

Seed fall and flowering in white box (*Eucalyptus albens* Benth.) trees near Cowra, New South Wales

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Summary

There are few studies of the factors affecting the recruitment of white box (*Eucalyptus albens*), a woodland tree of the inland slopes of south-eastern Australia with limited recruitment in recent times. One of these factors, seed fall, was monitored for periods ranging from 18 to 43 months (September 1995 to April 1999) at 14 *E. albens* trees in central western New South Wales. Seed collectors were located beneath the canopies of all trees and also outside the canopies at 12 of them. Flowering was also assessed — both visually and from the numbers of opercula in the collectors. Seed fall was highly variable between trees. Although one tree shed seed most of the time, and all those that were monitored for 43 months ultimately shed seed, there were lengthy periods when very little seed was collected. It appeared that most of the early-mature capsules present on all trees in mid-1995 did not shed seed until 1998. Seed fall beyond the canopy was low and from the limited data collected, it appeared that seed was evenly dispersed around the canopy. Flowering was similarly variable between trees, for example some produced abundant flowers every second year whereas others flowered in two or three consecutive years. However, averaged across all trees, flowering was abundant in 1997 and 1999 and was associated with above-average winter and spring rainfall in the previous year. Despite the presence of short-term seedbeds during the early period of monitoring and the absence of grazing at 12 of the trees, seedling recruitment was minimal during the 3.5 y of observation.

Keywords: regeneration; flowering; seed crops; seed collection; viability; seed dispersal; seedbed preparation; survival; rain; *Eucalyptus albens*

Introduction

Eucalypt regeneration depends on processes that need to operate synchronously or at particular times. It can fail if any one of the processes fails. In their introduction to a study of the Western Australian woodland eucalypt, *Eucalyptus salmonophloia* F.Muell., Yates *et al.* (1994, p. 532) cited J.L. Harper to explain the operation of the main processes:

For recruitment to occur, trees have to flower, the flowers have to be pollinated and set and disperse viable seed; the seed then

has to escape predation so that it can be incorporated into a soil seed bank where it must persist until the right conditions stimulate germination; the young plant then has to survive and grow.

They noted that these processes were poorly understood in *E. salmonophloia* but could have added that this also applies to many other woodland eucalypts, including *E. albens** (white box), the subject of this paper. General principles of eucalypt biology, including regeneration from seed, have been built up over many years in high-rainfall areas where most of the commercial timber species of eucalypt occur. Much of this information has been compiled by, for example, Jacobs (1955), Penfold and Willis (1961), Hillis and Brown (1984), Cremer *et al.* (1990) and Florence (1996), and with respect to seed, very comprehensively by Boland *et al.* (1980). As noted by Windsor (2000), however, the extent to which these principles apply to woodland species is less well studied.

Observations on the inland slopes of New South Wales (NSW) indicate that eucalypt regeneration is uncommon in grazed paddocks compared to roadsides (Schabel and Eldridge 2001), but even on the latter it is quite variable (Nowland 1997). Some regeneration, possibly from lignotuberous seedlings, was reported (Spooner *et al.* 2002) following fencing of selected stands.

Factors affecting regeneration of woodland eucalypts on the inland slopes and adjacent tablelands of south-eastern Australia have been described by Curtis (1989, 1990) and Windsor (2000), but observations on seed fall are very limited — for example Curtis (1989, 1990) and Lawrence *et al.* (1998). Capsule dehiscence in eucalypts is initiated by twig death or the formation of an abscission layer that cuts off the sap flow to the capsules. Fertilised ovules are shed as seed and unfertilised ones (the majority) as ‘chaff’. Seeds are dispersed by wind for short distances — up to 1.5 times the height of the tree, but this can be exceeded if trees are in exposed situations. With respect to woodland eucalypts in the highly modified rural environments of central western NSW, a number of questions arose. Is seed fall and seed viability sufficient for seedling recruitment in most

*Except where indicated, botanical nomenclature follows that of Harden (1990–93).

years? When do peaks of seed fall occur, and is recruitment likely to be successful at this time? Are asymmetrical distributions of seedlings around tree canopies due to uneven wind dispersal of seed as noted by Venning (1988), or are other factors such as protection from frost or desiccation (e.g. Curtis 1990) involved?

Despite extensive clearing, *E. albens* is still relatively common throughout most of its former range, southern Queensland to northern Victoria, even though most of the area originally occupied by these woodlands is now cropped and/or grazed. Intact woodlands are rare (Prober 1996) but stands with relatively intact structure and moderately to highly modified groundstoreys are more common, albeit small and fragmented. The species most commonly occurs in roadside corridors and as scattered paddock trees. The latter occurrence provided an opportunity to monitor seed fall beneath and around the canopy of individual trees in the absence of contamination from other trees. The specific objectives of the study were to:

- determine the amount, viability and seasonal pattern of seed fall
- test the hypothesis that seed is dispersed, at least over short distances, evenly around the canopy
- document the cycle of flowering during the period of observations.

Originally, it was also intended to promote synchronous seed fall onto a receptive seedbed by burning beneath the trees (Florence 1996) in an attempt to promote seedling recruitment. This was subsequently abandoned, but relevant results are reported.

Methods

Tree selection

The main study site was located on rolling country at Walli, about 30 km north-east of Cowra at an altitude of 560–600 m asl and with a mean annual rainfall (MAR) exceeding 650 mm. The site was largely cleared of trees, relatively fertile (enhanced by past applications of fertiliser) with a pasture (groundstorey) dominated by *Phalaris aquatica* and grazed by cattle. In June 1995 we searched for relatively isolated *E. albens* trees (at least 1.5 × tree heights apart to avoid the possibility of collecting seed from adjacent trees) with relatively abundant early-mature undehisced capsules (that may have been the product of flowering the previous year). Twelve trees satisfying the criteria were located (Table 1), though all had some older capsules from an earlier flowering. Samples of twigs containing the early-mature capsules were collected, allowed to dry and examined for the presence of viable seeds. Germination testing (using the method described below) of a sub-sample of all seed collected indicated that 81% of the seed was viable.

Supplementary data were obtained from two isolated *E. albens* trees — one at the Department of Environment and Climate Change's research facility at Cowra (~380 m asl, MAR ~640 mm) and another west of Molong (~620 m asl, MAR ~705 mm).

Seed collectors

The design of the collectors was based on that of Curtis (1989). The bottom of a plastic garbage bin was removed and a circular piece of cloth mesh glued to the underside. An earlier seed-collecting exercise (Lawrence *et al.* 1998) indicated that 'Petlee's polyester-cotton 2125 La Coste' fabric was durable and retained eucalypt seed and chaff while allowing the passage of water. Mean diameter of the bin opening was 0.385 m, giving a collection area of 0.116 m².

Collectors were suspended, with their tops about 1 m above the ground, from two steel pegs with two additional pegs serving as stabilisers (Fig. 1). A circular piece of rabbit netting was placed on top of each collector to prevent falling twigs from damaging the mesh and the entry of small animals. A sticky material ('Rentokil Bird Off') was applied near the base of the droppers to prevent ground-based invertebrates from gaining access to the collector. Herbage growth beneath collectors was controlled by applications of herbicide as required.

As cattle were expected to damage seed collectors, the 12 trees at Walli were individually fenced so as to include the canopy and an area 5 m beyond mean canopy diameter. The fenced areas therefore varied in size, but all were square with sides aligned north-south and east-west with the trunk of the tree at the centre. As no cattle were present at the Cowra and Molong sites, the trees there were not fenced. Over the period of observation, collectors sustained various types of damage, for example from falling limbs and cattle breaking down fences during dry times, or simply wearing out. Repair or replacement was an on-going activity. Missing data were therefore more common than was desired.



Figure 1. A modified garbage bin seed collector (127/25)

Table 1. Details of 14 *Eucalyptus albens* trees where seed fall and other monitoring was carried out between August 1995 and June 1999

Tree no.	Aspect (compass bearing °)	Slope (°)	Approx. height (m)	Approx. canopy diameter (m)	Trunk diameter at 1.3 m (m)	1995–1996 groundstorey treatments				Seed collection period		
						Herbicide	Burn	Mow	Outside canopy, from:	Under canopy, from:	To:	Total (months)
274^a	116	7	24	18	1.1	11 Sep 95	10 Oct 95		29 Aug 95	12 Sep 95	7 Apr 99	43
279^b	93	8	18	17	2.0	11 Sep 95	10 Oct 95		29 Aug 95	12 Sep 95	1 May 97	20
270	78	3	21	21	1.3	27 Sep 95	26 Oct 95		29 Aug 95	12 Sep 95	1 May 97	20
273	305	4	16	11	1.0	27 Sep 95	26 Oct 95		29 Aug 95	12 Sep 95	1 May 97	20
276	5	5	25	19	1.2	26 Mar 96	1 Apr 96		29 Aug 95	28 Sep 95	1 May 97	20
277	90	4	15	12	0.7	26 Mar 96	1 Apr 96		29 Aug 95	12 Sep 95	16 Jun 97	22
275	105	3	24	19	1.2	10 Oct 96		29 Oct 96	29 Aug 95	28 Sep 95	25 Aug 97	24
280	103	9	20	21	1.1	10 Oct 96		29 Oct 96	29 Aug 95	12 Sep 95	24 Feb 98	30
278	95	2	24	19	1.1	10 Oct 96 ^c		29 Oct 96	29 Aug 95	12 Sep 95	7 Apr 99	43
272	101	3	19	14	0.8	12 Nov 96		5 Dec 96	29 Aug 95	12 Sep 95	7 Apr 99	43
281^c	330	8	24	19	0.9	12 Nov 96		5 Dec 96	29 Aug 95	28 Sep 95	7 Apr 99	43
271^d	110	2	19	17	1.1	12 Nov 96 ^e		5 Dec 96	29 Aug 95	28 Sep 95	7 Apr 99	43
Molong						n.a.			n.a.	14 Oct 95	28 Apr 97	18
Cowra						n.a.			n.a.	28 Sep 95	28 Apr 97	19

^aTrees where seed fall monitoring was extended beyond mid-1997 are shown in bold.

^bOne seedling was observed beneath the canopy in March 1996 but recorded as dead in late May 1996.

^cOne seedling was observed outside (SSE of) the canopy in November 1996. It was protected from subsequent herbicide and mowing and was alive in April 1999.

^dOne seedling was observed near the edge of the canopy in July 1996. It was protected from the second herbicide and mowing and was alive in July 1997 but subsequently died.

^eAn earlier application of herbicide on 24 October 1995 was intended to be followed by burning of the groundstorey in November 1995 but the latter was abandoned due to potential fire hazard. The groundstorey was re-herbicide in November or October 1996, followed by mowing.

Seed fall beneath the canopy was assessed at Walli by locating four collectors below the edge of the tree canopies at the four cardinal points of the compass. The total collection area beneath each tree represented 0.1–0.5% of the area beneath the canopy. At Cowra and Molong, only two collectors, diagonally opposite, were located near the edge of the canopies. Recorded seed fall was therefore not from beneath the whole canopy but rather from the ‘vicinity of the canopy edge’. Collectors were installed at Walli during August–September 1995 and shortly afterwards at Cowra and Molong.

Short-distance seed dispersal was assessed only at Walli by locating collectors 4 m beyond the mean diameter of the canopy (i.e. 1 m inside the fence) at the four cardinal points of the compass at each of the 12 trees.

Monitoring seed fall

At Walli, seed fall was monitored from spring 1995 until autumn–winter 1997 for all 12 trees. Six of these trees were monitored for a longer period: until February 1998 for one tree, and until April 1999 (a total of 43 months) for 5 trees. Seed fall at Cowra was monitored from September 1995 to April 1997 (19 months) and at Molong from October 1995 to April 1997 (18 months).

Collectors were emptied at approximately monthly (initially fortnightly) intervals by inverting the collectors into a large funnel. The contents of each collector were stored in a paper bag and later passed through a sieve with a mesh of 1.56 mm to extract coarser material. The finer material was examined under a binocular microscope. Dark-coloured seeds were readily distinguishable from the smaller brown-coloured chaff. Seeds, including those with obvious insect damage, were counted and stored for germination testing, which was carried out in a germination cabinet set at a regime of 12 h 30°C day / 12 h 20°C night. Covered Petri dishes, filled with wet cotton wool and overlaid with filter paper, provided the germination medium. Water was checked and topped up twice per week and germinants were counted weekly over a four-week period.

For each tree at each collection time, the amount of seed was totalled and used to indicate the rate and time of seed fall. Seed numbers in each of the collectors outside the canopy were recorded separately and used to indicate the direction of seed fall. All seeds collected (i.e. from under and outside the canopy) were tested for viability.

Apart from occasions when collectors were damaged, the total seed collection area remained constant at Molong and Cowra but varied at Walli, where the maximum seed collection area ranged from 11.2 m² at the start when all 12 trees were monitored to 4.7 m² at the end when only 5 trees were monitored.

Monitoring of non-seed material at Walli

A wide range of non-seed material (e.g. mature and immature capsules, flowers, floral buds, opercula, chaff and insect frass) was also found in the seed collectors. Opercula (as an indicator of flowering from February 1996) were counted, and chaff (as an indicator of capsule dehiscence) was qualitatively assessed on an abundance rating of 0 = nil to 3 = abundant. In some cases, only basal parts of reproductive structures were present. These were not counted as they could not be reliably attributed to buds, flowers or capsules. Where damaged structures could be reliably identified, they were included in the counts of buds or flowers. As these aborted structures were considered peripheral to the main study, only a sample of the data is presented.

In anticipation of the removal of some of the collectors, visual monitoring of bud and flower abundance on all trees commenced in autumn 1997. Abundance was rated on a five-point scale: 0 = none, 1 = one to very few, 2 = scattered or a few small clumps, 3 = flowers obvious and dispersed across most of the canopy, and 4 = abundant to maximum possible. All ratings were made by the same observer. Final observations were made in early July 1999, 3 months after the last of the collectors was removed and 41 months after flowering records commenced. As some trees had not commenced flowering when observations ceased, the abundance of buds and the past temporal pattern of flowering (which varied between trees) were used to estimate subsequent flowering. The two flower abundance assessment methods, which overlapped for varying periods at individual trees, yielded a record of flowering from mid-February 1996 to July 1999, and by extrapolation until December 1999, that is for four complete flowering periods.

Seedbed treatments to encourage natural recruitment at Walli

Seedbeds were prepared on three occasions at Walli by burning herbicide-treated groundstoreys beneath randomly selected pairs of trees (Table 1) during periods of low fire danger (a reasonable condition imposed by the landholder). None of the fires was sufficiently intense to scorch even the bases of the canopies and this approach was abandoned. The groundstoreys of the remaining six trees (Table 1) were subjected to a one-off herbicide applica-

tion followed by mowing to disperse the thatch of collapsed grass and expose some bare ground. All exclusions were searched for seedlings at regular intervals, though this became progressively more difficult as exotic herbage rapidly recolonised the burnt and/or herbicide-treated areas.

Data analysis

Due to differing numbers of functional seed collectors at each tree and varying time intervals between collections, total seed collected below the canopy at each tree on each occasion was converted to the number of seeds per square metre per week. The variable seed collection periods were represented by variable bar widths on histograms of seed fall. As a general indicator of the occurrence of capsule dehiscence over time, chaff abundance, averaged across all collectors at each tree at each observation, was superimposed as a line graph on the seed fall histograms.

During the period when the two methods of assessing flower abundance overlapped, correlations were not high, primarily due to one measure (numbers of opercula in collectors) being an accumulation over time and the other (visual abundance ratings) an instantaneous assessment. Both sets of data are presented using an intuitive scale for opercula numbers per square metre per week relative to the 0–4 abundance rating. As relative flower abundance over time was the main interest, the data are presented as line graphs.

Due to zero or very low total seed falls outside the canopy at 7 of the 12 trees at Walli, only 5 could be used for an analysis of directional differences in seed fall beyond the canopy. Total seed fall for these trees was analysed using an analysis of variance for a randomised complete block design, with the four cardinal compass points forming the treatments and assigning the trees as blocks.

Results

Total seed fall and viability over time at Walli

Aggregate seed fall from all trees during the first 2 y was low relative to that recorded during the following 1.5 y (Fig. 2). Seed fall began to increase in late 1997 and peaked in the summers of

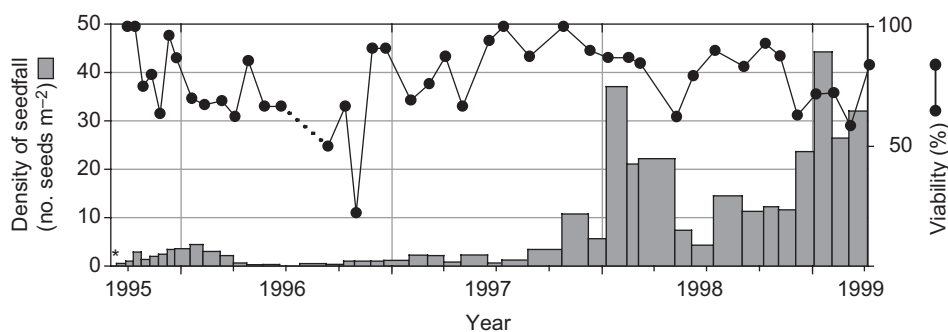


Figure 2. Total seed collected beneath all trees at Walli from 29 August 1995 to 7 April 1999. Varying periods of seed collection are indicated by varying bar widths. * = missing data. The proportion (%) of the seed that was viable at each time of collection (excluding an unreliable value for July 1996) is shown as a line graph.

1997–1998 and 1998–1999. Over the full observation period, viability of all seed collected averaged 76% and was usually in the range of 60–100%. Lower-than-average viability was evident in seed collected between July (0%) and October (22%) 1996, a period when little seed was collected.

Seed fall beneath the edge of the canopy

Seed fall was highly variable between trees (Fig. 3) such that presenting the data as means would be misleading. During the first 20 months when all 12 trees were monitored at Walli, 7 trees shed virtually no seed or very little seed. Of the remainder, seed fall peaks of variable magnitude occurred from spring 1995 to autumn 1996 and, to a lesser extent, from spring 1996 to autumn 1997. Seed fall below the trees at Molong and Cowra was quite discontinuous even during the minor peaks.

All trees monitored beyond autumn 1997 at Walli shed seed, more-or-less continuously, from summer 1997–1998 to autumn 1999 when observations ceased. This included three of the 'shy seeders' (no. 271, 272 and 278) from the earlier period. Tree no. 274 shed seed for most of the time.

Chaff, an indicator of capsule dehiscence, was found in the collectors much more frequently than seed. It was present, albeit sometimes in low amounts, at all trees during much of the observation period (Fig. 3). As would be expected, abundant chaff was associated with the presence of seed in the collectors.

Seed fall outside the canopy at Walli

Seed fall 4 m beyond the mean canopy edge was considerably less than beneath the edge of the canopy. Across the five trees where appreciable seed falls were recorded, average numbers of seeds in collectors at each of the four cardinal compass directions were not significantly different for the full period of observation. Analysis of only the latter part of the observation period (January 1998 to April 1999 when most of the seed fell) indicated that differences were

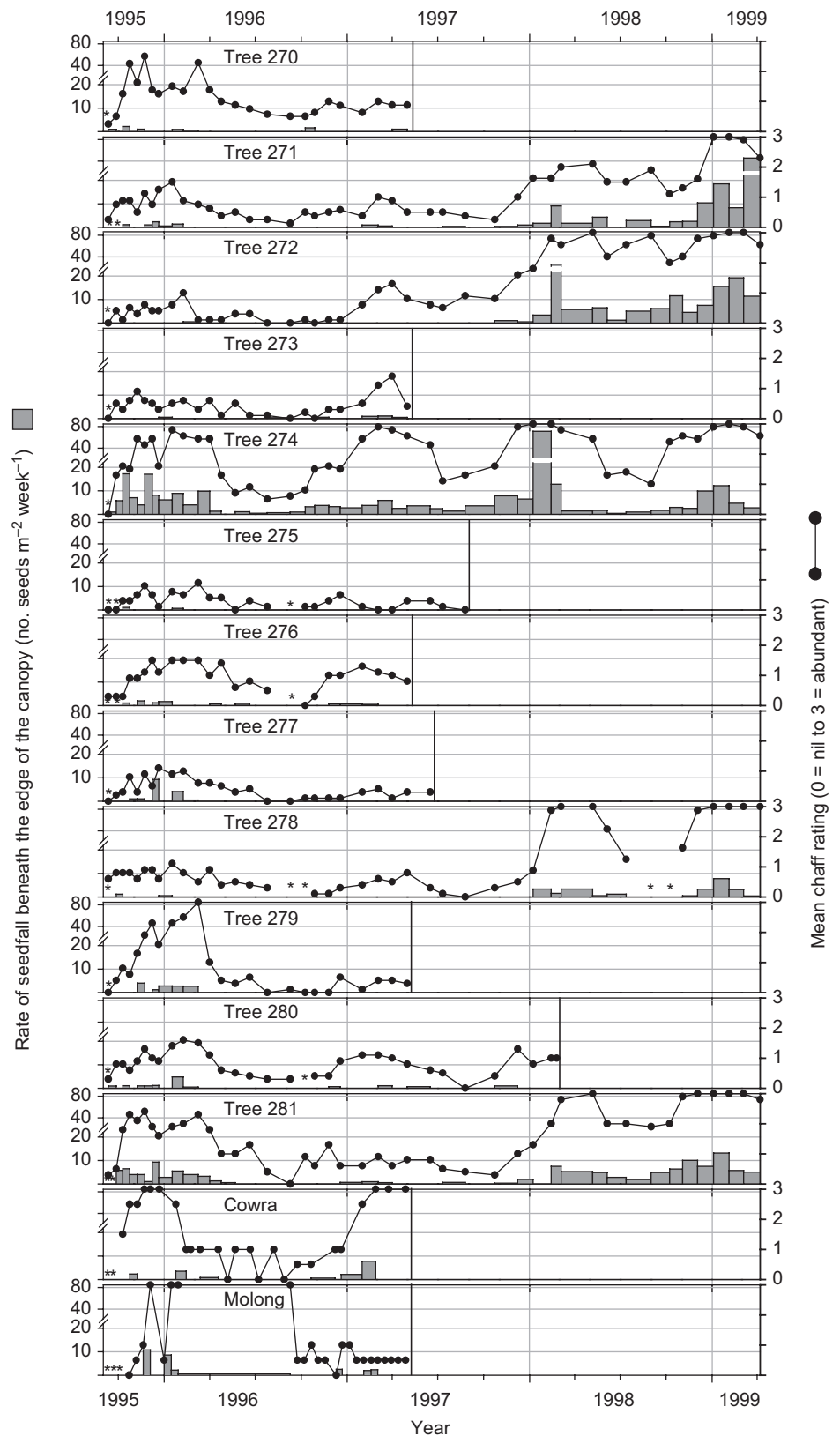


Figure 3. Seed fall under the edge of the canopy of 12 *Eucalyptus albens* trees at Walli (trees no. 270–281), one tree at Cowra and one tree at Molong that were monitored for variable periods between September–October 1995 and early April 1999. Seed fall expressed as numbers per square metre per week (aggregate of up to four collectors per tree), with bar widths indicating variable times over which seed accumulated in collectors. * = missing seed fall and/or chaff data. The line graph represents the mean ($n = \leq 8$ collectors at each observation) chaff abundance rating (0–3).

Table 2. Total seed fall per 0.116 m² collector at 4 m beyond mean canopy diameter in four directions averaged across five *Eucalyptus albens* trees. Differences between the four directions were not significant ($P > 0.05$) during either period of record.

Recording period	North	East	South	West
All records (Sep. 1995–April 1999)	13.2	24.0	20.6	22.6
Main seed fall period (Jan. 1998–April 1999)	9.0	16.2	16.4	15.8

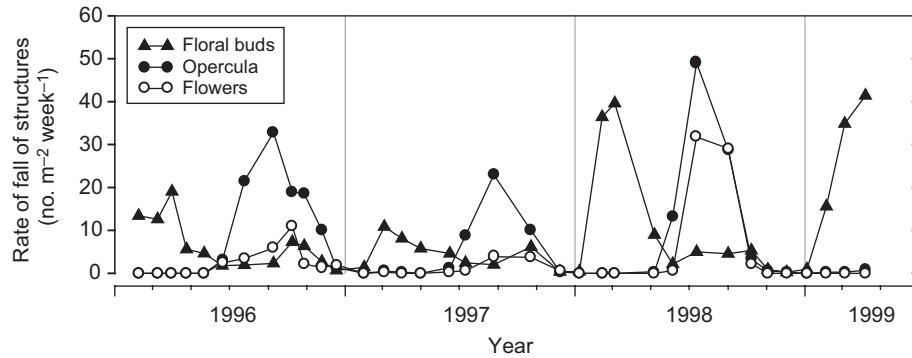


Figure 4. Quantities of buds and flowers (including part flowers) shed beneath and around the edge of the canopy of tree no. 274 at Walli from early February 1996 to early April 1999. To assist in gauging the size of the crop of flowers present each season, quantities of opercula are also shown.

also not significant (Table 2). However, because of high variability between trees and the small amount of seed collected, this result should be treated with some caution.

Bud production

Inflorescence buds were usually evident by early November, and pin buds shortly afterwards. Buds were ‘plump’ by about February. Very few inflorescence buds or young pin buds were found in the collectors, but older buds were commonly aborted before flowering commenced. Quantities beneath one of the regularly flowering trees at Walli are presented in Figure 4.

Flowering at Walli

A flower abundance rating of 1 or 2, or opercula numbers below $\sim 10 \text{ m}^{-2} \text{ week}^{-1}$ (unless over an extended period) indicated minimal flowering by any particular tree during any one year. Even a nil record of flowering did not necessarily indicate that no flowers were produced, as scattered flowers may have been missed between observations or the few opercula shed may have missed the collectors. Though occasional flowers could be present at any time, flowering mainly occurred between autumn and late spring. Some trees flowered for much of this period, but most had peaks in winter or spring. Some whole flowers were aborted, but many of those collected had the disc and part of the hypanthium severed — presumably by parrots before being discarded (Fig. 5). Flower losses at one tree are presented in Figure 4.

Flowering was minimal in 1996 for all trees except tree no. 274 (Fig. 6). In 1997, all trees produced flowers, though minimally in trees no. 275, 276 and 279. In 1998, a few trees produced

abundant flowers over a short period or less-abundant flowers over a longer period, but again there were trees that produced few flowers. In contrast, all trees flowered (or were presumed to do so from the abundance of buds present at the last observation) during 1999 — either abundantly for a short period or less abundantly but over a longer period.

Across the 4 y, differences in patterns of flowering were evident between individual trees:

- (a) four trees (no. 270, 271, 273, 278) produced moderate to abundant crops of flowers every second year



Figure 5. A flowering branchlet from tree no. 281 at Walli in July 1997. The disc and part of the hypanthium have been severed (presumably by parrots) from nearly half of the flowers (128/26).

- (b) three trees (no. 275, 276, 279) produced moderate to abundant crops two years in a row
- (c) three trees (no. 274, 277, 280) produced for three or more years in a row
- (d) two trees (no. 272 and 281) were intermediate between (a) and (c).

Averaged across all trees, flowers were relatively abundant in 1997 and 1999, low in 1996 and intermediate in 1998 (Fig. 7a). Years of abundant flowers were associated with above-average winter and spring rainfall in the previous year (Fig. 7b).

Natural recruitment at Walli

Only three naturally-recruited seedlings were seen during the period of observation (Table 1). Two were first observed in autumn–winter 1996 beneath the canopy of two trees (no. 271 and 279) where the groundstorey had been treated the previous spring; but both were dead when observations ceased. The effect of seedbed treatment, whether by burning, herbicide or both, was relatively short-lived, with exotic groundcover returning to around 100% within 6 months. The only survivor was first observed in spring 1996 outside the canopy of tree no. 28, the only tree with a predominantly native groundstorey. It emerged before the groundstorey was treated with herbicide.

Discussion

Though the main focus of the work reported here was on seed fall and to a lesser extent flowering of *E. albens*, the results are discussed in terms of the seed production sequence, at least as far as it is known.

Buds and flowers

Inflorescence buds became visually evident in November with bracts shed shortly afterwards exposing ‘pin buds’ that matured to ‘plump buds’ by about February. Many floral buds were aborted, consistent with observations in other eucalypts (Florence 1996). Despite reports of flowering commencing in January–February (Costermans 1983; Schrader 1987) or of occurring between March and May (Brooker and Kleinig 1990), observations at Walli were consistent with those of Clemson

(1985), namely April–November. Although there was variability between trees, peak flowering generally occurred during winter or spring but in some cases extended across much of this period. Most of the trees produced at least a few flowers every year. Many flowers were destroyed by parrots or otherwise aborted.

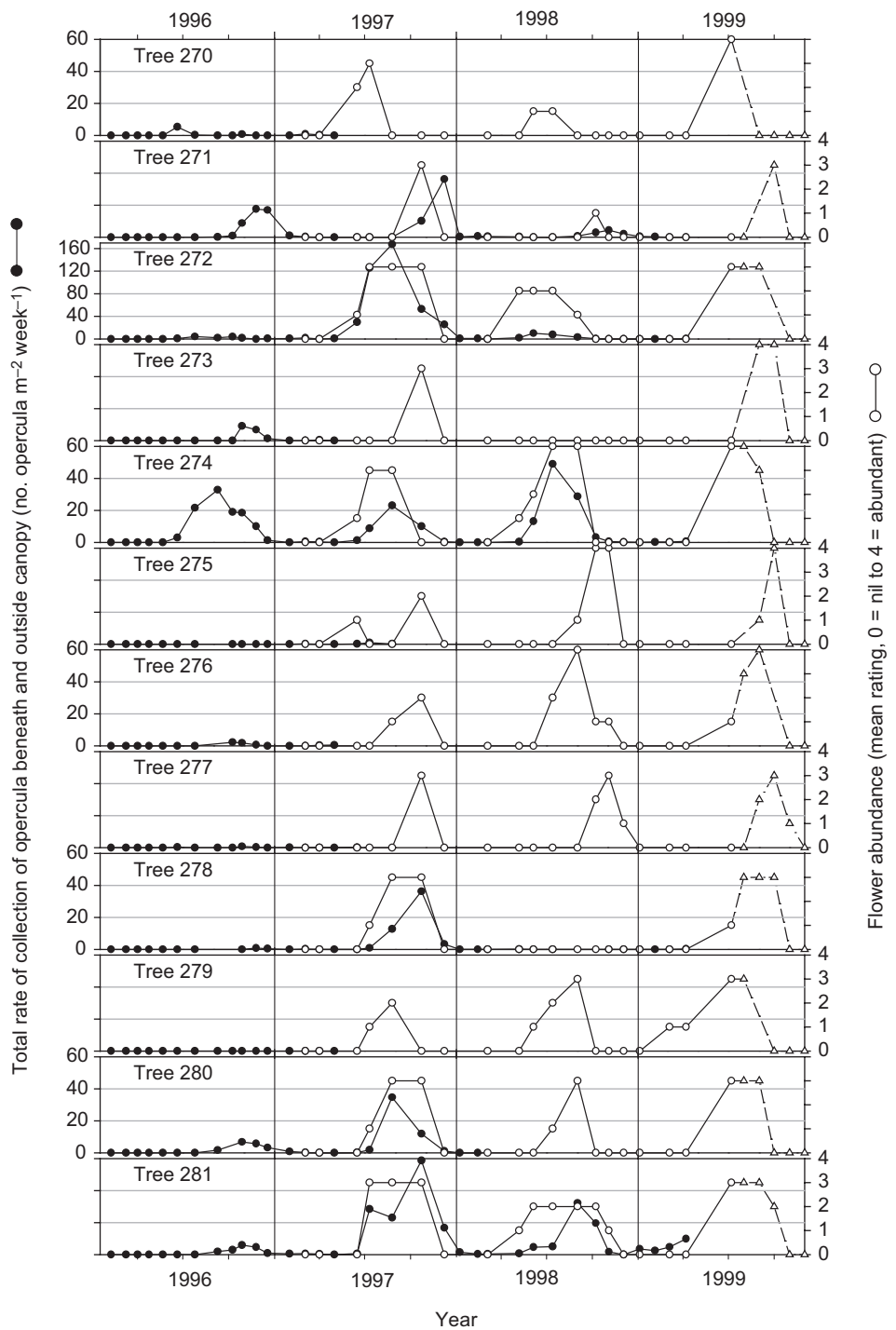


Figure 6. Flowering abundance and duration at 12 *Eucalyptus albens* trees at Walli from early February 1996 to early December 1999. Two methods of assessment, with varying periods of overlap, are shown: (1) solid circles indicate numbers of opercula, expressed as numbers per square metre per week (aggregate of up to eight collectors per tree); (2) open circles indicate visual abundance rating (0–4) until early July 1999 and open triangles indicate estimated abundance ratings based on bud abundance and previously observed patterns of buds flowering at each tree. Note that the y-axis scale for tree no. 272 differs from all the others.

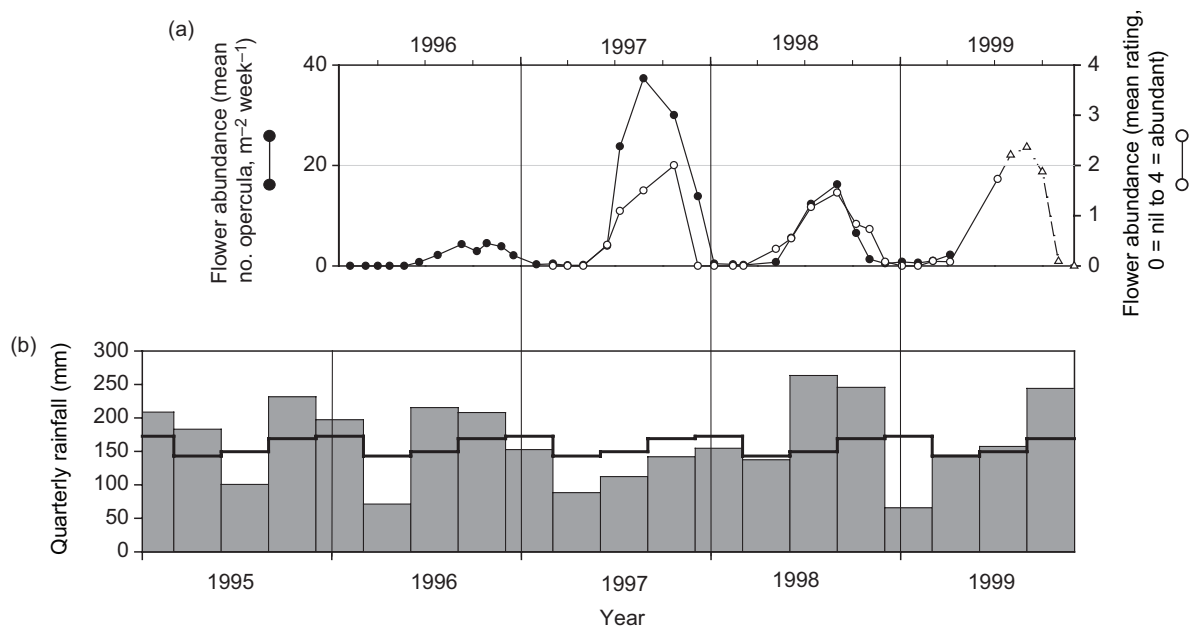


Figure 7. (a) Flower abundance, as assessed by opercula numbers and/or visual rating, averaged across all 12 trees at Walli; (b) quarterly (seasonal) rainfall at Cowra during and immediately preceding the period of observations. The thickened line indicates long-term seasonal means.

The average pattern of abundant flowering was every second year (Fig. 7a) but some trees flowered abundantly in two or more consecutive years (Fig. 6). Whether each tree had a distinctive pattern of flowering independent of environmental conditions or whether it was modified by (or entirely dependent on) prevailing environmental conditions could not be determined from only 4 y of observation. From 1996 to 1999, however, average flowering abundance was positively associated with above-average winter and spring rainfall in the previous year (Fig. 7).

As noted earlier, averaging across all trees can be misleading. For example, in a 30-y study of flowering synchrony of four box-ironbark species in Victoria, a graph of average flowering intensity suggested considerable synchrony between the species; yet actual overlap of flowering periods was low due to variable flowering of the species between years (Keatley *et al.* 2004). It should also be noted that as trees at Walli were deliberately and not randomly selected, overall patterns of flowering (and seed fall) should not necessarily be considered representative of what may occur in a natural stand of *E. albens*.

Seed maturation and seed fall

In the first 20 months (spring 1995 to autumn 1997), very little seed was collected from all but two trees even though the presence of chaff in collectors indicated that some capsule dehiscence was occurring in all trees. However, for the five trees that were monitored until autumn 1999, seed fall was markedly greater in the subsequent 20 months. It is likely that had all trees been monitored for the full period, a similar pattern would have occurred. Seed fall during the first 20 months may have been mainly from older capsules, rather than from the 'abundant early-mature capsules' for which trees were selected in mid-1995. The crop of early-mature capsules (containing viable seed) appeared to have shed seed mainly during 1998. This suggested that viable

seed was held within capsules for about 3 y before being shed, mainly during the warmer months, over a period of a year or so. Where peak flowerings occur in consecutive years, seed from a number of capsule crops can be present in the canopy and it may be shed simultaneously.

Timing and abundance of seed fall varied between individual trees. This is not uncommon in forest eucalypts and has been attributed (Jacobs 1955) to varying dominance, age, health and aspect of individual trees within a stand. To what extent these (or other) factors affected seed fall was not investigated. Some trees produced very little seed, at least during the first 2 y, whereas two trees produced seed for much of the time (Fig. 3). As suggested above, this may have been due to varying proportions of capsules of different ages within the canopies of individual trees. This suggestion was supported by the variable patterns of flowering, that is, abundance and frequency, subsequently observed. Peak seed falls tended to occur in the warmer months, consistent with Lawrence *et al.*'s (1998) short-term observations of *E. albens* in the central western NSW.

Viability of seed extracted from a sample of early-mature capsules present on all trees in mid-1995 was 81%, somewhat less than that reported (97%, Burrows 1995) from capsules of presumed similar age, suggesting the presence of some immature seed. Viability of seed within collectors ranged between about 60% and 100% (mean = 76%) over time, though lower values were recorded in mid- to late 1996, a period when few seeds were collected. Some seed was obviously damaged by insects when collected (though whether prior to seed fall or whilst in the collector was unknown), but in other cases no damage was evident and/or seed appeared to be immature. As most trees were relatively isolated (i.e. spaced at least, but usually considerably more than, 1.5 times the height of adjacent trees apart), it was possible that seed quality and quantity may have been adversely

affected by isolation as reported by Burrows (2000) for seed collected from *E. melliodora* trees.

Seed dispersal

Asymmetrical distributions of established seedlings have been reported to the south of parent trees and have been attributed to protection ('shading') afforded by the parent against frost and/or desiccation by Curtis (1989) in northern NSW and by Lawrence *et al.* (1998) in central western NSW and north-eastern Victoria. On NSW's southern tablelands, Edgerton (1996) reported an additional possibility, that is protection of frosted seedlings from early morning sunlight and subsequent death from 'cold-induced photoinhibition' (but no evidence of an adverse effect of early morning sunlight on seedling survival was evident in pot trials or in the distribution pattern of *E. albens* at high altitude on the central tablelands of NSW — Semple and Koen 2005). However, in SA and Victoria (Venning 1988; Dalton 1993), clumpiness has been attributed to asymmetrical dispersal of seed by prevailing winds at the time of seed fall as reported in forest situations (e.g. Cremer 1966).

No evidence was found for asymmetrical distribution of seed, albeit over relatively short distances, at Walli. Very little seed was collected at ~4 m from the edge of the canopy and there were insufficient data to examine whether asymmetry may have occurred in particular seasons, for example those that experienced high winds at the time of seed fall. Even allowing for the possibility of diminished seed fall close to the canopy edge, as reported by Cremer (1966) for an isolated ~76-m high *E. regnans* tree, the numbers of seeds collected at 4 m from the canopy edge were surprisingly low. Clearly a more targeted approach, that is seed collectors located over a wider area, would have provided a better test of asymmetrical seed dispersal. Though asymmetrical seed dispersal may provide an acceptable explanation of many cases of clumped seedlings elsewhere, the data presented here, albeit limited by the low numbers of seed collected, suggests that the 'protection hypothesis' is an equally likely explanation — at least in central western NSW.

Seed fall and seedling recruitment

The main reason for monitoring seed fall was to determine whether or not seed supply was likely to be limiting successful recruitment of *E. albens* in highly modified environments. At least two issues are involved here. First, studies elsewhere (e.g. Wellington and Noble 1985b) indicate that all seed shed is likely to be removed by seed-harvesting ants unless seed supply exceeds the rate of removal. Second, other studies (e.g. Lawrence *et al.* 1998; Semple and Koen 2003) suggest that seedlings arising from autumn–winter germinations are unlikely to survive in modified woodlands due to competition from annual exotics that germinate at the same time; and as noted by Prober (1996), cool-season annual exotics are particularly common in the southern part of the distribution of *E. albens* woodlands. Hence, in central western NSW at least, abundant falls of seed in spring and early summer are more likely to result in successful recruitment than falls in autumn and winter — particularly if some warm-season rainfall can be expected.

As only three naturally-recruited seedlings were seen during the course of the observations, it is difficult to relate their occurrence to seed fall. However, if a late 1995 emergence is assumed (see below), then Curtis' (1989) estimates of minimum seed quantities for recruitment, in the order of 100–200 seeds m⁻² in the 6 months prior to emergence, may be too high. Prior seed fall, aggregated from September to December (data for a full 6-month period were unavailable) at the three trees where recruitment occurred, was ~10 (no. 271), ~20 (no. 279) and ~70 (no. 281) seeds m⁻². However, no recruitment was observed at tree no. 274 where a seedbed had been prepared in spring 1995 and aggregate seed fall during this period exceeded 100 seeds m⁻². It would seem, therefore, that 'instantaneous' seed fall (not necessarily as high as 100 seeds m⁻² but at least sufficient to satiate ants) at the time of suitable rainfall, rather than an aggregation over a 6-month period, may be a more useful predictor of the likelihood of recruitment.

Other factors involved in seedling recruitment

Availability of sufficient seed at an appropriate time is only one of the factors necessary for successful recruitment. Having observed abundant eucalypt seedlings in Australian Capital Territory woodlands only when rainfall was above average for at least three successive years, Jacobs (1955) considered rainfall to be the most important of these factors. However, subsequent work on surface-sown or naturally deposited seed in modified rural environments (summarised in Table 4 of Lawrence *et al.* 1998) suggested that, for successful recruitment following seed fall in spring or early summer, above-average rainfall in spring and December followed up by at least 80 mm in either January, February or March were necessary. An examination of monthly rainfall recorded at Cowra (summarised in Fig. 7b) indicated that rainfall during the period of observation was likely to have been suitable for natural regeneration only in 1995–1996.

The presence of a suitable seedbed satisfies a number of requirements for successful regeneration: seed access to mineral soil, a lodgment site for the seed, and at least for a time, absence of herbaceous competition. Seedbeds created by fires have been effective in high-rainfall forests (e.g. Florence 1996) and mallee (e.g. Wellington and Noble 1985a,b) but have yielded variable results in woodlands, especially those with non-native groundstoreys (Curtis 1990). Similarly variable results have followed herbicide treatments (e.g. Whalley and Curtis 1993; Semple and Koen 1997, 2003), though herbicide followed by slashing was associated with higher numbers of naturally-recruited seedlings than a herbicide-alone treatment on the tablelands not far from the Walli site (Lawrence *et al.* 1998). In contrast, native groundstoreys may require little or no treatment to be an effective seedbed (e.g. Venning 1985; Curtis 1990) and this may explain the presence of the sole surviving seedling at Walli.

Apart from occasional incursions, cattle were excluded from most of the trees at Walli but wingless grasshoppers, abundant in the summers of 1995–1996 and 1996–1997, were not. When in plague numbers, these insects have been observed to be particularly damaging to young eucalypts established by direct seeding (Dalton 1993) or from tubestock (Semple *et al.* 1995).

Of the three naturally-recruited seedlings observed, all were at least six months old when first noted in mid- to late 1996 and were probably survivors from an earlier and larger cohort that probably emerged in late 1995 or early 1996 when rainfall satisfied Lawrence *et al.*'s (1998) criteria. Low seedling survival was probably due to competition from exotic herbage, browsing by grasshoppers and possibly 'competition' from the parent tree in the case of seedlings beneath or near the canopy.

Conclusions

Floral buds of *E. albens* were evident in November and flowering occurred between autumn and late spring of the following year, with peaks usually evident in winter or spring. Although most trees produced some flowers every year, abundant flowering of individual trees ranged from 2 y in a row, 3 y in a row to every second year. Collectively, however, at least one and usually more trees flowered abundantly in each of the 4 y of observation (see Fig. 6), giving rise to potentially multi-aged seed crops, not only in individual trees, but had the trees been together, in a stand.

Seed fall was also highly variable such that (assuming short longevity on the soil surface) it would have been limiting for seedling recruitment at most trees for periods of a year or more. Collectively, however, some viable seed was shed in the warmer months of all years of observation (see Fig. 2). It appeared that the abundant crop of early-mature capsules (with viable seed) for which the trees were selected in mid-1995 did not shed seed until 1998.

Very little seed was recorded at 4 m beyond the edge of the canopy and the limited data suggested that it was dispersed equally in all directions. This suggests that factors other than seed dispersal (e.g. protection from desiccation) may explain asymmetrical distributions of seedlings around parent trees. However, because of limited data, asymmetrical distribution of seed cannot be ruled as an explanation in some situations.

Despite exclusion of stock and preparation of seedbeds beneath trees early in the observation period, seedling recruitment was minimal. Though the quantity of seed shed was low at this time, other factors, particularly competition from exotic herbage, were more likely explanations for recruitment failure.

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