

Post-Fire Demography in the Resprouting Shrub *Angophora hispida* (Sm.) Blaxell: Flowering, Seed Production, Dispersal, Seedling Establishment and Survival

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After fire, the resprouting shrub *Angophora hispida* (Sm.) Blaxell rapidly forms an extensive canopy from epicormic and lignotuberos shoots, culminating in most plants in extensive flowering and fruiting. Flowering was virtually absent in populations which had not been recently burnt. There are virtually no predispersal seed predators in mature fruits.

Seed dispersal was minimal and confined to the immediate vicinity of the parent plant. In this study, released seeds were all viable and germinated following the first heavy rains. Seedling mortality was highest in the establishment phase (i.e., before the first leaves were produced) and declined markedly afterwards, remaining at a much lower rate for the following eight years. Seedling growth and lignotuber development were slow and after eight years the young plants may not be fire resistant. The importance of the length of inter-fire period for the survival of populations of this species is discussed.

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INTRODUCTION

Two modes of post-fire regeneration have been documented. These are regeneration solely from seed following the death of all adult plants during a fire (obligate seeders), and regeneration from protected vegetative buds on surviving plants (resprouters) (see Gill, 1981). Whilst several workers have categorized plants according to their mode of recovery after fire (Purdie and Slayter, 1976; Purdie, 1977; Benson, 1985), information relating to the long-term survival and reproduction of species is sparse.

Keeley and Zedler (1978) developed a model to explain the evolutionary development of these two major modes of post-fire recovery in relation to fire frequency, in fire-prone Californian vegetation. Based on the demography of several representative species, they predicted that high fire frequencies favoured the evolution of resprouters over that of obligate seeders. One aspect of the life cycle which they did not consider was the importance of the primary juvenile period in resprouters. Bradstock (1985), who worked on two resprouting and two obligate seeding species, predicted that repeated fires of short frequencies may eliminate both resprouters and seeders. In resprouters, this was because of the slow growth rate in plants originating from seed (juveniles), and their delay in gaining fire resistance. Hence, frequent fire may prevent recruitment of plants. Abbott (1985) found a similar result for the resprouting *Banksia grandis*. Auld (1987) has shown that short fire frequencies (with <10 year intervals) are likely to reduce the abundance of the obligate seeder *Acacia suaveolens* by a decline in the buried seed bank. Consequently, any model trying to predict long-term changes in plant popu-

lations in relation to the fire regime should consider vegetative survival, growth, sexual reproduction, establishment and the subsequent length of the primary juvenile period, as well as the longevity of adult plants.

Angophora hispida is a common understorey shrub found in heaths and woodlands on Hawkesbury Sandstone around Sydney (Leach, 1986). It grows to 2-3m in height and 3-4m in width and flowers from November to January (Price, 1963). Plants are usually able to survive fire (Beadle, 1940), and regeneration occurs by a combination of ligno-tuberous and epicormic shoots from protected bud strands, as is typical of many species in the closely related *Eucalyptus* (McArthur, 1968).

Several components of the life cycle of the resprouter *Angophora hispida* (Sm.) Blaxell were examined using demographic methods in an effort to link post-fire regeneration to survival and reproduction. These components included seed production, dispersal, seedling recruitment and seedling survival. Predictions were made of the long-term behaviour of *A. hispida* populations under different fire regimes.

METHODS

Study sites were chosen in Ku-ring-gai Chase National Park and Manly Dam Reserve, some 10-30km north of Sydney. Annual precipitation for the region is around 1300mm with the wettest period being, on average, from January to June. The average maximum temperatures are 27°C in summer and 17°C in winter, whilst the average minimum temperatures are 17°C and 4°C, respectively.

Eleven study sites were chosen, each with a different time since fire. A range of times from one to 13 years was available, with replication for 1, 6 and 13 years. The sites are briefly described in Table 1. The soils at each site are derived from Hawkesbury Sandstone. Rainfall levels are roughly uniform across all sites throughout the study period. Rainfall data during this study were taken from the station at Manly Dam, approximately 1km from Site 1. Plant names follow Beadle *et al.* (1982).

TABLE 1

Location of study sites with time since burnt and characteristic vegetation. Vegetation type after Specht (1970)

Site	Years since fire	Vegetation and notes
1	1	Open heath with occasional emergent <i>Eucalyptus gummifera</i> and <i>E. haemastoma</i> . Understorey dominated by <i>A. hispida</i> , <i>Banksia ericifolia</i> and <i>Casuarina distyla</i> .
2	1 or >10	Vegetation as for site 1. This site was divided into two neighbouring populations of <i>A. hispida</i> . In both populations the fire which had burnt the site had stopped in the middle of the population, once through natural causes and once because of a small fire trail. This left one half of each population burnt and one half unburnt for at least 10 years.
3	3	Low woodland of <i>Angophora costata</i> , <i>E. gummifera</i> , <i>B. serrata</i> and <i>Xylomelum pyrifforme</i> . Low (1-2m) shrub understorey of <i>A. hispida</i> , <i>Eriostemon australasius</i> and <i>Dillwynia floribunda</i> .
4	4	Open scrub of <i>A. hispida</i> and <i>B. oblongifolia</i> .
5	5	Open heath with occasional emergent <i>E. haemastoma</i> . Heath dominated by <i>A. hispida</i> and <i>B. oblongifolia</i> .
6	6	Open heath with <i>A. hispida</i> and <i>B. oblongifolia</i> .
7	6	Open heath with <i>A. hispida</i> , <i>B. marginata</i> and <i>Petrophile pulchella</i> .
8	7	Closed scrub of <i>A. hispida</i> , <i>Leptospermum attenuatum</i> and <i>P. pulchella</i> . Occasional emergent <i>E. haemastoma</i> .
9	10	Low woodland of <i>E. gummifera</i> and <i>E. haemastoma</i> . Understorey dominated by <i>A. hispida</i> and <i>D. retorta</i> .
10	13	Closed scrub with <i>A. hispida</i> and <i>P. pulchella</i> .
11	13	Closed scrub with <i>A. hispida</i> and <i>L. attenuatum</i> .

Fruit production

At each site, 20 individuals were randomly selected using a transect/baseline method. From randomly selected points along a baseline placed adjacent to the population to be sampled, 1m-wide transects were run into the population. A 1m interval was randomly chosen along these transects and any individuals touching the transect in this interval were sampled. The number of ripe fruits on each individual at the time of fruit maturation (February 1978) was counted. Where no fruiting individuals were encountered, the population was searched for any flowering and fruiting plants. Where possible, a sample of ripe fruits was harvested.

A further 10 individuals were similarly chosen and the number of living leaves on each counted, as an indicator of growth since the last fire, at sites 1,3,4,5,6,8,9 and 10.

For each fruiting individual that was sampled three size components were measured:

- i) plant height (m);
- ii) girth of the main stem (cm) at 15cm above ground; and
- iii) total girth of all aerial stems (cm) at 15cm above ground.

Diameter at breast height (DBH) is not a useful measure in *A. hispida* because of the species shrubby, frequently multistemmed habit. Two girth measurements were included because of the heterogeneous nature of regeneration after fire, i.e. epicormic and/or lignotuberous regeneration. The data were analysed using a multiple regression.

An additional 21 individuals were randomly selected at Site 1 and fruit production on both types of regrowth i.e. epicormic and lignotuberous shoots recorded. This gave a better estimate of the variation in fruit production and allowed a comparison of fruiting success in relation to type of regrowth.

Predispersal seed predation

The components of each fruit harvested at Site 1 were examined to estimate the proportion of seeds that were intact, eaten by a seed predator, or undeveloped.

Seed dispersal

Initial seed fall on the soil surface was mapped along four, 50cm-wide, transects radiating from the centre of a cluster of *A. hispida* individuals.

Potential secondary dispersal by ants was examined:

- i) Using 20 permanent quadrats (50 × 50cm) at Site 1 with 10 seeds of *A. hispida* and 10 seeds each of *Acacia linifolia* and *Acacia suaveolens*, both known myrmecochores (Berg, 1975; Auld, 1986). Movement of seeds by ants was observed intensively for five days. This trial was set up during seed fall for the acacias (December) and not when abundant *A. hispida* seeds were on the ground.

- ii) During seed fall of *A. hispida* at Site 1 (March 1978), a permanent 1m² quadrat was set up near eight individuals. Thirty *A. hispida* seeds, each marked with a small white paint dot for ease of recovery, were placed in each quadrat. The fate of these seeds was followed for a month.

Seed dormancy and viability

Samples of 32 seeds from the seed lot collected from ripe fruits at Site 1 were tested for dormancy and viability monthly for six months. Seed collected from the soil surface some two weeks after seed release was also tested. Seeds were placed in petri dishes on Whatman's Seed Test Thick filter paper with distilled water. These were placed on a laboratory bench at room temperature. Germination was determined by the emergence of a radicle.

Seven replicates of 50 seeds in small hessian bags were randomly buried at a depth of between 0-5cm in Site 1. Mesh sides on the bags allowed the penetration of water, soil air and small soil animals, whilst preventing the movement of the large *A. hispida* seeds. One bag was to be recovered each month for seven months, with the component seeds being extracted and examined for dormancy, viability and signs of predation.

Seedling survivorship

The transect/baseline sampling method was used to locate 10 permanent quadrats at Site 1. Within these, the locations of 143 germinating seeds were mapped. The fate of these seeds was followed at weekly intervals for six months and then sporadically for a further seven years. Where possible, causes of mortality were identified.

At Site 1, 30 eight-year-old plants were unearthed in August 1986 and the depth of burial and size of the developing lignotuber were measured with a vernier caliper. The volume of the lignotuber was estimated by assuming it was an ellipsoid. The height and the number of live aerial stems and leaves of these plants was also measured.

RESULTS

Fruit production

Flowering and fruit set were confined to those plants which had been burnt in the past 12 months i.e. plants at Sites 1 and 2. This was most evident at Site 2, where only half the plants had been burnt. Here burnt plants regrew extensive canopies and some flowered, whilst unburnt plants remained largely inactive and failed to produce any flowers or fruits. Whilst all burnt plants showed vigorous regrowth (Table 2) not all flowered (75% of plants at site 1 and 65% of burnt plants at site 2). No extensive, regrowth was evident at those sites not recently burnt (Table 2).

TABLE 2
Mean number of living leaves per individual

Site	Time since last fire (years)	mean number of leaves per plant (\pm S.E.)
1	1	2452.8 (373.1)
3	3	399.5 (107.8)
4	4	284.5 (49.5)
5	5	465.1 (173.1)
6	6	219.7 (101.1)
8	7	68.1 (22.3)
9	10	49.1 (24.2)
10	13	104.6 (27.0)

The immediate post-fire growth and reproduction were evident at other sites as indicated by either the presence of fruits from previous seasons (Sites 3 and 4), or typical inflorescence structures, i.e. terminal cymes (Sites 5-11), from past flowering.

At Site 1, significantly more fruits were produced on epicormic shoots than on lignotuberous shoots (1 — Factor Analysis of Variance (ANOVA), $P < 0.005$). This, in part, reflects the greater abundance of epicormic shoots produced after the fire. However, even where individuals produced both epicormic and lignotuberous shoots, more fruits were found on the epicormic shoots (paired t-test $0.01 > P > 0.001$). Where the main stem had a sufficient bark thickness to survive the fire and produce epicormic

shoots, successful fruit production was virtually assured (94% of such plants set fruit). However, where the main stem was killed and regrowth was entirely lignotuberous, the chance of an individual successfully fruiting was greatly reduced (35%), and was confined to those plants which produced a new shoot of at least 50cm in height. Most of these plants had small fruit-crops (<100 fruits), and only one plant had a large fruit-crop which was totally lignotuberous in origin (871 fruits).

The number of fruits produced varied greatly between individuals. At Site 1, around half the fruiting plants sampled produced less than 100 fruits (Fig. 1), though some plants produced up to 1500 fruits. This variation could be partially explained by size of individuals. The linear regression of the number of fruits per fruiting plant on girth of the main stem (Fig. 2) was significant ($P < 0.001$) and accounted for some 44% of the variation in fruit-crop size. Adding the height and total girth components did not significantly improve the regression. This is expected, as all three variables were significantly correlated. A large amount of the variation in fruit production remained unexplained.

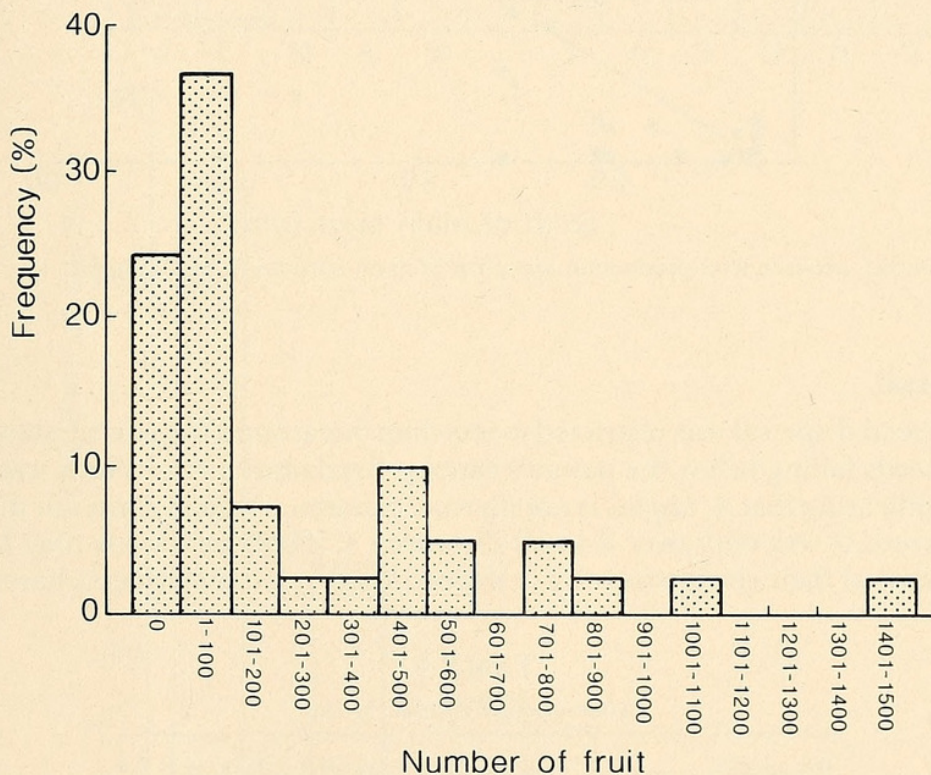


Fig. 1. Number of *A. hispida* fruits produced after fire at Site 1.

Predispersal seed predation

At Site 1, some 463 ripe fruits were harvested, with a maximum of 10 fruits being taken from any one plant. The majority of locules in a fruit contain an intact seed (Table 3). Seed predation in fruits was negligible (0.4% seeds lost), with occasional unidentified hymenopteran wasps reared from seeds.

TABLE 3
Extent of predispersal seed predation in A. hispida

	mean (\pm S.E.)	% of available locules
locules/fruit	2.996 (0.013)	100
intact seeds/fruit	2.361 (0.039)	78.8
seeds/fruit lost to predators	0.011 (0.005)	0.4

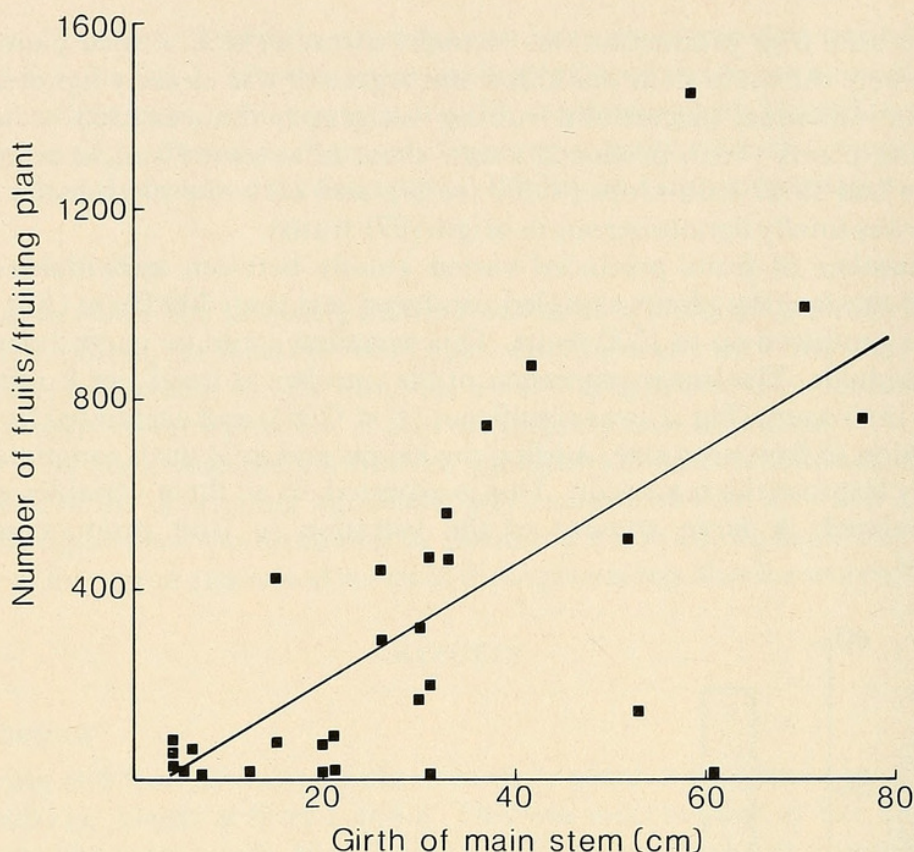


Fig. 2. Relationship between fruit production and girth of main stem for *A. hispida* at Site 1. $y = -43.9 + 12.1x$.

Seed dispersal

Initial seed dispersal was restricted to less than 5m around the parent plant (Fig. 3), with most seeds falling below the parent's canopy. Seed movement by ants was minimal (Table 4), indicating that *A. hispida* is not myrmecochorous. Where some ant dispersal of seeds occurred, it was only over a small distance (<50cm) and seeds may have been moved because of their close proximity to the two known *Acacia* myrmecochores.

TABLE 4

Evidence for seed movement by ants

Test species	% seeds remaining after 5 days (\pm S.E.)
<i>Angophora hispida</i>	79 (5.6)
<i>Acacia linifolia</i>	6 (4.7)
<i>Acacia suaveolens</i>	9 (5.5)

For the marked seeds, some *in situ* seed predation by an unknown seed predator occurred ($20\% \pm 7\%$), along with seed germination ($18\% \pm 6\%$) following heavy falls of rain in March 1978 (300mm). A large component of the seeds could not be traced ($62\% \pm 9\%$). These seeds were either: i) buried by moving sand, ii) washed away from the sampling area during heavy thunderstorms during the sampling period or iii) removed by seed predators or over small distances by ants. In all cases, the seeds would have germinated and established following sufficient rainfall in March 1978 (see below), unless they were destroyed by predators or buried too deeply for successful establishment. Seed movement during storms was small (<2m) as this was impeded by vegetation and litter.

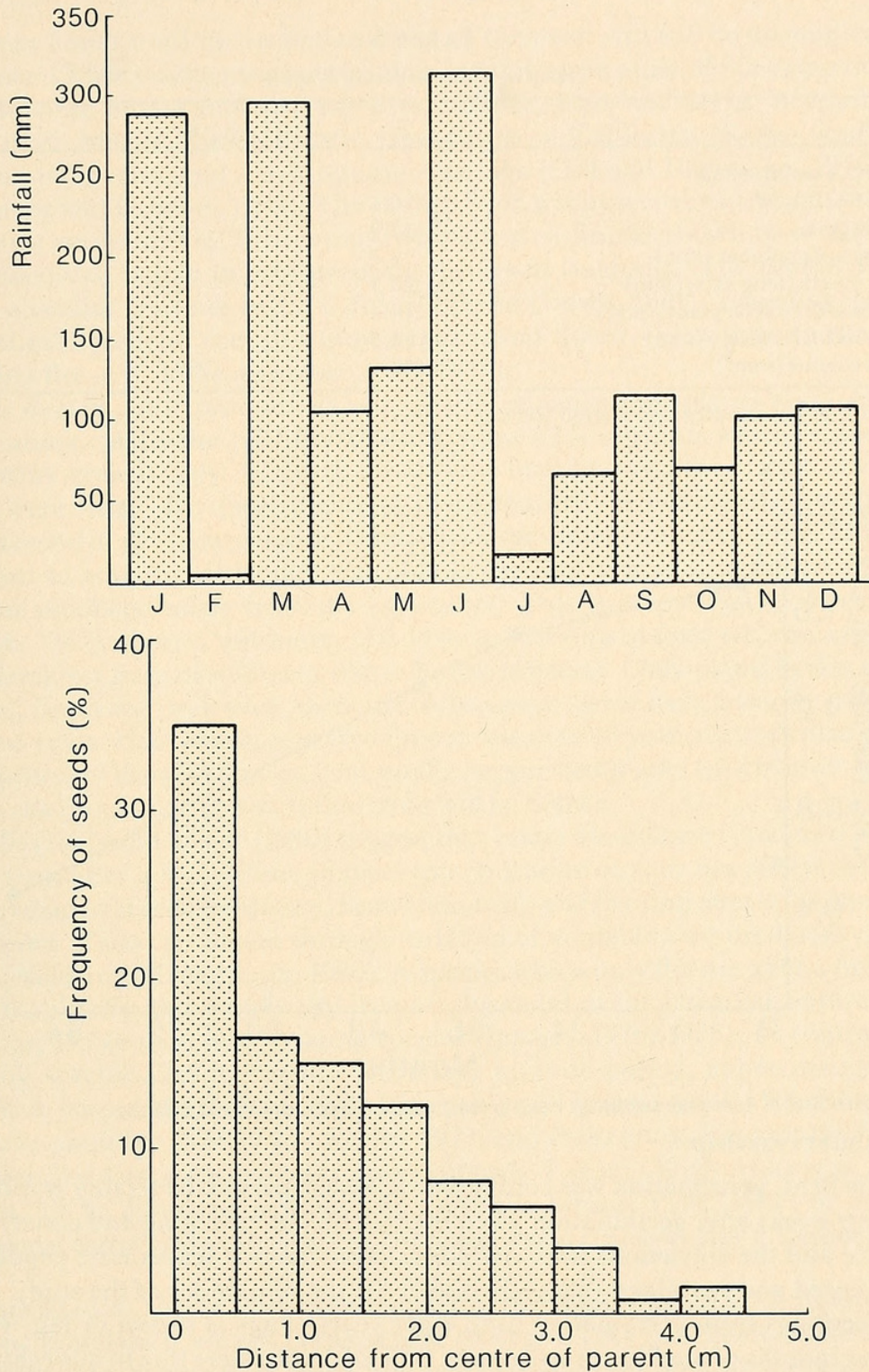


Fig. 3. Initial seed dispersal around *A. hispida* parents.

Seed dormancy and viability

All seeds showed 100% viability for up to six months after collection. There was no indication of any dormancy mechanism.

Seeds buried in hessian bags germinated within the first month of burial presumably following good rainfall in March (300mm). The remaining seed bags were retrieved two months after burial and all seeds had germinated.

TABLE 5
Size of eight year old plants, $n = 30$

Dimension	\bar{x}	s.e.	range
number of live aerial stems	1.8	0.3	1-8
number of live leaves ^a	8.1	0.9	2-27
plant height (mm)	140.2	8.0	40.5-220.2
depth to top of lignotuber (mm)	2.7	2.1	-25-29
lignotuber length (long axis) (mm)	20.3	1.6	5.9-36.1
lignotuber width (widest point) (mm)	16.4	1.0	6.3-26.7
lignotuber width (orthog.) (mm)	13.8	1.0	4.7-24.7
lignotuber volume (mm ³)	4736	780	213-16297

^a None of the leaves sampled was of adult leaf size.

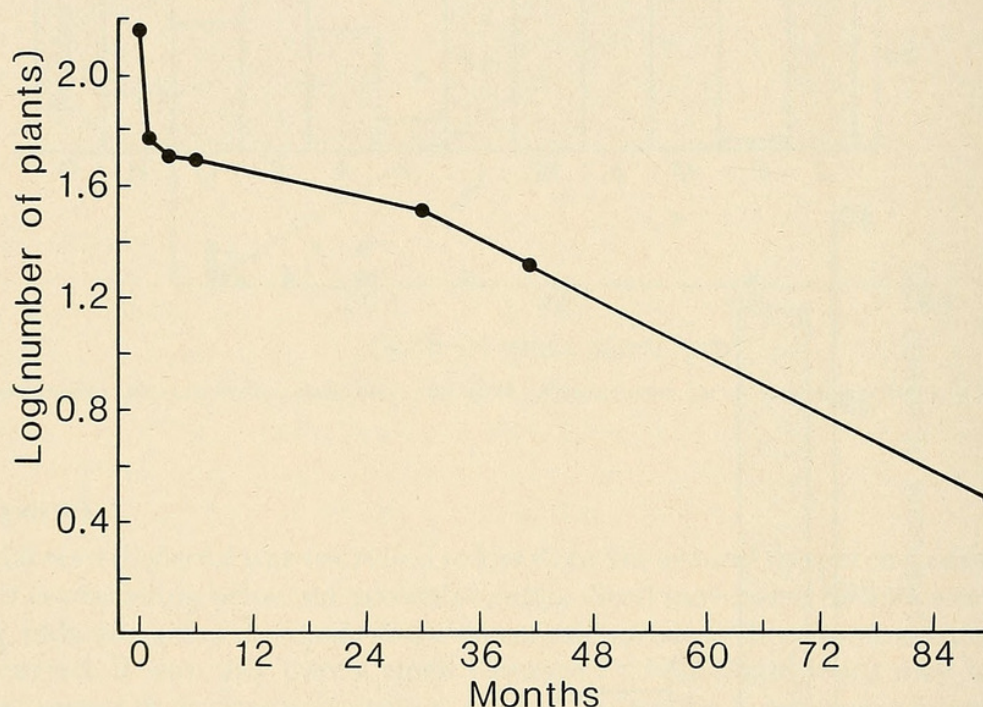


Fig. 4. The survival of *A. hispida* seedlings from germination to 8 years of age at Site 1.

Seedling survivorship

In the field, germination was confined to a 3-week period. Mortality was highest in the first few weeks after germination when the radicle was emerging and penetrating the soil surface and the cotyledons were unfolded. Once the first leaves were produced survival increased and remained relatively higher for the remainder of the study. The survival of seedlings from germination until eight years of age is shown in Fig. 4. During the first six months of seedling growth some 60% of deaths were due to desiccation; 16% to seedling predators; 5% to burial by moving sand; and 19% to unknown agents. The 8-year-old plants were small with small lignotubers close to the soil surface (Table 5).

DISCUSSION

A. hispida is a typical resprouter (Gill, 1981) with regrowth after fire from a combination of epicormic and lignotuberous shoots. It is among the fastest resprouting species in those communities in which it occurs, and where the main stem is not killed an extensive new canopy is formed some 6-8 months after fire. These mature plants have a very short secondary juvenile period and are potentially able to flower in the first flowering season (Nov-Feb) following a summer fire. Plants burnt in autumn to spring will

probably not flower until the second summer as regrowth will still be incomplete in the first summer. Other resprouting species showing this same pulse of flowering in the immediate post-fire period include; geophytic orchids, lilies and herbs in South Africa (Levy, 1966; Martin, 1966), coastal sage shrubs in California (Keeley and Keeley, 1984), *Xanthorrhoea* spp. and *Kingia* spp. in Australia (Gill and Ingwersen, 1976; Baird, 1977; Lamont and Downes, 1979). The change from a suppressed shrubby individual in long unburnt communities, to vigorous regrowth after fire, as shown by *A. hispida*, has not been recorded before in a resprouting species in Australia. The berries *Vaccinium* spp. show a similar response in the U.S.A. (Gill and Groves, 1981). Some non-sprouting plants (obligate seeders) can also grow rapidly and flower extensively in the first 18 months after fire, e.g. *Acacia suaveolens* (Auld, 1987).

In *A. hispida*, fruit production was clearly enhanced on plants resprouting via epicormic shoots. After the 1977 fire at Site 1, some 65% of plants which resprouted by lignotuberous growth only, failed to flower and may be juveniles. Most of these individuals were small. For these plants to reach maturity a sufficiently long inter-fire period is needed to allow development of a stem large enough to survive fire. However, it is important to note that one plant was able to produce a large seed-crop from a 1.5m aerial stem produced solely from the lignotuber. This is in contrast to *Banksia serrata* (Bradstock, 1985) where a minimum of 6-10 years is required for a resprouting juvenile plant to develop a stem of sufficient size to be fire resistant. Only plants of this size were capable of flowering and even then the subsequent secondary juvenile period was around two years. In *B. serrata*, repeated fires at less than 10 year intervals may produce, in a proportion of the population, continually suppressed plants which never flower. In *A. hispida*, the proportion of plants flowering will be higher.

Jacobs (1951) and Majer (1980) suggest that insect abundance is reduced at least in the short term after a fire. Although there are no studies on how fire affects the populations of predispersal seed predators, heavy flowering and fruiting after a fire may lead to reduced levels of seed predation through satiation of available seed predators e.g. *Acacia suaveolens* (Auld and Myerscough, 1986). A species which only flowers after a fire is likely to be both spatially and temporally irregular because of the irregular nature of fires. This is comparable with mast seeding species (Janzen, 1976; 1978). In contrast, other resprouting species after a post-fire secondary juvenile period, either maintain their reproductive output throughout their life span (e.g. *Banksia serrata*, Bradstock, 1985; *Arctostaphylos glandulosa*, Keeley and Keeley, 1977; and *Protea nitida*, Kruger, 1983) or show a peak after fire with a decline after approximately 2 years (*Xanthorrhoea* spp., Gill and Ingwersen, 1976; *Telopea speciosissima* and *Lambertia formosa*, Pyke, 1983) or around 10 years (*Isopogon anemonifolius*, Bradstock, 1985; and *Protea cynaroides* and *P. speciosa*, Kruger, 1983).

Dispersal of *A. hispida* seeds is minimal and seeds will remain in the boundaries of the existing population, except perhaps near its edges. Like the closely related *A. bakeri* (Auld, 1986), ant dispersal of seeds was not extensive. As well as the possibility of decreased seed predation (Majer, 1982) and increased nutrient levels (Siddiqi *et al.*, 1976) the immediate post-fire environment has ample light for developing seedlings. For *A. hispida*, with no seed dormancy, successful establishment and growth is largely dependent upon lack of discovery by post-dispersal seed predators and the amount of available moisture. Specht (1981), Bradstock and Myerscough (1981) and Bradstock (1985) have shown that the seedling establishment of several proteaceous shrubs was directly dependent upon soil moisture immediately following a fire. With high moisture availability, establishment should be high, although unless moisture levels are maintained subsequent mortality will be high. As seed of *A. hispida* maintains its viability for up to six

months it is likely that sufficient rainfall will occur for germination. During drought periods, post-dispersal seed predation may severely reduce the available seed.

For recruitment in *A. hispida* to be effective, the inter-fire period must be sufficient to allow seedlings to reach a stage where they are fire tolerant. This will vary depending on the intensity of the fire and the depth of burial of the lignotuber. After 8 years, seedlings (or juveniles) were still distinct in size from all individuals which survived the 1977 fire at Site 1. Whilst the development of the lignotuber had commenced, its size was small and may not ensure survival in the next fire. Abbott (1985) found that 3½-year-old plants of the resprouter *Banksia grandis* were small in height (11cm), whilst the length of the long axis of the lignotuber of these plants was also small (1.04cm). He predicted that it takes 35 years for this species to reach maturity from seed, although no estimate was made of how large the lignotuber must be to survive fires of differing intensities. To ensure the continued survival of populations of *A. hispida* via seedling recruitment, a fire-free period of greater than eight, and possibly many more, years may be required if the small juveniles described here are not fire resistant. Clearly, for the long-term management of populations of *A. hispida*, an investigation of the minimum fire-free period that is required under varying fire intensities is required. Kruger (1983) has suggested that in fynbos the primary juvenile period is usually less than eight years, whilst for chaparral it is 8-10 years. Data from Abbott (1985), Bradstock (1985) and this study indicate that in fire-prone Australian plant communities the primary juvenile period may be much longer for resprouting species. This emphasises the importance of considering the minimum length of the fire-free interval required to maintain populations of resprouting species through seedling recruitment. Whilst many resprouters are vegetatively vigorous and floriferous after fire, this cannot be directly interpreted to mean that resprouters are capable of maintaining population levels under short fire frequencies. The length of time required for seedlings to become fire tolerant dictates the minimum fire interval, irrespective of any post-fire flushes in vegetative growth or flowering.

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