

LETTER TO EDITOR

Authors' reply: Is biological control using seed-reducing agents a waste of time?

Ruan Veldtman^{1,2,3*}  and Matthys Strydom⁴ 

¹South African National Biodiversity Institute, Cape Town, Western Cape, South Africa

²National Institute for Theoretical and Computational Science, Stellenbosch, Western Cape, South Africa

³Conservation Ecology and Entomology, Stellenbosch University, Stellenbosch, Western Cape, South Africa

⁴Academy for Environmental Leadership SA, Upington, Northern Cape, South Africa

In South Africa, the existing weed biocontrol programs are lauded as successful and considered an essential approach to addressing plant invasions nationally.^{1,2} Using the much-researched biological control program on Australian *Acacias* using seed-feeding agents; however, Veldtman and Strydom² illustrated the weak scientific base for claiming success of biological control agents in suppressing these species. Noteworthy, van Wilgen and Richardson¹ state that South Africa is a world leader in weed biocontrol; therefore, framing our arguments using the textbook Australian *Acacia* biocontrol program is appropriate. We thank van Wilgen *et al.*³ for responding to our review paper² as it advances further scientific discourse in the use of biological control agents on invasive weed species.

The criticisms by van Wilgen *et al.*³ regarding our review create the impression that several of the main points were missed. They state “Veldtman and Strydom’s paper points out, correctly, that pre-treatment baselines and monitoring data are necessary to accurately gauge the effectiveness of control. This has in fact been done in the case of Australian acacias in South Africa.”^{3,p.1} We are not sure if we misunderstood this statement. Our review cites every primary peer-reviewed study on Australian *Acacia* biological control, seed bank dynamics, and effects of fire, and none of these studies have proven an effect of the released agents. In addition, few, if any, of these investigations have been done with the purpose of serving as baseline data or for monitoring purposes. Furthermore, it is claimed that in our review, only seed abundance, and not the wider context, is considered. However, Veldtman and Strydom² considered all aspects listed by van Wilgen *et al.*³ to assess biological control success. This included reviewing the literature of the area of occupancy, dispersal rate, population dynamics, seed bank dynamics, and interspecific relationships of invasive Australian *Acacia* within their invaded ranges in South Africa.

Second, van Wilgen *et al.*³ state that we present insufficient evidence to indicate that the Australian *Acacia* biocontrol has been unsuccessful. A major point of our review is that appropriate hypothesis testing requires data to reject the null hypothesis of no effect to demonstrate that biocontrol on Australian *Acacia* is effective, otherwise the chance of a Type 1 error is too great. As shown in Table 2 of our review,^{2,pp.6-8} no studies have demonstrated that the release of biocontrol agents on the invasive Australian *Acacia* in South Africa has sufficiently impacted their population’s dynamics to the extent that it has reduced their invasive impact. Instead, the assertion that this biocontrol program has reduced the impact of these species is almost solely based on expert opinion or counterfactual arguments.^{1,4,5}

*Corresponding author:

Ruan Veldtman
(veldtman@sun.ac.za)

Citation: Veldtman R, Strydom M. Authors' reply: Is biological control using seed-reducing agents a waste of time? *Explora Environ Resour.* 2025;2(4):025360065. doi: 10.36922/EER025360065

Received: September 4, 2025

Accepted: September 5, 2025

Published online: September 26, 2025

Copyright: © 2025 Author(s). This is an Open-Access article distributed under the terms of the Creative Commons Attribution License, permitting distribution, and reproduction in any medium, provided the original work is properly cited.

Publisher's Note: AccScience Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Third, as van Wilgen *et al.*³ have noted, the broader question of whether biological control of weeds in general can result in desirable outcomes⁶ is not directly relevant when reviewing the success of a specific weed biocontrol program. For instance how can the successful biological control of cacti or water weeds⁷ be used to justify or predict the success of biocontrol efforts targeting Australian *Acacia*?

Van Wilgen *et al.*³ suggest that any reduction in seed production by seed-reducing agents will translate in a reduced rate of spread of invasive plants. However, this assumption overlooks thresholds below which seed-reducing agents need to reduce seed production to decrease the short- and long-distance dispersal rates of their invasive host plants.^{8–10} In addition, the level to which specialist seed-predators, such as all biocontrol agents released against invasive Australian *Acacia* in South Africa, can reduce host dispersal rate, is a function of the host plants' dynamics rather than that of the biological control agents.¹¹ For example, where a host plant population has no Allee effect, the dispersal rate cannot be slowed or reversed, even in the presence of strong predation. At present, the seed production thresholds required to reduce dispersal in invasive Australian *Acacia* have not been determined empirically, nor is it known whether these species exhibit Allee effects at low densities. The assumption that seed-reducing biocontrol agents limit dispersal rate is therefore not empirically substantiated.

We already critiqued the use of comparative invasion rates from Henderson and Wilson¹² to assess seed biological control,² who argue that invasive Australian *Acacia* display lower dispersal rates than other invasive plants in South Africa. This comparison is problematic as it compares species with differing growth forms, life histories, modes of dispersal, and invasion stages. Moreover, Henderson and Wilson¹² do not provide evidence that the rate of spread of invasive Australian *Acacia* species has declined over time.

Kotze *et al.*¹³ present data on changes in the invaded area of invasive plants with and without biological control in South Africa. However, due to a lack of appropriate control treatments these data cannot be used to infer causal impacts of biological control on their hosts distribution ranges. Their findings show that the invaded area of invasive plants not under biological control decreased, remained the same, or increased in South Africa. This indicates that there are factors other than biological control influencing the area occupied by invasive alien plants in South Africa (Veldtman and Strydom²). Therefore, the observed changes in the area occupied by the invasive plants in South Africa under biological control could alternatively be the consequence of other factors (*e.g.*, mechanical and chemical clearing, land

use change, *etc.*). Kotze *et al.*¹³ therefore provide, at best, circumstantial evidence that weed biocontrol has reduced the area occupied by Australian *Acacia* in South Africa.

Veldtman and Strydom² identified key methodological shortcomings in the works of both Wood and Morris¹⁴ and Impson *et al.*,¹⁵ whose long-term studies attempt to link biocontrol impact to reductions in population size or area occupied. Wood and Morris¹⁴ reported a reduction in stand density but did not quantify canopy cover. A reduction in stand density could therefore also be due to self-thinning.² Impson *et al.*¹⁵ in particular raises multiple concerns beyond methodological errors. These include (i) data integrity issues such as implausible tree density estimates (*e.g.*, 26533 plants/m²), (ii) internal inconsistencies such as contradictory fire records (*e.g.*, 2001 and 2017 vs. 2000 and 2017 for the 4-year burnt site), (iii) pseudoreplication, as all long-term monitoring plots were located in a single protected area (De Hoop Nature Reserve), which are 0.2–10 km from each other, and (iv) taxonomic inaccuracies, such as reporting that both *Dasineura rubiformis* and *Dasineura dielsi* were studied on *Acacia cyclops*. These issues raise valid concerns regarding the accuracy and credibility of Impson *et al.*¹⁵

The case study put forward by van Wilgen *et al.*³ that species interactions need to be considered when evaluating Australian *Acacia* biocontrol is at best circumstantial evidence. For example, Holmes¹⁶ suggested that reduced seed predation by rodents in closed canopy stands of *Acacia saligna* was due to reduced rodent activity within these stands. However, rodent population densities were not measured, and an alternative explanation of predator satiation in a seed-abundant environment, cannot be ruled out. Moreover, Holmes¹⁶ questioned the importance of seed predation by rodents, noting that ants removed and buried seeds at a faster rate than they were consumed by rodents. There is also no supporting empirical evidence for the claim that *Uromycladium morrisii* has caused a decline in the stand density of *A. saligna*, which translates into reduced canopy cover (*i.e.*, reduced area of occupancy).² Thus, the conclusion that declining canopy cover is associated with increased rodent seed predation within *A. saligna* populations lacks support. Furthermore, neither Holmes¹⁷ nor Ngwenya *et al.*¹⁸ demonstrated that biological control allowed for native species recovery after physical clearing. On the contrary, they demonstrated a reduced native species diversity and cover as well as depleted or absent native seed banks following invasion by *A. saligna*. Their findings underscore the need for active management and restoration efforts to recover indigenous plant communities after the removal of *A. saligna* populations.

Van Wilgen *et al.*³ state that a substantial reduction in seed production by seed-reducing biological control agents targeting invasive Australian *Acacia* species will reduce the number of regenerating seedlings after disturbance events, thereby making physical control feasible in areas where it was previously impractical. Despite the assertion that seed bank reduction through biocontrol will reduce management effort, there is no empirical evidence quantifying the level of reduction needed.² In fact, empirical studies suggest otherwise. Post-biocontrol assessments found that seed bank size was similar to pre-biocontrol levels¹⁹ or remained large enough to sustain post-disturbance seedling regeneration, which was comparable to the pre-control levels.² These findings imply that the number of seedlings and trees requiring active management within invasive Australian *Acacia* stands have remained unchanged. It is also stated that Strydom *et al.*¹⁹⁻²¹ only investigated seed banks in predetermined, but not necessarily representative sites. However, these three peer-reviewed papers are the only studies in South Africa to date that have collectively investigated all stages of the seed bank dynamics of three invasive Australian *Acacia* species regarded as under substantial biocontrol.² Furthermore, these studies were in close proximity (0–10 km) to the original release sites of the investigated biocontrol agents, and close to the sites where these agents' impact were previously assessed as successful.^{14,22-25} Thus, how can the sites sampled in Strydom *et al.*¹⁹⁻²¹ then not be representative?

In conclusion, the extent to which seed production of invasive Australian *Acacia* in South Africa has been reduced by their seed-reducing biological control agents remains largely unquantified as stated in our review.² For the gall-forming biological control agents whose impact on their invasive Australian *Acacia* hosts has been assessed, it has been demonstrated that 22–60% of the pods produced on a population level may be lost.²¹ These values fall short of the threshold required to cause a reduction in the area occupied by these plants.² Based on the evidence provided by van Wilgen *et al.*,³ there is currently no new published evidence supporting the claim that biocontrol has reduced physical management effort, or that earlier implementation would have done so. If it is argued that any seed reduction would result in fewer seedlings to manage, then the threshold of reduction required still needs to be experimentally determined. We contend that the status quo of assessing weed biocontrol requires urgent reform and we should in fact guard against placing expert opinion above empirically collected data. Rather, investment in experimentally sound data collection, especially before and after release, is required to assess whether classical biological control agents result in a significant reduction of the impact of their invasive plant hosts.

Conflict of interest

The authors declare that they have no competing interests.

References

1. Van Wilgen BW, Richardson DM. South African contributions to the understanding of plant invasion ecology and management. *S Afr J Bot.* 2025;181:391-404. doi: 10.1016/j.sajb.2025.04.029
2. Veldtman R, Strydom M. Prioritizing scientific data over expert opinion in the valid assessment of Australian *Acacia* biocontrol success. *Explora Environ Resour.* 2025;2(1):5876. doi: 10.36922/eer.5876
3. Van Wilgen BW, Richardson DM, Midgley GF, Holmes PM. Is biological control using seed-reducing agents a waste of time? *Explora Environ Resour.* 2025;025140028. doi: 10.36922/eer025140028
4. Van Wilgen BW, Moran VC, Hoffmann JH. Some perspectives on the risks and benefits of biological control of invasive alien plants in the management of natural ecosystems. *Environ Manag.* 2013;52:531-540. doi: 10.1007/s00267-013-0099-4
5. McConnachie M, Van Wilgen BW, Gaertner M, *et al.* Using counterfactuals to evaluate the cost-effectiveness of controlling biological invasions. *Ecol Appl.* 2016;26(2):475-483. doi: 10.1890/15-0351
6. Van Driesche RG, Carruthers RI, Center T, *et al.* Classical biological control for the protection of natural ecosystems. *Biol Control.* 2010;54:S2-S33. doi: 10.1016/j.biocontrol.2010.03.003
7. Hill MP, Moran VC, Hoffmann JH, *et al.* More than a century of biological control against invasive alien plants in South Africa: A synoptic view of what has been accomplished. In: Van Wilgen B, Measey J, Richardson D, Wilson J, Zengeya T, editors. *Biological Invasions in South Africa*. Vol 14. Cham: Springer, Invading Nature - Springer Series in Invasion Ecology; 2020. p. 553-572. doi: 10.1007/978-3-030-32394-3_19
8. Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology.* 1999;80(5):1475-1494. doi: 10.1890/0012-9658(1999)080[1475:sdnafp]2.0.co;2
9. Nathan R. Long-distance dispersal of plants. *Science* 2006;313(5788):786-788. doi: 10.1126/science.1124975
10. Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A. Mechanisms of long-distance seed dispersal. *Trends Ecol Evolut.* 2008;23(11):638-647.

- doi: 10.1016/j.tree.2008.08.003
11. Fagan WF, Lewis MA, Neubert MG, Van Den Driessche . Invasion theory and biological control. *Ecol Lett.* 2002;5(1):148-157.
doi: 10.1046/j.1461-0248.2002.0_285.x
 12. Henderson L, Wilson JR. Changes in the composition and distribution of alien plants in South Africa: An update from the Southern African plant invaders atlas. *Bothalia.* 2017;47:a2172.
doi: 10.4102/abc.v47i2.2172
 13. Kotze I, Wannenburg A, Van Wilgen BW. Changes in the cover of selected invasive alien plant taxa between 2008 and 2023 in South Africa. *Biol Invasions.* 2025;27:98.
doi: 10.1007/s10530-025-03558-9
 14. Wood AR, Morris MJ. Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa: 15 years of monitoring. *Biol Control.* 2007;41:68-77.
doi: 10.1016/j.biocontrol.2006.12.018
 15. Impson FAC, Hoffmann JH, Impson OR, Kleinjan CA, Moran VC. Densities of a perennial invasive tree, *Acacia cyclops*, decline in the 20 years since inception of biological control with two seed-reducing agents, a flower-galling midge and a seed-feeding weevil. *Biol Control.* 2024;189:105442.
doi: 10.1016/j.biocontrol.2024.105442
 16. Holmes PM. Dispersal and predation of alien *Acacia* seeds: Effects of season and invading stand density. *S Afr J Bot.* 1990;56:428-434.
doi: 10.1016/S0254-6299(16)31037-7
 17. Holmes PM. Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecol.* 2002;27:110-120.
doi: 10.1046/j.1442-9993.2002.01164.x
 18. Ngwenya DK, Holmes PM, Geerts S, Esler KJ. Delaying a prescribed burn to scale up the restoration of alien-invaded Lowland Sand Fynbos in South Africa. *Austral Ecol.* 2023;49:e13469.
doi: 10.1111/aec.13469
 19. Strydom M, Veldtman R, Ngwenya MZ, Esler KJ. Invasive Australian *Acacia* seed banks: Size and relationship with stem diameter in the presence of gall-forming biological control agents. *PLoS One.* 2017;12(8):e0181763.
doi: 10.1371/journal.pone.0181763
 20. Strydom M, Veldtman R, Ngwenya MZ, Esler KJ. Seed survival of Australian *Acacia* in the Western Cape of South Africa in the presence of biological control agents and given environmental variation. *PeerJ.* 2019;7:e6816.
doi: 10.7717/peerj.6816
 21. Strydom M, Veldtman R, Ngwenya MZ, Esler KJ. Questioning the effectiveness of seed-reducing agents on invasive *Acacia*: Pod production relative to gall abundance of classical biological control agents. *Perspect Plant Ecol Evol Syst.* 2024;64:125813.
doi: 10.1016/j.ppees.2024.125813
 22. Dennill GB. The effect of the gall wasp *Trichilogaster acaciaelongifoliae* (Hymenoptera: Pteromalidae) on reproductive potential and vegetative growth of the weed *Acacia longifolia*. *Agric Ecosyst Environ.* 1985;14:53-61.
doi: 10.1016/0167-8809(85)90084-2
 23. Dennill GB. Establishment of the gall wasp *Trichilogaster acaciaelongifoliae* (Pteromalidae) for the biological control of *Acacia longifolia* in South Africa. *Agric Ecosyst Environ.* 1987;19:155-168.
doi: 10.1016/0167-8809(87)90015-6
 24. Hoffmann JH, Impson FAC, Moran VC, Donnelly D. Biological control of invasive golden wattle trees (*Acacia pycnantha*) by a gall wasp, *Trichilogaster* sp. (Hymenoptera: Pteromalidae), in South Africa. *Biol Control.* 2002;25:64-73.
doi: 10.1016/S1049-9644(02)00039-7
 25. Impson FAC, Kleinjan CA, Hoffmann JH, Post JA, Wood AR. Biological control of Australian *Acacia* species and *Paraserianthes lophantha* (Willd.) Nielsen (Mimosaceae) in South Africa. *Afr Entomol.* 2011;19:186-207.
doi: 10.4001/003.019.0210