

Flowering and seed crop development in *Eucalyptus sieberi* L. Johnson and *E. globoidea* Blakely in a lowland sclerophyll forest in East Gippsland, Victoria

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Summary

Eucalyptus sieberi L. Johnson (silvertop ash) and *E. globoidea* Blakely (white stringybark) are two important timber species from East Gippsland, Victoria, where their regeneration following timber harvesting is usually attempted using the seed tree silvicultural system. Their seed crop development processes have not been well documented, however, and the information available for *E. globoidea* appears to contain inconsistencies. Consequently, this study was initiated, during the establishment of the Silvicultural Systems Project experiment near Cabbage Tree Creek, East Gippsland, to describe the morphological development of seed crops in the two species, and to determine the quantities, variation and losses associated with each stage in that development.

Eight funnel seed traps were located on a duplex soil site which supported a stand composed of 67% *E. sieberi* and 33% *E. globoidea*, by basal area. They were monitored at intervals of about a fortnight over the period from February 1989 to November 1992. A further six traps were located under individual trees of *E. globoidea* on a uniform sand site and were monitored for the period from February to December 1991. The timing, rates of fall and total fall of reproductive material at each site were determined. The results are reported here and some silvicultural implications are discussed.

Keywords: flowering; seed development; seed production; *Eucalyptus sieberi*; *Eucalyptus globoidea*; Victoria; Australia

Introduction

Regeneration of native eucalypt forests following timber harvesting often relies upon the seed from trees retained as a seed source. To effectively manage such seed for regeneration, it is necessary to know the seed crop development process for each species present. Silviculturally, this knowledge is important when:

- (i) judging whether the trees to be retained as a seed source carry sufficient seed to regenerate the area harvested around them;
- (ii) judging whether that seed will be mature at the appropriate time; and
- (iii) managing that seed so as to influence the stocking and species composition of the regenerating stand.

Errors in any of these instances could lead to patchy or failed regeneration, or to unintended changes in species composition.

Eucalyptus sieberi L. Johnson (silvertop ash) and *Eucalyptus globoidea* Blakely (white stringybark) are two important timber species from the coastal and foothill forests of East Gippsland, Victoria. They have been harvested for sawlogs since the 1960s, and their regeneration since that time has usually been attempted using the seed tree system (Campbell *et al.* 1984). However, there is scant information in the literature concerning either their flowering behaviour or their seed crop development processes. Further, for *E. globoidea*, the information that is available appears to contain inconsistencies (Table 1).

During the establishment of the Silvicultural Systems Project (SSP) experiment (Squire 1990; Squire *et al.* 1991) at Cabbage Tree Creek, East Gippsland, a study was initiated to describe the morphological development of seed crops in *E. sieberi* and *E. globoidea*, and to determine the quantities, variation and losses associated with each stage in that development. The results of the study are reported here, and a number of silvicultural implications are discussed.

Methods

Study sites

The SSP experimental area at Cabbage Tree Creek is located about 5 km north-east of Cabbage Tree Creek township (37°41'S 148°45'E). Altitude ranges from 70 to 200 m above sea level, and slopes range up to 20°. Mean annual rainfall for the period 1946 to 1991 at Cabbage Tree Creek was 1094 mm (Bureau of Meteorology, Victoria).

Two lowland sclerophyll forest sites (Forbes *et al.* 1982) within the SSP experimental area were selected for this study. Site 1 is a 4-ha multi-aged stand of mature forest situated on a westerly to south-westerly aspect of slope 10° to 20°. Stand height is 38 m and projected canopy cover is 37%. Hence the stand is classified as Open Forest II (Specht *et al.* 1974). Stand basal area (BA) is 26.4 m² ha⁻¹, made up of 67% *E. sieberi* and 33% *E. globoidea*. Scattered *E. sieberi* and *E. globoidea* regrowth, to 10 m tall, occurs throughout. A shrub stratum, 3–5 m tall, consists of *Persoonia linearis* Andrews (narrow-leaf geebung), *Acacia terminalis*

Table 1. Summary of literature references to flowering behaviour and seed crop development processes for *Eucalyptus sieberi* L. Johnson (silvertop ash) and *E. globoidea* Blakely (white stringybark)

Species and summary	Reference
<i>E. sieberi</i>	
Flowers September to January	Turner and Moncur (1991); Boland <i>et al.</i> (1984)
Flowers constantly from November to December	Blakely (1965)
Flowers September to December	Willis (1986)
Regular, and often massive, seed producer	Bridges (1983)
Does not seed freely every year	Hall <i>et al.</i> (1963) in Turnbull and Pryor (1978)
Flowers most years in August to December, with peaks between September and November	Dept of Agriculture (1973)
<i>E. globoidea</i>	
Flowers April to June	Blakely (1965); Boland <i>et al.</i> (1984)
Flowers July to February	Turner and Moncur (1991)
Flowers December to March	Willis (1986)
Flowers summer to autumn, but may be found flowering erratically throughout the year	Dept of Agriculture (1973)
Regular, and often massive, seed producer	Bridges (1983)

(Salisb.) Macbr. (sunshine wattle) and *A. mucronata* Willd. ex H.H. Wendl. (narrow-leaf wattle). A lower shrub stratum, 1.5 m tall, is dominated by *Platylobium formosum* Smith (handsome flat-pea) and *Tetrarrhena juncea* R. Br. (forest wiregrass). The soil is yellow duplex, with fragmented quartzite and granodiorite parent material exposed on the soil surface in ridge-top locations. Raison *et al.* (1991) described duplex soils elsewhere on the SSP experimental area as having very low (194 kg ha⁻¹) total phosphorus (P) and low rates of nitrogen (N) mineralisation (40 kg ha⁻¹ y⁻¹).

Site 2 is a 3-ha multi-aged stand of mature forest situated on flat terrain 2 km east of Site 1. It is classified as Open Forest III (Specht *et al.* 1974), with stand height being 20–28 m. Stand BA is 29.8 m² ha⁻¹, composed of 50% *E. globoidea*, 40% *E. consideriana* Maiden (yertchuk) and 10% *E. botryoides* Smith (southern mahogany). An open lower tree stratum of *Banksia serrata* L. f. (saw banksia) stands over a dense shrub stratum of *A. terminalis*, *Leptospermum continentale* J. Thompson (prickly tea-tree) and *Pteridium esculentum* (G. Forster) Cockayne (austral bracken). Raison *et al.* (1991) described the soil at Site 2 as a uniform coarse-textured sand, with a bleached A2 horizon overlaying two fragmented 'coffee rock' hardpans. Total P is very low (91 kg ha⁻¹), whereas N-mineralisation is moderate (60 kg ha⁻¹ y⁻¹), but limited when soil moisture is low.

Seed crop development

Morphological development

The basic stages in the morphological development of seed crops in *E. sieberi* (Fig. 1) and *E. globoidea* (Fig. 2) were first outlined for this study by collecting branchlet samples from various locations in East Gippsland and comparing them with information in the literature (summarised in Table 1). A spotting scope was used from time to time to observe and confirm various stages in development.

Detailed information was then obtained by monitoring the fall of material from the forest canopy at Site 1 during February 1989 to November 1992 (May 1993 for flowers and immature capsules). For this, eight plastic funnel seed traps, each 0.814 m² and attached

to a fine-mesh collection bag, were placed in fixed locations in the forest, using the simple random sampling procedure previously applied to *E. regnans* forest by Ashton (1956, 1975) and Cunningham (1957). The collection bags were changed every 12–24 days. Each collection was timed to represent the first or the last half of each calendar month during the study period. From time to time, a sticky insecticide was applied to the legs of each trap to minimise the predation of the trap contents by ants. At each collection, capsules were separated from the other contents of the bag, so that the seed they might contain would not contaminate the otherwise free-fallen seed in the bag. Some contamination, however, may have occurred prior to collection.

In the laboratory, the contents of each collection bag were passed through a two-tiered sieve, with pore sizes 1.39 mm and 2.70 mm diameter respectively, to separate eucalypt seed from the other contents. If the contents were moist, they were first oven-dried overnight at 30°C. The resultant fine fraction (<1.39 mm) contained most of the eucalypt seed. To it were added *E. sieberi* seeds that were too large to pass through the smaller sieve, and fines which might contain seed but were stuck to coarse material in the coarse fractions. The fine fraction from each collection bag was germination-tested on filter paper for 28 days at 20°C (adapted from Boland *et al.* 1980). The tests determined the number of viable eucalypt seeds in each collection bag, but could not reliably separate the seeds by species.

The remaining two fractions were re-combined and sorted by species, for inflorescence buds and their bract involucre (from *E. sieberi* only), umbellate buds, opercula and flowers (Figs 1 and 2). The capsules that had been separated at collection were also sorted by species. Immature capsules, in which the valve slits were not evident and the floral receptacles were underdeveloped, were sorted as flowers. Leaf litter was also sorted, as was insect frass on occasions during spring and summer when relatively large quantities were apparent.

Each aborted bud, flower and capsule was examined for damage inflicted by insects, fungal infection or the feeding activity of birds or arboreal mammals. Following sorting, the buds, bract involucre, opercula, flowers and capsules from each trap were counted by species, and the data were used to estimate:

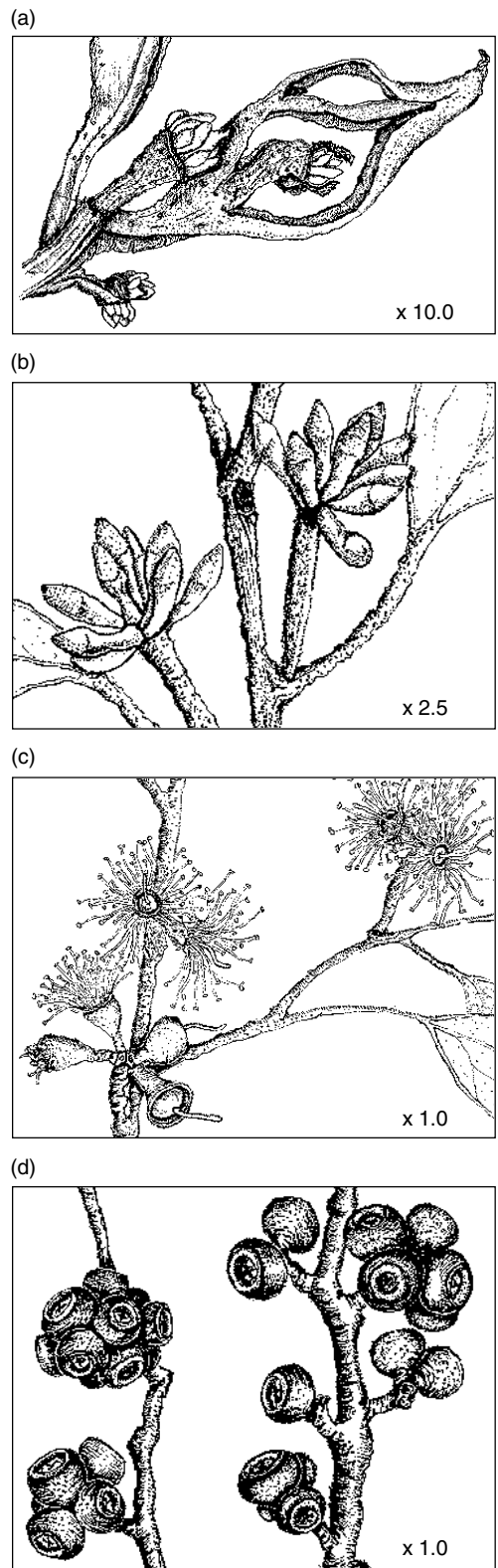
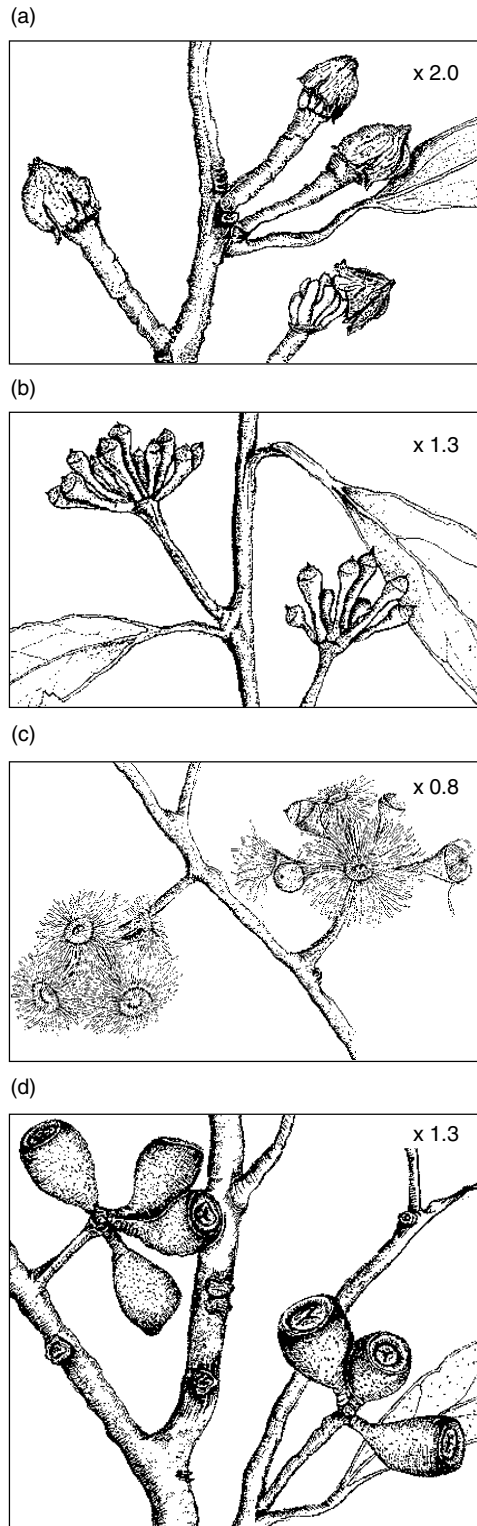


Figure 1. Stages in the morphological development of seed crops in *Eucalyptus sieberi* (silvertop ash): (a) shedding of the involucre of bracts from the inflorescence bud; (b) umbellate bud growth; (c) flowering and stamen fall; and (d) capsule maturation

Figure 2. Stages in the morphological development of seed crops in *Eucalyptus globoidea* (white stringybark): (a) shedding of the involucre of bracts from the inflorescence bud; (b) umbellate bud growth; (c) flowering and stamen fall; and (d) capsule maturation

- (i) the number that had fallen (no. ha⁻¹) during the collection period;
- (ii) the corresponding rate of fall (no. ha⁻¹ wk⁻¹) for the collection period;
- (iii) the total number that had fallen during the annual seed crop development cycle (no. ha⁻¹ y⁻¹); and

- (iv) associated coefficients of variation (Cvs).

Results from (ii) above were graphed against time, with the rate of fall calculated for each collection period being plotted against that half of the calendar month which the collection represented.

Table 2. Proportion of area (%) and the number of seed traps (in parentheses) in each stratum for *Eucalyptus sieberi* L. Johnson (silvertop ash) and *E. globoidea* Blakely (white stringybark) at Site 1, at the Silvicultural Systems Project experimental area, Cabbage Tree Creek

Stratum	<i>E. sieberi</i>	<i>E. globoidea</i>
1	28 (3)	09 (2)
2	72 (5)	65 (3)
3	—	26 (3)

Graphs concerning the fall of bract involucres (from *E. sieberi* only), opercula and seed were then used, in conjunction with live branch samples, to determine when inflorescence and umbellate buds emerged, and the timing and periodicity of flowering and seedfall.

The leaf litter fractions and insect frass from the eight traps were pooled following sorting, oven-dried to constant weight at 80°C and weighed. These data were also converted to a weekly rate of fall for the collection period and graphed.

After initial calculations, the collection of heavy tree litter was found to be biased, and so the sampling approach was divided into two. The simple random sampling approach was used for the light material from *E. sieberi* (inflorescence buds, bract involucres and opercula). Heavier material was sampled and analysed by imposing a stratification upon the trap locations as follows:

- (i) Stratum 1: directly beneath the projection of a tree crown;
- (ii) Stratum 2: outside Stratum 1, but within one tree height of any tree; and
- (iii) Stratum 3: beyond tree height of any tree.

For example, a trap could be in Stratum 1 for *E. sieberi*, being directly beneath an *E. sieberi* crown, but could also be in Stratum 3 for *E. globoidea*, being beyond tree height from the nearest *E. globoidea* tree.

The proportion of area occupied by each stratum was then determined for each species, using large-scale colour aerial photographs and ground measurements (Table 2). Weighted means and variances were calculated according to Husch *et al.* (1982).

To further study the flowering behaviour of *E. globoidea*, six individual trees of that species were also monitored at Site 2, where large variation in the timing of flowering had previously been observed. A single seed trap was located directly beneath the crown of each of these trees, so as to maximise the interception of opercula, and collections were made between February and December 1991, on the same dates as for Site 1 during that period. The resultant data were used only to indicate the relative timing and magnitude of flowering in the six trees being monitored.

Quantities and losses

The data from Site 1 were used to estimate the total quantities of reproductive material produced and the proportions lost from each species during each annual seed crop development cycle. A number of assumptions were made (after Ashton 1956, 1975):

- (i) the total number of inflorescence buds formed on *E. sieberi* in each annual seed crop development cycle equals the

number of bract involucres falling, plus the number of aborted inflorescence buds;

- (ii) the number of umbellate buds emerging from the inflorescence buds in either species equals the number of opercula falling, plus the number of aborted umbellate buds; and
- (iii) the number of capsules set in either species equals the number of opercula falling, minus the number of aborted flowers.

Thus, the total number produced in each seed crop development cycle, the proportion (%) lost and associated Cvs, were calculated for inflorescence buds (in *E. sieberi* only), umbellate buds, flowers and capsules. Further, the number of capsules set was calculated as a proportion of the number of umbellate buds initiated, as a measure of efficiency for each annual cycle.

Data concerning quantities and losses were also obtained in an 'inflorescence scar study' of pedicel and peduncle scars (Fig. 1), on umbels and twigs from sample branchlets collected specifically for the purpose. For this study, single branchlets were shot from three trees of each species at Site 1, and a further total of three branchlets was shot from two *E. globoidea* trees at Site 2. Each branchlet had a butt diameter of about 2 cm. Sampling took place in July 1991 using a .308 calibre rifle. The six branchlets from Site 1 each supported a crop of umbellate buds at the point of flowering, and a crop of capsules resulting from flowering in the previous year. A total of 2000–3000 umbels of umbellate buds and 2000–3000 umbels of capsules were examined for each species at Site 1.

Each pedicel scar represents the loss of an umbellate bud, flower or capsule, so the number of scars on an umbel at any time will indicate the losses from umbels up to that time. Likewise, peduncle scars represent the total loss of an umbel, for which an average value of the number of umbellate buds per umbel can be applied, to estimate the number of umbellate buds that have been aborted. A count of pedicel and peduncle scars was used to calculate the total number of umbellate buds that had emerged from the inflorescence buds, the losses that had occurred to the point of flowering, and the frequency distribution of the number of umbellate buds or capsules per umbel at each of these two stages.

The three *E. globoidea* branchlets from Site 2 each supported an umbellate bud crop at the point of flowering, and a second umbellate bud crop that had begun to emerge about one month prior to sampling. A total of 1500–1600 umbels in each of these crops was examined to estimate the total number of umbellate buds that had emerged, the losses that had occurred to the time of sampling, and the frequency distribution of the number of buds per umbel at each stage.

In this study, fresh pedicel or peduncle scars (found on <1% of umbels analysed) were assumed to represent losses during sampling. These infrequent scars were identified by their green appearance and were tallied as umbellate buds or capsules, as appropriate, rather than as losses.

Results and discussion

Data analysis

A deficiency in this study was the need, part-way through, to impose a stratification upon the layout of the seed traps at Site 1. Initially, all calculations had been based upon the data of

individual traps in their simple random layout at Site 1. With this method, seedfall and the lighter material from *E. sieberi* (inflorescence buds, bract involucre and opercula) generated relatively low Cvs, suggesting that, although the stand was open, this material was falling virtually homogeneously throughout, and that the calculated means were reliable. It was found, however, that the fall of other material from *E. sieberi* (umbellate buds, flowers and capsules) and all material from *E. globoidea* was biased, with the heaviest falls occurring directly beneath tree crowns. As a result, variances and Cvs for this material were unacceptably large and the means were unreliable. For example, simple estimates of the number of flowers aborted over each season for both species were larger than estimates of operculum fall over each respective season, a physical impossibility since, for Monocalyptus, operculum fall is a measure of the total number of flowers produced (Ashton 1975). The simple random allocation of seed traps had apparently given undue weighting to the area directly beneath tree crowns, and the fall of heavier material there. Consequently, as described above, the data for this heavier material had to be analysed by imposing a stratification upon the trap locations.

Three other studies have encountered problems in analysing seed trap data collected using simple random sampling procedures, and these are outlined below.

Ashton (1975) studied the flowering behaviour of *E. regnans* over a number of years. In years where flowering was heavy, the simple random layout of traps, and the simple analysis of data from them, proved adequate. For example, standard errors for the fall of flowers and sterile fruit were only 12–23% of the means of up to 12 million ha⁻¹ reported for 1954. Such homogeneity is perhaps to be expected in this mono-specific, even-aged forest type, as canopy cover is typically 60–80% (Gillison and Walker 1981) and stand height can be 50–80 m (Ashton 1976). Ashton (1975) also reported, however, that in years where flowering was poor (e.g. 0.5 million ha⁻¹ in 1955), the five to seven 0.52 m² traps used gave unreliable data because of insufficient replication.

Van Loon (1966) monitored the fall of reproductive material in a forest of *E. microcorys* F. Muell. (tallowwood) and *E. saligna* Sm. (Sydney blue gum) and, as in the initial analyses for this study, showed that the number of aborted flowers falling was greater than the number of opercula. No attempt was made to explain this irregularity, even though it is a physical impossibility as described earlier.

Thirdly, Gill (1966) also estimated flower-fall to be greater than operculum-fall, attributing this to the undue bias of one or two large values. These were most likely recorded directly beneath tree crowns.

It seems clear that stratification would have benefited the studies undertaken by Van Loon and Gill, and, although difficult to apply in *E. regnans* forest, it is possible that it would have reduced the stated need for additional replication in Ashton's study. Regardless, the experiences of these three studies are considered to support the decision taken here to impose stratification upon the data for the heavier material at Site 1.

Seed crop development in *Eucalyptus sieberi*

Bud formation and development

The first visible stage in the morphological development of seed crops in *E. sieberi* was the appearance of a pedunculate inflorescence bud in the axil of each new leaf primordium produced in mid- to late spring each year (Fig. 1). These inflorescence buds continued to appear through summer, as the flush of new leaves continued, resulting in a crop of inflorescence buds at various stages of development. The buds were solitary in each leaf axil, appeared in a dichasial cyme, and consisted of an umbel of umbellate buds enclosed by an involucre of six bracts. This number of bracts was also reported by Carr and Carr (1959) for series Fraxinales (Blakely 1934), to which *E. sieberi* belongs. The bracts were permanently fused at their tips, were joined below with separable seams, and swelled as an involucre, to a partly globose shape, as the inflorescence bud developed.

The involucre was first loosened by an irregular tearing along one of the seams on the middle of either its anterior or posterior face, and around the base of each bract at the apex of the peduncle (Fig. 1a). It was then carried upwards on the umbellate buds, as their growing tips elongated, and fell away when they began to arch outwards. This latter character has also been reported for *E. stellulata* Sieber ex DC. (black sallee) (Davis 1969). The involucre was shed as a whole, since the tips of the six bracts remained fused and four of the six seams generally did not separate. The inflorescence bud was 10–20 mm long at this point, much longer than the 2–5 mm reported by Carr and Carr (1959) as being typical for Monocalyptus.

Involucre were shed from December to June, although broad peaks occurred across several of those months (Fig. 3a). This long time-span is largely because the inflorescence buds appeared with the leaf primordia over a period of months, and so exhibited various stages of development. Individually though, the time taken from the appearance of each inflorescence bud to the shed of its bracts was 3–5 months. Ashton (1975) and Cremer *et al.* (1978) reported 14 months for *E. regnans*, as did Fielding (1956) for *E. delegatensis* R. Baker (alpine ash), *E. fastigata* Deane & Maiden (brown barrel) and *E. pauciflora* Sieber ex Sprengel (snow gum). A small proportion of the inflorescence buds produced each season did not shed their bracts. These buds were retained until most others had shed their bracts, but were all eventually aborted through abscission or fungal attack.

As the involucre split and fell, simple umbels of 4–12 pedicellate umbellate buds were exposed. Turner and Moncur (1991) reported 7–15 flowers per umbel for *E. sieberi*. Each umbellate bud was capped with a beaked, hemispherical operculum, and arched outwards, swelled and elongated, to take on the clavate appearance of the mature umbellate bud prior to anthesis (Fig. 1b). At anthesis they were generally 8–10 months old and, consequently, only one crop of umbellate buds was ever present on a tree at any time.

Flowering

The first sign of anthesis was the formation of an abscission layer about the base of the operculum. This structure fell away as the

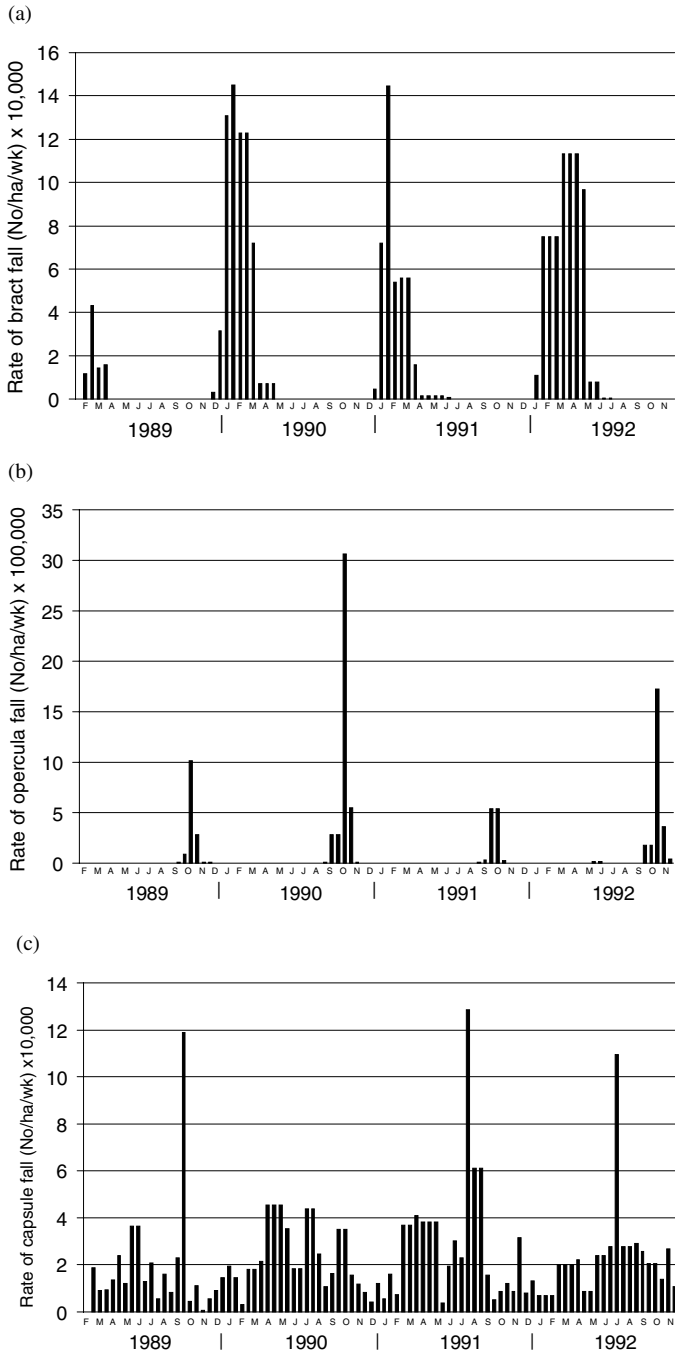


Figure 3. Rates of fall over time for (a) involucre of bracts; (b) opercula; and (c) capsules from *Eucalyptus sieberi* at Site 1, Cabbage Tree Creek

anthers unfolded outwards from the centre of the bud (Fig. 1c). Operculum fall was recorded from May to December, but peaked suddenly over the same short period in late October each year (Fig. 3b). Thus, flowering in *E. sieberi* generally occurred 12–13 months after the appearance of the first inflorescence buds. *Eucalyptus melliodora* A. Cunn. ex Schau. (yellow box) flowers after a similar time-span (Moncur and Boland 1989), whereas *E. stellulata* flowers after 5–12 months (Davis 1969), *E. pilularis* Smith (blackbutt) after 18–23 months (Florence 1964), *E. delegatensis* after 24–25 months (Grose 1960) and *E. regnans* after 27–29 months (Ashton 1975).

The very synchronised flowering of *E. sieberi* is emphasised in Figure 4a, which shows that operculum fall peaked in every seed

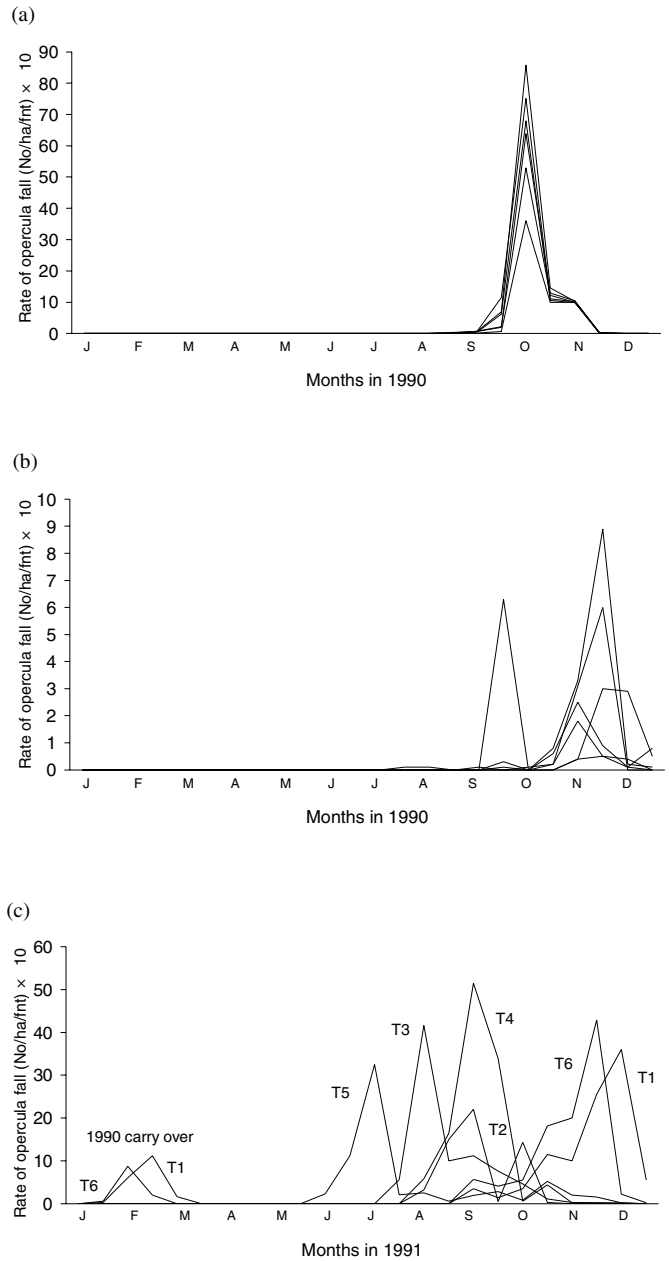


Figure 4. Rates of fall over time of opercula from (a) *Eucalyptus sieberi* at Site 1 during 1990; (b) *E. globoidea* at Site 1 during 1990; and (c) *E. globoidea* at Site 2 during 1991, Cabbage Tree Creek. 'T1'–'T6' denotes Tree 1 to Tree 6 at Site 2. 'fnt' = fortnight (2 weeks).

trap at Site 1 in the same fortnight in 1990. Similar patterns occurred in 1989, 1991 and 1992. Such synchronisation seems remarkable, given that the umbellate buds were released sporadically from the inflorescence buds over a period of 6–7 months. In contrast, flowering in *E. stellulata* occurs sporadically over the same number of months as the release of its umbellate buds (Davis 1969).

In East Gippsland, flowering in *E. sieberi* stands at a range of altitudes has been observed to peak within two weeks of the stand at Site 1. In Central Gippsland, about 350 km west, stands at altitude similar to that of Site 1 also peaked in the last two weeks of October in 1992. It thus appears that flowering in *E. sieberi* is

controlled by some factor which affects the whole stand and which is common to geographically separated stands.

Once their stamens were fully flexed, individual *E. sieberi* flowers remained in bloom for 2–3 weeks. *Eucalyptus sieberi* flowers are known to be poor producers of nectar (Henry and Murray 1993), possibly explaining why only a few birds were ever observed feeding on them during this study. Species that were observed feeding during the very heavy flowering year of 1990 (Fig. 3b) included honey-eaters (*Phylidonyris pyrrhoptera* Latham, *Lichenostomus chrysops* Latham, *Melithreptus brevirostris* Vigors & Horsf. and *M. lunatus* Vieillot), lorikeets (*Trichoglossus haematodus* Linne, *Glossopsitta concinna* Shaw and *G. pusilla* Shaw), a wattlebird (*Anthochaera carunculata* Shaw) and a spinebill (*Acanthorhynchus tenuirostris* Latham). Each is known to commonly feed upon pollen and nectar (Blakers *et al.* 1984). Nevertheless, insects are the major vector for pollen transfer in eucalypts (Griffin 1980), and swarms of bees (two species), hover flies (*Eristalis* sp.), beetles, moths (*Dorattfera pinguis* and others), butterflies and various other flies were observed, through a spotting scope, alighting on *E. sieberi* flowers each year.

Capsule development and seed dissemination

In the five months following flowering and pollination, the floral receptacle developed into an immature, obconical-pyriform capsule (Fig. 1d). Some seed capable of germination was present by 7–8 months, although observations of capsule morphology and routine viability tests undertaken by the Department of Natural Resources and Environment, Victoria, suggest that it was a likely to be a further 12 months before maximum viability was reached. Bassett *et al.* (in press) reported that mature *E. sieberi* capsules, two years following flowering and sampled from the SSP experimental area, contained an average of 1.4 viable seeds per capsule. By the second year following flowering, such capsules were largely free of subtending leaves. Leaves abscinded and fell throughout the year, but with peak rates of fall in late summer and early autumn (Fig. 5a).

Dissemination of seed from a particular capsule crop generally began 28–30 months after flowering and could continue for up to four years. Thus, as individual *E. sieberi* trees flowered every year, they could hold portions of up to six consecutive capsule crops at any time. Figure 5b does not differentiate between seedfall from *E. sieberi* and *E. globoidea*, but it shows that seedfall at Site 1 occurred year round. It also shows that peaks tended to occur in autumn, winter and spring; with comparatively little seedfall during summer. This is consistent with the view of Cunningham (1960) that, for many eucalypts, peak seedfall does not necessarily coincide with the hottest months of the year.

Seedfall in *E. sieberi* occurred as a physiological response to the gradual senescence of branchlets within the crown. Figure 5 suggests a linkage between leaf-fall and seedfall, and observations showed that it was often associated with the abscission and death of less dominant branchlets following the peak fall of leaves in late summer and early autumn. As these branchlets senesced, the capsules they supported dried, opened and released their seed, with seedfall from them being enhanced by warm, windy days. Ashton (1975) likewise reported the abscission of capsules at the

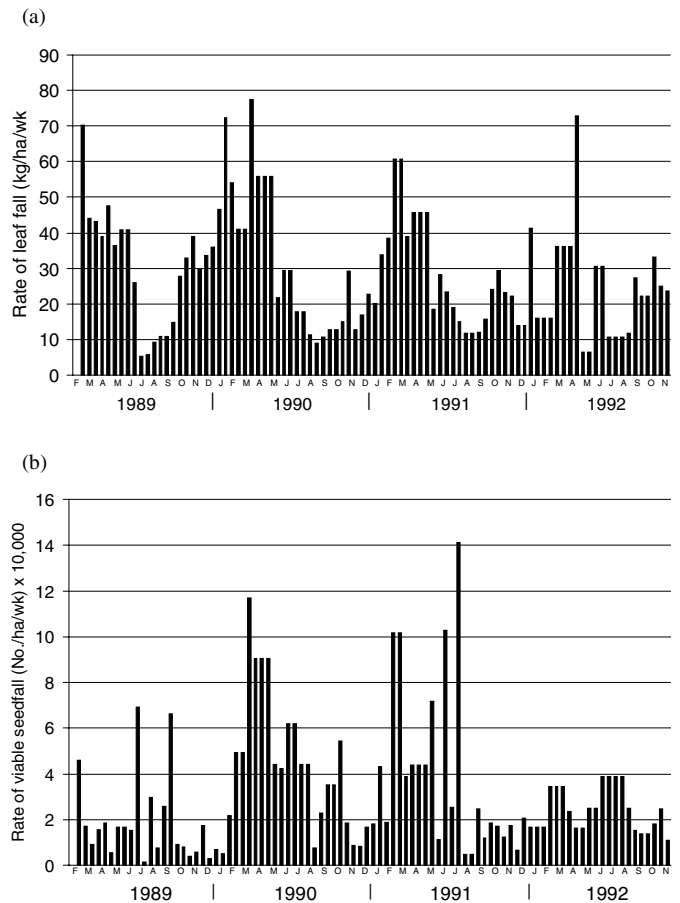


Figure 5. Rates of (a) leaf fall; and (b) seed fall over time from *Eucalyptus sieberi* and *E. globoidea* at Site 1, Cabbage Tree Creek

pedicel or peduncle in *E. regnans* as a result of this process. Cremer (1965) and Gill (1966) found that the general timing of seed release was principally determined by the initial cause of that release, which is physiological, rather than subsequent external environmental conditions. Other studies support this view (Ashton 1956; Cunningham 1960; Grose 1960; Wallace 1971; Loneragen 1979).

Wind and warmer temperatures were not the only agencies to influence weekly rates of seedfall at Site 1. Abnormally large peaks in seedfall occurred in September 1989, July 1991 and July 1992 (Fig. 5b), which were attributed to the feeding behaviour of crimson rosellas (*Platycercus elegans* Gmelin). At these times, *E. sieberi* crowns contained many recently-abscinded branchlets, 1–2 cm in diameter, each of which still held up to 200 capsules. The valves of most of these capsules had just opened, and a number of flocks of 20 to 30 rosellas were often observed feeding upon the easily accessible seed they contained. Each bird would pick off a capsule at the pedicel, place the valve end into its beak, throw its head back and spill the seed out into its crop by agitating its beak on either side of the capsule. During these observations, the sound of beaks clicking vigorously against capsules could be heard across the forest, and seed and capsules could be felt and heard spilling to the ground. This method of feeding was therefore by no means efficient. Each capsule was usually dropped after about 15 seconds and another chosen nearby. Hence it was estimated that a flock of 20 birds could empty over 4000 capsules h⁻¹.

Through a spotting scope the birds were often observed competing for canopy position. If an individual was forced from its position whilst feeding, a small stream of seed could be seen spilling from the capsule and the bird's crop whilst it was in flight, with subsequent effects on seed dispersal. Loyn (1993) reported a winter influx of crimson rosellas to lowland sclerophyll forest in East Gippsland, from their preferred summer habitat of damp and wet sclerophyll forest. This may, in part, be due to the ready availability of *E. sieberi* seed at this time. Loyn also reported that gang-gang cockatoos (*Callocephalon fimbriatum* Grant) were observed feeding on eucalypt seed in lowland sclerophyll forest in winter.

Capsule crops were often retained for up to 6 y following anthesis, with capsules falling throughout this time (Fig. 3c). Their fall followed a very similar pattern to seedfall, including the broad peaks resulting from branchlet senescence and the abnormal peaks due to crimson rosellas. An average of 73% of capsules fell already opened, having released their seed prior to fall, although at the time of rosella activity all capsules tallied were open. Capsules usually fell singly (72%), with the remainder falling still attached to twigs and/or as umbels.

Seed crop development in *Eucalyptus globoidea*

Seed crop development in *E. globoidea* (Fig. 2) had a number of fundamental differences from that in *E. sieberi*. Its interpretation was also more complex, due to the variation that occurred within key events such as flowering.

Bud formation and development

Solitary inflorescence buds were initiated in the axils of new leaves and became visible in the apical bud primordia as early as June each year, 3–4 months earlier than in *E. sieberi*. Carr and Carr (1959) emphasised that most eucalypt species shed the involucre of bracts from the inflorescence bud at an early stage. In *E. globoidea*, these bracts were commonly fragmented and shed at 2–3 weeks of age, even before the inflorescence bud was totally free of the surrounding fused leaf primordia (Fig. 2a)*. Florence (1964) found inflorescence buds in *E. pilularis* to be similarly short-lived.

By the time the new leaves accompanying the inflorescence buds in *E. globoidea* had separated from the apical buds, the involucre

*This characteristic of *E. globoidea* can be used for taxonomic purposes. *E. globoidea* is regarded as a highly polymorphic species in Victoria (Willis 1986), and has many features in common with *E. agglomerata* Maiden (blue-leaved stringybark). Because of the confusion that has occurred between the two, the genuine occurrence of *E. agglomerata* in Victoria was not confirmed until 1971 (Willis 1986). The main characteristic used to distinguish *E. agglomerata* has been its more sessile and congested fruits (Boland *et al.* 1984; Willis 1986), but assessment of this is somewhat subjective. It now appears that the two species can also be differentiated, from June to October, by the relative persistence of their inflorescence buds. Unlike those in *E. globoidea*, the inflorescence buds in *E. agglomerata* near Combiobar, 36 km north-west of Cabbage Tree Creek, persisted for some months before shedding their bracts. They therefore became much larger and associated with more advanced leaves, somewhat like those in *E. sieberi* (Figure 1a).

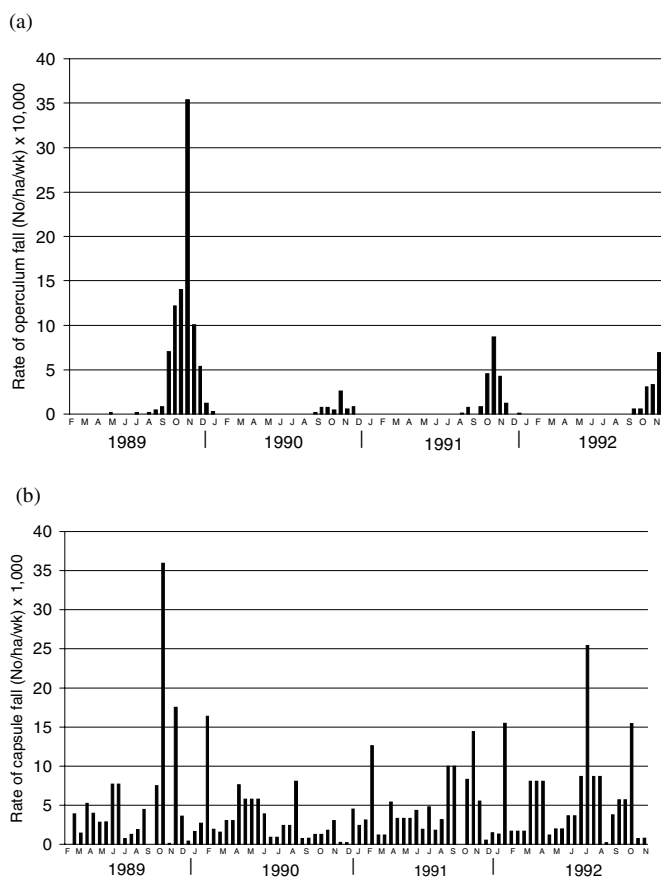


Figure 6. Rates of fall over time for (a) opercula; and (b) capsules from *Eucalyptus globoidea* at Site 1, Cabbage Tree Creek

bracts had fallen away to expose 1–24 shortly pedicellate, umbellate buds. Unlike those in *E. sieberi* though, the bracts in *E. globoidea* were not permanently fused at their tips, and separated completely as the involucre fragmented. Hence, they fell away individually and could not be identified once they had mixed with other material in the seed traps. Data on bract fall are therefore unavailable for *E. globoidea*.

At this stage, the umbellate buds in *E. globoidea* were only 1–2 mm long and tightly clustered, and possessed a fusiform shape similar to that of older buds at the point of anthesis (Figs 2a, 2b). They continued to swell after the bracts were shed, as their ovules and anthers developed, and eventually parted into two groups which arched outwards in opposite directions (Fig. 2a). This was the first step in the separation of the tight cluster of umbellate buds in each umbel.

The umbellate buds continued to develop until the beginning of anthesis, when they each shed a single, conical operculum (Fig. 2). Figure 6a shows that most *E. globoidea* opercula at Site 1 were shed over the period September to December, so that anthesis generally occurred 14–17 months after the appearance of the first inflorescence buds. Consequently, for a period of several months leading up to anthesis, *E. globoidea* supported two umbellate bud crops, one having just emerged and the other being about to undergo anthesis. *Eucalyptus baxteri* (Benth.) Maiden & Blakely (brown stringybark) at Cabbage Tree Creek was also observed to simultaneously hold consecutive umbellate bud crops during

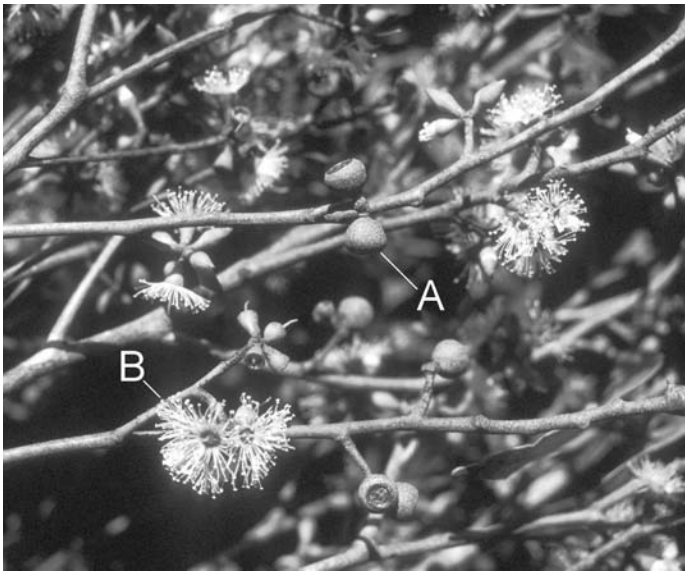


Figure 7. A single developing seed-crop on *Eucalyptus globoidea*, initiated in June 1989 at Site 2, Cabbage Tree Creek, showing: (A) capsules resulting from the usual spring flowering in 1990; and (B) flowering of buds that did not originally flower, but which were carried over from the previous 1990 spring to flower in autumn 1991.

March, one having been initiated the previous spring and the other, at the point of anthesis, having been initiated the spring before that. This has also been observed in *E. baxteri* at Wilsons Promontory, Victoria (Dr D.H. Ashton, *pers. comm.*). However, one of the bud crops on each branchlet so affected in *E. baxteri* at Cabbage Tree Creek was usually quite small relative to the other.

Flowering

Overall, the timing of flowering (Fig. 2c) in *E. globoidea* was quite variable and provided a stark contrast to the synchronised flowering reported for *E. sieberi*. Individuals in the same stand could differ in flowering time by several months. For example, during 1990 at Site 1, a number of *E. globoidea* individuals flowered 2 months earlier than most others, as indicated by the August–September peak in Figure 4b. Further, at Site 2 in 1991, four neighbouring, dominant *E. globoidea* trees flowered most heavily in June, July, August and November respectively (Fig. 4c). These individuals may have been genetic relatives, considering their close proximity, but little overlap in operculum fall was recorded. Similar observations have been made concerning neighbouring *E. globoidea* trees on other sites in East Gippsland (Cummings 1990), so it seems that flowering in *E. globoidea* is sensitive to factors affecting individual trees, rather than the whole stand uniformly. Thus, the apparently conflicting reports in Table 1 may well each be correct for the populations they were based upon, and serve to further highlight the variable nature of flowering in *E. globoidea*. Florence (1964) measured similar variation in the flowering time of *E. pilularis* on Fraser Island sands, recording up to 5 months difference between individuals. Ashton (1975) and Griffin (1980) also noted significant, but less, within-stand variation in their studies of *E. regnans*, as did Gill (1966) for *E. cypellocarpa* L. Johnson (mountain grey gum).

Further variation was apparent in the flowering behaviour of individual *E. globoidea* trees. At Site 2 especially, the rate of fall

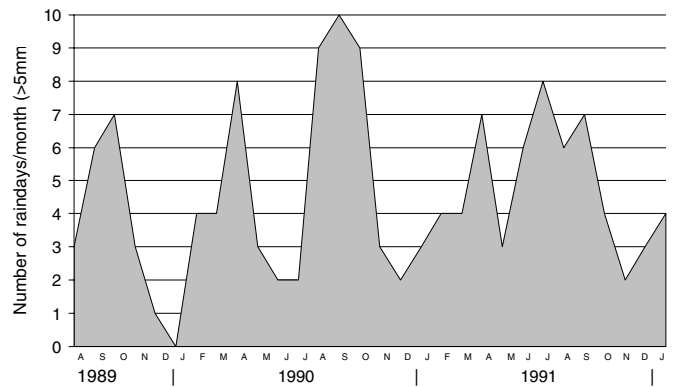


Figure 8. Number of rain-days per month with rainfall greater than 5 mm ('effective rainfall', after Byram and Keetch 1968) during 1989–92 at the SSP experimental area, Cabbage Tree Creek

of opercula from individuals was found to fluctuate, presumably in response to changes in factors affecting those individual trees. In one extreme case, two trees that began anthesis late in 1990 paused mid-way for some months, only to recommence in autumn 1991 (Fig. 4c). The resulting singular crop therefore displayed two different stages of development (Fig. 7). Cummings (1990) unknowingly reported the same flowering behaviour after observing *E. globoidea* individuals on coastal sands in East Gippsland to express 'two flowering seasons in the one (calendar) year'. Ashton (1975) recorded similar, but minor, carry-over of *E. regnans* umbellate buds to the following season, and Davis (1969) reported that umbellate buds which developed in summer on *E. stellulata*, as opposed to those which developed in early spring, would carry over from the normal period of anthesis (February to May) to flower at any time up to the following summer. Further, M. Moncur (CSIRO, Canberra, *pers. comm.*) observed *E. grandis* Hill ex Maiden (flooded gum) to commence flowering in late autumn, stop when low temperatures occurred and resume when temperatures increased again. Moncur also restarted flowering in *E. lansdowneana* F. Muell. & J. Brown (crimson mallee) by returning plants to a warm glasshouse in the middle of winter. Nevertheless, these carry-over mechanisms are unusual in eucalypts, as most species will generally abort unused reproductive material. For example, during years of light, irregular flowering in *E. diversicolor* F. Muell. (karri), umbellate buds that fail to flower are aborted (Loneragen 1979; Breidahl 1983).

Loneragen (1979) and Breidahl (1983) also reported an apparent correlation between drought and the likelihood of light flower crops in *E. diversicolor*. It is speculated here that soil moisture levels are also implicated in the variable flowering behaviour of *E. globoidea*. Soil moisture levels are dependent on both rainfall and the water-holding capacity of the soil. Sands (1983) and Flinn *et al.* (1980) both emphasised the low water-holding capacity of uniform sand profiles. A consequence is that rainfall is less effective in replenishing soil water on uniform sands than on other soil types (Squire 1982, 1983), and would therefore need to be more frequent to maintain the same levels of soil moisture and biological activity. Figure 8 shows the incidence of effective rainfall (raindays per month with rainfall >5 mm) at the SSP experimental area during the study period. Figure 9 shows the Byram–Keetch Drought Index (BKDI) (Byram and Keetch 1968) for Orbost, 25 km west of the SSP experimental area, for the

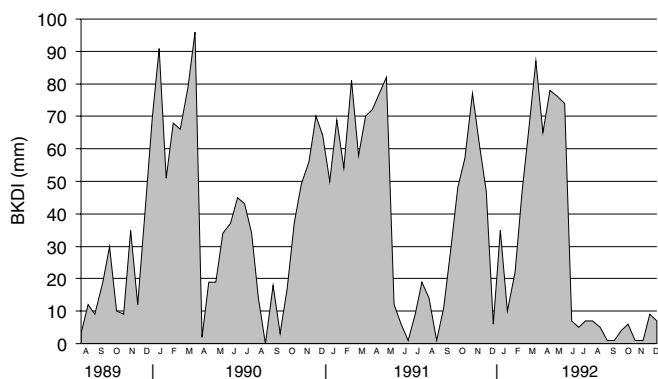


Figure 9. Byram-Keetch Drought Index (BKDI) (after Byram and Keetch 1968) during 1989–92 at Orbost, 25 km west of the SSP experimental area, Cabbage Tree Creek

same period. The figures indicate that the interruption to flowering at Site 2 in spring 1990, and the interruption to or cessation of flowering in spring 1991 (Fig. 4c), correspond to sharp decreases in rainfall incidence and sharp increases in BKDI. Further, they show that the increase in rainfall incidence and subsequent fluctuations in BKDI in autumn 1991 coincide with the recommencement of flowering in the carried-over buds.

That the general climatic conditions above did not affect all *E. globoidea* trees at Site 2 in the same way is possibly attributable to the variation evident in the sandy soils there, including surface and sub-soil drainage, and to the completion of anthesis in some trees prior to the onset of dry conditions. Likewise, the virtual absence of carry-over at Site 1 is possibly attributable to the more favourable soil moisture conditions associated with the gradational soil at that site. Florence (1964) perhaps recorded a similar effect where stands of *E. pilularis* on Fraser Island sands showed significant variation in the flowering time of individuals, but in general flowered four months later than stands of the same species on kraznozem and podsol soils at a similar longitude on the mainland.

It is not uncommon for flowering in eucalypts to show a dependence on rainfall. Mullin and Pswarayi (1990) detected a possible dependence of flowering in *E. camaldulensis* Dehnh. (river red gum) on rainfall or flooding regimes. Similarly, Thomson and Kube (1990) could not report a flowering season for *E. intertexta* R. Baker (gum-barked coolibah) on poorer sand sites in the Northern Territory because it flowered at any time of year in response to rainfall. Further, Breidahl (1983) confirmed the view of Loneragen (1979) that a correlation exists between drought and seed production in *E. diversicolor*. He found that, once inflorescence buds had been initiated in that species, anthesis depended upon high winter and early spring moisture levels. If those levels fell short, the buds failed to flower and were subsequently aborted.

Other genera are also known to express a flowering response to rainfall. Pozzera (1959), quoted in Mathews (1963), found that flowering in *Pinus pinea* L. (Italian stone pine) and *Cryptomeria japonica* (L. f.) D. Don (Japanese cedar) depended on rainfall incidence. Likewise, Paul and Marts (1931) recorded additional cone production in *P. palustris* Mill. (long-leaf pine) exposed to regular irrigation. However, further increases were produced with

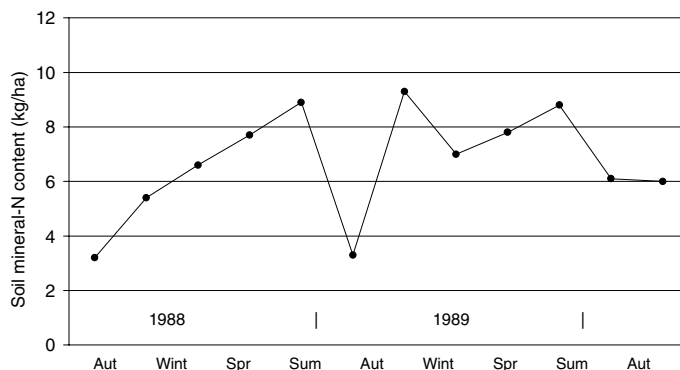


Figure 10. Temporal pattern of soil mineral nitrogen (N) content at Site 2, Cabbage Tree Creek (Raison *et al.* 1991)

the application of fertiliser, so it must be questioned whether nutrition could also be implicated in the flowering behaviour of *E. globoidea* at Cabbage Tree Creek.

For example, on the basis of the nutrient-vegetation relationship studies conducted by Lambert and Turner (1983), the total N-content of 2571 kg ha⁻¹ recorded for the 0–40 cm horizon of the uniform sand at Site 2 by Raison *et al.* (1991) is average for a typical site supporting *E. globoidea*. However, Raison *et al.* found that the rate of N uptake by vegetation at Site 2 (and elsewhere on the SSP experimental area) paralleled the rate of N mineralisation, suggesting that growth was limited by N availability. Further, it was found that, at Site 2 in particular, soil mineral-N content was reduced during drought periods (Fig. 10) to levels below the average found by Lambert and Turner (1983). It also seems that sharp increases in available N during autumn coincide with recovery of flowering in carried-over buds. Hence, it seems possible that N availability is also implicated in the variable flowering behaviour of *E. globoidea*.

The insects and birds seen visiting *E. globoidea* flowers during this study were similar to those observed for *E. sieberi*, but larger in number. This is possibly due to a greater flow of nectar and the more prominent nectaries in this species. In addition, feathertail gliders (*Acrobates pygmaeus* Gray), sugar gliders (*Petaurus breviceps* Waterhouse) and yellow-bellied gliders (*P. australis* Shaw) were observed feeding on the nectar of *E. globoidea* in heavy flower during winter nights at Site 2. At the completion of each such night's feeding activity, masses of flowers smeared with nectar were found scattered on the ground below the trees. The flowers had been bitten off, either individually, at the base of the floral receptacle, or as an umbel, at the peduncle. The use of different foods by foraging gliders follows an annual cycle that can be correlated with the phenological patterns of the forest (Kavanagh 1987), and Turner (1984) has shown that the feathertail glider is a regular and potentially important visitor to eucalypt flowers. However, the success of arboreals in achieving pollination in such instances is not known.

Griffin (1982) expressed the view that eucalypt species possessing a floral receptacle with a disc diameter of less than 5 mm could not be a viable source of nectar for arboreals. The disc in *E. globoidea* is usually 2–4 mm diameter, and Henry and Craig (1984) used this simplistic measure to explain the absence of

Table 3. Quantities and losses of reproductive material produced over four years by *Eucalyptus sieberi* L. Johnson and *E. globoidea* Blakely at Site 1 of the Silvicultural Systems Project experimental area, Cabbage Tree Creek. Coefficients of variation are in parenthesis (). Stand basal area was comprised of 67% *E. sieberi* and 33% *E. globoidea*.

Feature	<i>E. sieberi</i>				<i>E. globoidea</i>			
	1989	1990	1991	1992	1989	1990	1991	1992
Inflorescence buds aborted (no. ha ⁻¹) (A)	#	2 023 130 (24.6%)	3 084 473 (13.2%)	1 450 575 (28.9%)	#	#	#	#
Bract involucre fallen (no. ha ⁻¹) (B)	#	1 576 445 (28.2%)	926 263 (21.2%)	1 433 690 (31.4%)	#	#	#	#
Total inflorescence buds produced (no. ha ⁻¹) (A + B)	#	3 599 575 56.2%	4 010 736 76.9%	2 884 265 50.3%	#	#	#	#
Proportion of inflorescence buds aborted (%)	#							
Umbellate buds aborted (no. ha ⁻¹) (C)	2 081 386 (14.0%)	3 783 339 (15.1%)	4 255 320 (16.0%)	5 014 312 (12.2%)	2 973 204*	421 151*	624 330*	800 592 (19.0%)
Opercula fallen (no. ha ⁻¹) (D)	3 119 120 (22.9%)	10 488 655 (23.3%)	2 634 060 (23.0%)	6 051 295 (29.6%)	1 880 867 (34.4%)	130 405 (8.1%)	426 085 (11.0%)	326 112 (30.2%)
Total umbellate buds produced (no. ha ⁻¹) (C + D)	5 200 506 39.9	14 271 994 28.9	6 889 380 61.7	11 065 607 45.3	4 854 071 61.2	551 556 76.3	1 050 415 59.4	1 126 704 71.0
Proportion of umbellate buds aborted (%)								
Flowers aborted (no. ha ⁻¹) (E)	2 972 238 (16.4%)	8 316 656 (13.4%)	2 570 604 (14.1%)	6 066 850 (24.8%)	580 994 (43.4%)	128 801 (22.0%)	299 431 (27.1%)	200 327 (30.4%)
Capsules set (no. ha ⁻¹) (D - E)	146 882 95.3	2 171 999 79.3	63 456 97.6	0	1 299 873 30.9	1 604 98.8	126 654 70.3	125 785 61.4
Proportion of flowers aborted (%)								
Proportion of umbellate buds set as capsules (%)	2.8	15.2	0.9	0.0	22.0	0.3	12.1	11.2

#Data unavailable as sampling of the event was not possible or was incomplete.

*Estimated using a calculated proportion of umbellate bud fall from two consecutive crops.

gliders feeding on *E. globoidea* nectar in Boola Boola State Forest, Victoria, at the same time as they were commonly found feeding on nectar from species with larger floral receptacles. At the time of the Cabbage Tree Creek observations above, alternative food sources such as insects and sap flow would have been minimal (Henry and Craig 1984; Elliot and deLittle 1984), as would have been nectar from other species. Hence, it is suggested that, if alternative food sources had likewise been limited at Boola Boola, *E. globoidea* would have been used. Kavanagh (1987) provided further evidence that gliders will extract nectar from floral receptacles with disc diameters <5 mm, by finding that the population densities of yellow-bellied gliders and sugar gliders were correlated with the flowering intensity of *E. ovata* Labill. (swamp gum). The disc diameter of that species is commonly only 3–4 mm at the time of flowering (Costermans 1983; Willis 1986).

At the completion of flowering in *E. globoidea*, the stigma usually remained for at least 3–4 days beyond the fall of stamens (Fig. 2c). *E. sieberi* did not display this character as it commonly shed the stigma at the beginning of stamen fall. Moncur and Boland (1989) noted that the stigma abscinded from *E. melliodora* flowers up to 4 days before they shed their stamens.

Capsule development and seed dissemination

Following fertilisation, the floral receptacle in *E. globoidea* began to expand and push the depressed disc up towards the staminal ring. Thus, *E. globoidea* capsules assumed a truncate-globose appearance 5–6 months after anthesis, and attained their full shape after 12 months (Fig. 2d), although they remained green (immature) at this age. Cummings (1990) monitored seed viability for eight months following flowering in a number of *E. globoidea* individuals in East Gippsland. He found that viable seed was present on some trees as early as in March, and that viability generally increased throughout his study period. At Cabbage Tree Creek, the external valves on twelve-month-old *E. globoidea* capsules could appear dry and capable of releasing seed, but this drying was caused by an abscission layer which had formed at the point of connection of the valve with the internal ovary wall, which was still fleshy, green and incapable of naturally releasing seed. For seed to be released from such capsules on the SSP experimental area, either scorching of the capsules by fire or the death of the twig which supported them was required. Under normal circumstances, these capsules matured for a further 9–12 months, by which time they contained an average of 1.2 viable seeds per capsule (Bassett *et al.* in press). This is lower than the 1.3–1.8 viable seeds per capsule reported for *E. globoidea* (as *E. scabra* Dum.-Cours.) by Grose and Zimmer (1958). Gill (1966) reported that the additional 12 months maturation is also required for *E. obliqua* L'Hérit. and *E. radiata* Sieb. ex DC. to reach maximum viability, and Cunningham (1960) suggested the same for *E. regnans*.

At maturity, the capsules on *E. globoidea* were largely free of subtending leaves, and associated side branchlets had begun to senesce. The dissemination of seed largely

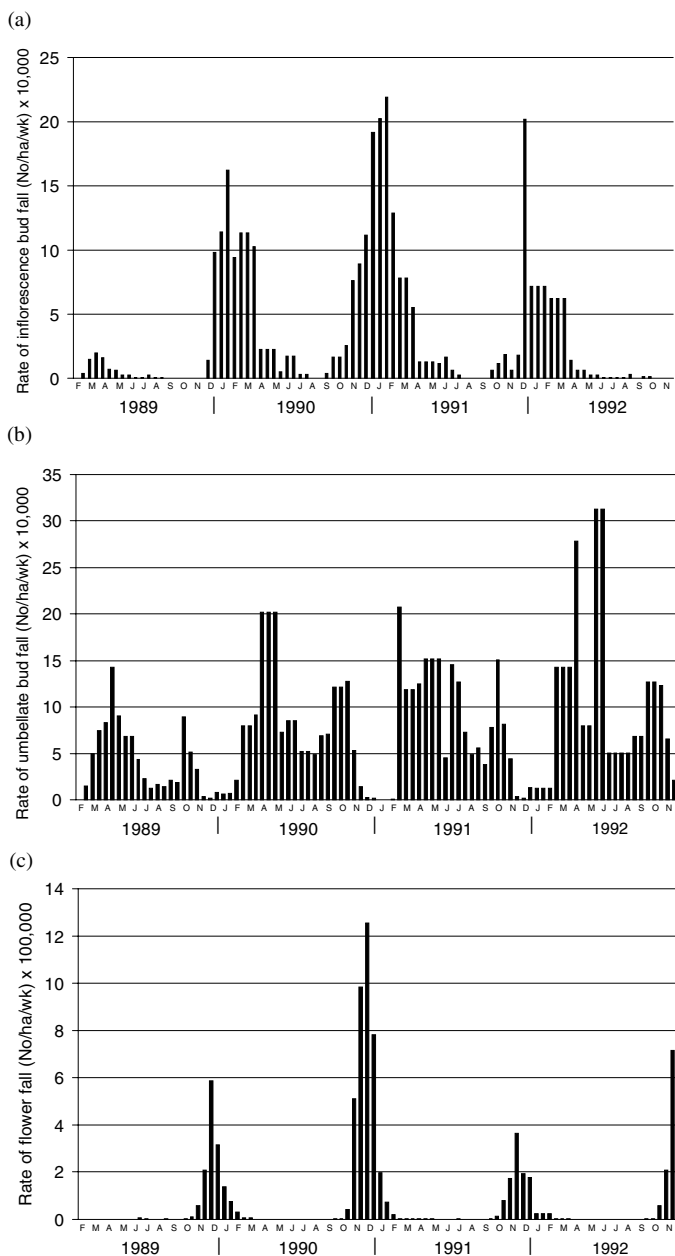


Figure 11. Rates of fall over time for (a) aborted inflorescence buds; (b) aborted umbellate buds; and (c) aborted flowers and immature capsules from *Eucalyptus sieberi* at Site 1, Cabbage Tree Creek

occurred in the second year following flowering, and although seedfall could not be differentiated between species at Site 1, inspection of capsules seemed to confirm an autumn seedfall. This is similar for *E. sieberi*, except that no winter seedfall was apparent in *E. globoidea*, based on frequent capsule assessments. Most capsules on *E. globoidea* had been shed two years after flowering, so that, usually, only two capsule crops were ever present. Occasionally though a fraction of a third, older crop persisted and became woody and embedded in the secondary xylem of the widening branchlets. Figure 6b shows that *E. globoidea* capsules were shed throughout the year, as were those of *E. sieberi* (Fig. 3c). Although it is likely that crimson rosellas may feed on seed from *E. globoidea*, no such feeding was observed during this study.

Quantities and losses in *Eucalyptus sieberi*

Estimates of the quantities and losses of reproductive material produced by *E. sieberi* over the four years studied at Site 1 are given in Table 3. The timing and rates of fall of aborted material (inflorescence buds, umbellate buds and flowers) are shown in Figure 11.

The number of inflorescence buds produced was relatively consistent over the three years for which data are complete, ranging from 2.88 to 4.01 million ha⁻¹ (Table 3). However, losses were high (50% to 77%), probably due, in part, to the relatively long residence time of inflorescence buds in *E. sieberi*. This would make them more susceptible than, for example, the short-lived inflorescence buds in *E. globoidea*. In *E. sieberi*, the loss of inflorescence buds generally began in September each year, as soon as the buds began to be initiated. The losses were heaviest at the time of bract shed through the summer months (Figs 3a and 11a). Over this period each year, falls were homogeneous across the stand: simple Cvs were relatively low for a native forest stand (Table 3). About 5% of inflorescence buds remained intact at the conclusion of bract shed and all of these were eventually aborted as well.

The number of umbellate buds produced each year (5.20–14.27 million ha⁻¹) was influenced more by the proportion of inflorescence buds lost than by the total number of inflorescence buds produced. Further, Table 3 indicates that the heavier crops of umbellate buds recorded in 1990 and 1992 were due, in part, to the greater numbers of umbellate buds initiated per inflorescence bud in those years (9.1 and 7.7 respectively, compared with 7.4 in 1991).

The proportion of umbellate buds lost in *E. sieberi* was quite variable between years (29–62%). Aborted umbellate buds generally began falling in December to January each year, as soon as bract shed had commenced, and peak rates of fall occurred in April, immediately following the peak in bract shed (Figs 3a and 11b). These initial losses probably occurred as the rapid swelling of the pedicel of each umbellate bud caused competition for space on the apex of the peduncle. This view is supported by the fact that the proportion of umbellate buds lost was greater for larger umbels than smaller umbels. An example of this also occurred in *E. globoidea*, and further supports this theory; i.e. the inflorescence scar study from both *E. globoidea* sites showed that umbels commencing with four umbellate buds lost only 25% of their buds on average, whereas umbels commencing with 12 umbellate buds lost 66% ($n = 4582$). Florence (1964) and Gill (1966) likewise attributed the loss of immature umbellate buds in the eucalypts in their studies to competition for space on the developing peduncle. Each bud may also be affected by competition for nutrients (Dr D.H. Ashton, *pers. comm.*). The loss of umbellate buds subsequently slowed over winter, as tree growth slowed (Raison *et al.* 1991) and insect activity decreased, but it increased again with the onset of warmer weather prior to flowering in spring each year (Fig. 11b). Insect abundance at Site 1 was at its greatest during this period, as indicated by collections of about 15 kg ha⁻¹ wk⁻¹ of insect frass. A large proportion of the umbellate buds aborted during this time displayed insect damage, usually in the form of a small entrance

hole with a larval instar inside. Cunningham (1960) recorded similar pre-anthesis losses of umbellate buds in *E. regnans*, and this pattern of bud fall, with two peaks, is common to *E. pilularis* (Florence 1964). Umbellate buds that failed to flower in *E. sieberi* were not carried over, rather, they were aborted in November–December after the completion of anthesis.

The quantity of flowers produced each year in *E. sieberi* ranged from 2.6 to 10.5 million ha⁻¹. Little can be concluded about the periodicity of that flowering though, as only four flowering seasons were observed. There is clearly considerable year-to-year variation, and there is some suggestion of a two-year periodicity (Fig. 3b), in keeping with tentative observations made by Squire *et al.* (1984). However, Bridges (1983) found no such periodicity in *E. sieberi*, as flowering intensity steadily decreased from year to year during his four-year study.

Cunningham (1957), Grose (1960), Van Loon (1966), Ashton (1975) and Loneragen (1979) found, in the various species they studied, that flowering intensity in the year following a heavy flowering season was small. At Cabbage Tree Creek, the heaviest flowering in *E. sieberi* was recorded in 1990 and was followed immediately by the lightest flowering, in 1991 (Table 3). Table 3 shows that the number of inflorescence buds initiated in each case was similar, yet the number of flowers produced was far smaller in 1991. Contributing factors were the larger proportion of inflorescence buds lost in 1991 (77 cf. 56% in 1990); the smaller number of umbellate buds initiated per inflorescence bud (7.4 cf. 9.1); the smaller total number of umbellate buds subsequently initiated (6.9 cf. 14.3 million ha⁻¹); and the considerably greater proportion of umbellate buds lost (62 cf. 29%) (Table 3).

The heavy losses of buds prior to flowering in 1991 could have been due to a need for recovery of carbohydrate reserves following the heavy flowering of the year before (Hall 1960), except that similar numbers of inflorescence buds were produced each year. Gill (1966) suggested that bud initiation is not influenced by carbohydrate reserves, but rather that these reserves influence the intensity of flowering and thus the numbers of aborted buds. The heavy bud losses recorded in 1991 may also have been due to random external influences, such as unfavourable environmental conditions, or to fluctuations in the populations of insects or other browsing organisms, perhaps related to the heavy flowering season the year before. Either could cause flowering intensity to be somewhat ad hoc, as observed by Grose (1957) in stands of *E. delegatensis*.

The data do suggest that unusually large crops of umbellate buds will experience lower proportional losses (Table 3). Insect browsing was a major cause of losses of umbellate bud in this study, hence predator satiation by the larger crops may well be a factor. Ashton (1956) noted similar occurrences in *E. regnans*, and Loneragen (1979) recognised that smaller bud crops in *E. diversicolor* were associated with larger proportional losses than were normally recorded. The largest proportional loss of umbellate buds during this study (62%) was recorded in 1991 (Table 3). This also happened to be the year in which the largest proportional losses of inflorescence buds, flowers and immature capsules occurred (Table 3), and, as indicated, it followed immediately after the heavy flowering season of 1990.

The proportional loss of flowers and immature capsules from *E. sieberi* at Site 1 was high and homogeneous across the stand during all four years for which data are complete (Table 3), suggesting that flowering is a consistently inefficient stage in seed crop development in that species. During 1992 and early 1993, the number of flowers estimated to have been aborted exceeded the number of opercula estimated to have fallen by 0.009% (Table 3). However, this is considered an acceptable margin of error and the result is taken to suggest that all flowers undergoing anthesis during 1992 were lost. Losses of such magnitude are not uncommon in eucalypts, as Loneragen (1979) recorded a flower loss of 91% in a stand of *E. diversicolor*, and Ashton (1975) measured losses of up to 89% in *E. regnans*. For *E. sieberi*, most aborted flowers and immature capsules fell in the period October–January (Fig. 11c), with the rate of fall peaking 1–2 months after anthesis (Fig. 3b). Most of the immature capsules that fell showed signs of fungal attack, insect attack, or damage caused by birds such as crimson rosellas and gang-gang cockatoos. These birds ripped apart the soft floral tube of the developing capsule in an effort to reach the immature seed and, in 1990–91, accounted for 5–10% of those capsules. Ashton (1975) likewise observed cockatoos and parrots ripping open green *E. regnans* capsules in an attempt to lick out the seed and, in so doing, spilling about 30% of the capsule contents.

The number of capsules that survived to reach the green, valvate stage, about five months after anthesis, varied from 0 ha⁻¹ in 1992 to 2.17 million ha⁻¹ in 1990. This represented 0.0% and 15.2%, respectively, of the umbellate bud crops initiated in those years (Table 3), and indicates that proportional losses can be significant for this species. In comparison, Ashton (1975) reported annual capsule sets of between 69 000 and 7.1 million ha⁻¹ for mature *E. regnans* forest over a five-year study period.

The results of the inflorescence scar study on *E. sieberi* at Site 1 are consistent with those above from the seed traps. Figures 12a and 12b indicate that 36% of the umbellate bud crop examined in the inflorescence scar study had been lost by July 1991, 3 months prior to the commencement of flowering in spring 1991. Peak umbellate bud fall occurs just prior to flowering (Fig. 11b) and, accordingly, the seed trap data indicated that 62% of that umbellate bud crop was lost (Table 3). The inflorescence scar study also indicated that average umbel size in the umbels remaining in July 1991, 3–5 months after the initiation of umbellate buds (Fig. 3a), had decreased from 8.4 to 5.4 umbellate buds per umbel, and that only 3% of the original umbels retained their full complement of umbellate buds. Further, average umbel size in the capsule crop resulting from flowering in 1990 was found to have decreased to 0.8 capsules per umbel by July 1991 (Fig. 12c), and that capsule crop was found to represent around 9% of the umbellate bud crop that would have flowered in 1990. This is consistent with the seed trap data, which indicated that 15% of the umbellate buds initiated in 1990 survived to capsule set in early 1991, and that further substantial losses occurred thereafter.

Figure 3c shows the rate of fall of all *E. sieberi* capsules during the study period. The proportion of these that had shed their seed naturally or had been caused to fall prematurely could not be determined. It was determined, however, that the valves were closed on an average of 27% of the capsules falling. Cremer *et*

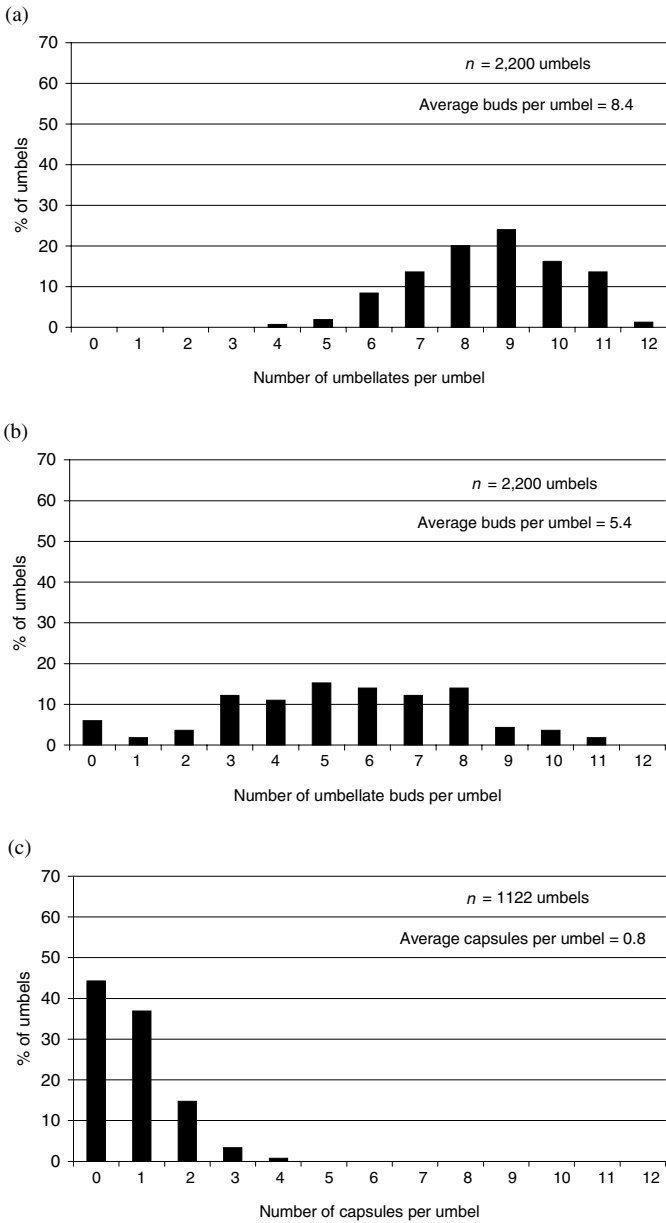


Figure 12. Frequency distributions (number per umbel) for (a) umbellate buds just initiated; (b) the same umbellate bud crop three months prior to anthesis; and (c) capsules approximately nine months post-anthesis, determined from a study of pedicel and peduncle scars on branchlets of *Eucalyptus sieberi* in July 1991 from Site 1, Cabbage Tree Creek

al. (1978) emphasised that the seed in such capsules should be regarded as being lost to regeneration. Small seedlings were sometimes observed emerging from the valves of fallen *E. baxteri* capsules at Cabbage Tree Creek, but the potential of these to survive was questionable. Some of the other *E. sieberi* capsules that fell were galled, hollowed out by the larvae of insects or showed signs of fungal attack, with mycelium evident in the valve slits. Eldridge (1963) and Drake (1974) indicated that losses due to these agencies could account for 20–50% of capsules in eucalypts. If such losses are considered in conjunction with those listed in Table 3, it would appear that a maximum of perhaps 10% (rather than 15%) of the umbellate buds that emerged from the bract involucre each year in *E. sieberi* developed seed that fell naturally.

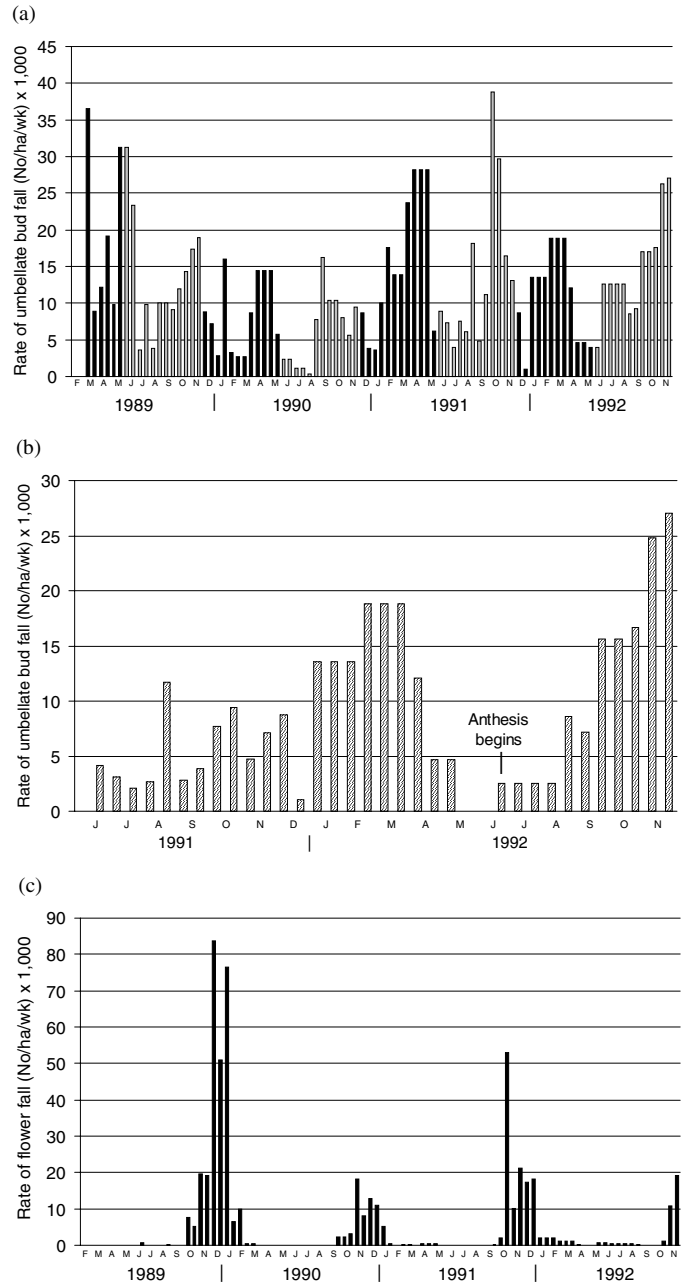


Figure 13. Rates of fall over time for (a) all aborted umbellate buds, where dark bars include buds from consecutive crops; (b) aborted umbellate buds from a single crop measured from the time it shed bract involucre in 1991 to its completion at anthesis in 1992; and (c) aborted flowers and immature capsules from *Eucalyptus globoides* at Site 1, Cabbage Tree Creek

Regardless, total annual seedfall at Site 1 averaged 1.71 million viable seeds ha⁻¹, with Cvs of 26–29%. Although the proportion that fell from *E. sieberi* is unknown, it is likely to have been at least equal to its proportion of stand basal area (67%, or ≈1.15 million viable seeds ha⁻¹). The capacity of *E. sieberi* to produce large quantities of seed was also reported by Bridges (1983) and Squire *et al.* (1984), and is evocative of the consistent and vigorous regenerating nature of the species in East Gippsland.

Quantities and losses in *Eucalyptus globoidea*

Estimates of the quantities and losses of reproductive material produced by *E. globoidea* at Site 1 are given in Table 3. The timing and rates of fall of aborted material are shown in Figure 13. Since the involucre bracts falling from *E. globoidea* could not be identified, the quantities and losses of inflorescence buds produced could not be estimated. Aborted leaf bud primordia may have contained some inflorescence buds, but these were not tallied. However, such losses are likely to have been small relative to those of *E. sieberi*, since the inflorescence buds in *E. globoidea* persisted for only 2–3 weeks.

The rates of fall of umbellate buds from *E. globoidea* are shown in Figure 13a. Those falling from the two crops held simultaneously for several months prior to flowering each year were tallied separately for the period June 1991 onwards only. This late adjustment to methodology occurred with the realisation that buds from these two crops could be largely distinguished by size. Hence, accurate data for the number of umbellate buds aborted and the total number of umbellate buds produced are available only for the crop that flowered in spring 1992 (Table 3). These data confirmed observations that from December to May of a particular year there appeared to be only one crop of umbellate buds in the crown, having been initiated the previous June and being likely to undergo anthesis the following spring. By June that year a second crop had been initiated and so from June to about November aborted buds from both crops were tallied from trap samples. It was determined that the larger proportion of these came from the crop about to undergo anthesis (about 60%), while the smaller proportion (about 40%) came from the crop just initiated (Fig. 13b). These proportions were used to estimate umbellate bud fall from the crops due to flower in 1990 and 1991 and, on this basis, Table 3 shows that the total number of umbellate buds produced by *E. globoidea* ranged from 0.55 to 1.13 million ha⁻¹. This is substantially less than the number produced by *E. sieberi* in any year, even when stand composition is considered. Losses were substantially higher than in *E. sieberi* too (59–76%), but they may not be entirely typical of *E. globoidea* as they occurred following a comparatively heavy flowering event in 1989 (Table 3).

Figure 13b shows that the rate of fall of umbellate buds from the crop due to flower in spring 1992 gradually increased following bract shed, and peaked in autumn several months later. This is somewhat different to the pattern in *E. sieberi*, where bract shed peaked during January–March and the loss of umbellate buds peaked soon after (Fig. 11b). As with *E. sieberi*, however, the rate of loss decreased through winter and subsequently increased again to peak just prior to anthesis. The buds lost at this time were commonly found to display insect entrance holes and to contain insect larvae that had emptied the buds of their contents. Some fungal mycelium and small fruiting bodies were also often evident on the exterior of the buds, but it was not apparent whether these were primary or secondary infections. Figures 13a and 13b show that the same patterns of fall occurred for umbellate buds in each of the four years monitored, with peak rates of fall in each of autumn and spring, and low rates of fall in winter.

The quantities of flowers produced by *E. globoidea* at Site 1 ranged from 0.13 to 1.88 million ha⁻¹ y⁻¹ and were substantially less than those produced by *E. sieberi* (Table 3). No conclusions

can be drawn about periodicity, though, as one comparatively heavy flowering season was followed by three light flowering seasons (Fig. 6a; Table 3). Notably, though, the heaviest flowering season was followed by the lightest flowering season, as in *E. sieberi*.

The proportional losses of flowers and immature capsules from *E. globoidea* at Site 1 were variable between years and usually somewhat less than for *E. sieberi* (Table 3). Figure 13c shows that the peak rates of loss occurred soon after anthesis (Fig. 6a). The comparatively small loss (31%) sustained during the heavy flowering year of 1989 could have been a result of predator satiation, or it could indicate the ability of this species to retain high proportions of initiated buds. It could be considered to indicate a different seed development strategy to that expressed by *E. sieberi*. But virtually all flowers and immature capsules were lost in the next year (99%; Table 3). Thus, capsule set ranged from just 1604 ha⁻¹ in 1990 to 1.30 million ha⁻¹ in 1989, representing 0.3% and 12.1% of the initial umbellate bud crops respectively. When stand composition is taken into account, the maximum capsule set recorded is not dissimilar to that for *E. sieberi*. Observations during this study, however, showed that the quantities of reproductive material produced and the losses experienced were much more variable between trees of *E. globoidea* than of *E. sieberi*; whereby some may have lost all their crop, while others very little. This is illustrated for operculum fall in Figures 4b and 4c and the high Cvs in Table 3. For example, during 1989, referred to as a ‘heavy’ flowering year for *E. globoidea*, the Cv between traps for flower fall was 43%, suggesting that a large proportion of aborted flowers may have originated from only a few individuals in the stand. Observations support this view as many individuals were seen to have either failed to flower or to have had sparse crops during this year.

As with *E. sieberi*, the results of the inflorescence scar study on *E. globoidea* at Site 1 were consistent with the results from the seed traps. The study showed that 53% of the umbellate buds initiated in 1990 had been lost by July 1991 and that umbel size in the umbels remaining had decreased from 7.7 to 3.6 umbellate buds per umbel (Figs 14a and 14b). In comparison, the seed trap data suggested that 59% of umbellate buds in that crop were lost prior to flowering (Table 3). The study also showed that the size of umbels remaining in the capsule crop resulting from flowering in spring 1990 had decreased to 1.5 capsules per umbel by July 1991 (Fig. 14c). The seed trap data suggested that 0.3% of these umbellate buds became set as capsules by July 1991 (Table 3).

The results from the inflorescence scar study in *E. globoidea* at Site 2 are different in two respects. Firstly, they show that initial umbel size was larger than at Site 1 (Figs 14a and 15a). Secondly, they show that it decreased rapidly from 15.2 to 9.1 umbellate buds per umbel, with 45% of the buds initiated having been aborted within about one month (Figs 15a and 15b). Losses did not appear to occur so rapidly at Site 1 (Figs 13a, 14a and 14b), where smaller umbel size may have induced less competition for space and nutrients between umbellate buds. However, the average size of umbels remaining in the umbellate bud crop initiated in 1990 and due to flower in spring 1991 at Site 2 was found to have decreased to 3.2 umbellate buds per umbel (Fig. 15c), more in keeping with the results from Site 1 (Fig. 14b).

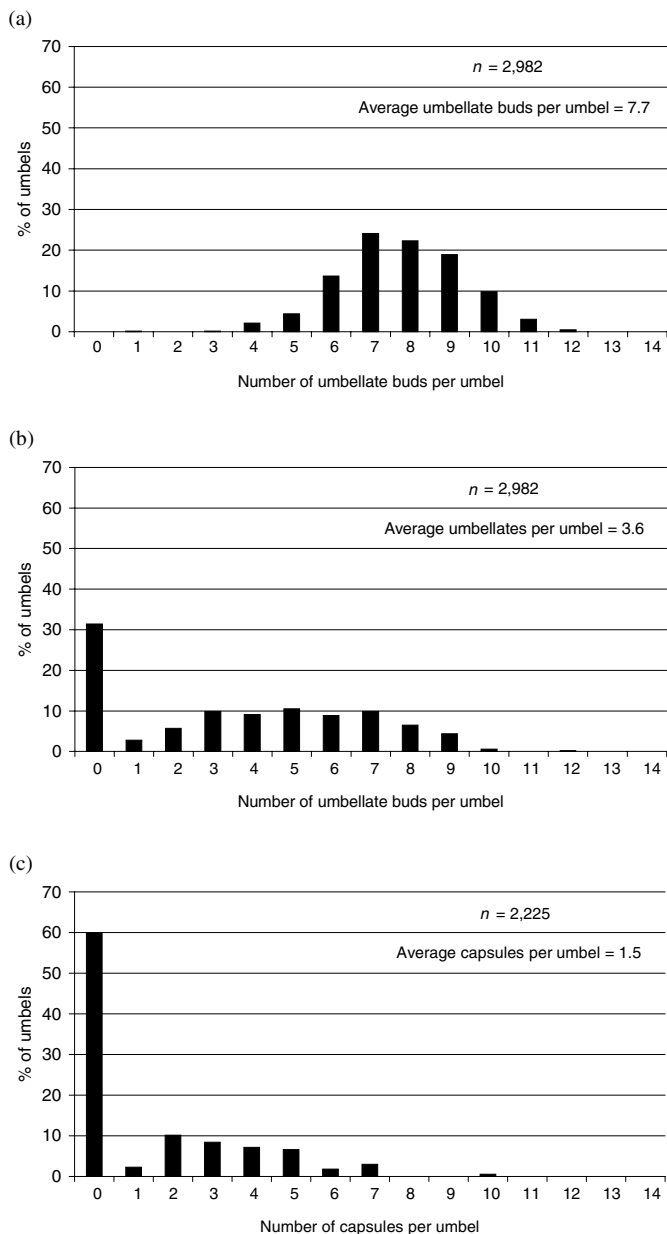


Figure 14. Frequency distributions (number per umbel) for (a) umbellate buds just initiated; (b) the same umbellate bud crop just prior to anthesis; and (c) the same crop following anthesis from *Eucalyptus globoidea* in July 1991 at Site 1, Cabbage Tree Creek

The destruction of seed by insects prior to its dispersal was more prevalent in *E. globoidea* than in *E. sieberi* during this study. Such damage was usually evidenced by small exit holes in the seed-coats or by the hollowed, enlarged shells that remained after the seed content or chaff had been eaten. Small grubs were often dislodged whilst inspecting this damage. Boland and Martensz (1981) found that losses due to insects accounted for an average of 0.6 viable seeds per capsule, or 20% of capsule contents, in *E. delegatensis* across New South Wales and the Australian Capital Territory. Further losses of seed in *E. globoidea* occurred when closed capsules fell due to abscission or mechanical damage. As in *E. sieberi* at Site 1, this amounted to 27% of capsules intercepted by the seed traps (Fig. 6b).

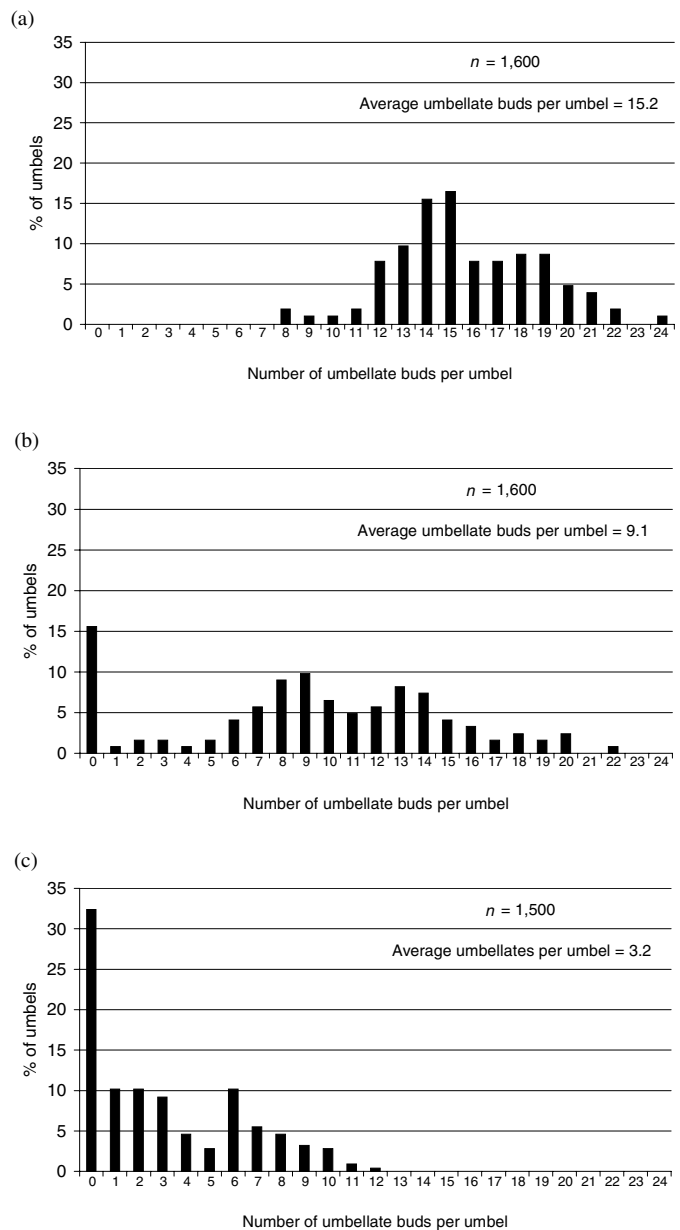


Figure 15. Frequency distributions (number per umbel) for (a) umbellate buds just initiated; (b) the same umbellate bud crop one month later; and (c) umbellate buds just prior to anthesis, determined from a study of pedicle and peduncle scars on branchlets of *Eucalyptus globoidea* sampled in July 1991 from Site 2, Cabbage Tree Creek

Silvicultural implications

The differences evident from this study in the development of seed crops in *E. sieberi* and *E. globoidea* highlight the need in silviculture to consider individually each species being managed.

The results clearly show that *E. sieberi* is well suited to regeneration operations that make use of retained trees for their seed. It is capable of producing large annual seed crops, and its capacity to store portions of up to six consecutive crops provides a buffer against years when the amount of seed produced is small. Furthermore, seed production in any one year in *E. sieberi* appears to be relatively uniform across the stand, so that any healthy, mature individual can reasonably be expected to carry sufficient

mature, viable seed to regenerate the area harvested around it at any time. For example, Bassett *et al.* (in press) physically counted 27 600 and 62 600 capsules on two selected *E. sieberi* trees, of 44 and 56 cm diameter breast height over bark respectively, and reported an average of 1.4 viable seeds per capsule in *E. sieberi* at the SSP experimental area. They also recorded average seed crops of 138 000 viable seeds tree⁻¹ (Cv 26%) on *E. sieberi* seed trees retained on two seed-tree coupes at the SSP experimental area. The recommended rate for the artificial sowing of *E. sieberi* seed following timber harvesting in Victoria is currently 150 000 viable seeds ha⁻¹ (Squire *et al.* 1984) and the usual number of seed trees retained in East Gippsland is 5 ha⁻¹ (Bartlett and Lugg 1993). It thus appears that only a cursory assessment of seed crops should be needed when selecting individuals of *E. sieberi* to be retained as seed trees.

The synchronised flowering behaviour of *E. sieberi* may be advantageous to the species, as it is known to maximise the potential for outcross pollination (Griffin 1980). Outcrossing tends to result in more prolific seed production, higher germinative energy and more vigorous offspring than geitonogamous pollination (Pederick 1976; Griffin 1980; Savolainen and Kärkkäinen 1992). These natural features of *E. sieberi* may well be factors contributing to the reportedly increasing proportion of the species in both fire and logging regrowth forests in East Gippsland (Forests Commission Victoria 1928; Incoll 1940; Loyn *et al.* 1980; Featherston 1985).

In contrast, *E. globoidea* is less suited to regeneration using seed trees, particularly on sites where variations in flowering time and quantity occur. Like *E. sieberi*, *E. globoidea* is capable of producing large annual seed crops, but the variation between trees and the fact that each new seed crop is shed within about two years of flowering means that the amount of seed present on an *E. globoidea* tree at any time can be highly variable. Thus, at a given time within a stand, it is highly probable that many *E. globoidea* trees carry little or no seed, and it is possible that neighbouring individuals can carry very large quantities of seed or no seed, respectively. Combined with the variation in flowering time that occurs, and the subsequent effects of that on seed crop maturation, these factors dictate that the choice of seed trees in *E. globoidea* needs to be based upon a careful assessment of each individual's seed crop, and it appears probable that supplementary seeding would be required in some instances.

The variation in flowering time in *E. globoidea* is likely to reduce the probability of outcrossing occurring and subject individuals to an increased rate of selfing and subsequent inbreeding depression. If selfing is possible in *E. globoidea*, it may result in poorer progeny (Pederick 1976) and place the species at a competitive disadvantage to others such as *E. sieberi*. Savolainen and Kärkkäinen (1992) found that increased selfing in natural stands resulted in selection against inbreds during the establishment of regeneration. Muona (1989) found average outcrossing rates of 0.7 in insect-pollinated eucalypts, whilst Griffin (1980) estimated that 51% of individuals in a stand of *E. regnans* had the potential to outcross due to synchronous flowering times. In the latter study, however, outcrossing largely occurred between groups of trees within the stand that flowered concurrently. No such group flowering patterns were evident in *E. globoidea* at Site 2. Instead, adjacent individuals often seemed to flower in isolation from each other, suggesting that the

outcrossing rate was likely to be somewhat less than 51%. This behaviour has the potential to result in the genetic isolation of individuals (Florence 1964) and may well encourage speciation in eucalypts (Gill 1966), perhaps as is evidenced by the polymorphic nature of *E. globoidea* and the taxonomic confusion that has surrounded it.

On the other hand, outcrossing between unrelated, distant individuals may be promoted in *E. globoidea* by the mechanisms of isolated synchronous flowering and the distant transfer of pollen by arboreal gliders, particularly during winter when few alternative food sources exist for them, although it is acknowledged that pollination by arboreal gliders is likely to be sporadic and less consistent than by other pollen vectors. The nightly home range of gliders observed at Site 2 varies from a 200 m radius for feathertail gliders (Fleming and Frey 1984) and 1.5 ha for sugar gliders (Suckling 1984), to 40–60 ha for yellow-bellied gliders (Henry and Craig 1984). Ellstrand *et al.* (1978) confirm the importance of tree spacing to outcrossing where animals are the pollen vectors.

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