

## Chapter 5

### Study Sites

Thirty four study sites were chosen on 16 properties in the southern half of the Northern Tablelands (see Fig 5.1). Most of the sites were between Uralla and Walcha with eight being close to or north of Armidale. They were chosen to display a full range of pasture and vegetation types, tree health, topography and capacity to regenerate naturally within a single ecological province which had been badly affected by dieback (Plate 5.1). It was decided to focus on the Gara-Chandler Plateau Province (Morgan, 1981b) with a few similar sites outside that system rather than spread the sites over the entire Tablelands for four main reasons: the area was one of the worst affected by dieback; because the properties were close together it was hoped they would form a nucleus from which the fruits of the research would spread; comparisons between sites would be easier within the same ecological province than across many; time and cost constraints.

Sites varied in size from 0.3 to 45 hectares with most being less than 8 hectares. A total area of about 150 hectares over the 16 properties was included in the study. Except for a few sites used only for phenology work (4a, 7, 15a) all sites were fenced off from stock by the landholders before or soon after the project began. Appendix VII includes details of each site.

#### TOPOGRAPHY, RELIEF AND ASPECT

Most of the sites were on gently sloping land of less than 5°. Some were on steeper hills or had steep portions with a slope of more than 10° (2a, 3a, 4a, 4b, 5, 12a, 12b). All sites were between 1,000 - 1,200 m above sea level except Malpas Dam (5) which is in an area 1,200 - 1,400 m above sea level. Most of the sites were positioned mid to upper slope and many also included a crest. Only four were in a lower slope position and only Malpas (5) included drainage lines. None were positioned in or near depressions or plains. Slopes were measured with an inclinometer and were classified according to McDonald *et al.* (1984).

#### GEOLOGY AND SOILS

Most of the sites had a similar geology, that is Palaeozoic metasediments. The exceptions to this were Birrhalee (2a) with porphyritic leucoademellite, Belhaven (1) with granite and basalt, parts of Malpas (5) with some basalt, Newholme (7) with adamellite and Spyway (11) with basalt.

Except for Yalgoo (16a) which had a yellow earth, all the sites on the metasediments had podzolic soils with red, yellow or grey-brown podzolics occurring on the upper slopes and gley or lateritic podzolics occurring on lower slopes. A few sites were so rocky their soils could only be classified as lithosols (eg. 12a). Sites on adamellite had grey podzolics, sometimes with laterite,

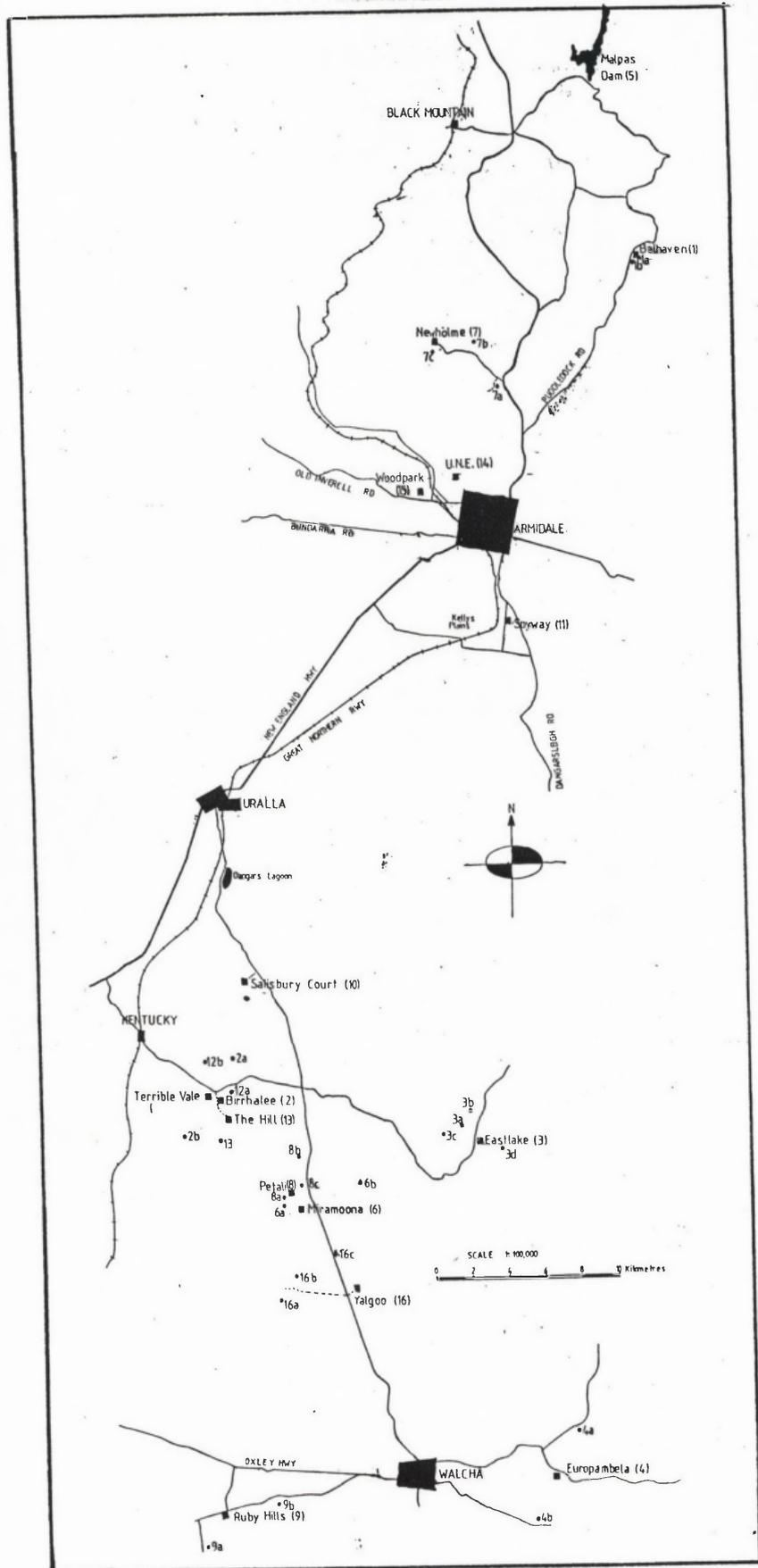


Figure 5.1: Location of Study Sites

while sites on basalt had chocolate or prairie soils.

### VEGETATION CLASSIFICATION

The three main structural classification systems for vegetation in use are those by Beadle and Costin (1952), Specht (1970) and Walker and Hopkins (1984). Beadle and Costin's system has recently been updated by Williams (ca 1987) who added the subforms: tropical, subtropical, warm-temperate, cool temperate, and dry rainforest; grassy sclerophyll forest; swamp woodland and wetland. Williams' system best describes the vegetation types observed on the sites in this study and was the one used throughout this thesis (see Table 5.1). The following minor changes were made:

- The term "savannah woodland" was replaced with Specht's "grassy woodland";
- The term "tree savannah" was replaced with Specht's "open woodland" although this was not confined to trees less than 10m high as used by Specht;
- Walker and Hopkins' terms "isolated trees" and "isolated clump of trees" were added - neither Williams nor Specht covered the situation of isolated remnant trees or clumps of trees in a pasture.

Pasture types were defined as native (comprising only native grasses and forbs), natural (consisting predominantly of native species but with a significant component of naturalized exotic species) and improved pastures (consisting of a major proportion of exotic pasture and weed species) (Lodge *et al.*, 1984).

### VEGETATION ON THE SITES

The sites covered almost the complete range of vegetation types found on the main Tablelands area, including grassy sclerophyll forest, tall woodland, sclerophyll scrub woodland, open woodland, scrub, and open grassland with few or no trees. Likewise a full range of pasture types was included from improved pasture to native although most of the sites had natural pasture with a few being completely native and some being improved. Most of the main eucalypt associations were represented in the sites (Appendix I).

### VEGETATION DENSITY

The density of the trees, shrubs and tree regeneration was measured on most sites by counting all the individuals (sometimes after dividing the site into zones). On the bigger sites or where trees and/or seedlings were too dense to count, plotless sampling was done using the quarter method (sites 9a, 16a) (Williams ca 1988). This involved selecting 9-20 points at random through the site (depending on its size). At each point four quadrats based on compass bearings were determined and the distance (metres) to the closest tree, shrub or seedling measured ( $s$ ) in each quadrat. Density could then be determined using the formula:  $Density = \frac{10,000}{(\text{mean } s)^2}$  units/hectare.

At two sites where regeneration was profuse circular quadrats of 10m<sup>2</sup> were used to estimate seedling density (sites 2a, 16a). Seedlings were frequently clumped together. In such cases the average density for the whole area was estimated.

Density was described using the system of Walker and Hopkins (1984) - see Table 5.2

Table 5.1: Structural Classification of Plant Communities

SUBFORM Williams†	DEFINITION	EQUIVALENT USING Specht (1970)	EQUIVALENT USING Walker and Hopkins (1984)
*Wet Sclerophyll Forest‡	Trees tall (20-70m) Mesomorphic shrub layer with tree ferns Grasses common or scarce	<i>Tall Open Forest</i> Trees > 30m Projective foliage cover 30% Dense understorey of shrubs, tree ferns Trees of forest form	<i>Very Tall Open Forest</i> or <i>Woodland</i>
*Dry Sclerophyll Forest‡	Trees small - medium (9-25m) Xeromorphic shrub layer Grasses and ferns scarce	<i>Shrubby Open Forest</i> Trees 10-30m Projective foliage cover 30-70% Trees of forest form Well defined xeromorphic shrub layer	<i>Tall Open Forest</i> or <i>Woodland</i>
*Grassy Sclerophyll Forest‡	Trees medium-tall (12-35m) Shrubs sparse, herb layer continuous of tussock grasses	<i>Grassy Open Forest</i> -as in shrubby open forest but with well developed grass layer and shrubs rare	<i>Tall or</i> <i>Very Tall Open</i> <i>Forest or Woodland</i>
		<i>Layered Open Forest</i> - as in shrubby open forest but shrubs and grass layer of equal importance	"
		<i>Low Open Forest</i> Trees 5 - 10 m (grassy, shrubby or layered)	<i>Mid-high Open</i> <i>Forest or Woodland</i>
*Tall Woodland§	Trees tall - medium Crown depth approximately equal to bole Grass layer abundant	<i>Tall Woodland</i> Projective foliage cover <30% Trees tall (>25m)	<i>Very Tall</i> <i>Woodland</i>
<i>Savannah</i> <i>Woodland</i> §	Trees low-medium Crown depth >> bole length Tussock grasses abundant Shrubs sparse	* <i>Grassy Woodland</i> Trees 10-25m, woodland form Projective foliage cover 10-30% Grass layer dominant	<i>Tall Woodland</i> or <i>Open Woodland</i>
*Sclerophyll Shrub Woodland§	Trees low-medium, often crooked Shrub layer prominent, Xeromorphic shrubs	<i>Shrubby Woodland</i> Trees 10-25m, woodland form Projective foliage cover 10-30% Shrub layer prominent	<i>Tall or Mid high</i> <i>Woodland or</i> <i>Open Woodland</i>
§		<i>Layered Woodland</i> As above but herbs and shrubs of equal prominence	<i>Tall or Mid-high</i> <i>Woodland or</i> <i>Open Woodland</i>
*Subalpine Woodland §	Tree crowns closely spaced Trees stunted (4-9m) Dense herb layer of tussock grasses and forbs Some shrubs. High altitudes.	?	<i>Low-Mid high</i> <i>Woodland or</i>
		<i>Low Woodland</i> Trees 5-10m Grassy, shrubby, or layered	
<i>Mallee</i> (Tall shrubland) Dry and Wet	Eucalypts with mallee growth form dominant	<i>Open Scrub</i> Projective foliage cover 30-70% Grassy or shrubby	<i>Closed mallee</i> <i>shrubland or forest.</i> <i>Mallee shrubland or</i> <i>open mallee forest</i> <i>Open mallee shrubland or</i> <i>mallee woodland</i> <i>Sparse mallee shrubland or</i> <i>open mallee woodland</i>
*Scrub (Tall shrubland thicket)	Dominant shrubs >2m high Mallee eucalypts not dominant	<i>Closed Scrub</i> Projective foliage cover >70% <i>Tall shrubland</i> dominated by multistemmed shrubs (2-8m) Projective foliage cover 10-30% <i>Tall open shrubland</i>	<i>Closed shrubland</i> <i>Shrubland</i> <i>Open shrubland</i> <i>Sparse shrubland</i> <i>Isolated shrubs</i> <i>Isolated clumps of shrubs</i>
*Grassland -hummock -dry tussock -wet tussock -sod tussock	Trees and shrubs absent Grasses dominant	<i>Hummock grassland</i> <i>Closed Grassland</i> <i>Tussock grassland</i>	<i>Hummock grassland</i> (closed-isolated clumps) <i>Tussock grassland</i> (closed-isolated clumps) <i>Sod grassland</i> (closed-isolated clumps)
<i>Savannah</i> (tree and shrub savannah)	Trees and shrubs present but very sparse Grasses dominant	* <i>Open Woodland</i> -scattered low trees, single or in clumps Projective foliage cover < 10% Grassy or shrubby	<i>Open woodland</i>
			* <i>Isolated trees</i> (> 20 diameters apart) * <i>Isolated clumps of trees</i> (> 20 diameters apart)

\* Terms used in this thesis †Based on Williams (ca 1987). Forms not included: Rainforest, saltbush, heath, feldmark, bog, herbfield, wetland. Subforms not included: Swamp sclerophyll forest, swamp woodland, mangrove scrub. Also not included are Specht's closed heath, open heath, low shrubland, closed herbfield or Walker and Hopkins' heath shrub, chenopod shrub, sod grassland, sedge, rush, forb, fern, moss, lichen, liverwort, vine. ‡Sclerophyll forest defined as sclerophyll trees dominant, spaced 1 diameter apart or less, open canopy, trees of forest growth habit. §Woodland defined as tree crowns widely spaced (1 - several diameters), trees of woodland growth habit.

Table 5.2: Vegetation Density Descriptions and Associated Structural Formations

Crown Separation	<i>Trees Dense or closed</i>	<i>Trees Mid-dense</i>	<i>Trees Sparse</i>	<i>Trees Very sparse</i>	<i>Trees Isolated</i>	<i>Trees in Isolated clumps</i>
Field Criteria	Touching - overlap	Touching - slightly overlap	Clearly separated	Well separated	Isolated	Isolated clumps
Crown Separation Ratio	< 0	0 - 0.25	0.25 - 1	1 - 20	> 20	> 20
<i>Structural Formations</i>						
	Closed Forest	Open Forest	Woodland	Open Woodland	Isolated Trees	Isolated clump of trees

From Walker and Hopkins (1984)

### SPECIES

Detailed lists were prepared of all vascular plant species on the sites

(see Appendix VII). This information was valuable in comparing sites and the relative ease of establishing trees on them.

### PREVIOUS LANDUSE OF SITES

All of the sites had been cleared at some stage for grazing, in some cases completely or almost completely. The trees growing on the forest sites were mostly regrowth from clearing for grazing 50-60 years ago. Generally these more timbered sites had been allowed to grow back because of their poorer soils and were used to provide timber or protection for sheep. Some sites had apparently never had their trees systematically ringbarked but their trees had simply been removed over time for fence posts etc. Most sites were still being used for grazing prior to this study.

### TREE HEALTH ON THE SITES

The general health of the eucalypts at each site was recorded at the beginning of the project using the Dieback Vitality Scale of Nadolny (1984) (Appendix II). These measurements were made on individual trees throughout the study. In addition an overall scheme was devised to classify the sites themselves with respect to tree health or decline, which incorporated the degree of clearing, the proportion of dead trees, and the general health of the living trees. These data were of value in the comparative studies on regeneration (Table 5.3).

Estimating the percentage of timber removal from the individual sites was difficult, for in all cases except one no early photographs were in existence. Hence the proportion of tree removal was based on the landholder's descriptions, the density of remaining trees and stumps and examination of early survey plans in the way described by Jeans (1978). Estimating timber removal was complicated on the two forested sites because they had regenerated following clearing 50-60 years previously, and the timber was probably more dense than had existed prior to clearing. Nevertheless the estimates allowed an expression of the obvious differences among the sites. All the sites originally were covered in forest or woodland and had been cleared completely or incompletely - none were originally treeless. It is likely that most of the sites had been cleared

Table 5.3: Site evaluation of tree decline and tree health

.....%	Trees removed/present	.....%	Trees poor
.....%	Trees dead	.....%	Trees very good.
.....%	Trees very poor;		
.....%	Trees good;		
<b>Key:</b>			
Tree dead	- tree completely dead with no chance of regrowth (DB 0*)		
Very poor health	- only epicormic growth on trunk, lower branches or upper branches (DB 1-4)		
Poor health	- 50-75% of crown dead (DB 5-6)		
Good health	- 25-50% of crown dead (DB 6-7)		
Very good health	- less than 25% of crown dead (DB 7-8)		
Most trees removed	- more than 75% of trees removed		
Many trees removed	- 25-75% of trees removed		
Most trees present	- less than 25% of trees removed		

\*DB values refer to Nadolny's scale (Appendix II)

during the last century; indeed some of them may have been cleared more than once.

Generally the health of the living trees remaining on the sites was good (DB 6-7),<sup>1</sup> irrespective of the proportion of trees that had been removed, had died, or were still alive. On only a few sites were the bulk of trees in very good health (sites 4a, 9a) or in very poor health (sites 6a, 10, 15a). The proportion of trees which were dead varied from over 3/4 on some sites to very few on others.

#### WEATHER DATA

Daily rainfall records were kept at each property. Monthly rainfall averages are plotted of a representative sample of these plus the median monthly values for Armidale in Fig 5.2. Despite some local discrepancies (see particularly the summers of 1983 and 1985) which could probably be explained by local storms, all of the sites followed the same basic trend.

Temperature records for each site were not kept. The mean monthly maxima and minima of Armidale are given in Table 5.4.

Table 5.4: Mean Monthly Maximum and Minimum Temperatures For Armidale N.S.W.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean Monthly Maximum Temperatures (°C)											
26.6	26.2	24.2	21.2	16.5	13.9	12.7	14.2	17.5	21.1	24.0	26.1
Mean Monthly Minimum Temperatures (°C)											
13.5	13.6	11.5	7.7	3.5	1.7	0.0	1.4	3.5	7.1	9.7	12.7

Source: Bureau of Meteorology (1975)

<sup>1</sup>"DB" values refer to the ratings according to the Dieback Vitality Scale (Appendix II)

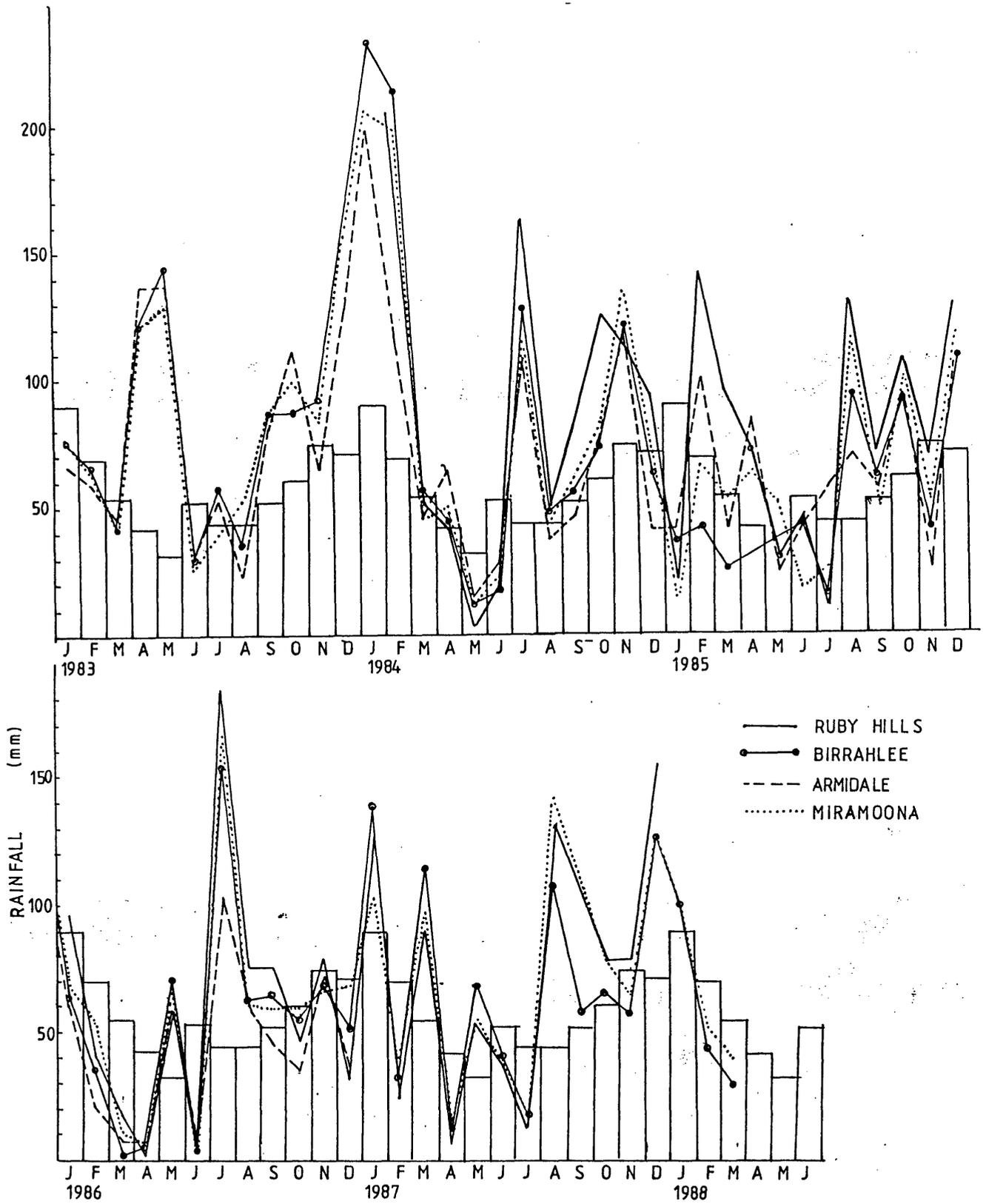


Figure 5.2: Monthly Rainfall for Representative Sites Plus the Median Rainfall of Armidale, 1983-88



Sclerophyll Scrub Woodland: Eurompambela  
Healthy trees, much regeneration.



Grassy Sclerophyll Forest: Yalgoo reasonably  
healthy trees, much regeneration.



Grassy Woodland: Petali Dam some dieback,  
poor regeneration.



Grassy Woodland: Eastlake healthy trees, good  
regeneration. Some pine trees planted.



Open Woodland: Salisbury Court bad dieback,  
little regeneration.



Isolated clump of trees: Miramoonna some  
dieback, little regeneration.

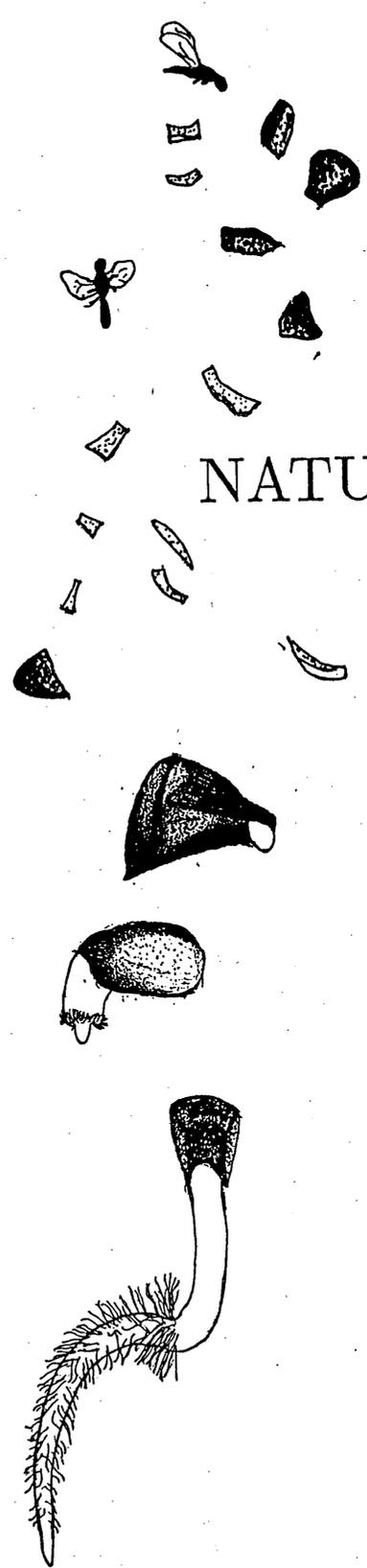


Isolated Trees: Terrible Vale bad dieback,  
no regeneration.

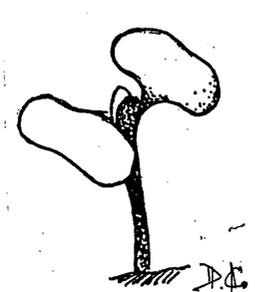
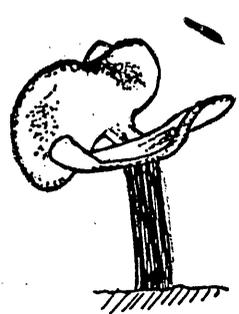
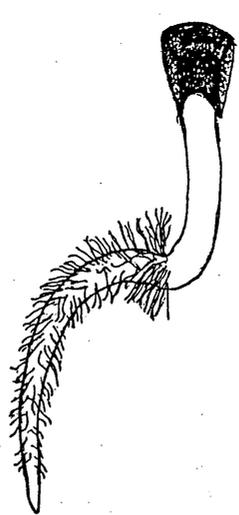
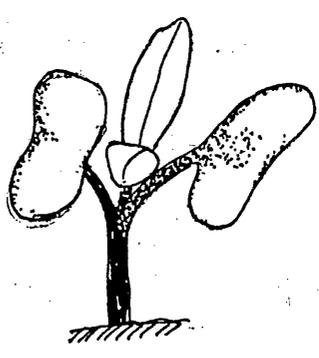
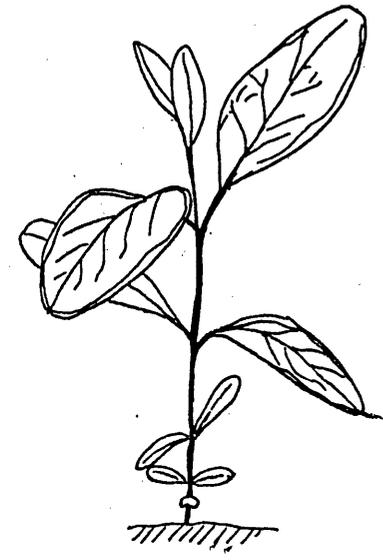


Grassland: Malpas Dam trees absent, no  
regeneration (white dots) are planted trees in  
milk cartons.

Plate 5.1: Representative Sample of sites, showing the range of tree density,  
health and regeneration



PART II  
NATURAL REGENERATION



## Chapter 6

### Flowering and Seedfall

The process of flowering and seedfall of local eucalypts was studied for two main reasons:

- To gain a greater insight into aspects of natural regeneration such as the factors affecting the seed crop, seedfall timing, and seedbed and weather conditions that favour seedling establishment.
- To use this information to gain a greater understanding of why natural regeneration has occurred in some places and not in others, to be able to encourage it where it is desired and to aid in the design of direct sowing techniques.

The flowering and seedfall process in *Eucalyptus* can be divided into a number of stages, all of which merge into the next but which nevertheless are relatively distinct. They are: **inflorescence buds - pin buds - buds - flowers - young fruit - mature fruit - seed shed - old empty fruits** (Cremer *et al.*, 1978; Boland *et al.*, 1980; Brooker and Kleinig, 1983; Plate 6.1).

#### 6.1 Flowering and Seedfall process in eucalypts

##### Flower Bud Formation

Flower development begins with the formation of inflorescence buds. Each one forms in the axil of a leaf and contains a cluster of tiny "pin buds". These are revealed when the two bracts which cover them fall off, after which they gradually grow into the flower buds ( Fig 6.1, Plate 6.1).

Flower buds are borne on a single stalk (the peduncle) in clusters of 3-11 or more, depending on the species. The clusters are cymose umbels (Pryor and Johnson, 1975) but are commonly simply called umbels. Each flower bud has one or two operculums (or caps) covering the sexual parts of the flower (Fig 6.1). The operculums represent sepals and/or petals and there are seven distinct types among the different subgenera – five types which are mono-operculate and two types which are bi-operculate. In the two common subgenera of the Tablelands, *Monocalyptus* (eg. snowgums, stringybarks, ashes) has one operculum only, representing fused sepals, while *Symphomyrtus* (eg. gums, boxes) has two operculums - the outer one representing fused sepals and the inner one representing fused petals. These two caps are shed together or separately depending on the species (Pryor and Johnson, 1975; Johnson, 1972; Williams, 1975a; 1975b).



New leaves with inflorescence buds forming in leaf axils



Inflorescence buds and pin buds 26.10.1988.



Young flower buds 7.12.1987.



Flower buds 1.5.1987.



Flowers and buds 26.10.1988.



Flowers 26.10.1988.



Old flower (just finished flowering) 26.10.1988.



Young fruit 7.12.1987.



Mature fruit and some opening to release seed 26.10.1988.

Plate 6.1: Stages in the flowering cycle of *Eucalyptus pauciflora* (snow gum).

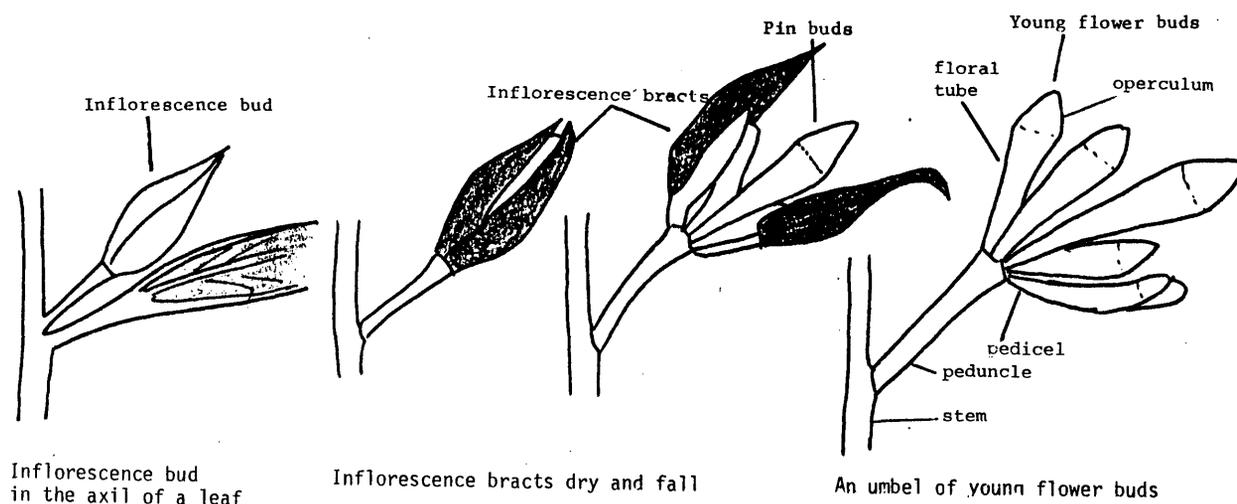


Figure 6.1: Inflorescence and Flower Buds of *E. nova-anglica* (New England peppermint). Collected from site 7c, 6 Dec. 1983

### Flowering and Pollination

Flowering occurs when the cap(s) fall off (anthesis) and the stamens spread to give the characteristic eucalypt flower (Fig 6.2, Plate 6.1). Mostly the flowers are bisexual. Some species have been found which have functionally unisexual flowers with reduced non-functional female parts, in which case the ratio of male flowers to bisexual flowers varies from tree to tree (Carr, Carr and Ross, 1971). The fruit from the unisexual flowers either do not develop or are deformed.

Pollination of eucalypts depends largely on insects although some birds and small mammals also visit the flowers and effect pollination (Turnbull and Doran, 1987a). In *E. regnans* bees, hoverflies, flies, wasps, beetles, ants, moths, and butterflies (amongst others) have been observed visiting flowers as well as nectar feeding birds (honey eaters) and small nectar feeding mammals, eg. lesser gliders (Ashton, 1975).

Pryor and Boden (1962) also found many insects (especially blow flies) pollinating eucalypt flowers. Indeed if insects were kept from the flowers, seed set did not occur. Loneragan (1979) reported the importance of honey bees in increasing seed production in *E. diversicolor* through good pollination. Christensen (1971a) observed interesting examples of bird pollination in many of the western Australian eucalypts (eg. *E. diversicolor*). The Purple Crowned Lorikeet is adapted to eating pollen, and follows the trees as they flower (which in karri is over an extended period), feeding on the pollen without damaging the flowers, and in the process pollinating many species. Wind pollination is infrequent in eucalypts and has only been reported as being significant in a few species with loose non-sticky pollen, eg. *E. tereticornis* (Pryor, 1979).

At the time of anthesis, anthers have mature pollen but the stigmas are not receptive until a few days later. In this way self-pollination is usually avoided, although pollen may still come from another flower on the same tree (Pryor, 1978; 1979). Species vary in their need for pollen from another tree – some being completely self incompatible, while others are able to set seed

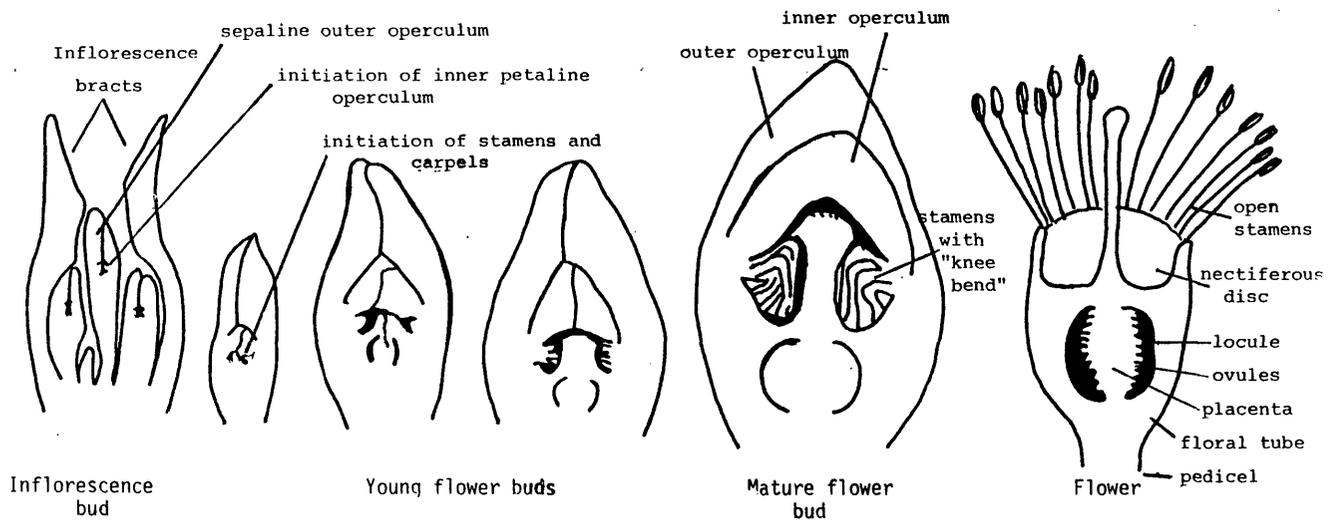


Figure 6.2: Development of the Eucalypt Flower - adapted from Davis (1968) for *E. melliodora* (yellow box)

when isolated (Pryor, 1979).

#### Fruit and Seed Formation

The stamens fall from the flowers after a few days but the style is persistent as the fruit develops. The fruit is an inferior capsule consisting of 3-5 locules, each locule containing 0-2 fertile seeds and 0-10 infertile seeds (chaff) - Fig 6.3. Chaff and seeds are borne in 2 rows in the subgenus *Monocalyptus* and 4-6 or more in the subgenus *Symphyomyrtus* (Boland *et al.*, 1980). In *Monocalyptus* species the chaff looks very similar to the fertile seed while in *Symphyomyrtus* the seeds are usually quite distinct, being black against the orange colour of the chaff. Seeds of most eucalypt species have been described by Grose and Zimmer (1958b) and Boland *et al.* (1980).

#### Seed Shed and Seed Dispersal

Seed shed occurs when a mature fruit dries out, either after being knocked from the tree or while still on the tree. Cremer *et al.* (1978) reported that the proportion of seed shed from fallen fruit is about 20% in *E. regnans* and 30-50% in *E. delegatensis*. Most fruit seem to open while still on the tree after a separation layer forms below the fruit, umbel, or twig, cutting the vascular supply to the fruit. What initiates this abscission layer is not really known, although there is some indication that it may be promoted by fire or drought and inhibited by wet or humid conditions (Turnbull and Doran, 1987a).

As the fruit dries the seeds separate from the placenta, the locules widen, the valves open and the seeds fall out. Soon after seedfall the fruit also falls from the tree, being only loosely connected by this stage (Cremer, 1961; 1965a; Christensen, 1971b). This type of seedfall occurs over an extended period unless stimulated by a fire or drought, both of which cause rapid desiccation of all fruit and rapid seedfall. Foresters manipulate fire to induce hastened seedfall and to get faster seedling establishment; the hotter the fire, the faster and more complete the

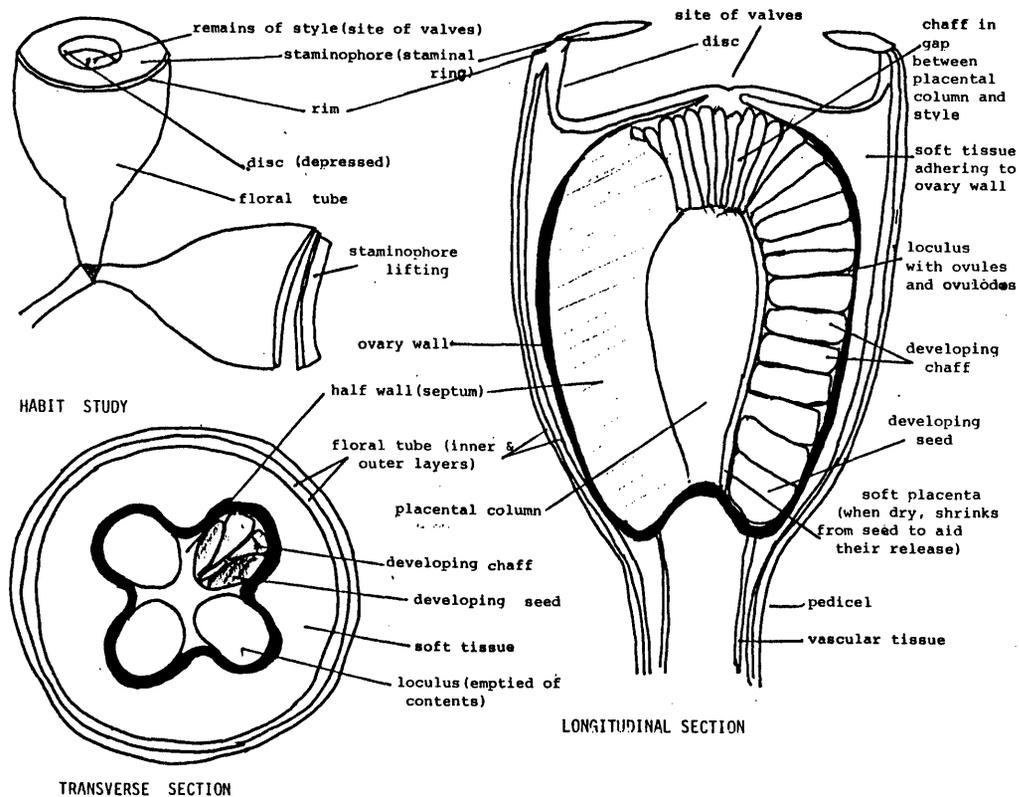


Figure 6.3: Young Fruits of *E. melliodora* (yellow box), collected from site 15a, 16 Dec. 1983

seedfall (2-10 days – Christensen, 1971b; Andersen, 1988a). A few species have circumscissile dehiscence, where instead of valves opening, a lid that will be shed completely is formed on top of the fruit, eg. *E. curtisii*, *E. setosa*, *E. botryoides* (Brooker, 1975).

The chief agent of seed dispersal is wind although other agents occasionally play a role (eg. water disperses the seed of *E. camaldulensis*). In studies on *E. regnans* most seed fell within a distance equal to the height of the tree and none was recorded beyond a distance equal to twice the height of the tree (Cremer, 1966a; 1977). Wind speed, seed weight, height of release, and the slope of the ground all influence the dispersal distance. Isolated trees, because of more exposure to wind currents, have seed dispersed further than trees within a stand. Cremer (1977) released seed of 15 species from a height of 40m in winds with speeds of 10km/hr. Dispersal depended on seed weight but most travelled 20-30m (eg. *E. viminalis* 29m). Heavier seed travelled 20m (eg. *E. globulus* while the lightest seed went 53m (eg. *E. deglupta*).

#### FACTORS INFLUENCING SEED PRODUCTION

Seed production varies considerably from year to year and from tree to tree. For example Pederick (1960) found great differences in seed yield of *E. obliqua* in different years, where the numbers of seeds varied between 31 and 115 per gram of seed plus chaff in three consecutive years while numbers of seed per capsule varied from 1.9 to 3.9. He attributed these differences to varying abundance of seed infesting insects. Cremer (1971) and Ashton (1975) in *E. regnans*, Floyd (1961) in *E. grandis*, and Fielding (1956) for *E. fastigata*, also recorded great variation in seed production between years (Fig 6.4).



Various factors have been found to influence flower abundance and the size of the seed crop. Fires and drought both result in lower seed crops. Conversely, heavier crops can result from high rainfall at bud formation or before (Floyd, 1961; Loneragan, 1979), although not always eg. Porter (1978) could find no correlation between flower abundance and rainfall for *E. sideroxylon*. Weather conditions at the time of flowering may also be important as Ashton (1975) found for *E. regnans*, and so can the availability of pollinating insects. In the year or years after a heavy crop a tree will often produce lighter crops. Young or suppressed trees produce less seed than mature ones (Cremer *et al.*, 1978). Trees near the edge of a stand frequently have heavier crops than trees within a stand and genetic differences between individuals account for a great deal of variation in seed crops.

Insect attack of flower buds can reduce flower crops considerably and damage to seed while it is still in the fruit is common. For instance, Boland and Martenz (1981) found about 20% of seed of *E. delegatensis* destroyed by a small wasp (*Megastigmus* sp.) as well as by other insects. This damage was widespread, occasionally reaching 80%, and also occurred in other species. The wasps lay their eggs in the young ovules and the grubs emerge and eat the embryo, leaving the seed coat. Andersen (1988b, 1989) found that many previous studies had underestimated seed losses due to insect predation and that it may be as high as 60-70%. The insects reduce the number of seed per fruit and the viability of the seed. Damage by birds, (eg. parrots chewing the fruit), and insect galls on flower buds have also been reported (eg. Cremer *et al.*, 1978). Fungal and insect damage of seed was reported by Drake (1974) in *E. crebra* and other species, affecting up to 20-50% of seed on some trees. Drake (1981a) found fungal damage to be fairly low (1-4%) in most trees examined of *E. melanophloia*, *E. crebra*, *E. populnea* and various hybrids, while about 6-11% of seed was damaged by insects. The hybrid *E. melanophloia* x *crebra* in contrast lost 33% of seed to insects. A proportion of seed is also aborted. Aborted seed appears collapsed compared with viable seed, but is different from chaff. Drake (1975) found 3-8% of seed in 7 species of box and ironbark to be lost in this way.

## 6.2 Review of phenological studies of eucalypts

“Phenology is generally described as the art of observing life phases or activities of plants and animals in their temporal occurrence throughout the year. These studies permit a phenological calendar to be constructed and superimposed on the astronomic or civil calendar...” (Leith, 1970)

Plant phenology can be depicted descriptively or analytically (Leith, 1970). In the descriptive methods the life phases of the plant are presented in a “phenodynamic strip” with the relative durations of each phase being shown. This technique has been used by Cremer (1971) to illustrate the phenology of *E. delegatensis* and by Loneragan (1979) for *E. diversicolor*. In the quantitative methods, accumulated quantities of each life stage (eg. number of flowers) is graphed against time. This technique has been used to illustrate the phenology of different eucalypts by Dexter (1967), Ashton (1975), Porter (1978) and Griffin (1980).

In this thesis most of the phenological data have been depicted using a modified version of Cremer (1971), in phenodynamic strips, which show what happens on the trees and when. Most of the figures also incorporate crude estimates of the relative quantities of each life stage. Seedfall has been treated more quantitatively. In many phenological studies all the life stages of the plant are illustrated (Leith, 1970). While this is suitable for short lived plants, for trees it is more usual to focus on flowering and seedfall, and leaf growth and death, over a few years only.

Detailed phenological studies in eucalypts have largely concentrated on the important timber species, most of which grow in moist forests, while the woodland species common in grazing country have largely been neglected. Fig 6.4 summarizes the available information for the seven species on which most work has been done. Most of these are in the subgenus *Monocalyptus*.

In eucalypts the length of each stage in the flowering cycle and the time of flowering and seedfall vary between species and between subgenera (as well as between individual trees and sites). In particular *Monocalyptus* species are characterized by very long development times, with inflorescence buds, flower buds and young fruit all taking one year to develop, fruit remaining on the tree for 1–2 years (or more) and the total time taken from bud initiation to seedfall being 4–5 years (Fig 6.4). Consequently a tree may have more than one crop present at one time. It is common for example on trees of *E. pauciflora* or *E. diversicolor* to find inflorescence buds, flower buds, young fruits and 1–2 crops of mature fruits, all present at one time (Fig 6.4).

*Symphomyrtus* species, in contrast, are much quicker in their development. Flower buds only take a few months to form, and are present for only 9–12 months before flowering. Fruits take less time to mature and seed has mostly fallen 12–18 months after maturation. Therefore there is no<sup>long</sup> accumulation of seed crops in the canopy. Usually by the time a crop has matured, the previous one has fallen (Dexter, 1967). Species of *Angophora* are faster still, completing bud initiation to seedfall in under five months (Prakash, 1969), while *E. deglupta* can initiate and complete two seed crops within a year (Turnbull and Doran, 1987a).

Flowering times vary among species. Of the seven species in Fig 6.4, *E. pauciflora*, *E. delegatensis* and *E. fastigata* flower in summer, *E. camaldulensis* flowers in autumn and *E. grandis*, *E. regnans* and *E. diversicolor* flower in autumn–winter. Among the eucalypts generally it is possible to find species flowering in every month of the year (Clemson, 1985).

The time of flowering can vary considerably within a species, depending on where individual trees are growing, their age, weather conditions etc. For example trees of *E. regnans* at lower altitudes flower earlier than those at higher altitudes and younger trees flower earlier than older ones (Ashton, 1975). Milder seasons can lead to earlier flowering. Ashton (1975) found that finishing and starting times varied by 3–4 weeks in *E. regnans* between individuals and between localities and that the peak flowering time varied between April and June in different trees (most had their peak in May). Griffin (1980) also found variation in *E. regnans* in flowering times with the peak flowering occurring in late March in 1979 and early March in 1977, the overall flowering peaking up to two months earlier than the trees observed by Ashton (1975) – which were in a different locality. He also observed that trees with a similar phenology clustered together.

Length of flowering is another factor with a great deal of variation between and within species. Some species have a fairly short well-defined flowering period (eg. *E. camaldulensis* – Fig 6.4) while others flower over an extended period. Individual *E. diversicolor* trees may flower for six months with a 2–3 month peak (Loneragan, 1979) while *E. sideroxylon* can flower in all months of the year with a minor peak in March and major peak in July–August, the start and length of flowering varying between localities (Porter, 1978). Individual flowers last 1–2 weeks in *E. regnans* (Ashton, 1975).

Seedfall mainly occurs in late summer–autumn in *E. diversicolor*, *E. delegatensis*, spring–summer in *E. camaldulensis* (to coincide with receding flood waters), and spring in *E. grandis* (Fig 6.4). Seed is shed earlier by fruit on small branches which die after leaf fall than fruit on main branches which continue to grow (Loneragan, 1979).

### 6.3 Phenology of selected Northern Tablelands species

#### 6.3.1 Methods

A total of 117 trees of 13 eucalypt and angophora species were monitored to follow their flowering and seedfall patterns over 3–4 years. The species were *Angophora floribunda*, *E. blakelyi*, *E. bridgesiana*, *E. caliginosa*, *E. dalrympleana*, *E. laevopinea*, *E. melliodora*, *E. nicholii*, *E. nova-anglica*, *E. pauciflora*, *E. radiata*, *E. stellulata* and *E. viminalis* (Table 6.1). Most of these species are common, widespread species on the Tablelands and all have suffered extensively from dieback, although to varying degrees.

In the early period of the study only one tree of each species per site was monitored. Trees were climbed and branchlets containing buds and/or fruits were tagged with aluminium labels. Numbers of umbels and buds etc. were counted every 1–3 months. Samples varied from 170–2,000 buds per tree but were usually 200–400. Seed traps were made from fine nylon mesh on a wooden frame and were hung from a lower branch of each tree to catch seed, fruits etc. (Appendix IV). They were emptied with a portable vacuum cleaner.

As the study developed and 12 new sites and 100 new trees were added these techniques were modified and monitoring of the earlier trees was discontinued. Trees were marked with plastic flagging tape, usually 3 of each species per site. Trees which were healthy and reproductively active were preferred. Observations were made on the various flowering stages on the tree 3–4 times per year. Crop size of each was estimated on a three point scale with the assistance of photographs (Plate 6.2). Tree health was estimated using the dieback scale designed by Nadolny (1984) (Appendix II). Tree height was measured using an Haga inclinometer. All this information was recorded on standardized data sheets (Appendix III). Seed trap design was modified also. New traps were made from plastic buckets with nylon in the bottom (Appendix IV). These were tied between two steel fence posts – 2 seed traps per tree. Chicken netting was placed over the top to prevent damage to the mesh from falling twigs. These traps proved to be

Table 6.1: Numbers of trees monitored for phenology and seedfall of each species on each site. The upper number in each square is the number of trees monitored at the particular site of that species. The lower number is the number of trees that were fitted with seed traps.

SITE	<i>Angophora Floribunda</i>	<i>Eucalyptus Blakei</i>	<i>E. bridgesiana</i>	<i>E. caliginosa</i>	<i>E. daalrympiana</i>	<i>E. laevopinea</i>	<i>E. melliodora</i>	<i>E. nicholii</i>	<i>E. nova-anglica</i>	<i>E. pauciflora</i>	<i>E. radiata</i>	<i>E. stellulata</i>	<i>E. viminalis</i>	TOTAL
Belhaven 1a, 1b														0
Birralee 2a														0
2b	1/-		1/-									3/2	3/2	8/4
Eastlake 3a				2/0		1/0	3/1							6/1
3b		1/-			3/1				3/1	3/1	2/-			12/3
3c, 3d														0
Europambela 4a											3/1			3/1
4b														0
Malpas 5														0
Miramooona 6a		3/-					4/1							7/1
6b													3/1	3/1
Newholme 7a		1/1	1/1				1/1							3/3
(1982-84) 7b									2/2					2/2
7c		1/1	1/1				1/1						1/1	4/4
Petal 8a		3/1	2/-		1/-	3/1	3/-							12/2
8b														0
8c		2/2					1/1							3/3
Ruby Hills 9a			1/-	3/1				2/-		4*/1	4/1			14/2
9b														0
Salisbury Court 10		3/-											3/-	6/-
Spyway 11										1/-				1/-
Terrible Vale 12a										3/1				3/1
12b	3/-			3/2										6/2
The Hill 13														0
U.N.E (1982-84) 14	2/-									2/2				4/2
Woodpark (1982-84) 15a	1/-	1/1					1/1						1/1	4/3
15b		1/1												1/1
Yalgoo 16a			2/-			3/1	1/-							6/1
16b									4/2	3/1		3/1		10/4
16c														0
Total No. Trees 1982-84	3	4	2	0	0	0	3	0	2	2	0	0	2	18
Total No. Trees 1985-88	4	12	6	8	4	7	12	2	7	14	9	6	9	100
Total No. Seedtraps 1982-84	0	4	2	0	0	0	3	0	2	2	0	0	2	15
Total No. Seedtraps 1985-88	0	3	0	3	1	2	3	0	3	3	2	3	3	26

much better than the earlier ones which were too shallow and unstable.

Collecting area of one bucket = 453 cm<sup>2</sup> Collecting area per tree (2 buckets = 905 cm<sup>2</sup>).

### 6.3.2 Results and Discussion

The flowering cycle of each of the species studied is summarized in Fig 6.5 together with data from selected closely related species from the literature. Species are arranged in phylogenetic order (after Pryor and Johnston, 1975). Clear patterns are evident, with closely related species having a similar flowering cycle.

#### a) Flower bud initiation

Inflorescence buds were first visible in most species in early summer (December), appearing with the new flush of leaf growth. Some species were observed initiating buds in November also (*Angophora floribunda*, *E. caliginosa*, *E. laevopinea*, *E. nicholii*, and *E. pauciflora*). *E. radiata*, *E. stellulata* and *E. viminalis* possibly initiated their buds in mid-summer.

There are few published descriptions of when flower buds are initiated in the species I examined. My results agree with those of Clemson (1985) for *E. blakelyi*, *E. caliginosa*, *E. melliodora*, *E. nova-anglica*, *E. viminalis* and *Angophora floribunda*; Davis (1968) for *E. melliodora*; Prakash (1969) for *Angophora floribunda*; and Clark and Dallwitz (1974) for *E. blakelyi*. Davis (1969) recorded that inflorescence buds of *E. stellulata* on the tablelands are initiated in September to December, which may mean my observations were inaccurate for this species. Inflorescence buds of *E. stellulata* are very small and easily confused with leaf buds so it may be that I missed their early initiation. The same could have happened for *E. radiata* and *E. viminalis* for which I was unable to get good observations of early bud initiation, although my results for *E. viminalis* agree with those of Clemson (1985) who reported that *E. viminalis* buds were formed in mid summer.

#### b) Flower bud development

Although flower buds are initiated in about the same period for all species, the time taken for the buds to develop and the way they develop is markedly different. Bud development, as with other aspects of the flowering cycle follows a distinct pattern between subgenera (see Fig 6.5, Table 6.2).

The flower buds of *Monocalyptus* species all take 2–2½ years to develop before flowering – with summer flowering species taking less time (about 2 years) than autumn flowering species (close to 2½ years). In the stringybarks pin buds emerge quickly with the new flush of growth and the flower buds slowly develop over about two years before flowering. In the ashes, sallees and true peppermints however, the pin buds do not emerge until the November–December period, one full year after they are first initiated. Pin bud emergence coincides with the next crop of inflorescence buds being formed with the new flush. The buds then take a further year or so



*E. nova-anglica*  
Heavy crop of flowers.



*E. radiata*  
Heavy crop of flower buds.



*E. viminalis*  
Heavy crop of flower buds.



*E. radiata*  
Heavy crop of young fruit.  
Moderate crop of flower buds.



*E. laevopinea*  
Heavy crop of flower buds.  
Moderate crop of mature fruit and young fruit.

Plate 6.2. Examples of crop sizes of some eucalypt species.

- |               |   |   |
|---------------|---|---|
| Heavy crop    | - | most potential sites for fruits or buds are filled; crops are massed. |
| Moderate crop | - | crop is easily seen, throughout the crown but not massed.             |
| Light crop    | - | crop is only very scattered; buds or fruit often hard to see.         |

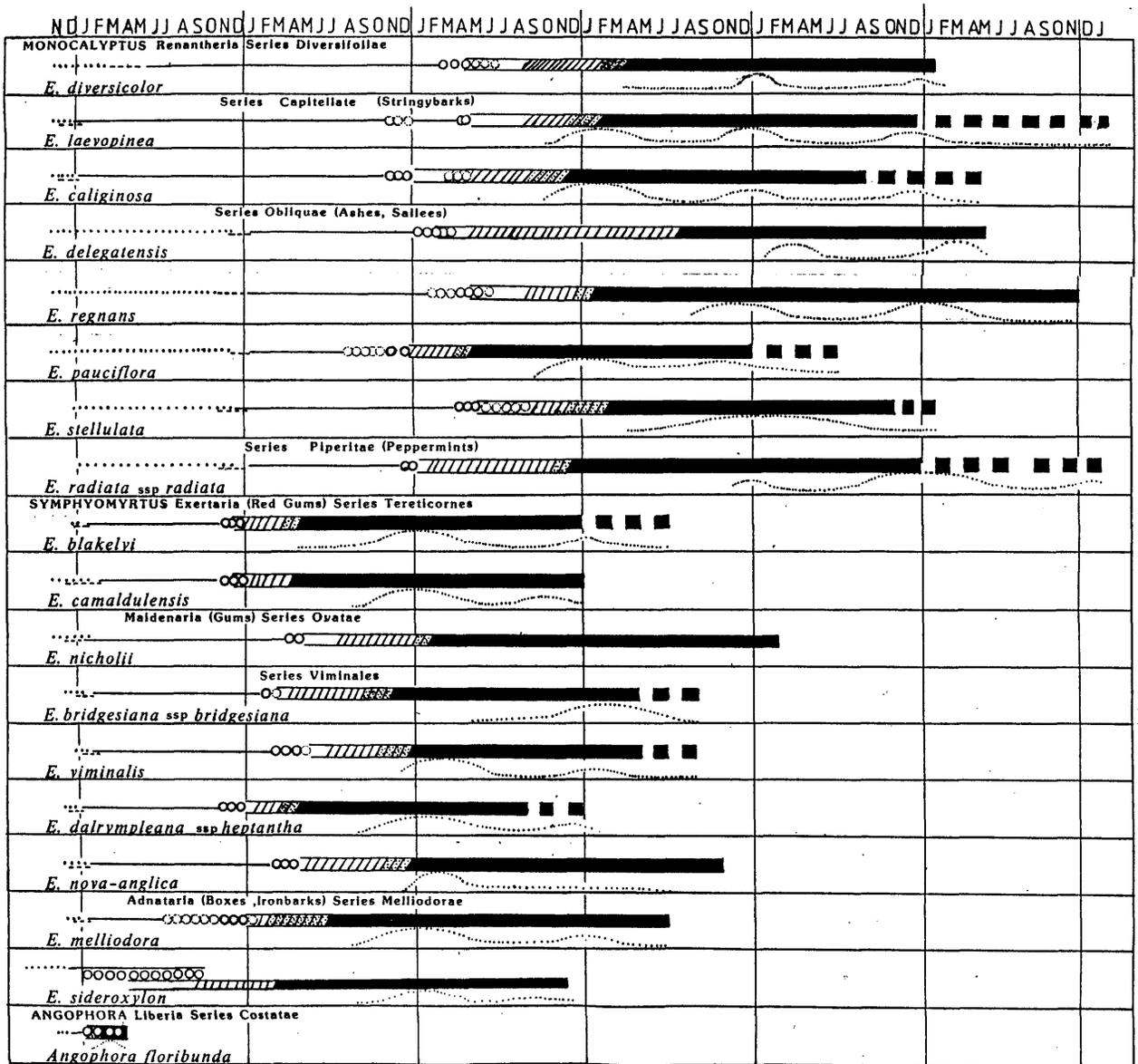


Figure 6.5: Flowering cycles of thirteen *Eucalyptus* species of the Northern Tablelands and some of their close relatives. Species are arranged in phylogenetic order after Pryor and Johnston (1975). + Insufficient data. The following species have been compiled from the literature (see Fig 6.4) – *E. diversicolor*, *E. delegatensis*, *E. regnans*, *E. camaldulensis*, *E. sideroxylon*. Symbols as in Fig. 6.4)

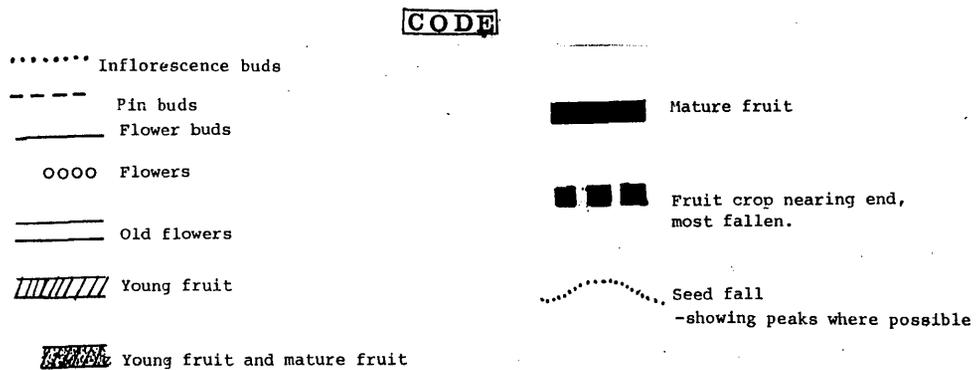


Table 6.2: Length of phenological stages for the twelve common *Eucalyptus* and one *Angophora* species of the Northern Tablelands examined in this study.

Species	Length of time for flower bud stages			Total bud time before flowering (mth)	Length of time for fruiting stage		Total Cycle length: bud initiation to seedfall (years) +	
	Inflorescence buds (mths)	Pin buds (mths)	Flower buds (mths)		Fruit maturing time (months after flowering)	Length of time fruit held after maturation (mths)		
MONOCALYPTUS						Mean	Range	
Stringybarks								
<i>E. laevopinea</i>	1-2	1-2	22-28	24-30	9-14	25	9-45	5-6
<i>E. caliginosa</i>	1-2	1-2	22-28	24-30	7-12 (mostly 9)	28	16-40	5-5½
Ashes, Saltees								
<i>E. pauciflora</i>	11-13	1-2	7-12	21-26	4-6	21	6-30	4-4½
<i>E. stellulata</i>	11-12	1-2	15-17	27-30	7-10	26	14-33	5
<i>E. radiata</i>	10-11	1-2	11-12	23-24	10-11	36	24-40+	5-6
SYMPHYOMYRTUS								
Red Gums								
<i>E. blakelyi</i>	1	1	9-11	12-13	3-5	21	8-30	3-3½
Gums								
<i>E. nicholii</i>	1-2	1-2	14-15	17-18	8-9	33	32-34	4
<i>E. bridgesiana</i>	1-2	1	12-13	14-15	7-9	26	20-32	3½
<i>E. viminalis</i>	1	1	13-16	14-17	6-9	21	12-24+	3½
<i>E. dalrympleana</i>	1	1	10-12	11-13	3-5	17	14-20+	3
<i>E. nova-anglica</i>	1-2	1-2	13-15	15-18	8-9	21	12-30+	4
Boxes								
<i>E. melliodora</i>	1	1-2	5-11	7-13	4-7	22	8-30	3½
ANGOPHORA								
<i>A. floribunda</i>	1		1	2-4	1	1	1-2	½

\* Species arranged in phylogenetic order after Pryor and Johnson (1975).

+ Compiled from Fig. 6a.

to develop before flowering. The summer flowering species (*E. pauciflora* and *E. radiata*) take slightly less time to develop than the autumn flowering species (*E. stellulata*) – see Table 6.2. All the Monocalyptus species therefore take 2–2½ years for their buds to fully develop – the difference among the major groupings being how long inflorescence buds are held.

The Symphyomyrtus species, in contrast to Monocalyptus, all take 1–1½ years from bud initiation to flowering – the main difference among species being due to flowering times. Thus spring flowering species (*E. melliodora*) has buds for 7–13 months before flowering, the early summer flowering species (*E. blakelyi* and *E. dalrympleana*) take 12–13 months to develop and the late summer–autumn flowering species (*E. viminalis*, *E. bridgesiana*, *E. nicholii* and *E. nova-anglica*) take 14–18 months to develop. *Angophora floribunda* flower buds develop in only 2–3 months.

Aberrations to these patterns can occur. Two such exceptions were observed as part of this study. *E. melliodora* produced a second flower bud crop in late summer on two trees. Pin buds were observed in March–May, and buds developed slowly over winter. This bud crop was lost before flowering. In one specimen of *E. pauciflora* pin buds emerged in the same season of initiation (rather like a stringybark) and remained on the tree for 12 months (instead of inflorescence buds), after which flower buds developed at the normal time.

### c) Flowering

All flower crops observed have been plotted in Fig 6.6. Because observations were made at

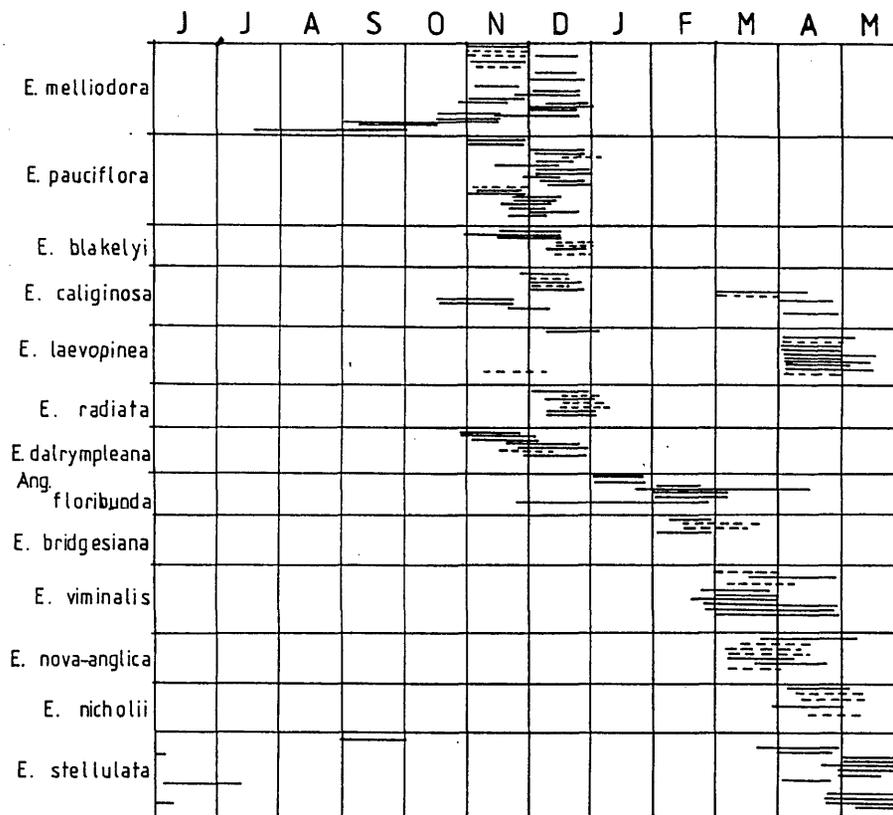


Figure 6.6: Flower crops of twelve *Eucalyptus* and one *Angophora* species: 1985–88. Dotted lines are crops which were estimated. See text for method of crop length estimation

3–4 month intervals some extrapolation has been necessary. Thus if flowers were observed at a certain date the flowering period was assumed to have extended one week either side of that date. If flowers and buds were present the flowering time was assumed to have lasted two more weeks, three weeks if the flowering had only just commenced and the crop was heavy. If flowers and old flowers were present the flowering period was assumed to have been already occurring for two weeks prior to the time of observation, three if the crop of old flowers was heavy. It was possible to make a calculated guess when flowering could have taken place for some trees, based on what was present on the tree or neighbouring trees even though no flowers were actually present. These are shown on Fig 6.6 as a dotted line. This method probably underestimates the length of time flowering occurred. However despite this limitation, clear trends are apparent. Fig 6.7 summarizes the flowering data.

#### Flowering Times – Differences between species

The flowering times of the twelve common eucalypts and one *Angophora* of the tablelands span most of the year. It would theoretically be possible to find a eucalypt tree flowering virtually any time of the year on the tablelands. *E. melliodora* can be found flowering any time from June to the beginning of January although most trees seem to flower in November–December. Early summer flowering species are *E. pauciflora*, *E. dalrympleana*, *E. blakelyi*, and *E. caliginosa* (all November–December). *E. radiata* flowers slightly later in December and early January. *Angophora floribunda* flowers in mid to late summer (late December to March and

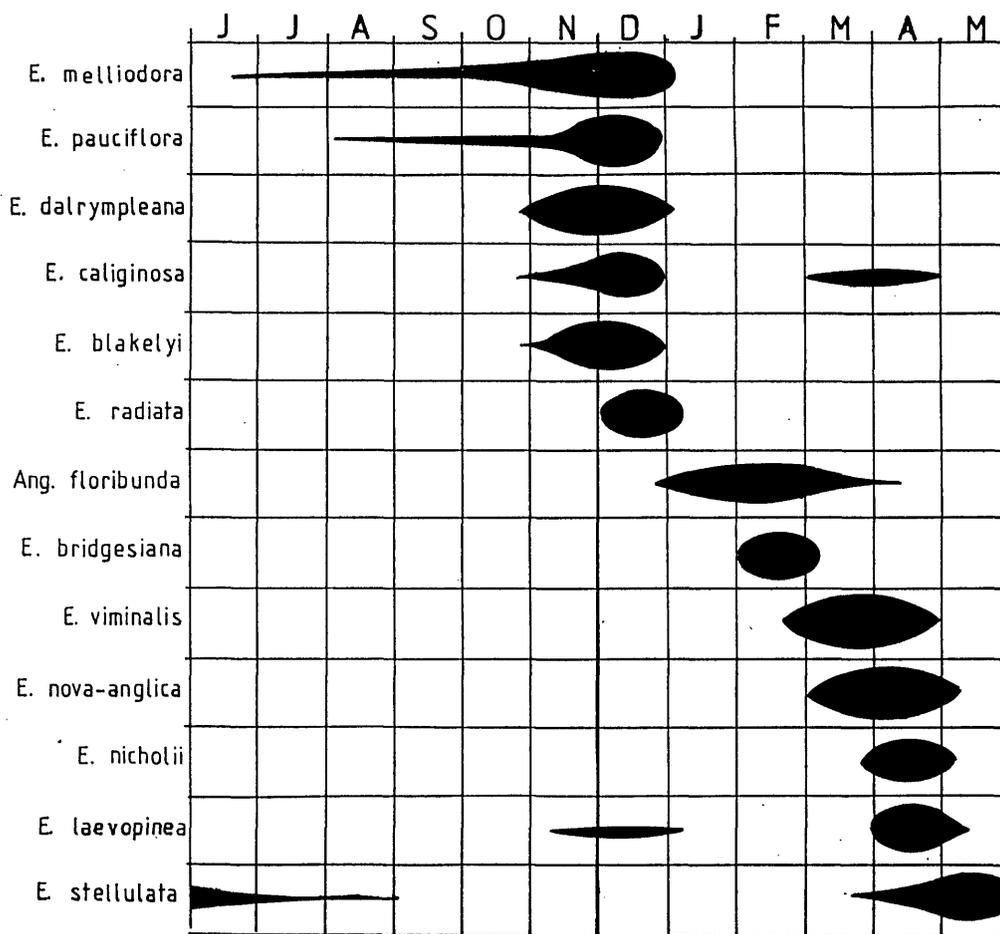


Figure 6.7: Summary of flowering times of the 12 common *Eucalyptus* and one *Angophora* species of the Northern Tablelands

extending to April). Late summer to autumn flowering species are *E. bridgesiana* (February to early March), *E. viminalis* and *E. nova-anglica* (March to April), and *E. nicholii* (April to early May). *E. laevopinea* flowers mainly in April and *E. stellulata* flowers in autumn to early winter (April–June).

Table 6.3 summarizes the flowering times observed as part of this study and compares them with records of other authors, some of which cover a bigger geographic range (eg. Clemson, 1985 and Kelly, 1974) while others are specifically for the Northern Tablelands (eg. Bowen, unpublished data).

In most cases my results agree with the records of the species elsewhere.<sup>1</sup> They show however that in the area I was examining, flowering times were in a smaller spectrum of the total range for each species. For local conditions the general texts give only a guide for flowering times of most species. Even the Tablelands records of Bowen (unpublished data) and Beadle (1976) indicate greater ranges than I have recorded. This is partly a function of the limited area under study and the interval between monitoring times.

There are three cases where my observations diverge from the literature. *Angophora floribunda* is reported by Beadle (1976) as a late winter to spring flowering species. My observations, in line with all other reports encountered, indicate this species flowers in mid-summer to autumn (Table 6.3). Local and other records of *E. caliginosa* indicate that it flowers in autumn to winter,

<sup>1</sup>References not included in Table 6.3 but with which my data also concurs are Goodacre (1958) and Goodacre (1973).

Table 6.3: Flowering times of the twelve common eucalypts and one *Angophora* of the Northern Tablelands

Species	My records	Other records
<i>E. melliodora</i>	Mostly Nov.-Dec; recorded anytime from June-Jan.	Clemson (1985) Variable, depending on altitude, season, locality. May-June on slopes. Main flowering in N.S.W.. Sept.-Feb.. Boland <i>et al.</i> (1987) Sept.-Feb.. Kelly (1974) Summer. Penfold and Willis (1961) Sept.-Feb., sometimes June. Blake and Roff (1958) Oct.-Dec. <u>Tablelands records</u> Davis (1968) Late Sept-Dec. Bowen (unpub.) Mid Sept.-late Jan. Beadle (1976) Spring-Summer.
<i>E. pauciflora</i>	Mostly early Nov.-late Dec.; occasionally flowers as early as July.	Clemson (1985) Nov.-Jan. Boland <i>et al.</i> (1987) Oct.-Jan. Kelly (1974) Summer. Penfold and Willis (1961) Nov.-Dec. Boland <i>et al.</i> (1980) Oct.-Jan. <u>Tablelands records</u> Beadle (1976) Early summer.
<i>E. dalrympleana</i>	Late Oct. - late Dec.	<u>Tablelands records</u> Beadle (1976) Spring.
<i>E. caliginosa</i>	Late Oct. - late Dec. mostly Dec. Some trees in Mar.-Apr.	Clemson (1985) Mar.-Jun. <u>Tablelands records</u> Beadle (1976) Winter. Bowen (unpub.) Early May - mid Aug.
<i>E. blakelyi</i>	Early Nov. - late Dec.	Clemson (1985) Oct.-Dec. Boland <i>et al.</i> (1987) Aug.-Dec. Kelly (1974) Aug.-Dec. Clark and Dallwitz (1974) Nov.-mid Jan. <u>Tablelands records</u> Beadle (1976) Late winter - early summer.
<i>E. radiata</i>	Early-late Dec. into Jan.	Clemson (1985) Sept.-Feb. (peak in early summer). Boland <i>et al.</i> (1987) Oct.-Jan. Boland <i>et al.</i> (1980) Oct.-Jan. Kelly (1974) Spring - summer. <u>Tablelands records</u> Beadle (1976) Spring - early summer.
<i>A. floribunda</i>	Late Nov. - mid Apr. Most in Jan.-Feb.	Clemson (1985) Dec.-Mar., most in Jan.-Feb. <u>Tablelands records</u> Beadle (1976) Late winter - spring. Bowen (unpub.) Early Dec.-late Feb. Prakash (1969) Jan. Davidson (1981b) Jan.
<i>E. bridgesiana</i>	Early Feb. - mid Mar.	Clemson (1985) Early Feb. - late Mar. Boland <i>et al.</i> (1980) Jan.-May. Kelly (1974) Autumn <u>Tablelands records</u> Beadle (1976) Late summer - autumn. Bowen (unpub.) Early Feb. - late Apr.
<i>E. viminalis</i>	Late Feb. - late Apr.	Clemson (1985) Mostly Mar.-Apr., beginning in Feb. Boland <i>et al.</i> (1987) Jan.-May. Boland <i>et al.</i> (1980) Jan.-May. Penfold and Willis (1961) Feb.-Apr. Blake and Roff (1958) Mar. <u>Tablelands records</u> Bowen (unpub.) Early Nov.-late Apr.
<i>E. nova-anglica</i>	Early Mar. - late Apr. sometimes into early May.	Penfold and Willis (1961) Jan.-May. <u>Tablelands records</u> Bowen (unpub.) Early Jan. - late Apr. Beadle (1976) Late summer - autumn.
<i>E. nicholii</i>	Late Mar. - early May. Most in Apr.	Kelly (1974) Autumn. <u>Tablelands records</u> Beadle (1976) Autumn
<i>E. laevopinea</i>	Mostly in early Apr. - mid May. Sometimes in Nov.-Dec.	Clemson (1985) Mid Jan. - Mar. Boland <i>et al.</i> (1987) June-Aug. <u>Tablelands records</u> Beadle (1976) Winter. Bowen (unpub.) Early May - Mid Aug.
<i>E. stellulata</i>	Late Mar. - Sept. Most in Apr.-May.	Clemson (1985) Feb.-May. Boland <i>et al.</i> (1980) Apr.-Oct. Kelly (1974) Winter - spring, sometimes in summer. <u>Tablelands records</u> Beadle (1976) Autumn - spring. Bowen (unpub.) Mid Mar. - late May.

in contrast to my records of *E. caliginosa* trees flowering in early summer, with some trees only flowering in autumn to early winter (Table 6.3). There is much variation in the literature for flowering of *E. laevopinea*, some reporting it as flowering in winter (Beadle, 1976; Boland *et al.*, 1987; Bowen, unpub.) and others reporting that it flowers in late summer to autumn (Clemson, 1985). My records indicate that *E. laevopinea* mostly flowers in autumn (early April–mid May), with some trees flowering in late spring to early summer. These two species therefore are quite variable in their flowering and have considerable overlap. This variable pattern of flowering was exemplified at Eastlake which had a mixed population of *E. caliginosa* and *E. laevopinea* and probably some hybrids. In this stand both species were found flowering in either autumn or early summer. This cross-over of flowering has probably been responsible for hybridization between the two species, or it may be a result of hybridization between them.

Within a site it was usual to find trees of the same species flowering at about the same time. Individual trees would exhibit some variation within a site but generally their flowering would be synchronous (Fig 6.8). However, it was not unusual to find considerable variation in flowering times among trees of the same species growing in different localities or in different years. Some variation of this nature was observed as part of this study, but insufficient replication of sites, trees or years was available to be able to analyse this aspect in detail. Fig 6.8 summarizes the data of the two species with the most complete data sets (*E. pauciflora* and *E. melliodora*). *E. pauciflora* showed little variation among the four sites it was growing at (all within 20 km of one another) or among the three years observed. *E. melliodora* showed a little more variation. The trees observed in 1982 flowered earlier (mid October to mid November) than the trees observed in later years but it was impossible to deduce from the data whether these differences were because of different weather patterns or because the trees were growing some 50 km apart. The trees observed in 1985–1988 were all growing within 10 km of each other and it appeared that 1986 was a slightly later year (early–late December) than 1985–1987 (early to late November). In 1989 some *E. melliodora* trees were flowering at the University of New England in April to June indicating that in a very mild year this species could flower very early.

#### Flowering times and ecological significance

Within associations it is usual for flowering times to be spread over an extended period. As well as providing a barrier to hybridization this spread also allows the trees to provide a more or less continuous food supply for the array of animals which visit their flowers, among them valuable predators and pollinators. Most flowering occurs on the tablelands between early spring and autumn when pollinators are active and very little occurs in winter when pollinators are mostly inactive. Table 6.4 summarizes the species growing in each alliance and the spread of flowering in each (see Appendix I for the main eucalypt alliances on the Northern Tablelands).

Providing a spread of flowering times has significance in planning planting programmes. Plantations should attempt to duplicate the range of flowering times in natural stands to provide a continuous food supply for beneficial wildlife

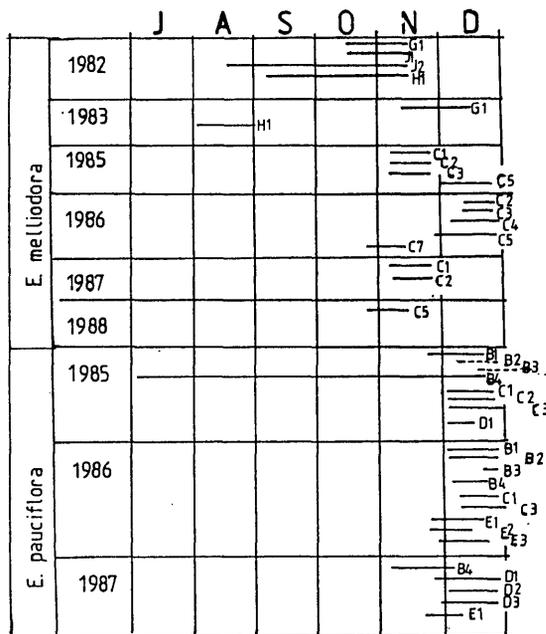


Figure 6.8: Flower crops observed of *E. melliodora* and *E. pauciflora* and variation between sites and years. Each horizontal line represents the flowering period observed at a site. Site code: B = Ruby Hills; C = Yalgoo, Miramoonna and Petali which are all very close to each other; D = the Kentucky sites Birralee and Terrible Vale; E = Eastlake; G = Woodpark and U.N.E.

Table 6.4: The spread of flowering times within the main eucalyt associations of the Northern Tablelands.

§ Alliance/Suballiance	Spring	Early summer	Mid summer	Late summer	Autumn	Winter
<i>E. melliodora</i> - <i>E. blakelyi</i> Alliance	<i>E. melliodora</i>	<i>E. blakelyi</i> <i>E. caliginosa</i>	<i>Angophora floribunda</i>	<i>E. bridgesiana</i> <i>E. caliginosa</i> <i>E. viminalis</i>		
<i>E. pauciflora</i> Suballiance	* <i>E. acaciiformis</i>	<i>E. pauciflora</i>		<i>E. viminalis</i>	<i>E. stellulata</i>	
<i>E. stellulata</i> Suballiance		<i>E. pauciflora</i>		<i>E. viminalis</i> <i>E. nova-anglica</i>	<i>E. stellulata</i>	
<i>E. dalrympleana</i> Alliance		<i>E. dalrympleana</i> <i>E. caliginosa</i> <i>E. pauciflora</i> <i>E. radiata</i>			<i>E. caliginosa</i>	
<i>E. viminalis</i> - <i>E. rubida</i> Suballiance	<i>E. melliodora</i>	<i>E. pauciflora</i> <i>E. caliginosa</i> <i>E. dalrympleana</i>		<i>E. nova-anglica</i>	<i>E. laevopinea</i> <i>E. stellulata</i>	
<i>E. nova-anglica</i> Alliance	<i>E. melliodora</i>	<i>E. pauciflora</i>		<i>E. bridgesiana</i>	<i>E. viminalis</i> <i>E. nova-anglica</i> <i>E. stellulata</i>	
<i>E. laevopinea</i> Suballiance		<i>E. dalrympleana</i> <i>E. pauciflora</i> <i>E. caliginosa</i>		<i>E. bridgesiana</i> <i>E. viminalis</i>		
<i>E. caliginosa</i> Suballiance	<i>E. melliodora</i>	<i>E. caliginosa</i> <i>E. dalrympleana</i>		<i>E. bridgesiana</i>	<i>E. caliginosa</i> <i>E. laevopinea</i> <i>E. nicholii</i>	

§ Based on Beadle (1981)  
\* Flowering time based on Beadle (1976).

#### d) Fruit Maturation

The time taken for fruit to develop followed a similar pattern to bud development (see Table 6.2). With the exception of *E. pauciflora*, Monocalyptus fruit took longer to mature than those of Symphyomyrtus species, taking approximately 9–12 months. The summer flowering *E. caliginosa* took less time to mature than the autumn flowering *E. laevopinea*, probably because there is little development in the fruit over the winter in *E. laevopinea*. The ashes and sallees took slightly less time to mature than the stringy barks. *E. pauciflora* was atypical for the Monocalyptus species, its fruit maturing in 4–6 months, more like a Symphyomyrtus species.

Among the Symphyomyrtus species, average maturation time was 6–8 months. The early summer flowering species developed faster (mean 3–5 months) than the late summer - autumn flowering species (mean 7–9 months), probably because little development takes place over the winter. Whereas the early flowering species are largely mature by winter the late flowering species do not mature until the following spring/summer. *Angophora floribunda* fruit matured only one month after flowering.

#### e) Seedfall

Seedfall per unit area has been graphed against time for each tree monitored in Fig 6.9 (see Appendix III for calculations). Table 6.5 and Fig 6.5 summarize the seasons and period in which seedfall occurs in each species. A major limitation with the seedfall measurements was the small number of readings per year (3–5). Consequently peaks and troughs in the graphs are less pronounced than if more frequent records were taken.

Table 6.5: Timing of seedfall for the twelve common *Eucalyptus* and one *Angophora* species of the Northern Tablelands.

§Phenology graphs – see Appendix V. \* Seedfall data – see Figure 6.9

Species	Major Season of Seedfall	Period of Seedfall (time after flowering)	Other Records
<i>Eucalyptus laevopinea</i>	Summer - autumn some in spring	1-3 years after flowering. <u>Seedfall data</u> * --> major peak 9-12 months after flowering and secondary peaks 2 and 3 years after flowering. <u>Phenology graphs</u> § --> most seedfall 2 and 3 years after flowering.	
<i>E. caliginosa</i>	Summer - autumn, some in spring.	1-3 years after flowering. <u>Seedfall data</u> --> major peak 1 year after flowering and secondary peaks 2 and 3 years after flowering. <u>Phenology graphs</u> --> most seedfall 1 and 2 years after flowering with some 3 years after.	
<i>E. pauciflora</i>	All year. Peak in summer.	1-2 years after flowering. <u>Seedfall data</u> --> most seedfall in 1-2½ years after flowering. <u>Phenology graphs</u> --> most seedfall in second year after flowering, with some in first and third years.	
<i>E. stellulata</i>	All year. Peak in summer - autumn.	1-2 years after flowering, sometimes up to 3 years. <u>Seedfall data and Phenology graphs</u> --> most seedfall in second year after flowering and extending 2½-3 years after flowering.	
<i>E. radiata</i>	Spring - summer, some in autumn, winter.	2-3 years after flowering, sometimes up to 4 years. <u>Seedfall data and Phenology graphs</u> --> most seed falls in third year after flowering with some extending into the fourth.	
<i>E. blakelyi</i>	Spring - summer, some throughout year.	½-2 years after flowering, occasionally longer. <u>Seedfall data and Phenology graphs</u> --> most in summer 1 year after flowering, and extending over the following year, some before.	Seedshed in spring-summer 9-12 months after flowering. (Clarke and Dallwitz, 1974).
<i>E. nicholii</i>	Spring-summer possibly.	1-3 years after flowering.	
<i>E. bridgesiana</i>	Summer possibly.	1-3 years after flowering, mostly in 2nd year after flowering with an apparent peak in the summer 2 years after flowering.	
<i>E. viminalis</i>	Summer-autumn.	1-2 years after flowering. <u>Seedfall data and Phenology graphs</u> --> most in summer-autumn one year after flowering and then secondary peak in the summer-autumn of the second year.	
<i>E. dalrympleana</i>	Summer, some in spring and autumn	1-2 years after flowering. <u>Phenology and Seedfall graphs</u> --> most seedfall in summer 1 year after flowering, and a secondary peak the following summer.	
<i>E. nova-anglica</i>	Summer-autumn, small amounts all year.	1-2 years after flowering, extending until 3 years. <u>Phenology and Seedfall graphs</u> --> main seedfall peak in the summer 9 months after flowering, with some seed falling over the next 1-2 years.	
<i>E. melliodora</i>	Summer, some all year.	1-2 years after flowering. <u>Phenology and Seedfall graphs</u> --> main seedfall in summer 12 months after flowering, and secondary peak the following summer.	Seedshed begins in spring 1 year after flowering (Davis, 1968).
<i>Angophora floribunda</i>	Late summer- autumn.	1-2 months after flowering.	

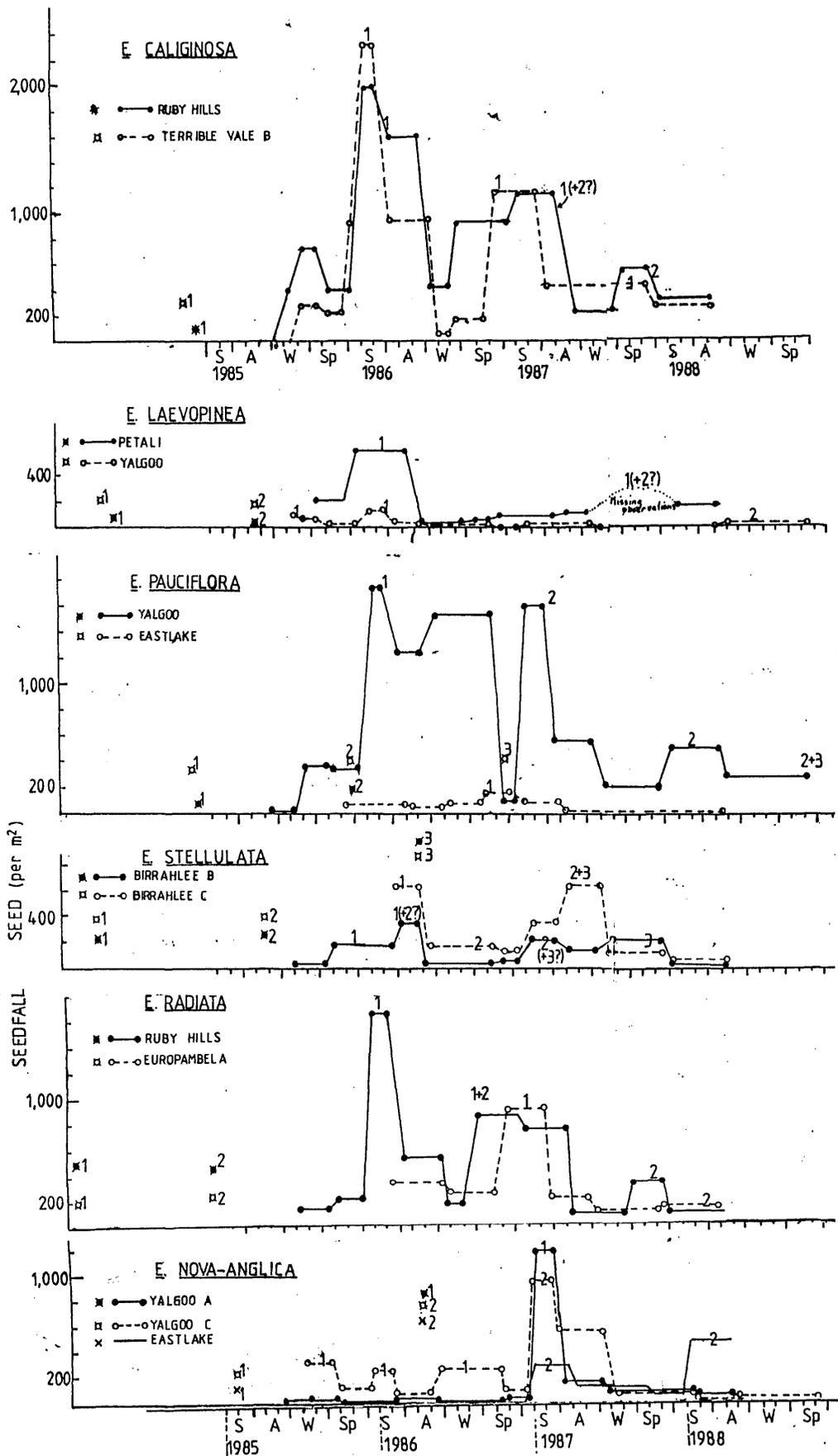
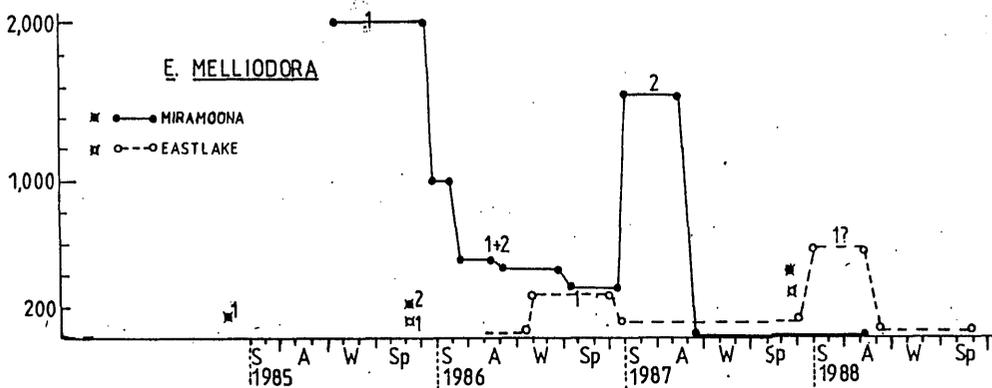
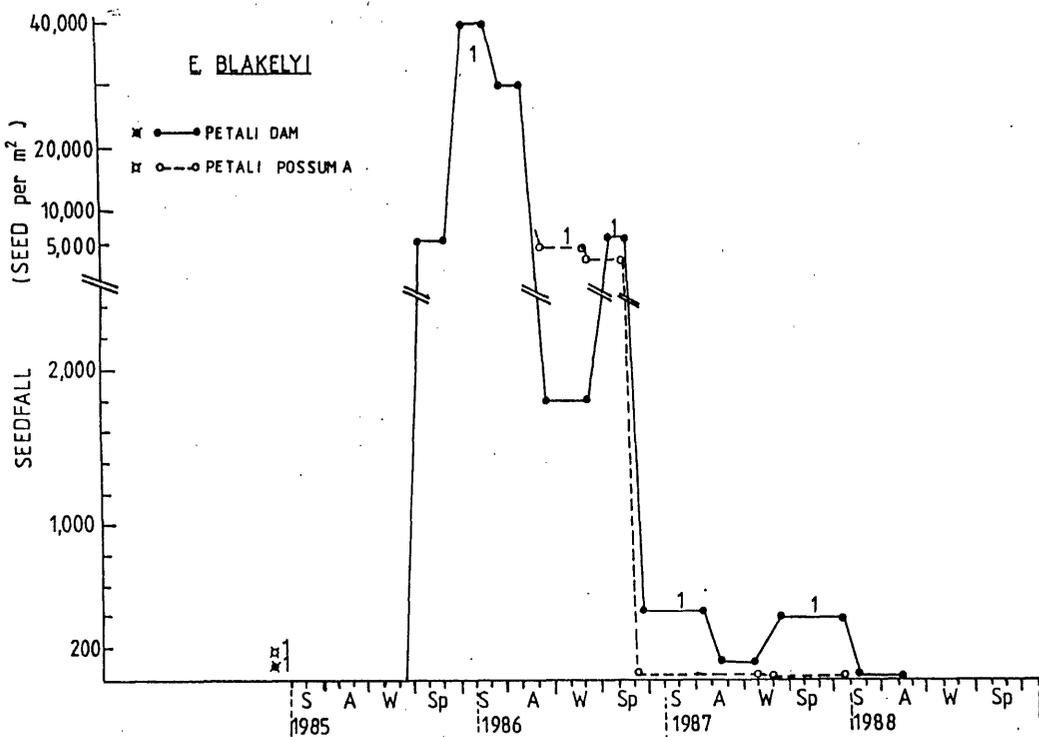
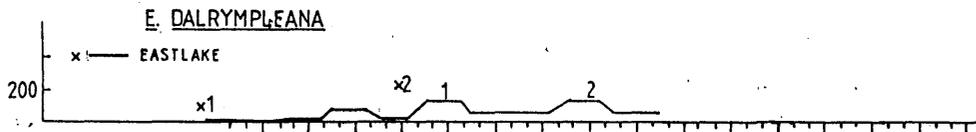
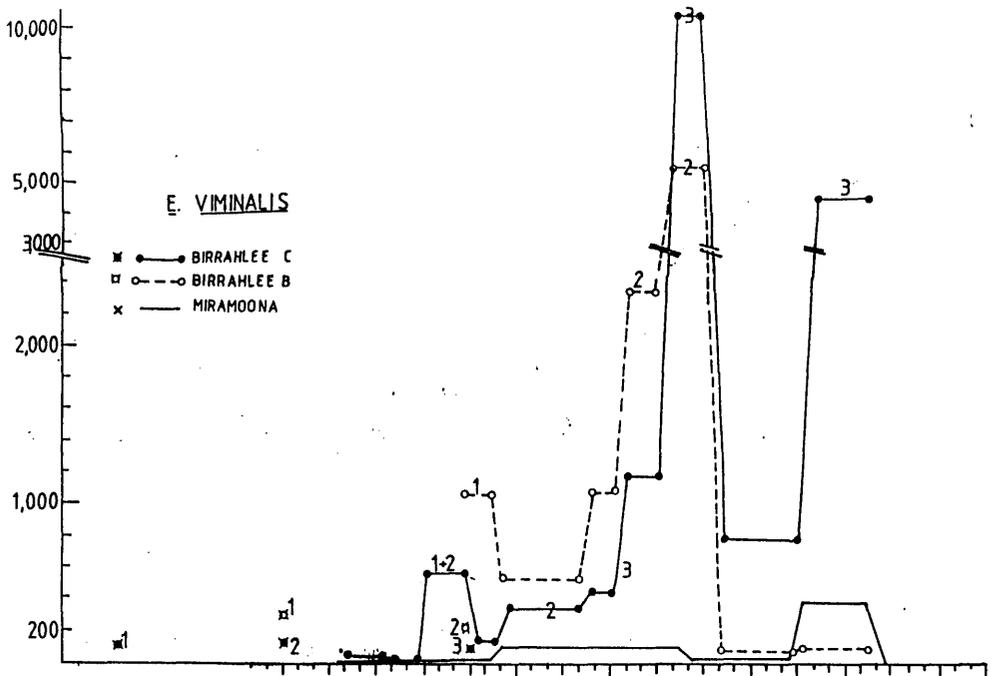


Figure 6.9: Seedfall per m<sup>2</sup> over time for ten eucalypt species. The sites where each tree was growing are shown in each figure. Where more than one tree of the species was monitored at the site (Table 6.1), the actual tree (or trees) are indicated by the letters A, B, or C. Some trees monitored had very low amounts of seedfall within the time monitored and these are not included in the figure. The symbols \* □ × represent flowering times of each tree. The numbers 1, 2, and 3 represent the different flowering crops. The figure is continued on the back of this page.



Despite the limitations of the data, clear seasonal trends were apparent in the seedfall of most species, particularly where good crops of fruit were present. The major period of seedfall for all species was summer – this period extending into spring and/or autumn. Some seed was found falling throughout the year although very little fell in the winter. Species with a predominantly spring– summer seedfall were *E. radiata*, *E. blakelyi*, and *E. nicholii*. Those with a predominantly summer– autumn seedfall were *E. laevopinea*, *E. caliginosa*, *E. stellulata*, *E. nova-anglica*, *E. viminalis*, and *Angophora floribunda*. *E. melliodora*, *E. stellulata*, *E. dalrympleana*, and *E. pauciflora*, while having a summer peak, tended to have seedfall throughout the year.

Most species had a major proportion of their seed fall in the summer one year after flowering with secondary peaks in the summer (or summers) following. Seedfall fell into five broad groupings. *E. nicholii* and *Angophora floribunda* had insufficient data and are not included here.

1. Major seedfall in summer one year after flowering with secondary peaks in the following two summers *E. laevopinea*, *E. caliginosa*.
2. Major seedfall in summer one year after flowering with a secondary peak in the following summer only. *E. pauciflora*, *E. blakelyi*, *E. viminalis*, *E. dalrympleana*, *E. melliodora*.
3. Major seedfall in the summer one year after flowering. *E. nova-anglica*.
4. Major seedfall in the summer  $1\frac{1}{2}$ –2 years after flowering. *E. stellulata*, *E. bridgesiana*.
5. Major seedfall in the summer 3 years after flowering with minor peaks in the summer 2 and 4 years after flowering. *E. radiata*.

The length of time fruit were held after maturation was much the same for all species examined – ie. 1–3 years with most having fallen 2 years after maturation. Although the mean values indicated that some species seemed to hold their fruit slightly longer than others (eg. *E. caliginosa*, *E. laevopinea*, *E. radiata* and *E. nicholii*) or for a shorter time (eg. *E. dalrympleana*), there was considerable overlap between the two ranges of species (Table 6.2).

#### f) Flowering cycle length

The length of time taken from flower bud initiation to seedfall followed a distinct pattern, which mirrors the evolutionary sequence. The more primitive Symphyomyrtus species all had a shorter flowering cycle ( $3-3\frac{1}{2}$  years) than the more advanced Monocalyptus species (5–6 years). *E. pauciflora* was slightly shorter than the other Monocalyptus species while *E. nicholii* was slightly longer than the other Symphyomyrtus species. The species examined on the Tablelands had very similar flowering cycles to their nearest relatives as described in the literature.

The different flowering cycle lengths between the subgenera are largely attributable to the length of time taken for buds to develop before flowering, and to a lesser extent the fruit maturation time while little overall difference could be detected in the length of time fruit were held (Table 6.2).

## 6.4 The effect of dieback on flowering

### Flowering in Eucalypts on the Northern Tablelands prior to 1982

Nadolny (1984) collected data on flowering, fruiting and tree health of eucalypts in the Armidale region from 1980 to 1982. In 1980 trees in the main dieback zone generally had no flowers, buds or fruits present. This was particularly so for *E. blakelyi*, *E. melliodora* and *E. viminalis* and less so for *E. caliginosa* which in general was less affected by dieback. Outside the dieback area (eg. Mt. Yarrowitch, the Pinnacle), these same species did flower so it was likely that dieback prevented flowering and seed production. At this time in dieback affected areas on the Northern Tablelands most trees predominantly consisted of epicormic growth as a result of the dieback and the presence of immature growth would have prevented flower initiation.

In 1981 there was a reasonable amount of flowering of *E. melliodora* in sites of grassy woodland near the Gara River in the winter and spring of 1981. Flowering of other species occurred in other localities also, eg. *E. blakelyi* and *E. nova-anglica*. Angophoras had a very heavy flowering in January 1981, to such an extent that articles commenting on it appeared in the local press (Davidson, 1981b). This general flowering seemed related to the general increase in the vigour of trees (tabulated by Nadolny, 1984). In 1982 the flowering was the heaviest seen on the Tablelands for many years, and it corresponded with improved health in the trees.

Nadolny monitored seven eucalypt species over 14 sites on the Northern Tablelands. The only trees which flowered at his sites were the healthier trees with less than 25% of the canopy defoliated. Sometimes trees flowered which had up to 50% of the canopy removed, but these were less common; trees which were more than 50% defoliated, and particularly those with predominantly epicormic growth, rarely flowered.

#### 6.4.1 Methods

All the trees at sites 15a and 7a and a representative sample of trees at sites 15b and 7b (132 trees in total) were examined in May 1982 and again in September 1983. Presence or absence of flower buds, flowers and/or fruits were recorded and the health of the tree was evaluated using the Dieback Rating Scale of Nadolny (1984) - see Appendix II. In 1985 and again in 1988 most of the trees monitored for phenology (Table 6.1) were evaluated in the same way (a further 86 trees). Table 6.6 lists the trees and species monitored. All species and monitoring times were pooled together.

#### 6.4.2 Results and Discussion

Trees which were badly affected by dieback and which only had epicormic growth present (DB less than 4)<sup>2</sup> were never seen with flower buds or fruit (Fig 6.10). Trees which had more than 50% of the crown defoliated or had predominantly epicormic growth (DB 4-5), sometimes had

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<sup>2</sup>“DB” refers to the Dieback Rating Scale - see Appendix II

Table 6.6: Trees monitored for dieback and flowering study. All sites are pooled together

	Number of trees monitored		
	1982/83	1985/88	Total
<i>Angophora floribunda</i>	0	4	4
<i>E. blakelyi</i>	60	9	69
<i>E. bridgesiana</i>	9	5	14
<i>E. caliginosa</i>	0	5	5
<i>E. darympleana</i>	0	5	5
<i>E. laevopinea</i>	0	7	7
<i>E. melliodora</i>	15	6	21
<i>E. nicholii</i>	0	2	2
<i>E. nova-anglica</i>	17	7	24
<i>E. pauciflora</i>	0	12	12
<i>E. radiata</i>	0	10	10
<i>E. stellulata</i>	0	8	8
<i>E. viminalis</i>	31	6	37
TOTAL	132	86	218

flower buds or fruit but they were only sparse compared with healthier trees. Trees which were 25-50% defoliated (DB6) tended to produce flower buds and fruits but not reliably; about half of trees in this category had buds or fruit but frequently they were only light crops. Trees less than 25% defoliated (DB 7-8) produced flower buds or fruits quite consistently. Many authors have reported great variation between years, sites and individuals in the abundance of flowering (Section 6.1). The size of the samples of healthy trees were not big enough to get a clearer picture in this regard.

It seems, therefore, that trees which are badly affected by dieback are prevented from flowering. The most likely mechanism that causes this is the destruction of flower buds at formation. This was observed in many trees in the summer of 1983. As well as preventing flower formation, it seems that dieback affects the percentage loss of flower buds from the canopy. Data collected for three *E. blakelyi* trees at sites 15a, 15b and 7a show this (Table 6.7). The tree in site 15a was less healthy than the other two and the leaves were distinctly more damaged by insects (Lowman, unpublished data). The malaise of the tree was reflected in the numbers of buds per umbel - only 2.1 compared with 4.7 and 5.2 in the healthier trees. *E. blakelyi* have an average of 7 buds per umbel when they first emerge (Beadle, 1976) so all 3 trees had probably lost considerable numbers of buds before the trees were initially monitored, but the less healthy tree had lost a greater proportion. Also a greater proportion of buds were lost before fruit formation. Umbels without buds were not counted so the values of fruit per umbel are a high estimate. The response of species to this form of damage will probably differ.

Dieback affects the ability for a eucalypt to produce seed by:

- Preventing formation of flower buds by the production of juvenile growth as a response to defoliation;
- Preventing the development of flower buds where insect damage causes the loss of new flower buds soon after initiation;
- Reducing the numbers of buds per umbel, and the abundance of buds in general, after formation;
- Increasing the percentage loss of buds before flowering and the young fruits before fruit maturity.

Table 6.7: Tree health and its influence on flower abundance and loss

TREE	Dieback Rating over 2 year period	START OF STUDY			AFTER FRUIT FORMATION BEFORE SEEDFALL			% loss of buds and/or flowers
		No. Umbels	No. Buds	Buds per Umbel	No. Umbels	No. Fruit	Fruit per Umbel	
<i>E. blakelyi</i> Site 15a	6-6.5	77 8 June 1982	167	2.1	29 1 March 1983	51	1.8	69
Site 15b	7.5-8	131 8 June 1982	600	4.7	78 1 March 1983	203	2.6	66
Site 7c	6	76 11 June 1982	395	5.2	64 11 May 1983	232	3.6	41

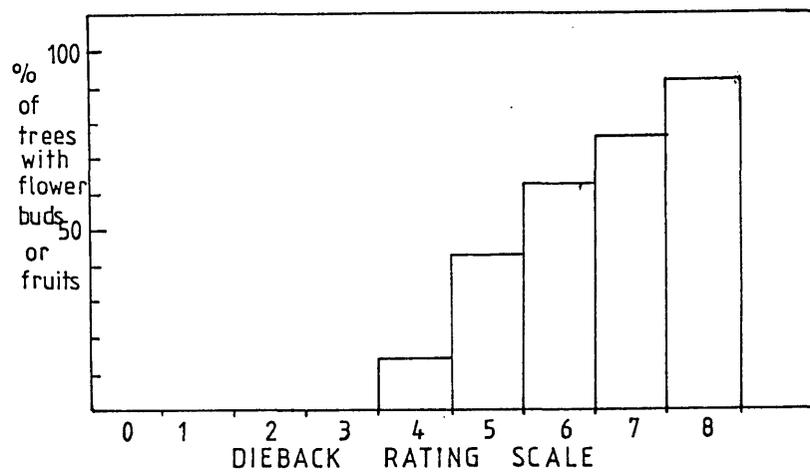


Figure 6.10: Effect of dieback on flower crop production. Pooled data over all species and sites. For explanation of Dieback Rating see Appendix II

## Chapter 7

### Seed in the Soil

The three main processes by which eucalypt seeds are lost from the soil's surface or from the soil seed pool are predation, germination and seed death (Fig 7.1). Published information on soil seed of woodland eucalypts is scarce so the following discussion is mainly drawn from the available literature on forest eucalypts.

#### 7.1 Predation

A varying proportion of eucalypt seed is lost to predation while it is still held in the fruit (section 6.1) but once the seed falls to the ground a major proportion of it seems to be taken by predators. Losses of 60-90% are typically cited, with higher or lower values possible (Cremer *et al.*, 1978; Ashton, 1979; Drake, 1981b). The animals found to be responsible for this predation are generally ants (Ashton, 1979; Drake, 1981b) although some bugs and other insects are also involved (Cremer, 1966b).  
lygaeid

The proportion of seeds taken seems to vary, depending on the activity of the insects and on the quantity of seed. Drake (1981b), working on Stradbroke Island, found that ants were more active later in the day. Ashton (1979), working in Mountain Ash forest in Victoria, also found that seed removal could be quite rapid and was quickest in dry periods in summer which was when most seed fell (60-90% removal in 14 days in warmer months compared with 40-50% in cooler months). Removal was more rapid and more complete if seeds were placed close to an ant nest (60% removal in 4 days if less than 10cm away compared with 20% removal if placed 30cm away). After 24 days, removal was fairly complete up to 30-40cm away from the nest. Time of day also influenced removal. Different species of ants had different foraging behaviour, some feeding in the late afternoon, others at midnight. Some were more active in cloudy conditions, others in hot conditions. Withers (1978) found that eucalypt seeds were predated at greater levels than seeds of *Acacia* or *Casuarina* species.

What attracts ants to eucalypt seed is not really known. Many plants have on their seeds an "elaiosome", a specialized appendage containing oils and fats, which attracts ants and is eaten without the seed being damaged. Eucalypt seeds lack such structures, so other attractants must be present. Cremer (1966b), working in Mountain Ash forest in Tasmania, tried to disguise eucalypt seeds to reduce their removal by insects. He coated seeds with many substances such as charcoal, kaolin and humus, to try to disguise them but they were still eaten, which suggested

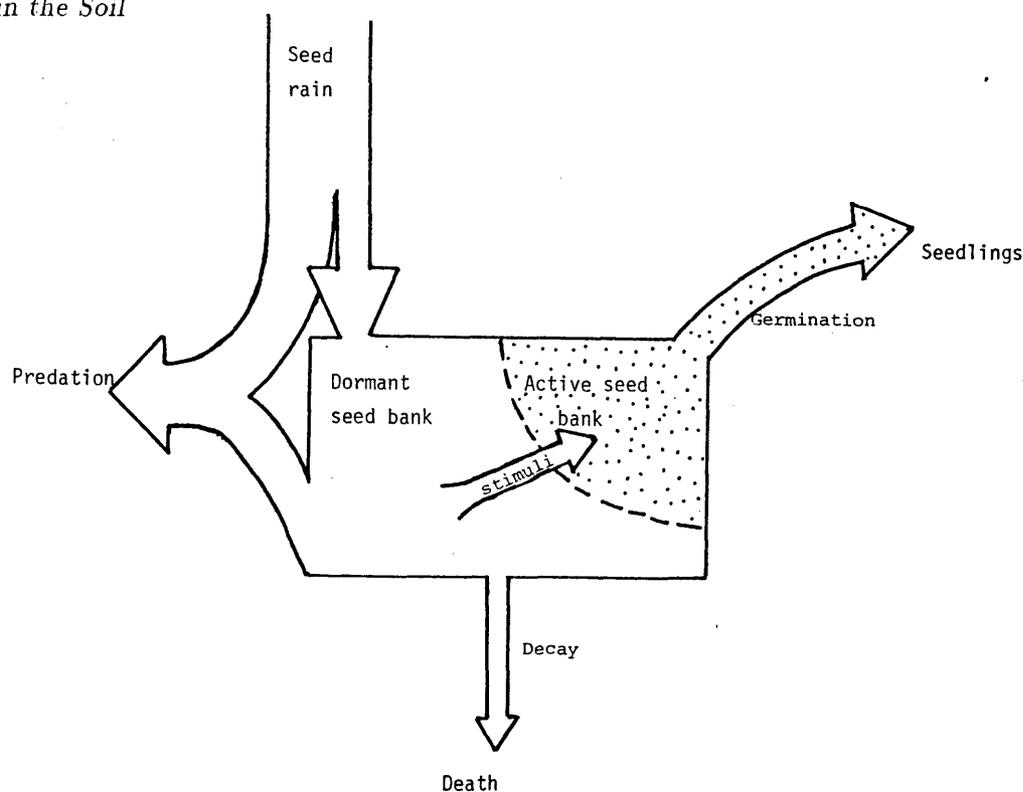


Figure 7.1: The Seed Pool (Adapted from Harper 1977)

that the insects were attracted by a smell. He then washed the seed with different chemical solvents to remove the smell but they were still eaten, suggesting that the attractant came from within the seed. Ashton (1979) found that some species of ant could distinguish between chaff and fertile seed and his tests suggested that some volatile compounds were the attractants. Drake (1981b) thought that ants were attracted to small oil glands in the cotyledons.

Once they have collected the seeds ants either eat them or store them. Both activities generally prevent the seeds from producing seedlings. Most eucalypt seed seems to be eaten, either whole or with the seed coat left intact. Ashton (1979) found very little storage of eucalypt seed in ant nests in moist forest, although he quotes other studies which have found some storage. Drake (1981b) also found that most seeds were eaten. Where seeds are not eaten their ability to ultimately grow will depend on how deeply they are buried. Eucalypt seedlings do not usually emerge from depths greater than about 2.0cm (Ashton, 1979), so although ants may account for some seed dispersal their actions generally seem to make seed unavailable for seedling production.

Silvertown (1982) described two defensive strategies which many forest trees have against seed predation – rapid seed germination (low seed dormancy) and masting (the occasional production of very heavy crops of seed). Whereas light seed crops may be entirely eaten, the heavier crops can fulfill the predators' requirements and still leave an excess of seed available for germination. Eucalypt forests frequently have massive seedling recruitment after fire because a fire can cause rapid and profuse seedfall when a heavy seed crop is present in the canopy. This causes a temporary satiation of seed-eating ants (Andersen, 1988a), and germinating seeds are likely to find a good seed bed.

A further defensive strategy of eucalypts against predation is the production of chaff which

may act as 'decoy' seeds (O'Dowd and Gill, 1984). This defense may not be as effective after a low intensity fire where chaff falls rapidly and successfully satiates ants but the seeds fall for several weeks after the fire, by which time predation levels have increased sharply and the seeds are more likely to be eaten (Andersen, 1988a).

Despite predation, which can account for large losses of eucalypt seed, eucalypts do regenerate quite successfully. Predation becomes critical when natural regeneration is hampered by other factors or when seed is sown in forestry or regeneration operations. Techniques for reducing predation in such situations are discussed in chapter 9.

## 7.2 Dormancy

Innate dormancy has only been found in the seed of a few eucalypt species and these all grow in temperate and alpine areas. Boden (1961) mentions 10 species with this characteristic, while Turnbull and Doran (1987a) list 11 species. Most species possessing dormancy belong to the subgenus *Monocalyptus* (eg. *E. pauciflora* and *E. delegatensis*) but some belong to *Symphymyrtus* (Boden, 1961; Glossop *et al.*, 1982). The dormancy is broken if seeds are exposed to cool moist conditions for a period of time and acts to ensure seedlings will emerge after winter when conditions are better for growth. This process is called stratification and can be done artificially by placing seeds on moist filter paper in a petri dish and held at 5°C for 4-6 weeks (Scott, 1972). Seeds stratified for longer periods (eg. 8 weeks rather than 0-4) have faster germination (Baker and Grose, 1961; Grose, 1957).

Bachelard (1967a and 1967b) examined *E. pauciflora* seeds to find the mechanisms controlling dormancy. He found that applying gibberellic acid overcame the necessity for stratification and that mechanical resistance by the seed coat prevented germination. Although seeds could imbibe water and the embryo could swell, further growth was prevented by the mechanically resistant seed coat. The gibberellic acid probably softened the seed coat, making germination possible. He does not say what sets off the production of gibberellic acid in the seed.

Innate dormancy only exists in a proportion of a seed lot, and some seed will germinate normally although the proportion may be small (about 20% for *E. delegatensis* - Grose (1963)). Dormancy also varies among trees at the same location thus ensuring a variation in the timing of germination. This may be important in spreading or reducing mortality of the total seed population due to frosts etc. Stratification increases the speed and completeness of germination as well as the range of temperatures at which seed will germinate (Grose, 1957; 1965; Baker and Grose, 1961). In effect stratification reduces the control that temperature has on germination. Species which show no dormancy at all have also been found to respond to stratification by germinating faster and more completely (Grose, 1957; 1965; Beardsell and Mullett, 1984 - see Table 7.1). For species which grow where there is a cold winter, eg. the Victorian species studied by Grose (1965), this faster germination could be important because many of these species shed their seed in summer or autumn. Some seed would germinate in autumn but most would lie

Table 7.1: Effect of stratification on the germination of seed of a non dormant eucalypt species, *E. melliodora*. Data from Grose, (1965).

Incubation Temperature °C +	Non Stratified Seed		Stratified Seed	
	Germination Percent	Germinative Energy §	Germination Percent	Germinative Energy §
25.5	99	6	100	4
32	99	7	99	3
35	50	9	97	2

+ Converted from °F - Incubation temperature was kept constant.  
§ Days to reach 90% of final germination.

imbibed or dry in the seed bed during winter to germinate in spring.

Some species are only “partially dormant” in that although they will germinate without pretreatment, they do so only slowly (Grose, 1957). Some species show a variation in the amount of dormancy displayed in the seeds, depending on where the trees are growing. For example the strength of dormancy increases with altitude in *E. pauciflora* (Beardsell and Mullette, 1984; Abrecht, 1985). The same is not true for *E. delegatensis* (Pederick, 1986). Smaller seeds have also been found to be more dormant than larger ones (Grose, 1963; Abrecht, 1985). Boden (1957) found that in *E. pauciflora* and *E. dives* the dormancy did not develop strongly until 3-5 weeks after the seeds had been extracted from the fruit.

Secondary dormancy can be induced in some species by exposing seeds to a high temperature after stratification (27°C or more) and seeds will not germinate until they are restratified (Boden, 1961; Ashton, 1979). Grose (1963) found that for *E. delegatensis*, primary dormancy could be strengthened or secondary dormancy could be induced by subjecting seed to high temperatures.

Induced dormancy could be an adaptation of alpine species such as *E. pauciflora* to prevent germination in summer or autumn. Seedfall of *E. pauciflora* mainly occurs in summer. Innate dormancy prevents germination until after stratification in the winter and secondary dormancy prevents germination in summer, thus ensuring that germination occurs in spring-early summer when conditions are most favourable for seedling establishment (Beardsell and Mullette, 1984).

There is a lack of information regarding seed dormancy and soil seed storage of most of the local Tableland eucalypts. Available evidence suggests that most local species do not possess innate seed dormancy, with the possible exceptions of *E. pauciflora* and *E. stellulata* (Scott, 1972).

### 7.3 Longevity

In dry storage eucalypt seed can remain viable for many years. In dry air at room temperature no loss in viability has been found in most species after 10 years or so (Floyd, 1961; Cremer, *et al.*, 1978), and there have been some reports of seed remaining viable for 30 years or more (Boden, 1961).

To find how many eucalypt seeds are viable in the soil Carroll and Ashton (1965) took soil to a depth of 10cm from six different types of plant communities, including wet and dry sclerophyll forests, grassy woodlands, mallees and heaths. They stratified and watered the soil in controlled conditions and identified seedlings as they emerged. Herbaceous species were very common germinants. In contrast, eucalypts, although they were the dominant species in most of the communities surveyed, produced no seedlings, except a few in a mountain ash community. This implied that there was virtually no storage in the soil <sup>of the seed</sup> or most eucalypts in the plant communities they tested or else the seed did not germinate under the conditions provided.

In another similar study in a Bimble Box Community (*E. populnea*, *E. intertexta*), Hodgkinson *et al.* (1980) took samples of soil and extracted seed. Most seed (78%) was in the top 1 cm of soil. Some eucalypt seeds were extracted but they were in very small quantities relative to the herbaceous and shrubs species present.

Ashton (1979) reported that although seed storage of *E. regnans* could be expected, none could be demonstrated. Most seed, he says, germinates within 3 weeks once moisture and temperature are adequate, although a small percentage may keep germinating for up to 2.5 years, probably due to 'hard seededness'. Cremer (1965b) reported that seed buried and ungerminated died within 14 months. Stratified or moist seeds have been found to lose viability very quickly in storage (Grose, 1963).

Thus it seems that most eucalypt seeds are eaten or disposed of by insect predators, and there is little seed accumulation in the soil. Some species show seed dormancy but most seeds, including dormant ones, do not survive in the soil for more than 1-2 years. Ashton (1979) found that annual seedfall in a mountain ash forest was 200,000-250,000 viable seeds per hectare; with most falling in summer and autumn. Emerging seedlings were only 0.4-0.7% of the seed fall - insect predation or seed death were the likely fates of most seeds. Baker and Grose (1961) found that most *E. delegatensis* seed fell in summer to autumn and 50-75% of seed was eaten by ants. A small percentage of seeds germinated in autumn but died in winter. Some other seeds became nonviable before spring leaving about 15-34% of seedfall available for germination in spring when they germinated readily if suitable conditions occurred. Seeds which did not germinate in spring usually became nonviable before favourable conditions returned. This general pattern of low seed dormancy and high losses of seed to predation, which seems applicable for most eucalypts, fits the general demographic pattern for many other trees (Silvertown, 1982).

## 7.4 Germination

A small proportion of seeds escapes predation, or death by other means, and given the right conditions are able to germinate and grow. To germinate seeds must have adequate moisture, favourable temperatures and oxygen. Seed size, salinity, light and dormancy also influence germination.

### (a) Moisture

Probably the most important factor limiting germination of eucalypt seed is moisture – seeds being prevented from germinating if conditions are too dry or too wet. Maximum germination occurs when there is no water stress (osmotic potential at 0 MPa – Zohar *et al.*, 1975). As water stress is increased germination is slower and less complete. Species vary in their response to water stress. For example germination of *E. cloeziana* is reduced when the osmotic potential falls below -0.4 MPa and is completely inhibited at -1.0 MPa (Turnbull and Doran, 1987a), while *E. occidentalis* can still have 70% germination at -0.9MPa (Zohar *et al.*, 1975).

*E. camaldulensis* is much more sensitive to water stress than *E. regnans*, its germination being significantly reduced even at -0.2 MPa and little germination occurring at less than -0.6 MPa, compared with less than -0.8 MPa for *E. regnans* (Edgar, 1977). The sensitivity of *E. camaldulensis* to moisture stress would help to ensure seeds germinate only when soil moisture is good e.g. after floods. For *E. regnans* high soil moisture could be less critical since it grows in moist, relatively drought free places.

Waterlogging as well as drought may inhibit germination (Cremer *et al.*, 1978) – an exception is *E. camaldulensis* seed which can survive after extended immersion (Dexter, 1967). Cremer (1965b) found that 4–10 weeks submergence killed the seeds of *E. regnans*.

### (b) Temperature

Temperature has an important influence on seed germination and has been extensively studied. The optimal temperature for germination is defined as the temperature which gives the highest percentage germination in the shortest time. Seeds may germinate over a large temperature range but at many of the temperatures germination will be slow.

Most eucalypts have optimal germinating temperatures of 20–25°C (Grose, 1965; Scott, 1972). Some species from tropical and inland areas have higher optimal temperatures of 30–35°C, eg. *E. camaldulensis* and *E. blakelyi* (Grose and Zimmer, 1958c; Grose, 1965; Scott, 1972). Species from temperate and mountain areas of south-east Australia and Tasmania tend to have lower optimal temperatures, between 15–20°C (Grose, 1965; Scott, 1972) or 15–17°C (Abrecht, 1985). Many of these latter species also frequently require stratification to break dormancy (Section 7.2). Many species from south-western Western Australia will only germinate in temperatures under 24°C (Turnbull and Doran, 1987a). Some species show no clear optimal temperature and will germinate well at temperatures ranging from 15–30°C (Scott, 1972). Optimal temperatures for germination for the species in the present study from Turnbull and Doran (1987a) are given in Table 7.2. These are virtually the same as those reported by Scott (1972).

Response to temperature may vary within a species growing over different altitudes (e.g. Abrecht, 1985 – *E. pauciflora*) but response to temperature does not seem to vary within species growing in different areas or in seed collected from different parts of a tree (e.g. Grose and Zimmer, 1958c – *E. camaldulensis*). In studies on *E. camaldulensis*, seeds did not germinate as well when subjected to alternating temperatures as in constant temperature, although combinations of temperatures could be found which gave good germination. Also near optimal germination could be achieved at lower, non optimal temperatures, by exposing seeds to short

Table 7.2: Optimal germination temperatures of the 12 species of *Eucalyptus* used in this study. (Data from Turnbull and Doran, 1987b)

Species	Optimal * Germination °C	First § Germinated (Days)	Last § Germinated (Days)
<i>E. blakelyi</i>	30; 25	7	21
<i>E. bridgesiana</i>	25	8	14
<i>E. caliginosa</i>	20	10	28
<i>E. dalrympleana</i> <i>ssp heptantha</i>	(25)	7	21
<i>E. laevopinea</i>	25	7	21
<i>E. melliodora</i>	25	5	21
<i>E. nichollii</i>	(25)	3	10
<i>E. nova-anglica</i>	(25)	3	14
<i>E. pauciflora</i>	15	7	21
<i>E. radiata</i>	15; 20	10	21
<i>E. stellulata</i>	15; 20	10	21
<i>E. viminalis</i>	25	7	14

\* Temperatures separated by semicolon are equally satisfactory; temperatures in brackets have been found to be satisfactory but a full range of temperatures have not been tested.

§ Number of days when "first" and "final" seeds germinate.

periods of the optimal temperature (Grose and Zimmer, 1958c). Stratifying seed lessens the effect temperature has on germination (section 7.2), as does exposure to light (Venning, 1988).

Freezing conditions (i.e. at or below  $-6^{\circ}\text{C}$ ) causes high mortality of eucalypt seeds that have just germinated or are about to germinate, while temperatures down to  $-2^{\circ}\text{C}$  cause no significant mortality. Air dry seeds are not affected by freezing but imbibed seed suffer significant mortality at temperatures below  $-5^{\circ}\text{C}$  (Cremer and Mucha, 1985).

### (c) Light

Twenty-one species of *Eucalyptus* have been found to require some light before they will germinate well (Turnbull and Doran, 1987a), and this requirement is usually satisfied in the laboratory by giving 10 minutes of light per day to the germinating seeds (Grose, 1965) and in the field by sowing the seeds on or near the soil surface. Other species require dark for good germination while others germinate equally well in dark or light (Clifford, 1953; Grose and Zimmer, 1957; Zohar *et al.*, 1975). Dependence on light for germination only affects a proportion of the seed lot, and this dependence varies with species, seed lots, seed maturity, prior stratification and temperature and moisture levels during germination (Turnbull and Doran, 1987a).

The light response is related to temperature and the need for light can be lessened or eliminated, in some species at least, by exposing seed to alternating temperatures, near optimal temperatures or stratification (Grose 1965; Grose and Zimmer, 1958c). Unfortunately none of

the authors above indicate why some eucalypts have a light requirement and others do not. In some other plants the adaptive significance of a light or dark response is clear. For example the sand dune grass *Spinifex sericeus* will only germinate in the dark. This ensures that germination will only occur when the seeds are buried and not when they are on the dry surface of the dune (Maze, 1982). Another grass – Channel Millet (*Echinochloa turnerana*) – has a requirement for light plus ample moisture to ensure rapid germination in times of flooding (Conover and Geiger, 1984 a;b). Perhaps a similar mechanism operates in some eucalypts native to wet places such as *E. camaldulensis* and *E. occidentalis*, both of which have a light requirement (Grose and Zimmer, 1957; Zohar *et al.*, 1975) but why there should be such a range in light requirements amongst other eucalypts is a question largely unanswered.

#### (d) Seed Size

There is large variation in the size of seeds of eucalypts, both within a species and between species – these size differences often being related to fruit size (Grose and Zimmer, 1958b). Seed size differences give rise to different germination behaviour with smaller seeds within a species generally germinating slower than the larger seeds, and tending also to give a lower percentage germination. Seedling growth and survival in the first few months of life are also affected by seed size (Grose and Zimmer, 1958a). Although differences can be observed in seedling vigour and survival for different sized seeds *within* a species, it does not necessarily apply when comparing different species or genera, and there is no evidence that seed size is related to ultimate growth rate (Cremer *et al.*, 1978).

## 7.5 Seed Germination Tests

In the course of the direct sowing trials (Chapter 9) seed samples of 25 local provenances of 7 eucalypt species were collected and measured for viability. In most cases ten samples of 0.10g of seed plus chaff were weighed – the only exceptions being one provenance of *E. laevopinea* for which samples of 0.20g were taken and *Leptospermum* species for which samples of 0.05g were taken. Each sample was placed in a clean glass petri dish and sufficient distilled water to provide an even film was poured over the seeds. No filter papers were used as seeds were found to germinate completely without them. Likewise as fungal problems were minimal, fungicides were not used.

The lids of the petri dishes were replaced and the dishes were left for two to three weeks at room temperature and checked daily. More water was added before a dish dried out. Numbers of germinants were counted and averaged over the ten samples. The number of viable seed per gram of seed plus chaff was then estimated and tabulated.

Table 7.3: Seed viability of the 9 eucalypt species used in direct sowing trials (Chapter 9)

Species	Number of Samples	Mean No. viable seed/g *	Range, viable seed/g *	Mean seed/g $\pm$ S.D. §	Highest on Record §
<i>E. blakelyi</i>	6	431	299 - 592	687 $\pm$ 524	2,080
<i>E. caliginosa</i>	1	125		48	193
<i>E. laevopinea</i>	2	37	29 - 64	51 $\pm$ 28	96
<i>E. melliodora</i>	2	137	49 - 224	354 $\pm$ 220	1,120
<i>E. obliqua</i>	1	26		88 $\pm$ 47	158
<i>E. pauciflora</i>	2	85	37 - 94	62 $\pm$ 23	112
<i>E. radiata</i>	3	177	125 - 234	143 $\pm$ 82	344
<i>E. stellulata</i>	5	122	44 - 251	355 $\pm$ 122	543
<i>E. viminalis</i>	3	280	124 - 259	349 $\pm$ 237	1,220

\* See Appendix VIII for complete data from which these values were calculated.

§ From Turnbull and Doran (1987b)

### 7.5.1 Results and Discussion

A summary of the seed data is presented in Table 7.3. Mean value of viable seed per gram of seed plus chaff has been calculated by averaging all the samples taken for that species. Measurements of Turnbull and Doran (1987b) are presented for comparison.

In all species my data lie within the general range for the species quoted by Turnbull and Doran (1987b). There was considerable variation between samples of a species and even adjacent trees were found to have quite marked differences in the amount of viable seed per gram. This becomes significant when direct sowing.

No dormancy was found in *E. pauciflora* in these viability tests – most seeds germinated adequately at room temperature. Likewise in extensive sowings of this species for the propagation of seedlings for planting trials (Chapter 10) no dormancy was obvious. This accords with the results of Beardsell and Mullett (1984) who found no seed dormancy in *E. pauciflora* from low altitudes, whereas dormancy became more pronounced at higher altitudes.