COMPARATIVE GROWTH RATES OF SEVERAL

EUCALYPTS IN MIXED-SPECIES STANDS IN

SOUTHERN TASMANIA

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Diameter increments, heights, and bark thicknesses are compared for trees of **Eucalyptus regnans, E. obliqua,** intermediates between these two species, and **E. globulus** occurring naturally in 13 mixed-species stands of even-aged tall-open forest aged 20–79 years in south-eastern Tasmania. **E. regnans, E. obliqua,** and intermediates did not differ consistently or substantially in growth rates in any of these parameters except that **E. obliqua** generally had thicker bark than **E. regnans. E. globulus** had higher diameter increments than the other species at about 20 years of age but lower increments after about 40 years of age. Height or bark thickness of **E. globulus** did not differ consistently from the other species at any age except that its bark was thinner than that of **E. obliqua.** It is concluded that **E. globulus** might be favoured for short rotations because of its higher diameter increments at younger ages and the other species might be favoured for longer rotations. There seemed to be no silvicultural reason to favour any one of **E. regnans, E. obliqua,** or intermediates over the others when these species are growing naturally in mixture.

INTRODUCTION

The tall-open, even-aged, regrowth eucalypt forests of south-eastern Tasmania normally consist of mono-specific stands of the various eucalypt species of the region. Sometimes, however, mixed-species stands containing several eucalypts occur. To maximise timber production in these mixed-species stands, it may be desirable to manipulate the species composition to favour the faster growing species.

This work compares diameter increments, heights and bark thicknesses of trees of *Eucalyptus regnans* F. Muell., *E. obliqua* L 'Herit., intermediates between these two species, and *E. globulus* Labill. occurring naturally together in even-aged, mixed-species stands aged 20–79 years. The results are considered in relation to stand dynamics and silviculture of these forests.

SOURCE OF DATA

Since about 1950, 88 plots have been established in a 20 km² area of the eucalypt forests of south-east Tasmania at about 43° 30′ S, 147° E. A few plots were also established on the nearby Tasman Peninsula. These areas are undulating to hilly, rising

from sea level to 450 m altitude. The climate is temperate with appreciable rain in both summer and winter, averaging about 1400 mm annually. The forests in these areas had regenerated naturally after fires from about 1860. Much of the virgin forest had been logged before burning.

The plots were located in both pure and mixed-species stands of *E. globulus*, *E. regnans*, *E. obliqua*, and intermediates between the latter two species. Trees of *E. regnans* were identified by the presence of 1–2 m of rough bark at the base of the stem, trees of *E. obliqua* had rough bark extending to the small branches, and intermediates had rough bark from about one-third to full stem height; Ashton (1958) has described other properties of this group of closely related species. The plots were located subjectively in stands judged to be even-aged, which meant they had not suffered any major fires after regeneration, and to have "full' stocking. They therefore do not represent properly the forests of the region but generally represent the commercially most valuable stands.

The plots varied in area from 0.1 to 0.4 ha and in age from 6 to 90 years. They have been measured several times at intervals varying from 3 to 8 years. At each measurement the diameter at breast height (1.3 m) over bark of each tree greater than 10 cm diameter (and occasionally smaller trees in younger plots) was measured with a girth tape. As well, a sample of trees was selected from each plot and measured for height and bark thickness at breast height. These samples were biased towards the larger diameter trees on the plot as described elsewhere (West 1979a).

METHODS

The object of this work was to compare growth rates of the different species in mixed-species plots. To do this, the whole data set available was reduced by removing data from single-species plots and those which contained only a few individuals of other species. When this was done 13 plots remained each containing 2 or more of the species of interest. Each species in these plots was represented by at least 20 trees, distributed over the range of diameters of all trees of the plot, and each species constituted at least 20% of the total trees of the plot. The ages, stockings, and basal areas of the selected plots are shown in Table 1. The two youngest plots selected were on the Tasman Peninsula and the rest were in the main study area.

Unfortunately, the selected plots had not been measured over a sufficiently long period to usefully examine changes in tree growth patterns with time in individual plots. Thus, one increment period was randomly chosen from all those available for each plot. The length of the increment period in each plot is shown in Table 1. Any data available from a plot after it had been affected by the disease known locally as regrowth dieback (West 1979b; Podger *et al.* 1980) were ignored.

For each species in each selected plot, the relationship between individual tree diameter increment and tree diameter at the beginning of the increment period was computed. It has been shown elsewhere (West 1980) that in these forests this relationship may be adequately represented by a quadratic function. Because of heteroscedasticity in the data, the relationship was fitted by weighted least squares regression in which it was assumed that the variance of the residuals from regression varied directly as the square of initial tree diameter. Examples of the relationships fitted in two

TABLE 1—Characteristics of the plots used in this work. Age, stocking, and basal area were determined at the beginning of the increment period used

Plot	Age (years)	Stocking (stems/ha)	Basal area (m²/ha)	Length of increment period (years)
R24	20	1501	30	4
R23	21	1788	29	4
069	24	1002	36	3
018	31	682	39	3
R4	37	913	56	3
R3	37	757	56	3
066	39	613	46	3
064	42	830	56	4
057	60	322	57	3
023	61	529	59	3
G8	66	294	50	8
G1	71	529	65	3
R5	79	306	83	3

arbitrarily selected plots are shown in Fig. 1. In this work tree diameter increments were studied rather than tree diameters since the latter are a consequence of the unknown history of stand development. Current diameter increments, on the other hand, express the present behaviour of the stand and by relating increments to tree diameters, differences between species resulting from past stand history are removed.

After the regression relationships for each species in each plot were computed, a covariance analysis was performed for each plot to test the significance of the differences between diameter increments of the various species in the plot. Firstly, a test was done to determine whether the fitted curved lines of the plot were parallel. If the lines were not significantly non-parallel, a subsequent test was done to determine the significance of the differences of the intercepts of the regression lines on the Y-axis. Where appropriate, significances of differences between adjusted means were then determined with a least significant difference test with $P = 0.05$. For the present work, it was necessary to compare the different species in each individual plot rather than to treat the plots as replicates and combine the data over all plots. This was due to the wide ranges of ages and sites of the plots which caused substantial differences in the coefficients of the regression equations of different plots; there was insufficient information available on plot characteristics for this work to adequately explain these differences.

It is known that both tree height and bark thickness are closely related to tree diameter in these forests (West 1979a). This allowed comparison of heights and bark thicknesses of different species in a particular plot at a given age. West (1979a) showed that the most appropriate relationship relating height and bark thickness to diameter in these forests was non-linear in its parameters. To facilitate covariance analysis, a relationship that was linear in its parameters was required. It was found that a quadratic relationship fitted by ordinary least squares was adequate for this purpose. Only some of the plots that were used to compare diameter increments of different species had had samples of trees selected for height or bark thickness measurement. These are indicated

in Table 2. In each of these plots covariance analyses were performed to compare heights and bark thicknesses of trees of different species at the same ages as shown in Table 1 for diameter increments.

TABLE 2—Diameter increments, heights, and bark thicknesses of different species in various plots. Results shown are the adjusted means from covariance analysis for each plot. The tree diameter at which the adjusted means of any one plot were computed is shown in the second column. Spaces left blank indicate the species concerned was not present in the plot

Plot	Diameter of adjusted mean (cm)	Significance of test of parallelism	Significance of differences between intercepts	Species			
				E. regnans	E. obliqua	Intermediates	E. globulus
				Adjusted mean tree diameter increment (cm/year)			
R24	15.4	*	—	**			**
R23	13.7	*	—	**			**
069	20.4	ns	*	0.20a	0.27b	0.22a, b	
018	25.2	ns	ns	0.30	0.31	0.32	
R4	26.7	ns	ns		0.33	0.35	
R3	31.2	ns	ns	0.50	0.40	0.47	
066	29.1	ns	ns		0.38	0.31	
064	28.2	ns	*	0.35	0.27a	0.28a	0.12
057	43.8	ns	ns		0.31		0.37
023	36.6	ns	ns		0.25	0.23	
G8	42.7	ns	*	0.36			0.24
G1	37.8	ns	*		0.28		0.21
R5	56.0	*	ns	0.50	0.39		
				Adjusted mean tree height (m)			
R24	19.6	*	—	**			**
R23	21.9	ns	ns	22.2			22.0
064	35.7	ns	ns	34.2	32.8	32.5	33.6
G8	49.8	*	—	**			**
G1	42.3	ns	*		32.4		37.9
R5	64.8	ns	*	50.5	47.2		
				Adjusted mean tree double bark thickness (cm)			
066	33.0	ns	*	4.6a	5.3	4.8a	
064	35.7	ns	*	3.9a	5.3b	4.9b	4.2a
G8	49.8	ns	ns	4.9			4.7
G1	42.3	ns	*		7.1		4.3
R5	64.8	ns	ns	6.6	7.7		

a, b Adjusted means with similar superscripts do not differ significantly, as determined by an LSD test with P = 0.05

*   Significant difference (P < 0.05 at least)

**   The species concerned was present in the plot, but adjusted means have no meaning since slopes of regressions differed significantly.

RESULTS

Diameter increment

Results of the covariance analyses are shown in Table 2. For diameter increments, the fitted regression equations were significantly non-parallel in the two youngest plots. Both of these contained *E. regnans* and *E. globulus.* The regression relationships fitted in one of these plots are shown in Fig. 1 (a). Results in the other plot were similar. The figure shows that diameter increments of trees of *E. globulus* were generally greater than trees of *E. regnans* of the same initial diameter. This effect became larger with increasing initial diameter. The other plots in which *E. globulus* occurred (064, 057, G8, G1) were all older than 40 years. In none of these were the regression lines significantly non-parallel, but in 3 of them intercepts differed significantly. Examinations of the adjusted means in these 3 cases shows that *E. globulus* had lower diameter increments than the other species. One of these cases is shown in Fig. 1 (b). These results suggest that *E. globulus* has higher rates of diameter growth than the other species at ages around 20 years but lower rates after at least 40 years of age. This result may have been confounded by the fact that the two youngest plots were located on the Tasman Peninsula.

Diameter increments of *E. regnans, E. obliqua,* and intermediates were then considered. In one plot (R5), the regression lines were significantly non-parallel. Examination of the fitted curves in this plot showed that this was due only to a greater number of small diameter low increment trees for one species than the other, causing a more pronounced curve in the relationship for that species at lower diameters. Among the larger diameter trees in this plot there were no significant differences between diameter increments of trees of the two species. If this is borne in mind, Table 2 then shows there were no consistent or large differences in diameter increments of trees of *E. regnans, E. obliqua,* or intermediates in any of the plots, although there were occasional specific differences in individual plots as follows. In one plot (069) *E. obliqua* showed significantly greater increments than *E. regnans.* In a second (064, which is shown in Fig. 1 (b)) the reverse applied, and in three others (018, R3, R5) there were no significant differences between these two species. In one plot (064) intermediates showed significantly lower diameter increments than *E. regnans,* but did not differ significantly from *E. obliqua.* In other plots containing intermediates, tree diameter increments did not differ significantly from those of trees of *E. regnans* or *E. obliqua.*

Height

In the limited data available there were no consistent differences between heights of trees of the different species. Table 2 shows that in two plots (R24, G8) the regression relationships relating tree height to diameter were significantly non-parallel. In both these cases trees of *E. globulus* were taller than trees of *E. regnans* at larger diameters, but this difference was less pronounced in the older plot. In one plot (064) *E. globulus* did not differ significantly from the other species and in another plot (G1) *E. globulus* trees were significantly taller than those of *E. obliqua.* In one plot (R5) trees of *E. regnans* were significantly taller than those of *E. obliqua* and in another (064) there were no significant differences among *E. regnans, E. obliqua,* or intermediates.
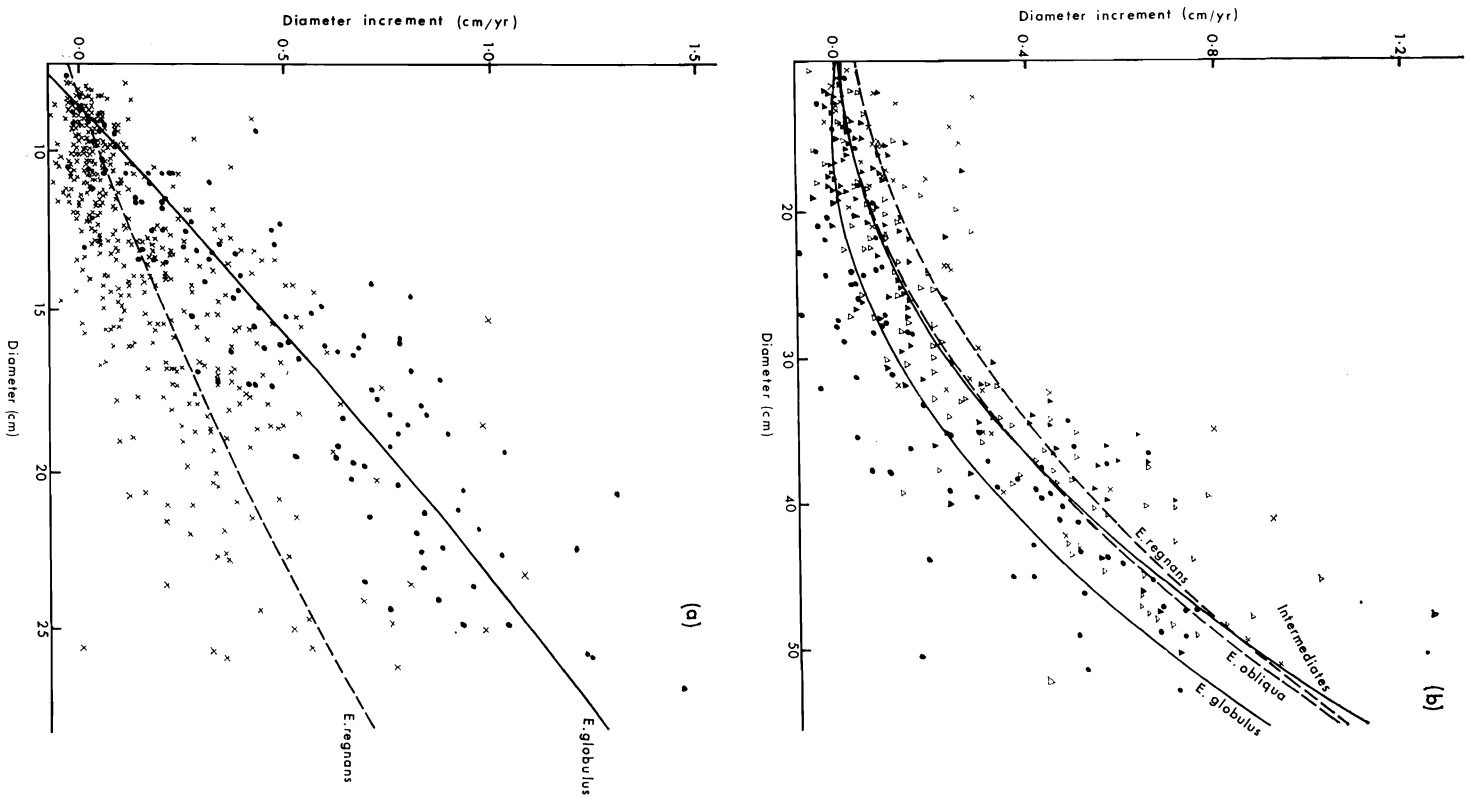
FIG. 1—The relationships between tree diameter increment and initial tree diameter, fitted
as quadratic functions by weighted least squares regression, for different species:
(a) plot R23; (b) plot 064. ✕ **E. regnans**, △ **E. obliqua**, ▲ intermediates,
● **E. globulus**.

Bark thickness

Trees of *E. obliqua* generally had significantly thicker bark at breast height than the other species in the limited data available. Table 2 shows that, except for the oldest plot, *E. obliqua* had significantly thicker bark than *E. regnans* or *E. globulus*. *E. regnans* and *E. globulus* did not differ significantly in bark thickness. In one plot (066) intermediates had bark significantly thinner than that of *E. obliqua,* and in another (064) bark thickness of intermediates did not differ significantly from that of *E. obliqua.*

DISCUSSION AND CONCLUSIONS

Because eucalypts tend to be intolerant of shade and competition (Opie *et al.* 1978), it might be expected that a species which showed more rapid growth than other species would dominate a site and possibly exclude the other species at an early stage of stand development. Whether or not this happened would depend on a complex interaction between the particular species present, their relative frequencies of occurrence, and their adaptation to the particular site on which they were growing. The complexity of these dynamic processes has been well described for a mixed-species forest of north-west USA (Wierman & Oliver 1979).

The results of the present study showed that, after age 24 years, there were no consistent or large differences in growth rates between *E. obliqua, E. regnans,* and intermediates growing in mixed-species stands containing two or more of these species. The few small differences that did occur may have reflected a better adaptation of the faster growing species to the site concerned. In general, there was little evidence that once such mixed-species stands have developed past age 24 years (at most), they are likely to change appreciably either in their species composition or the relative position in the stand occupied by the different species. In silvicultural terms, this suggests that there would be little gain in manipulating the forest to favour any of these species over the others unless any one had more desirable wood properties than the others.

Ellis (1971) and Griffin & Eldridge (1980) showed that when the two species were grown at the same location, *E. regnans* grew faster than *E. obliqua* in diameter and height up to 15 years of age. *E. regnans* showed this advantage even when growing on a site which formerly carried natural, mono-specific stands of *E. obliqua.* This suggested that *E. regnans* might normally have a competitive advantage during early development of a mixed-species stand. The results in the present work suggest that this advantage may not continue in later years. It should be noted that the circumstances of the earlier experiments differed from the present case in that seedlings had been raised from seed collected from parent trees that were growing in mono-specific stands. This meant that the seedlings would have been adapted to different sites since *E. regnans* tends to occur naturally on moister and more fertile sites than *E. obliqua* (Cochrane 1969; Ashton 1976). In the present work, stands had developed naturally from parent trees which had evolved under the same environmental conditions. Further work needs to be done to determine the genetic relationships between *E. regnans, E. obliqua,* and intermediates, and their interaction with the environmental conditions under which they are grown, before the dynamics of mixed-species stands may be properly understood.

The diameter growth rate of *E. globulus* was found to be greater than that of the other species at about 20 years of age. This suggests that *E. globulus* might tend to dominate a site during early development of a mixed-species stand. The plots in which

the rapid growth of *E. globulus* was observed had in fact been measured at several ages since 7 years of age. Examination of these early records suggested that there were sufficient *E. regnans* trees present in the stands to prevent complete domination by *E. globulus*. At ages past 40 years it was found that *E. globulus* generally had lower rates of diameter growth than the other species. This suggests that *E. globulus* might tend to lose its relative position as a stand develops to maturity. In silvicultural terms these results suggest that *E. globulus* might be preferred if short rotations were envisaged but not for longer rotations.

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