus*, making it difficult to target WSG exclusively in management efforts when the species co-occur, particularly by land managers without botanical expertise.

The five WSG are highly competitive against other locally occurring species due to their size and fast growth rate which negatively impact agricultural and natural ecosystems. WSG are widely distributed across Australian states and territories especially the eastern states, and they often co-occur with native *Sporobolus* species (Fig. 1 f & g; Biosecurity Queensland 2016). WSG produce copious amounts of tiny seeds, which are spread by wind, water and mud, attachment to clothes, fur, vehicles and equipment, and in contaminated agricultural produce such as grains and fodder (Biosecurity Queensland 2018). Established plants form a long-lasting seedbank of 20,000–85,000 seeds m^{-2} per year with 90% initial viability which can last for up to ten years (Walton 2001; Department of Agriculture and Fisheries 2020). WSG plants mature within three months, growing to 60–200 cm in height. Their root bases are large, and tussocks are difficult to manually remove (Bray and Officer 2007). Mature WSG leaf blades are tough to chew and can result in damage to the teeth of horses and cattle if grazed, and therefore infestations which displace desired pasture species greatly reduce carrying capacity of pastureland (Biosecurity Queensland 2018).

The economic impact of WSG to beef production in Northern Australia was estimated to be a loss of $60 million per year (Walton 2001). If left unmanaged, WSG can form vast monocultures, excluding native species and completely displacing desirable pasture species, thus lowering land values (Yobo et al. 2009). Ecoclimatic modelling shows that giant rat's tail grass (*S. pyramidalis* and *S. natalensis*) alone has the potential to spread to over 30% of Australia, and so the impact of WSG is expected to substantially increase in the future (Business Queensland 2020).

Historically a range of tools have been used to lessen the impacts associated with WSG including chemical, mechanical, fertilising, stocking rates and competitive pasture species (Bray and Officer 2007). Fire is often used to reduce the biomass of WSG and destroy surface seed. However actual mortality is low with large tussocks surviving the burn often become fragmented into smaller tussocks resulting in the formation of a denser WSG population (Bray and Officer 2007). Broadacre or wick wipe treatment with the selective herbicide flupropanate, or spot spraying with the non-selective herbicide glyphosate tend to be the management options of choice in invaded landscapes. These options, however, require repeated treatment application, are expensive and labour intensive, and generally not feasible on a property scale. Sustained use of these chemicals may also result in off-target damage and individual WSG plants developing herbicide resistance (Officer 2006; Ramasamy et al. 2008). An inability to successfully control these plants has caused WSG to spread into new areas (Grice 2002).

Control efforts are now shifting to the development of integrated, cost-effective and environmentally sound WSG management, including biological control (AgriFutures Australia 2020). Effective biological control agents could become a vital part of this arsenal, and one reason for this is that the level of land manager engagement required for successful and long-term control of WSG is lower than other control options.

Background: biological control of grasses

The use of pathogens to control problematic grass species is gaining increased attention (Witt & McConnachie 2004; Sutton 2019) despite the long-term views that they provided a lack of selectivity and posed too high a risk to important crop and pasture species (Wapshere 1974).

Classical biocontrol

Rusts and smut fungi are often favoured in classical biocontrol due to their high levels of host specificity and ease of spread via rain and wind (Berger et al. 2007; Bettgenhaeuser et al. 2014; McTaggart et al.

2016; Morin 2020). This allows for easy dispersal of the disease across vast populations of the weed (Charudattan 1988). Smuts are generally either foliar pathogens (mainly in Exobasidiomycetes), or they transform the inflorescences of their hosts. Classical biocontrol requires a very narrow host range because otherwise regulators (i.e., the Australian Department of Agriculture, Water and the Environment) would not approve introduction of the agent to the invaded range in case of non-target damage to other host species. Approved classical biocontrol agents are therefore introduced with the knowledge that they will likely disperse to create natural epidemics in populations of their target species (Barton 2012; Berestetskiy 2021).

Several pathogens have historically been investigated as possible classical biocontrol agents of other grass species. The rust *Uromyces pencanus* (Dietel & Neger) Arthur & Holw is being tested for the classical biocontrol of Chilean needlegrass (*Nassella neesiana* (Trin. & Rupr.) Barkworth) in Australia and is undergoing assessment for release in New Zealand (Anderson et al. 2010; pers comm. Dr A Den Breeyen, Manaaki Whenua – Landcare Research); and another rust, *Puccinia tsinlingensis* Y.C. Wang is undergoing host range testing for the biocontrol of downy brome (*Bromus tectorum* L.), also in New Zealand (Barton 2020). Of note, neither is specific to just their target weed with *U. pencanus* infecting three *Nassella* spp. and five *Stipa* spp., and *P. tsinlingensis* found on five *Bromus* spp. as well as *Elymus semicostatus* (Steud.) Melderis. Several smut fungi have also been investigated as classical biocontrol agents of grasses in New Zealand including the stem smut *Ustilago hypodytes* (Schltdl.) Fr. and fluorescence smut *U. bullata* Berk. targeting *Bromus* spp. (Barton 2020), and the fluorescence smut *U. quitensis* Lagerh. targeting several species of pampas grass (*Cortaderia* Stapf.) (Probst 2020).

Between 2001 and 2003 an extensive host range survey in southern Africa was conducted for candidate classical biocontrol agents of WSG (Palmer 2004, Vánky and Vánky, unpublished, Yobo et al. 2009). The African survey collected both pathogens and arthropods associated with *S. natalensis*, *S. pyramidalis* and *S. africanus*, and each were examined for their feasibility as biocontrol agents in Australia based on climatic suitability, pathogenic and herbivory traits, and ecological factors. The survey found only two promising candidate biocontrol agents for WSG: the leaf and fluorescence smut fungus, *U. sporoboli-indici* L. Ling and the stem galling wasp, *Tetramesa* sp. Walker (Palmer 2004). The latter having two species undergo field-based host-specificity testing on 49 grass species including nine *Sporobolus* spp. in South Africa (Sutton et al. 2021). The studies culminated in two *Tetramesa* spp. being imported into Australia in September 2022, but both failed to establish in quarantine. Insect agents are outside the scope of this review.

Inundative biocontrol

Inundative biocontrol involves the mass production and application of a pathogen that needs to be regularly reintroduced at infested sites to effectively manage the target weed (Charudattan 1988; McRae and Auld 2000). This is applied at a time when the target plant is likely to be most susceptible, resulting in a localised, artificial epidemic (McRae and Auld 2000). Unlike classical biocontrol where the agent is usually sourced from the target species' native range, inundative biocontrol uses endemic (or indigenous) microorganisms, or introduced microorganisms which may occur at endemic levels for formulating bio/mycoherbicides. These require similar application methods to herbicides, at doses containing $\pm 10^6$ infective units per ml of inoculum (TeBeest et al. 1992). For inundative biocontrol agents, a host range which is slightly broader than the target weeds will not automatically rule out a candidate pathogen as it will likely be applied selectively and require augmentation or reapplication to persist (Charudattan 1988; McRae and Auld 2000; Berestetskiy 2021). Even so, the host range boundary must be investigated so that suitable advice for application of the inundative biocontrol agent can be provided. This can be achieved, for example, by avoiding application of the bio/mycoherbicide in the vicinity of co-occurring, susceptible plant species, or by adjusting the application method.

For decades researchers and landholders in Australia have been looking to integrate inundative biocontrol into WSG management strategies, as conventional options are often expensive when controlling

this widely dispersed and aggressive group of weeds. The use of an inundative agent in the form of a pest or pathogen would be a vital additional tool in the arsenal of options available in the management of WSG (Vitelli et al. 2019). Only one inundative microbial agent, the Proteobacterium *Xanthomonas campestris* pv. *poae*, has been developed as a bioherbicide (Camperico™) for control for grasses, this being *Poa annua* L. in Japan (Imaizumi et al. 1999; Anderson et al. 2011, 2017; Morin 2020).

There have been 15 bioherbicides formulated with living organisms registered worldwide, but only two were currently commercially available as of November 2019 (Morin 2020). One of those is Di-Bak© Parkinsonia developed by BioHerbicides Australia for the control of the invasive leguminous tree *Parkinsonia aculeata* L. Each injectable capsule contains three fungal actives, *Lasiodiplodia pseudotheobromae* A.J.L. Phillips, A. Alves & Crous, *Neoscytalidium novaehollandiae* Pavlic, T.I. Burgess & M.J. Wingf., and *Macrophomina phaseolina* (Tassi) Goid (Galea 2021). Di-Bak© is currently the only bioherbicide to have so far navigated the regulatory framework in Australia and be approved for commercial use by the Australian Pesticides and Veterinary Medicines Authority (APVMA). While the fungi used are not completely host specific to *P. aculeata* (Galea 2021), the mode of application (injection of the capsules directly into the stem of the target weed) mitigates against the risk of spread to other non-target hosts.

The main purpose of this review was to collate and discuss biocontrol research on *Sporobolus* spp., specifically to determine which classical and inundative biocontrol pathogens have been tested and the details of the methodologies used in those studies. Much of the research in this space has only been published in reports or as university theses (i.e., not as peer-reviewed scientific articles and therefore not as easily available to researchers) so it is important to analyse why certain pathogens are no longer considered as potential agents against WSG, and specifically to determine whether the choice of pathogen(s), identification methods, pathogenicity and/or host specificity testing can be improved upon. Learnings from the review of these studies will improve our knowledge and assessment of classical and inundative biocontrol feasibility for WSG. We aim to lay the foundation for the future development of a bio/myco-herbicide against WSG.

Past research on WSG biocontrol

A survey of published literature from global databases (United States National Fungus Collection (Farr and Rossman 2021) and Kew Royal Botanic Gardens (Sivanesan 1987; The Herbarium Catalogue 2021)) identified 272 fungal pathogen species that were associated with *Sporobolus* species (n = 51; Supplementary material Table S1). To narrow down this range to the context of biocontrol of WSG, the Web of Science database was searched in July 2022 using all five WSG species names alongside various combinations of the words "bio* control", "agent", and "pathogen". Only 110 relevant journal articles were returned (Luttrell 1976; Alcorn 1982; Hetherington and Irwin 1999; Vánky 2003; Cunnington and Shivas 2006; Yobo et al. 2009; Vitelli et al. 2017; Sutton 2019; Sutton et al. 2021; Steinrucken et al. 2022) so we also added reports, conference papers and university theses which we classified as 'grey' literature. The resulting list was further divided into classical and inundative biocontrol (Supplementary material Table S2). The literature on the impacts of WSG, and of WSG biocontrol using pathogens, is henceforth discussed.

Fungal pathogens associated with ***Sporobolus*** globally

The following summarises information presented in Supplementary Table S1. Most fungal pathogens associated with *Sporobolus* globally were found to have a wide host range where 57% (n = 155) were associated with host species from > two host genera, and 39% (n = 107) were associated with host species from > two families. Some pathogens were found on hosts in up to 774 genera and 178 plant host families. Of the 272 pathogen species documented from *Sporobolus* hosts, 121 of them (from 54 fungal genera) were recorded from WSG, with the rust fungi *Uro. tenuicutis* McAlpine the only pathogen found on all five weedy *Sporobolus* species. *Uromyces tenuicutis,* however, is also associated with an additional ten *Sporobolus* species. Giant rat's tail grass (*S. natalensis* (n = 72) and *S. pyramidalis* (n = 41)) is host to almost 83% of the WSG-associated pathogens with only *U. sporoboli-indici*, *Nigrospora oryzae* (Berk. & Broome) Petch and *U. tenuicutis* common to both

host species. *Nigrospora oryzae* is associated with 127 genera and 53 families and *U. tenuicutis* is associated with three genera and two families. Pathogens that were only associated with *Sporobolus* hosts but contained a wide host range within the genus included *Phyllachora sporoboli* Pat., *Curvularia crustacea* (Henn.) Y.P. Tan & R.G. Shivas, *Phyllachora afra* Syd., *Puccinia cryptandri* Ellis & Barthol., *Jamesdicksonia sporoboli* (H.S. Jacks.) M. Piepenbr., *Curvularia ryleyi* Y.P. Tan & R.G. Shivas and *U. sporobolicola* J.C. Lindq. which respectively infected nine, eight, six, five, five, five and five species within the *Sporobolus* genus.

Classical biocontrol of WSG: *Ustilago sporobili-indici*

After its discovery in South Africa, *U. sporoboli-indici* was shown to significantly damage *S. africanus* and as a biotrophic pathogen was thought to likely be host-specific (Valverde et al. 1999; Vánky 2003; Palmer 2004; Vánky and Vánky, unpublished). *Ustilago sporoboli-indici* was subsequently tested in South Africa on Australian-grown populations of all five WSGs, as well as on several native Australian *Sporobolus* spp. to determine host range (Palmer 2008). Inoculation of seedlings from Australian-sourced seeds with *U. sporoboli-indici* with a suspension of either basidiospores or teliospores successfully caused infection and damage to all WSG species apart from *S. jacquemontii* (Yobo et al. 2009). The infection caused by *U. sporoboli-indici* was thought to be systemic, causing all shoots of an infected plant to be sterile, thereby reducing seed production (Vánky 2003; Cunnington and Shivas 2006). Additionally, the black/brown powdery spores that formed on the leaves of infected plants could be easily collected or spread by wind or movement between plants (Vánky and Vánky, unpublished). *U. sporoboli-indici* was therefore deemed a potential classical biocontrol agent of WSG.

Despite the promising results, in 2008 *U. sporoboli-indici* was ultimately rejected for importation into Australia due to its ability to also infect four of the 13 native Australian *Sporobolus* species tested (Palmer 2008; Yobo et al. 2009). Two of these, *S. creber* and *S. elongatus*, were severely infected in pathogenicity screening trials, with symptoms including dead leaves, flower malformations, and sori forming in both leaves and tillers (Palmer 2008; Yobo et al. 2009). Although rejected as a classical agent for import into Australia, *U. sporoboli-indici* has since been recorded infecting *S. natalensis* at several sites in eastern Australia beginning in Taunton Queensland in 2017 (Rapley 2020). Its identity was confirmed by morphological and genetic analysis at the Queensland Plant Pathology Herbarium (Vitelli et al. 2017). Its distribution was later found to extend over 300 km from Miriam Vale to Conondale in Queensland (Vitelli et al. 2017; Rapley 2020), and more recently an additional 370 km into Casino, New South Wales (David Officer, personal communication). The introduction of *U. sporoboli-indici* to Australia was unauthorised, and it is not known how it arrived in Australia (Vitelli et al. 2017). Its detection in 2017 was immediately reported to the Consultative Committee on Emergency Plant Pests, a committee that provides national technical and scientific advice in response to exotic plant pest and disease outbreaks in Australia (NCP 2017). Consensus was reached that *U. sporoboli-indici* was not an 'emergency plant pest' as defined by the Emergency Plant Pest Response Deed (EPPRD) as no crop was represented by industry parties to being hosts to *U. sporoboli-indicii* (NCP 2017).

In 2019, Australian strains of *U. sporoboli-indici* were tested on three cohorts of potted *S. natalensis* plants (seedlings, juveniles and adults) in a glasshouse, but failed to show infection (Rapley 2020). A parallel in vitro host-specificity study of eight *Sporobolus* species in clade A (the five WSG plus native species *S. creber*, *S. laxus* and *S. sessilis*) as well as four other closely related grass species showed infection of all WSG species apart from *S. jacquemontii* (Rapley 2020). The discrepancy in host-specificity or virulence on target and non-target species from these studies could be explained by genetic differences between the strains tested, which should be investigated. Unfortunately, *U. sporoboli-indici* also infected the tested native species *S. creber* and *S. sessilis* (as per Yobo et al. 2009) and *S. laxus*, which confirmed that infection is not specific to WSG but potentially to other clade A species. However, since *U. sporoboli-indici* is now widespread on the east-coast of Australia, its removal from the environment is not feasible. Options for incorporating this pathogen into existing WSG management practices, such as augmentation, are being investigated at state and

regional level (Nichols 2020). Further work using *U. sporoboli-indici* will need to consider any off-target effects carefully.

Augmentation of an obligate biotroph

Augmentation of an obligatory biotrophic pathogen (including smut or rust fungi), stands as a promising approach to biological control, but is one not widely used on pest plants at an operational scale in pastoral systems. The aim of augmentative biological control is to manage a pest using natural enemies or the inoculation and inundation of biocontrol agents, using parasitoids, predators or microbial organisms (Collier and van Steenwyk 2004). Augmentative biocontrol is considered a 'system management' approach, which was tested on *Senecio vulgaris* L. using *Puccinia lagenophorae* Cooke., aiming to cautiously manage the weed pathosystem to maximise a biocontrol agent's spread, and increase disease severity (Müller-Schärer and Frantzen 1996). Such system management parameters can include vegetation density, amount of inoculum, and/or the concurrent use of herbicides (Wyss and Müller-Schärer 2001; Frantzen and Müller-Schärer 2006). The head smut *Sporisorium ophiuri* (Henn.) Vánky was shown to infect *Rottboellia cochinchinensis* (Lour.) Clayton, a serious weedy grass of sugarcane and maize with stems that grow up to 3 m tall. It was initially trialled as a classical biocontrol agent and was highly pathogenic at high levels of infection, but, using a population dynamic model, the authors show that by augmenting *Sporisorium ophiuri* application with one or two weedings of the target grass per year, the smut could achieve a significantly higher level of control of emergent seedlings (Smith et al. 1997).

An example of augmenting an endemic fungal pathogen is the rust fungus, *P. canaliculata* (Schw.) Lagerh., which occurs naturally and seasonally in parts of southern USA on yellow nutsedge (*Cyperus esculentus* L.). The rust does not build up to epidemic levels until the plant is several weeks old and at that point is already affecting crop yields (Eilenberg et al. 2001). Phatak et al. (1987) found that releasing the rust spores a few weeks earlier in spring (thus augmenting its prevalence in the landscape at an opportune time), resulted in higher crop yields as nutsedge flowering and new tuber formation were inhibited. As obligate pathogens, rust teliospores must be harvested from infected hosts and so *P. canaliculata* was never commercialised because sufficient inoculum could not be efficiently produced to make a commercial product viable (Berestetskiy 2021). The same fate befell WoadWarrior (*Puccinia thlaspeos* C. Schub), a once-licensed biocontrol agent for Dyer's Woad (*Isatis tinctoria* L.; Bailey 2014, Flint and Thomson 2000).

Realistically, for a biotroph to be readily incorporated in an integrated weed management program, mass production of the agent needs to be cost effective, have a shelf life long enough to allow periodic releases when required, have an ability to rapidly spread, and must exert a measurable decline in the dominance of the targeted pest. Amendments to the formulation of a biocontrol agent can also augment its effectiveness. For example, an invert emulsion with the pathogen *Colletotrichum coccodes* (Wallr.) S. Hughes increased the level of control and mortality achieved in the target weed, *Solanum ptycanthum* Dunal (Batta 2016; Boyette et al. 2018).

Augmentation of *U. sporoboli-indici* already in the field, or of other tested agents, could optimise the impact of the application to target WSG. The aim would be to slow the growth of the host, significantly reduce host seed production, and/or allow productive pastures to be more competitive. When used in conjunction with traditional control methods, augmentative biocontrol could become a vital component of the integrated management of WSG.

Inundative biocontrol of WSG

While the search for classical biocontrol agents of WSG is continuing in Africa, efforts are ongoing to investigate options for inundative biocontrol of WSG in Australia (Sutton 2019; Vitelli et al. 2019; Sutton et al. 2021; Steinrucken et al. 2022). As of January 2023, 127 fungal pathogens from 56 genera have been isolated from *Sporobolus* spp. in Australia, with almost 65% (n = 82) novel species (Table 1). A further 21 fungal species are associated with host species in between two and 70 plant families and can be considered generalists with a wide global distribution. An additional 12 pathogens have been isolated from species in 2–12 host genera. *Phyllachora afra*, *P. sporoboli*, *C. crustacea*, and *C. ryleyi* are all pathogens known to infect several species of *Sporobolus* and were respectively isolated from one, four, seven

Table 1 Fungal species (n = 127) isolated from diseased or symptomatic native or weedy *Sporobolus* grasses in Australia between *1896–2014 (49) and #2015–2021 (70)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
Amphisphaeriales	Pestalotiopsidaceae	#*Neopestalotiopsis nebuloides* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1, 10	(2; 1; 1)
		#*Neopestalotiopsis* sp. BRIP 68236	10	
		#*Neopestalotiopsis* sp. BRIP 68237	10	
		#*Neopestalotiopsis* sp. BRIP 71163	10	
		#*Pestalotiopsis etonensis* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	13	(1; 1; 1)
		#*Pestalotiopsis chiaroscuro* Rapley, Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1	(1; 1; 1)
Capnodiales	Mycosphaerellaceae	^*Mycosphaerella* sp. (1989)	17	
		**Mycosphaerella tassiana* (De Not.) Johanson	5	(210; 123; 36)
Chaetosphaeriales	Chaetosphaeriaceae	#*Dictyochaeta* sp. BRIP 69686	1	
		#*Dictyochaeta* sp. BRIP 69688	1	
		#*Dictyochaeta* sp. BRIP 69691	1	
	Insertae sedis	#*Neoleptosporella* sp. BRIP 70659	1	
Diaporthales	Gnomoniaceae	@*Diplodina* sp. (1982)	5	
Dothideales	Saccotheciaceae	#*Aureobasidium* sp. BRIP 68300	1	
		#*Aureobasidium* sp. BRIP 70138	1	
		*$*Selenophoma donacis* var. *stomaticola* ≡ *Pseudoseptoria stomaticola* (Bäumler) B.Sutton (DAR32618)	5	(71, 23, 1)
Glomerellales	Glomerellaceae	*$*Colletotrichum coccodes* (Wallr.) S. Hughes (DAR72347)	10	(73; 50; 28)
		#*Colletotrichum gigasporum* E.F. Rakotonir. & Munaut	10	(20; 18; 17)
		#*Colletotrichum karstii* Y.L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai	1, 10	(84; 64; 38)
		#*Colletotrichum* sp. BRIP 68299	1	
		#*Colletotrichum* sp. BRIP 68820	10	

Table 1 (continued)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
Helotiales	Hyaloscyphaceae	#*Scytalidium* sp. BRIP 69689	1	
Hypocreales	Clavicipitaceae	#Clavicipitaceae gen. nov. BRIP 70643	1	
		**Dothichloë* sp. BRIP 21053 a (1930)	9	
		**Epichloe cinerea* Berk. & Broome	2, 5, 10, 12, 16	(34; 12; 1)
	Nectriaceae	*#*Fusarium chlamydosporum* Wollenw. & Reinking	1, 2, 11, 16	(87; 66; 34)
		*#*Fusarium proliferatum* (Matsush.) Nirenberg ex Gerlach & Nirenberg	1	(112; 92; 42)
		**Fusarium* sp. BRIP 12520 a (1977)	15	
		#*Fusarium* sp. BRIP 72816	1	
	Sarocladiaceae	#*Parasarocladium* sp. BRIP 68235	1	
Incertae sedis	Dothideomycetes	**Zymoseptoria tritici* (Desm.) Quaedvl. & Crous	12	(9; 6; 1)
	Incertae sedis	**Urohendersonia stipae* H.C. Greene	2, 9, 10, 16	(4; 2; 1)
Magnaporthales	Magnaporthaceae	#*Magnaporthiopsis meyeri-festucae*	1	(3; 2; 1)
Microbotryales	Microbotryaceae	^*Sphacelotheca* sp. (1989)	17	
Myriangiales	Elsinoeaceae	#*Elsinoe* sp. BRIP 67450	1	
Myrmecridiales	Myrmecridiaceae	#*Myrmecridium* sp. BRIP 69701	1	
Phomatosporales	Phomatosporaceae	*$*Dinemasporium graminum* ≡ *Phomatospora dinemasporium* J.Webster (ADW8241)	17	(22; 18; 5)
Phyllachorales	Phyllachoraceae	**Phyllachora afra* Syd	17	(6; 1; 1)
		*$*Phyllachora* sp. (484)	17	
		**Phyllachora sporoboli* Pat	2, 7, 16, 17	(9; 1; 1)
		**Phyllachora sylvatica* Sacc. & Speg	7, 10, 16	(15; 3; 1)
Pleosporales	Didymellaceae	#*Epicoccum* sp. BRIP 70661	1	
		#*Epicoccum* sp. BRIP 70883	1	
		#*Epicoccum* sp. BRIP 70507	10	
		#*Epicoccum* sp. BRIP 70564	10	
		#*Epicoccum* sp. BRIP 70565	10	
		#*Epicoccum* sp. BRIP 70566	10	
		#*Epicoccum* sp. BRIP 72811	1	
		#*Epicoccum* sp. BRIP 72813	1	
		#*Epicoccum* sp. BRIP 72814	1	
		#*Leptosphaerulina queenslandica* Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1	(1, 1, 1)

Table 1 (continued)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
		#*Leptosphaerulina* sp. BRIP 70187	10	
	Didymosphaeriaceae	#*Neptunomyces* sp. BRIP 66596	1	
	Lentitheciaceae	#*Darksidea* sp. BRIP 69697	1	
		#*Keissleriella sporoboli* Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1	(1, 1, 1)
	Massarinaceae	**Neottiosporina* sp. BRIP 16262 a (1988)	2	
	Periconiaceae	^*Periconia* sp. (1989)	17	
	Phaeosphaeriaceae	**Eudarluca caricis* (Fr.) O.E. Erikss	2, 17	(136; 90; 24)
		#*Parastagonospora* sp. BRIP 70642	1	
		**Phaeosphaeria* sp. BRIP 23040 c (1995)	6	
		#*Phaeosphaeria* sp. BRIP 70506	10	
		#*Phaeosphaeria* sp. BRIP 70650	1	
		#*Phaeosphaeria* sp. BRIP 70656	1	
		#*Phaeosphaeriopsis* sp. BRIP 70189	10	
		*$*Stagonospora* sp. (DAR50283a)	17	
		#*Stagonospora tauntonensis* Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1	(1, 1, 1)
	Pleosporaceae	#*Alternaria* sp. BRIP 68520	1	
		#*Alternaria* sp. BRIP 68540	1	
		#*Alternaria* sp. BRIP 70508	10	
		#*Bipolaris axonopodicola* Y.P. Tan & R.G. Shivas	10	(1; 1; 1)
		**Bipolaris panici-miliacei* (Y. Nisik.) Shoemaker	11	(7; 5; 1)
		#*Bipolaris secalis* Sisterna ex Y.P. Tan, Madrid, Crous & R.G. Shivas	10	(1; 1; 1)
		**Bipolaris* sp. BRIP 12926 a (1979)	10	
		**Bipolaris* sp. BRIP 39956 a (2003)	2	
		**Bipolaris* sp. BRIP 43651 a (2004)	2	
		**Bipolaris* sp. BRIP 43741 a (2004)	2	

Table 1 (continued)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
		**Bipolaris* sp. BRIP 43881 a (2004)	2	
		**Bipolaris* sp. BRIP 46533 a (2005)	16	
		**Bipolaris* sp. BRIP 46790 a (2005)	2	
		**Bipolaris* sp. BRIP 48144 a (2006)	2	
		#Bipolaris sp. BRIP 72815	1	
		**Cochliobolus queenslandicus* McKenzie	7	(1; 1; 1)
		**Curvularia australis* (Alcorn) Y.P. Tan & R.G. Shivas	4, 7, 10, 15	(7; 3; 1)
		**$Curvularia clavata* B.L. Jain (DAR63277a)	12	(99; 77; 36)
		**Curvularia crustacea* (Henn.) Y.P. Tan & R.G. Shivas	2, 5, 9, 10, 11, 12, 16	(8; 1; 1)
		**Curvularia dactyloctenicola* Y. Marín, Senwanna & Crous	1	(3; 3; 1)
		**Curvularia eragrostidis* (Henn.) J.A. Mey	6	(68; 47; 22)
		**Curvularia hawaiiensis* (Bugnic. ex M.B. Ellis) Manamgoda, L. Cai & K.D. Hyde	10	(113; 94; 51)
		**Curvularia ovariicola* (Alcorn) Manamgoda, L.Cai & K.D. Hyde	12	(9; 2; 1)
		**Curvularia papendorfii* (Aa) Alcorn	7	(1; 1; 1)
		**#Curvularia ravenelii* (M.A. Curtis ex Berk.) Manamgoda, L. Cai. & K.D. Hyde	1, 2, 3, 5, 8, 9, 10, 11, 12, 13, 16	(20; 8; 3)
		**Curvularia ryleyi* Y.P. Tan & R.G. Shivas	5, 8, 9, 10, 12, 13, 14, 16	(5, 1, 1)
		**Curvularia* sp. BRIP 8836 a (1973)	5	
		#Curvularia sp. BRIP 65595	1	
		#Curvularia sp. BRIP 66294	1	
		#Curvularia sp. BRIP 69020	1	
		**Curvularia spicifera* (Bainier) Boedijn	10	(118; 90; 26)
		**Curvularia sporobolicola* Y.P. Tan & R.G. Shivas	6	(1, 1, 1)
		**$Drechslera* sp. (DAR30804)	8	
		#Drechslera yamadae (Y. Nisik.) Subram. & B.L. Jain	1	(10; 5; 2)

Table 1 (continued)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
		**Exserohilum rostratum* (Drechsler) K.J. Leonard & Suggs	1, 7	(29; 22; 5)
		#*Exserohilum* sp. BRIP 70140	1	
		#*Exserohilum* sp. BRIP 70177	1	
		^*Pleospora* sp. (1989)	17	
		#*Stemphylium* sp. BRIP 72812	1	
	Pyrenochaetopsidaceae	#*Pyrenochaetopsis* sp. BRIP 69695	1	
		#*Pyrenochaetopsis* sp. BRIP 69700	1	
	Roussoellaceae	#*Roussoella solani* (Crous & M.J. Wingf.) Jayasiri & K.D. Hyde	10	(4; 4; 4)
		#*Roussoella* sp. BRIP 70563	10	
Pucciniales	Crossopsoraceae	**Uredo* sp. BRIP 15780 a (1987)	9	
		**Uredo* sp. BRIP 25235 a (1998)	16	
		^*Uredo* sp. (1989)	17	
	Pucciniaceae	@*Puccinia* sp. (1982)	5	
		**$Uromyces tenuicutis* McAlpine	2, 5, 12, 17	(17; 3; 2)
Rhytismatales	Rhytismataceae	**Lophodermium arundinaceum* (Schrad.) Chevall	17	(110, 51, 8)
Sordariales	Chaetomiaceae	**Trichocladium* sp. BRIP 29159 a (2002)	17	
Trichosphaeriales	Trichosphaeriaceae	**#Nigrospora oryzae* (Berk. & Broome) Petch	1, 2, 11	(172; 127; 53)
		#*Nigrospora sphaerica* (Sacc.) E.W. Mason	10	(240; 183; 70)
Ustilaginales	Ustilaginaceae	**Macalpinomyces spermophorus* (Berk. & M.A. Curtis ex de Toni) Vánky	6	(37; 6; 1)
		**Macalpinomyces viridans* R.G. Shivas, McTaggart & Vánky	3	(1, 1, 1)
		**Sporisorium ryleyi* Vánky & R.G. Shivas	7	(5, 3, 1)
		**$Ustilago hypodytes* (Schltdl.) Fr	17	(223,54, 3)
		#*Ustilago sporoboli-indici* L. Ling	1, 11	(3; 1; 1)
Xylariales	Hypoxylaceae	#*Hypoxylon* sp. BRIP 68818	1	
		#*Hypoxylon* sp. BRIP 68819	1	
	Michrodochiaceae	#*Microdochium dawsoniorum* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1, 10	(2, 1, 1)

Table 1 (continued)

Order	Family	Pathogen name	Known *Sporobolus* host(s)	Known hosts (n) (species; genera; families)
		[#]*Microdochium ratticaudae* Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas	1	(1, 1, 1)

Fungal species are listed by alphabetical order of orders, then families and then species names. Australian *Sporobolus* hosts are indicated by a number with its corresponding key presented below the table. Number of recorded hosts (species; genera; families) from the literature with the associated pathogen is also presented. Isolates housed in the Brisbane Plant Pathology Herbarium (BRIP) are indicated by their accession number

Known *Sporobolus* hosts: 1: *S. natalensis* (Steud.) Dur. & Schinz, 2: *S. pyramidalis* P.Beauv, 3: *S. actinocladus* (F.Muell.) F.Muell, 4: *S. advenus* (Stapf) P.M.Peterson, 5: *S. africanus* (Poir.) Robyns & Tourn., 6: *S. australasicus* Domin, 7: *S. caroli* Mez, 8: *S. creber* De Nardi, 9: *S. diandrus* (Retz.) P.Beauv., 10: *S. elongatus* R.Br., 11: *S. fertilis* (Steud.) W.D. Clayton, 12: *S. indicus* (L.) R.Br., 13: *S. jacquemontii* Kunth, 14: *S. laxus* B.K. Simon, 15: *S. mitchellii* (Trin.) C.E.Hubb., 16: *Sporobolus sp.*, 17: *S. virginicus* (L.) Kunth. Other references: ^Cook & Dube 1989, [@]Sampson & Walker 1982, [$]Australian Plant Pest Database (APPD) Plant Health Australia, Canberra

and eight species in Australia (DAF Biological Collections 2023; Plant Health Australia 2023). Of the remaining 15 pathogens associated with *Sporobolus* in Australia, six species (*Bipolaris axonopodicola* [*Sporobolus elongatus*]; *Bipolaris secalis* [*S. elongatus*]; *Cochliobolus queenslandicus* [*S. caroli* Mez]; *C. papendorfii* [*S. caroli*]; *C. sporobolicola* [*S. australasicus* Domin] and *Macalpinomyces viridans* [*S. actinocladus* (F.Muell.) F.Muell.]) were only associated with native Australian *Sporobolus* species. Eight recently described pathogens found on *S. natalensis* (n = 7) and *S. jacquemontii* (n = 1) are undergoing virulence and pathogenicity testing.

Nigrospora and Fusarium

In 2005, reports of diseased *S. fertilis* in Victoria and New South Wales resulted in the isolation of a fungus identified at the time as *Nigrospora oryzae* (isolate RMIT0601), a known pathogen of rice and several other plants (Officer 2006; Ramasamy 2008). The symptoms reported included stunted growth, yellowing of leaves and rot of tillers (Ramasamy 2008). Several authors have studied RMIT0601 for its potential as a myco-herbicide against *S. fertilis* and later against *S. natalensis* and *S. pyramidalis* (Ramasamy 2008; Lawrie 2011, 2014; Fletcher and Leemon 2015). Subsequent genetic analysis showed that RMIT0601 is an undescribed *Nigrospora* sp., not *N. oryzae* (Lock 2018).

In a glasshouse experiment, inoculation by RMIT0601 significantly affected both seedlings and mature potted *S. fertilis* plants, resulting in necrotic leaves, marginal chlorosis, and wilting and yellowing of leaves and tillers (Ramasamy 2008). In the field, symptoms of blight of field-inoculated adults occurred, followed by death 12 months after inoculation (Ramasamy et al. 2011). Additional trials by Lawrie et al., (pers. comm. Prof. A.C. Lawrie, RMIT University 2020) investigated the host range of RMIT0601, where 14 additional grass species were tested including species from *Austrodanthonia*, *Austrostipa*, *Festuca*, *Pennisetum* and *Themeda*, though unfortunately the results were both inconclusive and inconsistent due to lack of replication, or failure of plants to thrive. Additionally, the host-specificity trials involving RMIT0601 did not include any species from within the Sporobolinae subtribe. The host range of RMIT0601 could therefore not be established and required further testing before moving it forward as a biocontrol agent.

Two follow-up field and pot studies failed to find evidence of a pathogenic relationship between *S. pyramidalis* or *S. natalensis* with RMIT0601. Similarly, two *Fusarium* isolates (*F. proliferatum* (Matsush.) Nirenberg ex Gerlach & Nirenberg and *F. chlamydosporum* Wollenw. & Reinking), isolated from *S. fertilis* in a previous glasshouse trial, also failed to produce consistent infections or mortalitity of the target weeds (Lawrie 2014). A subsequent trial combining RMIT0601 with the two *Fusarium* spp. may have contributed to the mortality of *S. pyramidalis* seedlings. However, when the same pathogens were applied to adult *S. fertilis* and *S. pyramidalis*

plants in pots, results were inconclusive due to low replication, without mention of any successful re-isolation (Lawrie 2014). In a subsequent study, treatment groups inoculated with either RMIT0601 alone or in combination with the *F. proliferatum* and *F. chlamydosporum*, unexpectedly resulted in a significantly greater dry matter yield, suggesting a positive effect on growth of *S. natalensis* and *S. pyramidalis* (Fletcher and Leemon 2015). These studies were the first time a combination of fungi was used to inoculate WSG in the hope of producing mixed infections but were ultimately unsuccessful. The combined results of these studies effectively ruled out RMIT0601 and the two *Fusarium* spp. as biocontrol agents for WSG.

Curvularia

The false smut *C. ravenelii* (M.A.Curtis ex Berk.) Manamgoda, L. Cai & K.D. Hyde (≡ *Bipolaris ravenelii* (M.A. Curtis ex Berk.) Shoemaker (1959) ≡ *Helminthosporium ravenelii* M.A. Curtis ex Berk., J. Linn.), was shown to infect the ovaries of *S. indicus* (L.) R. Br. var. *indicus* (≡ *S. poiretii (*Roem. & Schult.) Hitchc.) in south-eastern USA, replacing them with a fungal stroma, and causing a small reduction in seed germination (Luttrell 1976). This host–pathogen relationship was so prevalent in Florida and Georgia that the common name of this plant became 'smut grass'. Plant infection was achieved with a conidial suspension of *C. ravenelii* following a 12 h dew period, with symptoms appearing 48 h later, and conidia forming on the panicles after 60 h (Luttrell 1976). Following these experiments, the use of *C. ravenelii* as an inundative biocontrol agent looked promising.

Sporobolus indicus var. *indicus* has not been recorded in Australia. However, strains of *C. ravenelii* have been isolated from several native (*S. elongatus, S. laxus* and *S. sessilis*) and non-native (all five WSG) *Sporobolus* spp. in New South Wales and Queensland (McKenzie 1968; Alcorn 1982). Australian strains of *C. ravenelii* have since been tested for pathogenicity against the WSG (excluding *S. natalensis*) and one native species, *S. elongatus* (Hetherington and Irwin 1999). All the tested host species showed similar levels (> 60%) of susceptibility. However, seed production between *C. ravenelii* infected plants and control plants was also similar, as infected plants compensated for the reduced levels of seeds recorded within each inflorescence by producing a greater number of inflorescences (Hetherington 1997). Further, within each host species there was inconsistency in pathogenicity as the amount of genetic variability within the host increased (Hetherington and Irwin 1999). Two other *Curvularia* pathogens have also been tested as potential agents against WSG: *C. crustacea* and *Cu. ryleyi*. However neither were found to be suitable due to low rates of infection, or due to modes of pathogenicity that did not adversely affect WSG seed production (Hetherington 1997; Hetherington and Irwin 1999).

Microdochium, Neopestalotiopsis and Pestalotiopsis

The isolates found on *Sporobolus* spp. in Australia (Table 1) included three fungal pathogens endemic to Australia which were subsequently described for the first time (Lock 2018): *Microdochium dawsoniorum* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas from leaves of *S. natalensis*; *Neopestalotiopsis nebuloides* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas from leaves of *S. elongatus*; and *Pestalotiopsis etonensis* C. Lock, Vitelli, Holdom, Y.P. Tan & R.G. Shivas from leaves of *S. jacquemontii*. Lock (2018) showed that all three species caused disease in *S. natalensis* seedlings, with the highest levels of seedling mortality caused by *P. etonensis* and *N. nebuloides*. At the time, these results suggested that the pathogens could reduce *S. natalensis* seedling recruitment if applied as a myco-herbicide. A subsequent research project tested the same three pathogens in a pathogenicity trial on three host growth stages (seedling, juvenile and mature), and in a host range experiment (Kukuntod 2020). The former aimed to determine the most susceptible growth stage of *S. natalensis* for inoculation but was hampered by contamination issues and was therefore inconclusive. Unfortunately, the host range study showed that all three pathogens were not host-specific and were shown to infect several host grasses outside of the WSG, including the native *S. laxus*, and the improved pasture species Callide Rhodes grass (*Chloris gayana* Kunth; Kukuntod 2020).

Collection, identification and testing of further endemic pathogens

A more recent study analysed the diversity of fungal taxa associated with symptomatic plants in the *Sporobolus indicus* complex in Queensland, Australia (Steinrucken et al. 2022). These isolates were derived from the same samples collected by Vitelli et al. (2019), and included the taxa which are discussed in the previous section (i.e., *M. dawsoniorum*, *P. etonensis* and *N. nebuloides*). This diversity study identified 79 isolates via sequencing and analysis of multiple genes of interest, that were chosen based on the putative family to which each isolate belonged. The multi-locus phylogenetic analysis classified the isolates into 54 fungal taxa representing 22 Ascomycete families (Steinrucken et al. 2022). Many of the taxa identified were novel species, five of which have since been described as *M. ratticaudae*, *Stagonospora tauntonensis*, *Leptosphaerulina queenslandica*, and *Keissierella sporoboli* (authority for all these species is: Steinrucken, Vitelli, Holdom, Y.P. Tan & R.G. Shivas); and *P. chiaroscuro* Rapley, Steinrucken, Vitelli, Holdom & Y.P. Tan (Crous et al. 2021, 2022).

As a pre-requisite, a cost-effective myco-herbicide should be formulated from fungal pathogens which can grow quickly and easily in a laboratory setting, benefiting both in vitro and in vivo studies. All the taxa identified in this diversity study were easily grown in the laboratory, and by identifying them to the species level, the literature could be assessed to determine the likelihood of each species being a potential biocontrol agent against WSG. For example, several species identified within *Alternaria*, *Bipolaris*, *Colletotrichum*, *Epicoccum*, and *Stagonospora* have either a history of being grass pathogens, and/or have closely related species previously used in biocontrol research (Steinrucken et al. 2022). Hence, for future work, those putative pathogens will be prioritised by the authors of this review for virulence, pathogenicity, and host-specificity screening as potential WSG biocontrol agents.

Learnings from past studies

The lessons learned from previous studies on potential fungal biocontrol agents for weedy grasses and WSG are multifaceted. Some of the major issues identified relate to accurate identification of the tested pathogen (as with RMIT0601 *Nigrospora* sp. which was misidentified as *Nigrospora oryzae*), and of the target plant (an issue with the morphological similarity between *Sporobolus* species in particular); virulence of the pathogen(s) to different life stages of the targeted host; and host range evaluation. However, by reviewing these past studies, we found two main points on which to focus for future work.

Adequate host range testing

Host range testing is a crucial point for ethical production of a potential myco-herbicide, approval by regulatory authorities, and for take-up by end-users once a product is formulated. However, the required stringency of host-range testing is context dependent. The primary concern of most biocontrol scientists is to ensure that only agents with very narrow host ranges are put up for approval. However there are some applications for which this may be less important. For example, South African product Stumpout® is a myco-herbicide based on a non-pathogenic wood rot fungus (*Cylindrobasidium torrendii* (Bres.) Hjortstam), so stringent host-range testing is likely to be less important biologically, as it is applied directly to tree stumps which then rot and break down (de Jong and Zadoks 1990; Morris et al. 1999). Similarly, when targeting a weed in an intensive cropping situation, the safety to the crop is of primary concern. Some previous WSG biocontrol studies showed conflicting evidence of the level of host specificity of an agent. In the case of *U. sporoboli-indici*, Rapley (2020) found evidence of non-target impacts that were not identified during the initial host-testing process (Yobo et al. 2009). For *Nigrospora* sp. (RMIT0601), biocontrol targets consisted of *S. fertilis*, *S. africanus* and *S. pyramidalis* which showed some level of pathogenicity, but no conspecific species were tested in the host range study (A. Lawrie, unpublished data), although, this may have been due to time and budget constraints for that research group (Ramasamy 2008). Further testing of *Nigrospora* sp., *Fusarium proliferatum* and *F. chlamydosporum* on *S. natalensis* failed to yield

evidence of pathogenicity, negating the need for host range trials (Fletcher and Leemon 2015).

In the case of myco-herbicide control of weeds when using endemic phytopathogens, we emphasise the importance of selecting phylogenetically related non-target hosts as a matter of priority, and the inclusion of co-located species and species of concern to the end-users of the product, such as commercial pasture crops (Wapshere 1974; Charudattan and Dinoor 2000). Additionally, we advocate for the inclusion of risk assessments such as the work done with *Sclerotinia sclerotiorum* (Lib.) de Bary, *Chondrostereum purpureum* (Pers. ex Fr.) Pouzar and *Pseudolagarobasidium acaciicola* Ginns (Bourdôt et al. 2006; Hantula et al. 2012; Kotzé et al. 2015). In these cases, risk assessments of the agent either required mitigation of infection risk to non-target plants or herbivore species in the form of agent distribution or application restrictions thereby reducing risk, or the agent itself had a low risk of infecting non-target species due to its biology. There have been examples of biocontrol agents being approved for release despite not having a single-species host range, including the aforementioned *U. pencanus* in New Zealand (Anderson et al. 2017), and those in the Di-Bak© Parkinsonia formulation. The safe use of these agents was however dependent on risk analyses and/or the inoculation strategy used to reduce any potential off-target effects (Waipara et al. 2009; Galea 2021). Approval for the release of an agent that is not entirely host-specific would need to be considered by stakeholders and regulators on a case-by-case basis.

The 'Go Wide' approach

Like other plants, grasses are host to a myriad of fungal species including several active or latent pathogens (Saikkonen et al. 1998; White and Backhouse 2007; Rodriguez et al. 2009; Teasdale et al. 2018). By opportunistly selecting a narrow range of pathogens for testing as potential biocontrol agents, many more are ignored. In the aforementioned studies on *Fusarium*, *Nigrospora* and *Curvularia*, the pathogens were chosen because they were isolated from symptomatic tissue of WSG (for *Nigrospora* sp. and the two *Fusarium* spp., in a glasshouse from *S. fertilis*; for *Curvularia*, from infected inflorescences of *S. africanus* as inspired by research on *Curvularia* in *S. indicus* (McKenzie 1968; Hetherington and Irwin 1999; Lawrie 2014)). Yet, other than two examples (Vitelli et al. 2019; Steinrucken et al. 2022)), there is no mention of any other pathogens systematically isolated and/or tested as potential agents. To highlight *Nigrospora* sp. in particular, the isolate was misidentified as *N. oryzae*, which may have informed the decision to include it in the original experiments (Lock 2018). With the introduction of new technologies and analyses, we can now collect a diverse range of fungal species from symptomatic target hosts and identify them more accurately and quickly using multi-locus phylogenetic analyses (Steinrucken et al. 2022) or genomics (Rizal et al. 2022). Once identified, assessing as many of the collected isolates as possible via a series of prioritisation steps will thus reduce the chance of missing a potential biocontrol agent. Lock (2018) and Kukuntod (2020) tested three pathogens in *M. dawsoniorum*, *P. etonensis* and *N. nebuloides* for their respective year-long projects, chosen from the wider pool of isolates collected as part of Steinrucken et al. (2022). While the process of isolating, purifying, identifying and testing multiple fungal pathogens is time consuming, a systematic 'shotgun' approach to finding candidates for a myco-herbicide is likely to result in a wider range of putative pathogens with greater supporting evidence for their inclusion, compared with a more opportunistic 'rifle' approach à la McKenzie (1968), Hetherington and Irwin (1999), and Lawrie (2014). The authors acknowledge that there is a trade-off between finding and testing more potential agents or focusing on fewer agents in more detail. However, this review advocates for the inclusion of the 'go wide/shotgun' approach initially, with the prerequisite of a stringent prioritisation workflow to then focus on fewer pathogens in more detail.

Conclusion

The search to find a biocontrol agent for WSG continues. There are currently several promising fungal pathogens which may prove to assist in the management of WSG (Steinrucken et al. 2022). Although native *Sporobolus* grasses often co-occur with non-native species, susceptibility of these hosts does not necessarily preclude the use of said pathogen as a bioherbicide, particularly if the pathogen is endemic. However, bioherbicide application would need to be targeted or strategically applied, and potential non-target effects monitored closely. *Ustilago sporoboli-indici* has shown to be pathogenic

in vitro to all WSG species except *S. jacquemontii*, whilst in the Australian landscape has only been found on *S. natalensis*. The pathogen is easily spread, mainly by wind and remains a research focus of its inclusion as part of an integrated tool for the management of giant rat's tail (Rapley 2020) with potential for augmentative biocontrol. Several Australian endemic pathogens have shown damage to WSG in preliminary screenings during host-specificity and glasshouse virulence trials by the authors (ongoing). Though research remains to iron out the morphological and genetic relatedness of *Sporobolus* in Australia, any new agent would nonetheless need to comply with host-specificity testing, safety, and efficacy trials (Department of Agriculture Water and the Environment 2020). In the meantime, Australian livestock and agriculture industries continue to call for solutions to the management of WSG, as the impact to landholders and the economy increases with spreading WSG infestations and a desire to reduce reliance on herbicides.

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Declarations

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