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## **Growth of Hybrid Fir Trees in Connecticut**

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#### Summary

Crosses were made between various species of fir in the spring of 1960 and 1962. Progeny of successful crosses were sown in Connecticut in 1962 and measured for diameter, height, and crown profile when the trees were 17 years old. In addition, branch samples were collected for classification according to needle tip morphology.

In almost all cases, interspecific crosses grew better than intraspecific crosses Crosses between species of neighboring geographic ranges tended to grow better than crosses between species of widely separated ranges.

There were growth depressions as a result of selfing, and, on average, characteristics of selfed progeny were less variable than those of hybrids. The needle tips of the hybrid crosses exhibited a range of variability. The most variable crosses in this respect were those from widely separated natural ranges.

Key words: Abies hybrids, height, diameter, crown area, needle tip morphology.

#### Zusammenfassung

Im Frühjahr 1960 und 1962 wurden mit 10 Abiesarten intra- und interspezifische Kreuzungen durchgeführt. Von den erfolgreichen Kombinationen, die 1962 in Connecticut ausgesät wurden, konnten nach 17 Jahren Durchmesser, Höhe und Kronenprofil gemessen werden. Zusätzlich wurden Zweigproben für klassifikatorische Zwecke entnommen.

In fast allen Fällen wuchsen die interspezifischen besser als die intraspezifischen Kreuzungen. Kreuzungen zwischen Arten, die benachbarte Verbreitungsgebiete haben, tendierten zu besserem Wachstum als die Kreuzungen zwischen Arten mit entfernten Verbreitungsgebieten.

Als Folge der Selbstung wurden Wachstumsdepressionen und geringere Variabilität der Nachkommen gegenüber den Hybridnachkommenschaften beobachtet. Die Nadelspitzen der Hybridkreuzungen zeigten eine beträchtliche Variabilität, wobei die größte Variabilität bei Hybriden aus weit entfernten Verbreitungsgebieten zu beobachten war.

Schlagwörter: Abies-Arten, Höhe, Durchmesser, Kronenfläche, Nadelspitzenmorphologie.

#### Introduction

During the spring of 1960 and 1962, control crosses were made between various species of fir growing in the George P. Brett Pinetum of Yale University at Fairfield, Connecticut

The growth characteristics of the progeny surviving in 1981 are presented in this report. This study is part of ongoing research on the cytological, developmental, and growth characteristics of this genus. Previous studies dealt with the staminate flower phenology and pollen formation in four species (Mergen and Lester, 1961a), on the induction of polyploidy by colchicine in nine species (Mergen and Lester, 1961b), crossability (Mergen et al., 1964), and the karyotypes of seven species (Mergen and Burley, 1964).

The compatibility between species and species evolution in the genus Abies have not been widely studied. A search of the literature provided few references on hybridization with fir beyond those described by Klaehn and Winieski (1962) and by Mergen et al. (1964). A citation by Silen et al. (1965) showed that there was no significant genetic barrier to crossing A. procera and A. magnifica where the ranges overlap in southern Oregon and northern California. Korpel et al. (1982) described 8 spontaneous hybrids of A. sp. including A. borisii regis Matte. (A. alba × A. cephalonica), and A. nebrodensis Matte. (A. cephalonica × A. alba). The former occurs in the southern Balkan Peninsula and the latter occurs in Sicily. Kantor and Chira (1971, 1972) crossed A. cephalonica with pollen of six other species, including A. alba, and all crosses were compatible.

Data on total height, diameter at breast height, and crown area of putative hybrid progeny, along with abservations on their needle tip morphology, are given in this report.

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This information may provide some insight into the evolutionary relationships among the species tested.

## **Materials and Methods**

Species Represented in the Study

Abies cephalonica Loud. (Greek fir) occurs in the montane forests of Greece (Tree Code 23).

Abies cephalonica var. apollinis (Link) Beiss. (Greek fir) occurs in the mountain regions of Greece (Zinke, 1973), and was represented by two trees (Tree Codes 15 and 16).

Abies firma Sieb. and Zucc. (Momi fir) is native to Japan located in Honshu, Shikoku and Kyushu in the evergreen broadleaf forest type in the warm temperate zone (Anonymous, 1981) (Tree Code 5).

Abies homolepis Sieb and Zucc. (Nikko fir) occurs in Japan on the Pacific side of both Honshu and Shikoku in the cool-temperate and subalpine zones (Anonymous, 1981) (Tree Code 17).

Abies koreana Wils. (Korean fir) has its natural range in the central temperate zone of Korea. It occurs on hill-sides in the Chiri and Dukyu mountains on the southern tip of the peninsula, and in the Cheju province at elevations between 500 and 2000 meters (BAE, 1968) (Tree Code 8).

Abies lasiocarpa (Hook. NUTT. (Subalpine fir) occurs in northwestern North America, ranging along the Pacific coast from southeastern Alaska and the central Yukon territory, which is its northernmost limit, and south through British Columbia along the Coast Range to the Olympic Mountains of Washington. It also occurs throughout the Rocky Mountains (Fowells, 1965) (Tree Code 13).

Abies mariesii Mast. (Maries fir) grows in the Buna Forests of Honshu, Japan, in the cool temperate zone where the average annual temperature ranges between 6° and 13° C (Anonymous, 1981) (Tree Code 32).

Abies procera Rehd. (Noble fir) occurs in the Pacific Northwestern United States from Washington to northern California on the west side of the Cascade range at elevations between 450 and 1 200 meters (Franklin et al., 1972). Two trees were used (Tree Codes 2 and 3).

Abies recurvata Mast. occurs in the Ming River Basin of the western Szechuan province of China, in the upper Tebbu country of Kansu, and at elevations between 2 700 and 3 050 m in the Wen Chuan Hsien area of Szechuan (Lee, 1935) (Tree Code 11).

Abies sachalinensis (Fr. Schmidt) Mast. (Saghalin fir) occurs in the sub-alpine region of Japan on Hokkaido between 700 and 1 400 meters (Anonymous, 1981). Two trees were used (Tree Codes 18 and 20).

There is no information on the specific geographic origin of the trees used in this study because seed was obtained from commercial seed dealers or from leftover lots of various arboreta. The crosses that yielded viable seed and had surviving seedlings are shown in *Table 1*. A large number of additional crosses were made, but either viable seed was not obtained or the seedlings were not able to survive under the harsh climate of northwestern Connecticut (for details on crossability, compare with results given in *Table 2* of Mergen *et al.*, 1964). Final verification of hybrids awaits cone production.

### Experimental

The seed was germinated in a greenhouse during 1962 and after the seedlings had become established they were planted in the nursery at the Greeley Memorial Laboratory in New Haven, Connecticut and later transplanted to a

nursery at the Great Mountain Forest in Norfolk, Connecticut. When the seedlings were seven years old, they were outplanted in a randomized block design, with eleven blocks, in an experimental plot close to the nursery in Norfolk. There were 100 trees per block; unequal numbers of each cross were planted within a block, but the proportional representation of each cross was constant across blocks. If a seedling died during the first year after outplanting, it was removed and replaced with a seedling of the same cross. Blocks were 12 feet (3.6 m) apart, and trees were spaced every 8 feet (2.5 m) within blocks.

#### Mensurational

The fir trees were measured between October 1980 and January 1981. Diameter at breast height (dbh) in centimeters, total height in meters, and crown diameter in meters were recorded. Dbh was measured using a standard dbh tape, and height to the nearest half meter was measured with a graduated pole.

Crown diameter was measured perpendicular to the stem at the base of the tree and at one-half the height of the tree. For exceptionally tall trees, the second measurement was taken at one-third of the height of the tree. Each measurement was made at the widest point of crown projection.

The measured crown diameter was used to calculate the area of the crown in profile for each tree. Crown area was computed as 0.25H (A + 2B) where B = crown diameter at one-half height, A = crown diameter at the base of the tree, and H = total tree height. This equation represents the total area of the upper triangular portion plus the lower trapezoidal portion of the tree.

For the study of needle tip morphology, branches from 12 crosses were collected at the time the trees were measured. They were kept refrigerated until they were examined under a dissecting microscope (15x) to determine needle tip characteristics. The characteristics were grouped into four classes: Class I: needles broad, tips deeply forked with sharply pointed lobes; Class II: needles with narrow and shallow forks and pointed lobes; Class III: needles broad and shallow forked with rounded lobes; Class IV: needles broad and unforked with a sharply pointed tip.

#### Statistical

Weighted ANOVA's were performed to ascertain cross effects. The need for weighted analyses was indicated by the heterogeneous variances evident in the box-whisker and other raw data plots. The weights employed were the computed sample variances of the crosses, making the weighted analyses equivalent to those in which each observation is divided by the standard deviation of its cross.

The model employed for these analyses was:

 $\begin{array}{ll} Y_{ijk} \ = \ \mu + C_i + B_j + CB_{ij} + E_{ijk} \\ \text{where } Y_{ijk} \ = \ \text{tree characteristic (dbh, height, or crown area)} \\ \mu \ = \ \text{overall mean} \\ C_i \ = \ \text{cross (e.g., } 32 \times W, 32 \times 32 \dots) \\ B_j \ = \ \text{block, } j = 1, \dots, 11 \\ CB_{ij} \ = \ \text{cross} \times \text{block interaction} \end{array}$ 

 $E_{ijk} = sampling error$ 

The interaction can alternately be viewed as an experimental error (Steel and Torrie, 1960). In the absence of confounding by the blocking on the treatment (cross) effect, its variance should be close to that of the sampling error.

**ØIND** 6.43 6.33 s sachalinensis (20) 0.4.0 P 0 \*8.00.00 A. sachalinensis s (18) 6.9 500 A. recurvata 2.5.4 7.5.6 ASIA Table 1. — Average diameter (D), height (H), and crown area (C) for fir hybrids. A. Mariesii 4.6.6 P. 4.6 A. homolepis 0.44 8 <del>- 9</del> 9 A. firma 4. E. E. 8.8.4 3.0 20.53 A. cephalonica var. Apollinis (16) 0.0 5.0 MEDITERRANEAN \* 24.4 \*\*: 2 = 8 A. cephalonica var. Apollinis (15) 4.9 -A. cephalonica 8 - 9 A. procera (3) 1 - 8 A. procera (2) AMERICA 0.2 A. Jusiocarpa 7.5.4 7.5.5 3.6 4.2 متں OIU OIU ں یا م aru OIU OIC OIU ٥٤٥ Sachalinensis (18) sachalinensis (20) A. cephalonica var. Apollinis (15) A. cephalonica var. Apollinis (16) A. procera (2) A. homolepis A. Mariesii A. koreana A. firma Maje SOURCE

Usually, one or more contrasts were also coded into the analyses, and residual plots were examined to assess model adequacy. Each ANOVA was followed by a series of pairwise mean comparisons using the Fisher Significance Difference (FSD) procedure to test for specific differences. This is a usual t-test conducted after a significant F-test ( $\alpha = .05$ ) of model treatment effects has occurred (Carmer and Swanson, 1973; Carmer and Walker, 1982). For pairwise

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comparisons, a significance level af  $\alpha = .10$  was chosen in lieu of the customary  $\alpha=.05$  to increase the power of these

AISA

Mixed pollen from both trees. Diameter of Breast Height (m);  $C = Crown \ Area \ (d^3)$ .

An alternate set of analyses were made to determine whether all crosses were equally variable. For these analyses the cross X block sample standard deviations were treated as individual observations, and then a two-way ANOVA model was fitted.

#### Results

The average height, dbh crown area statistics for the progenies of all the crosses are presented in *Table 1*. Figure 1 graphically summarizes the aggregate statistics for the progenies of the female parents that yielded enough trees for meaningful statistical analyses.

In Table 2 are given the classification of the crosses according to their needle tip morphology. All of the intraspecific crosses produced progeny with the same tip characteristics as their parents. The characteristics of the hybrid and intraspecific offspring fell within the limits of the parents, but no parent showed complete dominance. On the average, A. sachalinensis seemed to dominate A. cephalonica var. apollinis and A. lasiocarpa, while A. firma and A. mariesii tended to dominate A. sachalinensis and A. firma.

There was greater variability in some hybrids than in others. For example, in the cross A. sachalinensis  $\times$  A. cephalonica var. appollinis (15, 16), only  $64^{\circ}/_{\circ}$  of the progeny fell into the dominant class, whereas  $98^{\circ}/_{\circ}$  of the progeny of A. mariesii  $\times$  A. firma, were in the same class.

It is interesting to note that the most variable cross in regard to needle tip morphology (A. sachalinensis  $\times$  A. cephalonica var. apollinis) was made between the two most geographically distant species.

The variation within each class differed with different crosses. Some crosses were difficult to assign into one of the four classes and accuracy of classification might be improved by using more classes or actually measuring the needle tips and carrying out a quantitative analysis. Details for individual species follow.

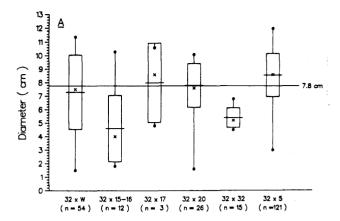
#### A. mariesii

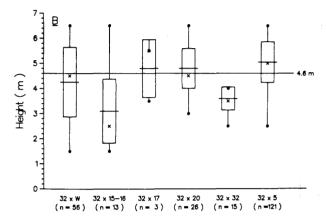
Summary values for dbh, height, and crown are shown in Figure 1a. For all three characteristics, the mean values for the selfed progeny and the progeny of the hybrid A.  $mariesii \times A$ . cephalonica var.apollinis were considerably lower than those of the other four crosses. The median values, less affected by exceptionally small or large trees, generally indicated this pattern even more strongly. On the other hand, the progeny of the A. mariesii with A. firma as the pollen parent displayed greater than average

Table 2. — Classification of the fir crosses on the basis of needle tip morphology.

Cross	wit		f branc le tips lass III		Percent of branches with needle tips in classes other than the main class as an index of variability	Geographical area of parents
5x5	22	44	34		56%	JxJ
2x3			50	50	50%	NA x NA
20x15-16		64	7	29	36%	JrG
32x15-16			80	20	20%	JIG
20x13		82	4	14	18%	JxNA
8 x 3			83	17	17%	K x NA
32x20			17	83	17%	JェJ
5x20		87	13		13%	JェJ
20x5		84	16		16%	JxJ
32xw	12		88		12%	J x 7
18x32	6		94		6%	JxJ
32x5	2		98		2%	J x J

Geographical area: J = Japan; G = Greece; NA = North America; K = Korea.





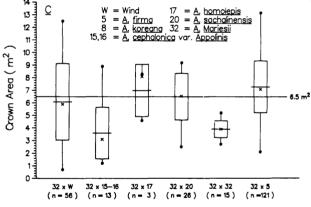
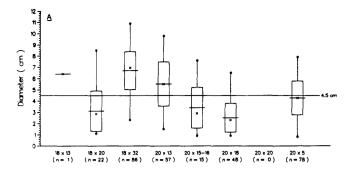


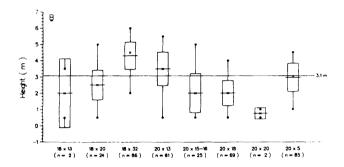
Figure 1a. — Box-and-Whisker plots of data of progeny of A. mariesti. A = Diameter, B = Height and C = Crown area. The horizontal line in the middle of each box is the mean value, X represents the median value, and the box extends one standard deviation on either side of the mean. The solid points represents the maximum and minimum values for each progeny. The horizontal line extending through all the boxes is the overall mean.

values for all characteristics. The differences apparent in these graphics were significant by the analyses of variance. Moreover, the FSD pairwise comparisons confirm that the selfed progeny and that of the A. cephalonica var. apollinis cross differed from all other crosses. Finally, the analysis of cross  $\times$  block standard deviations confirmed that the selfed progeny were significantly less variable for each of the three characteristics studied.

#### A. sachalinensis

The summary measures for diameter, height, and crown area are presented in Figure 1b. The box-whisker plots indi-





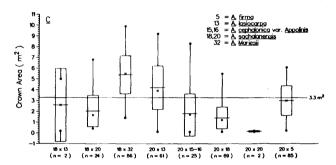


Figure 1b. — Box-and-Whisker plots of data of progeny of A. sachalinensis.

cate that the hybrids with A. mariesii and A. lasiocarpa generally were larger than the other crosses and greater than the overall mean. There was a paucity of dbh data for the selfed progeny because they were so short.

The ANOVAs revealed significant cross differences, thereby corroborating the impressions from the box-whisker plots. A contrast of the A. sachalinensis crossed with A. mariesii or A. lasiocarpa versus the other crosses was highly significant for all three characteristics. With few exceptions, pairwise comparisons of mean differences were significant. For example, when comparing dbh, the only non-significant difference was found between 18  $\times$  20 and 20  $\times$  15—16.

The analyses of cross  $\times$  block standard deviations revealed little support of the hypothesis that crosses differed in variability. In summary, of the 8 progeny groups, only A. mariesii and A. lasiocarpa displayed greater than average values for traits measured here, but generally, most crosses differed by statistically significant amounts from each other. All crosses were equally variable.

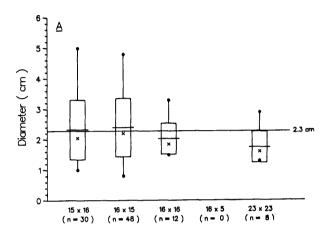
## A. cephalonica

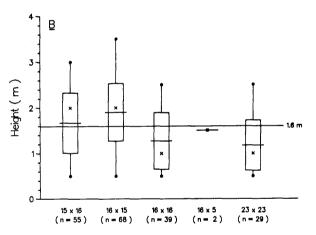
When used as a female parent with pollen from A. sachalinensis, a single tree was produced. This tree was exceptionally larger than any other A. cephalonica cross. The values for the other crosses are reproduced in Figure 1c.

The box-whisker and scatter plots indicated that the selfed progeny of both A. cephalonica and its variety apollinis were smaller than the two reciprocal crosses of A. cephalonica with A. cephalonica var. apollinis. The hybrid with A. firma was too sparsely represented to provide much information.

The analyses of variance for height and crown area indicated significant cross differences, whereas the ANOVA for dbh did not. For the height and crown area characteristics, both selfed progenies had significantly lower values than the hybrids based on the FSD tests.

Tests for differences in variability among the *cephalonica* crosses resulted in no significant results.





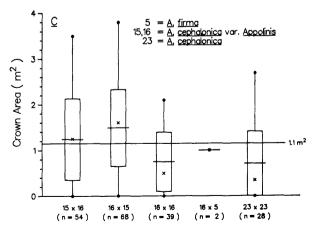
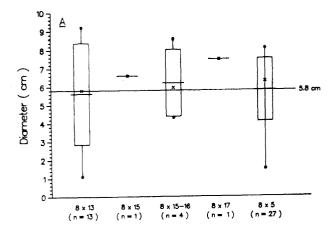
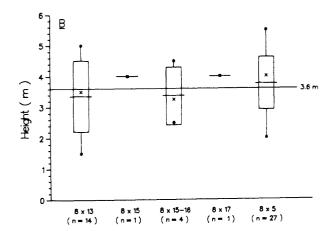


Figure 1c. — Box-and-Whisker plots of data of progeny of A. cephalonica.





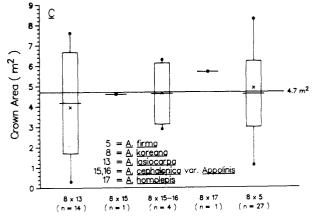


Figure 1d. — Box-and-Whisker plots of data of progeny of A. ko-reana.

#### A. koreana

The results for these crosses are given in Figure 1d. None of the ANOVA mean comparisons or treatment effects were significant, perhaps because of the small number of progeny available for analysis.

#### Discussion

In each case, selfing produced progeny that did poorly; A. mariesii showed the least inbreeding depression. A. firma also did well when selfed, whereas the largest inbreeding depression was with A. sachalinensis. These seedlings did not grow tall enough in 17 years to have a measurable dbh. Inbreeding depression has been shown previously in

conifers, e. g. Pinus elliottii var. elliottii (Mergen, 1954), Pinus monticola (Barnes, 1964), and Pinus resinosa (Fowler, 1965). It has also been reported in A. procera (Fowells, 1965). See Franklin (1970) for a detailed review.

When A. sachalinensis, A. procera, A. firma, and A. cephalonica var. apollinis were used as female parents, height, dbh, and crown area were greater in the interspecific crosses than in the selfed crosses.

Of all the interspecific crosses made, the progeny of A. mariesii, when used as the female parent, had the greatest growth. A. firma, when used as a male parent did well when crossed with A. koreana, A. mariesii, and A. sachalinensis. With the exception of A. koreana, all the formentioned species are native to Japan, suggesting that geographic similarity has a positive influence on hybrid survival and performance.

A comparison of the progeny, when grouped by geographic origin of the female and male parents, clearly indicates that the progeny from Asian parents were always superior in growth to those of American and European origin when planted in Connecticut. Trees in this group also had the greatest survival (unpublished data). Besides good growth characteristics, progeny of Asian species exhibited healty foliage and a large number of micro- und macrosporangiate strobili, and had little insect or disease damage. The progeny from crosses between parents with neighboring geographic ranges were generally more vigorous than crosses between parents of widely separated ranges. This indicates that geogaphic similarity has a positive influence on hybrid survival and growth.

Needle tip variability reflects plastic genetic control of this characteristic, indicating that it is of little diagnostic value in identifying putative hybrids in the field. For some crosses between Japanese species (32  $\times$  5 and 18  $\times$  32), however, there was little variation, and needle tip morphology could therefore be a useful characteristic for identification.

In the Norfolk, Connecticut region there are no native fir species. The closest natural forest of *A. balsamea* is some 65 km distant. Therefore, it was not possible to compare the growth of these hybrid fir trees with that of a native species. Planted *A. balsamea* trees in the area, however, were not as vigorous as many of these hybrids. Thus, further hybrid trials are warranted, especially for special purpose trees, e.g. specimen trees for landscaping, and for sale as Christmas trees.

#### Acknowledgement

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# Genetic Variation in Growth of Outcrossed, Selfed and Open-Pollinated Progenies of Eucalyptus regnans and some Implications for Breeding Strategy

By A. R. GRIFFIN1) and P. P. COTTERILL2)

(Received 4th May 1987)

#### **Summary**

Open-pollinated, selfed and outcrossed progenies were derived from thirteen parent trees in natural stands of Eucalyptus regnans, and evaluated in a field trial. Fortyfive months after planting, volume of outcross progenies averaged 37% more than the selfs. From the growth of open-pollinated progenies relative to selfs and outcrosses, the average outcrossing rates for the parent trees was estimated to be 0.69. The mixed mating system of this species complicates genetic interpretation of open-pollinated progeny test results. Heritability (hi2) for volume growth at 45 months was estimated as 0.16 from the selfs and 0.18 from the outcrossed progeny, compared wih an apparent value of 0.45 from the open-pollinated progeny. The variance between open-pollinated progeny appeared to be inflated by heterogeneity in both outcrossing rates and inbreeding depression.

The ranking of parents on outcross progeny performance was more highly correlated with self rankings than with open-pollinated rankings. It was concluded that vigorous open-pollinated progeny were indicative of high breeding value, but that the converse could not necessarily be claimed. Important implications for breeding strategy are that the role of family selection during the initial phase of domestication of *E. regnans* requires re-examination. Also that selfed progeny (which are more easily produced than outcrosses) may prove useful for estimation of genetic parameters and future breeding.

Key words: Eucalyptus, progeny testing, breeding, inbreeding.

## Zusammenfassung

Nachkommenschaften, entstanden aus freier Abblüte, Selbstbefruchtung und Kreuzungen, von 13 Elternbäumen aus natürlichen Beständen von Eucalyptus regnans wurden im Feldversuch untersucht. Fünfundvierzig Monate nach dem Auspflanzen lag das Volumen der Kreuzungsnachkommenschaft durchschnittlich 37% höher als das der Selbstun-

gen. Die durchschnittlichen Fremdungsraten der Elternbäume wurden auf 0,69 geschätzt basierend auf der Wachstumsrelation von Selbst- und Fremdbefruchtungsnachkommenschaften. Das Paarungssystem dieser Art komplizierte die genetische Interpretation der Ergebnisse frei abgeblühter Nachkommenschaften. Die Heritabilität (h;²) für das Volumenwachstum im Alter von 45 Monaten betrug 0,16 für die Selbstungen, 0,18 für die Fremdungen und bei den frei abgeblühten Nachkommenschaften 0,45. Die Varianz zwischen frei abgeblühten Nachkommenschaften schien durch die Heterogenität der Fremdbefruchtungsraten und durch die Inzuchtdepression erhöht worden zu sein. Eine Rangordnung der Eltern aufgrund des Erscheinungsbildes der Fremdungen war mit der Rangordnung der Selbstungen enger korreliert als mit der der Nachkommenschaften aus freier Abblüte. Es wird geschlossen, daß lebensfähige (kräftige) frei abgeblühte Nachkommenschaften ein Anzeichen für einen hohen Zuchtwert sind, aber daß der gegenteilige Schluß nicht notwendigerweise gezogen werden muß. Wichtige Folgerungen für die Züchtungsstrategie sind, daß die Rolle der Familienselektion für die Anfangsphase der Kultivierung von E. regnans eine erneute Untersuchung erfordert. Die Selbstungen, die leichter erzeugt werden können als Fremdungen, können sich für die Schätzung genetischer Parameter und die zukünftige Züchtung als nützlich erweisen.

#### Introduction

Eucalyptus regnans F. Muell. is a major commercial timber species in south-eastern Australia (Boland et al., 1984) and the subject of several genetic improvement programs (Eldridge, 1971; Pederick, 1976; Griffin et al., 1982a). It is pollinated by a variety of insects and in common with other eucalypts has a mixed mating system (Moran and Bell, 1983; Griffin et al., 1987). Open-pollinated seed from natural stands of E. regnans thus consists of a mixture of outcrossed and inbred seed resulting from selfing and from mating of related individuals. The actual outcrossing rate for any particular seed crop of an individual tree will be determined by a variety of genetic and environmental factors including self-fertility (Eldridge and Griffin, 1983),

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