Seed burial reduces seed predation in the endangered Clanwilliam cedar (*Widdringtonia wallichii*)

**Introduction**

The critically endangered Clanwilliam cedar, *Widdringtonia wallichii* (formerly *W. cedarbergensis*) typically has poor recruitment (White, Midgley & Bronner 2017). It has long been known that high levels of seed predation by small mammals are an important component of this poor recruitment. For example, over 30 years ago Manders and Botha (1989) observed <3% of seeds placed on soil surface in post-fire cedar habitats in April had germinated by September, whereas 15% of those buried by 5 mm of soil survived and 44% of similarly buried seeds survived in rodent exclosures. Using live traps, Manders and Botha (1989) noticed three granivorous small mammals on their plots: (1) *Acomys subspinosus*, (2) *Praomys verrauxii* and (3) *Micaelamys (Aethomys) namaquensis*. Van Hensbergen et al. (1992) also recorded much higher germination rates of serotinous *Protea* seeds (72%) within small mammal exclosures compared with 33% in open sites. However, they observed that planting seeds 3 mm–5 mm below the soil surface made no difference to germination rates. Furthermore, they observed that germination rates in open sites that had been burned were only 16% lower than in small mammal exclosures, because seed predation rates were higher in unburned vegetation and thus differences inside and outside exclosures are more extreme in mature vegetation.

More recently, White et al. (2017, 2020) found that some nut-fruited Proteaceae and cedar seeds are removed and buried about 20 mm deep by the scatter hoarding rodent *A. subspinosus* (Cape spiny mouse). Therefore, not all removed seeds may be predated; some may be buried. White et al. (2020) also noticed similarly high cedar seed predation rates found by Manders and Botha (1989); however, by using trail cameras, they observed that predation was mainly by *Micaelamys namaquensis* (Namaqua rock rat).

This study test whether planting cedar seeds at 20 mm depth (the depth scatter hoarding rodents typically bury seeds) in unburned vegetation is a possible conservation intervention that may lead to substantial increases in the seedling bank. Small mammal populations collapse after fire (Midgley & Clayton 1990; Van Hensbergen et al. 1992) and thus seed predation by small mammals may be high in pre-fire, mature vegetation. However, this may be circumvented by planting the seeds.

**Methods**

Bright yellow cotton threads was attached to seeds with a small drop of fast-setting glue and buried at 20 mm depth to relocate buried seeds at the end of the experiment. Similarly, cotton threads were glued to seeds placed on the soil surface to control the thread and glue. Researchers did this for 160 seeds across two sites, with 80 seeds per site. At each site, 40 seeds was placed on the soil surface and buried 40 seeds at 20 mm depth. Soil surface and buried seeds were placed in 40 pairs, 0.5 m apart, and identified by a numbered metal peg between the seeds. Seed pairs were 5 m apart along a ± 200 m transect. Site 1 was at the Cedarhoutkloof site of White et al. (2020) and site 2 was 500 m away and 60 m higher in altitude from site 1. Cedarhoutkloof was chosen because previously White et al. (2020) had observed intense predation and limited burial at this site despite there being mature adult trees and relative shelter from fires.

Threads were glued to seed-sized stones and seeds (20 pairs of buried seeds and buried stones) to compare discovery rates of buried seeds and stones. The pairs were placed 0.5 m apart with central metal peg, with pairs located 5 m apart at site 1.

Seeds were placed out in April and the experiment terminated in August, with two surveys in between (not reported on). At the termination of the experiment, seed removal and germination rates were measured. This mirrors the autumn seed fall phenology (from March to May) and winter-spring seed germination patterns (from July to August) of the trees. Trail cameras were also used at site 1.
to determine the most common small mammal granivores. Seven cameras recorded visits to seeds from 30 March 2022 until 4 April 2022. Each was focussed on a thread labelled seed.

Results
At site 1, only 2 out of 40 seeds placed on the soil surface remained, whereas 33 of the 40 buried seeds remained ($\chi^2 = 45.71$, $p < 0.001$), 12 of which had germinated. At site 2, one soil surface seed remained whereas 34 buried seeds were relocated, 5 of which had germinated ($\chi^2 = 52.01$, $p < 0.001$). Overall survival rates for buried seeds were thus $84\%$ ($67/80$) compared with $4\%$ ($3/80$) for soil surface seeds ($\chi^2 = 100.80$, $p < 0.001$) (Figure 1). This is a minimum difference because it is possible some of the missing buried seeds became detached from the strings in the soil, because the threads of these were mostly still buried in situ. The thread of most of the seeds placed on the soil remained in situ, suggesting that seeds were predated in situ and very few of the seeds may have been removed and buried. The overall germination rate for remaining buried seeds was $25\%$ ($17/67$), which is $21\%$ of initially buried seeds (Figure 1). Nineteen of the 20 buried stones were relocated whereas 14 of the 20 buried seeds were relocated, indicating that limited learning was taking place. Of the 14 videos that captured small granivorous rodents visiting the seeds, 12 were of *M. namaquensis*.

Discussion
This simple experiment suggests that burying seeds $20$ mm below the soil surface, even in mature vegetation, will strongly contribute to increasing the seedling bank of the cedar. It additionally shows the importance of *A. subspinosus* scatter hoarding to natural cedar recruitment, by showing that naive rodents (those foraging for seeds other rodents buried, such as *M. namaquensis*, the most common at our site) will only find a very limited portion of buried seeds. Seed burial has other advantages besides avoiding predation: it reduces the incidence of desiccation, improves seedling success, reduces damage during fire (Moore & Vander Wall 2015). Some cones on adult trees had opened and others were still to open when this experiment was initiated in April confirming that seed release is in late autumn (White et al. 2020). Seeds should thus be planted in autumn, near large rocks for the shade, moisture and fire protection they provide (Manders & Botha 1989; Mustart et al. 1995; White et al. 2016). An effort should be made to recreate dense stands so that prolific seed release and subsequent predator satiation may allow the scatter hoarding process to be re-instated (White et al. 2020). Recently burned sites should be preferentially targeted to minimise predation and to give seedlings the longest possible period of growth before the next fire. Nevertheless, burial also avoids predation in mature vegetation and will increase seed-to-seedling transition success.

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Competing interests
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Authors’ contributions
J.M. and J.D.W. conceived the idea and J.M., G.H. and L.M.K. were involved with fieldwork and all authors contributed to write-up.

Ethical considerations
This article followed all ethical standards for research without direct contact with human or animal subjects.

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Data availability
The data that support the findings of this study are available from the corresponding author, J.M., upon reasonable request.

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References


