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SHORT COMMUNICATION

Seed germination, dormancy and longevity in the endangered shrub *Muehlenbeckia astonii* (Polygonaceae)

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ABSTRACT

Muehlenbeckia astonii Petrie (Polygonaceae) is a nationally endangered shrub undergoing widespread recruitment failure in the wild. Seed germination, dormancy and longevity were investigated to determine factors potentially constraining *M. astonii* regeneration and population persistence. *Muehlenbeckia astonii* seeds were collected from restoration plants sourced from Kaitorete Spit, Canterbury. Germination percentage of untreated control seeds in a growth room (20 °C with 16 hours of light daily) was compared with that of seeds in two treatments: (1) chilled at 4 °C for 2 weeks; and (2) chilled for 12 weeks. I also investigated seed longevity by comparing germination of unburied, 6-month old, cold-stratified *M. astonii* seeds with germination of seeds buried in the field and retrieved after 1–4 years. All seeds were sown in pots outdoors. In the growth room, 24% of untreated *M. astonii* seeds germinated, while cold-stratification for either 2 or 12 weeks increased germination significantly (to 76%). In the seed longevity experiment, 85.2% of unburied *M. astonii* seeds sown 6 months after collection germinated. *Muehlenbeckia astonii* seeds survived burial under the soil in the field for up to 4 years. However, germination declined rapidly to 27.6% after burial for 1 year, and only 2.8% of the seeds germinated after 4 years of burial. The high germination of cold-stratified seeds suggests that low seed viability is not limiting *M. astonii* regeneration at Kaitorete Spit. *Muehlenbeckia astonii* has the potential to form a soil seed bank, which may buffer small, isolated populations from local extinction in the short term (< 5 years).

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Introduction

To regenerate successfully plants need to produce viable seeds (which depends on successful flowering, pollination and seed set), disperse their seeds through space and/or time, germinate, establish and grow (Grubb 1977). These processes define a plant's 'regeneration niche' (Grubb 1977). Plant regeneration and population size may be constrained by the availability of safe sites for establishment ('establishment limitation') or by whether viable seeds reach suitable recruitment sites ('seed limitation'; Erikkson and Ehrlén 1992; Clark et al. 2007). Establishment limitation and seed limitation were typically

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viewed as mutually exclusive (Clark et al. 2007). In reality most plant species are limited by both seed supply and safe sites to some degree (Clark et al. 2007; Duncan et al. 2009). Both extrinsic factors and inherent species biology can influence the availability of seeds and safe sites, and so limit plant recruitment.

Several New Zealand plant species fail to regenerate where adults are present. For example, some forest tree species do not regenerate under their own canopy and may require disturbance for their light-demanding seeds or seedlings to establish (e.g. Payton et al. 1984; Lusk et al. 2009). Many threatened species in New Zealand produce few or no seedlings in the wild, although the reasons are often unknown (e.g. Rogers 1996; Widyatmoko and Norton 1997; Dawson et al. 2005). Understanding why species fail to regenerate is essential for threatened species conservation and restoration, and it may also enhance our understanding of the drivers of plant abundance and distribution.

Human impacts such as habitat loss, invasion by non-native species (e.g. herbivores, seed predators and weeds) and altered disturbance regimes may reduce, or even completely eliminate, the availability of safe sites and threaten species persistence. The loss of pollinators or seed dispersers and inbreeding depression in small populations may also limit regeneration by reducing the availability of viable seeds (Keller and Waller 2002; Robertson et al. 2011). Seed dormancy may delay germination in some plant species. Cold-stratification is one of the main environmental cues that can break physiological seed dormancy, and it is a common requirement for germination in temperate floras (Finch-Savage and Leubner-Metzger 2006).

Species with persistent seeds can form a soil seed bank and disperse their seeds in time, as well as space, increasing seed supply in years with poor seed production. The definition of seed persistence differs among studies, ranging from 1 to 5 years survival in the soil (Thompson et al. 1993; Leishman and Westoby 1998; Funes et al. 1999; Moles et al. 2000). There is little information on seed persistence in soil seed banks in New Zealand (Ogden 1985; Moles et al. 2000; Rowarth et al. 2007). Seed longevity in the soil can be difficult to estimate by germinating seeds from soil samples, as the spatial distribution of seeds is extremely variable (Sem and Enright 1995; Martin and Ogden 2002) and the age of seeds in the soil is unknown (Rowarth et al. 2007). Seed burial experiments provide a useful method by which the longevity of seeds in the soil can be measured accurately, although they do not confirm the presence of a soil seed bank.

Muehlenbeckia astonii Petrie (Polygonaceae) is a nationally endangered (de Lange et al. 2018), small-leaved, divaricating shrub endemic to New Zealand, undergoing widespread regeneration failure (de Lange and Jones 2000). It occurs in Wairarapa, Wellington, Marlborough and Canterbury regions (de Lange and Jones 2000). *Muehlenbeckia astonii* is gynodioecious; plants either have male and bisexual flowers or only female flowers (Allan 1961). At many sites only a single female plant remains, effectively preventing regeneration (de Lange and Jones 2000). Despite its distinctive appearance and proximity to major travelling routes used since the 1850s, *M. astonii* was only discovered by botanists in the early 1900s, suggesting that it was never particularly abundant (Given 2001). Its abundance has been further reduced by habitat loss, and by browsing and trampling by stock (de Lange and Jones 2000). Juvenile plants have been found in some populations, but almost no seedlings have been recorded in the wild (de Lange and Jones 2000).

Muehlenbeckia astonii fruits consist of a small (2–2.5 × 1.25 mm), black, three-angled achene (hereafter referred to as a seed), which is partly surrounded by fleshy, translucent

white tepals (Allan 1961). Although information on the ecology of *M. astonii* is largely anecdotal, seed germination is reported to be poor (1%–6%; Norton 2001). In Marlborough, ship rats and mice ate and destroyed *M. astonii* seeds, while intact seeds were found in a single unidentified bird dropping (Udy 2004). Skinks (*Oligosoma* species) disperse seeds at Kaitorete Spit, Canterbury, although dispersal effectiveness is low (Wotton et al. 2016). Seeds have also been found in common gecko (*Woodworthia maculata*) droppings and birds have been observed eating fruits (de Lange and Jones 2000).

I investigated aspects of *Muehlenbeckia astonii* seed ecology that may influence seedling recruitment and persistence of this threatened species. Specifically, I addressed the following questions: (1) what percentage of *M. astonii* seeds germinate, and does cold-stratification increase germination success? (2) Do *M. astonii* seeds have the potential to form a soil seed bank?

Methods

Study site

Field experiments were conducted at Kaitorete Spit, Canterbury (43°50′S, 172°31′E), which had an estimated population of c.3400 *M. astonii* plants in 2007, almost all of which were on private land (Dutton 2007). Some plants have since died, probably due to browsing by stock and natural mortality (DMW pers. obs.). Additionally, several hundred plants were killed in 2018 when the landowner sprayed paddocks with herbicide. *Muehlenbeckia astonii* seedlings have not been observed at Kaitorete Spit. At this site, *M. astonii* occurs in modified grassland that is extensively grazed by cattle and sheep, with dune ecosystems to the south and Lake Ellesmere to the north. Most adult *M. astonii* plants are browsed by stock and are significantly smaller than nearby plants protected from stock (DMW pers. obs.). The average annual rainfall at the nearby weather station at Lincoln is 599 mm, with mean daily minimum and maximum temperatures of 6.6 °C and 16.7 °C, respectively (NIWA 2017).

Seed germination and dormancy

Germination success of *M. astonii* untreated control seeds was compared with that of seeds in two treatments: (1) cold-stratification for 2 weeks; and (2) cold-stratification for 12 weeks. *Muehlenbeckia astonii* seeds were collected in late March 2010 from 21 plants at Travis Wetland, Christchurch, which were originally sourced from the Kaitorete Spit population. Plants at Kaitorete Spit produced too few seeds for use in this study. Seeds were washed in tap water to remove the pulp, then air-dried at room temperature on paper towels. Under field conditions the fleshy tepals of *M. astonii* fruits that fall from the plant are often dislodged from seeds. They also break down rapidly when still attached to seeds and are digested when fruits are eaten by birds and lizards (Wotton et al. 2016). Therefore, it is unlikely that washing the pulp off would have influenced seed dormancy compared with the conditions that seeds experience in the wild. Seeds from all plants were pooled and mixed thoroughly before being counted into plastic vials, and so randomised among treatments and replicates for each experiment. Control seeds were stored dry at room temperature for 6 months before sowing.

Cold-stratified seeds were stored dry at room temperature (for either 5.5 or 3 months, depending on cold-stratification period) then placed on germination paper moistened with water inside sealed ziplock plastic bags and refrigerated at 4 °C for either 2 or 12 weeks. All seeds were sown in early October 2010, c. 6 months after collection. For each treatment, 25 seeds were sown along the top edge of each of 10 sheets of regular-weight germination paper (Anchor Paper Company, St Paul, MN, USA) c. 22.5 cm wide × 30.5 cm tall and moistened with water (three treatments × 10 replicates = 30 sheets). Each sheet was folded in half widthways to cover the seeds, then folded six times lengthways and placed inside an upright ziplock bag with the seeds at the top of the bag. Seeds were germinated at 20°C in a growth room with 16 hours of light each day (from 3 × 400 W sodium vapour and 2 × 400 W metal halide lights) and germination papers were kept continually moist. I counted the number of seeds germinated (radicle emerged) every week or fortnight until germination ceased (no further radicle emergence was observed for 3 weeks).

Seed longevity

I conducted a seed burial experiment at Kaitorete Spit to determine how long seeds can remain viable in the soil. Seeds used in this experiment were from the same collection used in the germination experiment above. Twenty-five seeds were placed into each of 100 heat-sealed nylon bags measuring 10 × 10 cm with a mesh size of 200 μm. This mesh size excluded invertebrate seed predators but permitted soil particles, fine roots and fungi to enter. Seeds were kept at room temperature for c. 6 months (until October 2010) until the burial experiment began. Bags were buried beneath 5 cm of soil in grassland with scattered *M. astonii* plants, which was fenced to exclude cattle and sheep in 2009. Bags were buried in ten 0.5 × 0.5 m plots (replicates) c. 20 m apart. Ten bags were buried side by side in each plot, with most bags separated by at least 2 cm. To minimise disturbance when burying bags, soil from each plot was removed as a single piece of turf then replaced over the bags. Aluminium pegs were laid horizontally beneath the soil along the four edges of each plot to aid long-term plot relocation using a metal detector if required. Plots were also marked above ground with two aluminium plot pegs placed on diagonally opposite corners.

One bag was retrieved at random from each of the ten plots in the field in September–October in 2011, 2012, 2013 and 2014; all intact, empty and germinated seeds were counted and intact seeds were sown. Remaining bags were not disturbed and six bags were left in each plot for a longer-term trial. I compared germination percentage of these buried seeds with germination of unburied control seeds kept at room temperature for 5½ months then cold-stratified at 4°C for 2 weeks to break dormancy before being sown in October 2010. These unburied control seeds were from the same collection of *M. astonii* seeds, with 10 replicates of 25 seeds each.

For each replicate of buried and unburied seeds, I sowed all intact seeds in a separate 125 mm diameter (c. 500 mL) plastic plant pot containing potting mix, with a 4 cm layer of seed raising mix on top. Pots were used in this trial, as seeds sown on germination paper developed mould. Pots were placed outside and kept continually moist. Seeds were sown within 3 days of retrieval from the field. Pots were checked weekly and seed germination (emergence of cotyledons above the seed raising mix) was recorded.

Statistical analysis

I analysed data in R 3.0.0 (R Core Team 2013). To determine whether cold-stratification influenced seed germination, I fitted a generalised linear model, with number of successes (germinated) and number of failures (did not germinate) per replicate germination paper (i.e. $n = 25$ seeds in each replicate) as the response variable. I specified a binomial error distribution with seed treatment as a fixed effect.

To determine whether length of burial time influenced germination percentage, I fitted a generalised linear mixed model in the R package *lme4* (Bates et al. 2013) with number of successes and failures out of each set of 25 seeds as the response variable, years buried as a fixed effect and an observation level random effect to account for overdispersion (Harrison 2015). I calculated marginal (variance explained by fixed effects only) and conditional (variance explained by fixed and random effects) R^2 values for the model (Nakagawa and Schielzeth 2013).

Results

Seed germination and dormancy

Cold-stratification significantly influenced *M. astonii* germination success (Figure 1). Seeds cold-stratified for 12 weeks had significantly higher germination (76.0 ± 5.3%, mean ± SD) than untreated control seeds (23.6 ± 10.7%; estimate = −2.327, SE = 0.21, d.f. = 27, $z = -11.081$, $P < 0.0001$). The length of time seeds were cold-stratified did not affect germination percentage; seeds cold-stratified for 2 weeks germinated as well (75.6 ± 8.3%; estimate = −0.022, SE = 0.209, $z = -0.104$, $P = 0.917$) as those cold-stratified for 12 weeks. The *M. astonii* seeds in all treatments began germinating within 10 days of sowing and germination was complete within 6 weeks. The viability of ungerminated seeds was not tested.

Seed longevity

Some *M. astonii* seeds survived burial under soil in the field for at least 4 years (Figure 2). The number of years of burial significantly influenced germination percentage (estimate = −1.5, SE = 0.15, $z = -9.74$, $P < 0.0001$) and explained 50.8% of the variance (marginal R^2; conditional $R^2 = 0.636$). Seed germination declined by 67.6% during the first year of burial (from 85.2 ± 4.97% to 27.6 ± 11.3%, mean ± 95% confidence interval) and continued to decline in subsequent years (49.3% reduction in second year to 14 ± 8.28%; 57.1% reduction in third year to 6 ± 3.92%; and 53.3% reduction in fourth year). Only 2.8 ± 3.88% of seeds germinated after being buried for 4 years. Some seeds germinated shortly before retrieval while still in bags (7.4 ± 10.19% across all years, included in total number germinated). Only a few seeds were empty (3.5 ± 10.99%) or disappeared (0.6 ± 2.65) during the 4 years.

Discussion

Seed germination and dormancy

Seed viability does not appear to be limiting the regeneration of *M. astonii* at Kaitorete Spit. Although most seeds that a plant produces will die (Harper 1977), high seed viability

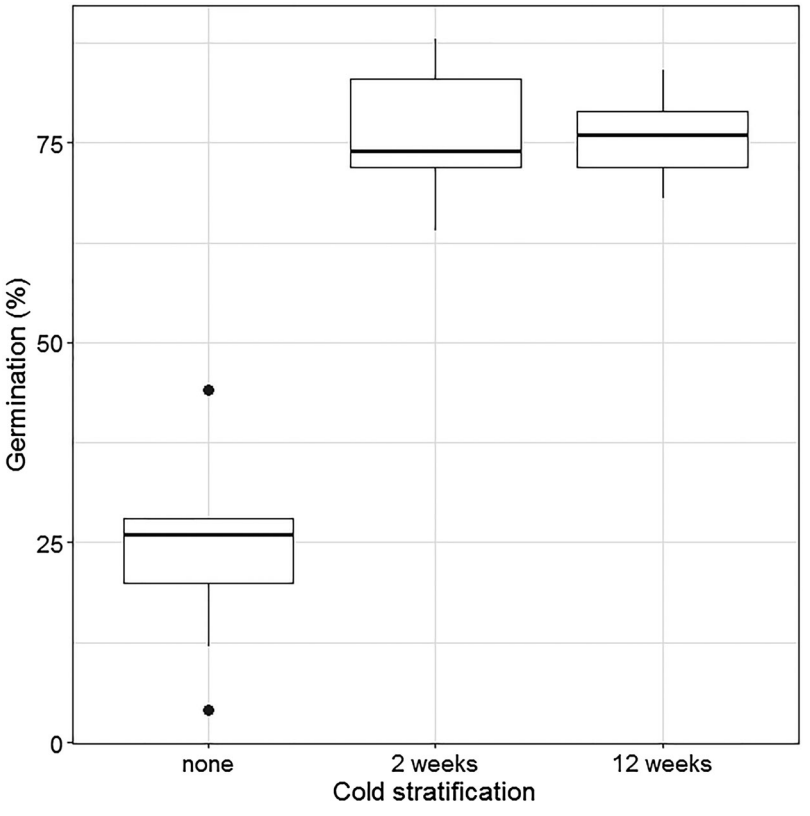

Figure 1. Effect of cold-stratification on germination percentage of *Muehlenbeckia astonii* seeds that had been after-ripened for 3–5.5 months. Batches of 25 seeds were sown on germination paper in a growth room maintained at 20 °C with 16 hours of light daily ($n = 10$). Boxplot displays median (solid horizontal bar), 25th and 75th centiles (upper and lower horizontal bars), 1.5 × interquartile range (whiskers) and outliers (points).

can maximise the likelihood of establishment if conditions are suitable. *Muehlenbeckia astonii* seeds collected from cultivated plants sourced from the Wairarapa had poor germination (1%–6%; Norton 2001). This may have been due to inbreeding depression in the small source population (Keller and Waller 2002). Kaitorete Spit has by far the largest *M. astonii* population (de Lange and Jones 2000), which probably has higher genetic diversity than other populations. Dormancy, after-ripening and/or germination conditions may also have limited germination in the Wairarapa population. Seeds were not cold-stratified and were stored at room temperature for 18 days after collection before being sown in Petri dishes in a growth cabinet under a cycle of 10 hours dark at 15 °C and 14 hours light at 25 °C, with five treatments ranging from 0% to 100% light (Norton 2001). After-ripening (dry storage at room temperature for a period of usually several months) is commonly used to break seed dormancy (Finch-Savage and Leubner-Metzger 2006), but was absent from Norton's (2001) study. This may have contributed to lower germination in Norton's (2001) study (1%–6%) than unstratified control seeds in this study (24%).

Cold-stratification enhances *M. astonii* seed germination, as it does for many temperate species (Schütz and Rave 1999; Finch-Savage and Leubner-Metzger 2006; Tsuyuzaki and

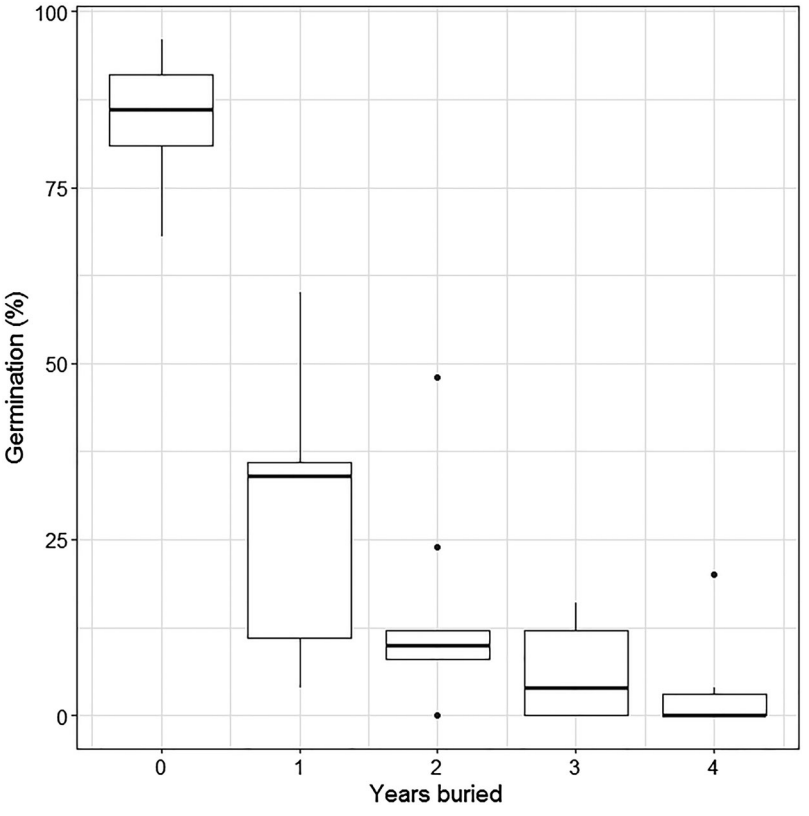

Figure 2. Effect of years of burial on germination success of *Muehlenbeckia astonii* seeds ($n = 10$). Seeds were buried in 200 µm nylon mesh bags (25 seeds per bag) under soil at Kaitorete Spit, Canterbury. One bag from each of 10 plots was retrieved annually and any seeds remaining in these bags were sown in pots outside to germinate.

Miyoshi 2009). In the wild, *M. astonii* seeds are produced in late summer and autumn, and experience cold temperatures during winter (June to August mean daily minimum 1.4–2.8 °C; NIWA 2017) before germinating in spring (D.M.W. pers. obs.). Exposure to a period of cold temperatures can signal the onset of favourable conditions for seedling establishment in spring (Finch-Savage and Leubner-Metzger 2006). Several New Zealand plant species have higher germination success when seeds are cold-stratified (Simpson and Webb 1980; Moore et al. 1994; Mackay et al. 2002). In contrast, cold-stratification did not increase germination percentage of *Muehlenbeckia australis* seeds (Mackay et al. 2002). Cold-stratification is commonly used in native plant nurseries to promote germination, so it is not surprising that it increases germination percentage in *M. astonii* and at least one other threatened New Zealand species (*Pittosporum obcordatum*; Moore et al. 1994). Dormancy behaviour varied within the *M. astonii* population, with 24% of seeds not requiring cold-stratification to germinate. The production of heterogeneous seeds that may differ in the extent of dormancy has been found in other plant species (Matilla et al. 2005; Finch-Savage and Leubner-Metzger 2006; DMW unpubl. data).

Seed longevity

Muehlenbeckia astonii has the potential to form a persistent soil seed bank, which may temporarily buffer small, isolated populations from local extinction. Species that occupy ephemeral habitats or with highly specific germination requirements may depend on a soil seed bank to persist (Bissels et al. 2005; Capon 2007). The current sites occupied by *M. astonii* have been modified by fire and grazing, so its habitat and in situ germination requirements are unclear (Given 2001). Although it seems unlikely that *M. astonii* is dependent on a seed bank for local population persistence, a persistent seed bank may enable recruitment to occur even in years when seed production is poor or absent. Species with short-lived seed banks are more strongly limited by seed availability than those with persistent seed banks where viable seeds accumulate in the soil over time (Clark et al. 2007). The degree to which a persistent soil seed bank may affect *M. astonii* recruitment is unknown, and depends on several factors, including the extent to which recruitment is limited by seed availability. Low seed production may limit regeneration at Kaitorete Spit, as most *M. astonii* plants are heavily browsed by stock and produce few or no flowers and seeds (DMW pers. obs.). *Muehlenbeckia astonii* has the potential to persist in the soil seed bank for at least 4 years, which may reduce the influence of annual seed production on regeneration at Kaitorete Spit. The presence of *M. astonii* in the soil seed bank at Kaitorete Spit, and in other populations, needs to be confirmed.

In temperate humid regions, including New Zealand, species with persistent seeds tend to have smaller seeds than species with transient seeds (Thompson et al. 1993; Funes et al. 1999; Moles et al. 2000). With its relatively small seeds, *M. astonii* fits this general relationship, even though it generally occupies relatively dry habitats within New Zealand. Although other threatened New Zealand plant species may form persistent soil seed banks, *Carmichaelia muritai* is the only species for which this has been confirmed; c. 10% of seeds survived burial under soil for 2 years and germinated after retrieval (Williams et al. 1996). *Muehlenbeckia astonii* plants can live for more than 80 years (de Lange and Jones 2000). Adult longevity combined with persistence in the soil seed bank may buffer small, isolated *M. astonii* populations from local extinction, at least in the short term.

Muehlenbeckia astonii can resprout (de Lange and Jones 2000), which decreases its dependence on seed for local persistence (Bond 1994). However, there may be a trade-off between investment in resprouting and regeneration from seed, making *M. astonii* vulnerable to any increases in adult mortality (Bond and Midgley 2001). In the face of extensive habitat loss and modification, and ongoing adult mortality, *M. astonii*'s lack of seedling recruitment threatens population persistence. Further research is needed on the role of seed supply and safe sites in *M. astonii* regeneration in the wild.

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References

Allan HH. 1961. Flora of New Zealand volume I. Wellington: P.D. Hasselberg. 1085 p.

Bates D, Maechler M, Bolker B. 2013. Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Bissels S, Donath TW, Hölzel N, Otte A. 2005. Ephemeral wetland vegetation in irregularly flooded arable fields along the northern Upper Rhine: the importance of persistent seedbanks. Phytocoenologia. 35:469–488.

Bond WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London B Biological Sciences. 344:83–90.

Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology & Evolution. 16:45–51.

Capon SJ. 2007. Effects of flooding on seedling emergence from the soil seed bank of a large desert floodplain. Wetlands. 27:904–914.

Clark CJ, Poulsen JR, Levey DJ, Osenberg CW. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. American Naturalist. 170:128–142.

Dawson PAC, Rapson GL, Robertson AW. 2005. Limitations on recruitment of the rare sand daphne *Pimelea arenaria* (Thymelaeaceae), lower North Island, New Zealand. New Zealand Journal of Botany. 43:619–630.

de Lange PJ, Jones C. 2000. Shrubby tororaro (*Muehlenbeckia astonii* Petrie) recovery plan: 2000–2010. Threatened Species Recovery Plan. Wellington (New Zealand): Department of Conservation. 24 p.

de Lange PJ, Rolfe JR, Barkla JW, Courtney SP, Champion PD, Perrie LR, Beadel SM, Ford KA, Breitwieser I, Schönberger I, et al. 2018. Conservation status of New Zealand indigenous vascular plants, 2017. New Zealand Threat Classification Series, Wellington (New Zealand): Department of Conservation. 82 p.

Duncan RP, Diez JM, Sullivan JJ, Wangen S, Miller AL. 2009. Safe sites, seed supply, and the recruitment function in plant populations. Ecology. 90:2129–2138.

Dutton P. 2007. *Muehlenbeckia astonii* re-survey at Kaitorete Spit, Canterbury 2007. Unpublished report prepared for Department of Conservation, Mahaanui Area Office.

Eriksson O, Ehrlén J. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia. 91:360–364.

Finch-Savage WE, Leubner-Metzger G. 2006. Seed dormancy and the control of germination. New Phytologist. 171:501–523.

Funes G, Basconcelo S, Díaz S, Cabido M. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. Seed Science Research. 9:341–345.

Given DR. 2001. The Wiggy-wig bush—orphan or geriatric? *Muehlenbeckia astonii* (Polygonaceae) in North Canterbury and Marlborough. Canterbury Botanical Society Journal. 35:48–51.
Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews. 52:107–145.
Harper J. 1977. Population biology of plants. London: Academic Press. 892 p.
Harrison XA. 2015. A comparison of observation-level random effect and beta-binomial models for modelling overdispersion in binomial data in ecology & evolution. PeerJ. 3:e1114.
Keller LF, Waller DM. 2002. Inbreeding effects in wild populations. Trends in Ecology & Evolution. 17:230–241.
Leishman MR, Westoby M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. Functional Ecology. 12:480–485.
Lusk CH, Duncan RP, Bellingham PJ. 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. New Zealand Journal of Ecology. 33:83–89.
Mackay AC, McGill CR, Fountain DW, Southward RC. 2002. Seed dormancy and germination of a panel of New Zealand plants suitable for re-vegetation. New Zealand Journal of Botany. 40:373–382.
Martin TJ, Ogden J. 2002. The seed ecology of *Ascarina lucida*: a rare New Zealand tree adapted to disturbance. New Zealand Journal of Botany. 40:397–404.
Matilla A, Gallardo M, Puga-Hermida MI. 2005. Structural, physiological and molecular aspects of heterogeneity in seeds: a review. Seed Science Research. 15:63–76.
Moles AT, Hodson DW, Webb CJ. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. Oikos. 89:541–545.
Moore S, Bannister P, Jameson PE. 1994. The effects of low temperatures on seed germination of some New Zealand species of *Pittosporum*. New Zealand Journal of Botany. 32:483–485.
Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution. 4:133–142.
NIWA. 2017. CliFlo: NIWA's National Climate Database on the Web. http://cliflo.niwa.co.nz/. Retrieved 6 October 2017.
Norton DA. 2001. Re-establishment of shrubby tororaro (*Muehlenbeckia astonii* Petrie), a nationally threatened plant. Science and Research Internal Report 188. Wellington (New Zealand): Department of Conservation. 21 p.
Ogden J. 1985. An introduction to plant demography with special reference to New Zealand trees. New Zealand Journal of Botany. 23:751–772.
Payton I, Allen R, Knowlton J. 1984. A post-fire succession in the northern Urewera forests North Island, New Zealand. New Zealand Journal of Botany. 22:207–222.
R Core Team. 2013. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.
Robertson AW, Kelly D, Ladley JJ. 2011. Futile selfing in the trees *Fuchsia excorticata* (Ongaraceae) and *Sophora microphylla* (Fabaceae): inbreeding depression over 11 years. International Journal of Plant Sciences. 172:191–198.
Rogers GM. 1996. Aspects of the ecology and conservation of the threatened tree *Olearia hectorii* in New Zealand. New Zealand Journal of Botany. 34:227–240.
Rowarth J, Hampton J, Hill M. 2007. New Zealand native seed germination requirements: a review. New Zealand Journal of Botany. 45:485–501.
Schütz W, Rave G. 1999. The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. Plant Ecology. 144:215–230.
Sem G, Enright NJ. 1995. The soil seed bank in *Agathis australis* (D-Don) Lindl (kauri) forests of northern New Zealand. New Zealand Journal of Botany. 33:221–235.
Simpson MJA, Webb CJ. 1980. Germination in some New Zealand species of *Gentiana*: a preliminary report. New Zealand Journal of Botany. 18:495–501.
Thompson K, Band S, Hodgson J. 1993. Seed size and shape predict persistence in soil. Functional Ecology. 7:236–241.

Tsuyuzaki S, Miyoshi C. 2009. Effects of smoke, heat, darkness and cold stratification on seed germination of 40 species in a cool temperate zone in northern Japan. Plant Biology. 11:369–378.
Udy G. 2004. Identifying pre-dispersal seed predators and seed dispersers of shrubby tororaro (*Muehlenbeckia astonii* Petrie). DOC Science Internal Series. Wellington (New Zealand): Department of Conservation. 10 p.
Widyatmoko D, Norton DA. 1997. Conservation of the threatened shrub *Hebe cupressoides* (Scrophulariaceae), eastern South Island, New Zealand. Biological Conservation. 82:193–201.
Williams P, Norton D, Nicholas J. 1996. Germination and seedling growth of an endangered native broom, *Chordospartium muritai* AW Purdie (Fabaceae), in Marlborough, South Island. New Zealand Journal of Botany. 34:199–204.
Wotton DM, Drake DR, Powlesland RG, Ladley JJ. 2016. The role of lizards as seed dispersers in New Zealand. Journal of the Royal Society of New Zealand. 46:40–65.