

Selfing Effects in *Eucalyptus regnans*

By K. G. ELDRIDGE and A. R. GRIFFIN¹⁾

(Received 16th February 1983)

Summary

A successful technique for self-pollination of *Eucalyptus regnans* was developed. Of 14 trees examined 13 were definitely self-fertile to some extent. However, the numbers of viable seed set from self-pollination per 100 flowers and per capsule were on average less than from open-pollination or cross-pollination and were highly variable from tree to tree.

In a field trial comparing four selfed families, four open-pollinated families and one outcrossed family the growth of the selfed families was not significantly different from the others until after two years. By 13 years the selfed families were suppressed and many trees had died, in contrast to the vigorous growth and high survival of the outcross. The growth and survival of the open-pollinated families were intermediate between the outcross and the selfed families. Implications for the eucalypt breeder and plantation grower are discussed. It is suggested that the results support the contention that the mixed breeding system of this species is maintained by selection against inbred trees through self-thinning of the stand.

Key words: *Eucalyptus regnans*, self pollination, self fertility, inbreeding depression.

Resumé

On a développé une technique réussie pour l'auto-pollinisation d'*Eucalyptus regnans*. Sur 14 arbres étudiés, 13 étaient nettement autofertiles dans une certaine mesure. La quantité de semis par 100 fleurs et par capsule produite après l'auto-pollinisation était cependant en moyenne moindre que celle résultant de la pollinisation ouverte ou de la pollinisation croisée, et variait considérablement d'un arbre à l'autre.

Au cours d'un essai pratique dans lequel on a comparé quatre familles autofécondées, quatre familles à pollinisation ouverte et une famille outcross, la croissance des familles autofécondées ne différait pas significativement avant l'âge de deux ans de celle des autres groupes. A 13 ans les familles autofécondées étaient supprimées et beaucoup d'arbres étaient morts, ce qui contrastait à la croissance vigoureuse et au taux élevé de survie de la famille outcross. En ce qui concerne la croissance et le taux de survie, les familles à pollinisation ouverte occupaient une position intermédiaire entre les familles outcross et les autofécondées. On discute les implications pour les sélectionneurs d'eucalyptus et les exploitants des plantations. On propose que les résultats soutiennent la thèse que le système à sélection mixte de cette essence se maintienne par une sélection dépendante de la densité contre des arbres consanguins pendant les premières phases végétatives du cycle vital.

Zusammenfassung

Ein erfolgreiches Verfahren zur Selbstbestäubung von *Eucalyptus regnans* wurde entwickelt. 13 von 14 untersuchten Bäumen waren mit Sicherheit bis zu einem gewissen Grad selbstfertil. Allerdings war die Zahl der lebensfähigen Samen pro 100 geselbsteten Blüten und pro Kapsel im Durchschnitt niedriger als nach freier Abblüte oder Kreuzung, aber die Unterschiede von Baum zu Baum waren sehr hoch.

¹⁾ CSIRO, Division of Forest Research, PO Box 4008, Canberra, ACT 2600, Australia.

In einem Feldversuch mit vier Selbstungsfamilien, vier aus freier Abblüte hervorgegangenen Familien und einer Kreuzungsfamilie war das Wachstum der Selbstungsfamilien in den ersten 2 Jahren nicht signifikant von den anderen Familien verschieden. Nach 13 Jahren waren die Selbstungsnachkommen aber im Vergleich zu dem kräftigen Wachstum und der hohen Überlebensrate der Kreuzungsnachkommen unterdrückt und viele Bäume davon abgestorben. Das Wachstum und Überlebensprozent der aus freier Abblüte hervorgegangenen Familien lag zwischen den Selbstungs- und Kreuzungsfamilien. Folgerungen für die Eukalyptuszüchter und Plantagenpflanzer werden diskutiert. Diese Ergebnisse scheinen die Behauptung zu unterstützen, daß das gemischte Breeding-System dieser Art durch die Selektion gegen ingezüchtete Bäume auf dem Wege einer natürlichen Läuterung erhalten wird.

Introduction

To develop sound breeding strategies it is necessary to understand the reproductive biology and breeding system of a species. The consequences of inbreeding are particularly important as they influence choice of breeding population size and seed orchard design.

Most conifer species, if self-pollinated, set some seed but the resulting progeny show inbreeding depression for early survival and growth rate (LIBBY *et al.* 1981). However under normal conditions where mixed self and outcross pollination occurs lack of viability of inbred zygotes may still lead to a high effective crossing rate. For example *Pinus radiata* D. DON is a self compatible species (PAWSEY 1964) but MORAN *et al.* (1980) estimated an outcrossing rate (t) in excess of 0.90 in a clonal seed orchard of this species. For practical purposes the conifer breeder and seed orchardist may therefore be able to ignore the effects of the most severe form of inbreeding, self-fertilization.

By contrast the few eucalypt species which have been investigated to date appear to be more self-fertile than conifers under controlled self pollination (PRYOR 1951, GUIMARAES and KERR 1959, ELDRIDGE 1970, HODGSON 1976).

Eucalypts have also been shown to produce a significant proportion of inbred progeny under open pollination. Using six morphological markers Hodgson (1976) estimated selfing rates of about 30% (10% to 38%) for 5 trees of *Eucalyptus grandis* HILL ex MAIDEN. ELDRIDGE (1970), using a marker with 'curled' leaves, estimated that 28% of the progeny from the lower part of the crown of a large tree of *E. regnans* F. MUELL. were selfs.

Recent studies using allozyme polymorphisms in germinating seed and young seedlings have led to the following estimates of effective outcrossing rates (t) between 0.69 and 0.84 in natural populations of nine eucalypt species (MORAN and BELL 1983).

The consequences of such a proportion of inbred individuals in open-pollinated progenies in terms of crop productivity and uniformity, or indeed for the breeder who wishes to screen selections by testing open-pollinated progeny, will largely be determined by the extent and variability of inbreeding depression expressed in each species.

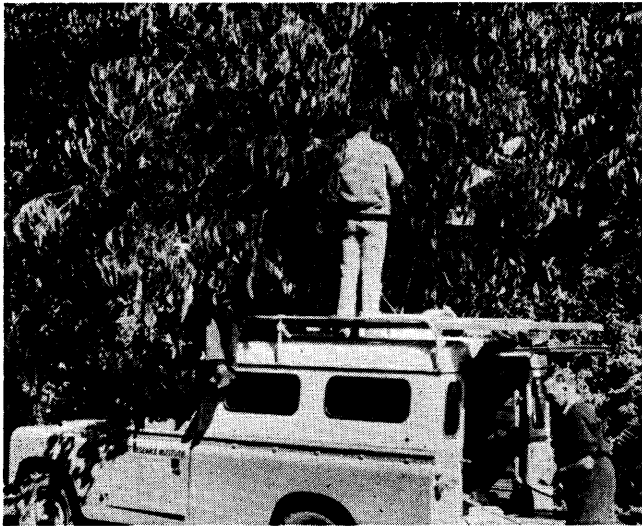


Figure 1. — Pollination of tree no. 184 on a roadside near Jeeralang in 1965 using silk organza bags and sleeves.

E. regnans (mountain ash) is an important timber tree in southeastern Australia (HALL *et al.* 1970). Breeding system studies of the species were commenced in 1962 near Traralgon, Victoria, on roadside trees (Fig. 1) scattered over a distance of 6 km in a continuous natural population. This paper reports some early studies designed to develop suitable controlled pollination techniques, assess levels of self-fertility in naturally occurring individuals, and to test selfed, outcrossed, and open-pollinated progenies in the field.

Controlled Pollination Technique

At the time work began (1962) techniques for reliable, efficient controlled pollination of eucalypts were not well developed. KRUG and ALVES (1949) had used paper bags in unsuccessful attempts to self-pollinate seven species in Brazil. PRYOR (1951) found that muslin or organdie bags had less harmful effects on flower development and obtained selfed seed from hand pollination of emasculated flowers. Subsequently GUIMARAES and KERR (1959) and PRYOR and BODEN (1962) used bees and blowflies as self-pollinating agents on bagged, unemasculated, flowers.

During the 1963–66 flowering seasons silk organza and cotton organdie bags were used for isolating flowers, and unwoven terylene was tested in 1967. The latter effectively excluded all pollen (as judged by lack of seed set on emasculated bagged flowers, Table 1), but the silk and cotton bags did permit some contamination. The pore size of the organdie was approximately 150 μ , considerably larger than the diameter of *E. regnans* pollen, 20 to 23 μ (PIKE 1956). Unwoven terylene was successfully used for the first time in 1967 (Table 1).

Table 1. — Test of contamination through bags. Emasculated flowers enclosed: O organza or organdie bags (1963–6), T unwoven terylene (1967).

Material	Flowers enclosed	Mature capsules	Seed germinated	Seed per capsule	Seed per 100 flowers
O	1110	51	40	0.8	3.6
T	154	0	0	0	0

Experience has shown that, where flowers are some distance from the growing tip, foliage damage is reduced if the bag is opened at the distal end and applied as a sleeve. Sleeves of loosely woven cotton fabric supported by a wire spiral are used in controlled pollination of *E. grandis* (VAN WYK 1977). Unwoven terylene bags and sleeves have been used successfully in all subsequent *E. regnans* pollination studies (e.g. GRIFFIN and HAND 1979).

Self-Fertility Studies

Capsule and seed yields were determined following three alternative methods of selfing (A, B, C), cross pollination of emasculated flowers (D), and open pollination (E). Pooled results by treatments over all test trees and seasons are given in Table 2. It should be noted that, because of the type of bag used, data collected in 1963–66 are subject to about 5 to 10% contamination (Tables 1 and 2), but such bias should apply equally to all treatments.

The data in Table 2 indicate that the percentage of flowers developing into mature capsules is apparently little affected by pollen source but on average a higher yield of viable seed per capsule is obtained from outcrossing compared with self pollination. Treatments A (2.3 seeds/capsule) and D (4.3 seeds/capsule) most directly bear

Table 2. — Seed set from self- and cross-pollination. Data combined from four seasons of pollination, 1963 to 1967.

Treatment	A selfed emasculated	B selfed not emasc.	C selfed, flies not emasc.	D crossed emasculated	E open- pollinated
Number of trees providing data	4	11	6	3	4
Number of bags	19	85	19	19	-
Flowers	402	2500	948	321	937
Mature capsules per 100 flowers	20	15	13	15	13
Seed germinated per mature capsule	2.3	2.3	4.0	4.3	2.8
Seed germinated per 100 flowers	47	42	22	90	71

on this point (Table 2). Open-pollinated seed yield in the trees sampled was similar to that from selfing.

Among the three selfing treatments hand pollination (A) resulted in lower seed set than that which occurred when un-emasculated flowers were bagged and allowed to pollinate through the action of gravity and wind movement (B). Support for the proposition that pollen can move within a bag of un-emasculated flowers comes from the occasional observation of pollen on leaves in the lower crown of *E. regnans* trees. Evidently pollen of this species can fall under the influence of gravity in some weather conditions. A possible explanation for the low seed set for treatment A is that the hand pollination was not carried out at the optimum receptivity stage for each flower (GRIFFIN and HAND 1979), whereas in treatment B variation in development rate of individual flowers (GRIFFIN 1980) would ensure that pollen would be present when all but the last stigmas were receptive.

The technique developed by PRYOR and BODEN (1962) using blowflies (*Calliphora auger* F.) (treatment C) as pollen vectors inside isolation bags, appeared to result in some increase in selfed seed set. However, subsequent

Table 3. — Variation between trees in seed set following self-pollination of 14 *E. regnans* trees. Data combined from 4 seasons of pollinations, 1963 to 1967, and from self-pollination treatments (A, B, C Table 2).

Tree number	No. of bags	No. seasons self attempted	No. of flowers enclosed	Mature capsules per 100 flowers	Viable seed yield			
					Total	per capsule	per 100 flowers	per gram of seed + chaff
181	20	4	941	3	12	0.9	3	160
182	6	2	202	42	24	0.3	16	50
183	6	2	184	7	12	1.0	7	150
184	18	4	810	20	280	1.8	34	170
185	6	2	159	0	0	-	-	-
186	2	1	50	2	4	4.0	8	570
187	6	2	185	34	14	1.1	28	200
188	4	1	166	10	18	1.5	17	130
189	16	3	520	39	975	4.7	180	420
191	16	3	679	3	46	3.1	10	410
192	16	2	475	7	240	6.9	51	720
193	20	1	458	6	45	1.5	10	130
194	4	1	101	9	4	0.6	4	60
195	1	1	25	28	5	0.7	20	60

work confirmed that treatment B was quite adequate for determining relative self fertility of individuals in this species, and for obtaining adequate seed for genetic studies. This treatment (B) is extremely simple as no emasculation is required and each bag is only handled twice: for application and removal. The additional trouble of obtaining and inserting pollen-free flies is therefore not justified.

The average germination per gram of seed plus chaff was 280 from self-pollination (A, B, C combined), 327 from open-pollination (E) and 445 from cross-pollination (D). Although on average selfing led to reduced seed yield, wide tree to tree variation was evident (Table 3).

Of the 14 trees tested four yielded more selfed seed per capsule than the open pollinated average of 2.8 seeds (Table 2) and are considered highly self fertile, while nine produced lesser quantities of seed. Only one tree (185)



Figure 2. — Plots of trees resulting from cross-pollination (193 × 181) left and self-pollination (193 × 193) right at 9 years.

produced no capsules or seed. Although selfing was attempted in two seasons the tests were not considered sufficient to clearly indicate that tree 185 was completely self-sterile.

Growth and Survival of Selfed Progenies

To evaluate the consequences of selfing on subsequent growth and survival of progeny, selfed, controlled outcross

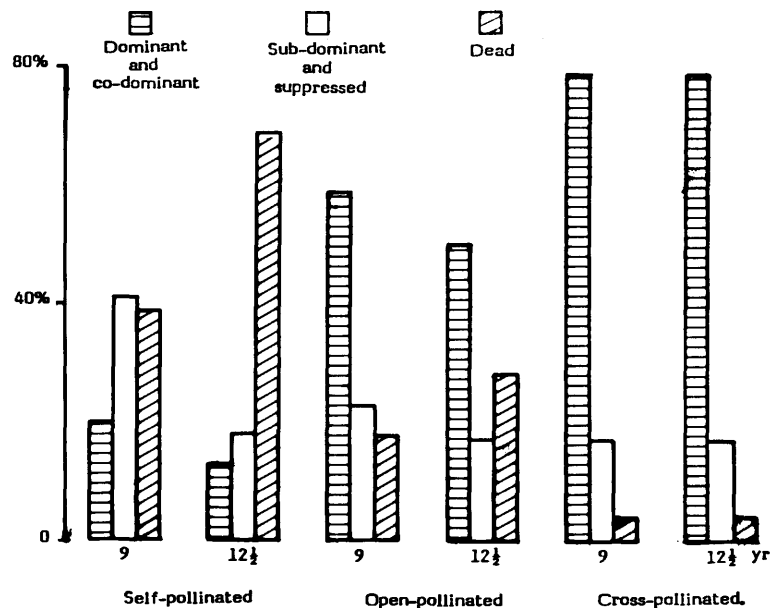


Figure 3. — Crown classification of self-, open-, and cross-pollinated trees in field trial at 9 and 12 1/2 years.

and open-pollinated seedlots were raised. Because of problems in the nursery only four selfed families were available for planting, together with four open pollinated seedlots from the same parent trees and one outcrossed family (193 × 181) (Table 4). The trial was planted at Jeera-

lang, Victoria (latitude 38° 27' S, longitude 146° 28' E, altitude 600 m) in August 1969 on a high quality *E. regnans* site with an annual rainfall of approximately 1300 mm. The nine families were laid out in a randomised complete block design with six-tree row plots at a spacing of 2.7 × 2.4 m

Table 4. — Comparison of selfed (S) and open pollinated (O) families of four trees with one outcross (C). Trait means over 4 replications of 6 tree plots.

Trait	Age from planting yr	Parent tree number												COMBINED					
		189			192			184			193			Sig. ^c	LSD _{0.05}	S	O	Sig. ^d	S-O
S	O	S	O	S	O	S	O	S	O	S	O	C							
Survival †	½	100	100	91.6	95.8	95.8	95.8	95.8	95.8	100	100	100	100	NS	5.0	96.9	97.9	NS	-1
Survival †	1½	95.8	95.8	83.3	79.2	83.3	95.8	66.7	91.6	95.8	95.8	95.8	*	17.8	82.3	90.6	NS	-9	
Survival †	5	95.8	95.8	70.8	70.8	41.7	91.6	62.5	87.5	95.8	95.8	95.8	***	12.0	67.7	86.5	***	-22	
Survival †	9	91.6	95.8	62.5	62.5	33.3	91.6	62.5	87.5	95.8	95.8	95.8	***	10.6	62.5	84.3	***	-26	
Survival †	12½	62.5	83.3	25.0	45.8	20.8	70.8	16.7	75.0	95.8	95.8	95.8	***	6.3	31.2	71.9	***	-57	
Height m	½	0.55	0.59	0.56	0.48	0.59	0.67	0.49	0.75	0.64	0.64	0.64	NS	0.09	0.55	0.62	NS	-11	
Height m	1½	2.06	2.07	1.93	1.90	1.81	2.10	1.68	2.46	2.22	2.22	2.22	*	0.42	1.87	2.13	**	-12	
Height m	5	9.75	9.88	8.14	8.44	7.86	9.27	8.23	9.97	10.03	10.03	10.03	**	1.17	8.49	9.39	***	-10	
Height m	9½	23.6	24.2	20.7	20.9	19.3	22.2	16.7	24.1	23.3	23.3	23.3	**	1.60	20.1	22.8	***	-12	
Diameter cm	5	11.4	12.7	9.2	9.7	10.4	11.2	8.4	12.4	13.3	13.3	13.3	***	2.15	9.8	11.5	***	-15	
Diameter cm	9	16.7	19.6	14.3	15.8	16.0	18.0	10.6	19.0	22.2	22.2	22.2	***	3.16	14.4	18.1	***	-20	
Diameter cm	12½	21.1	23.9	21.9	22.5	22.9	25.2	15.6	25.1	26.3	26.3	26.3	**	2.13	20.4	24.2	***	-16	
Branch angle	9	2.98	3.14	2.80	2.73	2.72	2.60	1.93	2.67	2.76	2.76	2.76	NS	1.03	2.61	2.78	NS	-6	
Branch size	9	3.32	3.41	2.87	3.13	3.00	2.95	2.71	2.76	2.81	2.81	2.81	NS	0.76	2.97	3.06	NS	-3	
Straightness	9	3.23	3.05	2.60	3.13	2.43	2.80	2.71	2.67	3.00	3.00	3.00	NS	0.71	2.74	2.91	NS	-6	

S self-pollinated

O open-pollinated

C cross-pollinated, 183 × 181

a height of tallest tree per plot only

b trees scored on 1-5 scale, 5 best

c significance of difference between all families

d significance of difference between S and O

NS no significant difference between means

* significant at 5% level of probability

** significant at 1%

*** significant at 0.1%

(1490/ha) and four replications. Each tree was fertilized with 50 g urea six months after planting and initial survival was excellent. At six months only 5 of the 216 seedlings had died (Table 4). After 9½ years the three tallest trees in the trial averaged 27 m.

In the first two years the selfed families grew only slightly more slowly than the open and cross-pollinated families, but by five years there were large and highly significant differences between families in survival, height and diameter (Table 4). By 12½ years the trend to suppression among the selfs had increased to the extent that there were fewer than 25% of the trees surviving in three of the four selfed families, and the cross-pollinated family was outstanding (Fig. 2). At 12½ years 79% of the 24 trees planted in the cross-pollinated family were classed as dominant or codominant (compared with the stand as a whole), only one was suppressed and one dead. The four open-pollinated families also declined in comparison with the cross-pollinated family, but not so much (Table 4).

As an index of inbreeding depression the ratio (S-O)/O was calculated, expressing the difference between selfed (S) and open-pollinated (O) families. By this index inbreeding depression was evident in all traits. Inbreeding depression for survival increased greatly with age. Inbreeding depression for height and diameter did not increase with age, reflecting this variation in mortality — more suppressed selfs died leaving the larger selfs as survivors.

There are indications of considerable variation between parents in inbreeding depression of their progeny. For survival at 12½ years the selfed progeny of tree 189 were much better than trees 192, 184 or 193 (Table 4). Also the selfing of tree 189 produced more seed per capsule and per 100 flowers than from selfing other trees (Table 3) or from the average of crossing or open-pollination (Table 2).

Stem and branch quality of selfs at nine years was on average less than that for open-pollinated families, but the differences were not statistically significant.

At 9 and 12½ years the proportion of trees in four crown classes was visually assessed. The combined data for dominant and codominant trees, and subdominant and suppressed are illustrated in Figure 3. The percentages were calculated in relation to the number of trees planted. The outcrossed family had 79% dominant and codominant trees at 9 and 12½ years while the selfed families had 20% at 9 years and 13% at 12½ years. The percentage of dominant and codominant trees also decreased from 9 to 12½ years in the open-pollinated families, from 59% to 50%.

The largest diameter tree in the selfed families was 29.5 cm at 12½ years, while 30% of the trees in the outcrossed family and 20% in the open-pollinated families were of larger diameter than this.

Discussion

The results presented here of the first investigations of the effects of selfing in *E. regnans* have several important implications for seed collection, breeding programs, and the population genetics of this species.

The structure and post-anthesis development of the flower of *E. regnans* may reduce the chance of autogamous pollination (GRIFFIN and HAND 1979) but there is certainly no effective barrier to geitonogamy (pollination between different flowers of the same tree). A receptive stigma may therefore receive self pollen and outcross pollen in varying quantities according to factors such as vector ac-

tivity, stand structure, heaviness of flower crop, and phenology. A highly self-fertile tree which is physically isolated from other individuals or which flowers out-of-step with adjacent trees may therefore be expected to produce a very high proportion of selfed seed, and consequently progeny with reduced viability and growth rate. Isolated open-grown trees are particularly attractive as sources of bulk quantities of seed for plantation establishment, but losses in productivity due to inbreeding will far outweigh the short-term benefits of reduced seed collection costs.

The variable levels of self fertility which we have demonstrated also complicate interpretation of progeny and provenance test results. If open-pollinated seed is used in an attempt to rank families for general combining ability (e.g. ELDRIDGE 1972) then the mean performance of each family will be a function of breeding value and the (unknown) degree to which it is inbred. The common practice of assuming that open-pollinated progenies are sets of half-siblings is obviously inappropriate for a species with a mixed breeding system, so one must also make some other assumption about the average degree of relatedness of progenies if derived estimates of additive genetic variance are to be unbiased (NAMKOONG 1966).

For eucalypts it seems necessary to explore alternative methods of progeny testing. BARKER and LIBBY (1974) discuss consequences of basing analyses on progeny performance following culling of plants showing the most severe inbreeding depression. This technique could perhaps be applied to open-pollinated progenies or to selfs, which can be produced quite cheaply by using method B (Table 2). We will have a better understanding of the options available following assessment of a more comprehensive series of controlled outcrosses, selfs, and open-pollinated progenies planted in 1979.

It is common practice in Brazil and elsewhere to attempt to remove inbred eucalypt seedlings by heavy culling in the nursery (GUIMARAES 1961). The gradual progressive expression of inbreeding depression observed in this experiment and also reported for *E. camaldulensis* DEHNH. (VENKATESH and VAKSHASYA 1977) and *E. grandis* (HODGSON 1976, VAN WYK 1981) suggests that such a procedure is unlikely to be very effective.

It would be better to reduce the proportion of selfed seed produced by selection and/or improved seed orchard management practice. Our data suggest that in *E. regnans*, as in *E. grandis* (HODGSON 1976), there are opportunities to select trees which have low self-fertility or alternatively those which are self-fertile but whose progeny do not show severe inbreeding depression. The level of outcrossing in orchards could be increased by matching flowering times, establishing more than one genotype at each spot (HODGSON 1976) and by ensuring that the orchards are located where pollen vectors are highly active.

Finally the results shed some light on the question of the mechanism whereby eucalypt species are able to maintain a mixed breeding system (BROWN *et al.* 1975). In the absence of a net heterozygote advantage, genes for self-fertility should become fixed in a population (FISHER 1941, ALLARD *et al.* 1968), yet the repeated estimates of outcrossing rate (*t*) of about 0.7 to 0.8 across a range of eucalypt species (MORAN and BELL 1983) suggest that the system is in equilibrium. If our progeny test is considered to approximate a naturally regenerating stand of *E. regnans* then the observed mortality rate (Table 4) of selfs represents differential selection against inbred genotypes

during the early pre-reproductive phase of the life cycle. In nature competitive effects are likely to be even more severe as our trees had the benefit of a wide spacing during establishment. ASHTON (1976) quotes estimates of over 2 million germinants per hectare following fire generation of *E. regnans*, decreasing to about 40 trees per hectare in a fully stocked stand at maturity (200 years). In such stands the probability that any particular genotype will survive to maturity might therefore be sensitive to very small differences in competitive ability.

It is important to note that if such selection, coupled with density dependent mortality (HARPER 1977), is a major determinant of population structure, then in a situation where regeneration is poor or seed widely distributed, some selfed progeny of *E. regnans* may be quite capable of successful growth and reproduction. At age 12½ years, 13% of our selfs were classified as dominant or codominant (Figure 3), despite the increasing competition from the other plots.

Conclusions

The series of observations reported in this paper (to be followed by as yet unpublished results from more comprehensive experiments planted in 1979) suggest that the eucalypt breeder and plantation grower must consider developing positive strategies for minimising the deleterious effects of inbreeding on growth rate. It is suggested that under natural regeneration conditions selection by self-thinning of the stand, operating in favour of more vigorous outcrossed individuals, is an important mechanism for maintaining the mixed breeding system of the species.

Acknowledgements

The authors thank the staff of the CSIRO, Division of Forest Research, Gippsland Research Station, Traralgon, Victoria for their contributions to the pollinations and the field trial over several years, and APM Forests Pty Ltd on whose forests the work was done.

References

ALLARD, R. W., JAIN, S. K., and WORKMAN, P. L.: The genetics of inbreeding populations. *Advances in Genetics* 14: 55–131 (1968). — ASHTON, D. H.: The development of even-aged stands of *Eucalyptus regnans* F. MUELL. in central Victoria. *Aust. J. Bot.* 24: 397–414 (1976). — BARKER, J. E., and LIBBY, W. J.: Use of selfing in selection of forest trees. *J. Genet.* 61: 152–168 (1974). — BROWN, A. H. D., MATHESON, A. C., and ELDRIDGE, K. G.: Estimation of the mating system of *Eucalyptus obliqua* L'HÉRIT. By using allozyme polymorphisms. *Aust. J. Bot.* 23: 931–41 (1975). — ELDRIDGE, K. G.: Breeding system of *Eucalyptus regnans*. Proc. IUFRO Sect. 22 meeting, Varparanta, Finland, vol. 1, 12 pp (1970). — ELDRIDGE, K. G.: Genetic variation in growth of *Eucalyptus regnans*. For. Timb. Bur., Aust., Bull. 46, 72 pp (1972). — FISHER, R. A.: Average excess and average effect of a gene substitution. *Ann. Human Genetics* 11: 53–63 (1941). — GRIFFIN, A. R.: Floral phenology of a stand of mountain ash (*Eucalyptus regnans* F. MUELL.) in Gippsland, Victoria. *Aust. J. Bot.* 28: 393–404 (1980). — GRIFFIN, A. R., and HAND, F. C.: Post-anthesis development of flowers of *Eucalyptus regnans* F. MUELL. and the timing of artificial pollination. *Aust. For. Res.* 9: 9–15 (1979). — GUIMARAES, R. F.: Resultados imediatos da selecao massal. Second World *Eucalyptus* Conf. Brazil, Rep. and Doc. vol. 1, 364–368 (1961). — GUIMARAES, R. F., and KERR, W. E.: Autofecundacao em *Eucalyptus alba*. Companhia Paulista de Estradas de Ferro, Sao Paulo, Servico Florestal, Boletim No. 11, 9 pp (1959). — HALL, N., JOHNSTON, R. D., and CHIPPENDALE, G. M.: Forest Trees of Australia. AGPS, Canberra, 334 pp. (1970). — HARPER, J. L.: Population Biology of Plants. Acad. Press, London, 892 pp. (1977). — HODGSON, L. M.: Some aspects of flowering and reproductive behaviour in *Eucalyptus grandis* (HILL) MAIDEN at J. D. M. Keet Forest Research Station. *Sth. Afric. For. J.* 97: 18–28; 98: 32–43; 99: 53–8 (1976). — KRUG, C. A., and ALVES, A. S.: *Eucalyptus* improvement. *J. Hered* 40: 133–49 (1949). — LIBBY, W. J., MCCUTCHAN, B. G., and MILLAR, C. I.: Inbreeding depression in selfs in redwood. *Silvae Genetica* 30: 15–25 (1981). — MORAN, G. F., BELL, J. C., and MATHESON, A. C.: The genetic structure and levels of inbreeding in a *Pinus radiata* D. DON seed orchard. *Silvae Genetica* 29: 190–3 (1980). — MORAN, G. F. and BELL, J. C.: *Eucalyptus*. In: TANKSLEY, D. S. and ORTON, J. J., eds. Isozymes in Plant Genetics and Breeding. Elsevier, Amsterdam (in press) (1983). — NAMKOONG, G.: Inbreeding effects on estimation of additive genetic variance. *For. Sci.* 12: 8–13 (1966). — PAWSEY, C. K.: Inbreeding radiata pine (*Pinus radiata* D. DON). For. and Timb. Bur., Australia, Leaflet No. 87, 31 pp (1964). — PIKE, K. M.: Pollen morphology of *Myrtaceae* from the Southwest Pacific area. *Aust. J. Bot.* 4: 13–53 (1956). — PRYOR, L. D.: Controlled pollination of *Eucalyptus*. *Proc. Linn. Soc. N. S. W.* 76: 135–9 (1951). — PRYOR, L. D., and BODEN, R. W.: Blowflies as pollinators in producing *Eucalyptus* seed. *Aust. J. Sci.* 24: 326 (1962). — VAN WYK, G.: Pollen handling, controlled pollination and grafting of *Eucalyptus grandis*. *Sth. Afric. For. J.* 101: 47–53 (1977). — VAN WYK, G.: Inbreeding effects in *Eucalyptus grandis* in relation to degree of relatedness. *Sth. Afr. Forestry J.* 116: 60–63 (1981). — VENKATESH, C. S., and VAKSHASYA, R. K.: Effects of selfing, crossing and interspecific hybridization in *Eucalyptus camaldulensis* DEHN. Proc. 3rd World Cons. Forest Tree Breeding, Canberra, Vol. 2, 683–92 (1977).

Short Note: Multiple Populations and Sublines

By R. D. BURDON¹) and G. NAMKOONG²)

(Received 1st October 1982)

Summary

Multiple populations and sublines are two concepts that have developed in recent years for tree breeding. They relate to subdividing breeding populations, and are defined as follows: multiple populations represent different selection criteria, to ensure that at least one such population will correspond roughly to any future selection goal; sublines represent replicate breeding populations that can

be intercrossed to ensure completely outbred offspring at any time in the future.

Key words: tree breeding, breeding populations, breeding strategy, multiple populations, sublines.

Zusammenfassung

Multiple Populationen und Sublines sind zwei Konzepte, die in den letzten Jahren für die Pflanzenzüchtung entwickelt worden sind. Sie lassen es zu, Züchtungspopulationen zu unterteilen und werden wie folgt definiert: multiple Populationen stellen verschiedene Selektionskriterien dar, um sicherzustellen, daß am Ende eine solche Population annähernd jedem zukünftigen Selektionsziel ent-

¹) Permanent address: NZ Forest Service, Forest Research Institute, Private Bag, Rotorua, New Zealand.

²) USDA Forest Service, Southeastern Forest Experiment Station, Department of Genetics, North Carolina State University, P. O. Box 5487, Raleigh, N. C. 27650, U.S.A.