

The seed ecology of *Ascarina lucida*: a rare New Zealand tree adapted to disturbance

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Abstract *Ascarina lucida* is rare in the North Island of New Zealand, occurring as small scattered populations. The seed ecology of this species was investigated by laboratory germination of fresh seed, and germination of samples from soil seed banks of two North Island populations. Seed collected from a submontane population had higher germinability (76%) than seed collected from a lowland population (32%). Seed collected from an isolated lowland garden tree had high germinability (82%). *A. lucida* seeds were abundant in both the surface and basal soil layers, and it was predicted that the species maintains a persistent seed bank for up to c. 8 years. *A. lucida* was the dominant component of the seed bank at the submontane site. The germination pattern of *A. lucida* was compared with other woody species in the seed bank and found to have similarities with species that often colonise disturbed sites. The maintenance of a persistent seed bank, coupled with the long period of time over which fresh seed germinates, gives this species flexibility in the timing of germination. Overall, the results indicate that the species is adapted to disturbed environments.

Keywords *Ascarina lucida*; seed ecology; seed bank; *Geniostoma rupestre*; germination; germination delay

INTRODUCTION

Ascarina lucida (Chloranthaceae) is a small tree endemic to New Zealand. The species is rare in the North Island occurring as small, scattered populations. It is only more widespread on the west coast of the South Island. Although *A. lucida* was more widespread in the early Holocene, it has become increasingly rare over the last 7000 years. This decline is usually attributed to climate change (McGlone & Moar 1977). Appropriate interpretation of the significance of “the *Ascarina* decline” with respect to climate change is reliant on a sufficient understanding of the ecology of the species. The research reported here is part of a larger body of work aimed at increasing ecological knowledge of the species.

Ascarina lucida is wind pollinated and has been described as dioecious (Poole & Adams 1963; Cockayne & Turner 1967; Metcalf 1991), and monoecious (Moore 1977). During the course of the present study, trees were observed to produce separate male and female flowers asynchronously.

Ascarina lucida produces a one-seeded fleshy drupe (Poole & Adams 1963; Cockayne & Turner 1967). The fruit is ovoid, 2.5 mm in diameter, and whitish with purple spots (Metcalf 1991) or reddish in colour (Burrows 1996). The small seeds, produced in large numbers, are mainly dispersed by silvereyes (*Zosterops lateralis*), an abundant bird species throughout most of New Zealand (Burrows 1996).

Literature on the seed ecology and germination of *A. lucida* is sparse. Burrows (1996) investigated the germination of *A. lucida* and his paper is the current knowledge base of *A. lucida* seed ecology. Burrows's (1966) study focused on the investigation of germination rates, percentage germination success, and mechanisms of germination delay under a range of experimental conditions. Burrows concluded that the long period of time over which seeds of this species germinate gives *A. lucida* ecological flexibility, which would increase the chances of a portion of each year's seed crop being exposed to appropriate environmental conditions for

germination and establishment. Burrows suggested that the investigation of the effects of burial on *A. lucida* might provide valuable insight as to why this species can be an important component of early successional vegetation.

Few studies of forest seed banks have been conducted in New Zealand. Ogden (1985) described the seed bank of a forest and shrubland community as having between 150 and 600 viable tree and shrub seeds m^{-2} . Enright & Cameron (1988) investigated the soil seed bank of a kauri (*Agathis australis*) forest remnant and estimated the average soil seed bank at 1131 seeds m^{-2} . The seed bank at that site was dominated by early successional species such as *Kunzea ericoides* and *Geniostoma rupestre*. These two studies have shown that the numbers of seeds m^{-2} for New Zealand forest soil seed banks are similar to those found in other temperate regions of the world (Harper 1977; Fenner 1985). However, the abundance of pioneer woody species has greater similarity to the seed banks of tropical regions (Garwood 1989) than the seed banks of temperate regions that are often dominated by herbaceous weeds (Enright & Cameron 1988). Ogden (1985) discussed the ubiquitous presence of certain woody species in the seed bank of the Kauaeranga Valley, Coromandel. Bird-dispersed tree species which require the relatively high light conditions of forest gaps for growth, were found to maintain a small but consistent seed bank of 10–100 seeds m^{-2} . Thus, some New Zealand tree species seem to be able to use transitory habitats by the maintenance of a widespread and persistent seed bank.

An extensive literature search revealed no papers that discuss the presence of *A. lucida* in New Zealand soil seed banks. However, the tendency for *A. lucida* to grow in forest gaps, forest margins, and in early successional vegetation (Burrows 1996), in combination with the production of large numbers of small bird-dispersed seeds, suggests that this species may be able to persist in soil seed banks.

MATERIALS AND METHODS

Seed germination (sown samples)

In April 2000, fruit was collected from a tree in the grounds at the University of Auckland, from three trees at Puhipuhi State Forest, Northland (a lowland population), and from three trees at Kohukohunui, Hunua Ranges, South Auckland (a submontane population). Three trees only were collected in order

to have sufficient seed from each to carry out some between-tree comparisons of germination characteristics, but these results are not presented in detail here. Variation between trees is discussed in Martin (2001). Fruit was collected from apparently healthy trees with a good fruit crop accessible from the ground. The flesh surrounding the seeds was removed prior to sowing.

Three lots of 100 seeds were taken from the fruit collected from the tree at the University of Auckland, and 100 seeds from each of the three trees sampled at the lowland and submontane populations.

Each lot was sown onto the surface of a 148 mm \times 148 mm \times 143 mm square pot filled with standard potting mix, and the pots arranged in a Latin Square design. The experiment was conducted in a shaded glasshouse with nightly overhead watering, and temperature extremes were monitored using a maximum/minimum thermometer. Germination was defined as the emergence of cotyledons above the surface. *A. lucida* seedlings were counted and removed weekly until germination had ceased.

Seed banks (soil samples)

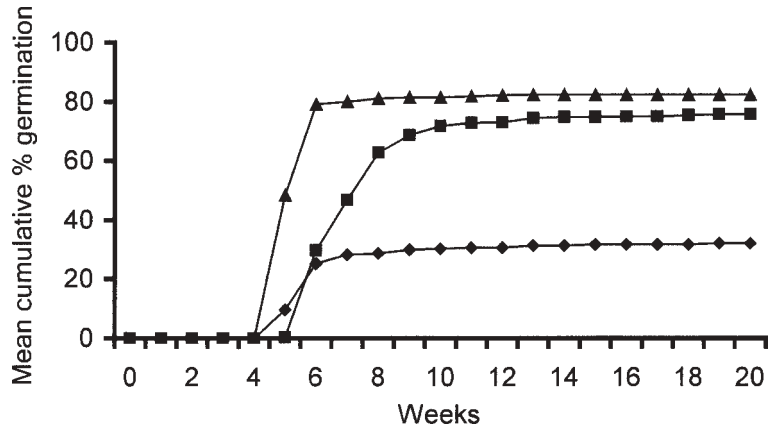
An investigation of the soil seed bank was conducted at the lowland and submontane study sites, to determine if viable *A. lucida* seeds were present in the soil. If *A. lucida* seeds were present, a second aim was to determine if the seeds formed a transient or persistent component of the seed bank.

The first soil samples were taken from the lowland and submontane study sites in early October 1999. Any *A. lucida* that germinated from these samples would have been either from the persistent seed bank, or from seeds that had overwintered since the autumn 1999 fruiting season (a transient seed bank).

As seed banks are highly variable in composition and patchy in nature, soil sampling was concentrated in areas most likely to contain *A. lucida* seeds. A large number of small samples are likely to be more representative of a seed bank than a smaller number of larger samples. Therefore, 10 samples were taken from each site, with each sample having a surface area of 10 \times 10 cm. The soil samples were taken close to fruiting *A. lucida* trees, from relatively flat ground without dense undergrowth.

The soil samples were taken using a soil corer 10 cm long \times 10 cm wide \times 8 cm deep. Recently deposited leaves and branches were carefully removed from each sample site, and the corer was pushed down until the top was flush with the soil surface. At some points, roots prevented sampling

Fig. 1 Cumulative percent germination of sown seeds from three *A. lucida* populations: ▲, garden; ◆, lowland; ■, submontane.



to the full 8 cm. The humus layer was removed and placed in a labelled plastic bag. The remaining soil was then removed and placed in a separate labelled bag. At the lowland site a distinct humus layer was often absent, and the top 2 cm of soil was arbitrarily deemed to be the “surface” layer.

Samples from each site were stored at c. 4°C for 35 days until sowing. The submontane samples were sown on 3 November 1999, and the lowland samples on 15 November 1999. Plastic seed trays 480 mm × 330 mm × 75 mm deep were filled with standard potting mix to a depth of 40 mm. Each surface or basal sample was broken up finely by hand and spread in a thin layer over the surface of the potting mix, each sample being sown in a separate tray. Several of the samples from the lowland site could not be broken up by hand due to their “putty-like” texture and these samples were slurried with water before being spread over the surface of the potting mix. The seed trays were placed in a temperature-regulated glasshouse with bright, indirect light and were kept moist by nightly overhead watering. Temperature extremes were monitored with a maximum/minimum thermometer.

The estimation of the composition and size of a seed bank, by the germination of seeds contained within soil samples, is based on the assumption that all viable seeds present germinate. To reduce the error caused by this assumption, complete germination was encouraged by subjecting the samples to stratification at low temperatures followed by the provision of warm, moist conditions. In addition to this, once germination appeared to have ceased, the soil surfaces of the trays were scarified in an attempt to cause any remaining seeds to germinate.

Germination, defined as the emergence of cotyledons, was monitored weekly for 12 weeks, after which germination ceased. Newly germinated seedlings were marked with a colour-coded toothpick, with a different colour each week. Seedlings that were not *A. lucida* were identified and removed, or transplanted into separate pots to allow for identification at a later date.

Glasshouse temperatures ranged between 14 and 36°C during the germination period.

The persistence of *A. lucida* in soil seed banks

To prevent further seed entry, each 10 × 10 cm cored sample site was covered with a 50 cm × 50 cm square of black polythene, which was securely pegged down at each corner. By excluding further seed entry to the core sites from October 1999 until June 2000, no *A. lucida* seeds produced during the 1999–2000 fruiting season would be present in the soil underneath the polythene sheets. Viable *A. lucida* seeds present after this period would represent only the survivors from the previous sampling date and thus help to determine if *A. lucida* forms a transient or persistent soil seed bank.

The soil moisture underneath the polythene sheets was regularly checked to ensure that the polythene did not cause the underlying soil to dry out.

In June 2000 at each of the original core sites, the polythene was carefully removed and a second core taken immediately adjacent to, but not overlapping, the original core. The surface and basal soil layers were sampled at the same depths as the cores taken in October. This allowed a direct comparison of the number of viable *A. lucida* seeds in each soil layer to be made, between the October sample, and the June sample, for each core site.

The germination methods for the June soil samples were the same as the methods used for the October soil samples.

Glasshouse temperatures ranged between 12 and 32°C during the germination period.

Statistical methods

Means and standard errors were calculated for each set of results. Means were regarded as different if their standard errors did not overlap.

RESULTS

Seed germination (sown samples)

From all three sites, germination commenced after five weeks (Fig. 1). The last seeds germinated from the University of Auckland population samples during Week 13, and seeds from the lowland and submontane populations ceased to germinate after 19 weeks. There was a noticeable delay of germination for seeds from the submontane population.

Table 1 Germination of sown seeds of three *A. lucida* populations (mean cumulative percent germination \pm s.e.).

	Tree 1	Tree 2	Tree 3	Mean \pm s.e.
Garden	96	83	68	82.3 \pm 8.1
Lowland	66	14	16	32.0 \pm 17.0
Submontane	89	60	78	75.7 \pm 8.5

The mean cumulative percent germination for the three populations was 82.3 \pm 8.1% for the tree at the University of Auckland, 32.0 \pm 17.0% for the lowland population, and 75.7 \pm 8.5% for the submontane population (means \pm s.e.) (Table 1).

Seed bank size and composition (soil samples)

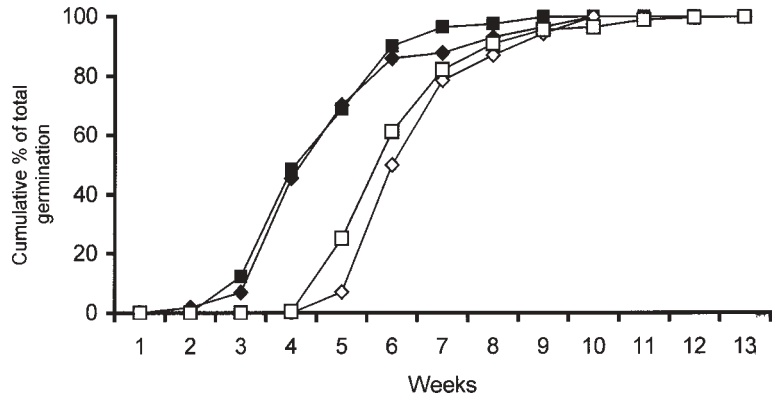
The October 1999 soil samples contained seed of *A. lucida* at both study sites (Table 2). At the submontane site *A. lucida* was the dominant component of the seed bank, comprising 71.3 \pm 7.6% of all dicot seedlings that germinated. *A. lucida* constituted a greater proportion of dicots present in the surface soil layers than in the deeper soil samples. The *A. lucida* seed bank in close proximity to adult trees was 7940 \pm 3654 m⁻². At the lowland site, *A. lucida* was a minor component of the soil seed bank, comprising 9.2 \pm 3.7% of all dicots germinated. The proportion of *A. lucida* seeds in surface and basal soil samples was very similar. The *A. lucida* seed bank in close proximity to adult trees was 650 \pm 192 m⁻².

Ascarina lucida remained in the soil seed bank at both sites after all seeds were excluded from entering the soil sampling sites for 9 months. At the submontane site *A. lucida* remained the dominant component of the seed bank, comprising 72.3 \pm 10.0% of all dicot seedlings germinated, and the proportion of *A. lucida* seeds in surface and basal soil samples did not change significantly. The *A. lucida* seed bank in close proximity to *A. lucida* trees was reduced to 3750 \pm 1053 m⁻². This represents an annual mortality rate of 70.4%. At the lowland site the results were very similar to the seed

Table 2 The composition and size of the lowland and submontane seed bank, \pm s.e., per 1000 cm². x, not recorded.

	Submontane		Lowland	
	October 1999	June 2000	October	1999 June 2000
Number of locations	10	10	10	10
Total dicot species germinated	14	17	23	27
Total dicot plants germinated	900	467	748	711
Total monocot plants germinated	17	x	3513	x
Total <i>A. lucida</i> plants germinated	794	375	65	70
<i>A. lucida</i> as % dicots	71.3 \pm 7.6	72.3 \pm 10.0	9.2 \pm 3.7	9.5 \pm 2.9
Average % <i>A. lucida</i> in surface layers	78.9 \pm 7.3	75.1 \pm 9.2	10.2 \pm 5.6	12.7 \pm 4.9
Average % <i>A. lucida</i> in basal layers	42.8 \pm 11.7	42.5 \pm 17.0	12.9 \pm 4.6	12.9 \pm 3.4
Dicots seeds m ⁻²	9000 \pm 3588	4670 \pm 1080	7490 \pm 1816	7110 \pm 1217
<i>A. lucida</i> seeds m ⁻²	7940 \pm 3654	3750 \pm 1053	650 \pm 192	700 \pm 213

Fig. 2 Cumulative percent germination of *A. lucida* from the lowland (diamonds) and submontane (squares) seed banks (original (filled symbols) and persistent (open symbols) samples).



bank composition for the site in October, and all percentage changes were within the standard errors, so that apparently no significant mortality occurred.

The abundance of monocot seeds in the soil seed bank varied considerably between the two sites. Germination of monocot seedlings from the October soil samples yielded a total of 17 individuals from the submontane site, and 3513 individuals from the lowland site. Seed bank species diversity also differed between the sites, which can be attributed to the higher number of adventive dicot species at the lowland site.

Rate of germination for the soil seed banks through time

Germination of *A. lucida* from the original October soil seed bank began during the 2nd week after sowing for the submontane samples, and during the 3rd week after sowing for the lowland samples, reaching 100% of total germination for both sites by the 10th week of germination (Fig. 2). Germination from the persistent *A. lucida* seed bank at both sites was delayed; germination from the submontane samples began during the 4th week, and from the lowland samples during the 5th week. Germination reached 100% for the lowland samples during the 10th week of germination, but the submontane samples reached 100% only during the 13th week.

The rate of decline of a seed bank can be assumed to be the difference in germinable seeds in repeated samples from which seed input has been excluded. In the current case, only the submontane seed bank showed a decline, but as germinable seed numbers were much larger in these samples than in those

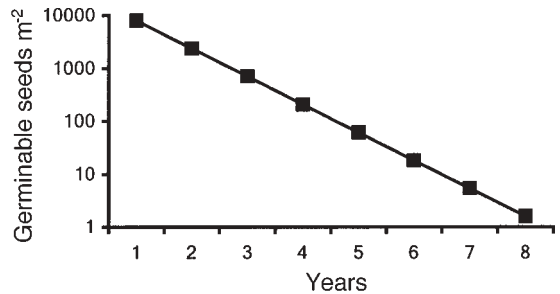


Fig. 3 Decline of *A. lucida* seed bank through time.

from the lowland site, the measured decline from that site has been used to estimate seed bank longevity. Using an annual mortality rate of 70% extrapolated from the data in Table 1, it is suggested that *A. lucida* seeds have the ability to remain viable in the soil for c. 8 years (Fig. 3).

Other native woody species present

Four other tree species were present in the submontane seed bank (*Pseudopanax crassifolius*, *Fuchsia exorticata*, *Olearia rani*, and *Carpodetus serratus*). *A. lucida* took longer to germinate than these four (Fig. 4). Germination of *A. lucida* and *Geniostoma rupestre* from the persistent seed bank at the lowland site was delayed compared with the rate of germination from the soil samples collected the previous year (Fig. 5). The timing of germination for these two species was very similar.

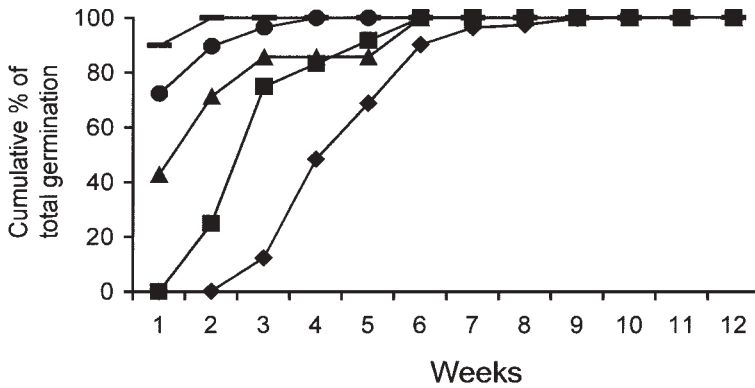


Fig. 4 Cumulative percentage germination of tree species in the submontane soil seed bank (original samples). ◆, *Ascarina lucida*; ■, *Carpodetus serratus*; ▲, *Olearia rani*; ●, *Fuschia excorticata*; —, *Pseudopanax crassifolius*.

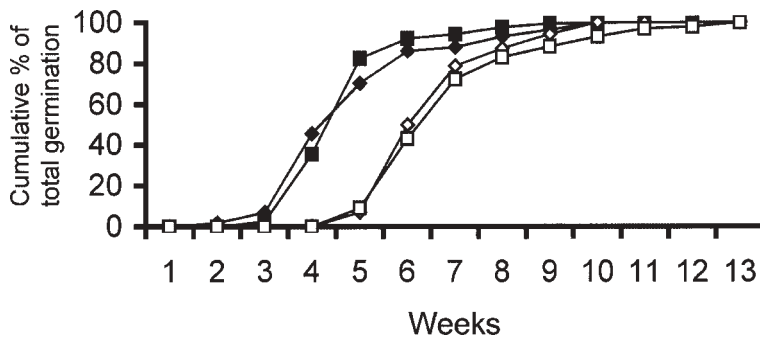


Fig. 5 Cumulative percent of total germination for *A. lucida* (diamonds) and *G. rupestre* (squares) in the lowland seed bank samples. Filled symbols, original samples; open symbols, persistent samples.

DISCUSSION

For a dioecious species to persist at a site, or for a new population to become established, both male and female plants must be present to allow the production of viable seed. The discovery that *A. lucida* is functionally monoecious may in part explain its ability to persist as small populations, as isolated trees are able to produce viable seed. New populations of *A. lucida* can potentially become established through the growth, survival, and seed production of a single tree.

Assuming the germination results presented are a true reflection of the seed viability for these populations, the results suggest that isolated trees can produce seeds of high viability, and that the submontane population may produce seeds of higher viability than the lowland population. High variability of seed viability between trees of the same population is suggested for the lowland site, where the trees sampled had seeds that ranged in germinability between 14 and 66%. The high

variability in seed germination proportion between trees of a single population may be a result of plants producing different types of inflorescences. *A. lucida* displays a type of monoecism whereby plants produce either inflorescences that produce male and female flowers simultaneously, or inflorescences that produce first male flowers and then female flowers after the male flowers have matured (Moore 1977). Thus, the high variability of seed germinability between plants may be explained by variation in inflorescence type.

The initial soil samples were taken primarily to determine if *A. lucida* maintained a seed bank and samples were taken only in close proximity to adult *A. lucida* trees. Comment on the composition of the seed bank at these sites is therefore restricted to describing the seed bank immediately under or adjacent to *A. lucida* trees.

The following discussion assumes that any seeds that failed to germinate were not viable, as opposed to being dormant. If this assumption is false, and 35 days of chilling followed by "ideal" glasshouse

conditions did not break dormancy in all cases, then the soil seed banks might have been underestimated. Furthermore, it is also a possibility that the chilling period might have had a differential effect on the germination from the lowland and submontane seed banks.

Ascarina lucida was an important component of the transient and persistent seed bank at both field sites. However, it constituted a significantly greater proportion of the total dicotyledonous seed bank at the submontane site than at the lowland site. The dominance by *A. lucida* of the seed bank at the submontane site may also be partly explained by the high germinability of the seeds sampled from this population.

Estimation of seed longevity from declining germination from soil samples is fraught with difficulty. In the present case no decline, but actually a slight increase, was recorded over 9 months at the lowland site. This increase between October and June samples must have been due to spatial heterogeneity in seed abundance, and this could likewise explain any decrease in the number of seeds between sample dates. However, the montane site appeared to have a much larger seed bank than the lowland site, and, on average, it did show a decline through time. The estimated seed longevity of c. 8 years is supported by the abundance of viable *A. lucida* seeds in the deeper soil samples at both sites.

The abundance in the seed bank of both *A. lucida* and *Geniostoma rupestre* at the lowland site enabled the seed ecology of these two species to be compared. *G. rupestre* seeds become dormant when buried, and have a high viability when unearthed (Burrows 1999). The presence of viable *A. lucida* seeds in the basal soil samples from both the lowland and submontane sites indicates that *A. lucida* may also become dormant when buried but maintain viability in the soil. Viable seeds found deeper in the soil column are regarded as being generally older than seeds at the soil surface (Enright & Cameron 1988).

Both *G. rupestre* and *A. lucida* exhibited a longer delay before the onset of germination from the June 2000 soil samples. Enright & Cameron (1988) attributed the increased delay for the germination of previously buried *G. rupestre* seeds to the action of enforced or induced dormancy. However, *G. rupestre* germinates very slowly in the dark, while *A. lucida* germinates faster, and with a higher success rate, under dark rather than well-lit conditions (Burrows 1999). This suggests that the dormancy of *A. lucida* seeds is not primarily caused

by low light. However, the similarities between the seed ecology of these two species suggests that, like *G. rupestre*, *A. lucida* is adapted to colonise disturbed environments.

Variation in the timing of germination from seeds of different populations is common, and may be attributed to genetic differences between populations and the different environments within which the seed matured (Fenner 1985; Lord 1994). Thus, the germination behaviour of a species can be adapted to the specific environment within which any particular population grows. Lord (1994) discovered that seeds of *Festuca novae-zelandiae* from high altitude provenances exhibited delayed germination compared with lowland provenances of the same species. Fenner (1985) attributed the delayed germination of seed from high altitude provenances to lower temperatures during seed maturation creating higher levels of seed dormancy. The seed germination and seed bank experiments presented here showed different patterns of germination delay for seeds sourced from the same populations. Seeds sown in the seed germination experiment from the submontane site showed delayed germination in comparison with seeds from the lowland site and the University of Auckland. However, germination delay was greater from the seed bank sampled at the lowland site than at the submontane site. The seed germination experiment was probably a more appropriate test for germination delay as the seeds from each provenance were of known age and treatment. The delayed germination of seeds from the submontane population suggests that the germination behaviour of *A. lucida* may be adapted to the environmental conditions of its source populations. Seeds produced in high altitude environments during autumn and winter may delay germination until the milder conditions of spring.

Seeds that exhibit germination delay also have a higher chance of being buried and incorporated into the soil seed bank than seeds that have the ability to germinate immediately after being shed from the parent plant (Grime 1979). Once buried, seeds may become secondarily dormant through the exclusion of light and the action of a gaseous environment (Burrows 1999). However, the ability of *A. lucida* to germinate successfully in the dark (Burrows 1996) indicates that the dormancy of this species when buried is not induced by lack of light. Seeds that are deeply dormant require the appropriate environmental stimuli to break dormancy, and are slow to respond to a change to more suitable

germination conditions (Enright & Cameron 1988). Thus, the increased delay of germination from the soil samples taken in June 2000 may be further evidence for the maintenance of a dormant seed bank by *A. lucida*. Alternatively, the increase in germination delay from the persistent seed bank samples may simply be attributed to a difference in germination conditions, as the samples collected in June 2000 were germinated at slightly lower temperatures than those taken in October 1999.

The long fruiting season of *A. lucida*, from February until July (Martin 2001), releases seed of this species into the environment for a period of six months. This long spread of seed fall, coupled with the delay between seed production and the onset of germination, ensures that seeds are ready to germinate during the autumn, winter, and spring of each year. The ability of buried seeds to maintain viability for longer than a year, and possibly for as long as eight years, also ensures that if the appropriate conditions are present, *A. lucida* seeds can germinate from the seed bank at any time of year. The maintenance of a dormant seed bank is an important part of the life strategy for a species, giving *A. lucida* the ability to disperse its seeds through space and time.

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