Regeneration of *Agathis australis* and associated species in a native bush stand on Limestone Downs

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Abstract
A predator-proof fence enclosing 270 m^2 of predominantly kauri (*Agathis australis*) bush on Limestone Downs was erected in February 2004. Regeneration of *A. australis* and other seed-dispersed species was monitored in permanent quadrats laid out within and immediately outside the enclosure. The quantity of viable *A. australis* seed entering the enclosure by natural dispersal and extent of viable *A. australis* seed within the soil seed bank were measured. Two thirds of the viable seed dispersed was lost, probably through mammalian predation. Eleven species were found in the soil seed bank. No viable *A. australis* seed was found in the soil seed bank. Seed rain was the source of viable *A. australis* seed. Regeneration of *A. australis* was greater within the protected environment of the predator-proof fence. There was a decline in seedling numbers between May 2007 and April 2008 both inside and outside the predator-proof fence suggesting that predation was not the only factor influencing seedling survival.

Keywords: *Agathis australis*, Xcluder™ fence, seed predation, seedling survival, regeneration, seed rain

Introduction

New Zealand's long isolation from other land masses has led to the development of a distinct flora (Martin 1961). Approximately 75% (Laing & Blackwell 1949) to 80% (Mark & Adams 1979) of the indigenous flowering plant species in New Zealand are not encountered elsewhere. The flora of New Zealand represents a unique genetic resource (Fountain & Outred 1991). Prior to settlement large herbivores were absent. The flora has therefore evolved in their absence. Successive waves of human settlement have introduced alien herbivores that now threaten this flora. In response to this threat pest-proof fencing is becoming an increasingly important tool for protection of native species (Kaplan 2003).

Kauri (*Agathis australis* (D. Don) Lindl. (Araucariaceae)) the New Zealand representative of the Southern Hemisphere genus is endemic and is a species of lowland forests extending from near North Cape (34° 25' 7" S) to latitude 38°S Kawhia harbour (Allan 1982). The once extensive kauri forests have been reduced to remnants: only 6.7% of the 1.2 million hectares of original forest remains (Shepherd, 2004).

A. australis seed matures from March to April and is dispersed from seed-bearing cones on the tree by wind and gravity. Seed quantity and viability can vary from year to year (Bergin & Steward 2004). *A. australis* seed and young seedlings are thought to be predated by mice (*Mus musculus* L) and possibly rats (*Rattus rattus* L.). Seedlings are also browsed by brush-tailed possums (*Trichosurus vulpecai* Kerr), rabbits (*Ortyctolagus cuniculus* L.) and/or hares (*Lepus europaeus* Pallas) and goats (*Capra hircus* L.) (Ecroyd 1982). Seed is also predated by insects such as the common weta (*Hemideina thoracica* White) (Mirams 1957).

Limestone Downs Station (37° 28' 48'' S, 174°S 44' 43' E) is a 3,200 ha coastal sheep and beef farm located 15 km south of Port Waikato. The original vegetation included extensive areas of *A. australis* forest (Macdonald 1993), of which a single remnant stand remains within a 419 hectare bush area. In the late 1930s, remaining *A. australis* on the station with a girth of over 1.2 metres was milled (Macdonald 1993). A girth of 1.2 m indicates a diameter of approximately 0.4m (diameter = girth/π), suggesting that the maximum age of the kauri in the remnant stand is 140-150 years, based on an estimated tree age of 70-80 years at a trunk diameter of 0.4 m (Burns & Smale 1990).

In this study seed recruitment and germination was measured inside and outside a mammalian predator-proof fence to determine (a) whether recruitment and germination were high enough to achieve regeneration and (b) whether there is evidence of predation by animals.

Methods

An Xcluder™ Tui Fence ('the fence') enclosing 270 m^2 of predominantly kauri bush on a ridge top within the 419 ha remnant bush area of Limestone Downs was erected in February 2004. Rodents and other mammals such as possums, rabbits and hares, are excluded by the Xcluder™ Tui Fence (Xcluder™ Pest Proof Fencing Company 2008). However, because the fence was erected within an *A. australis* stand complete removal of surrounding vegetation was not possible and ingress by rodents via overhanging vegetation can not be completely excluded. Possum and rodent bait stations were established within the enclosure in case of incursion. There was evidence of rodent bait being taken in August 2004 (shortly after completion of the fence), but none since then.

In April 2004 a total of 16 m^2 quadrat areas, subdivided into twenty 0.8 m^2 randomly distributed sites, ten inside and ten outside the fence, were laid out. All quadrats were within 2 m of an *A. australis* tree. Seedling emergence in these quadrats was scored by species in April and August 2004, July 2006, May 2007 and April and August 2008. A seedling was scored as emerged when it was visible above the leaf litter. Kanuka (*Kunzea ericoides* A. Rich.) and mingimingi (*Leucopogon fasciculatus* A. Rich.) seedlings were difficult to differentiate at an early stage, as were rewarewa (*Knightia excelsa* R. Br.) and lancewood (*Pseudopanax crassifolius* (Sol. ex A. Cunn.) C. Koch). Data for these species were included in the total number of seedlings but are not analysed at the species level. Seedling numbers in the quadrats were calculated as numbers/m^2 prior to analysis.

In January 2007, twelve funnel-type 'funnel' seed traps (funnel area at the opening: 0.20 m^2) and twelve tray-type 'tray' seed traps (tray area: 0.12 m^2) were set up within and outside the fence. The design of the funnel-type traps is such that rodents can only enter the traps by falling from above and once in the traps can not escape. All traps were within 10m of the *A. australis* stand, which is within the reported dispersal distances of *A. australis* seed of 0-50 m (Enright *et al.* 1999) and 0-150 m (Halkett 1983). Traps were emptied in April, May and July 2007 and April, May and August 2008. Seed was separated from the litter and identified. *A. australis* seed was separated into full (seed coat, embryo and nutritive tissues) or empty (seed coat only) seed. Full seed was placed in moist pleated paper (Anchor Paper Company, St. Paul, Minnesota) at 20°C (with light) to germinate. Germination was scored as normal seedling development. A normal seedling was defined as having a strong primary root and cotyledons that had expanded; otherwise the seedling was classified as abnormal. Remaining seed was cut. Seed that was flaccid and off-white in appearance was classified as dead. Seed that remained firm and white was classified as fresh ungerminated. The viable seed percentage was calculated as the percentage of full seed that produced a normal or abnormal seedling or remained fresh ungerminated expressed as a percentage of the total seed collected. Seed numbers in the seed traps were recalculated as numbers/m^2 prior to analysis.

The yearly dispersal numbers of *A. australis* seeds/m^2 within each category (total, full empty and viable) were estimated by adding the seed number/m^2 for the three collection dates for each year for funnel traps within the fence and averaging these over the two collection years. The loss of viable *A. australis* seeds as a result of predation was estimated by adding the seed number/m^2 for the three collection dates for each year for tray traps outside the fence and averaging these over the two collection years. These calcuations assume no *A. australis* seeds were dispersed between July and December.

Soil cores were taken from beside the tray traps in January 2007 and May 2008. At each sampling 24 soil cores (15mm diameter, 100 mm core depth) were taken from inside and 24 from outside the fence. Buried seeds within the core were identified by washing the seeds from the soil with a minimum of water on a fine mesh sieve (Cuisine Queen 250 mm sieve, fine mesh number 109).

Data Analysis

The general linear models procedure (PROC GLM) in SAS® for Windows (Release 8.02 TS Level 02M0, SAS Institute, Cary, North Carolina) was used to perform an Analysis of Variance (ANOVA) on the data. Data were checked for normality prior to analysis using the Shapiro-Wilk (W) statistic. A square root transformation was needed to normalise the data. Untransformed means are presented in all tables and figures.

The Least Significant Difference (LSD) procedure was used to compare means, but only where the ANOVA F-test identified a significant difference between treatments, i.e., a protected LSD (Ott 1988). For interaction effects the probability values for the hypothesis that two means being compared were equal were also determined using the LSD procedure.

Results

Seed rain and soil seed bank

Seeds of a limited range of species were found within the traps. The species were *A. australis*, kahikatea (*Dacrycarpus dacrydioides* (A. Rich.) de Laub.), miro (*Prumnopitys ferruginea* (D. Don) de Laub.), tarairi (*Beilschmiedia tarairi* (A. Cunn.) Benth. & Hook. f. ex Kirk), tawa (*Beilschmiedia tawa* (A. Cunn.) Benth. & Hook. f. ex Kirk), nikau (*Rhopalostylis sapida* H. Wendl. et Drude), *Coprosm*a spp., *K. excelsa* and hangehange (*Geniostoma rupestre* J.R. Forst. & G. Forst.).

The funnel traps contained more full seed (19.2 seeds/m^2) than the tray traps (11.0 seed/m^2) ($P<0.05$), but, there were no differences between total or empty seeds.

The total number and number of full and empty *A. australis* seeds differed between traps inside and outside the fence. Traps inside the fence contained more seed (Table 1).

Table 1 Total number and number of full and empty seeds/m^2 collected in all traps (funnel and tray) inside and outside the fence averaged over two collection years (2007 and 2008).

		Seed/m^2	
Location	Total	Full	Empty
Inside Fence	68.3a	18.9a	49.4a
Outside Fence	48.8b	10.7b	38.1b

Numbers followed by the same letter within a column are not significantly different ($P<0.05$)

The number of viable *A. australis* seed dispersed did not differ significantly between years (P<0.05). The average number of viable seed dispersed over the two-years of the study (measured as seed collected in the funnel traps within the fence) was 20.2 seeds/m^2. There were more empty seeds (P<0.05) collected in 2008 but there was no difference in the total amount or amount of full seed collected in the traps in different years (Figure 1).

There was a difference between years in the time when seed was collected in the traps (Table 2). In 2007 81% of the full seed had been collected by 13 April 2007. In contrast, in 2008 only 42% of the full seed had been collected by 2 April 2008 with the remaining 58% not collected until 28 May 2008 (Table 2). A higher number of full seed was collected within the fence on 13 April 2007 than at any other collection date, including 2 April and 28 May 2008. Viable seed percentage and the germination percentage of full seeds did not differ for any collection time (Table 2). In all germination trials, seeds that did not germinate were dead.

Species identified in the soil seed bank were *Agathis australis* (empty seed), *Collospermum hastatum* (Col.) Skottsb., manuka (*Leptospermum scoparium* J.R. Forst. et G. Forst.) (capsules), *P. ferruginea*, tanekaha (*Phyllocladus trichomanoides* D. Don), *Carex* spp., *Juncus* spp., nodding thistle (*Carduus nutans* L.), and three unidentified species. No viable *A. australis* seed was found in the soil seed bank.

Table 2 Total, full and empty seed/m^2, viable seed percentage and germination percentage of full seed collected in funnel traps inside the fence at each collection date.

Date	Total seed/m^2	Full seed/m^2	Empty seed/m^2	Viable seed (%)	Full seed germination (%)
13 April 2007	45.0a	24.6a	20.4b	44a	83a
25 May 2007	10.8b	5.0c	5.8c	26a	78a
4 July 2007	0c	0a	0d	-	-
2 April 2008	32.5a	8.3bc	24.2b	25a	82a
28 May 2008	45.0a	10.0b	35.0a	19a	77a
13 August 2008	0.4c	0d	0.4d	0a	-

Numbers followed by the same letter within a column are not significantly different (P<0.05)

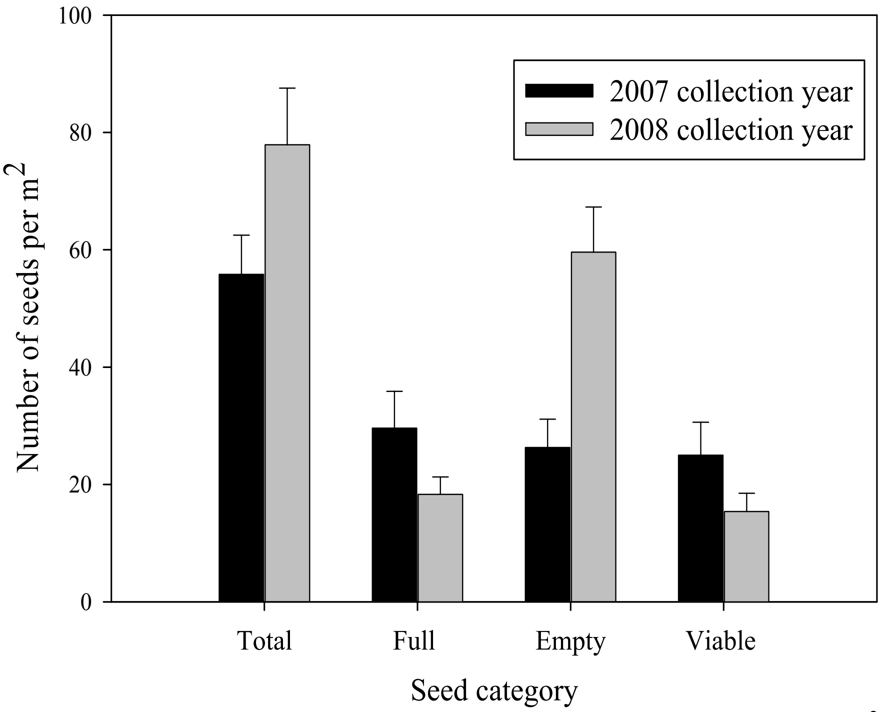

Figure 1 Total number and numbers of full, empty and viable seed/m^2 of *A. australis* seed collected in funnel traps within the fence in 2007 and 2008. Error bars are standard errors of the untransformed means.

Regeneration within and outside the Xcluder™ Tui Fence

The predominant seedling species found in quadrats within and immediately outside the fence were *A. australis*, *P. ferruginea*, *P. trichomanoides*, *D. dacrydioides*, *Coprosma* spp., mapou (*Myrsine australis* (A. Rich.) Allan), *K. ericoides, L. fasciculatus*, *K. excelsa*, *P. crassifolius* and *R. sapida.*

Total seedling number was higher (P<0.05) within the fence (44.2 ± 4.44 seedlings/m^2) than outside (29.1 ± 3.73 seedlings/m^2). Total angiosperm seedling number was also higher (P<0.05) within the fence (35.7 ± 3.31 seedlings/m^2) compared with outside (27.0 ± 3.49 seedlings/m^2) as were the number of *Coprosma* spp., *M. australis* and *R. sapida* seedlings (Figure 2). Similarly, total gymnosperm seedling number and those of *A. australis*, *P. ferruginea* and *D. dacrydioides* were lower outside the fence than within (Figure 2). In contrast there was no difference in the number of *P. trichomanoides* seedlings inside and outside the fence.

There was a significant interaction effect between scoring date and location inside or outside the fence for *A. australis* (Figure 3), but not for the other gymnosperms or angiosperms. At the first scoring (April 2004) there was no difference in the number of *A. australis* seedlings inside and outside the fence. However, there were more *A. australis* seedlings inside than outside the fence at all subsequent scoring dates. *A. australis* seedling numbers within the fence were at a maximum at the July 2006 and May 2007 scorings, but had declined by the April 2008 scoring. At the August 2008 scoring seedling numbers did not differ significantly (P<0.05) from those in May 2007.

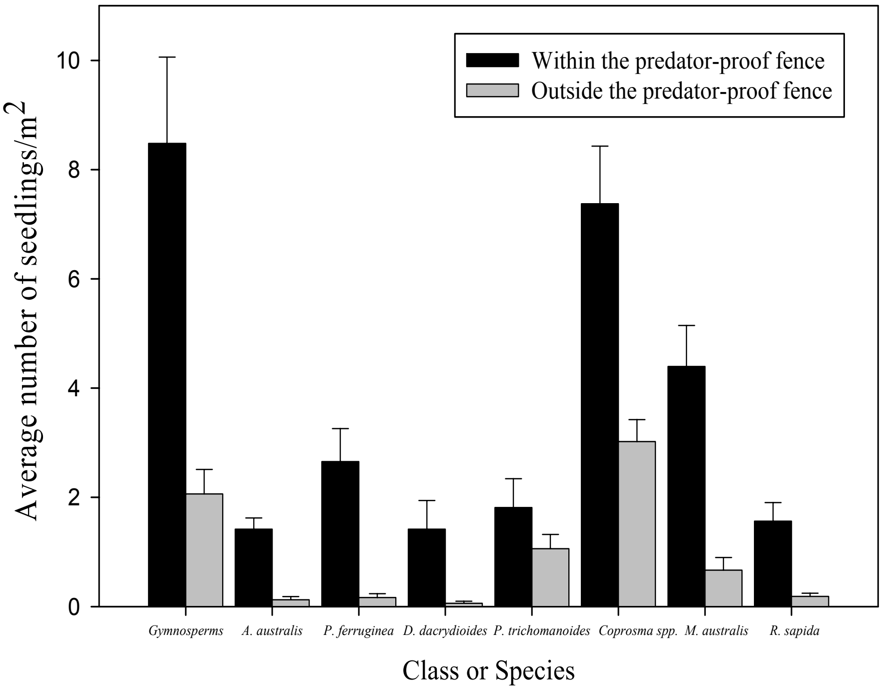

Figure 2 Emergence of total gymnosperms and selected species inside and outside the predator-proof fence averaged over scoring dates. Error bars are standard errors of the untransformed means.

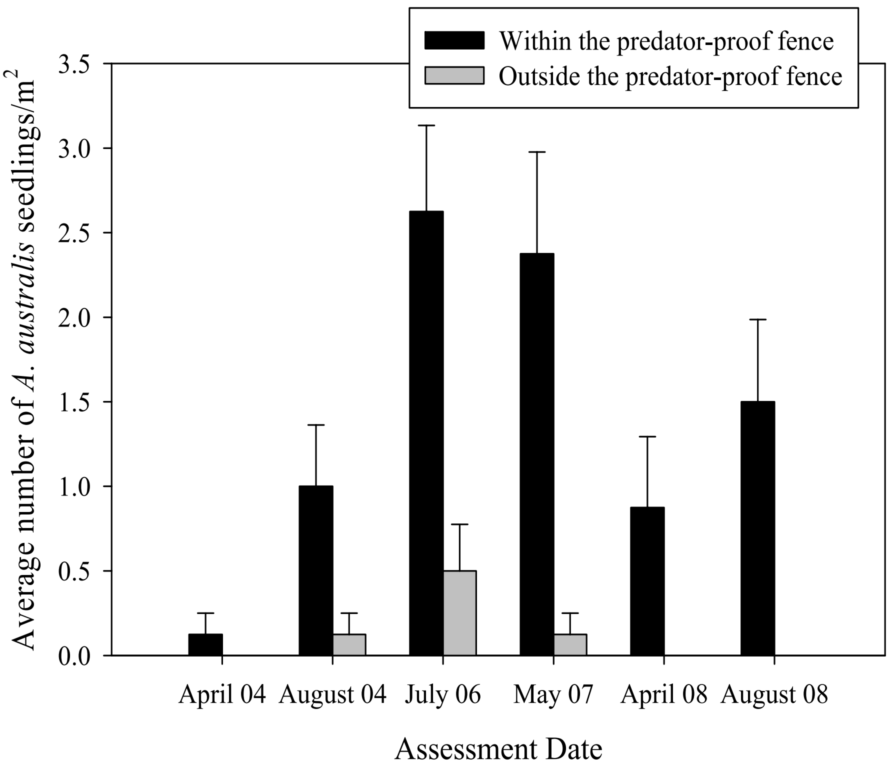

Figure 3 *A. australis* seedling emergence inside and outside the predator-proof fence over time. Error bars are standard errors of the untransformed means.

Discussion

Seed rain and soil seed bank

The yearly dispersal of viable *A. australis* seed was higher than that reported in some studies. Sem and Enright (1996) reported 10 viable *A. australis* seeds/m^2 from sites containing at least one *A. australis* tree within forest patches in the Waitakere Ranges. In this study there were 14 mature *A. australis* within the 270 m^2 enclosure. This suggests a much smaller seed source in the Sem and Enright (1996) study. In contrast Enright *et al.* (1999), using a viability of 5-23%, reported 15-69 viable seeds/m^2/year near parent trees declining to 0.5-2.3 viable seeds/m^2/year 50 m from the tree. The number of viable seeds/m^2 collected in this study was at the lower end of the Enright *et al.* (1999) range.

Enright *et al*. (1999) commented that viability declines with distance from potential parent trees. The seed viability in 2007 (37 ± 5.2%) was higher than the range reported by Enright *et al*. (1999), but was within this range in 2008 (21 ± 4.9%). The average of 28 (± 3.7%) viable seed over the two study years is consistent with Mirams (1957) who found 30-35% ‘sound’ seed in bulk *A. australis* seed lots, but also reported that the percentage of ‘sound’ seed is variable. Ecroyd (1982) also reports that the percentage of ‘sound’ seed varies from year to year.

The high number of empty seed dispersed each year indicates lack of seed set and/or development within the kauri cone is limiting the amount of viable seed produced.

There were more full seeds both inside the fence and in the funnel traps, suggesting that the best case scenario for full seeds surviving dispersal is represented by the funnel traps inside the fence and the worst by the tray traps, outside the fence. The number of viable seeds/m^2 collected in these traps, averaged over two years, is 20.2 and 6.6 seeds/m^2, respectively. This suggests that 67% of the viable seed dispersed is lost through predation by mammalian pests. This 67% loss will be aggravated by any subsequent loss of seedlings that germinate from surviving full seed.

A. australis seed is predated by mice and rats (Bergin & Steward, 2004) and these are likely to be the cause of seed loss outside the fence. There may still be predation loss of seed dispersed within the fence from predators not excluded by the fence such as the *H. thoracica*, (Mirams 1957), possibly crickets (*Teleogryllus commodus* Walker) (Ecroyd 1982) and any *Mus* spp. and *Rattus* spp. that gain entry into the enclosure via the overhanging canopy. Nonetheless exclusion, or at worst reduction, of mammalian pests by the fence has considerably enhanced the survival of full *A. australis* seed.

The lack of viable *A. australis* seeds in the soil seed bank means that regeneration is dependent on fresh seeds entering the area from seed rain.

Regeneration within and outside the Xcluder™ Tui Fence

The seedling species identified within the *A. australis* stand are typical of those found in a kauri forest (Cockayne 1928). Survival of *A. australis* seedlings was enhanced within the fence, presumably as a result of the fence protecting emerging seedlings from predation by the local mammalian population. However, the decline in *A. australis* seedling number in April 2008 compared with July 2006 and May 2007, indicates that predation is not the sole determinant of seedling survival. The thick litter characteristic of a kauri forest can prevent seedling roots from penetrating the soil A horizon (Sando 1936; McKinnon 1945). It is likely that the relatively dry March in 2008 (15 mm rainfall in March 2008 compared to a March average of 94 mm for 2005-2007, Limestone Downs weather station) resulted in a decline in *A. australis* seedling numbers. The increase observed in August 2008 is a result of the 2008 seed rain. The constant number of *A. australis* seedlings outside the fence suggests that there is continuous turnover of these species with predation being balanced by emergence from the annual seed rain but little or no long-term regeneration.

In addition to *A. australis*, *P. ferruginea*, *Coprosma* spp., *R. sapida* and *M. australis*, showed enhanced survival within the fence. Predation by *Rattus* sp. of seed of *P. ferruginea* (Wilmshurst & Higham 2004) and *D. dacrydioides* (Beveridge 1964) seedlings of *Coprosma* spp. (Campbell & Atkinson 2002) and seed and seedlings of *R. sapida* (Campbell & Atkinson 1999) has been reported. Pigs (*Sus scrofa* L.) will also eat seed of *P. ferruginea* (Beveridge 1964). Browsing of *P. ferruginea* by *C. hircus* (Pollock *et al*. 2007), *Coprosma* spp. by *C. hircus* and *T. vulpecai* (Husheer, 2006) and *M. australis* by *C. hircus* (Pollock *et al*. 2007) has also been reported. These observations are consistent with an increased number of seedlings of these species as a result of exclusion of mammalian predators from within the fence.

In conclusion, with no viable *A. australis* a seed identified in the soil seed bank regeneration is dependent on freshly dispersed seeds. Sufficient viable seeds are being dispersed for regeneration, however, outside the fence 67% of viable seed is lost through predation, with subsequent loss from seedling predation likely. While loss of viable seed may still be occurring within the fence, data from this study suggests that sufficient *A. australis* seed remains for regeneration.

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