

## **Chapter 6. PREDATION AND REMOVAL OF THREE SEED COHORTS: INFLUENCE OF FOREST FRAGMENTATION**

### **6.1 INTRODUCTION**

Forest fragmentation can alter animal-plant interactions and the reproductive success of plant species (e.g. Aizen & Feinsinger 1994b), as well as directly influencing species extinction and population decline (Wilcox & Murphy 1985). Pollinators, herbivores, parasites, dispersers or predators of fruit or seeds variously affect the ability of the tree to reproduce and ultimately, fecundity (Lovejoy *et al.* 1983). Any change in the abundance or behaviour of either the fauna or the plant resource could, therefore, affect plant reproductive success. At each plant life-stage (e.g. pollination, seed set, pre- and post-dispersal seed predation, seed dispersal, and early seedling survival), abiotic factors, as well as one or more animal species may be involved. The relative importance of each stage depends on the environment, the plant species, and the fauna with which it interacts. Thus, fragmentation may alter seed set (Lamont *et al.* 1994), pollinator abundance and pollination rates (Aizen & Feinsinger 1994a,b), seed predation and dispersal (Santos & Telleria 1994, Telleria *et al.* 1991) and/or germination rates (Menges 1991) and survival (Putz *et al.* 1990, Leigh *et al.* 1993). Whether this results in altered plant abundance is difficult to predict, so it is important to determine whether survival of new seedling recruits is affected by fragmentation, and to identify the cause, although this may not be immediately obvious (e.g. Yates *et al.* 1994b). Because of the coupling of plant life-stages and their associated fauna, it is useful to investigate more than one life stage.

Tropical moist forests are noted for a greater number of large-seeded tree species than sunlit, early successional habitats (Salisbury 1942, 1974, Foster & Janson 1985). There are several hypothesized adaptive values of large seeds in tropical moist forests (Foster 1986), for example, having sufficient seed reserves to sustain seedlings in shaded conditions until a gap in the canopy occurs. However, all of the hypotheses apply only if the seed escapes or can withstand partial predation. There is circumstantial evidence that large seeds often experience heavier rates of predation than small ones because they are often used as a food resource by a wider range of predators (Harper 1977, Janzen 1969, 1971 in Foster 1986). Estimates of seed predation in tropical large-seeded species range from 33 to 100% of seeds destroyed (Janzen 1982c, de Steven & Putz 1984, Becker & Wong 1985, Lott *et al.* 1995, Forget 1992a,b, Terborgh *et al.* 1993, Forget 1994). Moreover, newly germinated seedlings may suffer significant additional predation (e.g. De Steven & Putz 1984, Forget

1992a). Any alteration to these high levels of predation, as a result of fragmentation, could have important implications for the abundance of large-seeded species.

A great many studies document predation or record its magnitude but very few help determine whether predation is relevant to either the evolution or population dynamics of the plant (Harper 1977, Crawley 1992). The importance of seed predators in determining the number of plants and the character of the vegetation needs to be evaluated. Forest fragmentation offers a chance to explore the nature of such animal-plant interactions, since the system is perturbed in different ways from large tracts of forest.

Black Bean *Castanospermum australe* is a large-seeded species which occurs in subtropical and tropical rainforest of Australia. This chapter investigates its post-dispersal seed predation and survival rates in five fragments of forest, to determine whether or not there is any evidence of differential predation and seedling establishment among sites. There are several factors which could influence the level of predation for a seed species in a forest fragment, and this chapter I will examine seed crop size and the number of nearest neighbours bearing fruit, timing of seedfall and types of predation, and the presence *C. australe's* seed predators. Other factors which could affect level of seed predation will be covered in subsequent chapters.

## 6.2 STUDY SITE AND SPECIES

### *Study site*

The study area is located in the north-east of New South Wales, in a region surrounding Lismore (28°49'S, 153°17'E). Mean annual rainfall is 1358mm, with 127 raindays per year. Rainfall is higher along the coast and on adjacent plateau areas such as Alstonville (1700mm) (Firth 1979), and in the north near the Nightcap Range. Average maximum monthly temperature ranges from 19.8-29.7°C during the year, and the minimum from 6.4-19.2°C.

The main feature of the region is the low basaltic plateau (100-200m altitude) which is part of the residual slopes of the Mt Warning shield volcano to the north. The subtropical rainforest which occurred mainly on the low basaltic plateau near Lismore is referred to as the Big Scrub (see Figure 3.1). This rainforest has been estimated to have exceeded 75 000 ha (Floyd 1990b, Holmes 1987), forming one of the largest continuous expanses of rainforest in Australia. Clearing has reduced the area to approximately 556 ha (0.74%), much of this as remnants of forest less than 5 ha (Lott & Duggin 1993).

There are four major floristic suballiances within the Big Scrub (Floyd 1990b), of which the *Argyrodendron* suballiances include *C. australe*. Five remnants of suballiance 5 (*Castanospermum-Dysoxylum*) were selected for study: Big Scrub F.R., Boomerang Falls, Johnston's Scrub, Wollongbar and Davis Scrub. These remnants span a range of sizes (1.7 to 148.2 ha of primary rainforest) (see Table 3.4) and within them, *C. australe* are relatively common. Sites were not replicated for size, owing to a lack of suitable replicates. All five remnants are located on kraznozom soils (Tertiary Lismore Basalt), however, the valleys of Big Scrub F.R. and Boomerang Falls include alluvium from the Nimbin rhyolite which occurs on the Nightcap Range (Holmes 1987). In these sites, study trees on the basaltic slopes were selected.

### *Castanospermum australe*

*Castanospermum australe* is widespread in subtropical and tropical rainforests from Bellingen in New South Wales, northward to Atherton in North Queensland (Beadle & Beadle 1982). The trees are relatively abundant, and produce fruit in most years; thus demographic data are readily obtained. Flowering occurs from October-November. In northern NSW, ripe fruit falls between April and October of the following year. Pods dehisce from the terminal point, either releasing seeds from the tree, or more commonly, from the pod as it hits or lies on the ground. Seeds germinate during the rainy season following seedfall (December-April).

The pod is about 10-25 cm long and 4-5 cm broad (Boland *et al.* 1984), with a hard brown woody exocarp. Inside this is a spongy white mesocarp and a thin papery endocarp, within which rest 1-7 seeds (usually 1-4 seeds). Individual seed weights range between 17-93 g (Chapter 4). Although the seed is toxic to some eutherian mammals, it is known to be eaten by *Rattus fuscipes* and *Trichosurus caninus* and lepidopteran larvae (Chapter 5). The survival of *C. australe* is likely to be influenced by the presence of these seed predators, particularly mammals, in remnants, and the number of seeds which survive to germinate in the rainy season following the cessation of seedfall. The large woody pods are resistant to decay and when fresh, show a clear cavity where each seed has been produced. The seed cavities offer a unique opportunity to determine total seed crop size and coupled with the large seed size, allow an accurate determination of seed survival under the parent tree.

## 6.3 METHODS

### 6.3.1 Predation and survival of 1989 seed cohort

In 1989, three trees were selected at each site to span a range of apparent crop sizes, based on a binocular search of the number of pods in the crown of each tree. The range of seed crop sizes obtained was used to test whether this had an effect on seed predation rate. To avoid null data, trees which had no seed crop were rejected. Figure 3.5 indicates the location of the study plots and trees. Table 6.1 shows the trunk diameter (d.b.h), crown area and maximum % slope to the tree. For each tree, seedfall over time and the subsequent *in situ* fate of the seeds was determined. Seedfall commenced in April 1989, but the initial field trip was aborted owing to floods restricting access. Seeds and pods were counted and marked at 3-4 week intervals between May-October 1989, then checked at longer intervals through 1990-1994 (Table 6.2). The three trees at each site were usually visited on the same day. The order of visitation to the sites was determined using a latin square design.

At each visit, I recorded (1) new seedfall since the previous visit to the tree, and (2) the survival of seeds and pods marked on the previous visits. The newly fallen ('fresh') pods and individual seeds beneath the trees were marked with paint, using a different colour to identify each sampling interval. Only those seeds and pods which fell within the area of the crown of the parent tree were recorded. Subsequently, the occasional marked seed was found outside the crown area, by searching a 5-10m radius beyond the tree's crown.

For empty (dehisced) freshly fallen pods, the number of seed cavities was recorded. To avoid confusion with later samples, these pods were paint-marked in a different manner to undehisced pods. Loose, intact seeds were marked with a small paint spot on either side of the hilum, and with an additional spot on the underside of the seed, if conditions were fine enough to allow the paint to dry. The hilum is the most resistant part of the testa, and observations indicated that it would usually remain intact if separated from the seed. Seed content of fresh undehisced pods (including partly-dehisced pods) was estimated from the undulations on the pod exterior, and corrected at a later sampling date when the pod dehisced. Where possible, seeds exposed by a partly dehisced pod were also colour-marked. A small, numbered metal tag was placed in the ground adjacent to each undehisced pod or individual seed, to allow determination of seed fate on subsequent visits. Few pods disappeared from the site during the year and no additional unmarked pods were detected in later visits to the sites (December 1989/January 1990).

To determine seed fate, presence or absence of the individual pods and seeds, and their condition (intact or damaged *in situ*) was recorded at each visit. External damage to open, split or undehisced pods was noted. Seeds classed as damaged *in situ* included seeds with tooth marks only, and those paint-marked testas which were found peeled by animals and minus the seed. Consistent identification of the cause of seed damage proved difficult owing to time limitations and the heavy rain which occurred during several field trips. However, the type of damage was recorded opportunistically for 25-62% of those seeds damaged *in situ*. For these, evidence of damage from impact (after falling), decay or fungal attack, and whether the predator was vertebrate or insect was recorded. Two patterns of vertebrate damage were observed (Chapter 5). Sufficient notes were made to estimate the proportion of 'broad-toothed' (*T. caninus*) and rodent damage *in situ* at each site.

Those seeds surviving intact at the end of the fruiting season (October) were available for germination in spring/summer. The fate of these was followed to determine the number of seeds which germinated, and subsequent seedling survival. Once the stem was large enough, seedlings were tagged with a numbered metal tag. Seeds and seedlings from previous years were identifiable and distinguishable from the current cohort by colour, condition and size.

Data were used to calculate both the absolute number and proportion of seeds missing, surviving intact during seed fall, and damaged *in situ*. Absolute number of seeds damaged or removed is dependent on the density of predators (and alternative food sources available), as well as (limits imposed by) the seed crop size available. It is only a measure of between-site variation in seed consumption where comparable seed crops are available across sites. The choice of trees with a range of crop sizes was an attempt to control for this variation. The proportion of seeds damaged or removed is an indication of the predators' response to seed crop size, and is a measure of the probability of seed escape from predation.

Chi-squared analysis was used to compare sites for cumulative seed removal and seed predation *in situ* at the end of the fruiting season (October). Sites were also compared for seed removal over time relative to the total number of seeds which fell in that time period, and for subsequent seed germination and seedling survival. Mid-season, tagged seeds at two trees at Davis Scrub were vandalised: a subset was salvaged and studied at tree 1, and later seedfall was monitored at tree 3. At the end of summer, all seedlings produced from the 1989 cohort were counted at these trees. This gave an estimate of final seed survival, and allowed some retrospective estimation of seed survival.

### **6.3.2 Insect damage to seeds**

Insect attack of freshly fallen seeds appeared to be very low during the period April-October 1989. To verify this, levels of insect attack were determined for a sample of seeds in fresh undehisced pods, collected from the ground at four sites in 1990 (Big Scrub F.R., Boomerang Falls F.R., Davis Scrub, Wollongbar) and five sites in 1991. Pods were opened and the seeds inspected for signs of insect damage and decay. At the same time, a sample of fresh seeds which were lying loose on the ground (and therefore exposed to predators) was also collected and inspected for insect damage. Insects found in the seeds and pods were collected and preserved for identification (Appendix 1), but types of insect damage were not quantified.

### **6.3.3 Comparison between years: crop size and seed loss from 1990 and 1991 cohort**

In 1990 and 1991, the same trees were assessed for total seed crop size (but not timing of seed fall). Intact seeds were also counted, to give a one-off estimate of seed survival rate relative to seed production. Additional trees were studied at the control site, Big Scrub Flora Reserve and at Davis Scrub, to verify that the levels of predation observed in 1989 occurred throughout the remnant. Under each tree, all pods were collected, counted and the number of seeds they had held recorded. Pods from the previous year's cohort were discarded, based on prior observations of colour and texture of the woody outer and spongy mesocarp during the aging process (spongy mesocarp has generally disappeared by the following year). In 1990, seed survival was sampled in July. Trees were visited again in September, and subsequent seedfall was added to the estimate of seed crop size. Seed removal was not re-assessed. In 1991, trees were visited only in September. As before, the total number of pods, their seed content, and the number of intact seeds remaining was determined. Trees, sites and years were compared for seed crop size and the percentage of seed survival.

### **6.3.4 Fruiting status of nearest neighbours**

Neighbouring conspecific trees >30 cm diameter (dbh) within 20m of the study trees were assessed for presence or absence of a fruit crop in 1990 and 1991 (Table 4.2). These data allowed a test of the relationship between level of seed predation, and local abundance of neighbours with fruit.

**Table 6.1** Study tree statistics: Diameter at breast height (dbh), relative crown area and maximum % slope below the tree (measured at 10m distance).

Site and tree No.	dbh (cm)	Crown diameter (m)	Rel. crown area (m <sup>2</sup> ) (L x W)	% slope
<b>BIG SCRUB</b>				
1	120,54.3	7.0,12.3	86.1	19
2	113.5	13.6,12.6	172.3	17
6	52.8	10.8,7.7	83.4	19
<b>BOOMERANG</b>				
1	103	12.8,11.8	151.8	21
2	71,12.5,11.8	10.4,10.8	112.5	10
3	78.7	12.4,9.3	115.0	12
<b>JOHNSTON'S</b>				
1	112	11.8,15.1	178.7	28
2	61	6.1,10.5	64.2	35
3	163	14.6,11.6	170.2	19
<b>WOLLONGBAR</b>				
1	65.7	11.1,8.5	95.0	10
2	39	7.3,7.2	52.4	1
3	57	11.4,9.4	106.5	1.5
<b>DAVIS</b>				
1	144.5	8.1,8.4	68.7	7
2	81.3	9.5,6.9	65.8	1.5
3	89.8	9.7,12.5	121.2	10

dbh: some trees had more than one stem

**Table 6.2** Sample dates during study of 1989 seed cohort

Sample No.	Dates	Comments
1	6-15 May	all sites
2	25-28 May	all sites
3	7-13 June	all sites
4	25 June-2 July	all sites
5	17-22 July	all sites
6	17-20 August	all sites
7	8-11 September	seedfall only at Davis
8	19-25 October	all sites except Davis
8	4-7 December	Davis tree 2 only
9	23 Dec-2 Jan 1990	Johnst, Boom, Woll, Davis, no seeds surviving at BS
10	16 April-15 May	Johnst, Boom, Woll, Davis tree 1,3
11	23 July	Woll, Davis
12	17 Sept	Woll, Davis
13	22-23 Dec	Woll, Davis, Boom tree 3
14	18 Apr 1991	Woll, Davis
15	11 Sept-19 Oct	Woll, Davis
16	6-16 Jan 1992	Woll, Davis
17	18-22 Jul 1994	Woll, Davis

## 6.4 RESULTS

### 6.4.1 1989 seed cohort

#### *Seed fate*

Survival of seeds differed dramatically among sites (Table 6.3, Figure 6.1). Higher levels of seed loss and low-to-absent seedling establishment occurred under study trees at Big Scrub F.R. (148ha), Boomerang Falls (62ha) and Johnston's Scrub (21ha). By the end of the rainy season in April 1990, no seeds survived under the crown of the parent trees at the two largest sites. A small number survived at the 21 ha site, and large numbers and proportions survived at the two smaller sites (Wollongbar 2ha and Davis Scrub 11ha). Many of the seeds remaining at the two smaller sites germinated, and survival remained high until July 1994, at the termination of field study.

**Table 6.3** Seed crop size, and seedling survival over time for *C. australe* seeds produced in 1989

SITE	Tree number	No. seeds produced Apr-Sept 1989	% remaining:			
			Oct 1989 (seeds)	Apr 1990 (seeds/seedlings)	Apr 1991 (seedlings)	July 1994 (seedlings)
Big Scrub 148 ha	1	133	0	0	0	0
	2	278	0	0	0	0
	6	930	0	0	0	0
Boomerang 62 ha	1	980	20.5	0	0	0
	2	557	44.7	0	0	0
	3	755	49.1	0.1(1g)	0	0
Johnstons 21 ha	1	358	11.7	1.7(6g,5*)	≤0.6	0
	2	364	4.1	0	0	0
	3	276	19.9	0.4(1g*)	0	0
Davis # 11 ha	1	806	62.1	40.2	23.9	15.2
	2	268	92.5	62.3	27.2	15.3
	3	1404 est.	55.7	32.9	12.7	7.4
Wollongbar # 2 ha	1	905	55.7	52.9	26.5	10.2
	2	155	46.5	35.5	25.8	12.9
	3	633	63.5	34.8	16.9	10.7

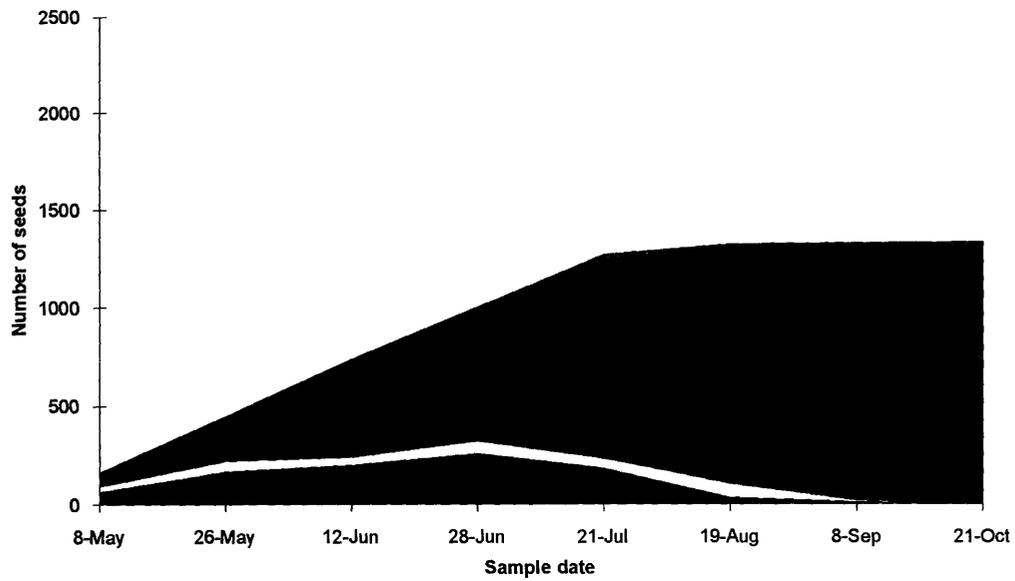
g Number of seeds germinated; \* seed germinated with stunted roots inside pod, or seedling weak. Bold type indicates estimate is based on seedling survival for half the canopy, corrected for original number of seedlings under whole canopy in April 1990.

# Mean survival July 1994: Davis 12.6% (std dev. 4.54), Wollongbar 11.3% (1.44); (students t test, T = -0.5, df=2, ns).

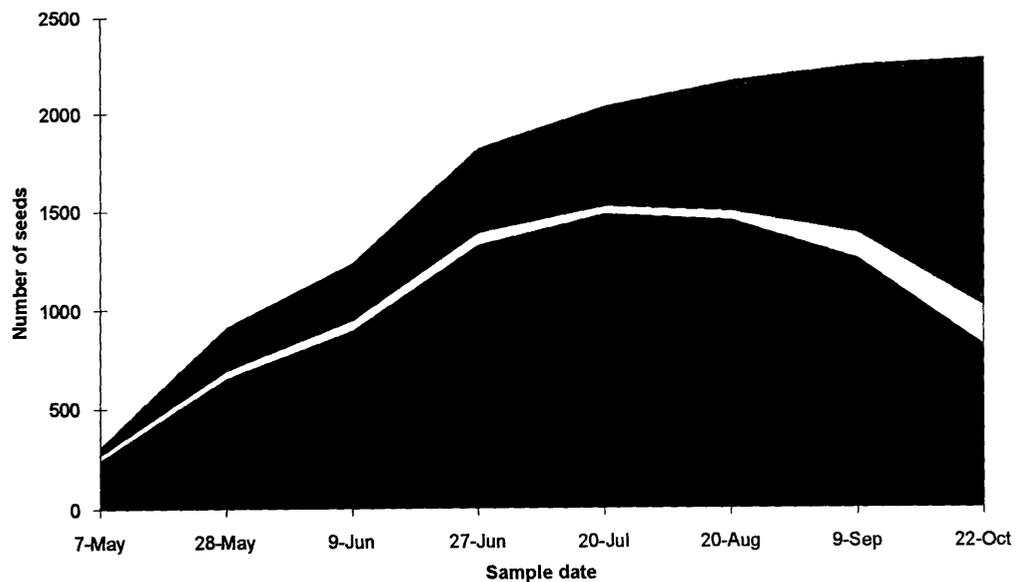
**Figure 6.1** Seed production over time and seed survival curves for the five sites in 1989.

(Black shading: intact seeds, white: seeds damaged *in situ*, grey: cumulative seeds missing. Upper line represents cumulative seed production for 3 trees at each site.)

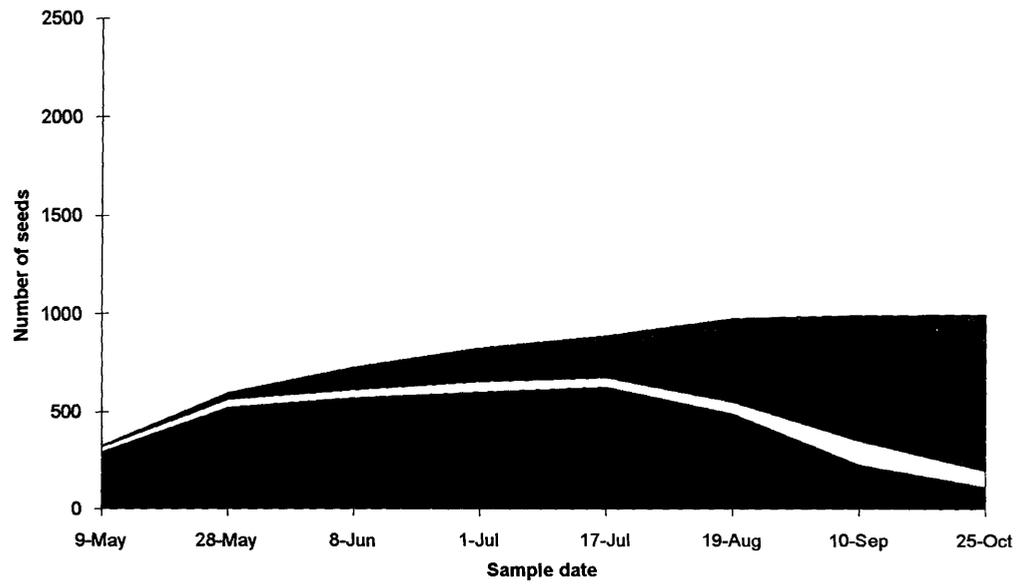
a) Big Scrub



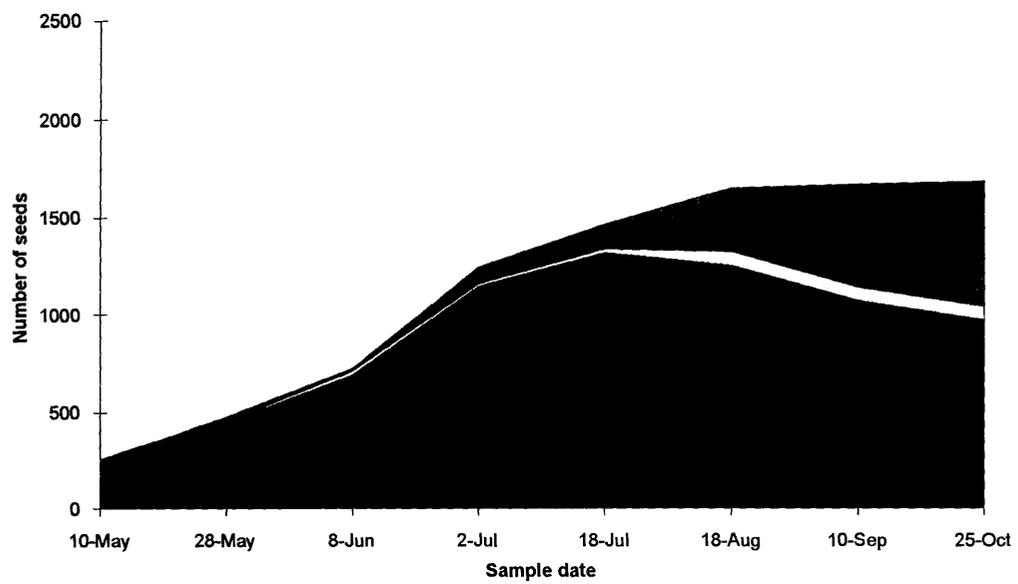
b) Boomerang Falls



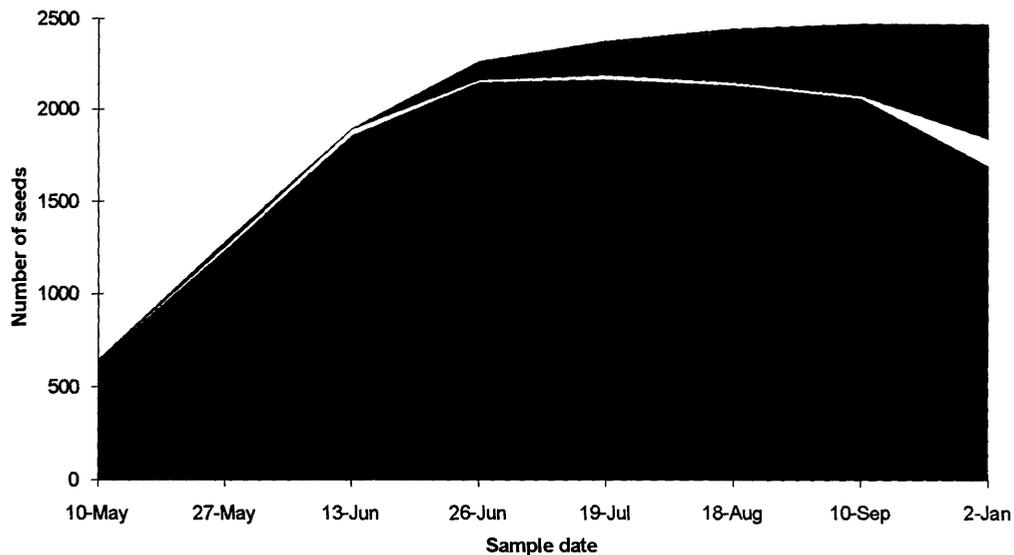
## c) Johnston's Scrub



## d) Wollongbar



## e) Davis Scrub



Individual trees varied in the distribution of general seed fates (intact, damaged *in situ*, missing) during the fruiting season (Table 6.4). However, broad trends were consistent within sites. A large number and proportion of seeds were missing at Big Scrub, while the majority of the remainder were damaged *in situ* by vertebrates. Missing seeds were probably removed largely by vertebrates and the passage of water downslope. Removal by water would have applied mainly to loose single seeds, as observation indicated that the heavy pods did not move far within the 3-4 week sampling intervals, and most were retrieved within the area searched. The number and proportion of seeds missing at Boomerang Falls and Johnston's Scrub was significantly lower than at Big Scrub ( $\chi^2=487.1$ ,  $\chi^2=315.1$  respectively,  $df=1$ ,  $p<0.05$ ), despite sometimes greater slopes, indicating that water removal did not explain at least 34% of the seed removal at Big Scrub.

In October 1989, Boomerang Falls and Johnston's Scrub had a similar proportion of seeds missing ( $\chi^2=0.67$ ,  $df=1$ , ns), however *in situ* seed damage was lower at Boomerang Falls ( $\chi^2=160.2$ ,  $df=1$ ,  $p<0.01$ ). The slower proportional seed removal at Boomerang Falls was due to the much larger seed crop, rather than a smaller number of seeds eaten - the absolute number of seeds damaged *in situ* at Boomerang Falls was the largest of any site, and the number of seeds missing was also large. Seed removal obviously continued after fruit fall ceased at Boomerang Falls, since both sites had similar numbers surviving in April 1990. The proportion of seed damage *in situ* per tree was variable at Johnston's Scrub. The higher seed survival at the two smaller sites is explained by a much lower proportion of seeds missing, and lower proportion of seeds damaged *in situ*. Most seeds stayed where

they fell below the trees. Some vertebrate predation occurred at Wollongbar, particularly at tree 1, which was adjacent to several houses that may have supported *T. caninus* among their fruit trees and compost heaps.

**Table 6.4** Cumulative fate of seeds underneath each parent tree in October 1989

SITE	Tree No.	% of seeds damaged <i>in situ</i>	% intact	% missing	Number of seeds produced Apr-Oct
Big Scrub F.R.	1	16.5	0	83.5	133
	2	39.9	0	60.1	278
	3	21.3	0	78.7	930
mean		25.9 (12.4)	0	74.1 (12.4)	447 (424.5)
Boomerang Falls	1	30.1	20.5	49.4	980
	2	22.8	44.7	32.5	557
	3	25.4	49.1	25.4	755
mean		26.1 (3.7)	38.1 (15.4)	35.8 (12.3)	764 (211.6)
Johnstons Scrub	1	56.7	11.7	32.4	358
	2	61.3	4.1	34.6	364
	3	26.4	19.9	53.6	276
mean		48.1(19.0)	11.9 (7.9)	40.2 (11.7)	332.7 (49.2)
Wollongbar	1	16.7	55.7	27.6	905
	2	23.9	46.5	29.7	155
	3	13.6	63.5	22.9	633
mean		18.1(5.3)	55.2 (8.5)	26.7 (3.5)	564.3 (379.7)
Davis Scrub	1	10.3	62.1*	27.6	806
	2	5.2	92.5	2.2	268
	3	7.0*	85.7	7.3	1404*
mean		7.5 (2.6)	80.1 (16.0)	12.3 (13.4)	826.0 (568.3)

\* estimate of fate is based on subsample

Values in parenthesis are standard deviations

### *Types of seed damage*

Table 6.5 indicates types of seed damage (insect, vertebrate, fungal, impact damage) observed in 1989. A small proportion (0.09%) of seeds were abnormal. These were classed as intact unless damaged subsequently. Some seeds were damaged by impact with the ground or other pods. This produced linear scars on the seed or forcibly separated the cotyledons. Impact damage was higher where the seeds were released from the pod at dispersal. Qualitative data from the 1989 cohort indicated that impact-damaged seeds were sometimes eaten, but otherwise were prone to fungal attack. In undamaged seeds, early stages of fungal attack did not preclude predation by insects or vertebrates, although this was rarely noted. Conversely, fungal attack was often recorded simultaneously, or subsequent to insect and especially vertebrate damage. Prior insect or vertebrate attack did not preclude subsequent vertebrate predation. Types of insect damage were not distinguished, but presumably a sequence of damage by different insect species occurred as the seed aged and decayed. Some seeds initiated germination despite previous damage, and some seeds were eaten after early radicle extension.

### Mammal predation

The proportion of seeds damaged *in situ* by mammals was greatest at Big Scrub > Johnston's = Boomerang > Wollongbar > Davis ( $X^2$  analysis,  $df=1$ ,  $p<0.05$ ). Seed production was larger at Boomerang Falls than at Johnston's, and although greater absolute numbers were eaten at Boomerang, this resulting in a similar proportion of seeds damaged by mammals. The site-ranking for predation by broad-toothed predators (*T. caninus*) was the same as that for mammals in general, except that Boomerang Falls showed a slightly higher number and proportion of seeds damaged than Johnston's ( $X^2=0.4$ ,  $df=1$ , not significant). The proportion of seeds damaged by broad-toothed mammalian predators was approximately 30% at both Boomerang Falls and Johnston's Scrub (Table 6.5) (probably higher at Boomerang if unspecified vertebrates are included in the dominant category) ( $X^2=0.43$ ,  $df=1$ , ns), however predation by rodents and insects was higher at Johnston's Scrub ( $X^2=24.3$ ,  $9.2$ , respectively;  $df=1$ ,  $p<0.05$ ). Most of the predation at Wollongbar was by *T. caninus*, and commenced in late May.

Rodent predation was <22% of seeds damaged *in situ* and was variable among sites. Rodent damage to seeds *in situ* did not differ between Big Scrub and Boomerang Falls ( $X^2=0.36$ ,  $df=1$ ). As calculated in Table 6.5, percentage predation by rodents at Wollongbar and Davis is an overestimate. This is because seeds damaged by rodents were rare, and were recorded especially. Therefore the six seeds damaged across the three trees

at Wollongbar represent total rodent predation for this site. Similarly, the seeds damaged by vertebrates at Davis represent total predation of their kind (3 seeds 'broad-toothed vertebrate', 2 rodent, 6 unspecified vertebrate). Nine of the 11 seeds damaged by vertebrates at Davis Scrub were obviously eaten subsequent to decay or attack by fungal pathogens.

### Insect damage

Of seeds damaged *in situ* in 1989, levels of insect attack ranged from 3-65% per site by October. Observed insect attack was lowest at Boomerang = Big Scrub <Johnston's <Wollongbar <Davis ( $\chi^2$  analysis,  $df=1$ ,  $p<0.05$ ). Insect attack was inversely proportional to damage by vertebrates (Figure 6.2). Analysis of seeds collected in 1990 and 1991 indicated that level of insect attack was low in recently dispersed mature seeds. Seeds which had lain on the ground during the fruiting season also showed less than 12% insect damage, although these data were confounded by the presence of some vertebrate damage. Whether vertebrate damage masked existing levels of insect attack, or lowered it at the larger sites is not known. However it appears that insect attack increases during the fruiting season, where seed survival is high.

### Other

Seeds at all sites were attacked by fungal pathogens. Higher levels of total fungal attack were evident at the three sites with intermediate vertebrate damage and seed survival (Boomerang Falls, Johnston's Scrub, Wollongbar), although proportions were not always significantly different from Davis. Of these sites, Boomerang Falls had significantly higher proportions of seed with damage by fungal pathogens without prior damage by other means ( $\chi^2>9.1$ ,  $df=1$ ,  $p<0.01$ ). Although fungal attack was low at Davis Scrub during the fruiting season, observation during December-January indicated that subsequently, many seeds at Davis Scrub decayed due to fungal attack and damping off.

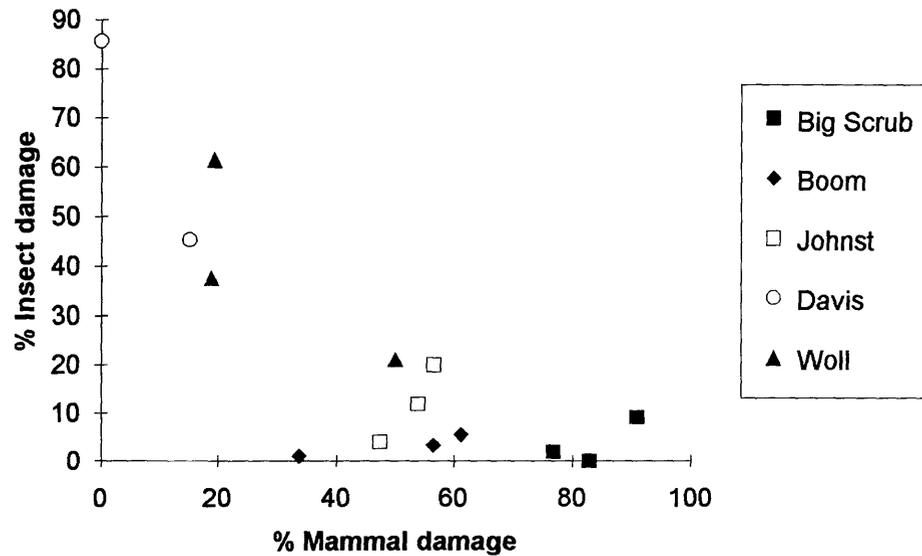
Seed damage from other sources represented only a small number and proportion of the seed crops, and there were no discernible differences among sites ( $\chi^2= 17.5$ ,  $df=4$ , ns; Table 6.5). Some interactions between damage types may have been responsible for secondary attack and resultant seed loss at some sites.

**Table 6.5** Proportion of seeds (expressed as percent of sample) with different types of damage, based on a sample of seeds damaged *in situ* for the 1989 cohort.\* (+/-v, with or without vertebrate damage; +/-d, with or without other damage; impact = seeds bruised or split from hitting the ground after seed release).

	broad tooth	rodent	unspec. vertebrate	insect		decay/ fungal		impact	<i>n</i>
				-v	+v	-d	+d		
BS	81.8	0	9.1	0	9.1	0	45.5	0	11
	35.7	7.1	39.3	1.8	0	17.9	25.0	7.1	56
	49.5	7.5	26.9	0	0	9.7	12.9	9.7	93
-----									
mean	55.7	4.9	25.1	0.6	3.0	9.2	27.8	5.6	
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Boom	30.6	12.0	18.5	5.6	0	29.6	13.0	6.5	108
	35.5	9.7	11.3	3.2	0	32.3	16.1	11.3	62
	23.8	4.0	6.9	1.0	0	58.4	6.9	10.9	101
-----									
mean	30.0	8.6	12.2	3.3	0	40.1	12.0	9.6	
-----									
Johnst	25.5	27.5	2.0	7.8	3.9	36.3	16.7	11.8	102
	22.4	28.9	0	3.9	0	43.4	19.7	6.6	76
	40.0	6.7	10.0	16.7	3.3	6.7	3.3	30.0	30
-----									
mean	29.3	21.0	4.0	9.5	2.4	28.8	13.2	16.1	
-----									
Woll	34.2	13.2	0	15.8	5.3	28.9	13.2	7.9	38
	12.5	0	6.2	25.0	18.7	37.5	25.0	25.0	16
	16.1	3.2	0	61.3	0	19.4	25.8	0	31
-----									
mean	20.9	5.5	2.1	34.0	8.0	28.6	21.3	11.0	
-----									
Davis	4.1	2.7	8.2	41.1	4.1	27.4	23.3	26.0	73
	0	0	0	85.7	0	4.8	9.5	14.3	21
-----									
mean	2.0	1.3	4.1	63.4	2.0	16.1	16.4	20.1	

\* percentages do not add to 100 since categories are not mutually exclusive

Data was only available for two trees at Davis Scrub, due to human interference with tagged seeds.

**Figure 6.2** Relationship between insect and vertebrate damage *in situ* (1989 cohort).

Proportions calculated as percentage of sample of seeds damaged *in situ*. Sample sizes indicated in Table 6.5. (Regression:  $y=59.03-0.78x$ ,  $R^2=0.65$ ,  $p<0.001$ )

### *Patterns of seed removal*

Except for Johnston's Scrub, seedfall peaked near mid June. At Johnston's Scrub, seedfall peaked early in the season, with a leptokurtic distribution of production. The timing of seed removal (*in situ* damage + missing) differed among sites (Figure 6.3). Highest removal occurred late in the fruiting season for the three smallest sites, but removal was fairly even throughout the season at Boomerang. At Big Scrub, removal closely matched seed release from the trees (Figure 6.3a). Within trees and sites, the slope of the survival curve for each seed sample was remarkably similar, indicating that the maturity of the seed had no influence on seed removal (Figure 6.4). Rather, the initial number of seeds released at each interval determined the survival time.

Seed removal comprises those seeds eaten *in situ* beneath the parent tree, and those missing. Although the fitted regression was not significant, the 1989 data show that number of seeds damaged *in situ* increased with seed crop size, particularly for the larger sites, Big Scrub and Boomerang Falls (Figure 6.5 a,b). The number of seeds missing (Figure 6.6),

also increased with seed crop size, and this was related to the number of seeds damaged *in situ* (Figure 6.7). However trees were selected to span a range of seed crops at each site (with less success at Johnston's). Analysis of covariance with seed crop size as the covariate indicated that site had the predominant effect on seed removal rate, and seed crop size did not explain a significant proportion of the variation in seed removal. There was no relationship between remnant area, and the numbers of seeds damaged *in situ* (Figure 6.8) or removed.

#### **6.4.2 Comparison between years: Crop size and seed removal rates**

Consistent with 1989, seeds collected from under the three study trees at each of the five sites in 1990 and 1991 (Tables 6.6, 6.7) showed that vertebrate damage was highest at Big Scrub, Boomerang Falls and Johnston's Scrub. Levels of vertebrate damage at Wollongbar and Davis were consistently lower. Levels of insect damage were too low to identify any differences among the five sites.

Samples from four occasions between 1989-1991 showed annual variation in seed removal levels, and differences between sites (Table 6.8). Across all sites, there was no relationship between tree size (dbh) and seed crop size (Table 6.1). Among sites, there was no clear relationship between total annual seed production (total for 3 trees) and total number of seeds removed, but within each site, the number of seeds removed tended to increase with total seed production.

Despite the year-to-year variation, proportional seed removal (loss) was consistently highest at Big Scrub. Seed loss at Boomerang Falls and Johnston's Scrub varied between years and seasonal stage (July or September). Compared with Boomerang Falls, loss was greater at Johnston's Scrub during the fruiting season in 1989 (but the sites subsequently equalized), but lower in 1990 and 1991. This corresponded with a switch in relative seed production (total crop for 3 trees) between the sites (Table 6.8). Seed removal occurred at a low level early in the season at Wollongbar, but increased later in the season. However, 1989 data indicated that seed removal remains low after seedfall ceases, so that seed survival and germination was still higher than at the larger sites. Seed loss at Davis Scrub remained low in all three years.

Whether proximity to the rainforest edge affected seed removal rates was tested at two sites. This was because the three trees selected for study at Big Scrub occurred within 72 m of the rainforest-eucalypt boundary, and those selected at Davis Scrub were all within 70-

80 m of the remnant's edge. Additional trees were selected at Big Scrub further downslope; these were assessed for seed crop size and seed loss in 1990 and 1991 and compared with four 'boundary' trees. The latter included the three main study trees. At Big Scrub, percentage seed loss at the 'boundary' trees (Table 6.9) was not significantly different from the additional 'interior' trees in 1990 and 1991 (students  $t=1.11$ ,  $df=7$ ;  $t=0.9$ ,  $df=4$ ). Seed loss at interior trees was variable, and the overall mean of all trees still indicated higher seed loss at Big Scrub than occurred at the other study sites. At Davis Scrub, seed loss was slightly lower at the three study trees than across the increased sample, but not significantly so (students  $t=0.91$ ,  $df=2$ ; Table 6.10).

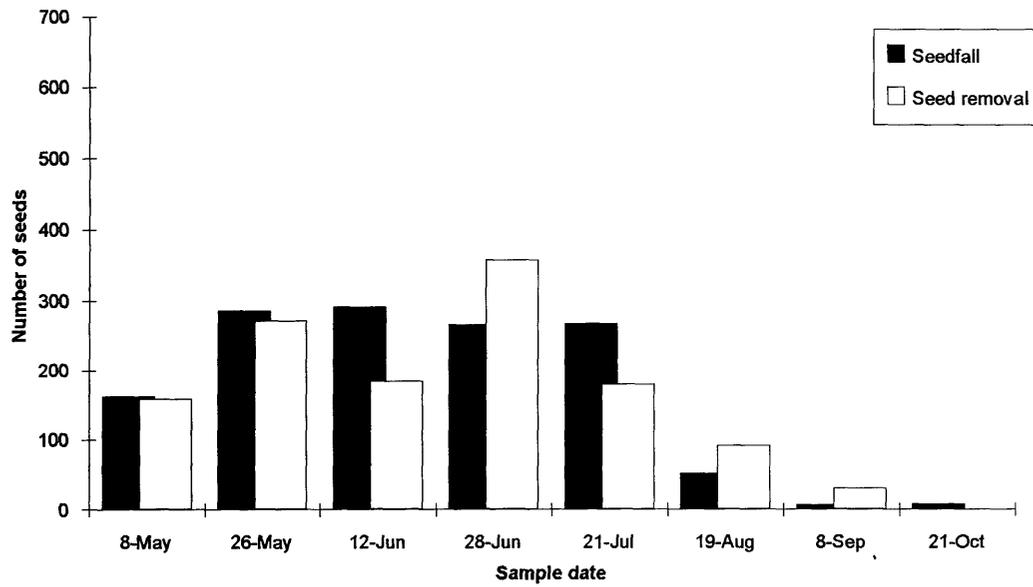
Determining the seed survival for crops in 1990 and 1991 also served to check whether seed predation from paint-marked seeds in 1989 was influenced by the paint. It is difficult to study seed predation at this scale without marking the seeds in some way. No trial was conducted to compare predation of marked and unmarked seeds in 1989 and it was possible that the paint deterred or attracted seed predators. There was some evidence early in the study that the paint was investigated: some seeds were found with incisor marks in the paint but the seed was otherwise untouched. Subsequently, these seeds were removed at the same rate as uninvestigated seeds, indicating that any effect lasted only until the paint dried. In addition, the estimates of seed survival in 1990 and 1991 seemed consistent with those in 1989, given the influence of other factors.

### **6.4.3 Fruiting status of nearest neighbours**

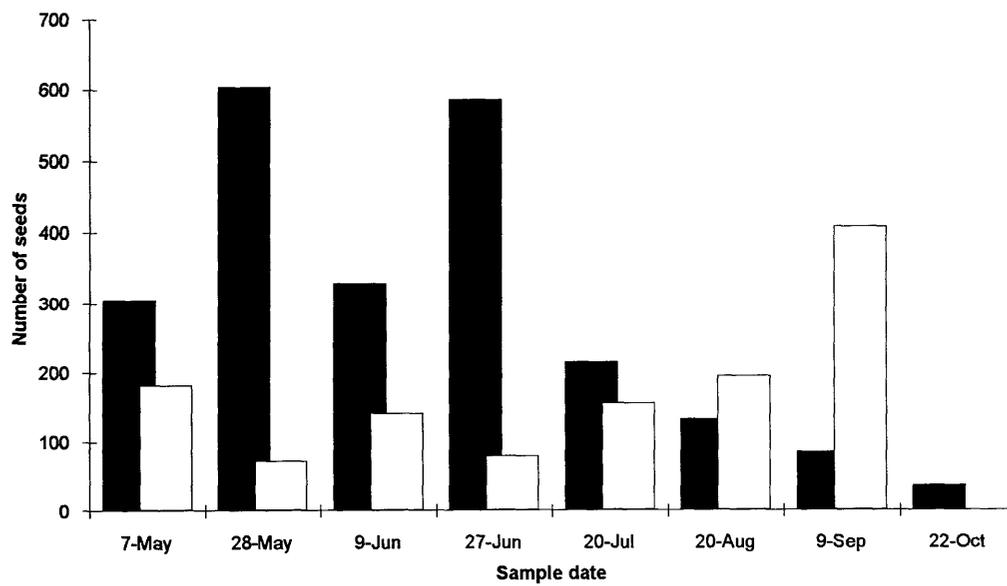
Analyses of covariance, with number or percentage of neighbours with fruit (Table 4.2) as the covariates, indicated that the covariates did not explain a significant proportion of the variation in seed removal. Rather, site had the predominant effect on seed removal in 1990 and 1991 ( $p<0.01$ ).

**Figure 6.3** Seed production and seed removal (missing plus damaged seeds) over time during 1989 for each of the sites. (n = 3 trees per site)

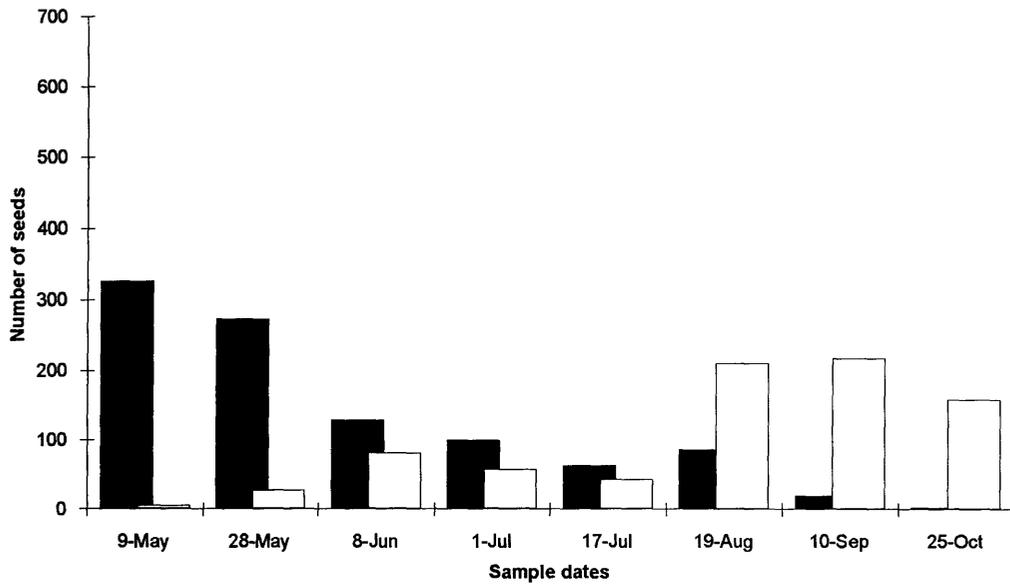
a) Big Scrub



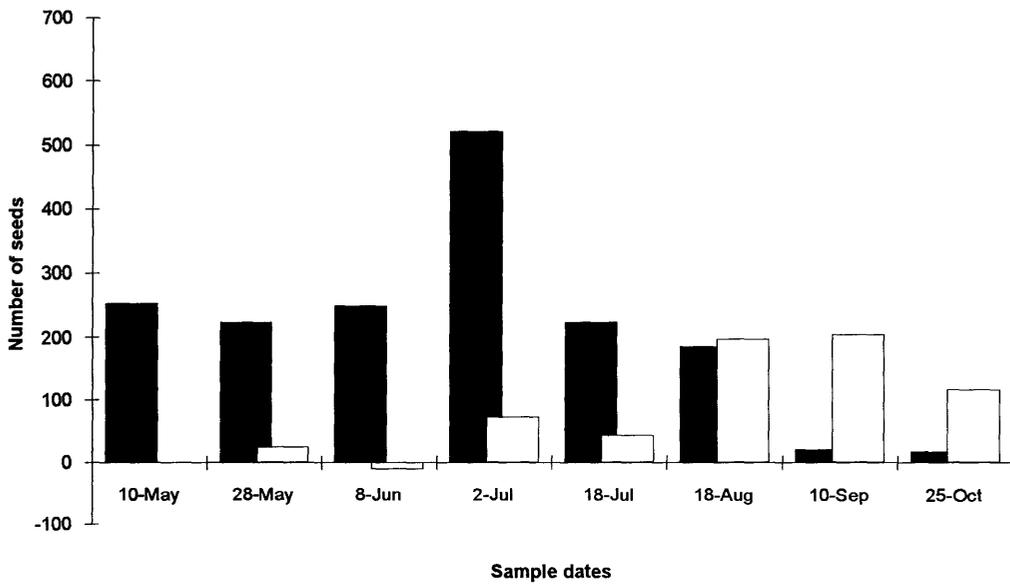
b) Boomerang Falls



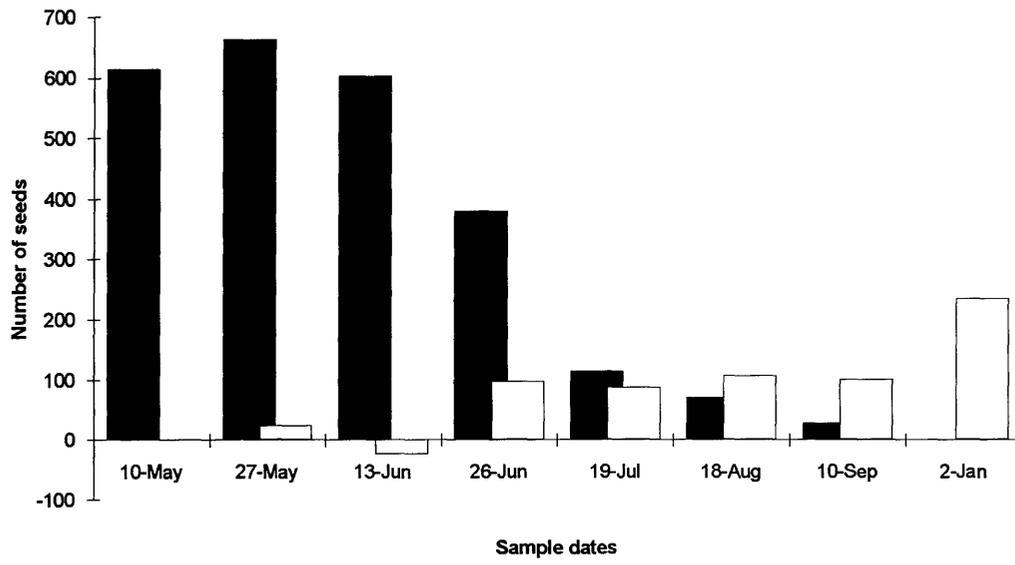
c) Johnston's Scrub



d) Wollongbar



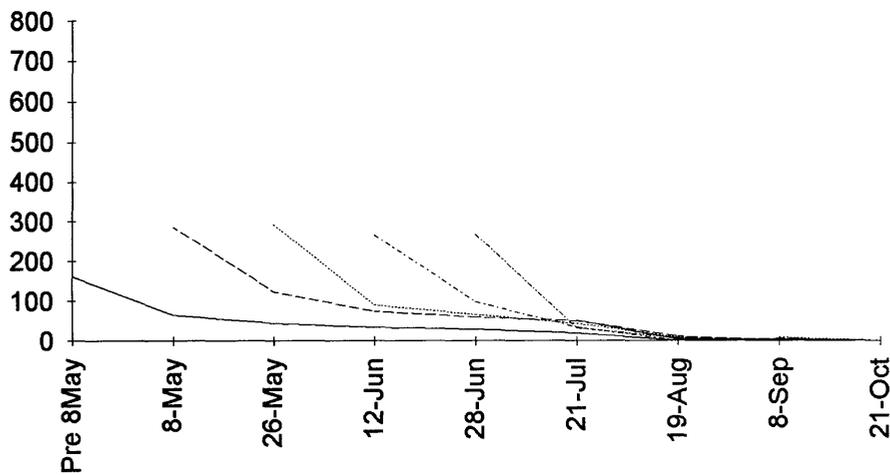
## e) Davis Scrub



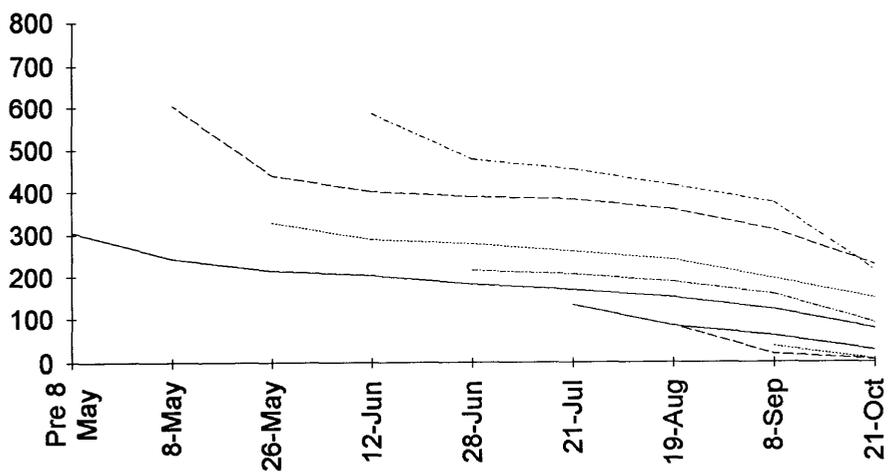
**Figure 6.4** Survival curves for seeds released at different times during seedfall.

(x axis: sample date, y axis: number of individuals. Initial number of seeds produced at each sample date is indicated by the starting point of each line. Data are pooled for 3 trees at each site)

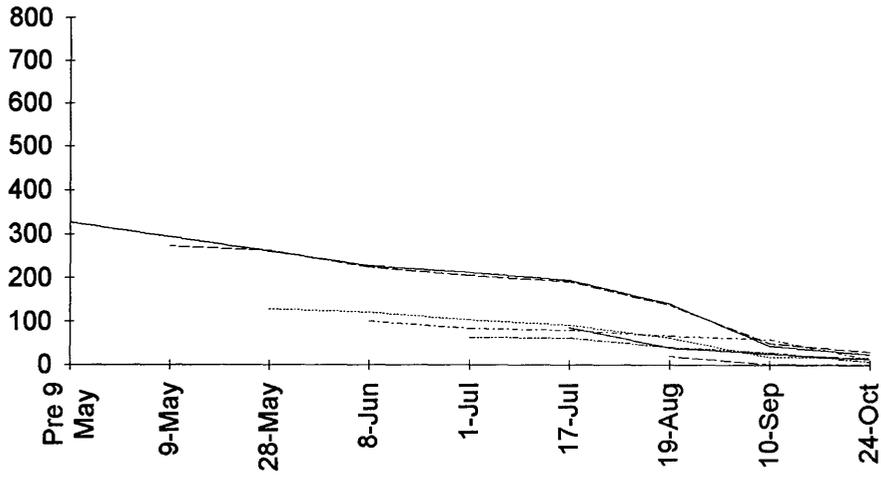
a) Big Scrub



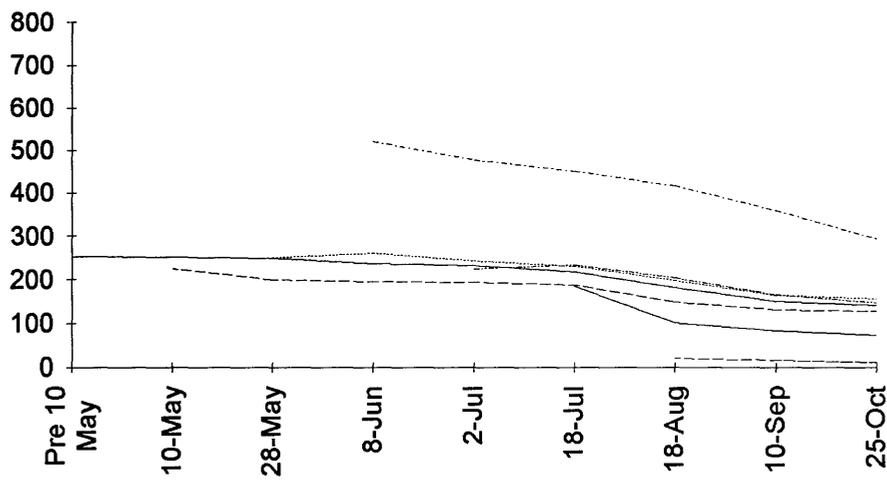
b) Boomerang Falls



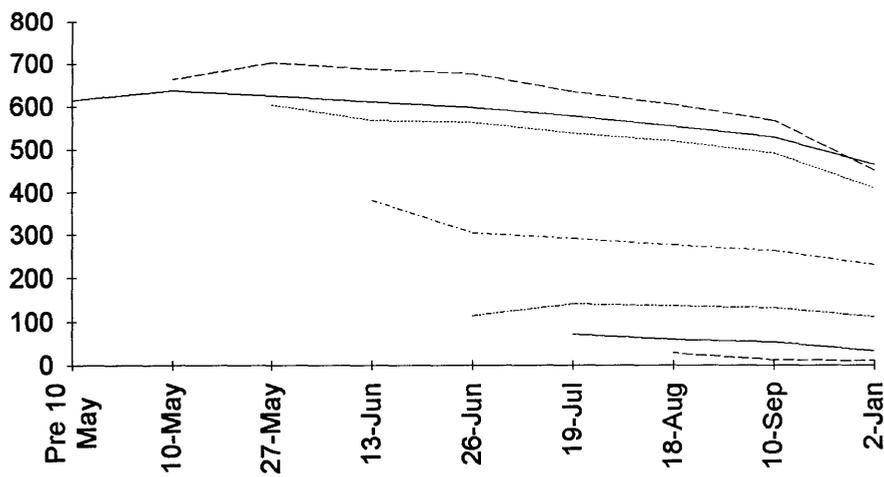
c) Johnston's Scrub



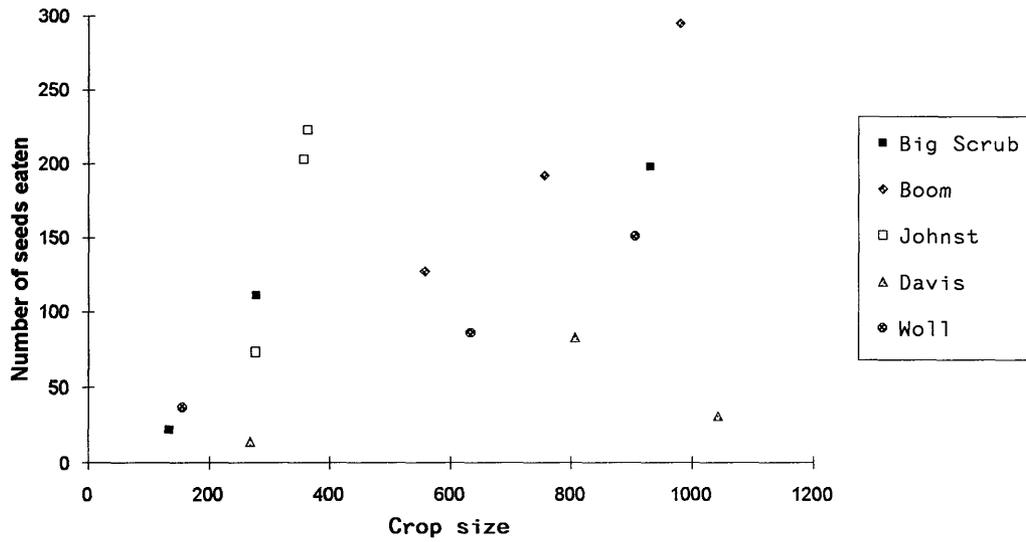
d) Wollongbar



e) Davis Scrub

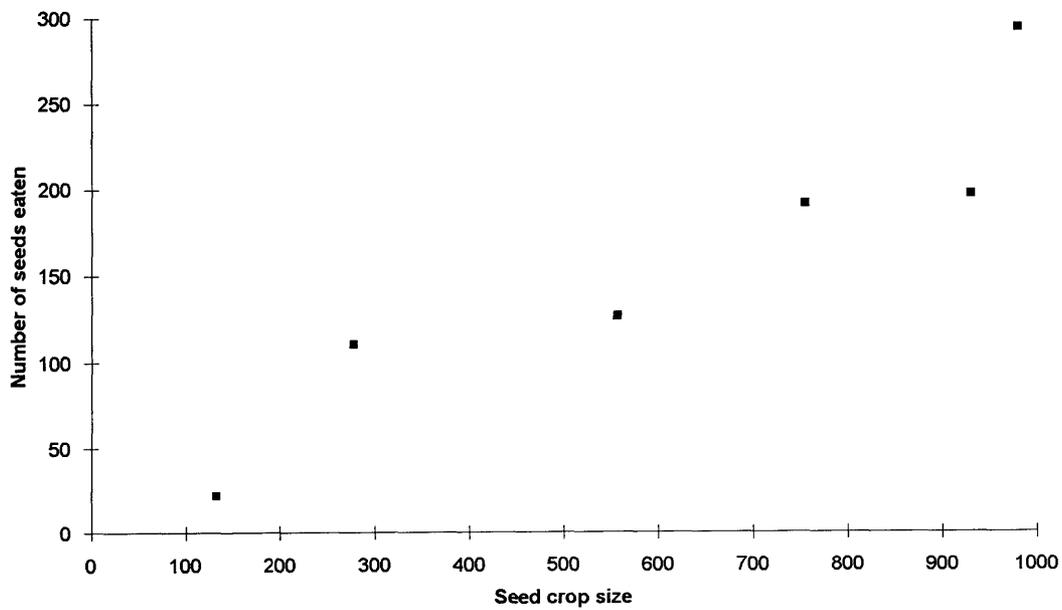


**Figure 6.5a** Number of seeds damaged *in situ* relative to seed crop size in 1989.

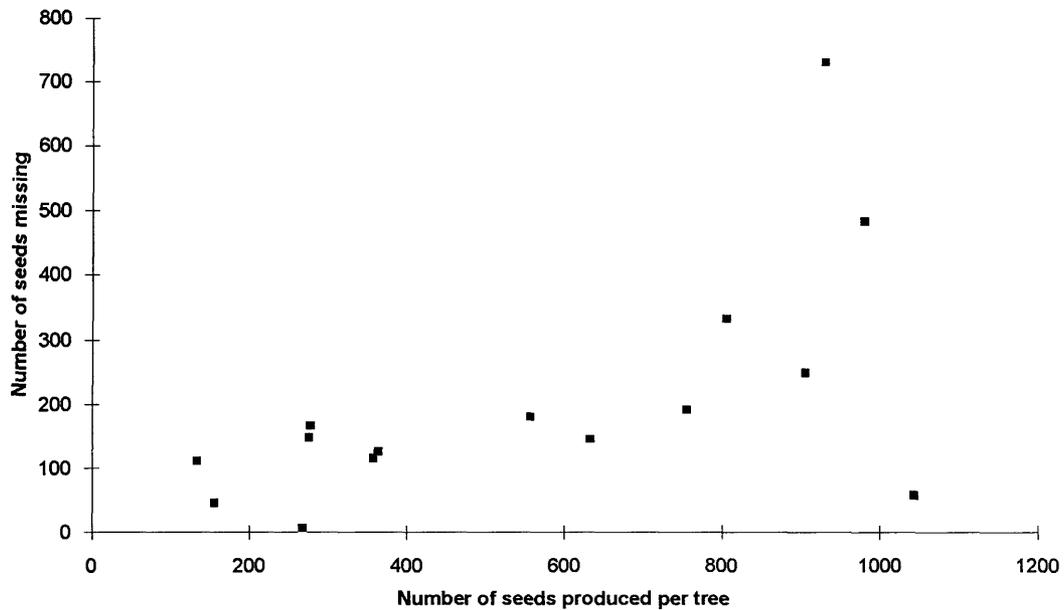


$(y=0.109x + 61.45, R^2=0.17, \text{ not significant } p<0.05)$

**Figure 6.5b** Relationship between seed crop size in 1989 and number of seeds damaged *in situ* for Big Scrub F.R and Boomerang Falls.

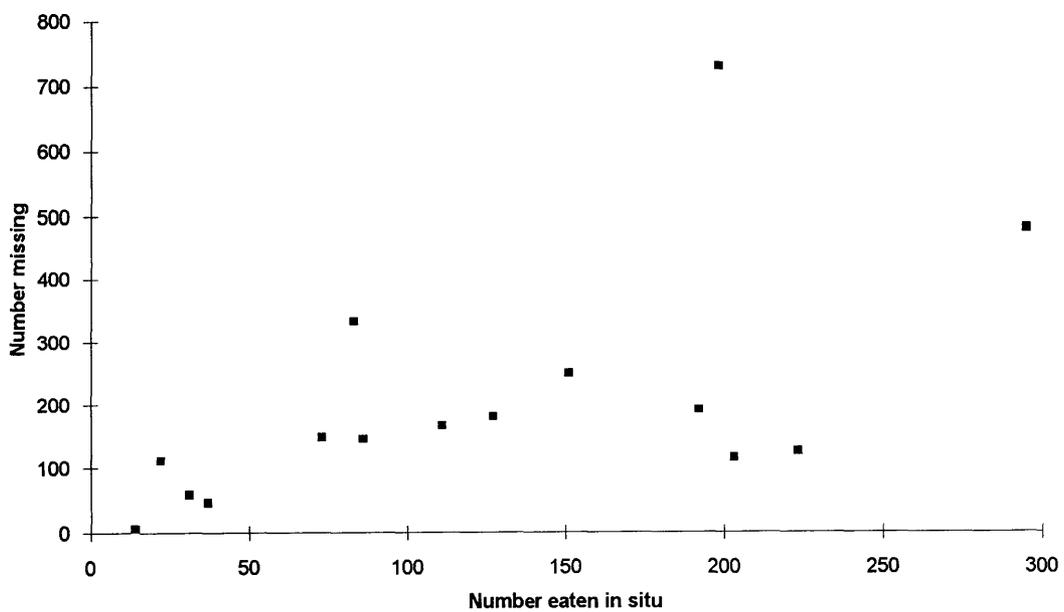


**Figure 6.6** Relationship between seed-crop size and number of seeds missing in October 1989 (all sites).

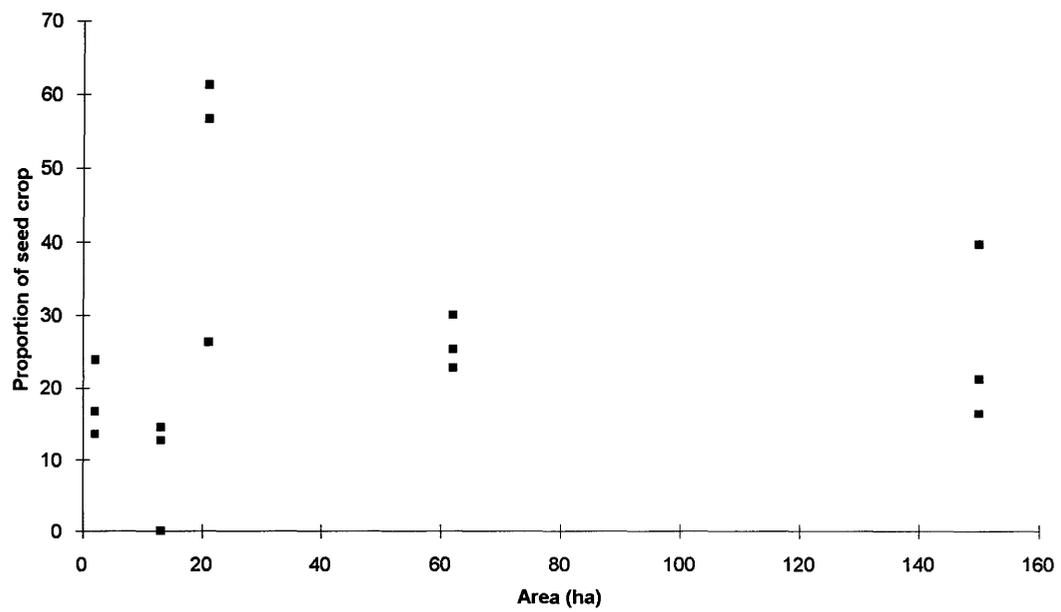


$$(y=0.35x + 9.317, R^2=0.36, p<0.02)$$

**Figure 6.7** Relationship between number of seeds damaged *in situ* and number missing per tree (October 1989, all sites).



$$(y=1.306x + 45.607, R^2=0.36, p<0.02)$$

**Figure 6.8** Proportion of seed crop damaged *in situ* as a function of area of remnant (1989)

**Table 6.6** Condition of seeds in fresh undehisced pods fallen beneath three trees per site in 1990 and 1991

## a) July 1990

	%	% Damaged					<i>n</i>
	Intact	insect	vertebrate	fungal/decay	impact	abnormal	
BS	88.8	3.3	1.0	2.6	0.7	3.6	304
Boom	97.2	0	0	0.8	0.4	1.6	247
Johnst	89.2	1.2	0	4.8	0	4.8	83
Woll	97.5	2.5	0	0	0	0	120
Davis	94.5	0.7	0	4.8	0	0	146

## b) September 1991

BS	86.4	9.0	2.3	2.3	0	0	44
Johnst	100	0	0	0	0	0	27
Davis	71.4	4.8	0	23.8	0	0	21

In 1991, only one fresh undehisced pod was found beneath the three study trees at each of Boomerang Falls and Wollongbar sites. Fresh loose seeds were assessed separately (see Table 6.7 below).

**Table 6.7** Condition of loose fresh seeds beneath three trees per site in 1990 and 1991.

## a) July 1990

	%	% Damaged					<i>n</i>
	Intact	insect	vertebrate	fungal/decay	impact	abnormal	
BS	63.6	2.6	27.9	0	4.5	1.3	154
Boom	72.3	0	26.5	0.6	0.6	0	155
Johnst	78.5	12.1	6.7	2.2	0	0.4	223
Woll	91.3	4.4	0	1.9	2.5	0	160
Davis	79.7	3.8	1.3	6.8	8.4	0	237

## b) September 1991

BS	60.0	3.3	23.1	10.2	2.9	0.4	480
Boom	69.7	3.0	21.2	6.1	6.1	0	33
Johnst	58.2	2.2	27.6	9.7	1.5	0.7	134
Woll	72.2	7.5	5.7	14.6	0	0	212
Davis	81.7	5.4	1.3	9.1	2.4	0	372

**Table 6.8** Proportional loss of seeds relative to seed crop size 1989-1991

Site and tree No.	July 1989		^Sept 1989		July 1990		Sept 1991	
	crop	% loss	crop	% loss	crop	%loss	crop	% loss
<b>BIG SCRUB</b>								
1	128	69.5	128	100	25	68.0	8	100
2	251	52.6	275	96.7	142	53.5	261	70.9
6	895	97.4	930	99.7	183	74.9	139	100
mean % loss		73.2		98.8		65.5		90.3
std. dev.		22.6		1.8		10.9		16.8
<b>BOOMERANG</b>								
1	901	34.5	965	49.4	316	72.2	17	58.8
2	512	22.5	550	40.4	144	53.5	20	45.0
3	625	20.0	741	39.5	379	64.6	30	73.3
mean % loss		25.7		43.1		63.4		59.1
std dev		7.7		5.5		9.4		14.17
<b>JOHNSTON'S</b>								
1	309	35.9	358	75.1	*824	13.9	18	61.1
2	361	27.4	364	89.6	22	45.5	18	33.3
3	221	23.5	274	63.1	719	19.3	141	46.8
mean % loss		28.9		75.9		25.9		47.1
std dev		6.3		13.3		17.25		13.89
<b>WOLLONGBAR</b>								
1	737	9.6	902	37.0	87	2.3	0	-
2	142	6.3	151	43.0	113	0	38	47.4
3	536	9.0	623	31.9	100	21	256	48.1
mean % loss		8.3		37.3		7.8		47.7
std dev		1.8		5.6		11.52		0.48
<b>DAVIS</b>								
1	776	6.7	806	27.3	*214	0	6	16.7
2	261	1.9	268	5.4	22	0	0	-
3	1342 <sup>#</sup>	7.3	1404 <sup>#</sup>	11.96	*322	2.4	0	-
mean % loss		5.3		14.9		0.8		5.6
std dev		3.0		11.2		1.39		-

<sup>^</sup>September 1989 values used in this table for comparison with 1991 results (October data used in Table 5.5 represent survival at termination of seed fall.)

<sup>#</sup>estimate based on incomplete sample

\*estimate based on sample of seeds beneath 1/2 or 1/4 crown

**Table 6.9** Seed crop size 1990-1991 and seed removal (July/September) at Big Scrub (Si denotes number of seeds intact)

Tree No.	July 1990			Sept 1991		
	crop	Si	% loss	crop	Si	% loss
1#	25	8	68.0	8	0	100
2#	142	66	53.5	261	76	70.9
4#	193	62	67.9	12	0	100
6#	183	46	74.9	139	0	100
3	8	3	62.5	3	1	66.7
5	96	41	57.3	33	11	66.7
7	*322	162	49.7	36	12	66.7
8	69	33	52.2	19	0	100
9	176	32	52.2	7	0	100
10	*279	148	46.95	275	67	75.6
2A				67	3	95.5
9A				25	0	100
9B				0		-
11				0		-
12				0		-
13				17	2	88.2
14				59	1	98.3
15				206	47	77.2
16				137	~5	
17				*45	3	93.3
18				*87	13	85.1
mean % loss			61.47	87.3		
std. dev.			11.52	13.66		

# trees near rainforest/eucalypt boundary

\* estimate based on sample of seeds beneath 1/2 or 1/4 crown

**Table 6.10** Seed crop size 1990-1991 and seed removal (July/September) per year at Davis Scrub (Si denotes number of seeds intact)

Tree No.	July 1990			Sept 1991		
	crop	Si	%loss	crop	Si	% loss
4#	*189	190	0	0		-
5#	11	11	0	0		-
5A#	14	11	21.1	-		
1	*120	126	0	6	5	16.7
2	22	22	0	0		-
3	*205	200	2.4	0		-
2A	15	15	0	0		-
6				55	52	5.5
7				0		-
8				2	2	0
9				7	6	14.3
10				16	10	37.5
11				0		-
12				21	24	0
13				29	26	10.3
14				3	3	0
16				13	16	0
17				42	37	11.9
18				132	122	7.6
mean % loss			3.4	7.98		
std dev			7.89	10.79		

# trees near edge of remnant

\* estimated based on sample of seeds beneath 1/2 or 1/4 crown

## 6.5 DISCUSSION

### 6.5.1 Relative importance of seed predators

Studies in other Australian vegetation types indicate that rates of pre-dispersal seed predation by insects are generally high, damaging 11-62% of ripe or developing seeds (Auld & Myerscough 1986, Anderson 1988, Auld 1991, Zammit & Westoby 1988, Vaughton 1990a; but see Anderson 1989). However this does not appear to be the case for ripe *C. australe* seeds, perhaps because of their alkaloid content. Rather, pre-dispersal predation evident at the time of seed maturation was very low ( $\leq 3.3$  percent).

Post-dispersal, the seeds predators of *C. australe* include lepidopteran larvae, and two or three species of mammal (*T. caninus*, *R. fuscipes* and possibly *M. cervinipes*; Chapter 5). Thus there are two kinds of predators - short lived and possibly synchronized with the phenology of the plant (insects), and longer-lived polyphagous feeders that take seeds during the season of abundance and eat other foods in other seasons or places (*sensu* Harper 1977). In the three larger remnants, vertebrates were the major seed predators, and a large proportion of the seed crop was removed, both as seeds damaged *in situ* (26-48%) and missing (36-74%) over the 6-12 months from commencement of fruitfall. At the largest site (Big Scrub F.R.), the quantity of seed removal matched seedfall, which suggests that missing seeds were predominantly removed by seed predators, rather than overland water flow after rain.

At the small sites, vertebrate predation was much lower and damage by insects increased over time, particularly in seeds which had aged and decayed (pers. obs). This trend was probably merely a function of increased insect visibility over time. Contributing factors could be that seeds lose their chemical protection over time, or that insect predators take some time to respond to seed availability. However, these hypotheses require testing. It is also possible that the populations of invertebrates have increased in the absence of vertebrates (see Herrera 1989), but if so, this is not significant: the high seed survival at the small sites indicates that insects are not a major cause of seed fatality.

### 6.5.2 Importance of seed predation to *C. australe*

This study demonstrated that the level of predation by vertebrates has a marked effect on seed survival to the seedling stage. The single most important correlative factor in explaining the difference in seed survival between sites was the presence or absence of the seed predators. At the three largest sites, both seed predators (*T. caninus* and *R. fuscipes*)

were present (Table 5.8), and the complete removal of the 1989 cohort from beneath the parent trees eventually occurred. Seed removal levels were also high at these sites in the two subsequent years. At the two small sites, no *R. fuscipes* were recorded and *T. caninus* were present in low numbers (Table 5.8). Seed removal levels were low, and there was also a delayed initiation of seed removal, which indicated either that, a) animals had moved into the remnant in late May, b) animals were able to find alternative food sources outside the remnant, and/or c) animal densities were much lower than at the large sites. Although not investigated in this study, density of the seed predators was probably important in determining levels of seed predation and removal. Density of predators would only be directly comparable between sites and years if a constant area, number of trees and seed crop size was available, and/or if intensive grid trapping was conducted at each site throughout the period of seed availability and predation. There was no evidence of 'compensatory' predation by insects in the absence of vertebrate seed predators.

Short-term studies of post-dispersal predation (e.g. Willson 1988, Lott & McIntyre 1991) which have not followed the fate of the seed until germination, do not necessarily predict the final survival of seedlings, although they are still useful for assessing the relative importance of seed predation to the plant species, the importance of different predators, or differences between habitats. Based on a 4-year study, Schupp (1990) concluded that seedling emergence could be predicted from a knowledge of seedfall and the probability of seed surviving until the peak of germination. Similarly, in *C. australe* the level of seedling emergence by the end of the first wet season in 1990 seemed to indicate subsequent survival (Table 6.3). By following seed fate until germination and subsequent seedling survival at a range of sites, I have demonstrated that (lack of) predation is an important determinant of *C. australe* seedling emergence. The lack of 1989 cohort seeds surviving under the parent trees at the larger sites suggests that in relatively undisturbed forest, only seeds dispersed beyond the parent, or seeds which survive in heavy-fruited years are likely to germinate.

### 6.5.3 Factors affecting level of seed predation

Crawley (1992) emphasized the wide range of factors which can influence levels of predation, and the resultant great variation detected. For both pre-dispersal (Anderson 1989) and post-dispersal predation (Schupp 1988, 1990), variation may be pronounced among plants and within and among years, seasons and sites. These factors may shift in importance during the fruiting and subsequent season, and among years. Anderson (1989) cautioned that it is important to consider between and within-site variation when assessing the impact of seed predation.

In this study, seed removal varied within sites and among years. Seed crop size contributed to variation in seed removal among individual trees, but this effect was evident at each site. Within site, cumulative seedfall also appeared to influence the annual number of seeds removed, but interpretation is limited due to the small sample size (3 years). Nevertheless, a large seedfall in a short period of time obviously took longer to be removed than a small one (Figure 6.3). For example, at both of the two largest sites Big Scrub and Boomerang Falls, seed removal in 1989 coincided with the commencement of seedfall. Percentage seed removal was lower, and seed removal took longer at Boomerang Falls, probably due to the satiation of predators by the larger overall seed production at the site. However, at both sites the vertebrate predators were effective in removing all but one seed by the end of the rainy season. Complete removal did not occur at the two small sites. Other seed availability measures which might have explained differences between sites, such as the abundance of nearest neighbours in fruit, did not have a significant effect on seed removal. Freshly fallen seed was removed at a similar rate throughout the season, indicating that predators did not have to wait for toxins to be leached out of the seed.

Slope and rainfall events would have affected the number of seeds washed downslope, the number remaining available for predation beneath the parent tree, and the level of fungal attack. However, the data indicated that these factors were of low importance: Rainfall in 1989 was higher than average, and included heavy rains in April, November and December. During very heavy rain, individual seeds were moved only small distances downslope (pers. obs.). Despite steeper slopes, Johnston's did not have a higher proportion of seeds missing, and the number of seeds missing was significantly lower than at Big Scrub and Boomerang Falls. In addition, the timing of peak seed removal at the large sites did not coincide with recent heavy rains. This indicates that vertebrates removed a large proportion of those seeds missing at the two large sites. A small contributing factor to seed loss at Boomerang Falls was also fungal attack, which was recorded more frequently than other sites during the fruiting season (fungal attack at Davis was high from October onwards). Boomerang Falls was the only site in the bottom of a shaded valley, and the soil and seeds were probably less mobile, and more moist.

The size of the remnant, and its position in the landscape mosaic are likely to determine the presence and abundance of fauna species and indirectly, the level of predation (Chapter 2). Big Scrub and Boomerang Falls are the two largest sites and they are contiguous with eucalypt forest along a large part of their boundary. This lack of complete isolation has probably buffered the forests and the fauna within them from the effects of invasion and fragmentation. Thus, they can be expected to function as larger tracts of forest. For example, fauna may be able to obtain additional food outside the rainforest : in northern

NSW, *T. caninus* occurs in rainforest and in eucalypt forest with a rainforest understorey, but not in dry eucalypt forest (Strahan 1983, H. Hines pers. comm.). However, an individual *T. caninus* has been seen feeding on flowers of *Xanthorrhoea* in eucalypt forest (A. P. Smith pers. comm.) and in early stage pine plantations at Clouds Creek, where they cause some damage (P. Jarman pers. comm.).

The results of this study suggest a level of predation and seedling survival at Johnstons that is intermediate between the larger sites (Big Scrub and Boomerang Falls) and the smaller sites (Wollongbar and Davis). Johnston's Scrub is connected to other small remnants by regrowth along the creek. This may buffer the 20 ha remnant and provide an increased area of habitat for the resident fauna, thereby allowing the seed predators and predation to occur. However, populations of predators could fluctuate more at Johnston's Scrub than at the Nightcap sites, due to the unstable nature of small populations, and the remnant's isolation and small size. If so, more variable levels of seed removal and overall survival of *C. australe* between years are predicted.

Davis and Wollongbar are small remnants isolated from other forest by roads and grazing land. Davis Scrub is completely isolated, with (until recently) either pasture or potato farms adjacent, which have presumably restricted movement by native mammals. Seed damage by vertebrates at Davis Scrub was mainly in seeds with prior decay and fungal attack, suggesting that these seeds could only be eaten once they had release their toxins and were digestible by *R. rattus* and *T. stigmatica*. The reason for the apparent absence of *T. caninus* within the core of the remnant is not known, but availability of ground cover (the remnant was grazed in the past), tree stumps for nesting, or lack of food trees are possible limiting factors. In contrast, Wollongbar is situated adjacent to houses with fruit trees and nearby agricultural lands. These might provide additional food sources to support transient *T. caninus* and explain the presence (rather than lack) of predation observed within the rainforest remnant.

#### **6.5.4 Forest fragmentation and altered interactions**

There is a large research literature on forest fragmentation which shows a strong relationship between decreasing remnant size, increasing isolation and the decline in fauna and flora species richness (see Saunders *et al.* 1987, Saunders *et al.* 1991). In small reserves, fruit-bearing trees (e.g. Howe 1984), other important food sources and/or habitat requirements may be a limiting resource for fauna. As a result, the remnant may not support a breeding pair or resident individual of some native mammal species. Edge effects, connection with corridors and species sensitivity are also important factors in determining

which species occur in a remnant (Laurance & Yensen 1991, Saunders *et al.* 1991). In the Big Scrub, there is preliminary evidence that there is a decline in faunal species richness in small sites (Chapter 3), with some sites showing a higher than expected richness due to proximity to large areas of forest or corridor (Holmes 1987, Lott & Duggin 1993).

Section 6.5.3 proposed that the position of the remnant in the landscape mosaic and its topography contributed to levels of fungal attack, levels of seed wash downslope, and between year variation in predator abundance and levels of predation. However, the analysis of seed fate demonstrated that the overriding differences between the two large sites and the three smaller sites were seed damage *in situ* by vertebrates, and the proportion of seeds missing. Seed removal by vertebrates also explains the majority of the seeds which went missing throughout the season, as peaks in seed removal did not coincide with rainfall events. Differences in seed predation rates and seedling establishment between sites correlate with the presence/absence of seed predators, which is almost certainly a response to remnant size and isolation. It is clear that survival of *C. australe* seed differs between large (Big Scrub, Boomerang) and small, isolated sites (Wollongbar, Davis), with Johnston's showing intermediate levels of predation. In small sites, there is (1) a decrease in seed consumption by native mammals; and (2) an increase in seedling recruitment beneath the parent trees, as a result of reduced seed predation. Chapter 8 will investigate whether there is any evidence that higher seedling establishment is a phenomenon that has occurred in previous cohorts.

## Chapter 7. PATTERNS OF SEED PREDATION - MECHANISMS OF SEED CHOICE

### 7.1 INTRODUCTION

Choice of seeds by predators may be a response to several factors, including seed chemical content, age, size, density and distance from the seed source. These factors operate at different temporal and spatial scales. For example, some seeds can be protected from predation by chemical means (Bell 1978). Differential palatability of seeds among sites could result in varying levels of predation. Within-site, the timing of seed predation could be determined by the seed aging process: seeds could become more palatable as toxins are leached out or broken down, or conversely, less attractive as seeds age. Both of these possibilities pose selective forces on the timing of seed release and dispersal.

At the spatial scale, levels of seed predation can be affected by seed density and distance from the parent tree. Seeds tend to be dispersed in a leptokurtic distribution, with highest densities near to the parent plant (Willson 1983). Both Janzen (1970) and Connell (1971) proposed that predators respond to seed density and distance from the parent plant by causing disproportionate mortality near to the parent, and seeds dispersed beyond the parent plant would have a greater chance of survival. Subsequent studies have shown that the evidence for disproportionate mortality near to the parent is equivocal (Clarke & Clarke 1984). The emerging trend is that insects cause higher levels of predation in dense areas of seed near to the parent source, and mammals do not (e.g. Howe *et al.* 1985). Both Terborgh *et al.* (1993) and Howe (1993) concluded that mammals are efficient searchers over their foraging area, and distance-dependent predation is unlikely to be observed. However, insects may show density- and distance- dependent predation on seed due to their uneven spatial distribution with respect to parent trees (Howe 1993, Terborgh *et al.* 1993, Terborgh and Wright 1994, Lott *et al.* 1995).

*Castanospermum australe* has a very large seed, containing a toxic alkaloid (0.3% castanospermine; Elbein & Molyneux 1987). Seeds are eaten by mammals and insects (Chapter 5). Seed dispersal has previously been assumed to be by gravity and water (Floyd 1990a, Adam 1992). Consequently, many seeds will remain beneath or near the parent tree and have little chance of escape from predation. These characteristics indicate that seed chemical content, age, and distribution with respect to the parent tree might be important in determining patterns of seed choice by predators. Alternatively, the very large size of the seed suggests that there is sufficient storage tissue to allow germination despite partial seed

predation (e.g. Zhang & Maun 1989). Such escape from seed mortality would depend whether the embryo is preferentially eaten, and how much of the seed reserves are left attached to the seed. If partially damaged seeds can germinate, or if the seed can germinate before the seed predator finds it, then large-seeded species have a chance to escape secondary predation after dispersal.

A series of experiments was undertaken to investigate whether seeds close to the parent tree suffer higher predation, whether seed age and source affect seed predation rates, and whether damaged seeds can germinate. These questions are important in determining the reason for the low predation rates observed at Davis Scrub (Chapter 6), whether *C. australe* seeds could be dispersed by mammals, and whether mammal fauna are likely to affect the dispersion of seedlings. The subsequent chapter will compare the density and dispersion of seedlings and juvenile *C. australe* plants between sites.

## 7.2 METHODS

### Predation experiments

#### 7.2.1 Effect of seed source on palatability of seed

There is no information on variation in *C. australe* seed alkaloid content among trees and sites. A possible cause for the lack of seed predation by mammals at Davis Scrub (Chapter 6) was low seed palatability. To test this, a reciprocal transfer experiment was used to compare the removal rates of Davis Scrub seed placed alongside Big Scrub seed at both sites. Ten, 1 m<sup>2</sup> plots were marked out at each site, with each plot placed under the crown of an adult *C. australe* tree. Each plot contained 10 groups of 2 seeds, with each pair comprising one Davis and one Big Scrub seed. Seeds within each pair were matched for size, to reduce the effect of seed size on choice by animals. Seeds were marked with a non-toxic acrylic paint to differentiate their source.

The experiment was set up in September 1991. The number of seeds remaining was checked every two days for the first 10 days, then at 33, 52-54 days and between 3-4 months (87 days Big Scrub, 113 days Davis). Seeds were recorded as intact or eaten and included those paint-marked seeds found in the buttresses of trees and on the ground within 20m of each plot. Damaged seeds were assessed for percentage damage, and condition of the embryo. Analysis of variance was used to test the effect of site on percentage of seeds surviving intact at 3-4 months.

Secondly, a pilot experiment was established to test for seed survival in the absence of *T. caninus* predation. Mesh enclosures (2.5 cm) were set up in three microsites at Big Scrub, in November 1991. These enclosures prevented entry by *T. caninus*, but were accessible to rodents. Each enclosure included five seeds from Big Scrub and Davis Scrub. Enclosures were placed in small forest gaps, and in the forest interior, both under large parent trees, and under large non-conspecific trees. Each microsite was replicated in five locations, and each replicate contained a pair of enclosures (10 cages per microsite per site). This experiment provided some evidence for rodent response to seed source and microsite.

### **7.2.2 Removal rate of fresh and aged seeds**

This experiment compared the removal rates for freshly fallen seeds (fresh) with seeds which have lain on the ground since early in the fruiting season (aged). This tested whether dispersed seed could become less attractive as it ages. Ten pairs of seeds (fresh and aged) were placed within each 2 x 1 m plot beside the trunk of 10 trees at Big Scrub. Seeds were marked with non-toxic acrylic paint to indicate their age. The experiment was set up from 11-13 July 1990. Seed survival (intact seeds) was assessed daily for the first week, then at 9 days, two weeks, and one, two, three, five, nine, fourteen and seventeen months.

### **7.2.3 Effect of distance from parent tree**

An experiment was conducted to test the effect of distance from fruiting tree on rate of seed removal, to determine whether there was an increased chance of survival, if seeds were dispersed from the parent trees. Fresh seeds were placed within 1 metre plots next to the trunk of the tree (10 seeds/plot), at the edge of the crown (3-11.5m from the trunk, 10 seeds/plot) and 10-20m away from the tree trunk (5 seeds). The proximity of neighbouring conspecifics prevented greater distances being tested. Fewer seeds were placed in the plots outside the parent crown, in order to simulate natural seed densities. Plots were placed near ten trees at Big Scrub, and near five trees at Davis Scrub. The experiment was set up 12-17 July 1990, and seed fate was determined daily for the first week, then at approximately 2 weeks, one month, 2, 3, 5, 9, 14, 18 months, and four years (July 1994). The percentage of intact seeds remaining after 1 and 5 months (33 and ~165 days) was used to test for an effect due to site and treatment.

#### **7.2.4 Analysis of patterns of damage to individual seeds: Proportion of seed damaged**

In several experiments where seed survival was determined (number of intact seeds), individual seeds were also assessed for the percentage of cotyledon tissue remaining after predation. Where possible the condition of the embryo and the type of predator was also determined. Experiments from which data was obtained were: the 1989 seed cohort study (chapter 6), palatability experiment (section 7.2.1), pilot trial for the enclosure experiment (section 7.2.1), and distance-effect experiment (section 7.2.2) : During study of the 1989 seed cohort (Chapter 6), all seeds under three *C. australe* trees at each of five sites (n=8441 seeds) were examined at three to four week intervals between May and October 1989. Freshly-eaten seeds were inspected opportunistically for tooth marks and patterns of seed predation, and the percentage seed remaining after predation was noted for individual seeds. In the following two fruiting seasons (1990 and 1991), the condition of seeds was examined more closely at Big Scrub and Davis Scrub. In July 1990, a total of 475 seeds were placed in plots beneath or near 15 trees and seed condition noted until September. In September 1991, 400 seeds were placed in plots and their condition noted until December. These data were combined to analyse the proportion of individual seeds left uneaten by insects, rodents and *T. caninus*, and the proportion of seeds where the embryo was left intact. Whether seed damage resulted in successful germination was also recorded.

#### **7.2.5 Germination trial**

Forty-three seeds with fresh damage by rodents were collected in the field and transferred to shadehouse conditions in Armidale. Of these, twenty-seven seeds with the embryo intact were planted in individual pots with kraznozem soil from Rous district, near Lismore. Seeds were collected and sown 14 November 1991. Seed germination and seedling height was determined periodically until 31 May 1992.

#### **7.2.6 Analyses**

Analyses of variance and paired t-tests were used to test for the effect of site when variation between trees or replicates was included. For these, a square root transformation was applied to the data (Snedecor & Cochran 1980). Nested analyses of variance (using square-root transformed count data) were used to test for the effects of treatments and sites in the palatability and distance-effect experiments.

### 7.3 RESULTS

In *C. australe*, seed predation is a continuous process, and affects both ungerminated seeds and seeds attached to young seedlings. Survival curves show survival of dispersal units (seeds/seedlings) over time irrespective of growth status. However, strict seed predation occurred until late December, at which time seeds commenced germination. Predation of seeds in the process of germination continued until late April, when peak germination was reached. Seed survival was analysed for mid December (~87 days) in the palatability experiment, July/August (3, 7 and 33 days) in the seed age experiment, and August (33 days) and late December (~165 days) in the distance experiment.

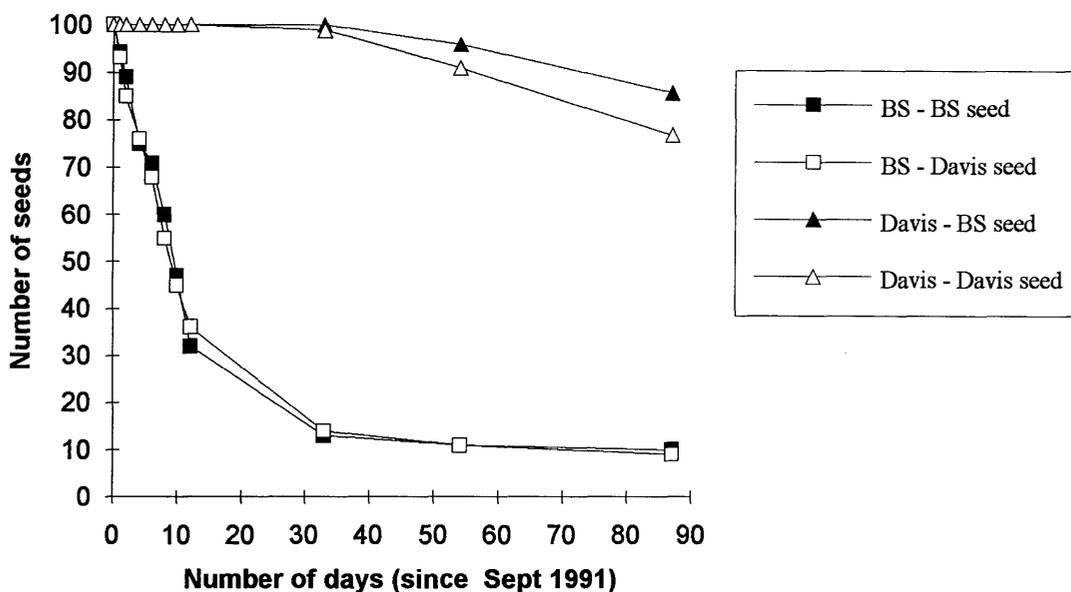
#### 7.3.1 Predation experiment - palatability of seed

Seed source did not have a significant effect on seed removal in the palatability experiment ( $F=0.77$ ,  $df=1$ , ns; Figure 7.1). Site differences explained all variation in seed removal patterns ( $F=158.96$ ,  $df=1$ ,  $p<0.001$ ). Except for one seed, there was no damage at Davis Scrub until November, when insect attack, small amounts of rodent damage (3 seeds nibbled), and decay caused some seed loss. Nearly half the seeds (44.5%) survived as seedlings until July 1994 (2 1/2 years later). At Big Scrub, seeds were removed rapidly over the first 10-14 days, then a small number survived the duration of the experiment. These were all within three plots. The pilot exclosure experiment also showed that there was no difference in removal of Big Scrub and Davis seed presented at Big Scrub. Over 11 days, rodents damaged 46 and 47 seeds respectively out of 150 from each seed source ( $F=0.005$ ,  $df=1$ , ns).

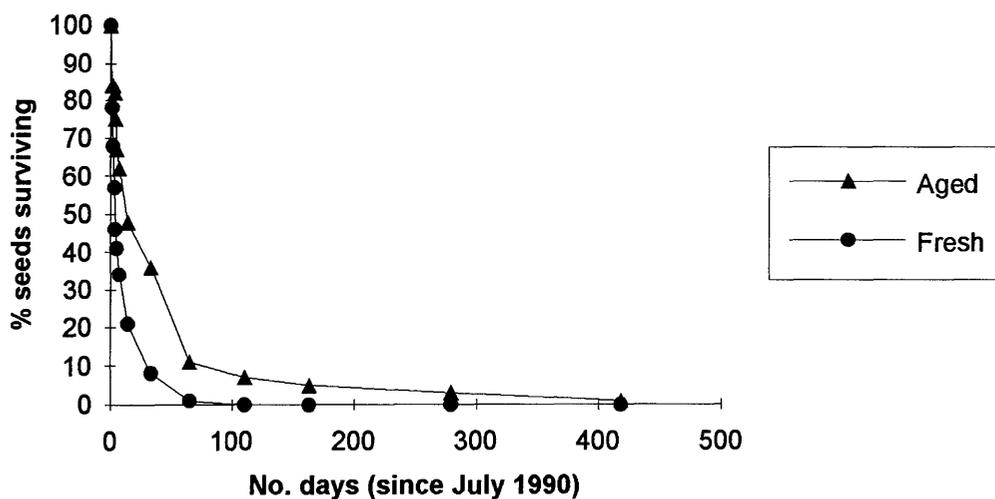
#### 7.3.2 Removal rate of fresh and aged seeds

Seed age did not have a significant effect on the proportion of seeds remaining at 3, 7, or 33 days ( $F\geq 1.13$ ,  $df=1$ ,  $p>0.02$ ). Fresh seeds were removed more rapidly than aged seeds (Figure 7.2) at seven out of 10 trees, but between-tree differences had a greater effect on removal rate than did seed age. For three trees, the removal rate was the same throughout or slower during one time interval only. Out of 200 seeds, one seedling remained after 1.5 years - this was from an aged seed, but did not survive subsequently.

**Figure 7.1** Survival over time for seeds in the palatability experiment. Seeds were collected from two different seed sources (Big Scrub and Davis Scrub), and placed together at each site. Figure legend gives location of plots (BS=Big Scrub, Davis=Davis Scrub), followed by seed source.



**Figure 7.2** Relative removal rate for fresh and 'aged' seeds at Big Scrub. (Seeds were placed together in ten plots. Fresh=freshly fallen. Aged seeds= seeds which had discoloured after lying on the ground for some weeks.)

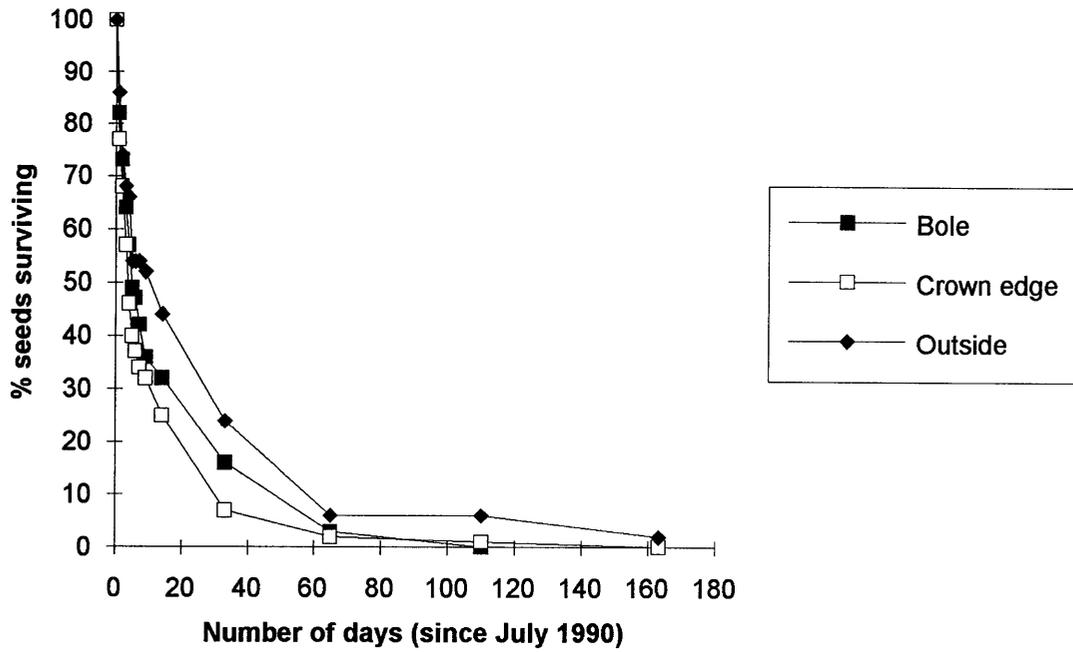


### 7.3.3 Effect of distance from parent tree on predation rate

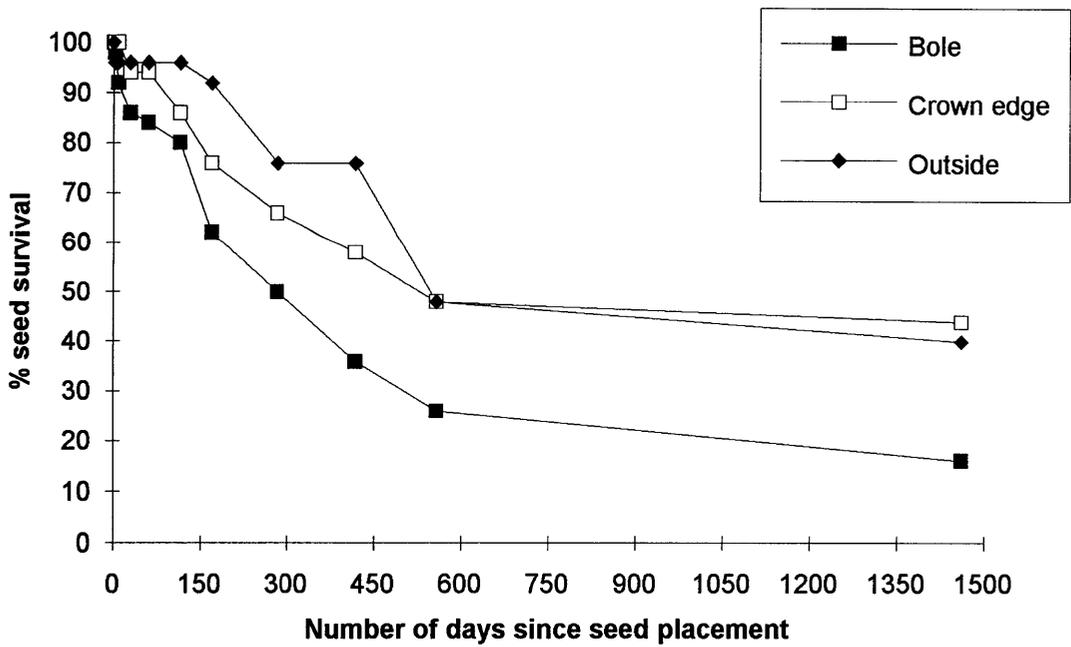
Analysis of variance on seed survival at 33 days showed a significant effect due to site ( $F=109.5$ ,  $df=1$ ,  $p<0.001$ ) and distance from parent tree ( $F=2.58$ ,  $df=2$ ,  $p<0.1$ ). The interaction was not significant. Both site and distance effects were also significant ( $p\leq 0.05$ ), 165 days after the experiment started. There was a clear difference between sites: Seed removal was much more rapid at Big Scrub (Figure 7.3 a,b) where, except for three seeds which germinated close to the parent trees in late April 1991, all seeds were removed. These seedlings did not survive until July 1994 (4 years later). In contrast, some seeds survived in all distance categories at Davis Scrub. At both sites, removal was slowest for seeds placed outside the parent crown. However, removal rates for seeds next to the trunk and at the edge of the crown were variable. Removal rates differed markedly between trees, particularly at Big Scrub (Figure 7.4 a).

**Figure 7.3** Survival over time for seeds at three distances from the parent trees

a) Big Scrub (10 trees)

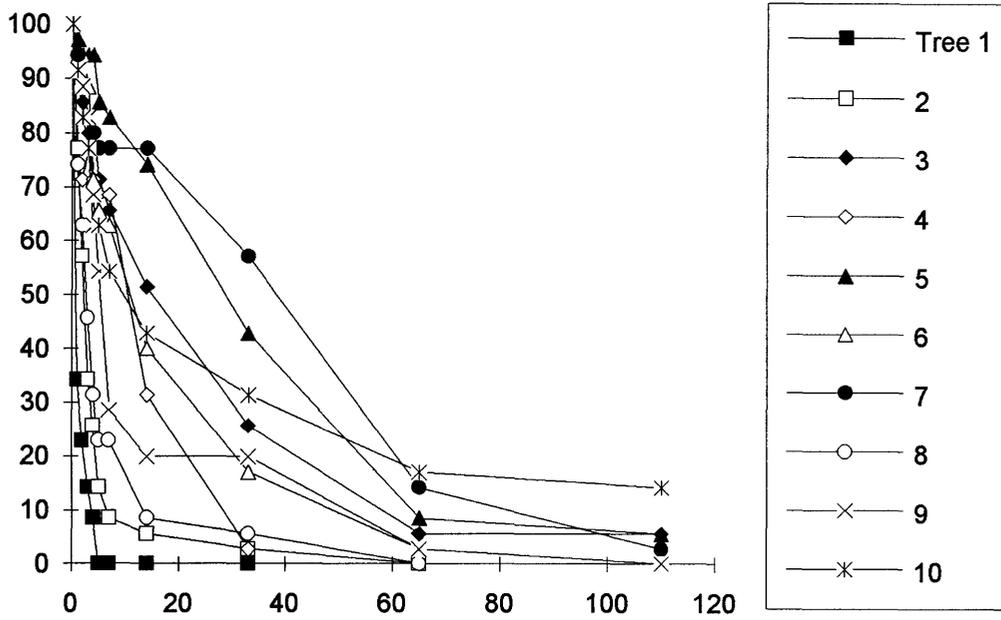


b) Davis Scrub (5 trees)

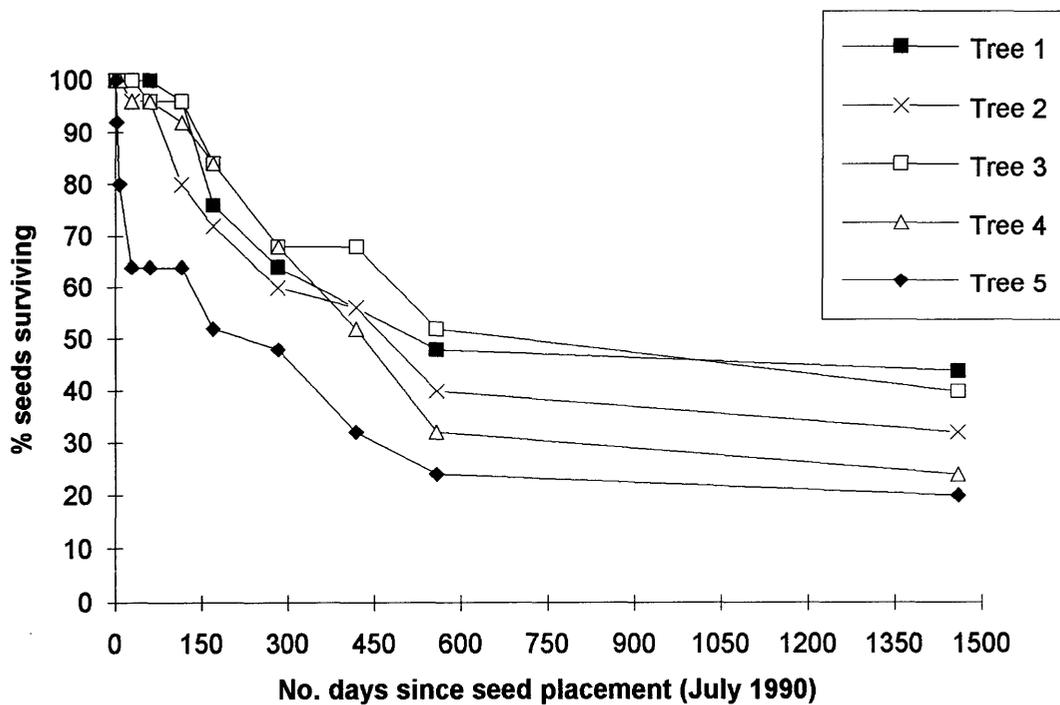


**Figure 7.4** Comparison of seed removal rates near different trees

a) Big Scrub



b) Davis Scrub



### 7.3.4 Proportional damage to individual seeds

At Big Scrub, damage *in situ* was largely by mammals. In contrast, most damage at Davis Scrub was by insects, and by seed decay, with rodents damaging only 2% of seeds in the palatability experiment. In January, most individual seeds at Davis Scrub had less than 20% damage, expressed as a proportion of seed volume (Table 7.1).

During the period of seedfall, insects damaged few seeds (Chapter 5), and only small proportions of each seed (Table 7.1). On average, 72 % of seeds escaped damage to the embryo (Table 7.2). Possums ate the largest proportion of each seed, and were most likely to damage the embryo. At the first visit, rodents generally left 99% of the seed intact, and in 54.5% of seeds, the embryo was left intact. Seed removal subsequent to this could have represented subsequent predation.

Some seeds germinated with previous or subsequent damage to the seed cotyledons. In October 1989, 22% of the 178 seeds with early root initiation were from seeds with 30-99% damage. Samples were too infrequent over the rainy season to be able to identify which of the seeds had germinated from each pod, and it was not possible to estimate the proportion of germinants which had previous seed damage. In the majority of cases, it appeared that damaged seeds either rotted, were killed by further predation, or germinated with weak multiple secondary roots which eventually died. However, sufficient data existed to demonstrate that nine seeds from Wollongbar and two from Davis tree 2 had germinated subsequent to damage, and had achieved shoot and leaf production by the end of the rainy season. In the 1990 and 1991 predation experiments, only 9 out of the 550 seeds from Big Scrub initiated germination prior to seed removal or death. Two of these seeds had 1 and 5% damage, but these seeds did not survive to shoot stage. At Davis Scrub, 29% (59) of the germinants during the rainy season had seed damage (1-50% damage). Twenty of these seedlings produced shoots and leaves.

Seeds with the embryo removed often remained for a subsequent 1-2 samples, and were eaten by insects, as well as showing evidence of fungal attack and softening of the cotyledon tissue.

### 7.3.5 Germination trial

Nineteen out of the 27 damaged seeds germinated (70%), with the remaining seeds being mouldy or rotten at the termination of the trial. The average height of seedlings after six months was 25.6cm (std dev=6.3), but seedling height was affected by the proportion of seed remaining at the start of the experiment (Figure 7.5).

**Table 7.1** Proportion of seed remaining after predation by rodents, possums (*T. caninus*) and insects. (Data are aggregated from three experiments at two sites. Cases where only the seed testa was recovered are excluded from this table.)

	Mean % seed tissue remaining (SE)	Mode	Range	n
<b>INSECT</b>				
<u>Distance experiment 1990</u>				
Davis Scrub	75.1 (4.4)	50	25-98	25
Big Scrub	93.6 (2.8)	99	80-99	7
<u>Palatability experiment 1991</u>				
Davis Scrub	89.7 (3.2)	99	50-99	19
Overall	83.1 (2.7)	90	25-91	51
<b>RODENT</b>				
<u>Distance experiment 1990</u>				
Big Scrub	83.8 (4.5)	98	2-99	32
<u>Palatability experiment 1991</u>				
Big Scrub	67.0 (4.7)	95	2-99	56
<u>Pilot exclosure experiment 1991</u> (possums excluded)				
Big Scrub	74.6 (2.9)	70	2-99	80
Overall	74.2 (2.3)	99	2-99	172
<b>POSSUM</b>				
<u>Distance experiment 1990</u>				
Davis Scrub	60.5 (9.7)	20	20-98	12
Big Scrub	47.2 (3.8)	20	2-98	80
<u>Palatability experiment 1991</u>				
Big Scrub	30.3 (7.4)	2	2-99	20
Overall	46.6 (3.3)	20	2-99	114
<b>PADEMELON ?</b>				
<u>1990 and 1991 predation experiment</u>				
Overall	77.3 (8.3)	-	60-99	4

Data does not include testas found as sole remains

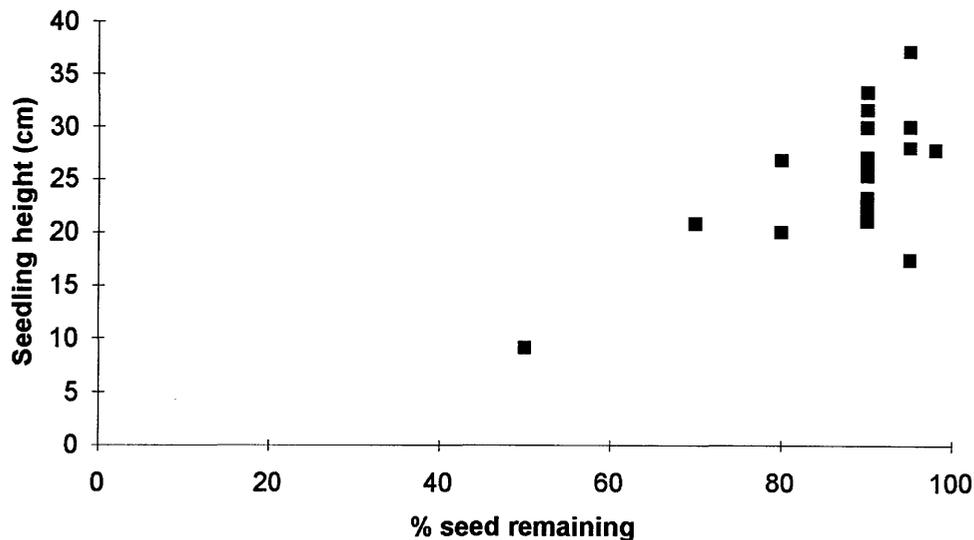
**Table 7.2** Percentage of predator-damaged seeds with the embryo intact

(*n*=number of predator-damaged seeds inspected. Distance-effect experiment commenced in July 1990, Palatability experiment in September 1991, Pilot enclosure experiment in November 1991.)

Predator	<u>Predation experiment:</u>						Overall Mean*
	Site	Distance-effect		Palatability		Pilot enclosure	
		Davis Scrub	Big Scrub	Davis Scrub	Big Scrub	Big Scrub	
<b>INSECT</b>							
% embryo intact		70.4	100.0	55.0	-	-	72.0
<i>n</i>		27	7	20			54
<b>RODENT</b>							
% embryo intact		-	58.1	-	55.9	50.6	54.5
<i>n</i>			43		59	85	191
<b>POSSUM</b>							
% embryo intact		46.2	52.5	-	27.3	-	37.1
<i>n</i>		13	81		22		124
<hr/>							
<b>TOTAL*</b>							
% embryo intact		61.7	35.6	67.0	32.6	50.6	48.7
<i>n</i>		60	205	94	135	85	357

\* Totals include additional damaged seeds where predator type was not distinguishable due to subsequent seed decay.

**Figure 7.5** Height of seedlings germinated from rodent-damaged seeds which had the embryo intact. Seedling heights were measured six months after sowing (n=19 out of 27 seedlings germinated).



$$\text{Regression } y=38.79x - 8.28 \quad (F=14.9, \text{ df}=1,17; p<0.001; R^2=0.47)$$

## DISCUSSION

Two experiments compared the relative seed predation from Big Scrub and Davis Scrub. Consistent with previous results for the 1989 seed cohort (Chapter 6), the experiments show that very little seed predation occurs at Davis Scrub. Further, there was no evidence that the lack of predation was because seeds were less attractive than those from Big Scrub. Therefore, a lack of mammalian seed predators within the Davis Scrub remnant explains the very low levels of predation.

The results indicate distance-dependent predation by both insects and mammals. The higher rate of seed damage near the tree trunk (bole) at Davis Scrub is consistent with density-dependent predation by insects, although the biology of the larval lepidopteran seed predators is not known. At Big Scrub, this effect if present, was masked by the much heavier predation by mammals. At both sites, seeds survived longest when placed away from the crown of parent trees. At Big Scrub, the distance-effect conferred only a temporary advantage, as eventually all seeds were damaged or removed. Nevertheless, the results indicate that there is a slightly higher chance of survival, if seeds are dispersed

beyond the parent. Survival could be assisted, at least during fresh seed fall, by the slight preference by mammals for freshly fallen seeds rather than those which have lain on the ground for several weeks.

The small dispersal distances (0- $<$ 20m) examined within this study were dictated by the proximity of adult trees. However, both of the seed predators are known to range over distances of 100-200m (*R. fuscipes*, Wood 1971; *T. caninus*, Owen & Thomson 1965). In years, or sites with high levels of predation, seeds which dispersed only short distances are likely to be eaten, as mammals can be efficient searchers throughout their territory (e.g. Terborgh *et al.* 1993). Nevertheless, the evidence is that most tropical species have a clumped distribution, and density-dependent predation may only operate to set the upper limits to abundance for each species, rather than being a strong force determining the coexistence of species (Hubbell 1979, Hubbell *et al.* 1990). This indicates that the advantages to seed dispersal may be for the seedling, rather than for seed escape from density-dependent predation. However, in plant species where seed predation rates are consistently high, escape from predation may require seed dispersal well beyond the parent tree, predator satiation during sporadic heavy crops, or occasional abandonment of seeds in a safe site for germination (see Howe & Smallwood 1982). For *C. australe* the presence of some seedlings close to adult trees in all sites visited (pers. obs. and Chapter 8), and the variation in predation rates between trees (this chapter) suggest that density-dependent predation is less important than seed crop size, habitat characteristics and the distribution of mammals, in determining spatial and temporal variation in seedling recruitment.

One of the hypotheses as to why large seeds may be an advantage in tropical moist forests is that large seeds have the reserves to withstand heavier seed (Foster 1986) or seedling damage (e.g. Armstrong & Westoby 1993). In this chapter, I have demonstrated that a very large-seeded species can withstand partial seed predation: in 48% of mammal-damaged *C. australe* seeds and a higher percentage of insect-damaged seeds, the embryo remained intact, and damaged seeds are capable of germinating in the wild. The ability to withstand partial predation also gives this species the opportunity for germination after seed dispersal by mammals. Observations of seeds during field research indicate that *T. caninus* and rodents carry seeds away from the seed source: Possums moved paint-marked seeds up to 19m away from parent tree (pers. obs.) and seeds have also been found on stumps (pers. obs.) and in trees (R.J. Haworth pers. comm.). Rodent-damaged seed has been found moved up to 10 m from the parent tree, and in a small number of cases, intact seeds were found placed in the buttress of a tree. As rodents damage a smaller proportion of the seed, they may be more effective seed dispersers than possums. Further research should investigate the distances that seeds are moved by mammals, and whether mammals are

important in seed dispersal. Whether the smaller seedlings which result from partially damaged seeds (Zhang & Maun 1989) survive within the forest, and have the ability to withstand herbivory (Janzen 1976) would also be instructive.

From the plant's perspective, escape from predation may be numerical (e.g. predator satiation), chemical, volumetric (e.g. seed size), or spatial (dispersal). These mechanisms may cause differences in levels of predation, and the subsequent patterns of seedling establishment, between and within sites. In this study, there was no evidence for a difference in seed palatability between sites. Removal rates varied between trees, but the main difference between the two sites was in the number of seeds removed from beneath or near adult trees. The most important factor determining this was the presence of mammalian seed predators.

## Chapter 8. SEEDLING GROWTH, SURVIVAL AND DISPERSION

### 8.1 INTRODUCTION

Plants produce far more seeds, than will establish as seedlings. Plant density is reduced to a supportable level by seed and seedling predation, and mortality due to the effects of overcrowding. If low seed predation allows seedling recruitment to exceed a supportable size, then usually there will be subsequent higher attrition due to fungal pathogens (Auspurger 1983a,b), herbivory (Howe *et al.* 1985), competition or other density-dependent causes (Harper 1977), i.e. the seedlings will self-thin. Because of this, it has been argued that seed predators are just eating the surplus in the system that would otherwise have died from density-dependent causes, and seed predation has little impact on plant recruitment (see references in Harper 1977, Crawley 1992). However, if a seed predator carries the seed density below that to which the plant population would be reduced by density-dependent process, then predation is important to the plant species (Harper 1977). Conversely, if seed predation is reduced or removed in time, and altered interspecific competition results, then the relative abundances of specific plants are likely to change (Janzen 1971). In both cases (increased predation, or reduced/absent predation), altered levels of predation could have an effect on the relative abundance of individual plant species within the vegetation community.

The number of seedlings which establish as a result of altered predation depends on the magnitude or frequency of the change in level of predation, the dispersal vector, the germination requirements of the plant species, and the seedling tolerance to crowding and herbivory. Seeds which are dispersed beyond the parent tree are generally expected to have a higher probability of survival, due to escape from predation (Janzen 1970, Connell 1971), competition, other causes of density-dependent mortality (Harper 1977), and potential allelopathic effects from the parent tree. The recruitment and dispersion pattern of seedlings beyond the parent tree is influenced by the dispersal vector and the germination requirements of the particular plant species (Howe 1989).

Forest fragmentation may indirectly cause altered levels of predation, through changed abundance or behaviour of the component fauna (Chapter 2). Seedling recruitment may also be affected owing to a lack of dispersal vectors for the target species, or a lack of seed dispersers to distribute seeds of competing plant species. In some cases, the balance between seed predation and dispersal may determine the number of seedlings which establish. For example, Santos and Telleria (1994) found evidence for decreased dispersal

efficiency of Spanish juniper *Juniperus thurifera* in small fragments, as a result of increased abundance and seed predation by mice *Apodemus sylvaticus*, and decreased seed dispersal by thrushes *Turdus* spp.

Previous study of *C. australe* has found that the levels of seed predation differed between rainforest remnants, and that this was correlated with the presence/absence of the mammalian seed predators within remnants (Chapter 6). As a result of reduced seed predation, there was a greater abundance of seeds remaining during the wet season, and a higher seedling establishment in the two smallest sites, Davis Scrub and Wollongbar. A large proportion of these seedlings survived 4 1/2 years. However, forest tree seedlings often exist as an abundant seedling bank, from which only small numbers grow into the next size class (Grime 1979). It is possible that subsequent self-thinning of seedlings in the small remnants results in a distribution and density of juveniles and saplings that is no different from those observed in the larger sites. The aim of this chapter is to investigate the abundance of seedlings and larger size classes, and their distribution with respect to adult trees, to test whether the existing vegetation at the five study sites shows any evidence of altered survival of *C. australe*.

The pattern of *C. australe* seedling recruitment beyond the parent tree is not known. Seeds are dispersed by gravity, water, and potentially, by *Rattus fuscipes* and *Trichosurus caninus*. If mammals are important in seed dispersal and in early seedling herbivory, then the five sites would be expected to differ in seedling dispersion and establishment. Seedling establishment, height and survival from the 1989 cohort study (Chapter 6) and from two experiments in Big Scrub and Davis Scrub were analysed to compare seedling growth and survival beneath and beyond parent trees. This is useful for understanding seedling age and spatial patterns of establishment within the forest. Results are compared with the dispersion and density of immature and adult *C. australe*, the floristic composition, and the number of adult nearest neighbour-conspecifics at each of the five study sites. The influence of site specific factors, and the potential for *C. australe* to increase in dominance are discussed.

## 8.2 METHODS

### 8.2.1 Germination, survival and growth of *C. australe* seedlings:

#### *1989 cohort (Davis Scrub and Wollongbar)*

In this section, the germination, individual seedling survival and height was determined beneath the trees' crowns at intervals until July 1994. In Chapter 6, survival of seeds from the 1989 cohort was determined. For three of the sites, all seeds had disappeared by 1990. In contrast, a large proportion of the seeds at Wollongbar and Davis Scrub remained undamaged at the end of seed fall (October), and many of these subsequently germinated. For trees with smaller seed crops, the fate of the entire seed(ling) crop was determined, using previously tagged individuals (Wollongbar trees 2 and 3, Davis tree 2). At the three trees with larger crops, all recently germinated seedlings beneath the parent crown were mapped in late April 1990, to give an estimate of seedling establishment, and a subsample of these were tagged. At this time, the majority of the cohort had germinated and were present as seedlings. At Wollongbar tree 1, all seeds and seedlings beneath half of the crown were re-tagged. At Davis Scrub trees 1 and 3, a sample of 131 and 94 seedlings were tagged respectively. All data were converted to percentage of original seed crop for each tree for analysis.

#### *1990 Distance-effect predation experiment (Big Scrub and Davis Scrub)*

Germination, height and seedling survival were determined for seeds remaining from the distance-effect predation experiment (Chapter 7) at periodic intervals until July 1994.

### 8.2.2 **Exclosure experiment: seed and seedling survival beneath conspecifics, nonconspecifics, and in canopy gaps**

This experiment simulates seed survival and resultant seedling survival and growth where seeds have escaped from vertebrate predation. The experiment compared Big Scrub and Davis Scrub, using seeds placed in small forest gaps (GAP), and in the forest interior, both under large parent trees (BB), and under large non-conspecific trees (NON). Seeds were protected in exclosures (mesh cages) to exclude vertebrate predators.

The position of the two treatments in the forest interior was dependent on the location of the gaps. Five gaps were chosen in each of Davis and Big Scrub. For each gap, the nearest large adult *C. australe* and non-conspecific were selected to place the other treatment

cages. Paired exclosures were set up in each replicate microsite. Each exclosure included five seeds from each of the two sites, in a reciprocal transplant experiment, to compare the response of the two seed lots to the same conditions, and to remove seed-source effects on microsite treatments. Seeds were collected from 5-8 trees at each site, and were marked with non-toxic acrylic paint to indicate their source.

Exclosures were made of soft metal mesh formed into a cylinder, supported by two wooden stakes, and with the top drawn together and tied with wire (Figure 8.1). Cages were approximately 1 m diameter and 0.8 m tall. Large steel pegs were used to anchor the base of the cages to the ground. A 2.5 cm mesh was used at Davis Scrub, where the experiment was set up in November 1991. After a pilot trial, the cages at Big Scrub were replaced with 1cm mesh cages between 3-5 December. Seed was collected from the ground at the two sites. The cage roof prevented coarse leaf litter fall reaching the ground within the cages. To allow for this, a handful of leaf litter was scattered into each cage in November.

Survival and growth were assessed 4-5 January (1 month for BS, two month for Davis), 19 February, 21-22 March, 23 May, 4-5 January 1993 (13-14 months). Seeds from each seed source were assessed for presence/absence, percentage seed remaining, type of predator (vertebrate, insect), decay (fungal attack, softening, necrosis), germination and seedling height (to terminal bud).

Seeds were classed as non-viable if the the embryo was missing (irrespective of percentage seed remaining), or if the seed was rotten, soft, or if there was  $\leq 10\%$  of the seed remaining. Seeds were regarded as present with such small percentages of tissue remaining, as seeds germinate concurrent with insect damage, late in the year (Chapter 7). In addition, greenhouse trials showed that seeds are capable of germinating with up to 90% of the seed removed (R. Lott unpublished data). In the latter stages of the exclosure experiment, the testa fell off the seeds, or the seeds rotted beneath the seedling, and seed source could not always be determined. These individuals were recorded separately, but such data was included in calculations of overall seed survival per cage.

A nested analysis of variance was used to test the effects of site, microsite, tree and seed source on percentage seed survival in January 1993 (15 mo).

### **8.2.3** *C. australe* immature plant survey at sites

To test the abundance of offspring from years prior to 1989, the abundance of *C. australe* immature plants was recorded along 50m transects at each site. Three transects were

sampled at all sites except Big Scrub, where four were sampled. Immature plants were classed into four height categories: <1m (seedlings), 1-3m (juveniles), >3m height but <5cm dbh (saplings), and 5-20cm dbh (sub-adults). Proximity to the nearest reproductive *C. australe* (>25 cm dbh) was also recorded. Transects were 2m wide, with the origin at the trunk of the study tree, and were chosen to travel in a direction away from the other study trees.

#### **8.2.4 Floristic composition of vegetation plots**

At each site, three 20 x 20 m plots were established, each centred on a study tree (Figure 8.2). All individuals  $\geq 5$  cm dbh were identified to species and measured for trunk diameter (dbh). Sites were compared for species richness, diversity, the proportion of secondary and mature forest species, and size and number of *C. australe* individuals relative to the size and abundance of other species. Species diversity was calculated using the Shannon-Wiener index (Krebs 1978), with the total known species recorded at each site (Holmes 1987) used to calculate H max, the maximum possible diversity.

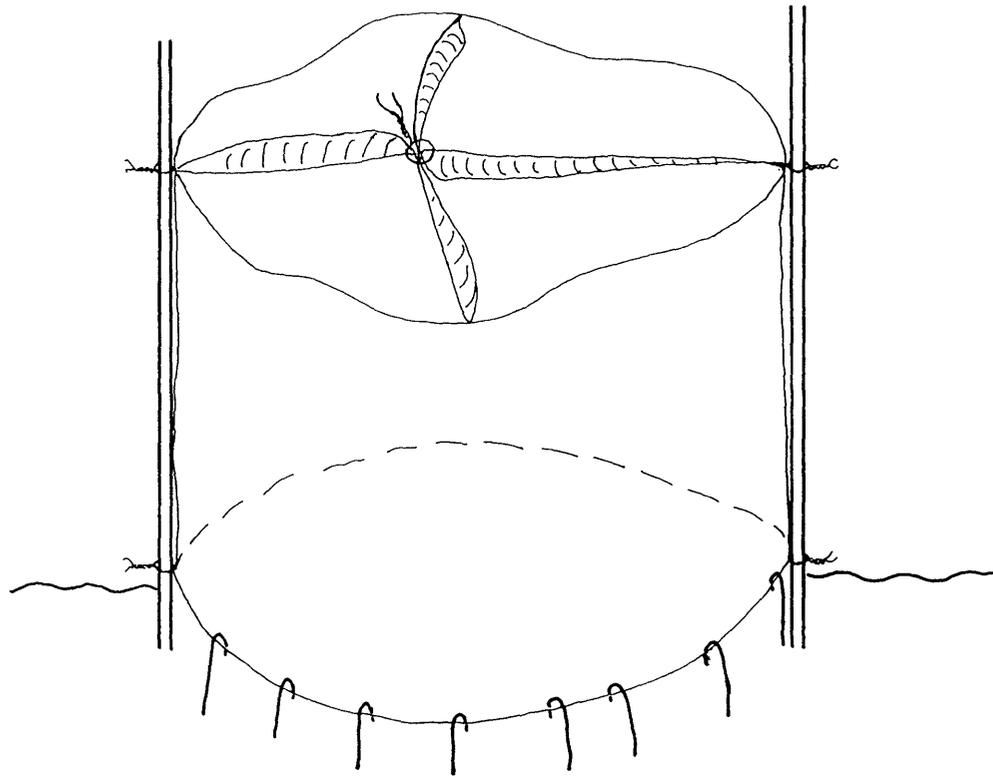
#### **8.2.5 Number of adult nearest neighbours**

To expand the sample size of adult *C. australe*, all trees >20 cm dbh within a 30m radius of the study trees were mapped and their dbh determined. These data allowed comparison of the size class distribution of adult *C. australe* between sites.

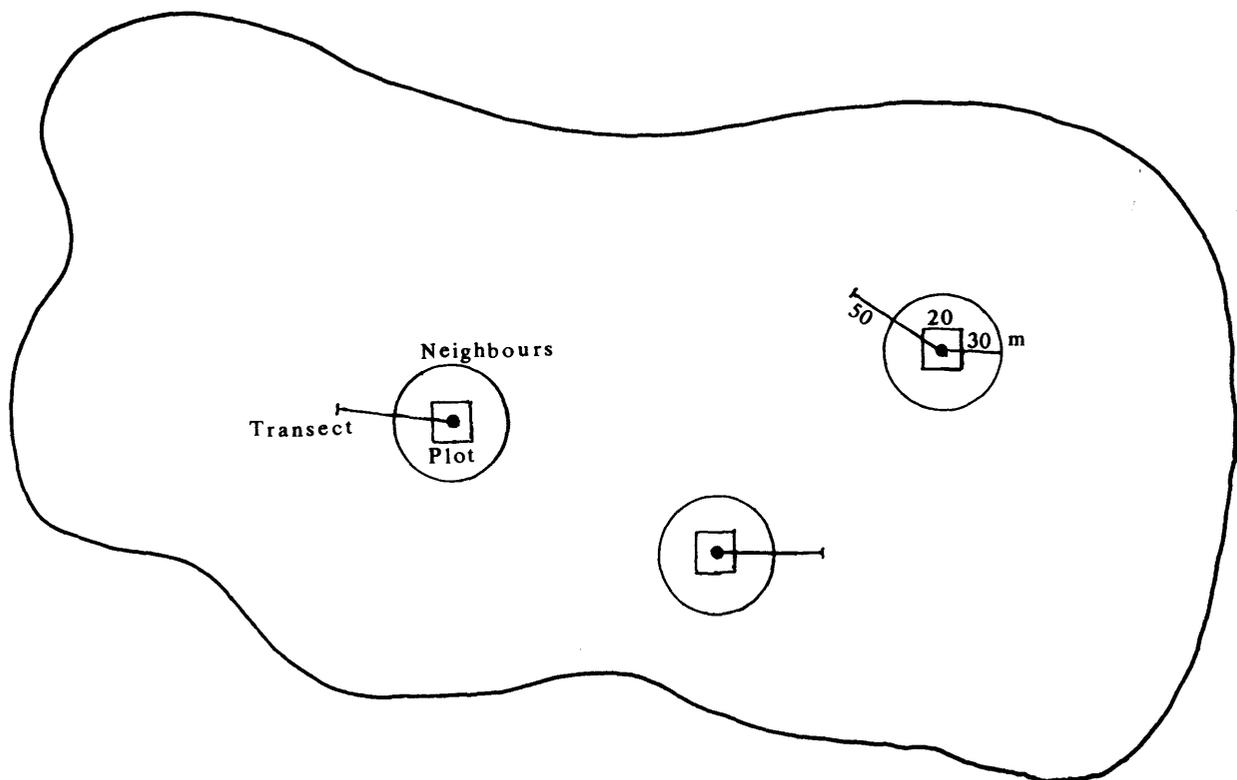
#### **8.2.6 Analyses**

A nested analysis of variance (using square-root transformed count data) was used to test for the effects of treatments and sites on seed survival, in the enclosure experiment. Chi-squared analyses based on count data were used to compare sites for the proportions of individuals in different plant size classes, and species groups. Some analyses of variance and paired t-tests were used to test for the effect of site when variation between trees or replicates was included. For these, a square root transformation was applied to the count data (Snedecor & Cochran 1980). For the distance and enclosure experiments, seed survival is expressed as a percentage of the original number of seeds, and survival data includes seedlings since they are still prone to seed predation after germination.

**Figure 8.1** Design of cages used to exclude mammals in enclosure experiment



**Figure 8.2** Vegetation sampling design at each site.



## 8.3 RESULTS

### 8.3.1 Germination, survival and growth of *C. australe* seedlings:

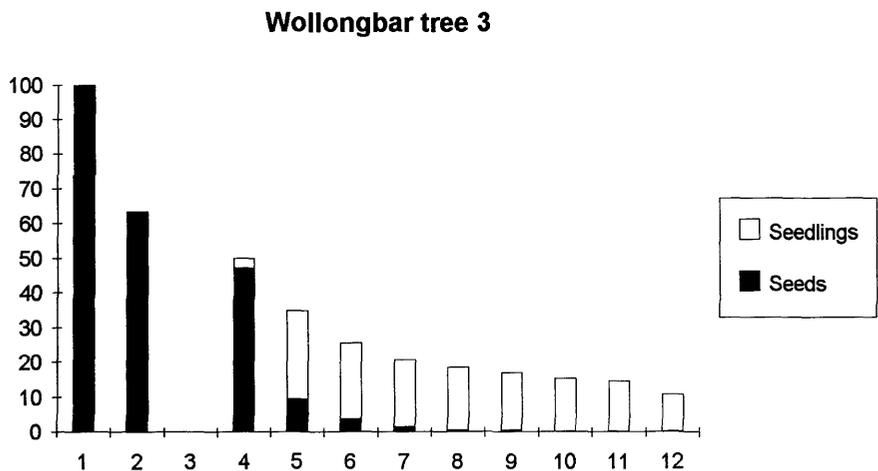
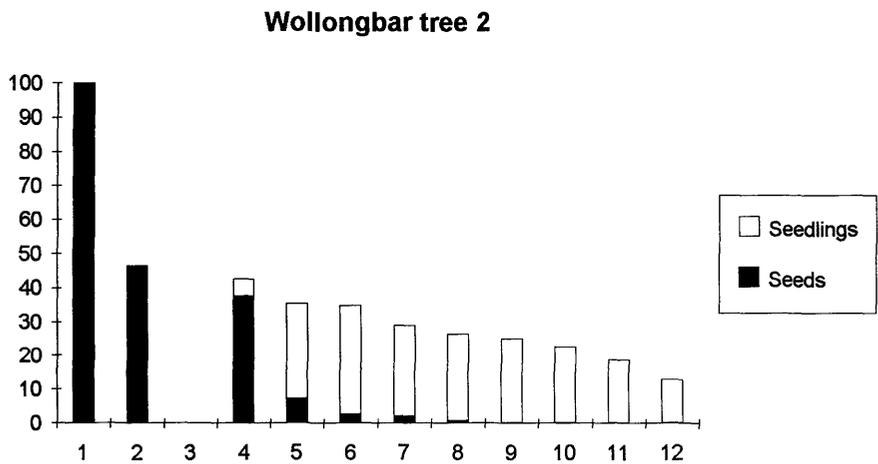
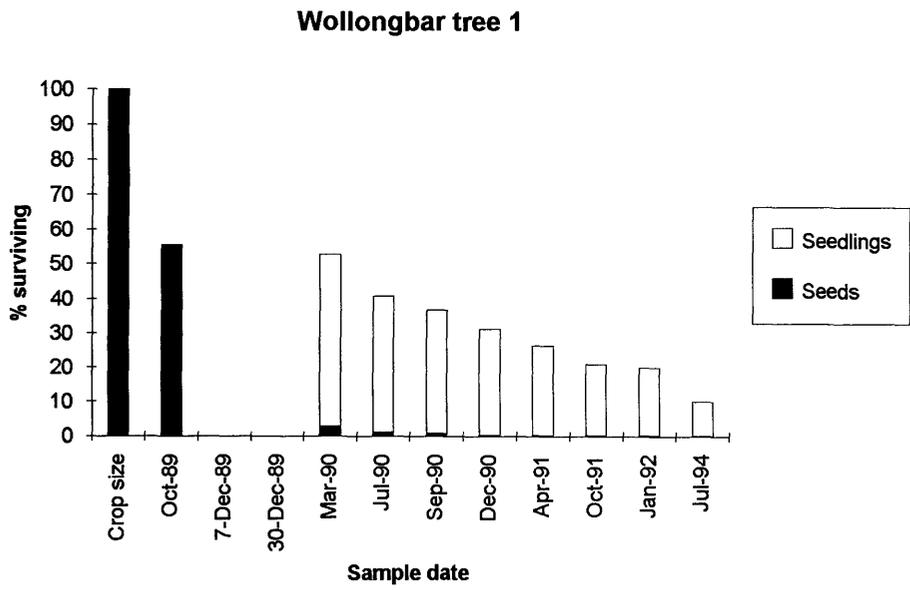
#### *1989 cohort (Davis Scrub and Wollongbar)*

Early extension of the radicle was noted from May 1989 onwards (in a small number of seeds), but shoot extension commenced in early December, after the onset of summer rain (see Figure 3.3). By April 1990, the majority of seeds at Davis and Wollongbar had germinated and produced stems 1-77 cm in height. A few seeds produced shoots in the winter of 1990 or during the second summer following seed fall (December-April 1991). No seeds survived at the other three sites. There was no discernible difference between sites in timing of radicle initiation, although seed survival at the commencement of germination obviously affected later numbers of germinants under each tree. Some seeds initiated germination despite previous damage, and some seeds were eaten after early radicle extension.

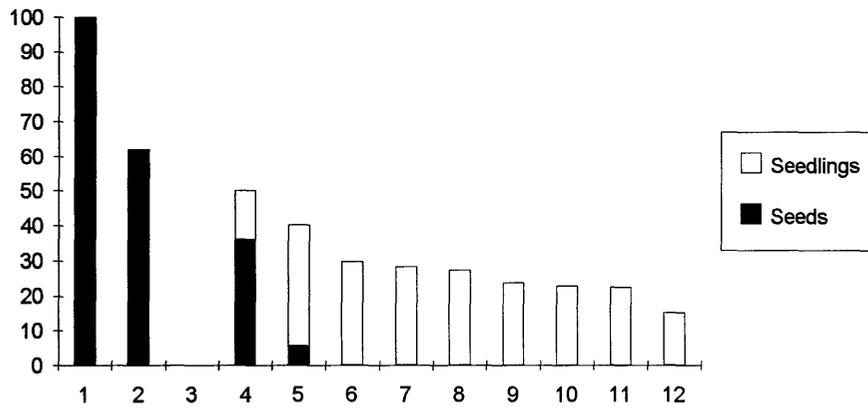
In July 1994, 10-15% of the original seed crop remained as seedlings beneath the six parent trees at Wollongbar and Davis Scrub. Seedling fatality was gradual over the five years (Figure 8.3). Seedlings gained height rapidly during the first summer, achieving an average height of 25-39 cm per tree by early May 1990. Height increased gradually over the following four years (final average height 50.1 cm (std. dev.14.1); Figure 8.4). At final census, seedlings from Davis Scrub were significantly taller than those from Wollongbar ( $T=4.99$ ,  $df=241$ ,  $p<0.001$ ).

Many seedlings showed evidence of insect damage and resprouting. Seedling mortality frequently followed observation of individuals with shrivelling stems and infestation by mealy bugs. Scale was found on leaves, on the stem and on the outside of seeds (see Appendix 1 for list of insects collected). Two large Geometrid caterpillars were found on seedlings; Geometrids are usually found feeding on foliage (CSIRO 1970). *Candalides absimilis* (Lycaenidae) larvae were not seen on seedlings at the study sites (although a decayed pupal case may have been collected on one occasion). This species feeds on the buds and young terminal leaves of plants in several families, including *C. australe* (Common & Waterhouse 1981) and is sometimes a minor pest of macadamia and *C. australe* in nurseries (D. Sands pers. comm.).

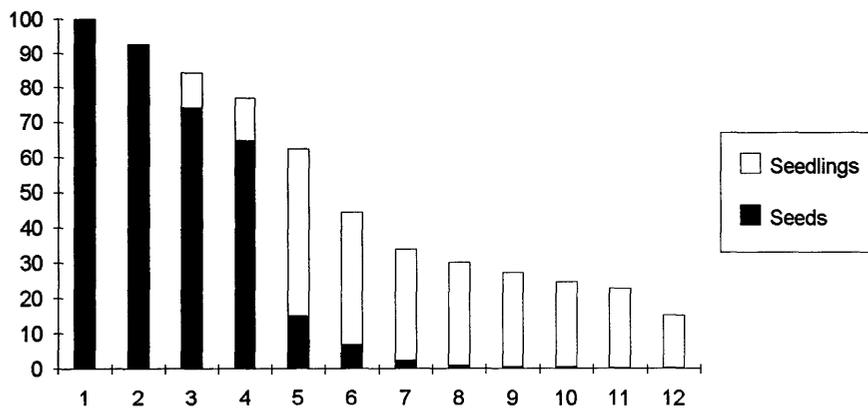
**Figure 8.3** Survival of seedlings from the 1989 cohort beneath three trees at each of Davis Scrub and Wollongbar. (The first graph gives axis labels: x axis=sample date, y axis= % of original seed crop surviving.)



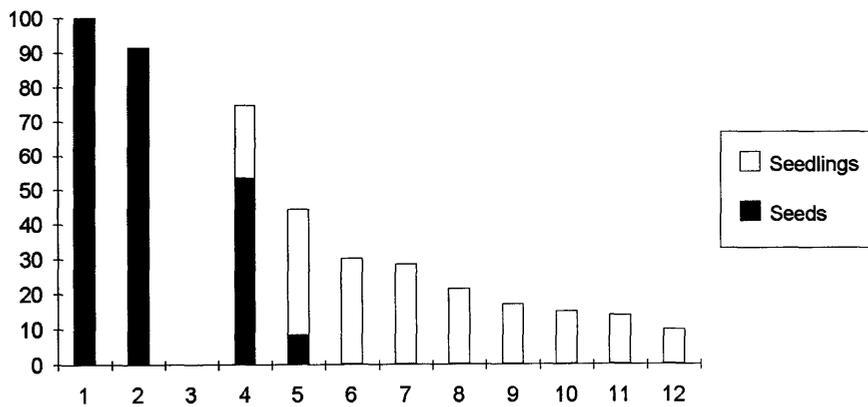
**Davis tree 1**



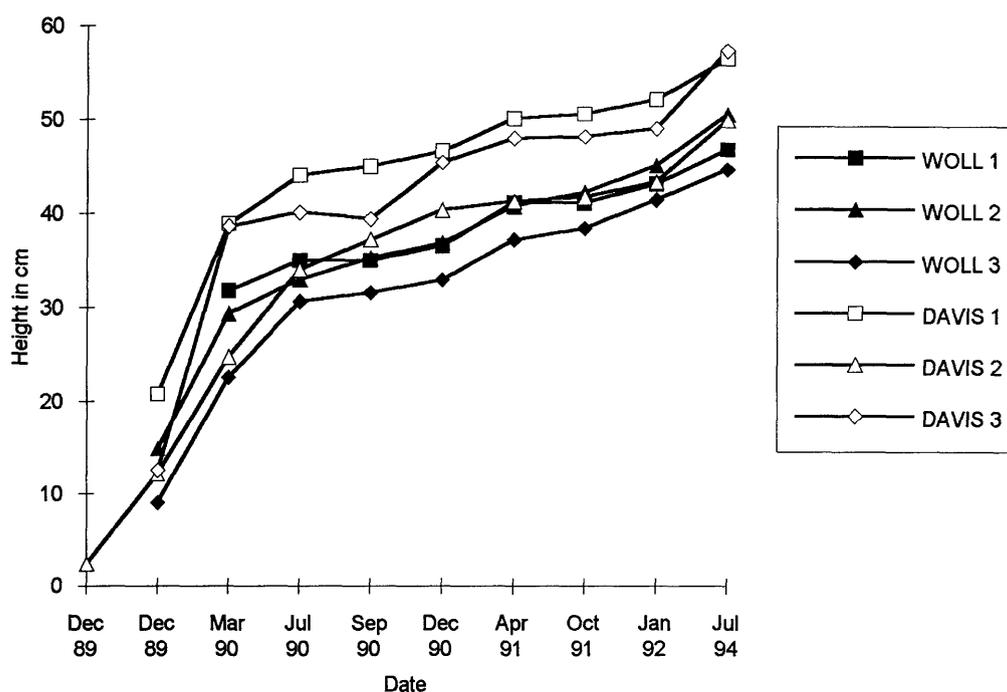
**Davis tree 2**



**Davis tree 3**



**Figure 8.4** Average height of seedlings from the 1989 cohort, beneath three trees at each of Davis Scrub and Wollongbar.

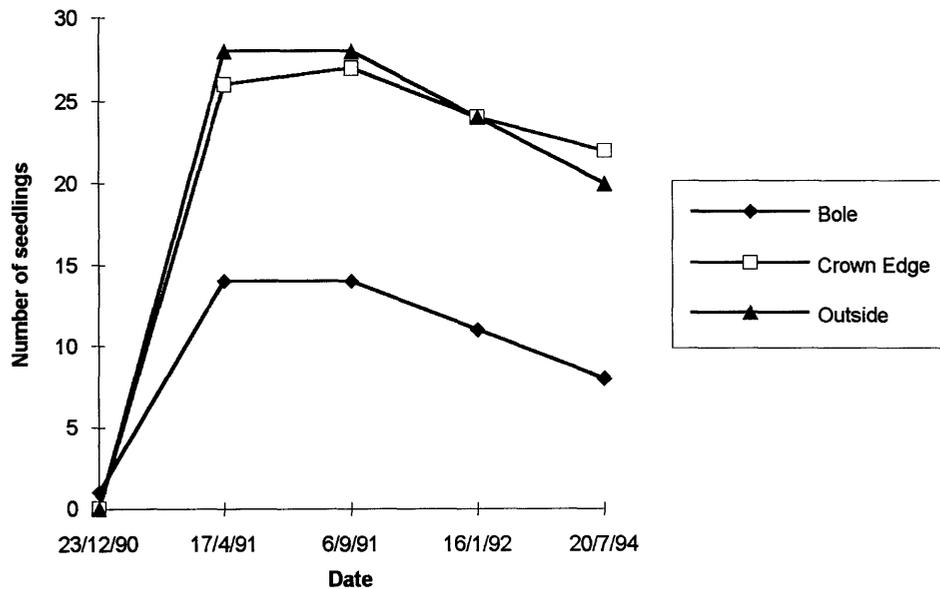


*1990 Distance predation experiment (Big Scrub and Davis Scrub)*

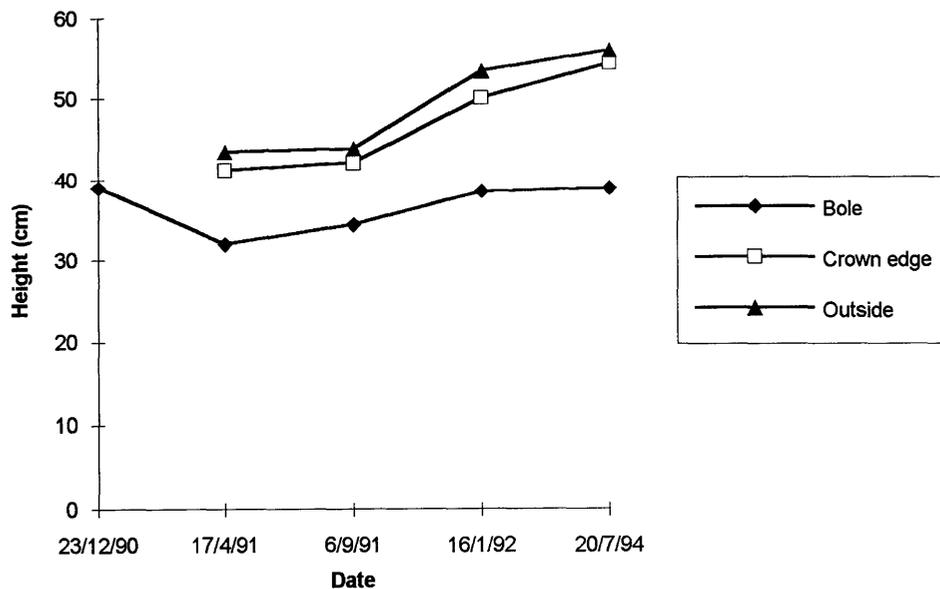
Out of 250 seeds, only four seedlings germinated within the plots at Big Scrub. Three of these showed early shoot initiation when inspected on 22 December (the other only had a root). In April 1991, one of the seedlings had disappeared, and the other three were 13.7, 15.9 and 30.1 cm in height. One seedling survived until December 1991 (height 34.5 cm), but subsequently died.

At Davis Scrub, fewer seeds survived predation beside the tree trunk than in plots at the crown edge and outside (Chapter 7). Of the seeds surviving, fewer seedlings (60%) germinated beside the tree trunk than at the other microsites (79% edge and 74% outside) (Figure 8.5). Distance had a significant effect on the height of seedlings surviving in July 1994 ( $F=2.3$ ,  $df=2$ ,  $p<0.1$ ; Figure 8.6). Average seedling height was significantly smaller beside the tree trunk (bole) than those at the crown edge and beyond (Student's  $T \geq 1.95$ ,  $df \geq 13$ ,  $p < 0.05$ ). Seedling height did not differ between the crown edge and outside ( $T = -0.2$ ,  $df = 13$ , ns). For all treatments, average seedling height increased slightly, and seedling survival decreased gradually between the end of the first rainy season (April 1991) and July 1994.

**Figure 8.5** Number of seedlings established at three distances from the parent tree, at Davis Scrub. (Initial  $n$  in July = 50 seeds per treatment. Number of intact seeds per treatment in late December: bole 31, edge 38, outside 46).



**Figure 8.6** Mean seedling height over time at three distances from the parent tree



Data point for 23 December 1990 is represented by one seedling only.

### 8.3.2 **Exclosure experiment: seed and subsequent seedling survival beneath conspecifics and nonconspecifics, and in canopy gaps (Davis and Big Scrubs)**

The first (pilot) exclosure experiment at Big Scrub demonstrated that seeds at all three microsites were prone to predation by rodents: There was no significant difference between Gap, BB and NON in number of seeds eaten over 11 days (29, 30 and 34% respectively,  $F=0.08$ ,  $df=2$ ,  $p=0.9$ ). In the subsequent 1 cm mesh trial, rodents also dug under two exclosures, and by early January, had damaged or removed eight out of ten seeds from one BB exclosure, and nine seeds from one gap exclosure. The remainder of the cages were intact. The invaded cages were treated as missing values, to give a balanced analysis of variance on final percentage survival.

In the full experiment, at least 19% of seeds survived as seedlings in all microsites. Seed source did not have a significant effect on seedling survival at each of the sites (Table 8.1). The interaction between site, microsite, and between-tree differences explained all significant variation in seed survival ( $F=6.04$ ,  $df=16$ ,  $p<0.001$ ). Throughout the experiment, seed survival was lower at Big Scrub than at Davis Scrub (Figure 8.7). In January, many of the seeds at Big Scrub were prone to fungal attack and by February, 86 out of 280 seeds were rotting. It is not known whether this is a site effect, or due to the re-installation of the experiment at Big Scrub three weeks after Davis Scrub. However, the relative survival of seedlings in the three microsite treatments was the same at both sites:

Peak seedling recruitment occurred in May. Expressed as a percentage of the surviving seeds, germination rate differed between treatments but was always high under non-conspecifics (Table 8.2). Pooled germination rate at Big Scrub was 79.4% and at Davis Scrub 74.7%. Final progeny survival (seedlings plus viable ungerminated seeds) was highest under non-conspecific trees at both sites, and lowest under adult *C. australe* (BB), but relative survival and survival over time occurred differentially at the two sites (Figure 8.7). Survival beneath conspecifics at Big Scrub was the lowest of all treatment combinations. There was significant variation between trees at both sites, resulting in a highly significant interaction between tree and microsite (Table 8.1).

Seedling height data showed a significant interaction between microsite and seed source ( $F=4.9$ ,  $p=0.01$ ). There was a significant effect due to seed source: although initially variable, from March 1992 onwards seedlings grown from Davis Scrub seed were taller than those from Big Scrub, within all treatments at both sites. However, the relative height of seedlings from the six treatment combinations (microsite x seed source) differed between

sites (Figure 8.8). Overall, when compared between microsites, seedling height was greatest under non-conspecific trees at both sites. However, the effect of microsite x seed source combination was variable. At Davis Scrub, seedling height in the Gap and beneath-conspecific (BB) treatments were similar in most samples, and generally less than both the NON treatments. At Big Scrub, seed source eventually had a greater effect on seedling height than did the treatments. Pooled average seedling height was higher at Davis Scrub than at Big Scrub, but site did not have a significant effect overall.

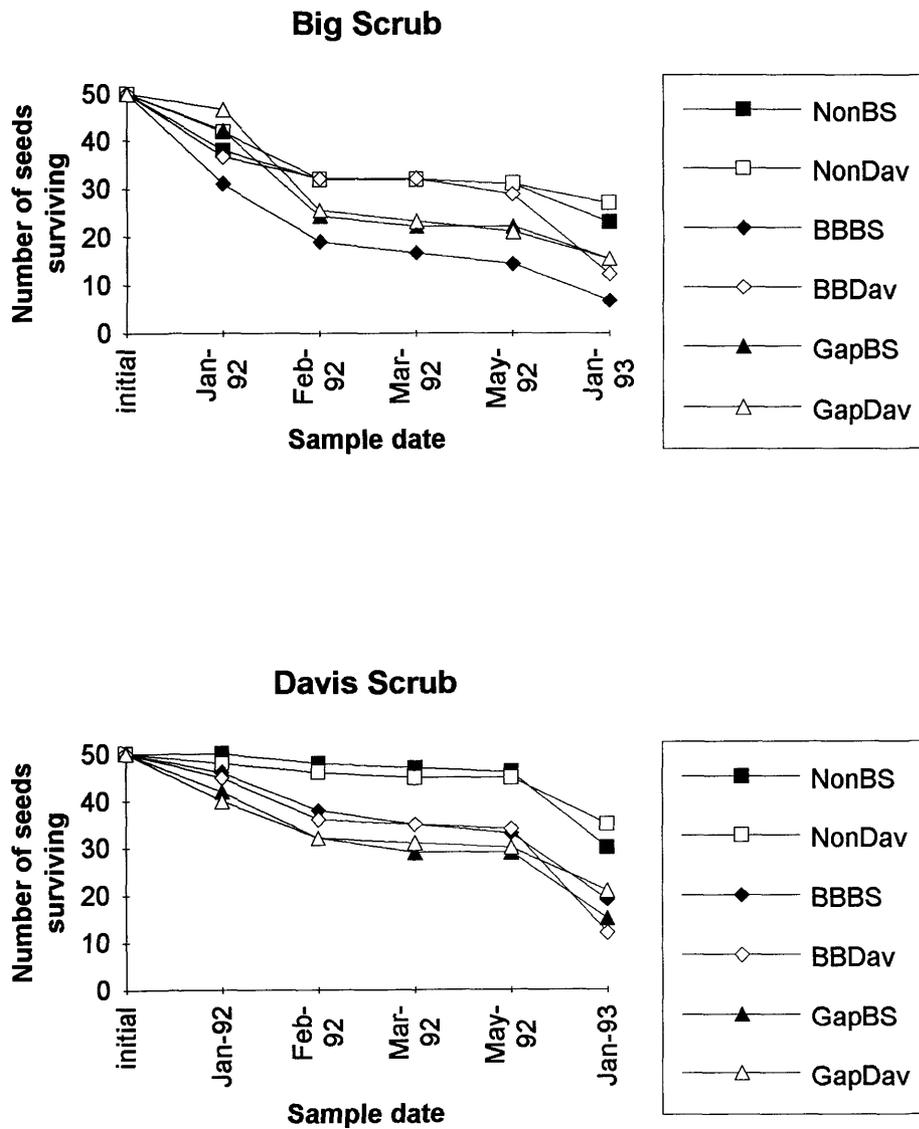
**Table 8.1** Nested analysis of variance on final seedling survival in enclosure experiment

Source	df	F	p
Site	1	9.49	<0.003
Microsite (within site)	4	19.18	<0.001
Seed source	1	2.52	0.118
Tree	4	2.60	0.045
Site*Seed source	1	0.13	0.721
Site*Tree	4	4.35	0.004
Seed source*Microsite	4	1.42	0.239
Tree*Microsite	16	6.04	<0.001
Tree*Seed source	4	1.08	0.376
Site*Tree*Seed source	4	0.60	0.664
Tree*Seed source*Microsite	16	1.56	0.109
Total	119		

(Two cages which were invaded by rodents were allocated a mean seed survival.)

**Figure 8.7** Survival over time for seeds in the enclosure experiment. Seeds were from two different seed sources (Big Scrub and Davis Scrub) placed together at three microsites within each site.

(Microsites: Small forest gaps (Gap), under adult *C. australe* trees (BB) and under adult non-conspecifics (NON). See Table 8.2 for description of ratio of seeds to seedlings in May 1992).



**Table 8.2** Germination as a percentage of seeds surviving in the enclosure experiment in May 1992.

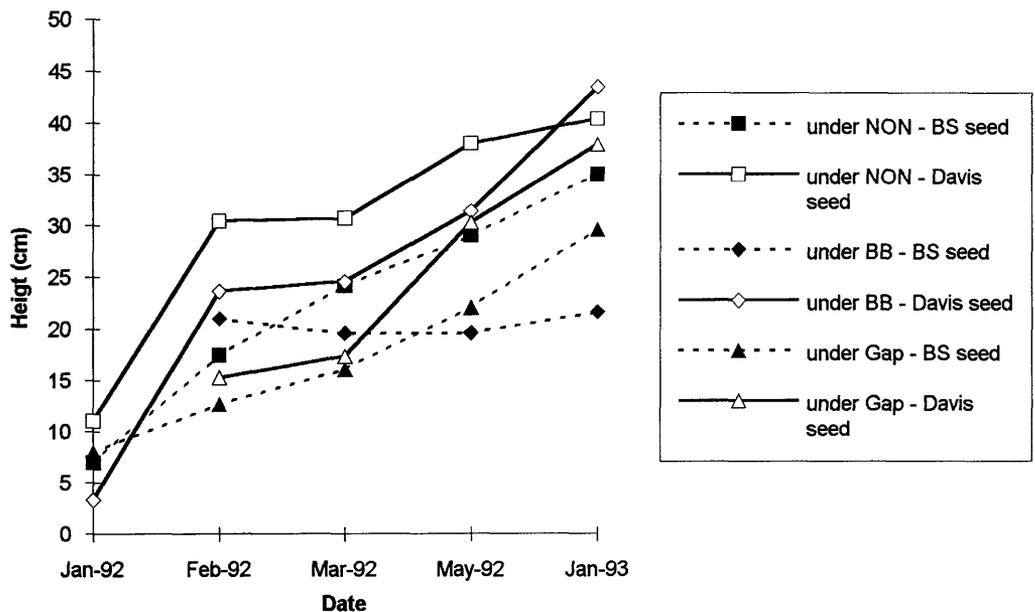
Initial number of seeds per treatment was 100. Davis Scrub enclosures were set up 8-11 November, Big Scrub 3-5 December. Seeds with the embryo and  $\geq 70\%$  of the cotyledon remaining were classed as viable.

Site	Microsite :			Total
	Non-conspecific	Beneath <i>C. australe</i>	Gap	
<b><u>Big Scrub</u></b>				
Seedlings	55	28	36	119
Seeds	11	13	6	30
Total	66	41*	42*	149
% germinated	83.9	66.7	85	79.4
<b><u>Davis Scrub</u></b>				
Seedlings	71	54	40	165
Seeds	24	17	25	66
Total	95	71	65	231
% germinated	74.7	76.1	61.5	71.4

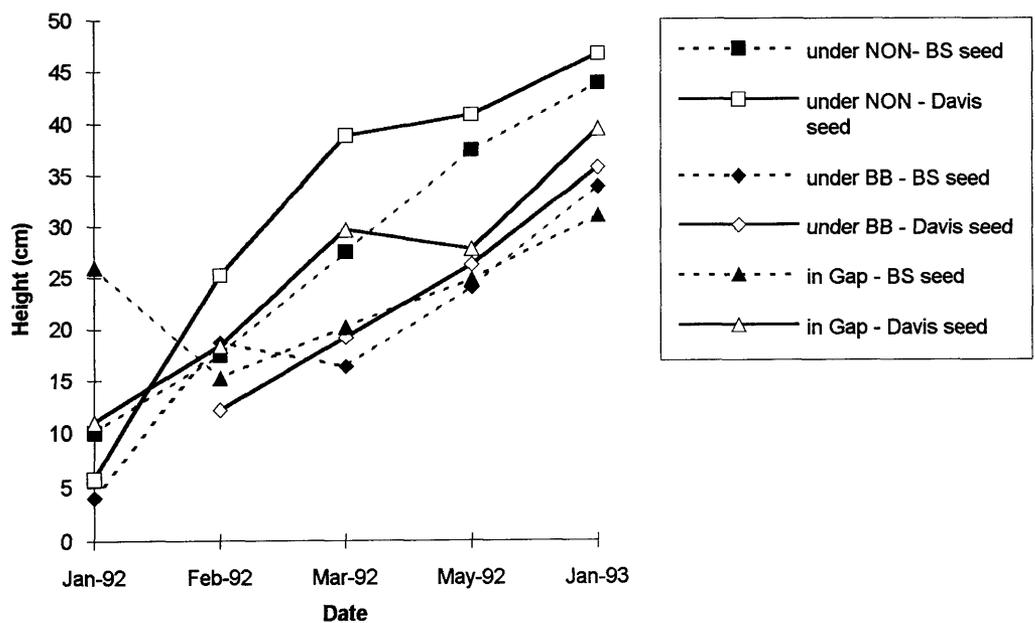
\* average survival allocated to one rodent-invaded cage.

**Figure 8.8** Mean seedling height over time at three microsites in the enclosure experiment

a) Big Scrub



b) Davis Scrub



**Table 8.3** Abundance of *C. australe* seedlings <1m height within 10m of adult trees at several sites.

Seedlings were censused in December-January 1989/90 within plots 5-10m wide and 10-20m long, centred on study trees.

Site	Tree No.	Area censused (m <sup>2</sup> )	Seedling abundance per 200m <sup>2</sup>	Mean no. m <sup>-2</sup>
Big Scrub	2	200	85	0.43
Boomerang	1	200	126	
Boomerang	2	200	210	
Boomerang	3	200	153	0.82
Wollongbar	1	100	840	
Wollongbar	2	160	687	
Wollongbar	3	100	986	6.9
Davis	1	200	472	
Davis	3	100	520	3.31

**Table 8.4** Mean total number of seedlings, juveniles, saplings and sub-adults along 50 m transects (2m wide) originating at study trees. (Four transects were censused at Big Scrub; three transects at each of the other sites, census date July 1994)

Site	Seedlings <1m	Juveniles 1-3m	Saplings >3m, <5cm dbh	Sub-adults 5-<20 cm dbh	Adults* ≥20cm dbh
Big Scrub	73	11	3.5	0.7	3.3
Boomerang	48.7	15	8	4	5
Johnston's	166.7	41	14.7	4.3	3.3
Wollongbar	321.3	12.3	4.3	4	3.3
Davis	536	31.7	15	5.3	5.3

\*Number of adults is measured within 10m either side of transect (i.e. 50 x 20m area).

### 8.3.3 Density and distribution of seedlings and larger size classes

Size class data was collected in three ways (Figure 8.2): within plots centred on study trees (seedling data, plus all sub-adults and adults), within nearest neighbour data (sub-adult and

adult), and within transects (seedling, sapling, sub-adult and adult). These three methods all sampled immature plants in the proximity of parent trees, but increasing distances were sampled away from the tree for the second and third methods. Analysis of size class data from all three methods will be presented together, to allow comparison of densities and size classes between near-tree (plot) and beyond-tree (parts of transect and near neighbours) individuals.

### *Seedlings (<1m)*

Prior to 1989, seedlings of *C. australe* were established under and near study trees at all sites (Table 8.3; pers. obs. at Johnston's Scrub). Both plot (pre 1989 seedlings) and transect (all seedlings) data (Table 8.4) showed that sites differed significantly in seedling abundance (one way ANOVA  $F=3.9$ ,  $df=4$ ,  $p=0.03$ ). Seedlings were significantly more abundant in plots and along transects at Wollongbar than at the two largest sites ( $t < -2.8$ ,  $df=2$ ,  $p < 0.05$ ). The mean density of seedlings in the transects was higher at Davis Scrub, but the variability between individual samples resulted in non-significant t-test comparisons. The higher seedling density recorded in the transects at Davis Scrub is because the transect originating at Davis Scrub tree 3 passed beside a treefall gap adjacent to a large productive *C. australe* tree, where seedlings were very abundant.

Analysis of transect data showed that seedlings were clumped with respect to adult trees, at all sites (Figure 8.9). The majority of seedlings occurred within 12 m of the trunk of an adult tree, with the largest number near the crown edge of the parent tree. The average radius of a *C. australe* tree's crown beyond the trunk was 4.89 m (std. dev.=1.66,  $n=25$  trees, four radian measurements per tree). Two transects at Big Scrub, three at Johnston's and one at Wollongbar appeared to have isolated seedlings dispersed beyond the immediate vicinity of an adult tree. However, there was no difference between sites in the position of seedlings beyond parent trees.

The relative abundance of seedlings <1m height in each site corresponded with the seedling survival from the 1989 seed cohort. However the relative abundance of the larger size classes differed between sites.

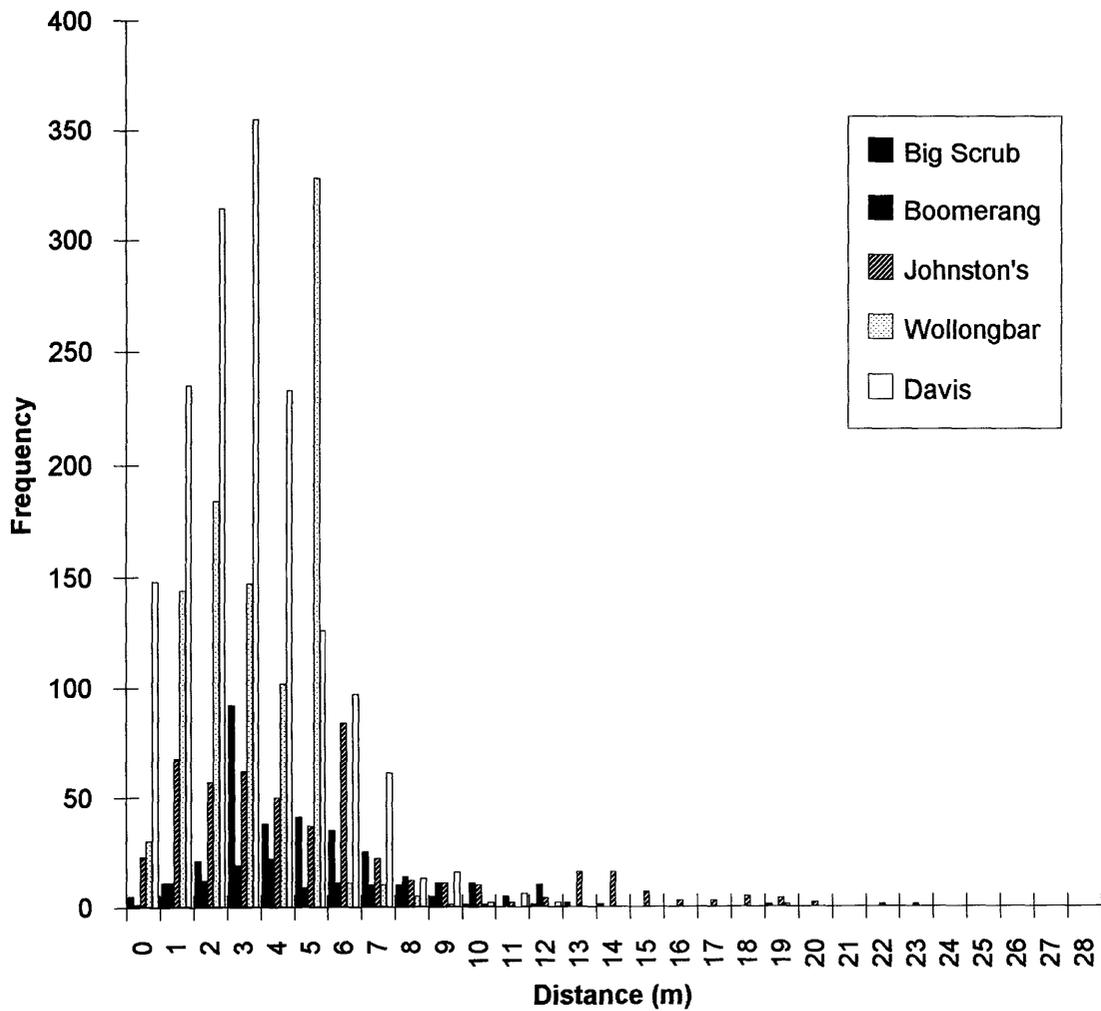
### *Juveniles (1-3m)*

The transect data (Table 8.4) showed that the abundance of juveniles was significantly higher at Johnston's and Davis Scrubs, when compared with Big Scrub and Boomerang Falls ( $t < -3.5$ ,  $df = 3$  or  $4$ ,  $p < 0.05$ ). Juveniles were less abundant at Wollongbar, which was

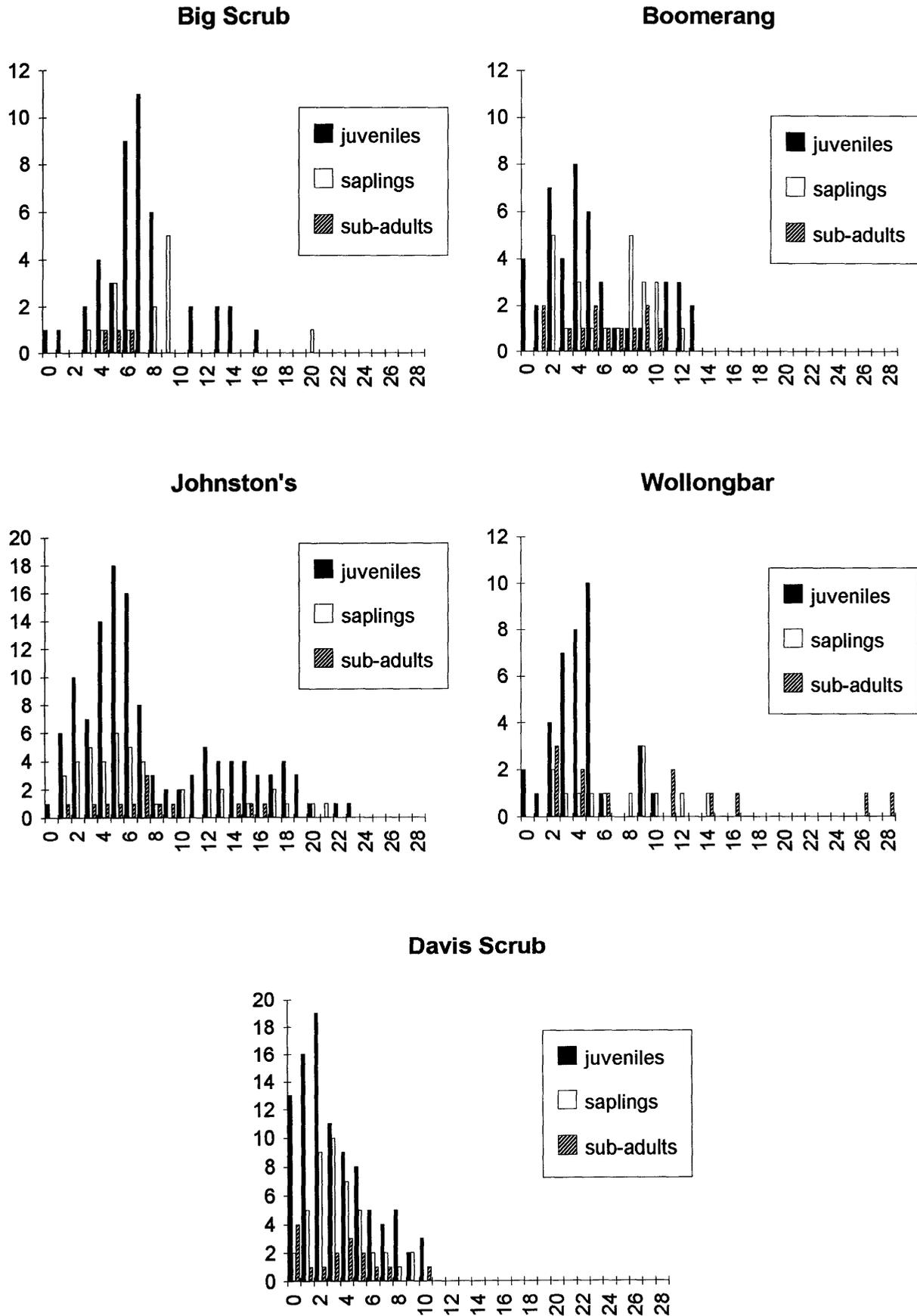
similar to the large sites. Juveniles were also clumped close to parent trees at the crown edge (Figure 8.10), and their distribution along individual transects matched that of the seedlings.

**Figure 8.9** Distribution of seedling distances from nearest adult conspecific at the five sites

(x axis: distance in metres from nearest adult *C. australe*, y axis: number of seedlings.)



**Figure 8.10** Comparison of the distribution of juvenile, sapling and sub-adult distances from the nearest adult conspecific, within each of the five sites



*Saplings (>3m and <5 cm dbh)*

The transect data showed a significant effect due to site on the abundance of saplings ( $F=5.31$ ,  $df=4$ ,  $p=0.013$ ). Abundance was low at Big Scrub and Wollongbar (Table 8.4). Saplings were significantly more abundant at Johnston's compared to Big Scrub and Boomerang ( $p<0.08$ ). The latter had significantly more saplings than at Big Scrub. The variability between replicates resulted in no significant differences between Davis Scrub and other sites, despite a higher mean. Across all sites, saplings generally occurred at distances where seedlings and juveniles were most abundant. The exceptions to this were two transects at Johnston's, and three at Wollongbar, where the tail of the distribution spanned the farthest seedling distances.

*Sub-adults (5-20 cm dbh)*

Close to the parent (plot data), numbers of sub-adults 5-20cm dbh were significantly greater at Johnston's and Davis Scrubs than at the other sites (Table 8.5). However averaged across a larger distance (transect), the number of sub-adults was similar between four sites (Table 8.4), the exception being Big Scrub which had fewer individuals (0.7 per transect). Most (87.5%) sub-adults occurred between 0 - 11 m from the nearest adult. However, seven individuals at Johnston's Scrub and Wollongbar were 14-16m and 26-28m from an adult.

*Adults*

Numbers of adults >20cm dbh did not differ significantly between sites for the transect data (one way ANOVA  $F=1.03$ ,  $df=4,11$ ;  $p=0.434$ ), but the sample size was too small to be conclusive (Table 8.4). Based on the larger sample of nearest neighbours, the number of individuals >20cm dbh differed significantly between sites (one way ANOVA  $F=3.73$ ,  $df=4,19$ ;  $p=0.02$ ), but was variable within all sites (Table 8.6). There were fewer neighbours at Big Scrub compared with the other sites, especially on the crest of the ridge where trees 1,3, 8 and 9 occurred. Number of neighbours at Boomerang was similar to the lower slopes at Big Scrub. Number of neighbours was markedly higher at tree 3 at Johnston's Scrub, in the previously logged side of the remnant, and at Davis Scrub. Abundance of trees at Wollongbar represents an underestimate, as two of the study trees did not have a full 30m radius within the canopy of the forest. There was no relationship between tree dbh or relative crown area and number of nearest neighbours (Table 8.6).

The nearest neighbour data showed that the distribution of adult size classes differed greatly between sites ( $F=9.4$ ,  $df=4,60$ ;  $p<0.001$ ; Figure 8.11). The relative proportions of nearest neighbours 20-50 cm dbh and larger did not correspond with the plot data, although they incorporated these trees (Table 8.5). This indicates that sizes of *C. australe* differ beyond, compared with the immediate proximity of the study trees. The plot data show that the most marked differences between sites were for the smaller size classes discussed above. The abundance of trees >20-50 cm dbh was slightly higher at Davis and Wollongbar, but not significantly different between sites for trees >50 cm dbh (Table 8.5). The nearest neighbour data showed a higher abundance of trees 20-40 cm dbh at Davis and Johnston's Scrub, but not at Wollongbar, although the latter could have been affected by the truncated sample area due to the remnant edge (Figure 8.11). Both near-study tree data (plot data, Table 8.5) and neighbour samples (Figure 8.11) confirm that trees 20-50cm dbh are most abundant at Davis Scrub.

### *Summary*

There are six common results, despite differing sample sizes and methods used to collect the data.

- Seedlings are more abundant at Davis and Wollongbar.
- Juveniles and saplings are more abundant at Johnstons' and Davis.
- Sub-adults and adult 20-50 cm dbh are relatively abundant at Davis Scrub (but not at Wollongbar).
- Seedlings and some medium-sized classes (saplings, sub-adults, small trees) are of intermediate to high abundance at Johnston's Scrub.
- Both the plot and nearest neighbour data show that the average number of *C. australe* is higher at Johnstons' Scrub, and significantly higher at Davis. The mean number of *C. australe* individuals at Wollongbar does not differ from Big Scrub F.R. and Boomerang Falls, although neighbours were clumped closer to the study trees at Wollongbar.
- Large trees >50cm dbh are less abundant at Wollongbar and Johnston's.

**Table 8.5** Mean number of sub-adults and adult individuals per size class (cm dbh) compared between *C. australe* and individuals of all other species.  
(Mean of three 20 x 20 m vegetation plots per site)

diameter (cm)	<i>C. australe</i>			Mean No.	Other species			Mean No.	Mean	std. dev. (of total No./plot)
	5-20 (subadults)	>20-50 (adults)	>50	<i>C. australe</i> individuals per plot	5-20 (subadults)	>20-50 (adults)	>50	of individuals other spp.	total No. all individuals per plot	
Big Scrub F.R.	1.3	0.3	2.0	3.7	36.3	8.0	2.0	46.3	50.0	(11.5)
Boomerang Falls	5.0	0	2.0	7.0	30.7	8.3	1.7	40.7	47.7	(9.7)
Johnston's Scrub	10.0	0.3	1.3	*11.7	15.3	4.7	3.0	33.0	44.7	(7.0)
Wollongbar	2.7	3.0	1.3	7.0	49.0	7.7	0.7	57.3	*64.3	(20.2)
Davis Scrub	20.7	2.7	1.7	*25.0	18.0	4.7	2.0	24.7	49.7	(10.0)

\* majority are 5-20 cm size class

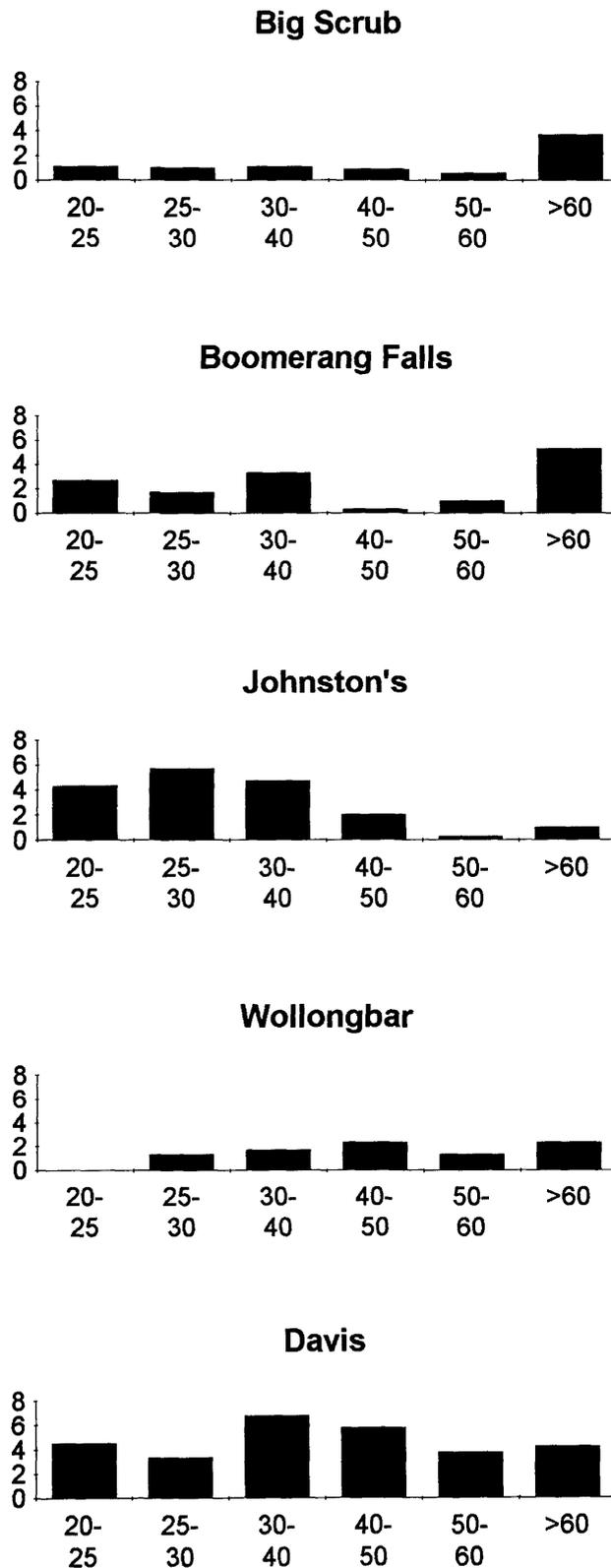
**Table 8.6** Study tree statistics: dbh, crown area and number of nearest neighbour trees ( $\geq 20$ cm dbh) within 30m radius. (Data are mean and (std. dev.).)

Site	No. trees	dbh (cm)	Crown radius	No. nearest neighbours
<b>BIG SCRUB</b>				
	10	100.3 (22.5)	5.1	8.4 (3.9)
<b>BOOMERANG</b>				
	3	84.2 (16.7)	5.2	14.3 (3.8)
<b>JOHNSTON'S</b>				
	3	112.0 (51.0)	5.3	18.0 (15.7)
<b>WOLLONGBAR</b>				
	3	53.9 (13.6)	4.3	8.7 (2.9)*
<b>DAVIS</b>				
	5	106.8 (27.8)	4.4	29.7 (7.2)*

\* One or two trees located near edge of remnant, with incomplete 30m radius of forest. Wollongbar estimate corrected for area = mean number of nearest neighbours 11.8 (2.4). Davis mean is based on 4 trees with complete circle of neighbours.

**Figure 8.11** Size distribution of adult nearest neighbours ( $\geq 20$  cm dbh) within 30 m radius. (n=3 core trees)

(x axis: size categories of adult trees in cm, y axis: frequency. Wollongbar sample includes two trees at the edge of the remnant, therefore the number of neighbours is lower than otherwise anticipated.)



### 8.3.4 Floristic composition of vegetation plots

#### *Species richness and composition*

Species lists from surveyed plots for the five sites are given in Appendix 6, and general species composition is discussed in Chapter 3. All four smaller sites had some species in common with Big Scrub F.R., the number of species decreasing with increased distance from Big Scrub F.R.

Wollongbar and Big Scrub had a higher species richness than the other three sites (Table 8.7). Out of 48 species for which regeneration strategy information was available (Appendix 7; Hopkins *et al.* 1976, Kooyman unpublished, Stewart 1995), Wollongbar had a significantly higher proportion of early and late secondary species ( $\chi^2 > 2.7$ ,  $df=1$ ,  $P < 0.1$ ). Seven of the eleven species recorded only at Wollongbar, were early or late- secondary succession species. Of the other four, three were introduced species. In contrast, the plots at Big Scrub F.R. and Boomerang Falls had the highest proportion of known mature phase tree species (Table 8.7).

Davis Scrub which had a lower species diversity (H and E) than the other four sites, which were similar (Table 3.6 and 8.7). This is due to the lower species richness and disproportionate abundance of *C. australe* relative to the numbers of individuals of other species.

#### *Tree numbers and overall size class distribution*

This section compares the abundance of *C. australe*, relative to individuals of other species within the vegetation plots. Size classes of trees from the vegetation plots are shown in Table 8.5 and compare *C. australe* to the total for all other species.

There was no significant effect due to site on total number of tree individuals per plot (one way ANOVA,  $F=1.1$ ,  $df=4,10$ ;  $p=0.41$ ). At Wollongbar, mean number of tree individuals per plot (65) and mean number of non-*C. australe* individuals between 5-20 cm dbh was higher than for all other sites, but variable. Davis scrub had a significantly higher number of *C. australe* individuals per plot and a lower total number of species, that is, *C. australe* was more dominant at Davis than at the four other sites ( $\chi^2 > 17.4$ ,  $df=1$ ,  $p < 0.0001$ ). Compared with the other sites, both Davis and Johnston's Scrub had a higher number of *C. australe* individuals 5-20 cm dbh, matched by a much lower number of individuals of other species in size classes 5-20 and 20-50 cm (Table 8.5). At Davis, this high number of *C. australe* was especially obvious in the 5-10cm size class for all 3 plots (Appendix 8). Number of mature

trees of all species (>50cm dbh) did not differ significantly between four sites, but was lower at Wollongbar.

**Table 8.7** Species composition and Shannon-Wiener species diversity of five remnants, based on a vegetation survey of three 20 x 20 m plots per site.  
H=Shannon-Wiener diversity index, Krebs 1978.  
Stage 3 species include early and late secondary tree species. Stage 4 species are primary forest species (after Hopkins *et al.* 1976).

	Mean number species per plot	std. dev.	Total species per site#	Diversity index H	Stage 3 (B/C) species	Stage 4 (or D) species
Big Scrub F.R.	18.7	4.6	38	4.0	8	18
Boomerang Falls	17.3	3.2	33	4.18	6	16
Johnston's Scrub	17.3	3.5	32	3.72	2	14
Wollongbar	20.0	4.0	35	4.13	13	11
Davis Scrub	12.0	1.0	26	2.8	6	10

# 2 species were common to all plots, 3 species were common to all sites.

## 8.4 DISCUSSION

### 8.4.1 Abundance of seedlings and larger size classes

A marked difference occurred between sites in seedling abundance. At the large sites, results showed that seedling establishment had occurred in previous years, but the density was markedly lower than at the smaller sites. Mammalian seed predation appears to remove most seeds at Big Scrub and Boomerang Falls, and it is hypothesized that only seeds produced in heavy-fruiting years or those produced when rodent populations are diminished, survive to germinate at large sites. Whether the survival of young seedlings is further affected by vertebrate herbivores in subtropical forest is not known. There are no data on vertebrate herbivory of (unprotected) *C. australe* seedlings in the Big Scrub, or other forests of northeastern New South Wales. However, two sources suggest that rodents, and perhaps other native herbivores damage young seedlings: In the rodent-invaded exclosures at Big Scrub, several seeds clearly had the root tip bitten off. In north Queensland, Osunkoya *et al.* (1992) found that survival of unprotected 3-5 week old

*C. australe* seedlings (ca 19-22 cm height) was markedly lower than those protected in cages, at a continuous forest site where *R. fuscipes* (Osunkoya 1994) and other potential herbivores occurred. In contrast, and perhaps similar to Davis Scrub, survival of unprotected seedlings was high in the remnant site where no *R. fuscipes* were caught (Osunkoya 1992). Mortality was apparently due to predation of the seeds still attached to the seedling: Osunkoya *et al.* (1993) found that protection of seedlings in cages had little effect on growth, suggesting that once seedlings had established and the seed was no longer a target for predation, the influence of vertebrates is negligible.

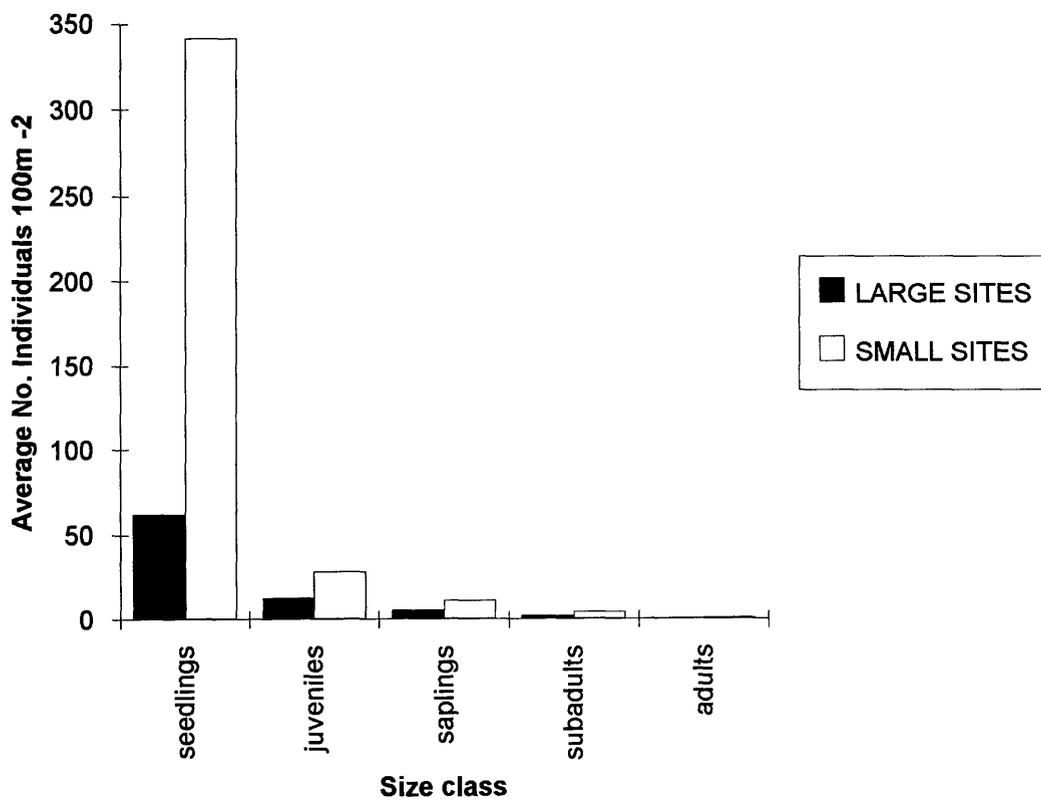
The three smaller sites showed a significantly larger total number of seedlings, and at two of these, Johnston's Scrub (21.5 ha) and Davis Scrub (10.5 ha), there was also a significantly larger number of juveniles and saplings (Figure 8.12). Assuming a relatively constant age-specific mortality across years, the size class data from the transects indicate that a significant proportion of seedlings survive to become juveniles and saplings at all sites. At Johnston's and Davis Scrubs, an elevated seedling establishment has transferred to an increased number of individuals in the next two size classes.

However, no sites showed an overall increase in number of sub-adults. It is not known whether this is because the increased survival of immature plants is a relatively recent phenomenon, or whether subsequent mortality reduces the saplings to a density of sub-adults similar to other sites. The similar numbers of sub-adults and adults across 50m transects at Johnston's and Davis Scrub, compared to other sites, indicates that any shift in vegetation dominance due to decreased predation has been operating for less than the lifetime of the saplings. This could represent a considerable period of time. The seedling survival curves for the 1989 cohort at Davis and Wollongbar show a slow attrition of seedlings over 5 years. The seedlings <1m height at each site are, therefore, probably more than a decade old, having achieved only a slow height increment from the 50 cm average achieved after 5 year's growth. The large seed would assist with nutrient supply and tolerance to defoliation (Foster 1986, Armstrong & Westoby 1993). Juveniles and saplings could also live a long time (see Clark & Clark 1992). Connell *et al.* (1984) found that roughly 80% of large saplings (0.8m height -2.5cm dbh) were still present in rainforest plots after 15 years, and many of these are still alive (P. Green pers. comm.).

There is some evidence of an increased survival to subadult size, close to the large adult trees (within 10m) at Davis Scrub: the plot data showed that there is a relatively high number of subadults, and a corresponding low number of subadults of other species. There is a similar but less marked increase at Johnston's Scrub. At these two sites, there is also a larger number of nearest neighbours in the 20-40cm size range. The conclusion reached is

that a combination of selective logging and grazing in the past, and altered seed predation levels as a result of forest fragmentation, has resulted in an increased establishment of *C. australe*. This effect is currently localised, due to the clumped distribution of seedlings close to parent trees.

**Figure 8.12** Size class distribution of *C. australe* in large (Big Scrub and Boomerang Falls) and small remnants (Johnston's, Wollongbar and Davis Scrub).



That an increase in larger size classes has not occurred at Wollongbar is probably due to edge effects (Chapter 2), such as drier soil conditions, increased sunlight, wind shear, and the greater competition from colonising species (Lovejoy *et al.* 1986, Ng 1983). Estimates of the width of the edge effect in rainforest range from 50 to 500m (Lovejoy *et al.* 1986, Laurance 1991b). Wollongbar is a narrow remnant with a maximum width of 60m, and is clearly all edge. This is evident in its higher proportion of secondary forest species (Table 8.7). *C. australe* is a shade tolerant primary forest species (Herwitz 1993, Osunkoya *et al.* 1992) and the conditions at the forest edge are likely to place it at a competitive disadvantage. In support of this, the enclosure experiment demonstrated that year-old seedlings had a greater survival and height under the forest canopy (beneath non-conspecifics) than in forest gaps. In contrast, Osunkoya *et al.* (1992, 1993) found that transplanted seedlings had a similar or higher survival and a greater seedling biomass in forest gaps than in the nearby forest interior, although height differed little. Three differences are important here. Firstly, the seeds collected from the Atherton Tableland (Osunkoya 1994) were nearly half the fresh weight of those collected in this study. Comparison of height data (see Figure 1 in Osunkoya *et al.* 1993) showed that seedlings from Big Scrub proper were taller, as expected from their relative seed size (e.g. Howe & Richter 1982). Large seeds have a greater adaptive value in the shade, enabling seedlings to be more tolerant of low-light conditions and competition (Foster 1986). Although light environment may not be critical until the endosperm is exhausted (Grime & Jeffery 1965, Howe *et al.* 1985), this does not explain the differences between the two studies: 38% of the seedlings in the enclosure experiment still had a portion of the seed attached after a year, and the same may be expected of those at Atherton. In addition, seedlings beneath non-conspecific trees remained taller than those in gaps at both Davis and Big Scrub F.R, after 2 and 1/2 years (R. Lott unpublished data).

Secondly, although average annual rainfall is very similar between Lismore (1358 mm) and Curtain Fig (1401mm), differences in seasonal distribution of rainfall can be expected to affect the climatic extremes experienced by seedlings in gaps at the two locations. Thirdly, desiccation of seeds within the gap prior to germination, may explain the lower seedling performance in gaps in this study compared with the transplanted seedlings used by Osunkoya *et al.* (1992). Many experiments which have used transplanted seedlings have not acknowledged this potential desiccation effect.

Other factors also contribute to differences between sites in seedling establishment and survival. For example, although predator choice and germination rates did not differ between seeds collected from Big Scrub and Davis Scrub, seedlings from Davis Scrub seed were taller than those from Wollongbar (Figure 8.4) and Big Scrub (Figure 8.8), and

potentially more competitive. Seedling height may have a genetic basis, as well as being due to seed size, as seeds collected from Davis Scrub were a similar weight to those from Big Scrub (Table 4.3). Seedling survival could also have differed between the study sites due to insect herbivory and fungal pathogens. Whether these compensate for the lack of vertebrate herbivory at the small remnants is not known, but the high survival of seedlings at Davis and Wollongbar suggests that this is not so. In conclusion, the overriding influence on seedling recruitment was level of seed predation.

#### 8.4.2 Seedling dispersion relative to adult trees

The combined effect of dispersal and seed and seedling mortality influences the spatial patterns of saplings and adult trees. Dispersal theory predicts that seeds which are dispersed away from the parent plant will escape disproportionate predation and within-species density-dependent mortality (Janzen 1970, Connell 1971), colonise disturbance, and/or locate microhabitats suitable for establishment and growth (Howe and Smallwood 1982). If seed and seedling mortality is disproportionate under the parent tree, then low numbers of established seedlings can be expected under the parent, and survival of those dispersed beyond the region of high seed density will be higher. For example, the high density *C. australe* seedlings which established in 1989 under parent trees at the small remnants could be expected to die at a greater rate than those few that establish further away. Alternatively, juvenile and adult tree distributions could reflect the seed shadow as originally dispersed, due to random mortality of seeds and seedlings with respect to distance from the parent (Hubbell 1979, Howe 1986).

At each of the five sites, *C. australe* seedlings, juveniles and saplings were clumped near the crown edge of the adult tree, with a small tail of the distribution away from adult trees. There was no evidence that seed survival, seedling recruitment or seedling growth was favoured in gaps. Several factors explain the clumped seedling distribution within the forest interior. Firstly, the distance experiment showed that seeds which fall close to the parent have a higher probability of predation (Chapter 7), and of those remaining, a smaller proportion successfully establish as seedlings (this chapter), compared with seeds at the edge of the parent crown, and those dispersed 10-20 m away. Secondly, there was some evidence of density-dependent mortality of young *C. australe* seedlings under parent trees: Invertebrate damage to seedlings was greater beneath conspecifics than beneath other trees or in gaps (R. Lott unpublished data, enclosure experiment). In particular, stem damage by Hemiptera often caused young shoots to wilt and die. Even though *C. australe* seeds can resprout several times after root tip and/or shoot damage, and partially damaged seeds will germinate (Chapter 7), invertebrate damage caused some seedling death. Observations at

Davis Scrub indicated that at times fungal or insect attack may kill several m<sup>2</sup> of seedlings beside the trunk of a parent tree. In addition, in the small remnants, undispersed seeds which germinated within the pod became root bound, and most subsequently died (pers. obs.). Thirdly, seedlings which establish away from the parent may have less competition for light and nutrients. The exclosure experiment indicated that seeds placed beneath the crown of other species were more likely to germinate, and seedlings were taller than those beneath the parent crown or in forest gaps. Possible reasons for this are escape from predation and fungal pathogens, increased light, and decreased competition from the parent tree. A fourth reason for the clumped distribution of seedlings at the edge of parent trees may be a lack of seed dispersal (in combination with *C. australe*'s apparent tolerance for germination close to adult trees).

The distribution of juveniles and saplings appears to match that of the seedlings, that is, mortality does not result in a different distribution with respect to adult trees. The distance experiment suggests that once established, seedlings at different distances from parent trees have a similar chance of survival: seedling survival curves beside the tree trunk (bole), crown edge and outside shared a similar slope, despite differing initial numbers of seedlings. In combination, these results indicate that seeds and seedlings suffer density-dependent predation, but this effect is less for larger size classes, so that their distribution reflects that of the seedling recruits. This is consistent with the clumped distribution of many other tropical trees (Hubbell 1979, Hubbell & Foster 1983). It does not mean that density-dependent predation is not operating (Clark & Clark 1984). Rather, unless density-dependent mortality is extreme, more immature plants are likely to be found under parent trees than away, because most seeds fall beneath parent trees (Hubbell 1980). A similar logic explains why density-dependent predation has not reduced the abundant seedlings at the small fragments to a similar number and dispersion as in the larger sites: Rates of mortality may not be extreme enough to deplete the increased number of seedlings in the small sites. Further, the small sites had an elevated density of older seedlings close to parent trees, indicating that seedling mortality has not been disproportionate in previous years, and that the pattern of seed survival observed in 1989 (Chapter 6) has also occurred within previous cohorts.

There is some evidence that juveniles and saplings are clumped closer to parent trees (inside the crown area) at Davis Scrub and Boomerang than at the other sites, and that fewer immature plants occur beyond the adult trees' crowns (none occur beyond 13 m). However lack of seed dispersal by fauna can not be argued for these sites, for three reasons. Firstly, if a conservative estimate of reproductive age is used, then adults >40 cm dbh occur less than 30 m apart at all study sites (Figure 8.11). Therefore, the maximum measurable

distance between a seedling and an adult is not much larger than the radius of the largest tree crown (10.2 m) and whether dispersal is by water, gravity or vertebrates would be difficult to distinguish. Vertebrates may only move the seeds short distances, such as the paint-marked seeds found transported up to 19m during this study. This could mean that the seeds found 10-28 m from an adult tree have been dispersed by vertebrates, but the distribution of distances are insufficiently different between the sites to demonstrate altered dispersal. Secondly, the higher abundance of adult nearest neighbour trees at Davis and Johnston's Scrub means that even if dispersed, seeds have a higher probability of landing close to an adult tree. Thirdly, sites differ in topography, and therefore some sites are more likely to have seed dispersed by water. This means that opportunities for dispersal differed between the sites pre-fragmentation.

In summary, there is clear evidence that the sites differ in number of *C. australe* seedlings, and that in the past this has resulted in higher relative abundances of some larger size classes at Davis and Johnston's Scrub. The data indicate that in small remnants, seed predation is the major factor influencing the number of *C. australe* germinants, and once germinated, seedlings have a relatively high survival rate. However, there is insufficient evidence to demonstrate that seedlings are distributed differently in space between the five sites. Further research should investigate whether there is a difference between sites in seed dispersal, seedling survival, and seedling herbivory by vertebrates.

## Chapter 9. GENERAL DISCUSSION AND CONCLUSIONS

### 9.1 Seed and seedling ecology of *Castanospermum australe*

#### *Seed production*

Seed crop size varied significantly between trees, and between years. In all three years, at least some individuals produced seeds at each per site, indicating a reliable annual seed production. *C. australe* is reputed to produce heavier crops than those encountered in 1989, although there are no data to substantiate this (NSW and Queensland Departments of Forestry, pers. comm.). If particularly high seed yields do occur, this could have a marked effect on levels of seed predation and seedling recruitment. For example, in natural forest, satiation of predators during heavy seed crops can result in reduced levels of seed attack (Silvertown 1980, Nilsson & Wastljung 1987) and allow some seeds to survive. The predator satiation hypothesis assumes that escape from predation results in seedling recruitment. This seedling recruitment would presumably be evident in the vegetation as a year-class effect. In a study of three shade-tolerant canopy tree species, de Steven (1994) found that each species had a year of exceptionally high seedling recruitment. Because seedling survival was relatively constant and high after the first few years of life, such large cohorts persisted as a year-class effect in the seedling population and thus maintained seedling numbers over time (de Steven 1994).

Such a year-class effect would explain the existence of previously established seedlings at Big Scrub F.R. and Boomerang Falls, where the distribution of previous seedlings under and at the edge of the parent crown, contrasts with the complete removal of seeds beneath the trees in 1989. This indicates that in some years, seed production is high enough to satiate the predators foraging beneath the tree. The effectiveness of mast-seeding may depend more on the functional response (proportion of the seed crop) than on the numerical response (number of seeds eaten) of the predators (Kelly 1994). For example, based on the relative quantity and timing of seed removal (Figure 6.3b), *C. australe* seed crops may not need to be much larger than those at Boomerang Falls in 1989, to satiate the predators until the germination season. Further research should investigate the spatial and temporal variation in seed production and seedling recruitment across several years, to determine the importance of large seed crops for seedling recruitment in natural forest, and in small remnants.

### *Seed predation*

Data from Big Scrub F.R. and Boomerang Falls indicate that mammals are the main predators of *C. australe* seed. An average of 2 to 3 seeds per tree per night were damaged or removed at Big Scrub and Boomerang Falls during the period of fruitfall. Estimates in October 1989, indicated that rodents ate 1.5 to 11.7% and *Trichosurus caninus* ate 7.8 to 12.9% of the seed crop *in situ* (beneath the parent trees) at Big Scrub, Boomerang Falls and Johnston's Scrub. A large proportion of the seed crop was carried away from beneath the trees. Assuming at least 34% of missing seeds at Big Scrub were removed by mammals (Chapter 6), total removal by mammals exceeded 60% at the end of the fruiting season. At this time, all seeds had been removed from beneath the three study trees. In contrast, insects were responsible for 0.001-5.7% of seeds damaged at the three largest sites. Other studies have reported 75-99% predation between seedfall and germination (Schupp 1990 and references within).

The reason for the higher *in situ* predation by rodents observed at Johnston's Scrub is not known, although increased seed predation in the absence of *T. caninus* is a possible explanation. Data recorded from the 2.5 cm mesh exclosures at Big Scrub showed that rodents ate 30% of the seeds when large mammals were excluded (and ate more of each seed). Terborgh & Wright (1994) also found higher predation levels in semi-permeable exclosures when large mammals were excluded. However they cautioned that when larger mammals are excluded, these exclosures may become privileged foraging grounds for small rodents. Nevertheless, whether seed predation by one species is higher in the absence of the other has ramifications for levels of seed predation and seedling recruitment in forest fragments.

Removal of seed varied between years. Although this study did not show an effect of seed crop size or abundance of neighbours with fruit crops, these factors probably influenced the level of seed predation in any one year. However, the timing of seed release and the relative abundance of fauna appeared to have a greater effect on the capacity for seed removal. Fluctuating mammal populations (see Table 5.8 and Appendix 3) would also affect annual levels of predation. In this study, small mammal trapping was only conducted once during June, in each year. Capture rates were not high in June 1989, however earlier in the year, Queensland Forest Service surveys found that *R. fuscipes* was more abundant than usual (G. Watts pers. comm.). This may explain the high rates of seed removal at Big Scrub in 1989. Factors including seed availability, availability of other foods, and each mammal species' population size are likely to cause the observed variations in seed removal within the season (Figure 6.3).

Proximity to adult trees, and between-tree variation affected the spatial pattern of seed predation. At both Davis Scrub and Big Scrub, distance- or density-dependent predation occurred, with insects most important at the former, and mammals at the latter site. At Big Scrub, all seeds and seedlings recruited in 1989 and 1990 were eventually removed, consistent with the prediction that mammals are efficient searchers over their foraging area (Terborgh *et al.* 1993, Howe 1993), however, older seedlings were clumped close to parent trees. Therefore, either density-dependent predation is not sufficiently strong to deplete crops in high seed years, or overall levels of predation are low in some years. Because seed predation by insects was minimal, density-dependent predation is expected to have little effect on patterns of seedling recruitment, in remnants where *T. caninus* and *R. fuscipes* are absent.

Topography has been shown to influence small-scale pattern of species composition and size class distribution of tropical forest trees (Basnet 1992, Williams *et al.* 1969). The largest site in this study, Big Scrub F.R., has a larger range of topography and microsites than occur in the smaller remnants. A larger number of trees were also studied at this site. During 1989-1991, total seed removal rates at Big Scrub varied between 47-100% per tree between July and September. Some trees, such as tree 1, consistently showed high removal rates (Tables 5.9, 5.10). Conversely, some trees consistently had large quantities of seeds lying untouched beneath them, such as trees 7 and 10. Plots under these trees were the only ones which still had seed remaining beyond November 1991 in the palatability experiment. Although trees 7 and 10 both had large seed crops and a high abundance of nearest neighbours with fruit, they also occurred on lower slopes, where the forest was more closed, dark and moist. Seed removal rates were apparently higher for trees on ridges, indicating that habitat factors may determine the activity of seed predators. For example, the presence of tree hollows, proximity to creeks, and topographic position are important factors determining the abundance of *T. caninus* in Victoria (Lindenmayer *et al.* 1990), although habitat requirements of rainforest *T. caninus* are not known. Climatic conditions may also be important, affecting fruit availability and mammal abundance. Observations during the drought subsequent to 1991 indicated that seed removal rates were lower than had been observed in 1989-91, and some intact seeds were seen under tree 1 in 1992 and 1994. Between tree variation was also evident at Davis Scrub, but to a lesser extent, reflecting the smaller area and more uniform topography of the site.

### *Seed dispersal*

Water and gravity dispersal have previously been assumed for *C. australe* (Floyd 1990a, Adam 1992). A test for flotation showed that individual seeds sink, but undehisced pods float (pers. obs.). Dispersal of the whole-pod unit seems most likely, due to its buoyancy, and may allow long distance dispersal from trees adjacent to creeks and rivers. This has been recorded for other legume species in the tropics (Connell & Lowman 1989, Kibutzki & Ziburski 1994). Observations also indicated that seeds which were buried under soil and leaf litter washed downslope, had a higher chance of escaping predation. However, comparison between sites of differing slopes suggested that seed removal by surface water flow and gravity did not explain at least 34% of the missing seeds at Big Scrub. Nor did the timing of heavy rainfall events explain seed removal. Most of these missing seeds were therefore removed by mammals, and possibly a small but unknown proportion of seeds is dispersed in a germinable condition by both of the mammalian seed predators. Observations of intact seeds uphill of rainforest in eucalypt forest (R. Lott pers. obs., R. Kooyman pers. comm.), in stumps of trees, and in open paddocks 50 m from their nearest source (R.J. Haworth pers. comm.) demonstrate that seeds are carried by mammals. Since some damaged seeds are capable of germinating, partially damaged seeds can also be regarded as dispersal units. Seedling distribution at the five sites indicated that most seeds which establish as seedlings are dispersed close to the parent tree (up to 12m), with a few individuals moved 14 to 28m. This is consistent with observations of seed dispersal by *Trichosurus* spp. (40 g seeds of *Macrozamia riedlei*, Burbidge & Whelan 1982) and large rodents in other systems (Forget 1994).

An alternative interpretation of adaptation for dispersal by *C. australe* is suggested by the slightly sweet-smelling spongy mesocarp, which was frequently found scraped away by mammals. In order to eat the edible mesocarp, animals may pick up the large pod and move away to gnaw it. In the process, they would dislodge the large seeds from the pod, thus dispersing them. This would need to be verified by pod-removal experiments and observation of *T. caninus* and *Trichosurus* spp., particularly the latter, which appear to eat the mesophyll but not the seed.

*C. australe* may not need long distance seed dispersal for maintenance of existing populations at the five sites. Adults occur within 30 m of each other, and seedlings are tolerant of growing near the parent tree. Therefore, only small movements are necessary to ensure that a seed receives a chance to survive. The dispersal of seeds by mammals allows for movement of seed uphill, and explains the existence of a small number of seedlings beyond adult trees, despite heavy predation at Big Scrub.

### *Germination and seedling survival*

*Castanospermum australe* seeds can lie on the ground for several months after seedfall, and then germinate *in situ*, if not eaten or decayed beforehand. Germination occurs mainly during the first wet season (summer) which follows seed fall. This tendency for relatively quick germination and a lack of dormancy is typical of many large-seeded tropical species which establish in shady conditions (Foster 1986, Ng 1978 in Primack 1987).

Seeds germinate readily (64% of seeds that survived intact in May 1990), and rapidly reach 30 - 50cm height. After this, the growth rate slows considerably. However, seedlings are large relative to a range of other common canopy species (Osunkoya *et al.* 1993). The seedling tolerates establishment under the parent, and in shaded conditions. It is also able to resprout after seed and seedling damage. As predicted by the large seed and seedling size (Foster 1986), *C. australe* is probably a superior competitor in shaded conditions, at least in the establishment stage.

Seedlings also grow in gaps, and at the forest edge (R. Lott pers. obs.). Relative to secondary forest species, their growth rate is slow (Herwitz 1993), both in gaps and the forest interior (Osunkoya *et al.* 1993). Differences in seedling response to gaps and forest interior are small, and may differ between sites and regions due to a combination of the effects of seed source, seed size, gap size, and climatic conditions. Perhaps more importantly, the exclosure experiment provided preliminary evidence that seeds dispersed or previously occurring in gaps are likely to be eaten, or suffer the effects of desiccation. Therefore, lack of seed survival may prevent many seedlings establishing in gaps. Those few that do survive, may then grow in sunlight. Observations indicated that seedlings appear to grow best when in partial sunlight patches caused by gaps between branches of an adult tree, or in more filtered sunlight at the edge of a treefall gap. Once established, *C. australe* has the capacity to modify its leaf physiological function to tolerate full sunlight (Myers *et al.* 1987). All studies agree that *C. australe* is a primary forest species which tolerates shaded conditions and narrow gaps.

Survival of seedlings for the first 5 years was high in the two small remnants. It was beyond the scope of this study to measure the rate of recruitment from seedlings to larger size classes. However, the results of studies of neotropical shade-tolerant canopy tree species (de Steven 1994; Forget 1994), show that survival of seedlings after the first few years, and of saplings (<1cm dbh) can be high. Demographic studies indicate that life expectancy of non-pioneer trees increases markedly after 10 years of age (Alvarez-Buylla & Martinez-

Ramos 1992). In addition, Forget (1994) found that *Vouacapoua americana* (Caesalpinaceae) showed no evidence of long term compensatory mortality, that is, the greater the initial density, the greater the final density of recruits surviving up to 8 years. This supports the conclusion that the high initial density of *C. australe* seedlings in the small remnants is indicative of an increased abundance of larger size classes in the future. The abundance of juveniles and saplings at Davis and Johnston's also suggests that enhanced seedling establishment has occurred in the past.

### *Seedling dispersion*

Howe (1989) has proposed that the pattern of seed dispersal is an important factor explaining seedling demography and susceptibility to density-dependent predation. Clump-dispersed species recruit many offspring from undispersed seeds near the parents, as well as from seeds dispersed away from parent trees by frugivores. Scatter-dispersed seeds are adapted for recruitment as isolated individuals, often in light gaps or other special habitats. Seed and seedling mortality near parents is very high, and overall seed and seedling survival is low. In terms of explaining the coexistence of many species in tropical forests, this hypothesis requires that there is a compensatory mechanism, such as temporal variation in relative recruitment rates (Chesson & Warner 1981), so that there is a greater relative recruitment of scatter-dispersed species. The seedling distribution of *C. australe* approximates that predicted for clump-dispersed species (see Howe 1989), but is due to a predominance of short-distance dispersal rather than deposition of seeds in small clumps.

Scatter-dispersed species are those with dispersal vectors which spread individual seeds widely, and are not necessarily rare species, which tend to be clumped in the permanent plot at Barro Colorado Island (Hubbell 1979). Howe (1989) has proposed that trees which are scatter-dispersed will be more vulnerable to loss of seed dispersal agents, than species which are clump-dispersed and pre-adapted for survival in dense aggregations near parents. The seedling dispersion of *C. australe* is consistent with this hypothesis. However for other plant species, overall vulnerability to habitat fragmentation will depend on the coupling of different plant processes and the animals which mediate them.

### *Importance of C. australe to fauna*

*C. australe* has a wide distribution in subtropical and riverine rainforests of northern New South Wales and southeastern Queensland (Chapter 2). Observations of seeds damaged by mammals span much of this range: seeds damaged by possums have been seen in large tracts of rainforest in the Border Ranges National Park (E. Date pers. comm.), as well as in

remnants of the Big Scrub rainforest region. Floyd (1990a) also noted a 'cache' of seeds at Numinbah Nature Reserve, closer to the coast.

In 1989, peak seed fall occurred from late May to late June. In lowland primary rainforest in eastern Australia, this early winter period is generally the season with the lowest number of species in fruit (Innes 1989, Crome 1975a) and a lower quantity of fruit available (Hopkins & Graham 1989) (but see Stewart 1995, House 1986). Although both *T. caninus* and *Rattus fuscipes* eat a large quantity of leaves in other habitats (Seebeck *et al.* 1984, Owen & Thomson 1965, Watts 1977), fruit and seeds may be a more important dietary component to those populations that live in rainforest, where large seeds and fleshy-fruited species are more common (Willson *et al.* 1989, 1990). In addition, female *R. fuscipes* and *T. caninus* captured during May to July 1989 and 1990 were either lactating or pregnant. It is possible that *C. australe* is an important source of food, in particular starch, for these mammals during the winter months, particularly as seedfall coincides with the breeding season of both species.

#### *C. australe* in north Queensland

The suite of rainforest-dwelling fauna in north Queensland is different to that in northeastern NSW, with only *R. fuscipes* in common. In North Queensland, the predators of *C. australe* seeds and seedlings are not known, although Osunkoya (1994) suggested that the main predators of seeds and seedlings were likely to be native rats (*Rattus*, *Uromys*). Observations of a paste resembling *C. australe* in the stomach of the Grey Cuscus *Phalanger orientalis* (Winter 1983), and of chewed pods near Tully and Atherton (R. Lott pers. obs.) in north Queensland indicate that a larger mammal also eats the seed. Experiments with transplanted seeds and seedlings showed that *C. australe* seeds (see Willson 1988, Osunkoya 1994) and seedlings (Osunkoya *et al.* 1992) are eaten at some sites in north Queensland, but not others. This appears to depend on the forest type and resident fauna. For example, in Osunkoya's study the continuous rainforest site (Lamins Hill) supports a different forest type (Tracey 1982) and has a more abundant and diverse fauna (Osunkoya 1994, A. K. Irvine pers. comm.) than that of the isolated, 200 ha rainforest fragment (Curtain Fig). The lack of survival of unprotected seedlings at Lamins Hill suggests that vertebrate predators were responsible for a large proportion of *C. australe* seedling mortality. Differences in soil and climate between the sites appear to have had little, if any, effect on survival of caged *C. australe* seedlings. *R. fuscipes* was only captured at Lamins Hill, so this species may have damaged the seeds and seedlings. In addition, the sites differ in possum fauna, and musky rat-kangaroos and possibly other wallabies are absent from the Curtain Fig remnant (A.K. Irvine pers comm.). Such fauna

could also have been responsible for the seedling predation. It is interesting to note that in four of the other five plant species tested by Osunkoya, seedling survival was higher at Lamins Hill, indicating that the vertebrate responsible for damage to young *C. australe* seedlings is not the same one that eats the other species.

Thus, there is preliminary evidence that vertebrate seed predation may also limit the survival or distribution of *C. australe* in north Queensland. However, levels of seed predation and seedling herbivory may differ between regions, as well as between continuous and fragmented forests.

### *Summary*

- In this study, the factors that influenced levels of seed predation and seedling survival were distance-dependent predation, between-tree differences (microsite), seedling response to forest canopy and gaps, and the presence or absence of mammalian seed predators.
- For *C. australe* in remnants of the Big Scrub region, the presence or absence of native seed predators was the factor which had the greatest effect on seed survival and seedling recruitment.
- The distribution of seedlings indicated that the species is clump-dispersed, and tolerant of establishment near conspecifics and in the shaded forest interior. Immature plant distance to nearest adult trees is similar to that for seedlings, indicating that density-dependent seedling mortality does not have a strong effect on dispersion patterns.
- Further research should investigate whether there is a difference between sites in seed dispersal, seedling survival, and seedling herbivory by vertebrates.

## **9.2 The effects of forest fragmentation on *C. australe***

Compilation of fauna surveys across a range of Big Scrub remnants (Lott & Duggin 1993), and in fragmented habitats throughout the world show that in general, small sites show a reduction in mammal and bird species richness, as was observed in the three smallest sites in this study. However, the presence of species within similar-sized remnants varies depending on random inclusion of fauna at the time of clearing, differences in site characteristics (e.g. Schwarzkopf & Ryland 1989) and position in the landscape matrix. In the Big Scrub, not all small sites lack both *R. fuscipes* and *T. caninus* (Appendix 2).

The presence of *C. australe* as a winter food source, is not sufficient to retain the native mammals within small remnants. In small reserves, fruit-bearing trees (Howe 1984), other

important food sources and/or habitat requirements may be a limiting resource. For *R. fuscipes*, the presence of dense ground cover has been found to be important in Victoria, where a survey of 39 remnants of *Eucalyptus* forests found that *R. fuscipes* were present in most patches of 4 ha or larger (Bennett 1990). For *T. caninus*, its requirements for tree hollows for shelter and nesting (Lindenmayer *et al.* 1990), particularly in short and broad trees with few holes (Lindenmayer *et al.* 1991) probably means that some remnants are not suitable as a permanent habitat. For medium-sized mammal species, their home range requirements would preclude their presence in small remnants (Table 9.1). The home range given for *T. caninus* indicates that, theoretically, remnants of 10 ha or larger may support an individual. In small remnants where *T. caninus* is absent or transient, seed predation is expected to be absent or sporadic.

The marked increase in seedling recruitment observed in this study only applied where seed predators were absent, or absent for part of the fruiting season (Table 5.8, and pers. obs., Wollongbar and Davis). Both seed predators occurred at Johnston's Scrub, but they were less abundant than at the large sites, and an intermediate effect on plant recruitment was implicated. Seed predation levels were relatively high from 1989 to 1991, but a few seedlings were detected. Seedling densities of older cohorts were high beneath some trees but not others, resulting in an intermediate seedling density for the site, and there was evidence of an increased recruitment of sub-adults at some time in the past (Chapter 8).

Davis Scrub was the only site of the five studied where seed predation by native mammals was virtually non-existent. There was no evidence to suggest that seeds from Davis Scrub were unattractive to animals, compared with those at Big Scrub. Rather, results across three experiments and years (Chapter 6 and 7), demonstrated that the lack of seed predation is a phenomenon that is repeated across years. Absence of mammalian seed predators remains the best explanation for the lack of seed predation at Davis Scrub. In contrast, mammalian seed predation appeared to remove most seeds at Big Scrub and Boomerang Falls, and it may be that seeds only survive to germinate at the larger sites in high seedfall years, or beneath highly productive trees.

As already discussed, the presence of seed predators in small remnants is variable. Inspection of several other Big Scrub remnants showed variable levels of seed predation and seedling abundance. Although classified as suballiance 5, Laurelbank did not have dense *C. australe* seedlings, probably due to the presence of vertebrate predation (pers. obs.) and dense invasion by the ground climber asparagus *Protasparagus* sp. Few seedlings were found at Booyong (suballiance 1 *Argyrodendron trifoliolatum*), despite the occurrence of several fruiting trees. Observations under five trees in 1994 indicated that all but one seed

was eaten by *T. caninus*. Seedlings were sometimes dense at Victoria Park (suballiance 1), but some seed predation by *T. caninus* was observed. At none of these sites were seedlings in the same densities as at Wollongbar or Davis.

**Table 9.1** Habitat area required for herbivorous rainforest mammals found in northeastern NSW\*

Species	Home range size (ha), density (No. ha <sup>-1</sup> ) or range (m)	Source
<i>Thylogale stigmatica</i>	estimated 120-130 animals in 29 ha area with supplementary food - i.e. 4 per ha, but normally fewer than this number. Similar to <i>T. thetis</i> in size but browses on fallen leaves, not grass and shrubs)	Cooke 1979
<i>T. thetis</i>	5-30 ha	Johnson 1980
<i>Potoroo tridactylus</i>	5.2 ha (females), 19.4 ha (males) 1.5 ha (females), 2.0 ha (males) - home ranges overlap. Range depends on habitat	Kitchener 1967,1973 Bennett 1987 Seebeck <i>et al.</i> 1989
<i>Pseudocheirus peregrinus</i>	low-23.5/ha - depends on eucalypt species & understorey cover. 2.43-2.84 adults/ha	Pahl 1984 Thomson & Owen 1964
<i>Trichosurus caninus</i>	1 per 10 ha (n-e NSW) 100-120 m (mean range length in dense Wet sclerophyll forest)	How 1981 Owen & Thomson 1965
<i>Melomys cervinipes</i>	50 m	Wood 1971
<i>Rattus fuscipes</i>	200 m	Wood 1971
<i>R. rattus</i>	?	
<i>Mus musculus</i>	3.8-20 m (depending on food availability)	Kirby 1974 Newsome 1969 a,b

\* Most home ranges or densities are from research sites other than northeastern NSW

? No home range found in literature

The occurrence of other sites where *C. australe* seedlings are abundant, supports the conclusion that *C. australe* has the potential to increase with a release from seed predation. Local National Parks and Wildlife Service personnel commented on the abundance of the seedlings at two other northeastern New South Wales sites, Maclean and Moore Park.

These sites are of vegetation suballiance 5 (*C. australe*-*D. muelleri*) and 24 (*C. australe*-*Grevillea robusta*) respectively (Floyd 1990b). Both sites are small disturbed remnants adjacent to a river. *C. australe* has formed dense stands of seedlings at both, and adult trees form a large proportion of the canopy (pers. obs.). There was little evidence of seed predation (R. Lott pers. obs.). This suggests that the particular disturbance conditions at Davis Scrub, Maclean, and Moore Park are those that promote establishment of *C. australe*.

Overall, comparison between sites with, and without the seed predators, showed that mammals have an important influence on the levels of seed predation and resultant seedling recruitment of *C. australe*. At the large sites, the timing, number and proportion of seeds removed differed from those at the small sites, and this resulted in markedly different seedling abundance (Chapter 6). These results show that faunal composition also has an important effect on seedling recruitment at different sites.

Prediction of the effects of increased seedling recruitment on long term forest structure and composition is difficult. The combined sample of adult neighbours within a 30 m radius of each study tree provided a sample of nearly 1 ha within each remnant. While such an area is insufficient to describe the diversity and spacing of trees in tropical forests (e.g. Hubbell 1979, Hubbell *et al.* 1990), it can provide a sample of stems of more common species (see Condit 1995). Therefore, the enhanced abundance of small adult *C. australe* observed at two remnants in this study can be regarded as, at least, a significant local phenomenon. Whether altered recruitment is more widespread requires sampling over a larger area both within the study sites, and in other remnants of appropriate rainforest types. Microsite conditions could allow the formation of dense clusters of adults at some locations, but not others. Density-dependence could set upper limits to adult tree abundance (Hubbell *et al.* 1990), which only operate in extreme cases where a plant species has increased in abundance. Forest fragmentation has begun to cause a change in plant-species interactions, and possibly, a shift in vegetation composition. This poses long-term management problems for maintenance of diversity of rainforest remnants.

Table 9.2 summarizes the effects of forest fragmentation on the life stages of *C. australe*. There is also preliminary evidence that there has been a change in pollination and seed set, due to fragmentation. The seed crop data showed that the number of seeds per fruit was higher at Davis Scrub and Wollongbar than at the other sites (Figure 4.6), suggesting increased pollination efficiency, or nutrient availability at the small sites. *C. australe* is probably pollinated by either, or several, of its insect and vertebrate flower visitors (*Apes mellifera*, birdwing butterfly, Uranid moth, D. Sands pers. comm.; *Pteropus* spp, Parry-Jones & Augée 1991a; Lewins honeyeater, rainbow lorikeet, scaly-breasted lorikeet, R.

Green pers. comm.). The vertebrates occur in small remnants of the Big Scrub (Holmes 1987, P. Eby pers. comm), including Davis Scrub (R. Lott pers. obs.). However, flower visitation rates are unknown and several aspects of the pollination system would need to be investigated, including ovule number per flower, to determine whether this is an effect due to fragmentation, or merely a trade off between number of seeds per pod, and number of pods.

**Table 9.2** Summary of effects of forest fragmentation on various life stages of *C. australe*

Life stage	Result for <i>C. australe</i> (Black Bean)
Pollination	At least some pollinator visitation to remnants. (Bats and generalist rainforest birds the main flower visitors. Depends on importance of insect pollination.)
Seed set	No indication of reduction in remnants, based on seed crop reaching the ground
Seed predation	Release from predation in small remnants
Seed germination	Much in small remnants, little in large (depends on both seed predation and seed production)
Seedling survival	Seedling survival high in small remnants. Insufficient data in large remnants due to very low numbers of seeds remaining after predation.
Juveniles and saplings	Larger numbers in two small remnants, but not in third remnant where edge effects probably prevent high seedling survival to next size class.
Subadults	Small increase within 12 m of adult trees at two small sites
Large Adults	No difference at present. May be a function of time.

### **Summary**

- The theoretical predictions of altered processes and animal-plant interactions in fragmented habitats are supported by this study, which showed decreased levels of *C. australe* seed predation, and higher seedling recruitment in small remnants.

- Differential abundance of immature *C. australe* plants among sites indicates that increased seed survival to seedling stage has resulted in a shift in species dominance in the forest understorey. The ultimate effect on structure and composition of continuous forest is difficult to predict, because of the long life span of trees, and the dynamic events within rainforest (treefalls, gaps etc.).
- However, a slow shift in species composition is expected in small fragments, because the small size and reduced environmental heterogeneity decrease the chance for random events to re-organise species assemblages. Coupled with this, *C. australe* possesses a very large seed, rapid germination, and seedling characteristics which enable it to withstand shade and seedling herbivory.

### 9.3 Implications for other fragmented rainforests

#### *Coupling of stages in the recruitment process*

There are several examples where the extinction or decline in mammalian herbivores has had an apparent effect on seed or seedling survivorship (DeSteven & Putz 1984, Sork 1987, Dirzo & Miranda 1991, Leigh *et al.* 1993) (see section 2.3.4). For example, higher seed and seedling predation rates have been found on Barro Colorado Island (BCI) in the Panama Canal, than on the nearby mainland (De Steven and Putz 1984, Sork 1987). On BCI, there is an absence of top carnivores and it is assumed that this allows higher densities of seed- and seedling-eating predators than on the mainland (Glanz 1990, Terborgh 1988). In the 600 ha of tropical rain forest at Los Tuxtlas, Mexico, no damage by folivorous vertebrates to seedlings was found. In comparison, seedlings in the 600 000 ha tract of tropical rainforest at Montes Azules showed 29% damage (Dirzo & Miranda 1991). In addition, the understorey vegetation at Los Tuxtlas showed a lower diversity, a much higher density, and a greater dominance by single species within quadrats (Dirzo and Miranda 1991). A reduced abundance of top carnivores is also implicated in the Mexican study. These studies document either an altered process in fragments, or a different vegetation composition, but have not directly linked the two. Thus, although tantalizing new information, interpretation of the long term importance of these studies is limited. This study of *C. australe* is an important step towards remedying this situation.

Plant population dynamics depends on the coupling of different stages in the recruitment process (Herrera *et al.* 1994), that is, between dispersal-seed rain- seed predation- and germination and seedling establishment. Species have different population bottlenecks and may respond to altered animal-plant interactions in different ways. Large-seeded tree species differ in their susceptibility to mammalian predation (Terborgh *et al.* 1993,

Molofsky & Fisher 1993), and they may not necessarily increase in abundance in the absence of seed predators. The following section considers the situations where rainforest fragmentation could be evident as altered mammal-plant interactions.

During predation, two factors are important in determining whether any seeds remain to germinate in fragments. These are the quantity of seed available and the ability of the predators to remove a large proportion. For *C. australe*, there was no evidence that the small fragments had a different availability of seeds. Indeed, the increased number of small adults at Davis Scrub could have meant an increase in overall seed availability, although this was not quantified. In two small remnants of the Big Scrub, a reduced abundance of *T. caninus* and an absence of *R. fuscipes* was sufficient for the animals to be satiated by *C. australe* seed crops. Similarly in other systems, the regular production of normal or large quantities of seed would potentially satiate a reduced abundance of seed predators. This is particularly so in southern Australia, as most seed predators are only partial granivores which include other foods in their diet.

However, a decreased seed production in fragments, along with decreased predation could result in a functionally similar level of predation and numerically similar seedling recruitment, that is, no change. Similarly, where a mammal species is a very efficient searcher, it could still eliminate normal seed crops, despite reduced numbers of animals. For example, Harrington *et al.* (in prep.) found no difference in final seed survival for several palatable large-seeded species in fragments and continuous forest. Although the principle seed predator, *Uromys caudimaculatus* occurred at lower abundance in fragments, this merely meant that seeds took longer to be eaten. There was no evidence that seedlings of these species differed in abundance between fragments and continuous forest. The authors concluded that it would take a local extinction of the seed predator to cause a change in the density of germinating seeds due to forest fragmentation. Therefore, for some plant species, the distinction between the absence and reduced abundance of fauna for seed survival will be important.

Whether seed dispersal differs between sites may be more difficult to determine.

Conceivably, a lower abundance of seed predators could result in a greater seed availability for dispersal and increased dissemination. This could result in a slow shift in seed germination rate and seedling dispersion, that may not be discernible for some decades after forest fragmentation. Alternative effects are: 1) a decreased dispersal due to a low of specialised dispersers or component of the disperser suite, 2) that a scatterhoarding rodent in reduced abundance may retrieve caches at a lower rate, or 3) an efficient forager looking for highly attractive seeds may still retrieve all cached individuals, resulting in no change in

seedling establishment. The latter is demonstrated by *U. caudimaculatus* which scatterhoards seeds, but the rate of seed damage *in situ* and seed retrieval did not differ between fragments and continuous forest (Harrington *et al.* in prep.). A knowledge of dispersal efficiency, relative seed production over several years, and seedling and sapling dispersion is required to answer such questions.

Whether other animals compensate for the decline in one member of the predator/herbivore guild, may also affect total levels of seed or seedling predation. In a comparison of levels of predation of five large-seeded species, Terborgh and Wright (1994) found no difference in overall seed survival between La Selva and Cocha Cachu, despite differential abundances of fauna. This appeared to be because the various seed predators compensated for the absence of their competitors.

Predation of seeds and seedlings has been shown to be the major limitation to recruitment in other large-seeded tropical species (Schupp 1990). However, interpretation of the importance of predation for population dynamics can only be made when the relationship between predation and emergence is directly addressed (Anderson 1987, Sork 1987, Borchert *et al.* 1989 in Schupp 1990). Seedling emergence and recruitment can differ significantly between years (Schupp 1990) and allow temporal variation in abundance and distribution within the forest. Density-dependence is important because it is a mechanism by which seedlings can be thinned to levels more consistent with adult density in natural forest. Density-dependent seedling mortality has been reported in a range of rainforest plants (Auspurger 1983a, Clark & Clark 1984), although whether this is a mechanism for coexistence of species is still being debated (Connell *et al.* 1984, Hubbell 1980, Clark & Clark 1984, Hubbell *et al.* 1990). For *C. australe* seedlings, density-dependent mortality due to insects was implicated in the enclosure experiment, but the distribution of older seedlings indicated that this effect is not strong. Whether density-dependence sets upper limits on abundance, as suggested by Hubbell *et al.* (1990), will be important for vegetation changes associated with fragmentation.

Alteration in seedling recruitment processes can have an important effect on community structure and dynamics (Ribbens *et al.* 1994). Forest fragmentation may alter spatial, as well as quantitative patterns of seed predation and dispersal. Future examination of Howe's (1989) hypothesis regarding clump- and scatter-dispersal will be interesting in this regard. For *C. australe*, release from predation has the potential to remove some of the spatial and temporal variation in seedling recruitment (e.g. variation between trees) which is hypothesized to permit coexistence (Chesson & Warner 1981, Chesson 1985).

Decreased levels of predation and dispersal in fragments will only effect a change in seedling recruitment, if the germination and seedling characteristics of the plant species include a tolerance to germination under the parent, or in increased densities. Assuming a reduction in seedling herbivores, with resultant low levels of herbivory, the second factor that may affect the establishment of a plant species is the competitive ability of the seedling.

In conclusion, the effect of forest fragmentation on a tree species depends on the type of pollination vector, seed predator, seed disperser and seedling herbivore, on the germination requirements of the tree species, and on the coupling of these processes. Figure 9.1 reviews some of the possible effects on plants, of altered animal-plant interactions due to habitat fragmentation, based on theoretical considerations and limited available evidence. The effects of specialist and generalist pollinator systems on seed set and genetic diversity are not likely to be distinct, as they will depend on the flight patterns and susceptibility of pollinator guilds to fragmentation, and in any case, cannot be clarified on the evidence currently available. The pollination system is not known for either of the two examples which have investigated genetic diversity in fragmented forests (see Table 9.4).

The long-term changes in composition and structure of small fragments (compared to the large ones) is hard to predict, given the current lack of knowledge of individual species life histories. Whether a species which shows increased seedling recruitment, will eventually increase in abundance in the canopy depends not only on its age-specific survival rates, but on the species composition and disturbance regime in the fragments. Since fragments are small isolated areas of habitat, with often little spatial heterogeneity, a single disturbance event, such as a cyclone, could completely alter the canopy structure. The creation of treefalls and gaps could result in a switch from dominance by a shade-tolerant species benefitted by altered animal-plant interactions, to the creation of a patch of secondary forest. Alternatively, the lack of spatial and temporal heterogeneity in a remnant could mean that enhanced recruitment under individual trees, rather than being a localised phenomenon (e.g. de Steven 1994), could occur throughout the remnant. This could lead to a dominance of that species throughout the remnant. Some of the mechanisms hypothesized to explain coexistence of species in tropical forest (e.g. Denslow 1980, Connell 1978, Chesson & Warner 1981, Chesson 1985) could also explain the potential shift in species composition and structure in forest fragments.

### *Future research*

This research entailed a detailed study of processes, coupling seed predation and seedling recruitment, across five sites. Its limitations stem from a lack of site replication, the need

for more expansive surveys of stand structure and composition within the study sites, and a lack of site-specific information on mammal population dynamics. However, this is more than one researcher can achieve. The few studies of plants which have documented seedling recruitment in habitat fragments have been confined to 2 to 4 sites (Table 2.4). The studies of plants in a larger number of sites (Santos & Telleria 1994, Telleria *et al.* 1992, Aizen & Feinsinger 1994a,b) have not determined the implications of the altered process for seedling recruitment or seed set, respectively. To link process and forest stand structure adequately requires an integrated research program, involving several researchers.

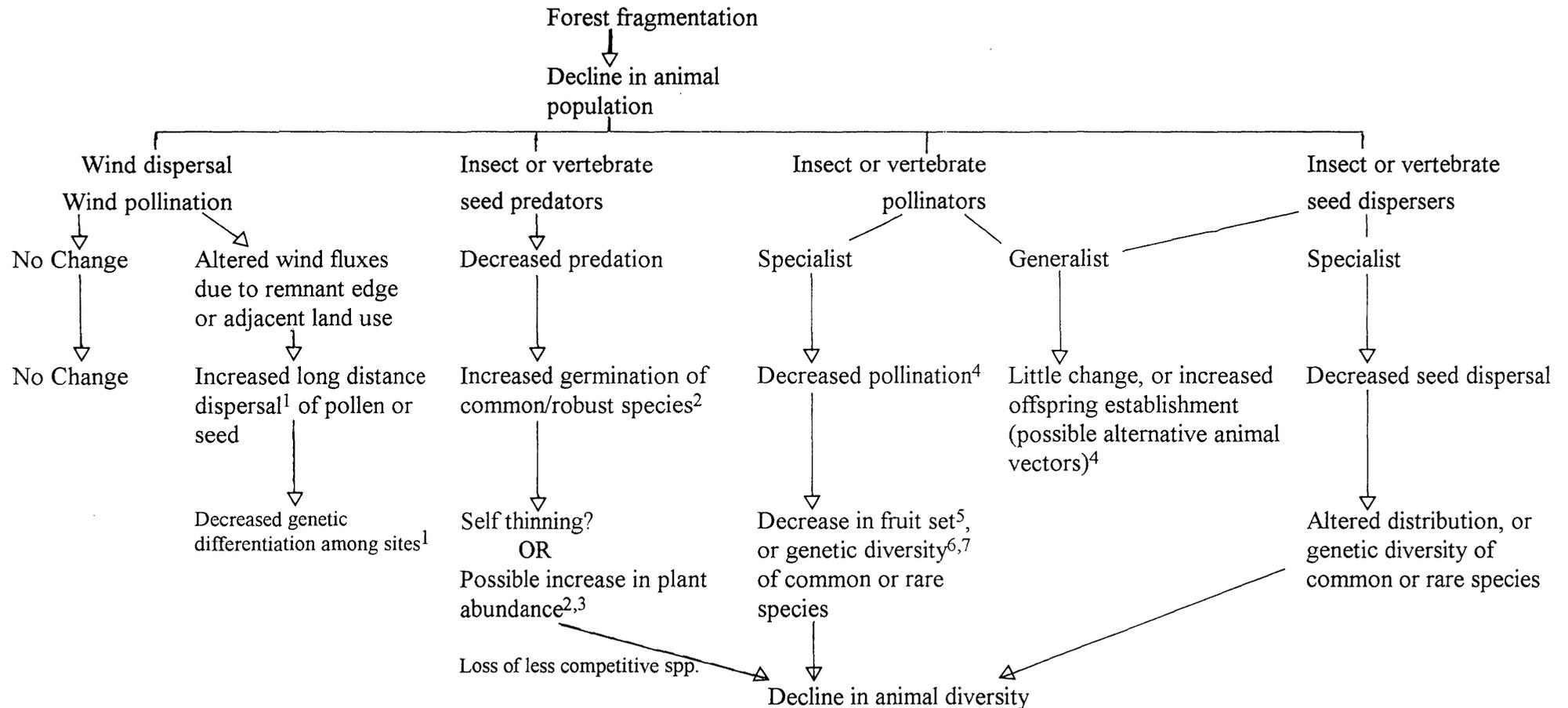
Due to the long lifespan of rainforest trees, it could be argued that any alteration in animal-plant interactions observed now, will have little effect on long-term species abundance. Conversely, a species could be on the increase, and it would take a generation of trees for us to recognize it, due to a lack of information on survival rates of larger size classes. Therefore, in studies of the effects of forest fragmentation on plants, size class information must include juveniles, subadults AND adults, and sufficient autecological study to identify the life stage at which there are bottlenecks in survival. Whether these bottlenecks are widened, as in *C. australe*, or constricted as expected with rare species and specialist interactions, will determine the long-term effects of fragmentation on species abundance.

Whether changes in process transfer to an altered diversity of species in the forest canopy will be difficult to prove. As shown by this study of *C. australe*, it is difficult to separate the effects of past disturbance and natural variation from those directly due to forest fragmentation. Increased site replication, both in fragments and in continuous forest, may have helped this study identify the applicability of these results to other remnants and regions. However, it is still likely that there would have been a range of seed survival rates at different sites. This reflects the complex set of factors that influence whether a species will increase in abundance. In this study, past grazing and logging disturbance, adjacent land use, presence/absence of seed predators and seedling herbivores, and edge effects all appear to interact to determine not only whether seed recruitment is altered, but whether this will transfer to larger size classes. Differences in remnant shape, isolation, topography, rainfall, germination conditions and disturbance history are also likely to have affected the abundance of *C. australe*.

However, even if the fragmentation effect is difficult to interpret, the autecological data allows an increased understanding of species dynamics, and the importance of processes within the rainforest. Information will be best used if the research targets species which are likely to demonstrate altered interactions due to a loss or decline in fauna. Examples are species with specialist pollinators or dispersers, mast-fruited species with high levels of

seed attack by insects, and large-seeded species with mammalian seed predators or dispersers.

**Figure 9.1** Predicted effects of forest fragmentation on plants due to altered animal-plant interactions.



1. Fore *et al.* (1992), Young *et al.* 1993; 2. this study, 3. Putz *et al.* (1990) and Leigh *et al.* (1993), 4. inferred from Aizen & Feinsinger 1994a, 5. Aizen & Feinsinger 1994b, 6. Hall *et al.* 1996, 7. Prober & Brown 1994.

#### 9.4 Management of remnants containing *C. australe*

*"So it's OK that we harvest the seeds (illegally) from the small remnants".*

Restoration ecology has new challenges, to estimate the range of population abundances which are 'natural' for each species, and to distinguish them from those that are due to 'unsuitable' anthropogenic disturbance. Superficially, it may seem that *C. australe* seeds are in overabundance in small remnants. This will only be true, if

- a) adults are common to dominant in the canopy, and regularly produce seed,
- b) there are no seed predators,
- c) there is little evidence of seed predation,
- d) seedlings are of a range of sizes and occur in high relative abundance, and
- e) seedlings recruit to the next size class.

If these conditions are met, removal of seeds or seedlings could be justified as a management option in the short term (Table 9.3), particularly if forest managers were prepared to plant seedlings of species which are in low abundance in the forest canopy. These should be mainly primary forest species. However, this appears to be treating the symptoms rather than the cause.

Long term planning requires 1) identification of keystone plants and animals which maintain fauna and process in remnants (Howe 1984), 2) research into the habitat needs of the fauna, and 3) some assessment of abundances of seedlings and whether they are within the range of natural variation, or due to altered interactions as a result of forest fragmentation. Planning should recognize that not all remnants of the Big Scrub are *C. australe-Dysoxylum* vegetation alliance, and species abundance will differ between vegetation types.

It seems plausible that *C. australe* is a keystone species: The seed suffers heavy predation, and is winter food for at least two of the five herbivorous mammals in the rainforest. The seedlings may be eaten by another species of vertebrate, and the nectar-rich flowers are visited by a range of vertebrate fauna. If the plant species is important to these fauna, then its removal could also have deleterious effects on the remaining flora and fauna in the remnants. Therefore, removal of adult individuals is inadvisable, and removal of seedlings or seeds requires better site-specific information than we now have regarding predation, seedling recruitment and growth rates. In the short term only, some seedlings could be removed from sites such as Davis Scrub - removal of individuals should be in regions of high abundance, but not where they are more sparse, as this is less likely to disrupt the spatial and genetic composition of the population.

A more sensible and long term action would be to expand the existing remnants, and/or plant corridors between remnants. While there has been some criticism of the validity of planting corridors (Simberloff *et al.* 1992), they remain the most viable means of expanding the area of habitat for fauna, and potentially facilitating movement between remnants of forest. This would be particularly relevant to Davis Scrub, which is furthest from the Nightcap Range, and isolated from other remnants of rainforest. Such revegetation could also allow eventual reintroduction of the native fauna into the remnant, from which it is assumed that animal-plant interactions would return to something more similar to continuous forest. This will require consideration of the habitat requirements of different fauna, and their willingness to use corridors. Some species will be more likely to use corridors than others. For example, *T. caninus* has adapted to living in urban and rural residential areas (S. Phillips *pers. comm.*) and it seems that surrounding land use may, at times, support a resident or transient individual within a remnant. During this study *Trichosurus caninus* were seen crossing roads (alive) and also as road kills, adjacent to vegetation corridors.

Studies of tropical rainforest mammals in north Queensland, showed marked differences between species in vulnerability to forest fragmentation. Of five arboreal marsupials, only two species had similar abundances in forest fragments and continuous forest, the remainder having reduced abundance or being absent from fragments (Pahl *et al.* 1988, Laurance 1990). The abilities of these species to use regrowth (a useful indicator of their extinction proneness) seemed to depend on their denning requirements, diet and degree of arboreality (Laurance 1990). Laurance (1991a) concluded that corridors enhanced mammalian diversity in fragments. Species which were detected in corridors included *Trichosurus vulpecula johnstoni*, *Pseudocheirus archeri*, *Antechinus flavipes*, *Melomys cervinipes* and *Rattus fuscipes*. Species which rarely if ever used corridors of secondary vegetation included *Dasyurus maculatus* and *A. stuartii*. However the ecological equivalents of the above species have rarely been detected in remnants of the Big Scrub. This may be because the Big Scrub was cleared 50 years prior to the Atherton Tableland, and remnants of the Big Scrub are generally more isolated and further from large tracts of forest than those studied by Laurance, which were 'linked' to large (>3000ha) tracts of primary forest, by streams or rivers which were often overgrown by secondary vegetation (Laurance 1990). Consideration of the habitat requirements and willingness of fauna to use corridors will require data gathered from the same region as that to be managed.

**Table 9.3** Possible management options for remnants containing *C. australe*.  
See section 9.4 for discussion of these options.

Small remnants	Large remnants
Remove some seedlings ? (short term only)	No action
Introduce seed predators	No action
Plant other plant species	Check other plant foods are available for fauna
Expand remnant	Expand remnant
Plant corridors	Plant corridors