Seed Longevity of Six Native Forbs in a Closed *Themeda triandra* Grassland

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**Abstract**

Seeds of six native forbs—*Arthropodium strictum* R.Br., *Burchardia umbellata* R.Br., *Bulbine bulbosa* (R.Br.) Haw., *Chrysocephalum apiculatum* (Labill.) Steetz, *Craspedia variabilis* Everett & Doust and *Leptorhynchos squamarus* (Labill.) Less.—were sown on and below the soil surface in a closed, native grassland dominated by *Themeda triandra* Forsskål. Replicate seed lots were recovered after 2, 4, 6, 9 and 12 months, and viability was assessed. Less than 7% of sown surface seeds of *B. bulbosa*, *B. umbellata*, *C. variabilis* and *L. squamarus*, and less than 10% of buried seeds of *A. strictum*, *B. umbellata* and *C. variabilis* remained viable after 12 months. Virtually all losses of Liliaceae seeds were due to germination. Fates of Asteraceae seeds were difficult to assess accurately after 6 months, but germination accounted for most seed losses. Burial significantly promoted longevity of *B. bulbosa*, *C. variabilis* and *L. squamarus* seeds. No obvious relationship existed between seed longevity and taxonomic group (Liliaceae versus Asteraceae) or seed mass, for surface or buried seeds; the response of the large-seeded lily, *B. bulbosa*, was most similar to that of the small-seeded daisy, *L. squamarus*. Of the six species, *C. apiculatum* appears to have the greatest potential to accumulate a soil seed bank beneath a closed grass canopy, owing to its small seed size, inhibition of germination beneath a closed canopy, both on and below the soil surface, and sustained viability of buried seeds. Naturally dispersed seeds of the other five species are likely to form smaller, transient or short-term seed banks.

**Introduction**

A knowledge of seed bank dynamics is imperative for predicting ecosystem responses to management and natural perturbations (Egler 1954; Noble and Slatyer 1980; Roberts 1981). Seed longevity is a critical factor, and three types of seed banks can be recognised: (1) 'transient' seeds, which persist in the soil for 1 year at most, (2) 'short-term persistent' seeds, which persist for 1–5 years, and (3) 'long-term persistent' seeds, which persist for at least 5 years (Thompson 1993).

Little information is available on soil seed banks in temperate grasslands or grassy woodlands in south-eastern Australia. These once-widespread ecosystems are now among the most threatened in Australia, due to widespread agricultural development (Specht 1981; Scarlett and Parsons 1982; Lunt 1991; McDougall and Kirkpatrick 1994). An enhanced understanding of seed bank dynamics is of considerable importance for conservation management. Many grassland remnants dominated by *Themeda triandra* require regular burning, grazing or slashing to promote regeneration, flower and seed production, and survival of smaller native herbs (Stuwe and Parsons 1977; McDougall 1989; Lunt 1994). The cessation of regular burning often leads to a rapid closure of the grass sward, and a dramatic reduction in the density of native forbs (Stuwe 1986; Scarlett and Parsons 1990). Importantly, if the inter-fire interval exceeds 7–10 years, the diversity of native species does not seem to be re-instated after eventual burning (Scarlett and Parsons 1990), which suggests that many native species do not form a long-term seed bank.

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Seed banks in regularly grazed native grasslands in Victoria and Tasmania are overwhelmingly dominated by exotic species, especially annual grasses and legumes and the geophyte, *Romulea rosea* (Lont 1990; Gilfedder and Kirkpatrick 1993). Morgan (1995) found that most seeds of the endangered composite, *Rutidosis leptorrhynchoidea*, germinated rapidly after the first autumn rains. Insufficient data are available to determine whether the presence of a transient seed bank is characteristic of rare and endangered grassland plants like *R. leptorrhynchoidea*, or whether it also occurs in many common grassland forbs.

The aim of this paper is to document seed longevity of a number of common and widespread grassland forbs over a 12-month period. Seed bank longevity beneath a closed grass canopy, rather than in open gaps, is assessed, due to the need to predict potential recruitment in long-unburnt grassland remnants. Since seed burial can greatly alter germination patterns (Bliss and Smith 1985; Pons 1991, 1992), both surface and buried seeds are studied.

**Materials and Methods**

A seed burial and recovery technique was used. Known quantities of seeds were buried in small envelopes made of nylon mesh, and replicate seed lots were recovered and seeds were inspected at regular intervals up to 12 months. This method allows accurate data to be collected on the seed dynamics of species with low soil seed densities or highly clumped seeds, which may not be sampled adequately by a small number of soil samples (Thompson 1986; Bigwood and Inouye 1988; Benoit et al. 1989). Six widespread and conspicuous grassland species were selected for study, including three perennial daisies (Asteraceae): *Chrysocephalum apiculatum*, *Craspedia variabilis* and *Leptorrhynchos squamatus*, and three geophytic lilies (Liliaceae): *Arthropodium strictum*, *Bulbine bulbosa* and *Burchardia umbellata*. Plant nomenclature follows Ross (1993).

**Study Site**

Seeds were buried in a native grassland dominated by *Themeda triandra*, at Hillside in eastern Victoria, south-east Australia (37° 50' 00" S, 147° 29' 35" E). Prior to European colonisation, the area supported a grassy forest dominated by *Eucalyptus tereticornis*, but most trees were cleared last century, and the site is now managed as a native grassland reserve surrounded by agricultural pastures. The 4 ha reserve is part of an unused railway siding which has been burnt regularly for over a century and was grazed occasionally by stock. Recent fires occurred in spring 1991, 1.5 years before this experiment began, and in March 1994, at the end of the experiment.

A loamy topsoil overlies Pleistocene alluvial gravels, consisting of coarse pebbles and stones (Aldrick et al. 1988). The gently sloping site is poorly drained, and the soil surface is often covered by a shallow layer of water, over 1 cm deep, in early spring. Mean annual rainfall at Bairsdale, 8.5 km south-east of the study site, is 702 mm and tends to be uniformly distributed throughout the year, with a slight peak in spring (Fig. 1; Land Conservation Council 1982). The percentage probability of receiving at least the effective rainfall ranges from 55% in February to 92% in September (Fig. 1). Effective rainfall is defined as the minimum amount of rain necessary to start plant growth and maintain soil moisture levels in the root zone above wilting point (Bureau of Meteorology 1976). The mean daily maximum temperatures range from 25°C in February to 14°C in July, and mean minimum temperatures range from 13°C in February to 4°C in July (Fig. 1; Land Conservation Council 1982). The study period was characterised by below average rainfall throughout most of autumn and winter (March to August 1993), above average spring rainfall (September and October 1993) and exceptional summer downpours in February 1994 (Fig. 2; Bureau of Meteorology, unpublished data).

**Seed Burial**

Seeds were collected from nearby grassland and woodland remnants in December 1991 and 1992, and were air-dried and stored in the dark at room temperature until used. Mean seed mass was calculated from the air-dry weight of 100 propagules of each species. The pappus was removed from daisy seeds before weighing. Daisy 'seeds' are properly termed 'fruits', but the term 'seed' is used for simplicity. Initial seed viability was assessed on 8 replicates of 25 seeds of each species using tetrazolium (Freeland 1976). The small seeds of *C. apiculatum* and *L. squamatus* stained poorly, so
viability of these species was assessed visually. Intact, filled, healthy seeds were assumed viable, and viability of both species was initially assumed to be 100%.

Twenty-five filled seeds of each species were placed in a 4 cm × 4 cm nylon mesh envelope, of mesh size 0.85 mm × 0.95 mm. Two layers of material were placed on the bottom of each envelope to prevent small seeds from falling through the mesh. The 480 seed envelopes were subjected to one of
two field treatments: (1) surface sowing beneath the closed canopy of *T. triandra* or (2) burial 3 cm deep below the grass canopy. Envelopes were sown on 18–22 March 1993, at 0.5 m intervals along 22 parallel transects, each 1 m apart, forming a 10.5 × 21 m grid. Samples in alternate rows were buried. Surface envelopes were firmly pinned to the soil to maximise soil contact.

Eight seed envelopes of each species were randomly recovered from each treatment after approximately 2, 4, 6, 9 and 12 months: in May, July, September and December 1993 and March 1994. Recovered seeds were inspected for evidence of germination or, where possible, predation and decomposition. As in the initial viability test, viability of intact, ungerminated seeds was assessed using tetrazolium (Freeland 1976), except for seeds of *C. apiculatum* and *L. squamatus*, which were assessed visually. The percentage of sown seeds that remained viable at 12 months, and at other selected intervals, was compared between surface and buried treatments using the non-parametric Wilcoxon two-sample test (Sokal and Rohlf 1981).

**Chrysocephalum and Leptorhynchos Viability**

After the final recovery in March 1994, ungerminated seeds of *C. apiculatum* and *L. squamatus* were placed on moist filter paper in petri dishes to assess final germinability. Petri dishes were placed indoors on a window ledge to promote germination. To ensure that conditions were suitable for germination, an additional 8 lots of 25 seeds of each species were sown under the same conditions, from seed stored in the dark at room temperature throughout the experimental period. Dishes were inspected and watered every 3–5 days for 57 days, and germinated seeds were removed at each inspection.

**Environmental Data**

Above-ground biomass at the study site was measured on 28 June 1993 by harvesting plant material from 10, 0.25 m² plots, placed at 2 m intervals on a transect immediately adjacent to the experimental grid. Samples were oven-dried at 80°C for 48 h, before weighing. Light transmission at the soil surface below the grass canopy was measured immediately prior to biomass harvesting, with a Li-Cor light meter (model Li-185) with quantum sensor. Twenty readings were taken above and below the plant canopy, at 1 m intervals along a transect adjacent to the experimental grid. Weekly maximum and minimum soil temperatures beneath the grass canopy were measured from July 1993, using two electronic temperature probes, on and 3 cm below the soil surface. From October 1993, two additional temperature probes were placed on the soil surface and at 3 cm depth, in a 1 m² gap, to compare soil temperatures beneath the grass canopy with that in the open. Regenerating plant material was cut regularly to keep the gap open. An extra, shielded probe was placed above the plant canopy, approximately 0.8 m above ground level to measure local air temperature. All temperature probes were removed in March 1994 when the site was burnt.

**Results**

**Seed Mass and Initial Viability**

Seed mass varied from a maximum of 2.19 mg for *B. bulbosa* to a minimum of 0.06 mg for *C. apiculatum*. All Asteraceae seeds were considerably lighter than Liliaceae seeds. Initial seed viability exceeded 90% for all species except *C. variabilis*, for which only 63% of seeds were judged as being viable using the tetrazolium test (Table 1). In an earlier germination test using seeds from the same lot (Morgan and Lunt 1994), only 45% of *C. variabilis* seeds germinated. The initial estimate of 100% viability for *C. apiculatum* and *L. squamatus* seeds was largely confirmed by the germination test at the end of the experiment, in which 100% of *C. apiculatum* seeds and 93% of *L. squamatus* seeds germinated (Table 1).

**Field Germination**

Some seeds of all species remained viable after 12 months in the field. *Craspedia variabilis* seeds declined most rapidly, and only 2% of sown surface seeds and 13% of sown buried seeds remained viable after 2 months; most seed losses were due to germination. Less than 7% of sown surface seeds of *B. bulbosa*, *B. umbellata*, *C. variabilis* and *L. squamatus*
Table 1. Seed mass and percentage seed viability for six species
Seed mass was calculated from the air-dry weight of 100 propagules of each species. The pappus was removed from all Asteraceae species before weighing. Seed viability was assessed using tetrazolium, except for *C. apiculatum* and *L. squamatus*, for which a germination test was used.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Mass of 100 seeds (mg)</th>
<th>% Viability</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arthropodium strictum</em></td>
<td>Liliaceae</td>
<td>206.6</td>
<td>99</td>
</tr>
<tr>
<td><em>Bulbine bulbosa</em></td>
<td>Liliaceae</td>
<td>219.3</td>
<td>97</td>
</tr>
<tr>
<td><em>Burchardia umbellata</em></td>
<td>Liliaceae</td>
<td>93.8</td>
<td>94</td>
</tr>
<tr>
<td><em>Chrysocephalum apiculatum</em></td>
<td>Asteraceae</td>
<td>6.1</td>
<td>100</td>
</tr>
<tr>
<td><em>Craspedia variabilis</em></td>
<td>Asteraceae</td>
<td>26.7</td>
<td>63</td>
</tr>
<tr>
<td><em>Leptorhynchos squamatus</em></td>
<td>Asteraceae</td>
<td>8.1</td>
<td>93</td>
</tr>
</tbody>
</table>

Table 2. Percentage of sown seeds that remained viable after 12 months in the field
Row values with different superscripts are significantly different at $P = 0.05$ (lower case) or $P < 0.01$ (upper case).

<table>
<thead>
<tr>
<th>Species</th>
<th>Surface</th>
<th>Buried</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arthropodium strictum</em></td>
<td>16</td>
<td>5</td>
</tr>
<tr>
<td><em>Bulbine bulbosa</em></td>
<td>$1^A$</td>
<td>$46^B$</td>
</tr>
<tr>
<td><em>Burchardia umbellata</em></td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td><em>Chrysocephalum apiculatum</em></td>
<td>36</td>
<td>61</td>
</tr>
<tr>
<td><em>Craspedia variabilis</em></td>
<td>$2^A$</td>
<td>$8^B$</td>
</tr>
<tr>
<td><em>Leptorhynchos squamatus</em></td>
<td>$1.5^A$</td>
<td>$36^B$</td>
</tr>
</tbody>
</table>

remained viable after 12 months. No buried seeds of *B. umbellata* remained viable after 12 months. At the other extreme, 36% of sown surface seeds and 61% of buried seeds of *C. apiculatum* remained viable after 12 months (Table 2).

With longer periods of burial, it became increasingly difficult to accurately determine the fates of decomposing seeds, especially for Asteraceae species, since seeds may have germinated or been eaten prior to decomposition. Seed fates could be readily determined for the larger-seeded Liliaceae species, *A. strictum, B. bulbosa* and *B. umbellata*, and nearly all seed losses for these species were due to germination. Less than 1% of *A. strictum* and *B. bulbosa* seeds, and 2% of surface *B. umbellata* seeds were eaten. All eaten *B. umbellata* seeds were in one seed envelope, which also contained an unidentified insect larva. Rotting accounted for 4% of surface and 2% of buried seeds of *B. umbellata*. The fate of *B. umbellata* seeds could not reliably be determined after 6 months of burial; consequently, the proportion of *B. umbellata* seed losses attributed to predation or rotting may be under-estimated. The cause of mortality of Asteraceae seeds often could not be determined, especially after 6 months of burial, and no such data are presented here. However, germination is suspected to have accounted for most seed losses. The initial, rapid loss of *C. variabilis* seeds and surface seeds of *L. squamatus* (Fig. 3), was largely due to germination.

Burial significantly promoted seed longevity for three species, *B. bulbosa, C. variabilis* and *L. squamatus* (Table 2). More buried than surface seeds of *C. apiculatum* persisted for 12 months (61% versus 36% of sown seeds), but this difference was not significant ($0.05 < P < 0.1$) owing to extreme variability between surface replicates. The percentage of sown seeds that remained viable after 12 months did not differ significantly between treatments for three species, *A. strictum, B. umbellata* and *C. apiculatum*, but rates of seed loss differed greatly between treatments. Buried seeds of *A. strictum* and *B. umbellata* germinated
significantly faster than surface seeds \((P < 0.01\) at 2 months; Fig. 3a, c), and surface seeds of \(C.\ apiculatum\) germinated significantly faster than buried seeds \((P < 0.05\) at 4 months; Fig. 3d).

The season of maximum germination differed markedly between species and treatments. The great majority of buried seed of all species except \(L.\ squamatus\) and \(C.\ apiculatum\) (for which few seeds germinated), germinated within 2 months of sowing (by May), as did most surface seeds of \(C.\ variabilis\) and \(L.\ squamatus\). By contrast, surface-sown lily seeds \((A.\ strictum,\ B.\ bulbosa\ and\ B.\ umbellata)\) germinated gradually throughout the year. Surface seeds of all species except \(C.\ apiculatum\) germinated readily in the low light environment under the closed grass canopy.

![Graphs showing temporal changes in the percentage of sown seeds remaining viable](image)

**Fig. 3.** Temporal changes in the percentage of sown seeds remaining viable on the soil surface (■) and at 3 cm depth (□) beneath a closed grass canopy.
No obvious relationship existed between taxonomic group (Liliaceae versus Asteraceae) and seed survival (Fig. 3, Table 2), or between seed mass and seed survival (Tables 1 and 2), for surface or buried seeds. The response of the large-seeded lily, *B. bulbosa*, was most similar to that of the small-seeded daisy, *L. squamatus*, with virtual complete germination of surface seeds, but enforced dormancy of most buried seeds.

**Final Germination Test**

After 12 months in the field, 84% of intact surface seeds and 87% of intact buried seeds of *C. apiculatum* remained viable, compared to just 7% of intact surface seeds and 51% of intact buried seeds of *L. squamatus*. By contrast, all control seeds of *C. apiculatum* (which were stored indoors for 12 months) were viable, as were 93% of control seeds of *L. squamatus*.

**Environmental Measurements**

Mean above-ground biomass on 28 June 1993, 20 months after burning, was $476 \pm 29$ g m$^{-2}$ (mean ± s.e.m.), and mean photosynthetically active radiation at ground level beneath the canopy was $32.2 \pm 5.6$ mmol m$^{-2}$ s$^{-1}$ (mean ± s.e.m.), just $3.7 \pm 0.7\%$ of incident sunlight. Soil temperatures beneath the grass canopy differed radically from those in gaps (Fig. 4). Temperatures beneath the grass canopy exhibited a steady, seasonal rise from winter through to late summer, and were largely insulated from weekly variations in air

![Fig. 4. Maximum and minimum air temperature, and soil temperature in an open gap and beneath the closed grass canopy, on and 3 cm below the soil surface. + = temperatures that exceeded 50°C, the upper limit of the temperature probes.](image-url)
temperature, except in mid-summer (Fig. 4). The surface soil temperature beneath the closed canopy was very similar to that at 3 cm depth (Fig. 4), with the maximum surface temperature being, on average, 0.6°C greater than that at depth (range 0.2–1.7°C), and nighttime minima being 1.0°C lower than at depth (range 0.6–1.5°C). Weekly temperature fluctuations (differences between weekly minimum and maximum temperatures), on the soil surface beneath the grass canopy, ranged from 7°C to 10°C from June to October, and from 10°C to 13°C from November to February, with a peak of 19°C in the hottest week of summer. A similar pattern occurred at a depth of 3 cm, where weekly temperature fluctuations ranged from 5°C to 8°C from June to October, and from 9°C to 12°C from November to February, with a maximum of 16°C in the hottest week of summer.

Maximum soil surface temperatures were higher and more variable in gaps than beneath the grass canopy, and exceeded 50°C (the upper limit of the temperature probes) on three occasions in summer. The soil at 3 cm depth was shielded from the extremes of summer surface temperatures, but temperatures still reached a maximum of 39°C in the hottest week of summer, which was 10°C above that recorded on the soil surface below the grass canopy. Weekly temperature fluctuations were considerably greater in gaps than beneath the grass canopy. The average weekly temperature fluctuation in surface gaps was 30°C, with a maximum over 43°C and minimum of 23°C. The average fluctuation at 3 cm depth in gaps was 21°C, with a maximum of 30°C in the hottest week of summer. Night-time minimum surface temperatures were, on average, 3.5°C lower in gaps than beneath the grass canopy (range 2.2–7.5°C).

Discussion

Rates of seed decline differed significantly between treatments for all species (Fig. 3, Table 2), with no obvious relationship between seed longevity and taxonomic group or seed mass. Except for C. apiculatum, relatively few seeds of any species remained viable after 12 months on the soil surface (Fig. 3). The response to seed burial was more complex, as burial strongly inhibited germination of some species, particularly B. bulbosa and L. squamatus.

Since some seeds of all species persisted for 12 months, no species possessed a ‘transient’ seed bank (sensu Thompson 1993) under the experimental conditions imposed. However, the experimental technique is likely to exaggerate, rather than under-estimate, the potential for seed persistence under natural conditions, as: (1) seed envelopes may preclude predation by organisms larger than the envelope mesh-size, (2) seeds were sown in March, about 3 months after the season of natural seed dispersal, and additional seed losses may have been recorded had the experiment begun earlier, and (3) many seeds that are capable of maintaining viability upon burial might rarely be buried under natural conditions (Thompson 1993). Since the experiment was undertaken at just one site in one remnant grassland, the results may not prove applicable to other sites.

Of the six species studied, C. apiculatum seems to have the greatest potential to accumulate a soil seed bank owing to its small seed size, inhibition of germination on and below the soil surface beneath a closed grass canopy, and sustained viability of buried seeds. Naturally dispersed seeds of the other five species may form, at best, ‘short-term persistent’ seed banks (sensu Thompson 1993), due to their possession of characteristics unsuited to either burial or sustained seed dormancy, including large seed size, which minimises opportunities for burial (A. strictum, B. bulbosa and B. umbellata), rapid germination on the soil surface beneath a closed canopy (C. variabilis and L. squamatus), rapid germination at depth (A. strictum, B. umbellata and C. variabilis), and possibly, short-term viability of intact buried seeds (L. squamatus). However, further studies are required to identify: (1) rates of seed burial and predation under natural conditions, (2) depth of seed burial in the soil profile, and (3) fates of dormant seeds over the medium-term (1–5 years), to see whether intact seeds remain viable or gradually germinate or decompose.
The germination behaviour of *L. squamatus* and *C. apiculatum* seeds in the field provides an interesting contrast to that under growth-cabinet conditions (Willis and Groves 1991). Willis and Groves (1991) found that *L. squamatus* seeds germinated over a range of temperatures below 30/20°C and did not require light to germinate. By contrast, in this experiment, surface seeds readily germinated in the low light environment under the closed grass canopy, but few buried seeds germinated.

Willis and Groves (1991) found that *C. apiculatum* germination was strongly temperature dependent, with maximum germination at 20/10°C. Germination was found to be promoted by light, although more than 80% of seeds germinated in the dark, and there was little difference between the rate of germination in the light and dark. By contrast, in this study, more seeds germinated on the soil surface than when buried (Fig. 3d), which might reflect decreasing light availability. However, few buried seeds germinated, whereas Willis and Groves (1991) found over 80% germination in the dark. The similar temperature regime on the surface and at 3 cm depth suggests that temperature differences were unlikely to have affected germination behaviour. By contrast to the decline in germinability of laboratory-stored seeds of *C. apiculatum* found by Willis and Groves (1991), 100% of filled seeds were still viable after 16 months storage at room temperatures in Gippsland, and 87% of intact seeds remained viable after being buried for 12 months. Further studies are required to determine whether these differences perhaps reflect genetic differences from different seed provenances.

**Soil Temperatures**

The closed grass canopy greatly ameliorated the micro-climate experienced by surface and buried seeds, and effectively insulated the soil from extreme summer temperatures (Fig. 4). Thus, the maximum surface soil temperature beneath the grass canopy in mid-summer was only 29°C, when the air temperature reached 43°C, the soil 3 cm below the surface in canopy gaps reached 39°C, and the surface soil in canopy gaps far exceeded 50°C (the upper limit of the temperature probes). The insulating capacity of the closed grass canopy was far greater than that of 3 cm of loamy topsoil in canopy gaps. Indeed, 3 cm of topsoil beneath the grass canopy imposed little additional thermal insulation, and there was very little difference between soil surface and buried temperatures beneath the grass canopy (Fig. 4).

The closed grass canopy is likely to have an enormous impact on the season of seed germination and on seed dynamics. High temperatures inhibit seed germination in some grassland forbs (Willis and Groves 1991), leading Willis and Groves (1991) to suggest that germination in the field might be delayed over summer until lower air temperatures are attained in autumn or winter. While this scenario might apply to seeds in gaps, the thermal insulation of a closed grass canopy may provide suitable temperatures for seeds to germinate at any time of the year, provided that adequate moisture is available, and that seeds have no after-ripening or light requirement.

Seeds of all species studied responded differently on the soil surface and at depth beneath the grass canopy, despite the similar temperature regimes in both micro-environments (Fig. 4), which would suggest that the differences in germination behaviour between surface and buried seeds were not temperature dependent. Different germination behaviours might reflect differences in light intensity and frequency on the soil surface and at depth, beneath the grass canopy. However, light levels below the canopy were very low (on average, only 4% of that above the canopy), so if the different germination behaviours of surface and buried seeds were due to light quantity or quality, they were manifested at very low light levels. A number of other ecological factors may have contributed to the different germination responses of surface and buried seeds, perhaps including more consistent soil moisture levels, better soil-seed contact for buried seeds, and different atmospheric and nutrient conditions.
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