SPP 93/0094. Establishment of jarrah (*Eucalyptus marginata*) in shelterwood areas and on dieback 'graveyard' sites

Exp B. Effect of stand density and fertilizing on seed-fall – Final Report

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Abstract

We studied the effects of stand basal area and fertilizer on the falls of buds, flowers, opercula, capsules, and seeds over 41 months on 24 thinned and 6 unthinned plots in the jarrah (*Eucalyptus marginata*) forest seven years after fertilizer application. The study plots were first thinned in 1964 and then rethinned in 1986 to nominal stand densities of 5.5, 10.9, 16.4, and 22.4 m^2ha^{-1} basal areas under bark, with control plots of 28.5 m^2ha^{-1}. Fertilizer treatments of: unfertilized; and fertilized with 400 kg ha^{-1} N and 229 kg ha^{-1} P were applied in 1987 and 1988 to produce a completely randomized design consisting of five thinning treatments by two fertilizer treatments by three replicate plots. Seed collection, from randomly positioned traps set in fixed locations, began in 1994.

The average rate of seed-fall across all plots was 448,000 seed ha^{-1} yr^{-1}. This equates to 4 kg ha^{-1} yr^{-1} of seed, which is one-hundredth of the total weight of the annual production of all reproductive parts (423 kg ha^{-1} yr^{-1} of buds, flowers, opercula, seeds and capsules). This is less than 6% of the total annual production of above ground biomass on the site.

The seed-fall, and the falls of the other reproductive parts, generally increased as the stand basal area increased. However this response was only statistically significantly for the falls of empty capsules and immature buds, and for the weight of the immature bud-fall. The falls of all reproductive parts varied widely within the treatments, and the response was not linear or consistent across the thinning treatments. This high variability may be due to our use of traps in fixed locations to sample the falls on each plot.

The fertilized plots produced a combined total of 24% more reproductive parts than unfertilized plots, though neither this nor any of the differences in the falls of the individual reproductive parts were statistically significant. The main impact of fertilizing was an increased production of buds and flowers, followed by a greater loss of these parts, leading to

a production of seed equivalent to that observed on unfertilized plots. We conclude that fertilizer application six years prior to this study did not effect seed production.

Only 7% of the buds that were initiated were retained on the trees to mature and become seed bearing. The greatest loss of buds occurred before flowering (55% of buds lost), followed by a large loss in the period shortly after flowering before the capsules fully developed (37% lost).

In jarrah the falls of mature and immature buds, and of immature, mature, and empty capsules are spread throughout the year and do not follow a regular seasonal pattern. However, flowers typically open in October, November, and particularly in December, with the fall of opercula reaching a peak in these months.

Seed-fall did follow a seasonal pattern. From a minimum in June each year, seed-fall increased through the months of July and August reaching early season peaks between August and October before declining slightly in November. The main seed-fall occurred between December and March, with annual peaks occurring in December, January, or February. Seed-fall consistently declined in March, April and May to again reach a minimum in June each year.

We describe the annual seed production cycle and comment on the reliability of estimating seed production across the seed cycle.

Introduction

In the south west corner of Western Australia the publicly owned tall forests occur over an area of 1.98 million hectares. The jarrah forest is the most extensive, covering 1.57 million hectares with 0.8 million hectares actively managed for timber production (Conservation Commission, 2002). It is typically a mixed forest of jarrah and marri (*Corymbia calophylla*) trees, but can grow as stands of almost pure jarrah. Multiple use jarrah forest is managed for water and mineral production, conservation of biodiversity, ecosystem health and vitality, soil and water, recreation, and the production of timber at sustainable levels. Regeneration of harvested stands is usually achieved by managing the various innate regeneration capabilities of the jarrah forest. During timber harvesting operations, areas of jarrah forest which are suitable for regeneration but do not have an adequate stocking of seedlings, saplings, or ground coppice to supply this regeneration, are cut to a shelterwood so that the retained trees provide a source of seed for regeneration. Prior to harvesting shelterwood areas, seed and habitat trees are marked to provide a minimum of 8 m^2ha^{-1} of retained basal area in the high rainfall zone (>1100 mm yr^{-1}), 10 m^2ha^{-1} in the intermediate rainfall zone (900 to 1100 mm yr^{-1}) and 6 m^2ha^{-1} in the low rainfall zone (< 900 mm yr^{-1}) (CALM, 1995, CALM 2002b). The objective of this treatment is to provide seed for regeneration from the retained seed trees, and to suitably prepare the site so that seed will fall and seedlings will establish after timber harvesting. Fire is used to promote seed-fall and to provide a receptive seed-bed. Over recent years approximately 18,000 ha of jarrah forest has been logged annually (1% of the extant forest per annum) and 41% of this is cut to shelterwood (or 0.4% of the extant jarrah forest) (CALM, 2002a).

This report covers Part B of a wider SPP (93/0094) that examines various aspects of seed-fall and seedling establishment. In this part of the study we aim to :

- Determine the effect of stand basal area and fertilizer on the quantity of seed produced
- Examine the seasonal variations in seed-fall.
- Examine the production and loss of buds, flowers, and capsules through the development sequence.
- Describe the seed production cycle.
- Provide seed-fall information relevant to improving the management and regeneration of shelterwood logged jarrah forest.

Methods

Study area

This study area was located in a high quality even-aged regrowth stand of *E. marginata* in Inglehope forest block (32° 45’S, 116° 11’E; AMG 423,500m E; 6,375,900m N) 9 km south east of Dwellingup, Western Australia. The overstorey trees on this site are predominantly jarrah with very few (~1% of stems) marri occurring in the stand. The soil is yellow sandy ferruginous gravel and is of low fertility. The climate in the area is typically mediterranean with an average annual rainfall over the period of the seed collection of 1177 mm at Dwellingup, and an average annual pan evaporation of 1277 mm. Long term average annual rainfall at the site is 1100 mm, 200 mm less than that at Dwellingup. Average monthly maximum temperature varies from about 30° C in January and February to 15° C in July.

Experimental design

The experiment consists of 30 plots (40 m x 40 m with an 8 m buffer on all sides) dispersed over approximately 40 ha (Fig.1). The plots were first thinned in 1964 (at age 40 years) to nominal stand densities of 7, 11, 15 and 18 m^2ha^{-1} basal areas under bark. The unthinned plots had basal areas of approximately 22 m^2ha^{-1}. In 1986 a second thinning was imposed (Table 1). Fertilizer treatments were then applied in 1987 and 1988. The two fertilizer treatments were: unfertilized, and fertilized with 400 kg ha^{-1} N and 229 kg ha^{-1} P. The resulting design consisted of five thinning treatments by two fertilizer treatments by three replicate plots in a completely randomized design (Table 1). Both thinnings aimed to remove the smallest and slowest growing trees from the stand (thinning from below).

Seed-fall collection

The fall of seed and associated reproductive parts (buds, flowers, opercula, capsules and seeds) was collected each month over the period February 1st 1994, to July 7th 1997 (41 months). For the first five months the falls were collected from nine trays randomly located about the central 20 x 20 m within each plot (9 x 0.097 m^2, total 0.873 m^2 per plot). For the remaining 36 months (July 7th 1994, to July 7th 1997) the falls were determined by collections from three traps, again randomly located about the central 20 x 20 m within each plot. These random trap locations remained fixed over the period of the study. Each trap had an area of 0.9025 m^2 (a total of 2.7075 m^2 per plot). Collections were air dried in a glasshouse or oven dried if wet (< 40° for up to 24 hours). Samples were lightly sieved to remove material less than 2 mm, and any leaves, twigs, or other foreign material was removed. Subsequently the sample was manually sorted and individual counts determined for: seed, flowers, mature buds, immature buds, opercula, mature capsules, immature capsules, and empty capsules (Collections for the first six months considered only seed, mature capsules, and empty capsules). After sorting, all reproductive parts other than seed were dried for 48 hrs at 70°, and then weighed. Collections were made on or close to the last day of each month, and thus reflect the average fall for each month.

The flower and seed-fall cycle

The growth and fall of flowers, capsules, and seed follow a regular annual progression and a longer term though irregular cycle. The flower and seed-fall cycle occurs over a four to seven year period, i.e. it is four to seven years between major seeding years in jarrah (Abbott and

Loneragan, 1986). Seed-fall commences about two years (21 months) after the incipient flower buds appear and may continue for 29 more months, i.e. a total period of 50 months from incipient flower bud appearance to final seed-fall (Loneragan, 1971). Several key stages occur in this cycle. Incipient flower buds appear in summer to early autumn along the last and current season's growth. Flowers then open in spring. Capsules ripen over early winter one year after flowering (Loneragan, 1971). Finally, seed-fall commences one year after flowering and two years after buds first appeared (Loneragan, 1971). One important consequence of this cycle is that seed collected in the first year of this study was linked to the cohort of buds and flowers that formed before the study began. Similarly, buds and flowers collected at the end of the study were linked to the seed crop that fell after the study finished. Because of the time lag in this cycle, it is not possible to relate total seed-fall to flower production (determined from the fall of opercula) over the entire period of collection. Also, the seed that matured in one winter will fall largely in the following summer, but may continue to fall and overlap with the seed-fall from the subsequent one or two years. Thus seed-fall in one summer is not strictly related to flower production in the previous summer. Our first collections occurred when buds were forming in late summer (we did not collect buds during the first five months). Our collection finished in late winter after the end of a seed-fall.

Results

Mean falls over the observation period

A total of 3,236 samples were collected on the 30 plots over 41 months, yielding 292,663 reproductive parts weighing a total of 10.8 kg. Over the 36 months in which all reproductive parts were collected, this collection consisted of 10,436 seed, 75,228 flowers, 56,647 mature buds, 52,020 immature buds, 90,201 opercula, 808 mature capsules, 368 immature capsules, and 5,381 empty capsules weighing a total of 10.3 kg (423 kg ha^{-1} yr^{-1}) (Table 2). Very little of this total production was seeds. The total weight of seed collected (98 g) was less than 1% of the total weight of all reproductive parts produced by the trees (seeds, buds, flowers, capsules and opercula). The weight of all capsules (mature, immature and empty capsules) produced by the trees was 43.3% of the total weight of all reproductive parts produced (seed, flowers, buds, opercula, and capsules). With a weight of 9.5 mg, individual seeds weigh very little when compared with an individual capsules (approximately 720 mg). The total weight of seed collected was approximately 2.6% of the weight of all empty capsules collected.

Mean seed-fall over the entire 41 month period of this study was 447,670 ha^{-1} yr^{-1} (1226 seeds per hectare per day) (or 427,889 ha^{-1} yr^{-1}, and 1172 seeds per hectare per day over 36 months). Daily seed-fall (averaged for each month) ranged from 0 to 6 seeds per m^2 per day in individual traps, with a mean for the entire collection period of 0.123 seeds per m^2 per day.

Effect of stand basal area and fertilizer on the fall of reproductive parts.

The fertilizer treatment had no statistically significant effect on the number or weight of seed, capsules, and reproductive parts produced over the observation period (Anova, $\alpha = 0.05$). However, large increases and decreases in the falls of these reproductive parts occurred with fertilizer application (Table 3). We observed a 37% increase in the fall of mature buds on fertilized plots, and a 17% increase in the fall of immature buds, resulting in a 27% increase in total bud-fall on the fertilized plots. Fertilizer also increased the fall of opercula by 24% (indicating a 24% increase in flowering). However these same fertilized plots had a 26% greater fall of flowers. A large proportion of the extra flowers that were produced on fertilized plots fell from the tree and did not develop to become capsules. From our data we cannot directly determine whether fertilized plots retained more or less flowers than unfertilized plots. However, the falls of capsules and seeds indicate that it is unlikely that fertilized plots retained more flowers in the tree crowns than unfertilized plots. The fertilized plots produced 9% less immature, empty and mature capsules, (9% less total capsules - the reduction in each capsules type being similar - about 9.3%) and 6% less seed. However these differences were not significant and the resulting fall of seed must be considered similar for both fertilized and unfertilized treatments, indicating that fertilized plots most likely retained similar numbers of flowers in the tree crowns as unfertilized plots. Thus fertilizer increased flower production, but also increased flower fall, resulting in a similar number of flowers being retained on both fertilized and unfertilized plots.

The mean weights of single reproductive parts produced on the fertilized plots were similar to those produced on unfertilized plots (Table 3). As the weights of individual parts were similar, the total weights of seeds, buds, flowers, capsules and opercula produced on fertilized and unfertilized plots followed the trends observed for the counts of falls of these parts (Table 3).

Analysis of covariance, with the basal area of each thinning treatment used as a covariate, established that treatment basal area had a significant effect on the number of immature buds ($p > 0.018$) and empty capsules ($p > 0.021$) that fell. The fall of immature buds increased as basal area increased (Table 4), and this response was further increased by the fertilizer treatment, though the response to fertilizer was not significant (Table 5). The weight of the immature buds that fell showed a similar significant increase with increasing basal area ($p > 0.032$) (Table 4), and again an increasing fall with fertilizer that was not significant. The fall of empty capsules also increased significantly as basal area increased, but in this case was reduced by the application of fertilizer. Again, the response to fertilizer was not significant. In this case the weight of empty capsules that fell was not significantly related to basal area or to fertilizer treatment. The falls of other reproductive parts were not significantly related to the thinning or fertilizer treatments.

Effect of stand basal area and fertilizer on the falls from individual trees.

Table 6 gives the mean falls of reproductive parts per tree for each of the five thinning treatments. In all cases the falls per tree consistently increase as the stand basal area decreases. This result is not surprising. As the a result of past thinning, the stands with the lowest basal area also carry the largest trees, and the largest trees have a larger branch structure, which would be expected to carry a larger crop of flowers, capsules and seeds. This situation is an outcome of the thinning treatments applied to these plots. There are several aspects of the thinning treatments that are relevant. The trees remaining on the plots in all treatments were retained from a single stand with high spatial uniformity in stand structure. The stand structures that existed on the plots during this study are a consequence of two thinnings over 39 years, which removed the smallest and slowest growing trees. This occurred to the greatest extent in the most heavily thinned stands. Consequently, the plots with the lowest treatment basal area have the largest trees (mean diameter under bark, DUB = 37.7 cm), and the lowest number of trees. Conversely the plots with the highest basal area have the smallest trees (mean DUB = 16.5 cm), and the greatest number of trees. Therefore it is not surprising that the treatments with the lowest basal area, which have the largest trees, also have the highest falls per tree.

Seasonal variation in the flower and seed-fall cycle

Figs. 2 to 5 show the monthly variation in the falls of buds, opercula, flowers, capsules and seeds over the period of observation. The monthly and seasonal falls of all reproductive parts varied greatly between years, particularly for flowers and opercula. Regular seasonal cycles are evident for the falls of seed, flowers and opercula (Figs. 3 and 5). The falls of immature and mature buds did not appear to follow a regular seasonal cycle, and the falls of immature, mature and empty capsules were spread throughout the years and did not have regular peaks (Figs. 2 and 4).

Discussion

Effect of stand basal area

The falls of reproductive parts generally increased as the stand basal area increased (Table 4). However these responses were only statistically significant for the falls of empty capsules and immature buds.

The response of seed-fall (Fig. 6) with stand basal area is similar to the response that Stoneman et al. (1996) described at this site for basal area growth and volume growth, with stand basal area. At low stand basal areas there were too few trees, and stand growth was less than maximal. As stand basal area increased, stand growth increased. Stand growth was greatest for intermediate stand basal areas, and declined slightly as stand basal area continued to increase. Similarly seed-fall was low on stands with low basal areas as there were insufficient stems and crown structure to produce a large seed crop. Above a basal area of about 10 m^2ha^{-1} seed production reached a plateau, and increases in stand basal area did not increase seed production. This response is similar to that found for cone production in *Pinus elliottii* (Florence and McWilliams, 1956) and also for fruit production in apple stands (Verheij, 1968). At low stand basal areas capsule and seed production is reduced and with increasing stand basal area a threshold is realised beyond which production is not influenced by stand basal area.

There was large variability about the mean falls for each thinning treatment, with falls on individual plots within treatments varying widely (eg. Fig. 6) and reducing the statistical significance of the differences that occurred with basal area. Some treatments produced distinctly larger or smaller falls of particular reproductive parts (Tables 3, 4, 5). This was most noticeable with thinning treatments T1 and T3. Treatment T1 had consistently lower falls than all other treatments for all seed, capsules, and flower parts except immature capsules. Treatment T1 also had the lowest total weights for all seed, capsules, and flower parts produced (Table 4). These results are consistent with the response observed by Stoneman et al. (1996) for leaf area and stem growth on treatment T1 which has insufficient numbers of stems to fully occupy the site. The response in treatment T3 was variable. Treatment T3 had the largest fall of opercula, indicating a large production of flowers. This treatment also experienced the largest fall of flowers prior to capsules set. However treatment T3 had the lowest fall of immature capsules and the second lowest production of seed. These various responses within treatment T3 are consistent with one another – a large flower fall following a large flower production followed by a low fall of immature capsules and finally a low seed-fall – but they confound the generally observed trend of increasing falls with increasing basal area. Consequently the response with basal area was not consistent across the thinning treatments.

The specific sources of the variability between plots within the thinning treatments are unclear. This variability may reflect genuine differences between plots with similar basal area, or may be due to bias in the sampling of these falls on individual plots. We collected seed, capsules, and flower parts from traps at three fixed positions randomly located across each of the three replicate plots in each of the ten basal area and fertilizer treatments – a sampling design intended to limit systematic bias. The fall of reproductive parts will vary with distance from the tree. Heavy parts, which are little effected by wind, would be expected to fall close to a tree, and be absent or in low numbers far from a tree, while lighter opercula and seed would be expected to be distributed more widely away from trees. However, winds below the canopy in this forest are typically light, and consequently falls of seed, capsules, and flower parts should have high spatial variability and be related to the distance of the collection point from flowering and fruiting trees. It is possible that traps on some plots were located directly beneath flowering and fruiting trees – these traps yielding high falls – while those on other plots were located away from such trees and recorded low falls. These types of consistent bias are possible when a small number of fixed trap locations are used. It is not possible to determine if this bias exists in this data set as a result of our sampling strategy or if the high variability observed within treatments is a true reflection of variability between stands of similar basal area which may be related to variations in crown structure, and/or conditions on individual plots. The observed variability may also result from a combination of bias in sampling and genuine variability between the plots.

Effect of fertilizer on the falls of seed, capsules, and flower parts

Fertilizer tended to increase, though not significantly, the number and total weight of the falls of reproductive parts in the early stages of the seed development sequence (immature buds, mature buds, opercula and flowers). The effect of fertilizer on the later stages of seed production tended to be the opposite, with the number and total weight of immature capsules, mature capsules, seed and empty capsules tending to be less on fertilized than on unfertilized plots. These responses could be related to the impact of fertilizer on plant water stress. Stoneman et al. (1996), in an earlier study on this site, identified increased water stress on the unthinned plots over the summer and autumn period associated with fertilizer application.

It is important to note that these plots were fertilized in 1987 and 1988, approximately six years before the seed-fall collection began. The major impacts of fertilizing on seed production would be expected to occur relatively soon after the fertilizer application. This six year interval between the fertilizer application and the commencement of our seed-fall study may in part explain the absence of significant responses to fertilizer in this study.

As fertilized plots produce 9% fewer capsules but only 6% fewer seed than the unfertilized plots, this could indicate that the capsules produced on fertilized plots contain a greater number of seeds per capsules than those on unfertilized plots (about 4% more).

Effect of thinning and fertilizer on the falls of buds, flowers, capsules and seeds

Analysis of covariance, which considered the effects of both treatment basal area and fertilizer treatment on the falls of reproductive parts, did not identify any significant interactions between the thinning and fertilizer treatments.

Number of seed per capsules

Considering all empty capsules and all seed collected over the study period, there were 1.86 seeds per capsules. This value presumes that the concordance between seed-fall and empty capsule-fall indicates that capsules fall soon after they lose their seed, and that these falls can be used to determine the number of seeds per capsules. Generally the capsule-fall tracked the seed-fall closely; however this did not occur in March and April 1997 at the end of our collection period. There was a large seed-fall which was not closely followed by an increased fall of empty capsules, which may have occurred after our study finished (Fig. 5). Over this period in March and April there were 4.28 seeds collected for every capsules collected. Excluding this, and a similar period prior to July 1994 at the commencement of this study, yields a calculated value of 1.6 seeds per capsules. This is proposed as the best estimate of the number of seeds per capsules from this study.

Bassett (2002) found that *E. globoidea* capsules contained an average of 1.2 viable seeds per capsules, and Grose and Zimmer (1958) reported 1.3 to 1.8 seeds per capsules for this same species. While *E. globulus* capsules contain an average of 20 seed and capsules of *E. deglupta* can contain up to 40 seeds, average viable seed numbers for these species typically range between 1.2 and 4.9 seeds per capsule (House, 1997). We did not test the viability of the collected seed. Jarrah seed is comparatively large and relatively easy to visually identify compared with the seed of some other eucalypts. Abbott and Loneragan (1986) cite work by

Kimber (unpublished) that demonstrated jarrah seed collected from trees in Teesdale block (approximately 15 km west of our study site) had a high viability (93%), and Abbott (1984) found 97% viability. Abbott (1984) (cited in Abbott and Loneragan, 1986) examined 3 batches of seed and found means of 1.2, 1.9, and 2.1 fertile seeds per capsules (mean = 1.7). We conclude that our estimate of 1.6 seeds per capsules is appropriate for viable seed.

The fate of buds, flowers and capsules

Fig. 7 shows the fate of the buds, flowers and capsules produced by trees in this study. The number of opercula that fall reflect the number of flowers produced. When combined with the falls of mature buds and immature buds, the sum of these falls provides an estimate of the total number of buds initiated. Of the 8.15 million buds initiated per hectare per annum, only 45% completed their development and became flowers (Fig. 7). Of the buds that fell before they developed into flowers (55% of all buds), approximately half fell as immature buds (26%), and half fell as mature buds (28%) (Fig. 7). By comparison with our observation over 3 years that a mean of 55% of buds were aborted annually, in a 4 year study Bassett (2002) found that *E. sieberi* aborted 44% of umbellate buds annually, while *E. globoidea* aborted 67%. The data of Cremer (1971) indicates that 50% of buds are aborted prior to flowering in *E. regnans* and White's (1971) observations indicate that 75% of *E. diversicolor* buds fall before flowering.

These findings indicate that substantial losses of buds prior to flowering are common in Eucalypts and that the losses of buds that we observed in jarrah are not unusually high. Florence (1964) observed consistent and extensive shedding of buds in *E. pilularis* and suggested that this may occur at the stage of major expansion of these buds and be due to competition for space or demand for water or nutrients. Loneregan (1971) noted that bud-fall may be caused by fire, insects, birds, disease, and irregular weather events, and proposed that strong annual leaf growth encourages abscission of much of the bud crop in jarrah. However, high losses of buds do not occur in all years. Loneregan (1971) notes intervals of 4 to 6 years between major flowerings in jarrah and observes that the majority of buds are shed in successive years until conditions favour the mass retention of buds that produces a prime blossom and subsequent seed year. Our three and a half year study may not have included such a prime blossom year (though an extremely abundant flowering was observed over summer in 95/96). However the seasonal variability of our observations of bud-fall, flowering and flower-fall indicate more complex interactions (Figs. 2 and 3). Monthly bud-fall had a low negative correlation with the monthly mean of maximum temperature ($r = -0.19$, $n = 36$). We observed moderate losses of mature buds throughout 1995, yet we also observed a strong flowering over summer 1995/96 and a massive fall of flowers soon after flowering in January 1996. Our data indicates that substantial shedding of buds can occur at any time during their development and that the largest losses of reproductive parts occurs during bud development, and shortly after flowering.

There were 3.7 million opercula collected per hectare per annum in our study, indicating that on average this number of flowers opened per hectare per annum. Of these 3.7 million buds that opened and flowered, 83% (3.08 million $ha^{-1}yr^{-1}$) fell after flowering and only 17% progressed and developed into some form of capsule. Bassett (2002) found that a similarly high proportion of *E. sieberi* flowers (93%) were aborted, leaving only 7% of buds to develop into some form of capsule. In contrast *E. globoidea* aborted only 65% of flowers leaving 35% of buds to develop into some form of capsule (Bassett, 2002), 30% of *E. regnans* flowers progress through to become mature capsules (Cremer, 1971) and more than 80% of *E. diversicolor* flowers progress through to become mature capsules (White, 1971).

The temporal concordance between the fall of operculum and the fall of flowers indicates that flowers typically remain on the tree for approximately 1 month after opening (Fig. 3). Of the 17% of jarrah flowers that opened and did develop further (0.61 million $ha^{-1}yr^{-1}$), what was their fate? At this point our estimates become much less accurate. Of the capsules and seed we collected over the study period many would have developed from buds that had been initiated before the study commenced, and a significant proportion of capsules produced over the study period would have been retained on the trees and fallen after the study finished. Consequently the seed and capsules fall collected over the study period cannot be directly related to the flower production over this period. This is evidenced by the large discrepancy between the calculated number of capsules set in the collection period (14,973) and the number of capsules accounted for (6,557, or only 44% of all capsules set) (Fig. 7). However, some conclusions can be reached, and this discrepancy can be used to correct the observed estimates. We collected only 368 immature capsules over the 36 month collection period, compared to 6189 empty and mature capsules. These figures indicate that after the initial and substantial fall of fully developed flowers, in most years very few immature capsules fall before they mature and bear seed (estimated as 6% of all capsules set). From these figures it can be estimated that only 16% of all flowers that open complete the cycle to form mature capsules (another 1% develop to immature capsules). This amounts to 7% of all buds initiated, i.e., only 7% of all buds initiated develop to become mature capsules. By comparison 15% of all buds in *E. regnans* and 30% of all flowers complete the cycle to form mature capsules (Cremer, 1971). *E. diversicolor* has much lower losses with 20% of all buds and more than 80% of all flowers completing the cycle to form mature capsules (White, 1971).

Seasonal variation in the flower and seed-fall cycle

Seasonal falls of buds

Although the falls of immature buds were low from September through to February in 1994/95 and 1996/97 (Fig. 2), immature bud-fall does not appear to follow a regular seasonal pattern. We found poor negative correlation between bud-fall and monthly mean of maximum temperature. Presumably buds fall at times of strong winds, or in response to other environmental factors. The fall of mature buds peaks from September through to December. Isolated peaks also occur in April and May (Fig. 2). However the September to December peak was missing in 1996/97 suggesting bud-fall is not seasonally regular. Possibly the large fall of immature buds in April, May and June of 1997, and the fall of mature buds in July 1997 are associated with the absence of a bud-fall in September through to December 1996/97. Van Noort observed bud-fall over the nine months from November to July in 1959/60 (Abbott and Loneragan 1986). A marked peak in bud-fall over this period occurred in March with little bud-fall in the spring and summer months of observation (November to January). This contrasts with our observed peaks in bud-fall from September through to December, reinforcing the impression of seasonal irregularity in bud-fall, and indicating that buds fall in response to unknown environmental factors.

Flowering and season

The fall of opercula peaked in October, November, and particularly in December, indicating flowers open in these months (Fig.3). This is consistent with the observations of van Noort in the same general area (cited in Abbott and Loneragan, 1986) and Abbott and Loneragan (1986) who noted that although the time of flowering in jarrah varies widely across its distribution, trees in the Darling range (which encompasses the area of this study) generally flower in November and December. The intensity of opercula fall, and hence flowering, varied widely (Fig. 3) across the years of our study. Flowerings occurred in Summer 94/95 (2,866 opercula collected), 95/96 (86,576 opercula collected), and 96/97 (759 opercula collected). The fall of flowers followed soon after the fall of opercula. The extremely abundant flowering we observed in 95/96 was accompanied by a similarly large fall of flowers in December 1995 and January 1996, however the number of flowers retained on the trees was still relatively large. The fall of flowers has a peak in December, January and

February. The data of van Noort for 1959/60 (Abbott and Loneragan, 1986) shows this peak earlier in November, December, and January. Although the intensity of these falls of opercula and flowers varied greatly between years, the timing of the falls was similar over the three years.

Capsule-fall and season

As previously noted relatively few immature capsules fell from the trees in this study. Over the three years of this study the peak fall of immature capsules was in the month of March, soon after flowering, with a particularly large fall in March 1996 which continued on into August 1996. The fall of mature and empty capsules is spread throughout the year and does not have regular seasonal peaks (Fig. 4). We also note that variations in the intensity of the fall of mature capsules usually align with the variations in the intensity of the fall of empty capsules (June 1994, March 1995, March 1997, Fig. 4). This may indicate that peaks in the fall of these capsules are driven by weather events, however we found a poor positive correlation between capsule-fall and monthly mean of maximum temperature ($r = 0.29$, $n = 36$).

Seed-fall season and cycle

Seed-fall followed a regular seasonal pattern with greatest falls occurring between December and March with smaller early season peaks occurring from August to November (Fig. 5). Seed-fall showed a consistent minima in June each year.

The major seed-falls occurred in the summers of 1993/94, 1994/95 and 1996/97. Seed-fall was greatly reduced in the summer of 1995/96. The peak seed-falls occurred in January and February 1994, December 1994 through to February 1995, January and February 1997. Van Noort's data (Abbott and Loneragan 1986) is consistent with our study, showing seed-fall for jarrah across the warmer months but particularly in January, February and March, with clear minima in June and July. Seed-fall had a moderate and significant positive correlation with the monthly mean of maximum temperature ($r = 0.57$, $n = 41$).

In all years we observed an early season peak in seed-fall between August and November before the main seed-fall in December through March (Fig. 5). These early season peaks occurred in August 1994, November 1995 and August and September 1996. This is clearly shown in Fig. 8 which plots the mean monthly seed-fall for each month of the year. The composite data of Fig. 8 shows seed-fall rising sharply in July to peak in August, and then decline in October and November before rising again with the main seed-fall in December. As these early season falls occurred before maximum temperatures had started to rise in November and December, it is most likely that this seed falls from capsules that have been held over from previous seed crops. Both White (1971), describing karri seed-fall, and Loneregan (1971), describing jarrah seed-fall, refer to ripe seed capsules retaining seed in the tree crowns through one (White, 1971) and two summers (Loneregan, 1971).

The main seed-fall of summer 1995/96 would have developed from flowers that opened in February 1995, i.e. buds set in 1994. The low seed-fall we observed could be due to a poor production of buds in 1994 (which our data would not directly identify), a large fall of immature buds in 1994 or of mature buds in 94/95, or a large fall of flowers around February in 1995. The latter is not evident. The falls of immature buds in 1994, and mature buds in 94/95 were of a typical magnitude. There was a relatively large fall of immature capsules in March 1996. This leads to the conclusion that the production of buds was poor in 1994, and the atypically large fall of immature capsules in April 1996 led to the poor production of seed in summer 95/96.

Abbott and Loneragan (1986) report estimates of mean seed-falls from a study by Kimber (1970) over five years. Kimber (1970) determined seed-fall using one fixed and four roving traps to collect monthly samples from each of three 2 ha plots. Mean annual seed-fall over the five years was 280,000 seed ha^{-1} yr^{-1} on a pole stand, 353,000 seed ha^{-1} yr^{-1} on an uneven-aged stand, and 90,000 seed ha^{-1} yr^{-1} on a veteran stand with few poles (Fig. 9). These values, and the mean for all stands, (251,000 seed ha^{-1} yr^{-1}) are substantially lower than both the mean observed in our study (448,000 seed ha^{-1} yr^{-1}) (Fig. 9) and that estimated from van Noort's study for the 1959 seed-fall event (~ 438,000 seed ha^{-1} yr^{-1})(Abbott and Loneragan 1986). However in 1967 and 1968 the seed-fall on the pole and mixed stands were similar to the mean value for our study (Fig. 10). The basal areas, and stand attributes of the stands studied by Kimber (1970) (local experiment no. 35) are not known and we cannot speculate on the effect of basal area on the seed-fall observed in his study. However, the mean seed-falls for the three stands studied by Kimber over the five years were not significantly different (Anova, $\alpha = 0.05$) (Fig. 9). Figure 10 shows the mean annual seed-fall for each year on each stand. Seed-fall on the veteran stand was relatively stable and low over the years (Fig. 10). As in our pole stand, the mixed and pole stands of Kimber's study show large annual differences in seed-fall, and large differences between the stands in some years.

Hatch (1964) determined the weight of the total annual fall of "floral litter" (flowers, buds, opercula, and capsules) over eight years at three sites in the northern jarrah forest described as sapling, pole, and virgin stands. Figure 11 shows the mean annual falls for these stands in comparison to the mean annual fall of "floral litter" collected over 36 months in our study at Inglehope. There was no significant difference between the falls on these stands, and the mean value we observed was close to the means for the three stands studied by Hatch. The standard errors show the large annual variations that Hatch (1964) recorded. The data of Hatch (1964), van Noort (presented in Abbott and Loneragan, 1986), and Kimber (1970) indicate that the falls of reproductive parts that we observed in our study are of a typical size found in the northern jarrah forest, and the data from these various studies highlight the large annual variations that occur in seed-fall.

Development and completion through the seed cycle

Following Loneregan (1971) and White (1971), Fig. 12 displays the percentage of the potential capsule crop expected to reach maturity, and the progressive fall of seed from these capsules over the months following capsule maturity. The percentage of the potential capsule crop expected to reach maturity was determined from the progressive loss of reproductive parts through the period of capsule development and growth. We derived this interpretation by combining data collected over the 41 months of this study. We combined the falls for each month of the year to calculate the mean monthly fall for each of the reproductive parts. For example, Fig. 8 shows the mean monthly seed-fall. These mean monthly falls, and the information displayed in Fig. 7, were used to develop the left hand side of Fig. 12.

The right hand side of Fig. 12 was derived from Fig. 8 and the observations of Loneregan (1971). Fig. 8 shows seed-fall reaching a minima in June and then rising in July and August before the mean of maximum monthly temperature starts to rise in November and December. We assume that much of this early seed-fall in July, August, September, and October falls from capsules that have been held over from previous seed crops. Fig. 13 shows the proportion of the seed-fall in July, August, September, and October that we assume has originated from a previous capsule crop, and Fig. 14 shows how we interpret seed from one years capsule crop falling over 14 months.

Biomass allocation

Loneragan (1961) (cited in Abbott and Loneragan, 1986) estimated that the annual above ground biomass production for a stand with a leaf area index of 1.0, was 5.9 t ha^{-1} yr^{-1}. This consisted of 2.7 t ha^{-1} yr^{-1} of wood, and 3.2 t ha^{-1} yr^{-1} of litter. The leaf fall contributed 1.9 t ha^{-1} yr^{-1} to the litter fall, the remaining 1.3 t ha^{-1} yr^{-1} presumably consisting of branchlets, twigs, and reproductive parts. The leaf area index across the plots on our study site ranged from 0.2 to 3.2 (Stoneman et al., 1996), depending on the plot and season, with a mean for all plots across all seasons between 1987 and 1989 of 1.45 (45% higher than that on Loneragan's study site). Adjusting Loneregan's estimate for this proportional difference in leaf area index gives an estimate of biomass production for our study sites of 8.6 t ha^{-1} yr^{-1}. Alternatively, using an allometric relationship for above ground biomass in jarrah (Hingston, 1990) we estimate the mean annual biomass production between 1987 and 1991 for the stands on this site to be approximately 7.6 t ha^{-1} yr^{-1}. The mean annual fall of reproductive parts observed across our study site was 0.423 t ha^{-1} yr^{-1}, which is approximately 6% of the estimated total annual biomass production, and approximately 10% of the estimated total litterfall. Thus the fall of reproductive parts is a minor proportion of the total annual biomass production.

This proportion (6%) of the total annual biomass production is comparable to that found in other environments. Kummerow et al. (1981) calculate biomass values for chaparral at two sites in California – Echo valley and Fundo Santa Laura. Flower and fruit biomass was 4.5% of total annual biomass production at Echo valley, and 1.9% at Fundo Santa Laura. For *Pinus pinaster* plantations near Canberra, Cremer (1992) estimated the annual weight of cones produced was equal to about 5% of the total annual above ground growth, though production of other reproductive components was not accounted for.

Implications for silviculture of jarrah forest

Seed forecasting

Results from this study indicate that seed forecasting can be undertaken with reasonable confidence once capsules have begun to form after flowering. Over the three years of our study only six percent of the capsules that set fell as immature capsules, and 13 percent of capsules that matured fell unopened, thus 81 percent of the capsules that set survived through to seed fall. Predictions of future seed crops during the bud development and flowering stages will be unreliable because of the potentially high losses between these reproductive stages and the seed-fall stage. With such high losses, small or moderate changes in the proportions aborted and surviving can lead to wide variation in the final seed crop. However predictions of the seed crop after flowering, when the capsules have begun to form, should provide relatively reliable estimates of the potential seed crop.

Stand density

Seed-fall was shown to be independent of stand basal area over a wide range of basal areas, with reduced seed fall occurring for stands with less than about 10 m^2ha^{-1} of basal area. When applying the shelterwood system in jarrah forest, the figure of 10 m^2ha^{-1} provides a target stand basal area that should provide near optimum levels of seed fall. This target basal area will also facilitate growth and development of seedlings that establish by reducing competition from the overstorey (Stoneman et al., 1995). The growth of retained seed trees will be enhanced by reducing stand density to this level which should produce little loss in stand growth (Stoneman et al., 1996).

In addition to the stand basal area, spacing of seed trees is important as jarrah seed in relatively heavy and does not disperse far beyond the tree crown. A basal area higher than 10 m^2ha^{-1} may be required to achieve the spacing of seed trees required to provide a relatively uniform spread of seed.

The relationship between stand density and the amount of seed fall is likely to change in response to site and stand factors. For low quality sites it is likely that near optimum seed fall would be provided at a lower stand basal area than for high quality sites, as full site occupancy will be achieved at a lower stand density. As a stand ages it is likely that near optimum seed fall would be achieved at progressively higher stand basal areas. In addition, stand height and crown dimensions, which are a reflection of stand quality, will effect the dispersion of seed across a stand. Seed from tall trees with wide crowns will disperse widely, while seed from short trees with narrow crowns will cover a smaller area. If the number of stems per ha is low on a stand, then it may be necessary to consider the dispersion of seed on the site as well as the quantity of seed produced.

Timing of regeneration establishment fires

In areas of jarrah forest cut under a shelterwood treatment, fire is used to facilitate establishment, survival and growth of jarrah seedlings by reducing competition from understorey species. Fire also creates a suitable seedbed for the seed to fall into, and ensures that seed-fall occurs at an appropriate time so that the chance of germination and establishment of seedlings is optimised.

In the Mediterranean climate of the south-west of Western Australia, options for timing of fire for regeneration establishment purposes are limited to the spring, summer and autumn period. The winter period is generally too wet and cold to carry a fire of sufficient intensity for regeneration establishment purposes.

If a spring fire is used, most of the potential seed crop will be in the canopy at the time of the fire, and consequently an appropriate fire intensity should be able to induce mass synchronized seed fall. However, seed fall in spring may expose seed to very high levels of seed predation during the long period before germination in the following winter (Abbott and van Heurck 1985, Stoneman and Dell 1994). The degree to which mass synchronized seed fall may offset the very high levels of seed predation that would otherwise be expected is unknown (O'Dowd and Gill 1984).

The second option is to use a summer fire. As most seed fall occurs over the summer period, particularly the month of February, mass synchronized seed fall into a newly created seed bed would be achievable if fire was planned to occur before seed fall would otherwise occur naturally. This option would limit the period of time, relative to spring fire, that seed is on the ground and available to seed predators, and so should reduce the amount of seed predation. However, given that seed fall would occur naturally over the summer period in the absence of fire, the advantages of using fire to induce mass synchronized seed fall are questionable. Another disadvantage is that summer fires are not usually applied in most of the jarrah forest because of the difficulty and cost of controlling such fires.

The third option is to use an autumn fire. Figure 5 shows that a large proportion of seed falls over the summer period, so the amount of seed fall that could be induced by an autumn fire will be much less than in spring. Additionally, an autumn fire may destroy seed that has fallen over the preceding summer period. An autumn fire would greatly reduce the period of time that seed is on the ground and available to seed predators and so should reduce the amount of seed predation. Whether the reduced seed predation offsets the reduced amount of seed that is supplied to the seed-bed from an autumn fire is unknown.

Research and development

Research and development is warranted to facilitate improvements to application of the shelterwood system in the jarrah forest. Two areas for research and development are identified.

Firstly, methods need to be developed to enable the prediction of seed crops so that disturbance activities can be planned to coincide with adequate seed crops. Such methods have been developed for a number of other eucalypts (Cremer 1971, White 1971, Harrison et al. 1990, Bassett 2002) and these methods may serve as models for jarrah.

Secondly, the timing of the regeneration establishment fire is worthy of investigation. Theoretically, fire in spring, summer or autumn each has advantages and disadvantages, but the degree to which each of the factors influences final seedling establishment is unknown. It is therefore unknown which fire season will provide the best outcome for establishment of jarrah seedlings. The effectiveness of regeneration in the absence of a regeneration establishment fire should also be tested, as fire may not be required to achieve near complete seed fall over the summer period.

Conclusion

Biomass and production

The mean annual fall of reproductive parts observed across our study site was 0.423 t ha^{-1} yr^{-1}. This is less than 6% of the total annual above ground biomass production on the site. We observed a mean seed-fall of 448,000 seed ha^{-1} yr^{-1}, and an average of 1.6 seeds per capsules. As viability is typically very high in jarrah these value are useful as estimates of viable seed.

Effect of basal area, and variability

This study was designed to examine the effects of thinning and fertilizer treatments on seed production. The treatment means for the falls of all reproductive parts except mature buds and immature capsules generally increased as the stand basal area increased. However this response was only statistically significantly for the falls of empty capsules and immature buds, and for the weight of the immature bud-fall. The falls on individual plots within the treatments varied widely, and the response was not linear or consistent across the thinning treatments. This high variability prevents us from identifying statistical significant relationships between stand basal area and seed production. The sources of this variability are unknown. Sampling bias on individual plots could be due to our use of fixed trap locations to sample the falls. Our replication of the treatments could have been insufficient, or the trends we observed could be random occurrences. The latter is unlikely. Although not statistically significant, this study shows a general increase in seed-fall with increasing stand basal area.

This study also showed that individual trees on thinned stands produced more seed than trees in unthinned stands, thus compensating on a stand basis, for the reduced number of trees that could produce seed on the thinned stands.

Fertilizer

Fertilized plots produced a total of 24% more seed, capsules, and flower parts than unfertilized plots. However these differences were not statistically significant. The weights of individual reproductive parts produced on the fertilized plots were similar to those produced on unfertilized plots. A large proportion of the extra flowers produced on fertilized plots fell from the tree and did not grow through to become capsules. Our data shows that fertilized plots produced 9% less immature, empty and mature capsules, (9% less total capsules - the reduction in each capsules type being similar - about 9.3%) and 6% less seed. The six year interval between the fertilizer application and the commencement of our seed-fall study may in part explain the absence of significant responses to fertilizer in this study. Fertilizer application six years prior to this study did not affect seed production.

Fate

Very few of the initial buds that form on the trees go on to complete the cycle and produce seed. Of all the buds initiated, 55% fall before they develop into flowers, approximately half falling as immature buds (26%), and half falling as mature buds (29%). Of those that remain and flower, 83% fall soon after flowering, leaving only 17% of the flowers to progress and develop into some form of capsules. A few then fall before they fully mature and bear seed (approximately 6% of all capsules) leaving only 16% of the flowers that open to complete the cycle and form capsules. This amounts to 7% of all buds initiated, ie., only 7% of all buds initiated mature to become capsules.

Seasonal cycles

In jarrah the fall of immature and mature buds does not follow a regular seasonal pattern Similarly the falls of immature, mature, and empty capsules are spread throughout the years and without regular seasonal peaks; however flowers typically open in October, November, and particularly in December, and the fall of opercula peaks in these months. Seed-fall was greatest between December and March with the largest falls occurring throughout the month of February, and much reduced falls occurring in October and November. The seed-fall minima occur in June.

Silviculture

Because of the high losses that occur through the early stages of the flowering and fruiting cycle, predictions of the future seed crop are most accurate if they are made after flowering, when the capsules have begun to form. The shelterwood system would be substantially enhanced and refined if a method for predicting seed crops was developed. This would greatly increase the likelihood of successful regeneration by enabling disturbance activities to be planned to coincide with adequate seed crops.

When applying the shelterwood system in jarrah forest, a target stand basal area of 10 m^2ha^{-1} should provide near optimum levels of seed fall. However a higher basal area may be needed to provide adequate spacing of the seed trees. For low quality sites it is likely that a lower stand basal area would provided near optimum seed fall as full site occupancy will be achieved at a lower stand density. As stands age, the optimum seed fall can be expected to occur at progressively higher stand basal areas.

Investigation of the timing of regeneration establishment fires is required to determine which fire season will provide the best outcome for establishment of jarrah seedlings. The effectiveness of regeneration in the absence of a regeneration establishment fire should also be examined, as fire may not be needed to achieve an adequate seed fall over the summer period. However, the absences of ashbeds may restrict opportunities for successful establishment, and the rapid early growth of seedlings required to compete with understorey.

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Table 1. Treatments applied to the Inglehope thinning plots. There was an initial thininng in 1964, followed by a thinning in 1986 to prescribed basal areas of: T1, 5.5 m^2 ha^{-1}; T2, 10.9 m^2 ha^{-1}; T3, 16.4 m^2 ha^{-1}; T4, 22.4 m^2 ha^{-1}; T5, 28.5 m^2 ha^{-1}. Fertilizing treatments was 400 kg ha^{-1} N and 229 kg ha^{-1} P applied approximately six years before the commencement of seed-fall collection.

Thinning treatment	**Fertilizer treatment**	**Nominal treatment basal area under bark in 1986** (m^2 ha^{-1})	**Actual basal area under bark in 1991** (m^2 ha^{-1})	**Stocking in 1991** (stems ha^{-1})	**Mean diameter under bark in 1991** (cm)	**Identification number of each replicate plot**		
T1	No	5.5	6.2	50	39.3	5	7	14
T1	Yes	5.5	5.6	44	39.1	15	22	28
T2	No	10.9	11.8	177	28.5	3	8	24
T2	Yes	10.9	11.7	129	33.2	1	19	20
T3	No	16.4	17.1	229	30.1	13	17	25
T3	Yes	16.4	18.4	321	26.1	6	18	27
T4	No	22.4	23.4	579	21.5	11	16	23
T4	Yes	22.4	23.6	548	22.5	9	10	21
T5	No	28.5	29.7	1083	16.7	4	29	31
T5	Yes	28.5	28.5	1092	16.6	2	26	30

Table 2. Total numbers and weights of seeds, capsules, and flower parts collected in traps over 36 months. Data from smaller seed trays used for 5 months at the beginning of the collection is not shown.

	Total count of collection	**Fall** (no. ha^{-1} yr^{-1})	**Percentage of all reproductive parts collected**	**Total weight of collection** (g)	**Total weight of fall** (kg ha^{-1} yr^{-1})	**Percentage of all parts weighed**	**Mean weight of a single reproductive part** (mg ± s.e.)
Immature buds	52020	2,132,882	17.9%	826	33.9	8.0%	15.87 ± 0.248
Mature buds	56647	2,322,595	19.5%	1857	76.1	18.0%	32.78 ± 0.363
Opercula	90201	3,698,349	31.0%	1491	61.1	14.5%	16.53 ± 0.659
Flowers	75228	3,084,438	25.8%	1580	64.8	15.3%	21.00 ± 0.967
Immature capsules	368	15,088	0.1%	58	2.4	0.6%	157.72 ± 10.964
Mature capsules	808	33,129	0.3%	600	24.6	5.8%	723.26 ± 14.531
Seeds	10436	427,889	3.6%	98	4.0	0.9%	9.48 ± 0.219
Empty capsules	5381	220,627	1.8%	3806	156.0	36.9%	698.53 ± 7.933
All reproductive parts	291089	11,934,998	100%	10315	423.0	100%	-

Table 3. The effect of fertilizer on the falls of seeds, capsules, and flower parts. Tabled values are: counts of the falls, the weight of the fall, the mean weight of individual parts on fertilized and unfertilized treatments, and the percentage difference between fertilized and unfertilized treatments. Falls of seed, mature capsules, and empty capsules were collected over 41 months. Flowers, mature buds, immature buds, opercula and immature capsules were collected for only 36 months of these months.

	Fall of reproductive parts (no. ha^{-1} yr^{-1})			**Weight of parts that fell** (kg ha^{-1} yr^{-1})		**Mean weight of single part** (mg)	
	Unfertilized	Fertilized	% difference	Unfertilized	Fertilized	Unfertilized	Fertilized
Immature buds	1,961,579	2,304,185	17	30.01	37.72	15.3	16.4
Mature buds	1,962,645	2,686,481	37	63.96	88.40	32.6	32.9
Opercula	3,300,268	4,096,512	24	56.42	65.85	17.1	16.1
Flowers	2,726,006	3,442,871	26	58.71	70.85	21.5	20.6
Immature capsules	15,826	14,350	-9	2.38	2.38	150.3	165.7
Mature capsules	44,667	34,439	-9	32.36	24.85	724.5	721.6
Seeds	468,165	427,174	-6	4.64	3.84	9.9	9.0
Empty capsules	256,176	225,892	-9	182.50	154.22	712.4	682.7
All parts	10,735,334	13,231,904	24	430.98	448.10	-	-

Table 4. The mean falls of seeds, capsules, and flower parts per hectare per year on each of the five thinning treatments, and the mean weight per part for each treatment. Falls of seed, mature capsules, and empty capsules were collected over 41 months. Flowers, mature buds, immature buds, opercula and immature capsules were collected for only 36 months of these months.

	Fall of reproductive parts (no. ha^{-1} yr^{-1})					Weight of parts that fell (kg ha^{-1} yr^{-1})					Weight of individual reproductive parts (mg)				
Thinning treatment	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5
Immature buds	1,302,391	2,074,846	2,237,620	2,516,425	2,533,030	21.99	31.55	35.81	39.96	39.94	16.8	15.2	16.0	15.9	15.8
Mature buds	1,916,993	2,428,068	2,697,649	2,313,676	2,266,320	69.65	76.35	87.63	76.80	70.61	36.4	31.4	32.4	33.2	31.1
Opercula	2,389,528	3,029,960	5,071,391	3,243,165	4,757,325	41.69	51.13	84.93	51.75	76.15	17.4	16.8	16.7	15.9	16.0
Flowers	1,896,493	2,673,458	4,283,765	2,627,947	3,940,384	47.58	62.21	85.92	48.75	79.36	25.1	23.2	20.1	18.6	20.1
Immature capsules	12,095	18,450	11,275	11,890	21,730	2.25	2.38	2.26	1.97	3.03	186.4	133.3	200.0	172.4	141.5
Mature capsules	23,972	44,947	31,962	45,346	51,539	20.68	34.79	21.64	31.95	33.97	866.7	773.3	675.0	704.8	658.9
Seed	333,205	502,405	384,345	497,011	521,382	3.47	4.81	3.45	4.32	5.18	10.2	9.5	8.8	8.8	10.0
Empty capsules	142,032	264,686	194,969	317,224	286,261	119.81	194.31	136.75	210.69	180.22	843.9	734.3	701.8	664.4	629.4
Total	8,016,709	11,036,824	14,912,979	11,572,689	14,377,976	328.11	459.53	461.4	470.19	493.47	41.2	41.9	31.0	40.8	34.3

Table 5. The mean falls of seeds, capsules, and flower parts per hectare (no. ha^{-1} yr^{-1}) for each of the fertilizer and thinning treatments.

Thinning treatment	**T1**		**T2**		**T3**		**T4**		**T5**		**All thinnings**		**All treatments**
Fertilized	N	Y	N	Y	N	Y	N	Y	N	Y	N	Y	-
Immature buds	1,066,021	1,538,761	1,924,988	2,224,704	1,814,696	2,660,543	2,358,777	2,674,073	2,643,323	2,422,738	1,961,561	2,304,164	2,132,863
Mature buds	1,498,170	2,335,817	1,965,169	2,890,968	2,137,373	3,257,925	1,904,488	2,722,864	2,307,936	2,224,704	1,962,627	2,686,456	2,324,541
All buds	2,564,191	3,874,577	3,890,158	5,115,672	3,952,069	5,918,468	4,263,265	5,396,938	4,951,259	4,647,443	3,924,188	4,990,619	4,457,404
Opercula	1,541,221	3,237,835	2,453,079	3,606,842	3,613,607	6,529,380	2,614,622	3,871,912	6,278,455	3,236,194	3,300,197	4,096,433	3,698,315
Flowers	1,169,343	2,623,642	2,155,003	3,191,914	3,109,092	5,458,439	2,072,181	3,183,713	5,124,282	2,756,485	2,725,980	3,442,839	3,084,409
Immature capsules	7,380	16,810	16,810	20,090	15,580	6,970	12,300	11,480	27,061	16,400	15,826	14,350	15,088
Mature capsules	20,775	27,168	42,749	47,144	35,158	28,766	53,137	37,555	71,515	31,563	44,667	34,439	39,553
Seed	347,588	318,822	528,973	475,836	375,555	393,134	491,018	503,004	597,692	445,073	468,165	427,174	447,670
Empty capsules	155,815	128,248	294,052	235,321	171,796	218,142	340,397	294,052	318,822	253,500	256,176	225,852	241,014

Table 6. The mean number of reproductive parts that fell, and total weight of reproductive parts that fell per tree per year on each of the five thinning treatments. Falls of seeds, mature capsules, and empty capsules were collected over 41 months. Flowers, mature buds, immature buds, opercula and immature capsules were collected for only 36 months of these months.

	Fall of reproductive parts (no. tree^{-1} yr^{-1})					Weight of parts that fell (kg tree^{-1} yr^{-1})				
Thinning treatment	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5
Basal area (m^{2}ha^{-1})	5.9	11.7	17.7	23.5	29.1	5.9	11.7	17.7	23.5	29.1
Immature buds	27,133	12,995	7,958	4,472	2,312	0.458	0.198	0.127	0.071	0.036
Mature buds	39,937	15,207	9,594	4,112	2,068	1.451	0.478	0.312	0.136	0.064
Opercula	49,782	18,977	18,037	5,764	4,341	0.869	0.320	0.302	0.092	0.069
Flowers	39,510	16,744	15,236	4,671	3,596	0.991	0.390	0.306	0.087	0.072
Immature capsules	252	116	40	21	20	0.047	0.015	0.008	0.004	0.003
Mature capsules	499	282	114	81	47	0.431	0.218	0.077	0.057	0.031
Seed	6,942	3,147	1,367	883	476	0.072	0.030	0.012	0.008	0.005
Empty capsules	2,959	1,658	693	564	261	2.496	1.217	0.486	0.374	0.164
Total	167,015	69,124	53,040	20,568	13,121	6.836	2.878	1.641	0.836	0.450

Fig. 1. The location and dispersion of the 30 plots (40 x 40 m) in the study of the effects of thinning and fertilizing on the seed-fall from jarrah (*Eucalyptus marginata*) trees at Inglehope in the south west of Western Australia.

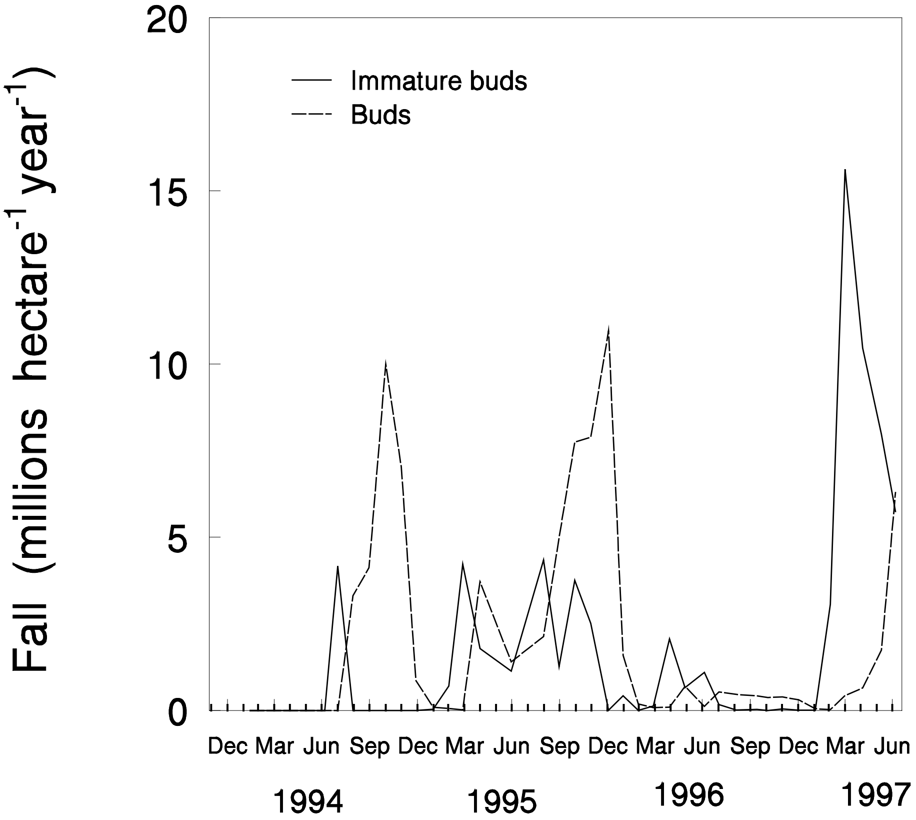


Fig. 2. The monthly falls of mature jarrah flower buds and immature flower buds over 36 months at Inglehope in southwest Western Australia.

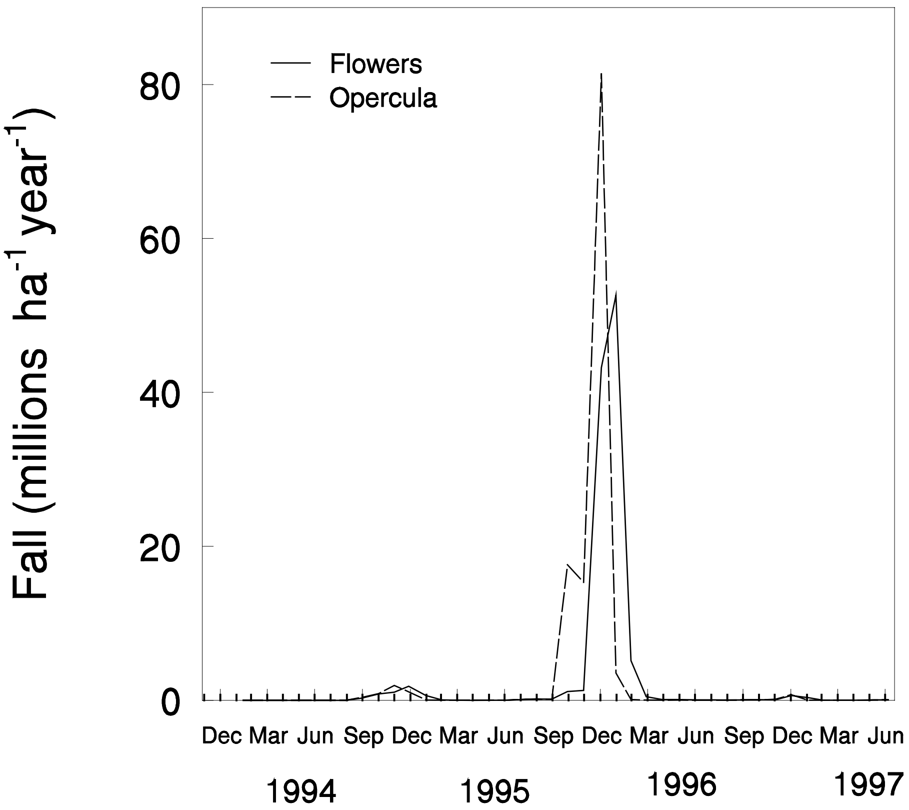


Fig. 3. The monthly falls of jarrah flowers and opercula over 36 months at Inglehope in southwest Western Australia.

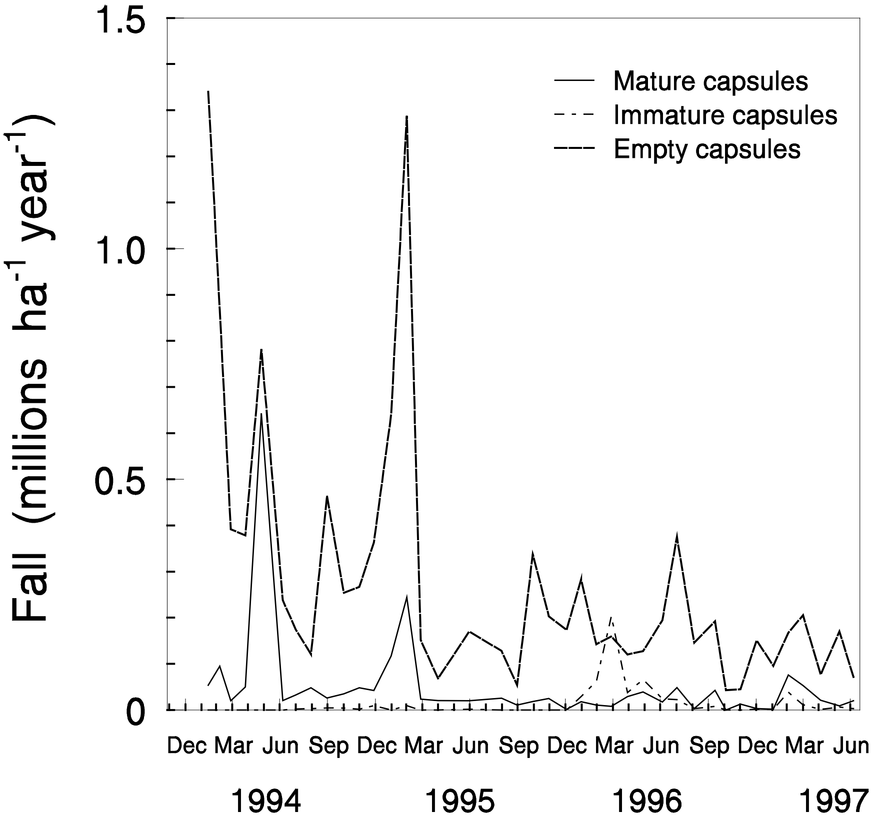


Fig. 4. The falls of immature, mature and empty capsules over 41 months at Inglehope in southwest Western Australia.

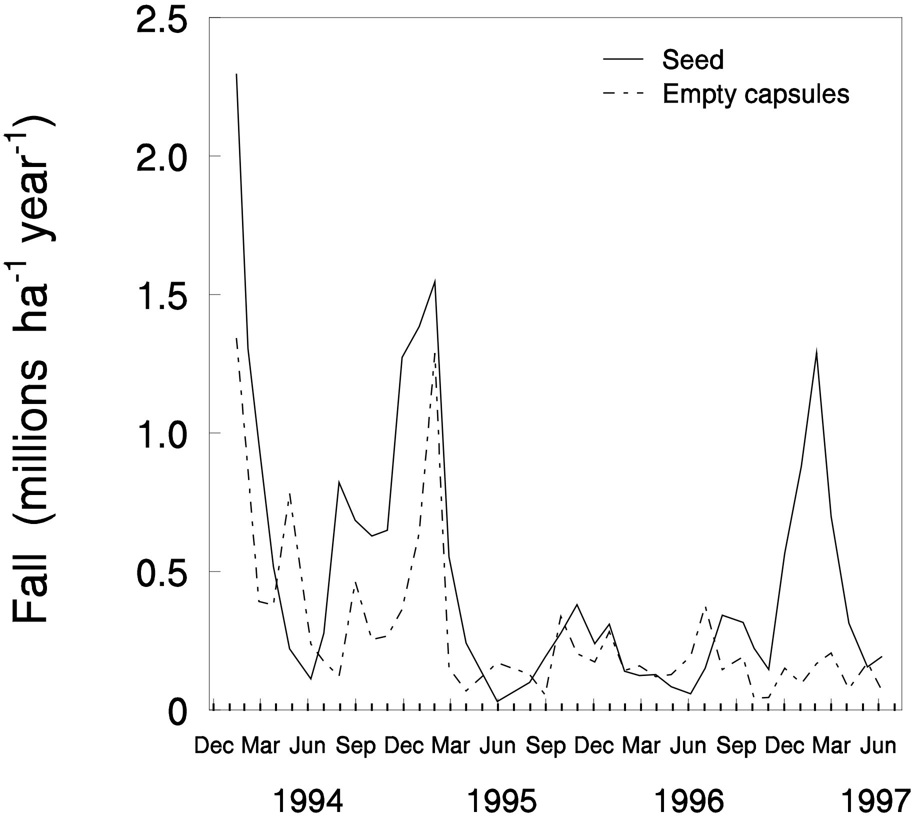


Fig. 5. The falls of seed and empty capsules over 41 months at Inglehope in southwest Western Australia.

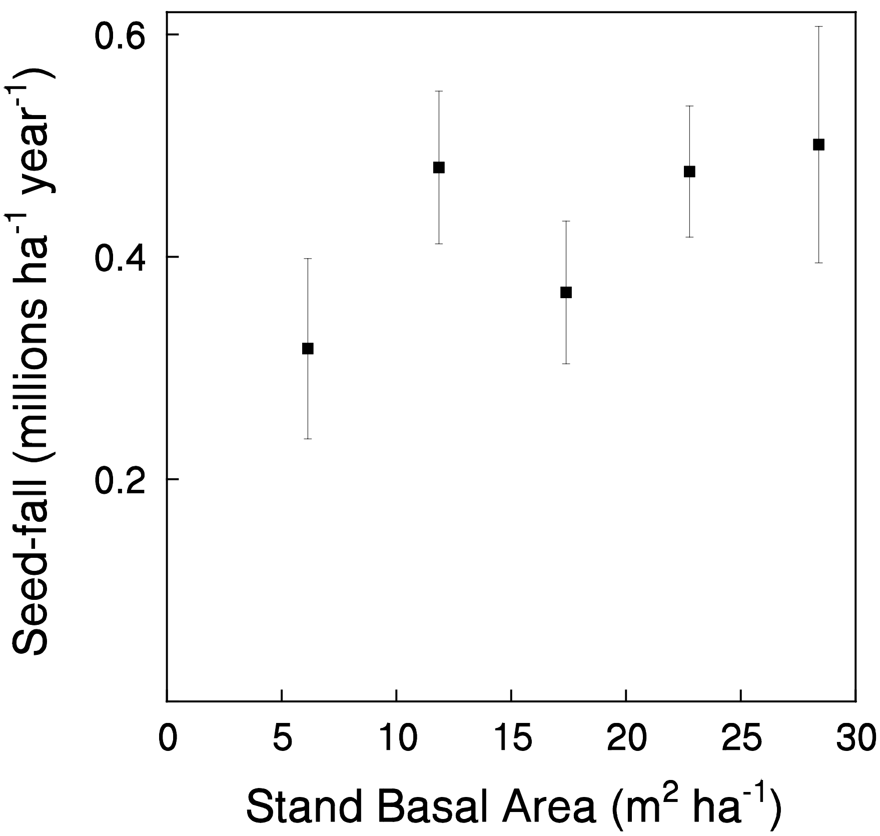
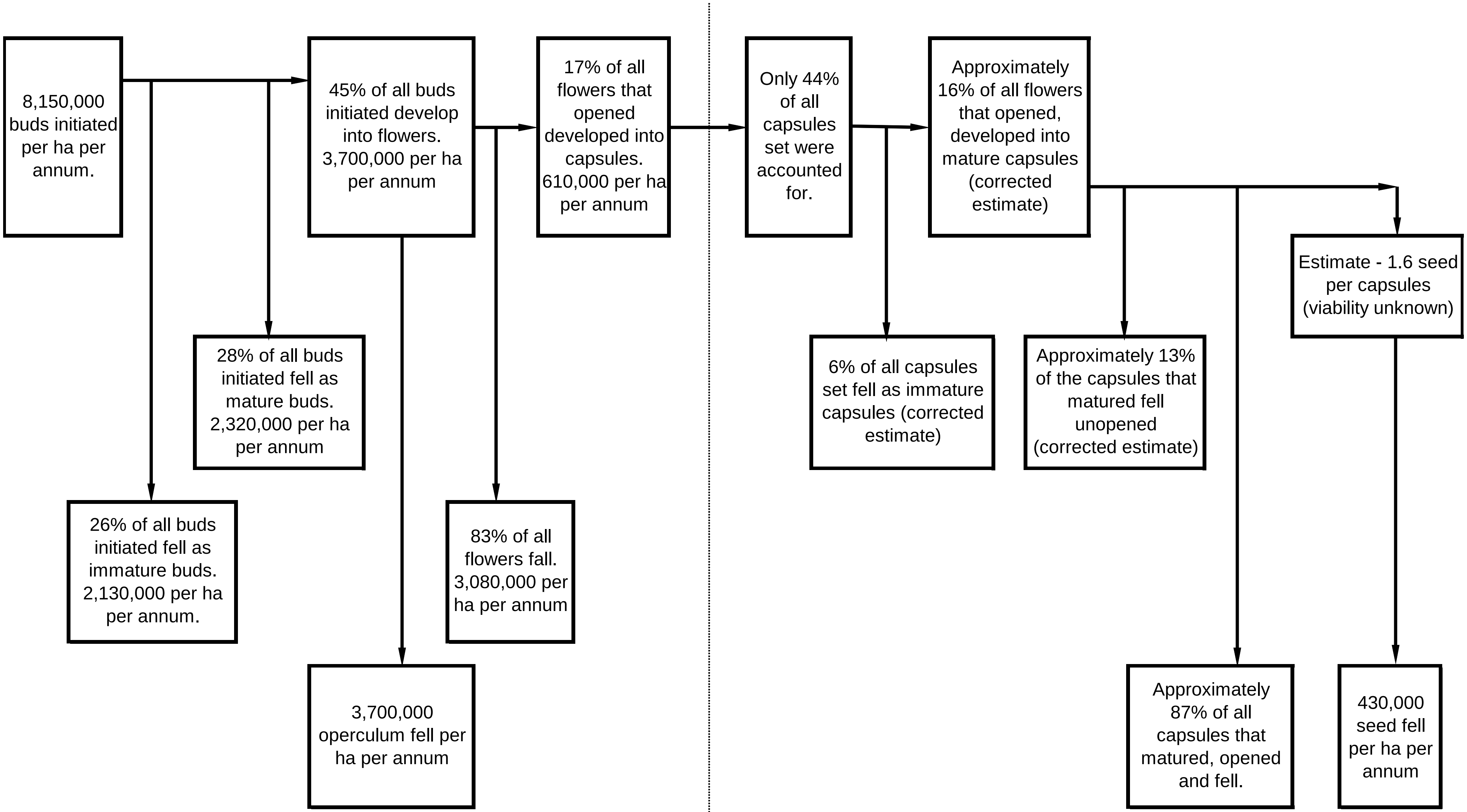


Fig. 6. The response of seed-fall with changes in stand basal area at Inglehope in southwest Western Australia. Each plotted value is the mean seed-fall from six plots of 40 x 40m determined from monthly collections over 41 months. Bars are standard errors.

Fig. 7. The fate of buds, flowers and capsules produced by trees in a 36 month study of the fall of reproductive parts in jarrah trees



Estimates of the fate of flowering parts are relatively accurate as these parts are not retained on the trees for a long period

Estimates of the fate of capsules are less accurate as capsules are retained on trees for up to 50 months after bud initiation. 14,973 capsules were set, yet only 6,557 capsules (44%) were accounted for within the observation period.

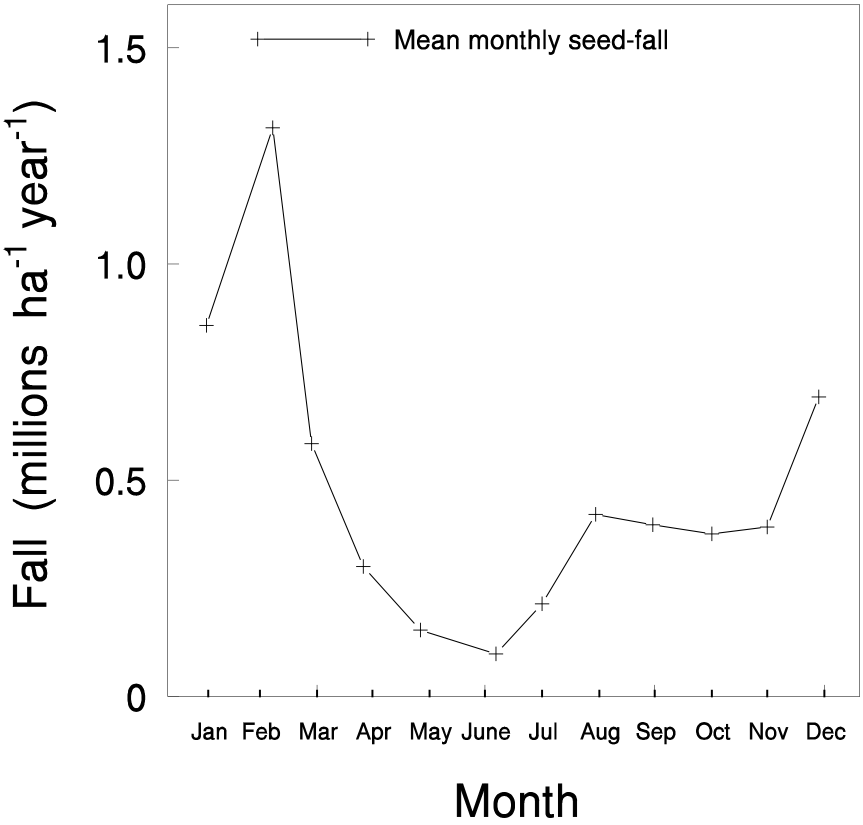


Fig. 8. The mean monthly seed-fall for each month of the year from observations of seed-fall over 41 months at Inglehope in the northern jarrah forest.

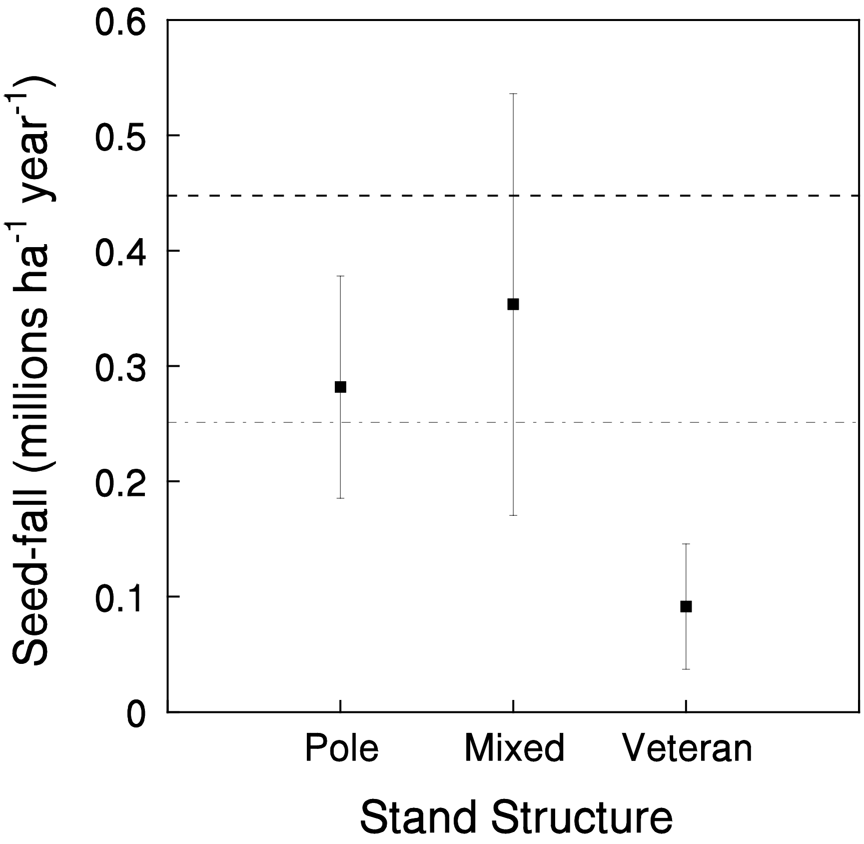


Fig. 9. Seed-fall from three types of jarrah stands over five years in the 1960's. Unpublished data of Kimber (1970). Sites are: a veteran stand at Banksiadale, a mixed stand at Amphion, and a pole stand at Plavins. The upper broken line is the mean annual seed-fall collected over the 41 months of the current study at Inglehope and the lower broken line is the mean annual seed-fall for Kimber's study.

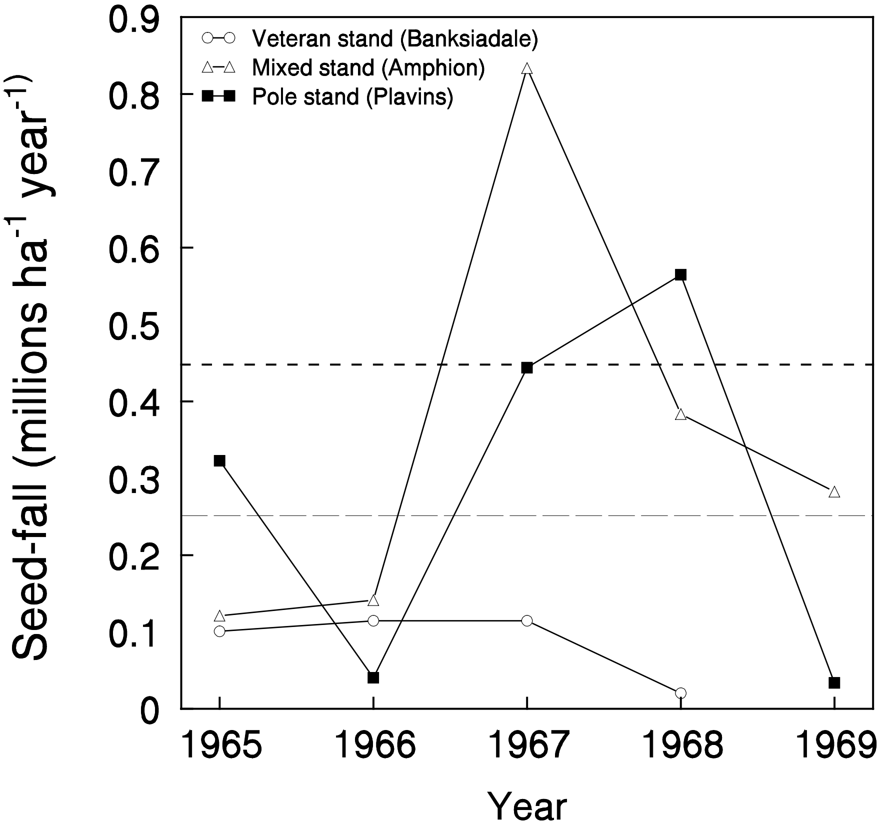


Fig. 10. The total annual seed-fall over five years at three sites studied by Kimber (1970) in the northern jarrah forest: a veteran stand at Banksiadale, a mixed stand at Amphion, and a pole stand at Plavins. The upper broken line is the mean annual seed-fall collected over the 41 months of the current study at Inglehope, and the lower broken line is the mean annual seed-fall for Kimber's study.

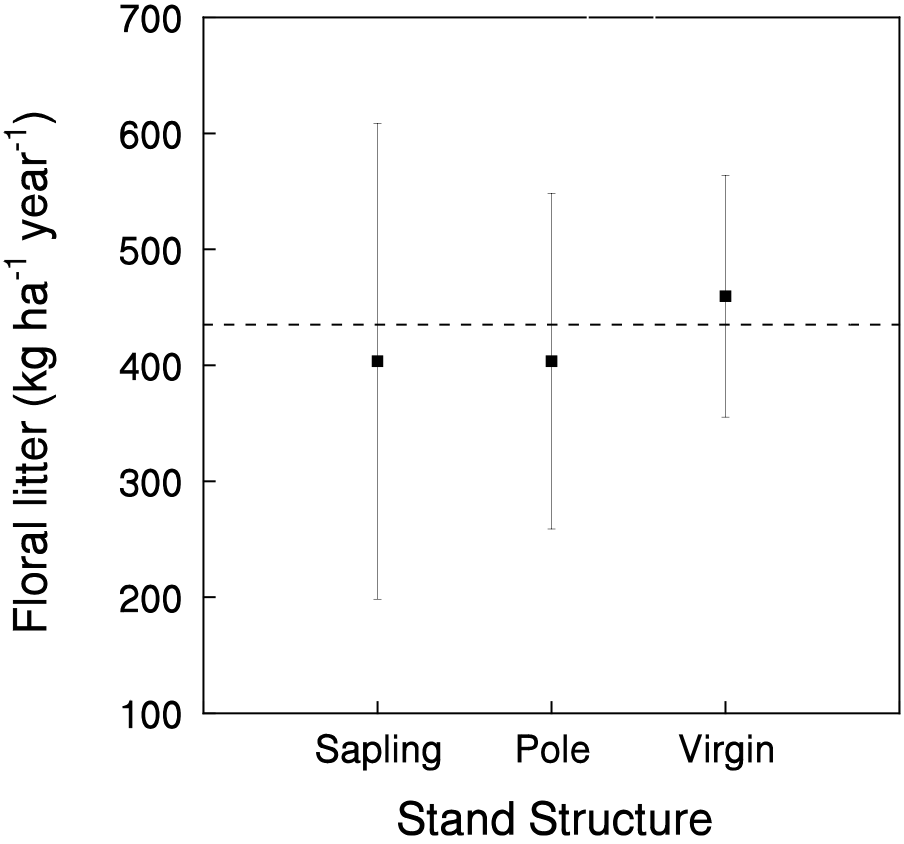


Fig. 11. Hatch (1964) collected the total annual falls of “floral litter” (flowers, buds, opercula, and capsules) over eight years at three sites with differing stand structures in the northern jarrah forest. The broken line is the mean annual fall of “floral litter” collected over 36 months of the current study at Inglehope.

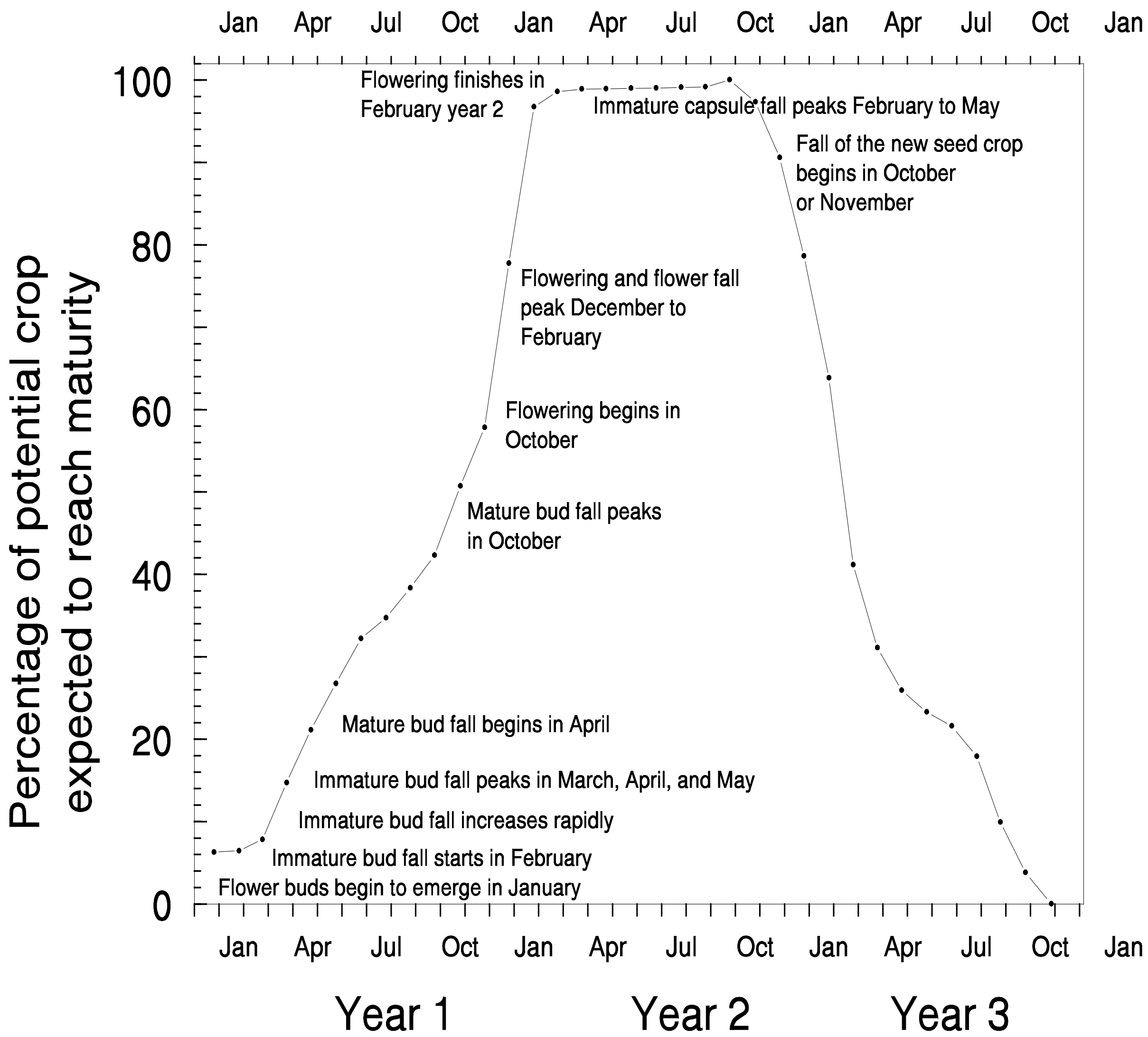


Fig. 12. The percentage of the potential capsule crop that is expected to reach maturity (on the left hand side), and the progressive fall of seed from these capsules over the months following capsule maturity (on the right hand side).

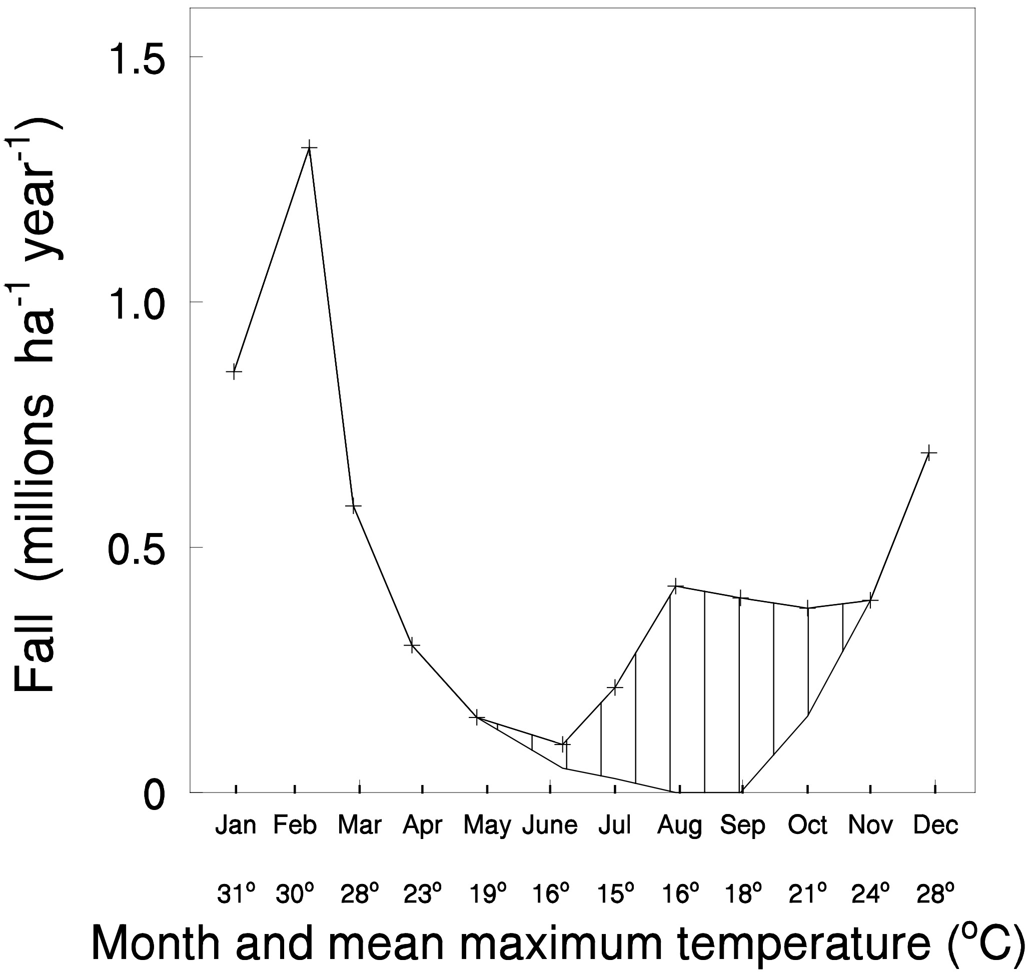


Fig. 13. The mean monthly seed-fall for each month of the year from observations of seed-fall over 41 months at Inglehope in the northern jarrah forest. The proportion of the seed-fall in July, August, September, and October that we assume has originated from a previous capsule crop is shown as the hatched area.

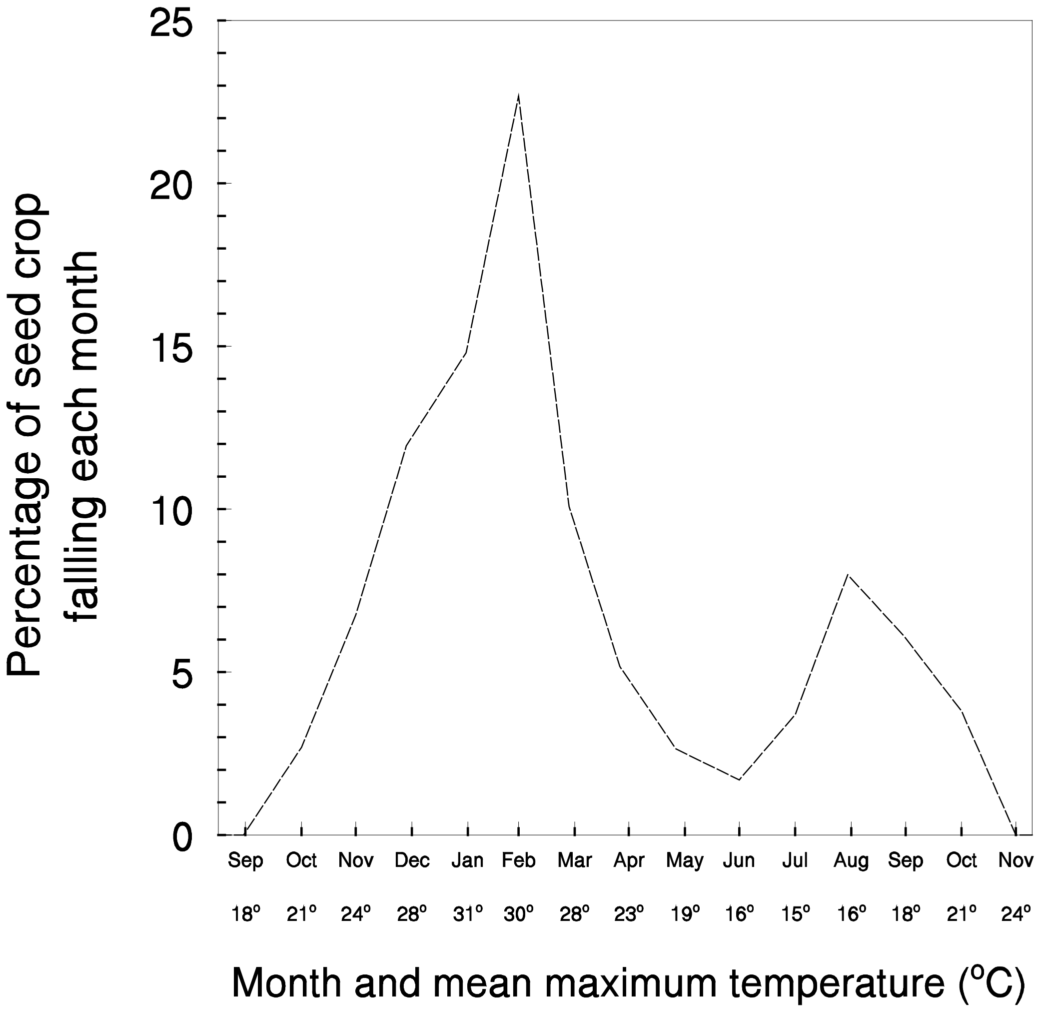


Fig. 14. This figure shows how we interpret seed from one years capsule crop falling over 14 months. The seed-fall on the right hand side of the diagram in July through to November was estimated from the hatched area in Fig. 13.