found in northern regions such as the Western Tiers and Cluan Tier, and occasionally on Fingal Tier and the adjacent Eastern Tiers. In these highland regions, *E. viminalis* may be confused with *E. dalrympleana*. The main flowering period is November to April, peaking in February and March (Figure 91).

Eucalyptus viminalis rarely forms pure stands, but may dominate grassy (Photo 28) and shrubby dry sclerophyll forests and woodlands in drought-prone habitats in south-eastern Tasmania. Forest stands dominated by *E. viminalis* that occurred throughout the alluvial valleys of the Midlands and northern coastal hinterlands have been extensively cleared (M.J. Brown, pers. comm. 1995). *Eucalyptus viminalis* is usually subdominant or co-dominant with



Figure 90. Altitude distribution of E. viminalis.



Figure 91. Flowering times for E. viminalis.

other eucalypts from the subgenus Monocalyptus in wet and dry sclerophyll forest. In wet sclerophyll forest, it has been observed to dominate stands on the drier, rocky dolerite sites of the lower slopes of the Western Tiers but more typically occurs as a subdominant species with *E. obligua*. It varies in form from a tall tree up to 90 m in some north-eastern wet forests (e.g. the 'White Knights' (Photo 2, p. 46) in Evercreech Forest Reserve) to a mallee shrub in coastal heathland. Where it occurs as a minor species in dry sclerophyll forests, it frequently forms an emergent crown over the more continuous canopy of peppermint eucalypts (i.e. *E. amygdalina, E. pulchella* or *E. tenuiramis*).

COMMENTS: In Tasmania, it is frequently difficult to distinguish the taxonomic limits of



Photo 27. Manna on a trunk of E. viminalis (manna gum) produced in response to feeding by the redeye cicada, Psaltoda moerens (top, left).

E. viminalis and E. dalrympleana because of continuous variation between the two (e.g. Maiden 1918; Barber 1955, 1956; Phillips and Reid 1980). The white-gum subgroup of the series Viminales is largely absent from western regions (Figures 21, 71, 89). However, some western outliers of E. viminalis occur near Strahan and the Henty River sand dunes (cells 3534, 3633), and other scattered outliers exist along the coast in the far north-west and around Smithton (e.g. cells 3045, 3049, 3347). The extent of E. viminalis on the west coast and the exact affinity of these forms to *E. viminalis* and *E. dalrympleana* require further study. One extreme, unverified outlier is recorded from inland forest of the north-west, near the Huskisson River (cell 3739), which may be indicative of a similar habitat to that of the south-western outliers

adjacent to the Picton River (cells 4721, 4722). Unverified outliers from the southern Central Plateau are likely to reflect intergrading forms with closer affinities with *E. dalrympleana* (i.e. 4433, 4532, 4535, 4631, 4632, 4731, 4733, 4933). Glaucous-leaved *E. viminalis* plants have been observed in localities such as New Norfolk, Snug and Nugent (F. Duncan, pers. comm. 1994). It is not clear whether these intermediates are clinal or hybrids with *E. rubida*, or a result of adaptation of populations of *E. viminalis* to local dry sites.

KEY REFERENCES: Almeida *et al.* (1994); Duncan (1981); Higa (1986); Ladiges (1974a, b, 1977); Ladiges and Ashton (1974, 1977); Paton (1972, 1980); Phillips and Reid (1980); Pryor (1955); Valentini *et al.* (1990); Withers and Ashton (1977).



Photo 28. Eucalyptus viminalis in grassy dry sclerophyll forest, its form markedly different from that seen under more favourable conditions (see Photo 2, p. 46).

Results and discussion

Sampling range of the distribution data

Eucalypts have been recorded in 757 of the 837 grid cells that cover Tasmania, King Island and the Furneaux Group of islands (Table 3). The number of eucalypt records per cell indicates the relative levels of sampling intensity between regions (Figure 92). For example, the greatest number of records is from the central east coast region where detailed transect studies were undertaken for multiple-use forest management zoning prior to the proclamation of a National Park (e.g. Blakesley and McDonald 1989). In this region, one grid cell may have as many as 2000 eucalypt records (e.g. cell 5937), and surrounding cells may be represented by 500 records or more. Nearly 60% of all cells in which eucalypts are recorded are represented by 20 or more records and relatively few cells (10.4%) contain only one or two eucalypt records. Gaps in the database, where eucalypts are expected to be present, are particularly apparent in coastal and inland localities of the west and south-west. Other isolated database omissions are indicated for coastal areas of the far north-west and north-east. and some parts of King Island. Apart from western regions, reduced sampling relative to other localities is evident for the Midlands, the central north-west and the Central Plateau, and coastal plains of the north-east and on Flinders Island. Records of eucalypt occurrences for some of these locations may exist but are uncollated. Conversely, these may represent real absences for eucalypts due to extreme environments or following the clearing of forests and woodlands for agriculture.

The data are derived from over 450 different sources, including published and unpublished articles or reports, numerous personal communications, and recent herbarium collections. Up to 29 different sources have been collated for any one grid cell (e.g. cells 5224, 5225). One-quarter of the cells with eucalypt occurrences are represented by three or less sources and 30% of the cells are represented by ten or more sources (Figure 93). The cells with many different sources represent the most accessible locations or specific localities and regions of economic or botanical significance. In particular, these include parts of the Eastern Tiers and the south-east near Nugent, Tasman Peninsula, southern Bruny Island and Snug, Mount Field National Park, the Southern Forests, the Western Tiers, the West Tamar and parts of the central north coast. In the south-east, for example, numerous independent studies of eucalypts have been undertaken close to Hobart (e.g. Barber 1955; Hogg and Kirkpatrick 1974; Ratkowsky and Ratkowsky 1976, 1977, 1982; Brown and Bayly-Stark 1979a; Kirkpatrick and Marks 1985; Potts 1986; Potts and Reid 1983, 1985c; Davidson and Reid 1985, 1987, 1989: Davidson et al. 1987; Gilfedder 1988; Wiltshire et al. 1991a, b, 1992; Pyrke and Kirkpatrick 1994), and herbarium records abound for the Wellington Range.

Eucalypt species richness

Eucalypt species richness, defined as the number of species recorded for each 10 km x 10 km grid cell, is given in Figure 94. There is clearly much greater species richness in eastern regions than western regions of Tasmania, with concentrations on the central east coast and in the south-east. Approximately 12% of the cells in which eucalypts have been recorded contain at least one-third of the Tasmanian taxa, and 12 of these cells contain 15 or more species. There is a noticeable paucity of eucalypt species in the south-west, and this is unlikely to change with increased sampling.

Species richness will be a function of several factors including environmental heterogeneity within a grid cell and adequacy of surveying. There are, for example, local concentrations of species richness around the Mount Field National Park and Cradle Mountain National Park that could reflect greater sampling than elsewhere, although both centres are also on geological transition zones. In other regions, such as the Midlands, the north and northeastern coastal plains, parts of the Central

Table 3. Summary statistics for altitude range, flowering times, eucalypt presence and aggregation. For altitude, figures given for the minimum, maximum, mean and standard deviation are in metres a.s.l. and the means and standard deviations are rounded to the nearest 10 m. The number of records used to calculate the altitude statistics is given by 'n'. The flowering times are given in months as the 5–95% range and the 25–75% interquartile range. Aggregation is calculated as the percentage of the number of grid cells in which a species is present and the number of grid cells within the envelope of its range. The ordering of species within subgenera follows Table 1 (p. 40).

| | | | Altitu | de | | Flowering time (range in months) | | No. grid cells | Aggregation |
|--------------------|-------|-----|--------|------|------|-------------------------------------|---------|-------------------|-------------|
| Taxonomic grouping | g n | min | max | mean | s.d. | 5%-95% | 25%-75% | present | (%) |
| Monocalyptus | | | | | | | | | |
| E. delegatensis | 2744 | 100 | 1240 | 655 | 211 | Jan-Mar | Jan–Feb | 349 | 68 |
| E. obligua | 4208 | 1 | 860 | 300 | 176 | Jan-Mar | Jan–Feb | 436 | 68 |
| E. pauciflora | 305 | 10 | 1080 | 531 | 255 | Dec-Feb | Jan–Jan | 170 | 55 |
| E. regnans | 1579 | 20 | 870 | 372 | 169 | Feb-May | Mar-Apr | 171 | 40 |
| E. sieberi | 331 | 1 | 720 | 277 | 179 | Sep-Mar | Oct-Nov | 37 | 73 |
| E. amygdalina | 2600 | 1 | 1020 | 305 | 209 | Aug-Jan | Oct-Nov | 417 | 87 |
| E. coccifera | 326 | 390 | 1290 | 938 | 195 | Nov–Feb | Dec–Jan | 139 | 49 |
| E. nitida | 551 | 1 | 1020 | 291 | 244 | Nov-Feb | Dec–Jan | 292 | 76 |
| E. pulchella | 493 | 10 | 740 | 286 | 167 | Aug-Feb | Oct-Dec | 126 | 70 |
| E. aff. radiata | 8 | 150 | 610 | 369 | 126 | na | na | 7 | 88 |
| E. risdonii | 33 | 2 | 280 | 123 | 68 | Aug-Dec | Oct-Nov | 4 | 100 |
| E. tenuiramis | 456 | 1 | 700 | 264 | 158 | Nov-Feb | Nov-Jan | 118 | 78 |
| Symphyomyrtus | | | | | | | | | |
| E. barberi | 79 | 130 | 500 | 298 | 96 | Mar-Oct | Apr-Jul | 17 | 68 |
| E. brookeriana | 125 | 10 | 720 | 392 | 193 | Sep-Apr | na | 81 | 22 |
| E. ovata | 954 | 1 | 830 | 233 | 186 | Jun–Feb | Aug-Nov | 412 | 49 |
| E. rodwayi | 186 | 60 | 1120 | 557 | 212 | Nov-May | Jan–Mar | 135 | 36 |
| E. dalrympleana | 596 | 150 | 1175 | 630 | 200 | Mar-May | Mar-Apr | 176 | 54 |
| E. rubida | 126 | 90 | 880 | 430 | 172 | Nov-Jan | Dec–Jan | 86 | 55 |
| E. viminalis | 2633 | 1 | 940 | 322 | 216 | Nov-Apr | Feb-Mar | 424 | 71 |
| E. johnstonii | 185 | 130 | 920 | 645 | 168 | Jan-Apr | Feb-Apr | 47 | 41 |
| E. subcrenulata | 103 | 550 | 1180 | 902 | 135 | Jan–Apr | Jan-Mar | 65 | 43 |
| E. vernicosa | 73 | 240 | 1250 | 840 | 208 | Dec-Apr | Jan-Feb | 76 | 41 |
| E. globulus | 1143 | 1 | 830 | 218 | 154 | Sep-Dec | Oct-Nov | 211 | 54 |
| E. archeri | 34 | 980 | 1350 | 1148 | 81 | Jan-Apr | Feb–Mar | 20 | 28 |
| E. cordata | 67 | 20 | 680 | 422 | 178 | May–Nov | Jun-Nov | 25 | 37 |
| E. gunnii | 157 | 330 | 1200 | 897 | 194 | Nov-Mar | Dec-Feb | 100 | 36 |
| E. morrisbyi | 4 | 10 | 80 | 45 | 35 | Mar–Apr | Mar-Apr | 2 | 33 |
| E. perriniana | 11 | 500 | 620 | 537 | 40 | Jan-Mar | Jan-Mar | 4 | 14 |
| E. urnigera | 59 | 420 | 1160 | 779 | 174 | Mar-Nov | May-Aug | g 29 | 21 |
| Full data range | 20169 | 1 | 1350 | 480 | 270 | | | 757 | 90 |

Plateau and the north-west, the depressed levels of species richness may be due to inadequate sampling of the environmental range per grid cell.

The relative distributions of the two subgenera are similar, although Monocalyptus species are present in 10% more grid cells than are Symphyomyrtus species (Figures 95, 96). Unexpectedly, Monocalyptus species are not verified from King Island. Species richness per grid cell for the Monocalyptus subgenus is greater in north-eastern, northern and northwestern regions than for the *Symphyomyrtus* subgenus, even though there are nearly 30% fewer Monocalyptus species than Symphyo*myrtus* species in Tasmania. However, this trend is consistent with the prevalence of Monocalyptus species such as E. delegatensis, *E. obliqua, E. amygdalina* and *E. nitida* across a wide range of sclerophyll forest, woodland and scrub habitats, and their frequent occurrence among the canopy dominants.

The relative distribution and species richness of the four Eucalyptus series (from Table 1) are given in Figures 97–100. In the Monocalyptus subgenus, the series *Obliquae* and *Piperitae* both include species with widespread distributions (e.g. E. obliqua and E. amygdalina). The series *Obliquae* reaches its greatest species richness in the north-east (Figure 97), and in the series Piperitae this is highest in the southeast (Figure 98). The series *Piperitae* species are broadly absent from the north-eastern montane forests and woodlands but extend into the far south-west and Flinders Island. Conversely, the series Obliguae species are largely absent from the far south-west, are not known from the Furneaux Group of islands and King Island but are well represented in the north-eastern highlands.

In the *Symphyomyrtus* subgenus, species in the series *Ovatae* and *Viminales* are also widely distributed in a range of habitats (e.g. *E. ovata* and *E. viminalis*). The series *Ovatae* species reach their greatest richness on the east coast and tiers (Figure 99), and the series *Viminales* species are richest in the highland regions of the south-east and, to a lesser extent, the

Eastern Tiers and the Central Plateau (Figure 100). Representative species from both series occur on King Island and Flinders Island. The series *Ovatae* species appear to extend more consistently into the north-west and the series *Viminales* species extend further into the environments of the south-west.

Endemism in the Tasmanian species of *Eucalyptus* (Table 1) is dominated by the series *Piperitae* (Figure 98) and *Viminales* (Figure 100). Species richness amongst the 17 endemics is centred in the south-east between the Huon and Derwent River estuaries, and at Mount Field (Figure 101). Endemism is also high in eastern regions and the Central Plateau, but is absent from King Island, and is sparse on Flinders Island, in the Midlands and in northern regions. Conversely, species richness among the 12 non-endemic eucalypts is highest in eastern regions, extends throughout northern regions including the Bass Strait islands, and into the Midlands and lower Central Plateau (Figure 102).

Altitude profiles

Altitude is an intuitively observed and easily recorded, indirect environmental descriptor of a species' habitat. It provides an immediate impression of the climate in a familiar locality. However, Tasmania-wide, altitude is confounded by continentality (distance from the coast) and the geographic trend in the degree of climatic exposure, induced by the prevailing westerly airstream. This effect is most readily observed in the upward shift of the altitude of the alpine tree-line in a southwest to north-east direction (see Jackson 1960; Kirkpatrick 1982). Consequently, a species may appear to grow in a broader range of environments than is actually the case. For example, E. vernicosa occurs in south-western habitats over a broad range of altitudes (240-1250 m, Figure 87), but the actual alpine or subalpine climatic range it grows in is likely to be much narrower than the altitude figures suggest.

Despite these limitations to ecological interpretation, altitude is a useful field guide

Tasforests Vol. 8



Photo 29. Eucalyptus vernicosa (foreground) grows as a low shrub in exposed alpine environments, occupying one of the harshest habitats in Tasmania.

to the general type of environment in which a species is likely to be found, and provides a basis for broad comparison of trends in habitat between taxa. For example, the local clinal variation between lowland and subalpine species that is commonly observed for the yellow gums (e.g. Potts and Jackson 1986) and white gums (e.g. Phillips and Reid 1980) reflects a continuum in habitat encapsulated in the altitude range. Altitude, in combination with other local site-factors such as slope, aspect and substrate type, and physical-process models for climate and soil, may be used to define more physiologically based environmental indices (e.g. water balance, growing degree-days, nutrient status) for assessing the nature of the ecological relationship between a species and its habitat.

The response of individual species to altitude (see Figures on pp. 49–121; Table 3) indicates some of the confounding factors involved in species identification due to clinal intergradation and hybridisation. The lower or upper altitude limits to a species' distribution are abrupt at sea-level due to the physical barrier or at the tree-line where plants are

physiologically limited by the seasonally low temperatures. Some of the distributions are apparently bimodal, potentially indicating geographically distinct ecotypes, while others are excessively peaked, skewed or long-tailed, which could represent error, sampling bias or a real effect. For example, the altitude profile for *E. pauciflora* may reflect the distribution of this species across two separate altitudinal ranges. The first is the lowland, coastal plateau between 100 m and 300 m, and the second is a mid-altitude, inland plateau in the range from 400 m to 700 m (Figure 51). In the case of *E. nitida*, the distribution extends across a broad altitudinal range and does not form distinct peaks (Figure 41). For this species, it is likely that more comprehensive sampling in the south-west would give a clearer indication of the environmental trend. The distribution for *E. nitida* is also confounded by possible separate ecotypes from Flinders Island and western Tasmania (Figure 40).

The geographic sampling range for which accurate altitudes were available is shown in Figure 103. Most regions are well sampled. Under-sampling is evident from western and south-western regions, parts of the Central Plateau and the Midlands. Apart from a probable under-sampling in highland areas, there is a natural bias in altitude for lowland environments since these are more common in the landscape (Figure 104).

The highest altitude recorded for any species was for *E. archeri*, found at 1350 m in the north-east. However, this altitude does not represent the most alpine habitat for eucalypts in Tasmania, which is occupied by *E. vernicosa* (Photo 29) in the south-west.

Flowering times

Geographic isolation or differences in flowering time are the main pre-mating barriers to hybridisation in natural eucalypt populations. However, once these barriers are removed, many species from the same subgenera will form viable hybrids following artificial pollination. The major post-mating barriers identified to date include differences in flower morphology and physiological incompatibility. Pollen tubes of smallflowered species are frequently unable to grow the full length of the style of large-flowered species (Gore et al. 1990). Eucalyptus globulus has the largest flowers of the Tasmanian species (Photo 9) and while it can successfully act as a pollen parent, no seed, or very little, is obtained when it is pollinated by the smaller flowered Tasmanian species (Potts and Savva 1989; Potts et al. 1992). When floral morphology is compatible, the success of controlled pollination tends to decline with increasing taxonomic distance between parents. Thus, intra-sectional hybrids tend to be more common (Griffin et al. 1988) and successful (Ellis et al. 1991) than intersectional hybrids. The major eucalypt subgenera are reproductively isolated and despite many attempts, no viable artificial hybrids have been obtained between Monocalyptus and Symphyomyrtus species (Griffin et al. 1988; B. Potts, unpublished data).

Monthly flowering times for each species are presented as Figures (see pp. 49–121), with a general summary in Table 3. No data are

currently available for *E.* aff. *radiata*, and few data are available for *E. perriniana*, *E. dalrympleana*, *E. johnstonii*, *E. regnans*, *E. rubida*, *E. sieberi* and *E. brookeriana*. The monthly flowering times for the taxonomic groups of subgenera and series are given in Figures 105a–g.

Most flowering of Eucalyptus occurs from September to March, with very little flowering over winter (Figure 105a). Eucalyptus urnigera is the only subalpine species in which flowering is centred over the winter period and it appears to be primarily bird pollinated (Savva et al. 1988). Other subalpine to alpine species tend to be summer flowering (e.g. E. vernicosa, E. subcrenulata, E. gunnii, E. archeri, E. rodwayi, E. delegatensis, E. pauciflora and E. coccifera). Many lowland species may commence flowering in the late autumn (e.g. E. barberi, E. cordata) or early spring (e.g. E. amygdalina, E. pulchella, E. risdonii, E. tenuiramis, E. sieberi, E. globulus and *E. ovata*), although their peak flowering generally occurs in spring. An apparent bimodality in flowering time for *E. cordata* is probably related to the different habitats of the eastern and western morphs (Figure 20). The strong bimodality in the flowering time of E. brookeriana requires investigation but is more likely to be a function of under-sampling or misidentification of west coast forms of E. ovata (compare Figures 14, 49). However, differences in flowering time between east and west coast occurrences of E. brookeriana cannot be excluded at this stage.

There is complete overlap in flowering between the *Monocalyptus* and *Symphyomyrtus* species (Figures 105b, c). Within the subgenus *Monocalyptus*, the series *Obliquae* species tend to flower in late summer or early autumn (Figure 105d), whereas the peak flowering of most series *Piperitae* species is in spring or early summer (Figure 105f). This difference in flowering time may partly explain the lack of extensive hybridisation between these series (Potts and Reid 1983), but is also a function of the general predominance of series *Piperitae* species in summer-dry habitats. The flowering of the

Tasforests Vol. 8

series *Ovatae* species is spread widely throughout the year (Figure 105e), whereas, with the exception of *E. urnigera*, the flowering of series *Viminales* species appears to be concentrated into the early summer to early autumn period (Figure 105g).

There are clear differences in the flowering of some groups of closely related species, and this would reduce the probability of hybridisation. In the Viminales, the alpine white gums (e.g. E. archeri, E. gunnii, E. urnigera and E. morrisbyi) differ markedly in their flowering times, and the peak flowering periods of the Ovatae species E. ovata, E. rodwayi and E. barberi also differ considerably. However, these generalised flowering curves underestimate the degree of reproductive isolation which may arise between species through differences in flowering time, and confound the large variations in flowering time which may occur within a species (e.g. Potts and Reid 1985a, c; Davidson et al. 1987; Savva et al. 1988; Gore and Potts 1995) and in different seasons. When flowering has been monitored in the same geographic locality, species from the same subgenus growing in close proximity are often well differentiated in flowering time. For example, the generalised flowering curves would suggest extensive overlap in the flowering of *E. amygdalina* and *E. risdonii*. However, detailed studies of an ecotonal area between these species have shown a significant difference in the time of peak flowering when species are in close proximity, although more distant populations may overlap (Potts and Reid 1985c). Flowering also tends to occur as 'waves' along altitudinal gradients, with higher altitude populations usually flowering later (e.g. Ashton 1975c; Savva et al. 1988).

There is little information available about the extent to which the differences in flowering time within species, or even between species, are determined by environmental (e.g. temperature) or genetic effects. Nevertheless, studies of populations of *E. globulus* have shown differences in flowering time within the same field trial to be highly heritable

(Gore and Potts 1995). Large, genetically based differences in flowering time occur between populations within this species, and even between trees within populations. Populations of *E. globulus* on the Furneaux Group of islands and eastern Tasmania flower in spring whereas those from western Tasmania, King Island and the Otway Ranges flower several months later, which corresponds with the pattern observed in natural stands. The flowering-time curve for *E. globulus* in the present study is based only on observations of *E. globulus* from eastern Tasmania.

Distribution types and conservation status

The natural continuum in the distribution of Tasmanian eucalypts can be divided into several types based upon categories for their geographic range and aggregation of occurrences (Table 3; Figure 106). Nine distribution types distinguish the widespread, dispersed or disjunct species from the more common species with widespread, clustered distributions (Table 4).

Within Tasmania, species with localised distributions and those with widespread distributions, at the 10 km x 10 km grid-cell scale, have representatives in each of the four *Eucalyptus* series. The rarest species always have localised distributions, but may exhibit different levels of aggregation across their respective ranges. For example, E. risdonii and *E. barberi* have a clustered aggregation of sites within a localised geographic range, whereas *E. morrisbyi* has a dispersed distribution. Other interesting distributions are species with dispersed or disjunct populations within regional or widespread occurrences. For example, the most disjunct species is *E. brookeriana*, with widely separated population centres in the northwest and the central east coast. Eucalyptus urnigera is a regionally disjunct species and *E. perriniana* exemplifies a locally disjunct distribution. Regional or widespread species with dispersed or disjunct patterns of occurrence typically occupy mid- to highaltitude habitat zones which are naturally dispersed in the landscape. Eucalyptus

Table 4. The nine distribution types of Tasmanian eucalypts as defined by their geographic range and aggregation level in 10 km x 10 km grid cells (see Figure 106). Species are listed in order of decreasing aggregation within each group. Taxonomic divisions are indicated by letters preceding the species name. M = Monocalyptus, S = Symphyomyrtus, Ob = Obliquae, Ov = Ovatae, P = Piperitae, V = Viminales (see Table 1). Species conservation status is from the Flora Advisory Committee (1994).

Criteria for the definition of conservation status (after Kirkpatrick et al. 1991a):

Ee—taxa that are likely to become extinct in native stands in Tasmania if present causal factors of decline continue.

- *R*—taxa that have limited distributions nationally following Briggs and Leigh (1988).
- r1—taxa that have a distribution in Tasmania that does not exceed 100 km x 100 km.

r2—taxa that occur in 20 or less 10 km x 10 km national mapping grid cells in Tasmania.

r3—taxa that do not fit r1 or r2, but which have very small and/or localised populations wherever they occur in Tasmania.

| Aggregation | | | | | | |
|-----------------------------|--------------------|---|---------------------------|--|---|--|
| (patterns of occurrence) | (< | localised 5 000 km²) | ı (5 000 | regional 1–25 000 km ²) | \ (> | videspread 25 000 km²) |
| Clustered (50–100%) | M P M P S Ov | E. risdonii R r1 E. aff. radiata r1 E. barberi R r2 | M P M Ob M P S V | E. tenuiramis E. sieberi E. pulchella E. rubida | M P S V M P M Ob M Ob S V S V | E. amygdalina E. viminalis E. nitida E. obliqua E. delegatensis subsp. tasmaniensis E. pauciflora E. dalrympleana E. globulus subsp. globulus |
| Dispersed (30–50%) | S V | E. morrisbyi Ee, r1 | S V S V S V S V | E. subcrenulata E. vernicosa E. johnstonii E. cordata R r3 | S Ov M P M Ob S Ov S V | E. ovata E. coccifera E. regnans E. rodwayi E. gunnii |
| Disjunct (< 30%) | S V | E. perriniana r2 | S V S V | E. archeri R r2 E. urnigera | S V | E. brookeriana |

regnans is an exception, being a lowland species with a narrow ecological range (e.g. Ashton 1958, 1981a). Most species with clustered distributions usually occupy midaltitude to lowland habitats, exceptions being the widespread species *E. delegatensis*, *E. dalrympleana* and the more enigmatic *E. nitida*. The distribution of *E. sieberi* is barely regional (Figure 74) using the type definition (Table 4), and may equally be considered as localised in Tasmania.

These distributions have important implications for the definition of conservation status and subsequent management in the context of genetic variation of the rarer species (Moran and Hopper 1987; Moran 1992). However, the 10 km x 10 km grid-cell scale used in this simple analysis of distributions does not accurately distinguish the species such as *E. barberi* and *E. risdonii* with small populations that are dispersed at a finer scale. Naturally rare species (clustered, dispersed or disjunct populations with a localised geographic range) are the most vulnerable to disturbance and reflect the highest priority for conservation (e.g. Pryor and Briggs 1981; Fry and Benson 1986; Briggs and Leigh 1988; Flora Advisory Committee 1994).

Priorities for conservation management of *E. morrisbyi* (Wiltshire *et al.* 1989, 1991b), *E. risdonii* (Wiltshire *et al.* 1989), *E. perriniana* (Wiltshire and Reid 1987), *E. cordata* (Potts

1989), E. barberi (McEntee et al. 1994) and, indirectly, E. archeri (Potts and Reid 1985a, b) have been considered, but little is known of the rare northern peppermint *E.* aff. *radiata*. Other more regionally distributed species with somewhat localised populations such as E. rubida, E. tenuiramis, E. pulchella and E. sieberi tend to be poorly conserved across parts of their range where this is characterised by intensive land-use practices such as agriculture and forestry. For these species, the conservation priority shifts to population and plant community considerations. Many other regional and widespread eucalypt species can also be identified with reservation needs within their distributions where conservation of the genetic and ecological variability is inadequate. These regional community conservation needs have been addressed in preliminary work combining generalised information on environment, land-use patterns and species or community occurrences (Working Group for Forest Conservation 1990; Kirkpatrick and Brown 1991; Kirkpatrick et al. 1994). However, the adequacy of these conservation measures needs to be more comprehensively addressed using ecological gradient analyses with collated data of species presence and absence (e.g. Austin et al. 1990; Austin 1992) coupled with information on patterns of genetic diversity within the eucalypt species (e.g. Potts 1989).

Key issues in clarifying eucalypt distributions

The propensity of eucalypts for intergradation due to hybridisation, clinal variation or parallel adaptation (Duncan 1989; Figure 1) has led to considerable difficulties in identification of taxa. The recognition of specific regional or environmental locations in which species identifications have been problematic or in which range extensions are likely to be encountered may assist future observers in naming taxa. Many of these problem situations are indicated in the annotated text for each species. However, this study has highlighted several key features of the distribution and taxonomy of the Tasmanian *Eucalyptus* species which require clarification.

Issues of biogeography, taxonomy and genecology

Eucalypts commonly form replacement series or intergrade along environmental gradients, particularly those associated with altitude and substrate, with underlying factors including temperature limits and water availability. For example, in lowland regions of the north and north-west, E. nitida intergrades eastward with E. amygdalina following a gradient of decreasing rainfall, coincident with the geological divide. The 'tongue' of *E. amygdalina* occurrences (Figure 2) on dry sites north of the Pieman River appears to be associated with Devonian or Cambrian volcanics and Ordovician sediments, whilst E. nitida occurs where substrates are underlain by the older Precambrian and Cambrian sediments.

The extension of predominantly eastern species such as E. obliqua, E. viminalis, E. ovata and E. globulus into the habitats of the southwest and west coasts is of considerable biogeographic and genetic interest. Populations in these areas may have adapted to the west coast environment and be genetically differentiated from eastern populations. Near Strahan, for example, white gums ascribed to either E. viminalis or *E. dalrympleana* appear different from their respective eastern populations. Similarly, populations of some different species may converge in their morphological and ecological characteristics. For example, on King Island, the same forest trees in the Kentford State Reserve have been identified as E. ovata and E. brookeriana by different observers. This epitomises the difficulty in distinguishing the two species in western Tasmania where they converge in both morphology and habitat. The maps of these species reveal the potential extent of overlap (Figures 12, 47). In the Eastern Tiers, morphological and habitat differentiation between E. ovata and E. brookeriana is more marked. Recent work by Li et al. (1996) using leaf oil chemistry confirms that the two taxa are distinct in the east (Ladiges et al. 1981, 1984) but difficult to differentiate in the west. The genetic and ecological relationships of the east and west coast forms of *E. ovata* and *E. brookeriana* (series *Ovatae*) require detailed study.

The distribution and affinities of the northern populations of *E. urnigera* on the southern edge of the Central Plateau also require study (Figure 83). Most of our knowledge of the ecology and taxonomy of *E. urnigera* is based on southern populations (e.g. on the Mount Wellington Range and Mount Field). Studies of the northern population at Alma Tier (Potts and Reid 1985a, b) suggest the possibility of consistent differences from the southern populations in morphology, habit and ecology.

Variation within *E. tenuiramis* requires further study. For example, the differences observed by Wiltshire et al. (1991a, 1992) for the northern populations of *E. tenuiramis* near Bicheno and Friendly Beaches may be specific to the granite substrates, whereas *E. tenuiramis* extends onto dolerite substrates in the Eastern Tiers (Figure 80). Similarly, the coastal mallee peppermint on Tasman Peninsula has been variously identified as E. tenuiramis. E. coccifera and E. nitida. but it is believed to have its closest affinities with E. tenuiramis which occurs nearby on mudstone and dolerite substrates (Marginson and Ladiges 1982; Wiltshire et al. 1991a, 1992). However, stabilised populations intermediate between E. coccifera and E. tenuiramis have been reported from near sea-level on Bruny Island and at high altitudes on Alma Tier (Wiltshire et al. 1992; see also Li et al. 1995). A glaucous peppermint in the south-west near Red Point Hills needs its affinities investigated in the context of the coastal mallee peppermints (Figure 80). It is certainly possible that other, as yet unidentified taxa may be lurking within the Tasmanian peppermints.

The peppermint on the Furneaux Group of islands has been classified historically as *E. nitida*, but the disjunction with other populations of *E. nitida* is difficult to explain (Figure 40). The affinities of this peppermint with the west coast ecotype of *E. nitida* and the other coastal peppermints, such as *E. amygdalina* from the north-eastern coastal

plains and related mainland coastal species, have not been adequately determined. Studies of seedling morphology have shown that the peppermint on Flinders Island has affinities with E. nitida (Wiltshire et al. 1992). Studies of leaf oils have suggested that the peppermint on the Furneaux Group of islands is intermediate between the narrower leaved west-Tasmanian E. nitida and a broader leaved E. aff. nitida population occurring on Wilsons Promontory (David Rankin, pers. comm. 1994). On Cape Barren Island, the large degree of variation observed in glaucousness amongst the peppermints is not typical of *E. nitida*. The waxy glaucousness suggests affinities with coastal populations of E. (aff.) tenuiramis which do not have the typical connate juvenile leaf morphology of E. tenuiramis (Wiltshire et al. 1992), and the affinities of these populations require investigation.

All the peppermints in Tasmania are endemic (except possibly E. aff. radiata) and display a high degree of variation due to hybridisation and intergradation (Figure 1). Sharp boundaries between the lowland populations of E. tenuiramis, E. pulchella and E. amygdalina exist in the south-east, usually associated with shifts in substrate. Toward the east coast, the sharp edaphic boundaries and narrow hybrid zones of the south-east break down and the morphological and ecological differences between the species are more diffuse (see Davidson et al. 1981). While hybridisation between all three species is common, the morphological similarity of E. pulchella and E. amygdalina makes identification uncertain where 'half-barked' forms exist. The northern limits to the distribution of *E. pulchella* are similarly difficult to determine. Kirkpatrick and Potts (1987) investigated the genetic affinities of the 'half-barked' forms of the fineleaved peppermint, and concluded this to be *E. amygdalina*. However, recent work on ecotypes of the three lowland peppermints (K. Williams, unpublished data) indicates that the fine-leaved peppermint in the Eastern Tiers is distinct from both the southeastern E. pulchella and E. amygdalina in morphological and ecological characteristics.

Table 5. Distributions of the Tasmanian eucalypts that require clarification. Problems are listed by subgeneric group in no order of importance.

Monocalyptus species

- 1. The putative absence of any *Monocalyptus* species from King Island.
- 2. The north-western extent of the range of *E. delegatensis*.
- 3. The south-western extent of *E. obliqua* from inland valley forests to coastal woodlands.
- 4. The north-eastern limits of E. coccifera, E. pulchella and E. tenuiramis.
- 5. The south-eastern extent of relatively low-altitude occurrences of *E. coccifera*.
- 6. The occurrences of *E. pulchella* and *E. tenuiramis* at relatively high altitudes on the Central Plateau.
- 7. The population discontinuity between the south-eastern and eastern forms of *E. tenuiramis*, and the apparent absence of this species from Maria Island.
- 8. The identity and disjunct distribution of the glaucous peppermint (*E.* aff. *tenuiramis*) in the southwest, and on Cape Barren Island and Flinders Island.
- 9. The northern occurrence of *E*. aff. *radiata*, and a putative location for it in the Murchison River valley.
- 10. The western extent of *E. risdonii* on the foothills adjacent to the eastern shore of the Derwent Estuary.

Symphyomyrtus species

- 1. The western and south-western distribution and taxonomic status of populations with affinities to *E. ovata* and *E. brookeriana.*
- 2. The north-western extent of *E. rodwayi* and the morphological differences between these and the Central Plateau and eastern populations.
- 3. The eastward extent of *E. subcrenulata* on the Central Plateau and its occurrence on southern mountains.
- 4. The eastward extent of *E. johnstonii* in the south-eastern mountains and eastern highlands.
- 5. The north-western and south-western extent of relatively low-altitude occurrences of *E. vernicosa*.
- 6. The putative absence of *E. dalrympleana* from Maria Island.
- 7. The distribution and affinities of populations ascribed to series *Viminales* in coastal regions of the west coast.
- 8. The putative north-eastern occurrence of *E. globulus* near Gladstone and the north-western occurrence near Sandy Cape.
- 9. The extent of *E. urnigera* on the southern Central Plateau, Midlands and Eastern Tiers, and its differentiation from southern populations.

Further work is needed to determine the distributional limits of *E. pulchella* in Tasmania in the context of the taxonomic and ecological variation of the lowland peppermints. Li *et al.* (1995) investigated the chemistry of leaf oils as a means of differentiating the Tasmanian *Piperitae* species but was unable to find suitable species-specific markers. Further work is needed to identify suitable markers, such as DNA or other biochemical traits (e.g. wax chemistry, Li 1993), to distinguish between members of the *Piperitae*.

Distributions requiring clarification

A summary of the main areas requiring clarification in the distribution of *Eucalyptus* species is given in Table 5. Many of these unresolved issues are associated with undersampling in some localities and some regions, particularly in the remote south-west and parts of the Central Plateau and Eastern Tiers. Other issues are associated with outlier or marginal occurrences of species at the limits of their known range. For example, the distributions of the series *Obliquae* and *Ovatae* species are reasonably well known, and the main unresolved issues concern range extensions toward the west. However, it is notable that species from the subgenus *Monocalyptus* are not verified from King Island.

Distributions of particular interest with regard to the series *Piperitae* species include the apparent population discontinuity between the south-eastern and east coast forms of *E. tenuiramis* in the vicinity of the Little Swanport River, Tooms Lake and the Macquarie River, the extent and identity of the glaucous peppermint in the south-west, the extent of *E.* aff. *radiata* in the north, and the north-eastern distribution limits for *E. coccifera, E. pulchella* and *E. tenuiramis* such as in the vicinity of the Fingal Valley.

Amongst the series *Viminales* species, the distributions of particular note for clarification include specific locations for *E. perriniana, E. gunnii* and *E. cordata* in the south-east; the north-eastern and north-western extent of *E. globulus*; and the north-western low-altitude occurrences of *E. vernicosa.* The extent of the yellow gum *E. subcrenulata* on the south-eastern Central Plateau, and the alpine white gum *E. urnigera* on the southern edge of the Central Plateau, also needs to be resolved.

Conclusions

The natural distribution of eucalypts in Tasmania is best explained by considering both historical and ecological factors. For example, the climatic conditions of the last glaciation resulted in a different pattern in extent and juxtaposition of alpine, subalpine and lowland habitats, and the selective nature of environmental gradients affecting clinal variation. It is estimated that mean temperatures were about 5°C lower than present (Davies 1974; Macphail 1979; Kiernan *et al.* 1983), and this equates with the tree-line near the present sea-level on the west coast, rising to about 400–500 m above the present sea-level on the east coast (Macphail 1979). Considering the bathymetric contours of the continental shelf surrounding Tasmania (e.g. Bureau of Mineral Resources 1980), the most extensive area of suitable habitat for eucalypts would have been in the east and south-east (Davies 1974), and the current distribution patterns of many of the endemic *Eucalyptus* species are consistent with their confinement to a south-eastern glacial refuge (Potts and Reid 1985b).

The major rise in mean temperatures between 12 000 and 10 000 years ago, accompanied by rising precipitation, resulted in the expansion of arboreal taxa inland and upslope onto mountains (Macphail 1979). Concomitantly, the distribution range and connectedness of many of the alpine and subalpine taxa would have contracted, and extant populations of species such as E. coccifera, E. gunnii, E. archeri, *E. urnigera* and *E. johnstonii* would have no doubt become isolated in small refugia on mountain regions and coastal hills in the east and south-east. Conversely, the lowland species may have expanded from their isolated refugial habitats into the new lowland areas following the retreat of the glacial and periglacial zones, and the flooding of their former habitat by rising sea-levels. Some of these previously isolated populations may have become genetically distinct (e.g. *E. tenuiramis* populations in the central east coast and the south-east). Other taxa, such as E. aff. radiata, E. regnans, E. brookeriana, E. cordata and E. barberi which currently occupy specialist habitats intermediate in altitude between the subalpine and lowland environments, may have experienced similarly narrow habitat ranges in both glacial and post-glacial times. This may be reflected in the distribution pattern of their extant populations which are frequently small and locally or widely dispersed. Few species truly transgress these altitude zones: exceptions may be the stepped distribution of E. pauciflora and the widespread predominance of *E. nitida* in the south-west.

Outliers in the present-day distributions of eucalypts may be biogeographically significant. For example, they may reflect



Photo 30. Eucalyptus rubida, a species whose occurrence has been greatly reduced by clearing. Mature eucalypts in paddocks have a special role in conservation, particularly for rarer species, because they may be the best evidence in some areas that certain species ever occurred there.

adaptive extensions of the ecological range of a species, or relict or remnant populations, important in the context of genetic resources for both conservation and exploitation.

The *Eucalyptus* species distributions presented in this atlas provide a basis for assessing the significance of population outliers and new localities. They also highlight areas most in need of further work. For example, it is clear from the study that the remoter mountain regions and the west of Tasmania, in general, require more intensive survey. More detailed work is also needed where present or past land-use practices are altering distribution patterns. For example, the introduction of non-provenance species and ecotypes in seed mixes sown for native forest regeneration following logging may confuse the future interpretation of natural eucalypt occurrence and patterns of genetic variation (e.g. Elliott *et al.* 1991). In other areas, where the land has been cleared during the early history of European settlement, remnant trees in farmland (Photo 30) are indicators of natural distribution limits for some eucalypt taxa (e.g. Fensham 1989). These remnants need to be assessed urgently given the rate of clearing of native forest, the increasing dieback of isolated trees, and artificial planting of eucalypts in rural areas that are not necessarily provenances from local sources.

Acknowledgements

The electronic data sources for eucalypt distributions were collated with the cooperation and enthusiasm of staff at Forestry Tasmania, the Tasmanian Parks and Wildlife Service, the Tasmanian Herbarium and the CSIRO Division of Plant Industry. We particularly wish to acknowledge the assistance of Simon Orr, Andrea Manson, Alex Buchanan, Sonya James, Eddie Steenbergen, Colin Reed, Andrew Slee, Peter Cinquini and Kevin Hortle in making these data available. Thanks also to individuals within these Departments and the University of Tasmania, and others who happily rummaged through paper and electronic files to provide additional distributions from specific surveys: Fred Duncan, Stephen Harris, Jamie Kirkpatrick, Mick Brown, Tony Moscal (Tasmanian Conservation Trust files), Mark Neyland, Jean Jarman, Michael Askey-Doran, Jayne Balmer, Jennie Whinam, Phil Barker, Jill Hickey, Karen Johnson, Andrew North, John Hickey, John Grant, Peter Kube, Rob Wiltshire, John Davies, Fiona Coates, Ross Peacock, Jon Marsden-Smedley, Michael Battaglia, Peter Gore, Mirranie Barker, Jill Packham, Ian Brooker and Rob Taylor. We also appreciate the letters, notes and other personal communications provided by other individuals who have assisted us in determining the validity of some occurrences: Stephen Mattingly, David Ziegler, Brett Cusick, Heidi Dungey, Greg Jordan, Alan Gray and Dennis Chester. Thanks to Bill

Jackson, Jamie Kirkpatrick, Fred Duncan, Mark Neyland, Rob Wiltshire, Jim Reid, Mick Brown, Alan Gray, Alex Buchanan and Tony Mount for their patience in the face of our persistent queries. The flowering data were collated with the co-operation of staff of the Tasmanian Herbarium and with the technical assistance of Peter Gore, Milton Savva, Heidi Dungey and Anne McEntee.

Thanks to Michael Henry and Tony Grainger at the University of Tasmania Computing Centre in Hobart who provided advice on databasing in ORACLE and cheerfully allocated sufficient space for the growing list of records. We are also indebted to Simon Orr, Tony Rainbird and Andrea Manson for cartographic assistance in the early draft production stages of the maps. The final distribution maps were produced using MAPSPECIES software (version May 1996) written for MacIntosh computers by Mark Fowler (Dept. of Geography and Environmental Studies, University of Tasmania). The inset Australia-wide distribution maps were reproduced from G.M. Chippendale's (1988) account in Bureau of Flora and Fauna, Flora of Australia, Vol. 19: Myrtaceae - Eucalyptus, Angophora, AGPS, Canberra (maps: 137, 141, 146, 154, 411, 413, 441, 451, 460, 462, 470), Commonwealth of Australia copyright reproduced by permission from the Australian Government Publishing Service and the Australian Biological Resources Study. We also thank Fred Duncan for allowing us to include his drawings of selected eucalypt species (Figures 5, 27, 46), and acknowledge the use of photos from Fred Duncan (Photos 14, 18), Humphrey Elliott (Photos 6, 17, 26, 27), Dennis Harding (Photo 2), Jean Jarman (Photos 5, 12, 13, 16, 19, 28, 29) and the Tasmanian Herbarium (Photos 3, 4, 7, 11, 15, 20, 24, 25).

We gratefully acknowledge Jean Jarman, Mick Brown, Jim Reid, Humphrey Elliott and Fred Duncan for their friendly cajolery and helpful comments on the manuscript, and suggestions in the editing and final production stages of this atlas. This work was undertaken by KJW as part of post-graduate study supported by a Commonwealth Department of Primary Industry and Energy Forestry Scholarship.



Figure 92. Sampling intensity. Figures shown in each 10 km x 10 km grid cell indicate the number of eucalypt records used.



Figure 93. The number of different data sources per 10 km x 10 km grid cell used to compile the atlas.



Figure 94. The number of eucalypt species recorded in each grid cell. (Twenty-nine taxa occur in Tasmania.)



Figure 95. The number of Monocalyptus species recorded in each grid cell. (Twelve taxa occur in Tasmania.)



Figure 96. The number of Symphyomyrtus species recorded in each grid cell. (Seventeen taxa occur in Tasmania.)



Figure 97. The number of series Oblique species recorded in each grid cell. (Five taxa occur in Tasmania.)



Figure 98. The number of series Piperitae species recorded in each grid cell. (Seven taxa occur in Tasmania.)



Figure 99. The number of series Ovatae species recorded in each grid cell. (Four taxa occur in Tasmania.)



Figure 100. The number of series Viminales species recorded in each grid cell. (Thirteen taxa occur in Tasmania.)



Figure 101. The number of endemic eucalypt species recorded in each grid cell. (Seventeen endemic eucalypt taxa occur in Tasmania.)



Figure 102. The number of non-endemic eucalypt species recorded in each grid cell. (Twelve non-endemic taxa occur in Tasmania.)



Figure 103. The number of altitude records in each grid cell that was used to compile the altitude profiles.





Figure 105. Flowering time of the genus Eucalyptus and its subgroups in Tasmania: Eucalyptus (a); subgenera Monocalyptus (b), Symphyomyrtus (c); and the series Obliquae (d), Ovatae (e), Piperitae (f) and Viminales (g).



Figure 106. Eucalypt distribution types. The display shows the number of grid cells in which a species occurs compared with the number of grid cells in the envelope which defines its geographic range (see Table 3). Species may be aggregated, dispersed or scattered within localised, regional or widespread distributions (see Table 4). A species is 100% aggregated if the number of grid cells in which it occurs is equivalent to the number of grid cells across its range. A species is 50% aggregated if it is at least present in half of the cells across its range. Abbreviations refer to the first three letters of the species name.