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Germination behaviour of seeds of the New Zealand woody species *Alectryon excelsus*, *Corynocarpus laevigatus*, and *Kunzea ericoides*

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Abstract Germination rates, percentage germination success, and phenomena related to germination delay were determined for seeds of *Alectryon excelsus*, *Corynocarpus laevigatus*, and *Kunzea ericoides*, taken from freshly collected fruit. The experimental treatments simulated natural conditions that the seeds could experience after dispersal.

In a treatment where seeds were cleaned and kept moist, in the light, germination success was 94% for *Corynocarpus* and 100% for *Kunzea* but only 48–56% for *Alectryon*. Seeds of each species germinated moderately to very well (50–100%) on soil and (except *Alectryon*) in the dark. The seedlings of the large-seeded *Alectryon* (seeds at 5 cm depth) and *Corynocarpus* (5 and 10 cm depth) reached the surface when seeds were buried in soil. Buried seeds of *Kunzea* (5 cm depth) germinated and the seedlings died underground. After seeds were kept dry for c. 5 months those of *Kunzea* germinated well (92%), those of *Alectryon* moderately well (58%), and those of *Corynocarpus* poorly (10%).

The seed germination behaviour of the three species accords quite well with the habitat conditions in which juveniles and adults are found.

Keywords seeds; germination tests; simulating nature; winter germination

INTRODUCTION

This is a further contribution to a series of papers describing the germination behaviour of seeds of woody plant species in New Zealand lowland forests in conditions similar to those that the seeds could experience in nature (cf. Burrows 1995a, 1995b). The aim of the study was to examine the germination rates, numbers of seeds which germinate, and features of the germination delay systems for freshly collected seeds from wild parents. As noted in the review by Fountain & Outred (1991), published information on the germination capabilities of seeds of New Zealand forest species is scarce. It is necessary to have information of this sort before the regeneration ecology of the forests can be well understood, or before decisions can be made about management of these forests for conservation or other purposes.

The disseminules of all three species are referred to here as seeds, although the fruit of *Corynocarpus* are drupes; tough endocarp tissue surrounds each seed.

The species tested

Alectryon excelsus Gaertn. (Sapindaceae)

A single, or few-stemmed, evergreen, dioecious tree, up to 15 m tall. It occurs in mixed forest, near the coast in the South Island. It is often a canopy species and may form groves. The paniculate infructescences, at the ends of branchlets, bear up to 20 large capsules, each containing one (rarely two) seed(s). When the capsule opens the upper part dehisces, revealing the shining black seed with its lower half imbedded in a fleshy, scarlet arillode.

Corynocarpus laevigatus J.R. et. G.Forst.
(Corynocarpaceae)

An evergreen, usually single-stemmed tree up to about 16 m tall. The bisexual flowers are borne in panicles on the ends of branchlets. The species occurs at margins or interiors of mixed forest, and near the coast in the South Island. It is believed to have been moved to many locations by Maori but is sub-

sequently naturalised in unmanaged vegetation. The fruit are large drupes with orange flesh, each with a single large seed surrounded by endocarp tissue.

Kunzea ericoides (A.Rich.) J.Thompson
(Myrtaceae)

An evergreen shrub or tree, up to about 15 m tall. It occurs widely in dense, often monospecific stands in areas where forest has been disturbed, or at forest margins and in openings, in lowland to lower montane habitats. The bisexual flowers occur singly or grouped, near the tips of branchlets. The fruit are small, three- or four-loculed, thin-walled capsules, each containing many tiny seeds, most of which were empty in the samples examined.

Seed dispersal

The minute seeds of *Kunzea* are wind-dispersed when the capsules open, in dry weather. The much larger seeds of *Alectryon* are exposed, with the arillode prominent, when the capsule opens. Those of *Corynocarpus* are enclosed by fleshy pericarp tissue. Kereru (*Hemiphaga novaeseelandiae*) were seen eating its fruit and the arillode-imbedded seeds of *Alectryon*. The single-seeded fruit of *Corynocarpus* are too large to be swallowed whole by birds other than kereru. Many of its fruit fall to the ground and some are eaten there by rats (*Rattus rattus*). According to Clout & Hay (1989) *Alectryon* seeds are eaten by all of the extant, medium-sized native and introduced forest birds.

METHODS

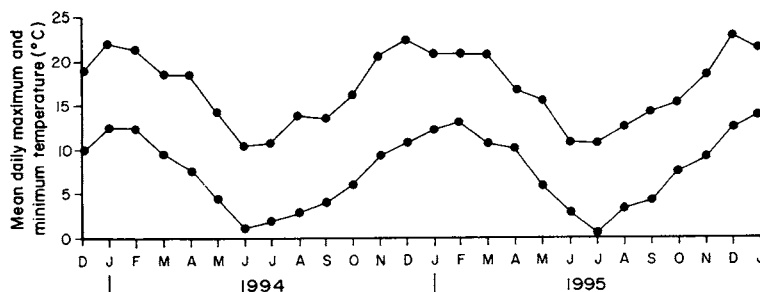
Fruit were collected from locations in Canterbury and (*Corynocarpus*) Marlborough, and kept cool, in an insulated bin with cooler pads, before the seeds were placed in the experiments. Table 1 summarises site location data, collection dates, and other information on fruit and seeds. One provenance of *Alectryon* was tested in 1989–90, by the methods described fully in Burrows (1995a). The other provenance of *Alectryon* and each of the other species were tested in 1994 by methods which were essentially the same as those used in earlier studies (Burrows 1995a, 1995b, 1995c) but with some modifications to the dark treatment and two additional treatments. The various treatments represent a range of conditions which could be experienced by the seeds in nature.

Except for one set of seeds left in the fruit, pericarp tissues were removed and the seeds sepa-

Table 1 Fruit and seed properties. Counts and measurements were done on random samples of freshly collected fruit and thoroughly air-dried seeds from the collection localities; unless otherwise indicated 10 individuals were counted and measured. The values are mean \pm standard deviations. No error values are provided for the mean seed weights which were obtained by weighing a given number of seeds. * measurements on opened capsules; + length of main axis; ** groups of fruit on branchlets – not strictly infructescences

Taxon Location	Collection date;		Ripe fruit length of main axis (mm)	Ripe fruit diameter (mm)	No. of full seeds per fruit	Seed length (mm)	Seed width (mm)	Mean seed weight (g)	n
	Grid reference (NZMS 260):	Altitude (m)							
<i>Alectryon excelsus</i> Town Reserve, Akaroa, eastern Banks Peninsula	26 Jan 1989 N36/076113	20	-	-	-	-	-	-	-
<i>Alectryon excelsus</i> Ahuriri Valley Bush, western Banks Peninsula	6 Mar 1994 M36/773248	140	20.9 \pm 1.19*	16.4 \pm 1.0+*	1	7.83 \pm 0.3+	7.97 \pm 0.19	0.2323	20
<i>Corynocarpus laevigatus</i> Goose Bay, Kaikoura Coast, Marlborough	25 Feb 1994 O32/540593	20	37.8 \pm 1.9	20.9 \pm 1.3	1	34.2 \pm 2.2	16.4 \pm 1.1	2.356	10
<i>Kunzea ericoides</i> Ahuriri Valley Bush, western Banks Peninsula	18 Apr 1994 M36/774245	100	2.9 \pm 0.32	2.4 \pm 0.31	12.0 \pm 4.9	1.03 \pm 0.05	0.45 \pm 0.07	0.000063	100

Fig. 1 Mean monthly maximum and minimum temperatures 1993–95 for the Christchurch Botanical Gardens site.



rated out by washing, sieving, and decantation in tap water. It proved very difficult to remove the last vestiges of the arillode tissue from *Alectryon* seeds. *Kunzea* fruit were stored in a large plastic bag; the capsules then opened and the seeds could be shaken out. All cleaned seeds were soaked in tap water for 12 h. The seeds were then carefully sorted under a stereomicroscope to ensure that empty, damaged, or diseased individuals were eliminated. The exit holes left by larvae of the moth *Conopomorpha cyanocephala* (cf. Sullivan et al. 1995) could be seen on many *Alectryon* seeds but sometimes were overlooked. There appears to be a second predator of these seeds, the larva of a small Dipteran, not identified as yet, which leaves no trace on the outside of the seed.

Modular replicates of 25 seeds were used for each test (with some exceptions noted later and in Tables 2, 3, 4). The **standard** treatment seeds were cleaned, soaked in tap water and placed in plastic petri dishes, each with a single filter paper, and kept continually wet. The large seeds of *Corynocarpus* were kept in bigger plastic dishes lined with filter paper (usually 4 replicates). In the **dark** treatment the standard procedure was followed but the petri dishes were kept in black, heavy duty plastic bags, with the mouths folded and fastened with clothes pegs (2 replicates). **In-fruit** treatment seeds were left in fleshy fruit tissues, but otherwise maintained as for the standard (2 replicates). This test was not done for *Kunzea*. The dishes and plastic bags for these three treatments were laid out in blocks on a table covered by a black plastic sheet in an unheated, partially-shaded glasshouse. In spite of the shading the dishes were relatively well lit during daylight hours.

Soil treatment seeds were cleaned, soaked and placed in shallow grooves in pasteurised soil, in small shallow plastic dishes with drainage holes (2 replicates). **Dry** treatment seeds were cleaned, washed, and kept dry for 5–6 months before being placed in the same conditions as for the standard treatment (2 replicates). **Buried** treatment seeds were

cleaned, washed, and buried in pasteurised soil in 30 cm long, upright cylinders made from 10.4 cm diameter plastic drainpipe, open at the top and with drainage holes in the baseplate. Seeds were placed (in separate cylinders) at 5 cm and 10 cm, either between two layers of nylon net or, if small, beneath sheets of nylon net at the bottom of small plastic pots fitted with 0.2 mm mesh stainless steel gauze for drainage (1 replicate at each depth). The soil treatment trays and burial cylinders were laid out in blocks on a separate table in the glasshouse and the soil was kept moist.

Except for the 1989 *Alectryon* collection no tests of seed viability by the tetrazolium method were done. It has proved to be only partially reliable in the past (cf. Burrows 1995a, b).

The experiments were maintained in a glasshouse, as described by Burrows (1995a). Shade is provided by a row of evergreen and deciduous trees on the north side. In summer direct sunlight reaches the house early in the morning and late in the afternoon and sunflecks through the rest of the day. Before the experiments were set up in 1994, the tables, glasshouse walls, plastic sheets, central concrete slab path, and gravel floor were washed with a strong solution of calcium hypochlorite to kill algae, mosses, liverworts, and animal pests.

Monitoring and, when necessary, watering were done at weekly intervals for all except the dark treatment. All preparatory work and watering was done with tap water. Maximum and minimum temperatures were recorded at weekly intervals with Casella thermometers kept on the tables and at ground level. However, the continuous temperature record from the Christchurch Botanical Gardens (Anon. 1994–95) (Fig. 1) is used as a proxy for the record in the glasshouse, which it closely resembles (Burrows 1995a). The extreme maximum and minimum temperatures recorded in the glasshouse during the experiment were, respectively, 36.5°C and –3.0°C in 1994 and 37.0°C and –2.5°C in 1995.

The first signs of germination for each species were splitting of the seed coat, or endocarp, followed by radicle emergence. As seeds germinated in the standard treatment they were removed and planted out into trays of soil. The dark treatment seeds were not examined until all or most seeds in the standard treatment had germinated. This was to ensure that, during monitoring, they were not exposed to light or other conditions which might trigger germination. They were examined in a darkened room under a Kodak photographer's safelight. If no germination had taken place they were returned to the dark conditions. Little, if any, water loss occurred from the dishes kept in black plastic bags.

Seedlings that emerged above the soil surface in the burial experiment were counted. In early September 1995, the remaining seeds were exhumed. Seeds which appeared to be alive (i.e., had not germinated, or rotted) were planted out in shallow grooves in trays of soil as for the soil experiment.

Within-treatment variability of the final germination success is relatively low (Table 2). Graphical representation of the results is considered adequate.

RESULTS

In the standard treatment the timing of germination of the first seeds and the subsequent rate of germination among the remaining seeds varied considerably, as is clear from Fig. 2–5 and Table 2.

Kunzea

A few *Kunzea* seeds germinated in June, less than a month from the start of the tests (Fig. 2). Most *Kunzea* seeds germinated by the end of July; all in the set had sprouted by late August. The germination rate in the soil treatment was markedly slower than in the standard. So was germination in the dark and the success was low (Table 2). No in-fruit test was done for *Kunzea*.

When placed in conditions suitable for germination, after being kept dry for 5 months, *Kunzea* seeds germinated rapidly with a high degree of success (Table 3). No seedlings appeared at the surface when *Kunzea* seeds were buried at 5 cm depth and no sign of them could be found in September 1995. It is likely that the seeds had germinated then died and rotted, as was apparent for other species with larger seeds (Burrows 1996) (Table 4).

Corynocarpus

Corynocarpus seeds in both standard and soil

Table 2 Seed germination data for standard, dark, in-fruit, and soil treatments. * two replicates only; ** one replicate only

Taxon	Starting date	Numbers germinated per treatment												
		Standard			Dark			In-fruit			Soil			
		Days to first germination	Days to complete germination	%	\bar{x}	s	%	\bar{x}	s	%	\bar{x}	s	%	\bar{x}
<i>Alectryon excelsus</i>	3 Feb 1989	2	42	12.0±3.6	48	0	2.0±2.8	8	14.0±5.6	56				
<i>Alectryon excelsus</i>	9 Mar 1994	20	223	14.0±3.9	56	5.0±2.8	20	14.5±2.1	58					
<i>Corynocarpus laevigatus</i>	6 Mar 1994	2	148	23.5±0.7*	94	18.7±0.7	75	24.5±0.7	98					
<i>Kunzea ericoides</i>	20 May 1994	24	77	25.0±0	100	21.5±0.7	86	19.0±0	76					

Fig. 2 Germination curves for *Kunzea ericoides* seeds.

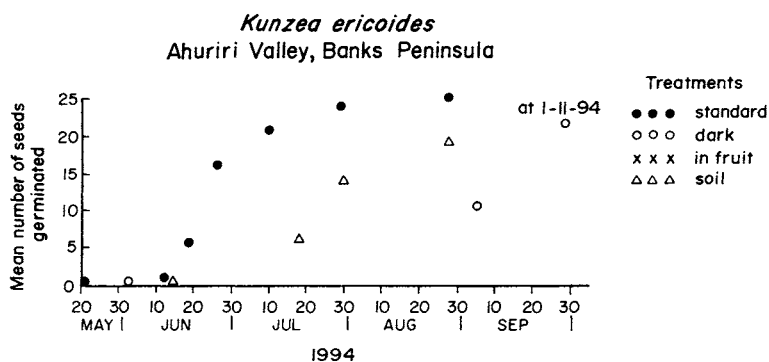
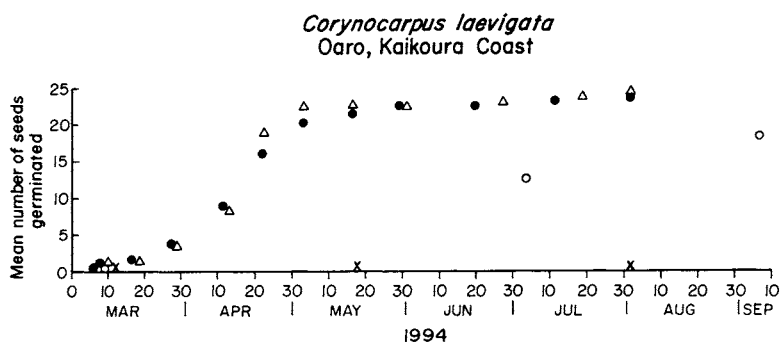


Fig. 3 Germination curves for *Corynocarpus laevigatus* seeds (symbols as for Fig. 2).



treatments germinated at about the same rate, beginning a few days after the experiment started (early March) (Fig. 3). Most (90%) had germinated by mid-May. Most of the remaining seeds germinated at a very slow rate through the coldest months (June–July) and the last few sprouted in early August. Dark treatment seeds of this species also germinated slowly. No in-fruit treatment seeds and few of the seeds that were dried for 5 months germinated. However, 70% and 80%, respectively, of seeds buried at 5 and 10 cm depths sent shoots above the soil surface. The remaining buried seeds died and rotted (Table 4).

Alectryon

In the standard treatment the two provenances of *Alectryon* seeds, collected from different places, in different months and different years, behaved somewhat differently (Fig. 4). In an early February collection (1989) the first seeds germinated a few days after the start of the experiment, a flush of germination followed, and the last few seeds germinated by the end of March. In the early March collection (1994) the first seeds germinated more than a month later, and only a few more seeds germinated in the next 2 months (up to early June). There was no

germination over the winter, but a flush occurred in September–October and the last seeds germinated in early November. The final success for this treatment in 1989 and 1994, was 48% and 56%, respectively, a much lower level than for most other species I have investigated so far. In the 1989 experiment 36% of the *Alectryon* seeds tested for viability with triphenyl tetrazolium chloride proved to have been attacked by seed predators (*Conopomorpha cyanospila* and possibly another) (cf. Sullivan et al. 1995). The rest were viable.

No *Alectryon* seeds germinated in the 1989 dark treatment; this was probably caused by fungal overwhelming of the seeds, as 20% of the 1994 seeds in this treatment germinated. Only a few *Alectryon* seeds germinated in the in-fruit treatment in 1989. Again the seeds were heavily affected by fungi. The soil treatment seeds in 1989 germinated at a very slow rate in autumn, but in September–October there was a slight flush with a few more seeds germinating as late as January 1990. The standard treatment seeds of *Alectryon* in 1994 followed a similar course. However, the soil treatment seeds of the 1994 collection germinated relatively well through the winter, with only a few seeds sprouting in spring (total of 48% success).

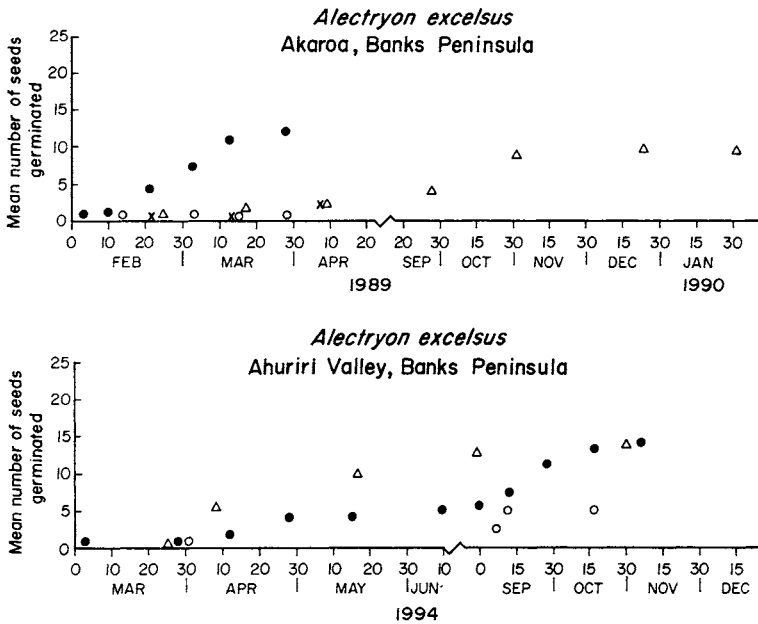


Fig. 4 Germination curves for *Alectryon excelsus* seeds (symbols as for Fig. 2).

Table 3 Seed germination data for dry treatment. * two replicates of 25 seeds; for location and date collected see Table 1; + remaining seeds rotted.

Taxon	Period seeds kept dry (months)	Starting date	Days to first germination	Days to complete germination	Mean number of seeds germinated		
					\bar{x}	s	%
<i>Alectryon excelsus</i> *	5	4 Aug 94	56	81	14.5±2.1		58
<i>Corynocarpus laevigatus</i>	5	4 Aug 94	82	—	1.0 ⁺ (n=10)		10
<i>Kunzea ericoides</i>	5	25 Oct 94	7	28	23.0 (n=25)		92

Table 4 Seed germination data for burial treatment. * one set of 25 seeds; for location and date collected see Table 1. ** as no seeds were found, despite careful search, it is assumed that they had germinated and the seedlings rotted.

Taxon	Burial depths (cm)	Date Started	Days to first seedling appearance	Days to last seedling appearance	No. that reached surface	%	Date of exhumation of buried seeds	No. of seeds that germinated and seedlings died underground	
								No.	%
<i>Alectryon excelsus</i> *	5	9 Mar 94	120	87	6	24	29 Sep 94	10	40
	10	9 Mar 94	—	—	—	—	12 Sep 95	13	52
<i>Corynocarpus laevigatus</i>	5	6 Mar 94	} 226	126	7	70	12 Sep 95	—	—
	10	6 Mar 94			8(n=10)	80	12 Sep 95	—	—
<i>Kunzea ericoides</i> *	5	20 May 94	—	—	—	—	5 Sep 95	25**	100

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After 5 months' drying in 1994, seeds of *Alectryon* germinated over a period of nearly 10 weeks, with 58% success (Table 3). Seeds buried to 5 cm depth germinated, with 24% reaching the soil surface. A further 40% germinated but did not reach the soil surface. The remainder (examined in September 1994) included one seed that had been attacked by a Dipteran larva, three that had been attacked by *Conopomorpha*, and five others which were apparently alive. These last were planted in soil, as for the soil treatment, but none germinated. Of the set of *Alectryon* seeds buried at 10 cm depth and examined in September 1995, 52% had germinated, probably in spring 1994, but none reached the soil surface. The rest had rotted (Table 4).

DISCUSSION

Germination success

High to very high germination success was achieved in the standard treatment for seeds of *Kunzea* and *Corynocarpus* but not *Alectryon* (Table 2). Three likely causes of the low result for *Alectryon* were identified. During the sorting of seeds to place in the experiments, it proved very difficult to detect all seeds which had been attacked by the larvae of the moth *Conopomorpha cyanospila*, an obligate predator of the young seeds of *Alectryon* (Sullivan et al. 1995). In that predation study, samples of seeds collected from trees or the ground on western Banks Peninsula revealed a 1% to 30% infestation. During the present study, 36% of a sample of 25 seeds from Akaroa, eastern Banks Peninsula, were damaged. *Conopomorpha* is considered to be the main reason for seed death in *Alectryon*. In addition, there may be another seed predator of *Alectryon* seeds as an unknown Dipteran pupa was found in one damaged *Alectryon* seed. Thirdly, it is impossible to remove all of the arillode tissue from the seeds before placing them in experimental conditions. The tissue becomes a focus in petri dishes for the growth of first fungi then algae, which may have smothered some seeds.

The timing of germination

The standard treatment results are being discussed unless otherwise indicated. The timing of flowering and fruiting is relevant to this discussion (cf. Burrows 1994a). Ripe fruit of *Corynocarpus* and *Alectryon* are displayed on the parent for periods of at least 3 months (sometimes more). Such long fruiting periods are achieved by having extended

consecutive flowering and resultant consecutive ripening of fruit on any one plant, as well as by having overlap of consecutive extended flowering and fruiting among individual parent plants in populations of each species. The period of presence of viable seeds of these species is lengthened probably both by inhibition of germination by the pericarp tissues and the preservative antibiotic influences of these tissues (Burrows 1995c).

This phenomenon of long drawn-out fruit display is likely to have been exaggerated by the local or total extinction since 1840 of native birds that were important frugivores and seed dispersers, as well the absolute numerical decline of numbers of the important native frugivores that still survive (cf. Burrows 1994a). Introduced frugivores such as blackbirds (*Turdus merula*) and silvereyes (*Zosterops lateralis*) cannot compensate entirely for the losses because they are not large enough to swallow fruit of some species (e.g., *Alectryon* (silvereyes) and *Corynocarpus* (both species)). The presence of fruit on parent plants for extended periods means that seeds from one cohort can experience different climatic conditions, pre-dispersal (Fig. 1, Table 2).

Some *Corynocarpus* seeds germinated very early, but Fig. 3 and Table 2 show that not all seeds in the set were in an advanced state of readiness to germinate. Such physiological differences in germination readiness among seeds in a cohort can be imparted to them before they leave their parents (cf. Gutterman 1992). Any seeds of this species which had not germinated by the end of April sprouted very slowly over the winter, when extreme low temperatures fell to -3°C in the glasshouse and mean minimum temperatures were below 5°C and maxima below 15°C . *Corynocarpus* seeds on soil and in the burial tests behaved similarly to those in the standard test, in contrast with the patterns for *Kunzea* and *Alectryon*.

The timing of *Alectryon* seed germination in relation to the seasons (Fig. 4) resembled that for *Corynocarpus*, but the overall results are more complex, with early- and late-collected seeds behaving differently. It is notable that the soil test seeds from the 1989 collection germinated with a very similar pattern to the standard test seeds from the 1994 collection. The causes of these variations in behaviour of seeds germinating in well-lit conditions and on soil are not known. Partial burial of the soil treatment seeds may influence light relations. There may be complex interactions between effects of changing temperature and light quality and quantity through the seasons (Gutterman 1992; Pons 1992; Probert

1992). *Alectryon* seeds germinate in two flushes in Banks Peninsula forests. A few seedlings from particular cohorts of seeds appear in late autumn, while many do so in spring–early summer (C. J. Burrows unpubl. data). This pattern may reflect the influences of the different times in the fruit season when seeds mature and are dispersed. This phenomenon was noticed for various other species with long-drawn-out fruiting periods (Burrows 1996).

The spread of the germination period evident from the standard test for *Kunzea* seeds (Fig. 2) differs from that recorded for the other two species in that, after a moderate delay before the first seeds sprouted, 80% of the seeds germinated within a month. *Kunzea* fruit on Banks Peninsula are ripe in April–May and almost all seeds are shaken out of the capsules by the end of May (C. J. Burrows unpubl. data). On soil the *Kunzea* germination pattern was similar to that for the 1994 *Alectryon* collection seeds, though confined to the late winter.

Other ecological implications

It is to be expected that germination behaviour of the three species explains at least some of the ecology and site preferences of seedlings, saplings, and adults in natural habitats. For species to succeed in natural conditions their seeds must be dispersed to places where there is a good likelihood that firstly, the seeds will germinate and secondly, the seedlings will establish and grow on to adulthood, in spite of all environmental hazards and competition.

Alectryon, *Corynocarpus*, and *Kunzea* are tolerant of the summer-dry environment of Canterbury-eastern Marlborough and are moderately to very abundant there. Autumn, winter, and spring are the times of most reliable supply of moisture, so selection in favour of germination at those times has probably occurred. Winter cold seems to be less of a problem for seeds in the New Zealand context than dry conditions (cf. Burrows 1994b). These species also occur in moderately wet climates such as that of the Marlborough Sounds or in the southern North Island; they are less prominent in very high rainfall areas. In Westland *Kunzea* is confined to very well-drained, young river flood plains. It would be interesting to establish the germination times of seeds from provenances from the wetter regions.

Kunzea is often regarded as a colonising species which flourishes after forest disturbance and otherwise is found at forest margins or in openings. After major disturbance (especially fire) *Kunzea* often forms extensive and dense monospecific groves. During their development, and when the plants reach

their full size after 80–100 years, other tree species are excluded and *Kunzea* itself does not regenerate (cf. Allen et al. 1992; Smale 1994). There is little or no replacement of the *Kunzea* unless there is further disturbance. Overall the capabilities of *Kunzea* for vigorous regeneration on disturbed sites are explicable in terms of its abundant seed production, the ready dispersal of its minute seeds by wind, and their rapid germination when moisture conditions are favourable. An additional benefit is the ability of its seeds to remain viable when dry, for a few months at least. Experiments are needed to determine how long the dry seeds will retain their viability. However, *Kunzea* cannot maintain buried seed banks (at least, if the soil is moist) because the seeds are not inhibited from germinating when buried.

Germination of *Kunzea* seeds is slow in the dark. Shading by canopy or litter would, presumably, affect the germination rate. The failure to regenerate under its own canopy is probably at the stage of early seedling growth, as it is for *Leptospermum scoparium*, a species with very similar seed biology and general ecological behaviour (Mohan et al. 1984a, 1984b).

Corynocarpus is not usually regarded as a colonising species, although it often occurs at forest margins and may form groves there. It has a scattered presence in quite dense, tall forest and is usually part of the canopy. The seed characteristics favouring *Corynocarpus* are the high germination success on soil and when the seeds are buried. The extension of shoots of buried seeds (from at least 10 cm depth) is an advantage accruing from their very large size. Large seeds are also a benefit in shaded sites. However, its poor seed germination after drying of the seeds with the pericarp removed (Table 3) suggests that *Corynocarpus* would be vulnerable when colonising open sites if there was a risk from drought.

Judged by the overall results from the present tests the best likelihood for establishment of seedlings of *Corynocarpus* would be if seeds are dispersed as soon as the fruit are ripe, to moist, shaded sites, or are buried in the soil or beneath litter. Burial of the seeds to 5 cm or more could result in better seedling establishment than if seeds lie on the ground surface, because of their vulnerability to drying (Table 3). *Dysoxylum spectabile* requires similar conditions for good germination and seedling establishment (Court & Mitchell 1988). It is possible that seeds in *Corynocarpus* fruit which fall to the ground with the pericarp intact and lie there through the summer (a common feature in Canterbury – Marlborough)

(C. J. Burrows unpubl. data) retain their viability better than seeds which have passed through birds.

The potential for long temporal spread of the germination period and to survive a period of drying (as well as surviving shallow burial) means that, at the seed germination stage, *Alectryon* is somewhat more versatile, ecologically, than *Corynocarpus*. *Alectryon* does not normally behave as a colonist except in forest gaps. It is part of the canopy in relatively tall forest, and can form groves. A limiting factor for other species in the sites where it lives is periodic summer drought, whereas *Alectryon* is drought-tolerant (Innes & Kelly 1992). Although many of its seeds are eaten by moth larvae it is a periodic but very prolific seeder and its juveniles are abundant on the forest floor in spring after a mass seeding (C. J. Burrows unpubl. data). The germination behaviour of *Alectryon* appears to match its site preferences quite well, as seeds germinate relatively abundantly on soil on the forest floor after being dried and when shallowly buried. However, it did not germinate so well in the dark treatment because fungi proliferated on the arillode remnants, a feature not quite compatible with its behaviour when the seeds were buried. In the soil there may be antibiotic effects which neutralise the adverse influence of such fungi.

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