### Concluding remarks

1) The gene frequencies of seed originating from different ramets of the same clone differ. Considerable variations within different sectors of a crown can also be detected in some cases. It seems to be difficult to expect random mating in the seed orchard. The diversity in the gene frequencies is not much due to the segregation of the mother trees but to the various composition of neighbours.

2) The dispersal of pollen is mainly depending on the coincidence of the time of flowering, the distance between parent trees and the wind direction during pollen shedding. The neighbour to the marker ramet, with all mentioned conditions favourable, received 31.4 per cent of fertilizing pollen to that ramet. It seems, as if in the prevailing wind-direction trees within 10 m contributed considerably to the fertilizations, trees at a distance of 10—20 m to a large extent, but less than trees within 10 m. Trees at a distance of more than 40 m and up-wind only make a small contribution.

3) The frequency of self-pollinated seeds originating from one clone in the Scots pine seed orchard was roughly estimated at 6 per cent with the lowest frequency in the top of crown. This points on the risks of mainly picking cones in the lower parts of the crowns both on practical and scientifical purposes.

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### References

Ashton, G. C. and Braden, A. W. H.: Serum β-globlin polymorphism in mice. Austr. J. Biol. Sci. 14: 248—253 (1961). — Dixon, W. J. and Massey, F. J.: Introduction to statistical analysis (1969). — Gregorius, H. R. and Müller, G.: Genetic structure in finite, open-pollinated plant populations. Theor. and Appl. genetics 46, 295—305 (1975). — Hadders, G.: Pollineringssituationen i tallplantager. (The situation of pollination in seed orchards of Scots pine (*Pinus sylvestris* L.). With English summary). — Fören Skogsträdsförädl. Inst. Skogsförbättr Arsbok 1971, 111—139 (1971). — Johnsson, H.: Självpollineringsfrekvensen i en tallfröplantage (The frequency of self-fertilization in a pine seed orchard). (Prelim Rep in mineo) (1972). — Jonsson, A., Ekberg, I. and Eriksson, G.: Flowering in seed orchard of *Pinus sylvestris* L. Studia Forestalia Suecica No. 135. 38 p. (1976). — Koski, V.: Natural pollination in seed orchards with special reference to pines p 83—91 in Seed orchards ed R. Faulkner. Forestry Commission Bulletin 54 (1975). — Müller, G.: A simple method of estimating rates of self-fertilization by analysing isozyme in tree seeds. Silv Gen 25, 15—17 (1976). — Müller-Starck, G.: Estimates of self- and cross-fertilization in a Scots Pine seed orchard. Proceedings of the Conference on Biochemical Genetics of Forest Trees, Umea, Sweden 1978: 170—179 (1979). — Rudin, D.: Inheritance of glutamate-oxalate-transaminases from needles and endosperms of *Pinus sylvestris*. Hereditas 80: 296—300 (1975). — Rudin, D.: Leucine-amino-peptidases from needles and macrogametophytes of *Pinus sylvestris* L. Hereditas 85, 219—226 (1977). — Rudin, and Lindgren: Isozyme studies in seed orchards. Studia Forestalia Suecica No 139, 23 p. (1977).

# Inbreeding depression in selfs of redwood

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### Summary

Given the polyploid chromosome constitution of *Sequoia sempervirens,* there was reason to question whether it would exhibit inbreeding depression. Preliminary results from studies of self and related outcross families are reported as a guide to the selection of trees for redwood seed-orchards and breeding-orchards. The data indicate that, compared to outcrosses, selfing produced no additional cone abortion, no consistent effect on number of seeds per cone, and variable effects on germination. Consequently, the relative proportions of inbred and outcrossed offspring produced are normally maintained.

Under good nursery conditions, survival of selfs and outcrosses was both high and similar. Under stress nursery conditions, survival was lower for both, but selfs had a much lower survival rate than outcrosses. The selfs were consistently 65—80% the height of the outcrosses in the nursery, and also after one year in the field. Then inbreeding depression appears to become much more severe. After fourteen years in the field, in the single family available, selfs averaged only 42% the height and 29% the diameter of related outcrosses. It thus appears prudent to restrict inbreeding in redwood seed-orchards.

*Key words:* Cone abortion, Diameter, Germination, Height, Nursery practice, Polyploidy, Seed-orchards, *Sequoia sempervirens*, Stress, Survival.

### Résumé

Etant donné la constitution chromosomique polyploïde de *Séquoia sempervirens* on pouvait se demander si l'autofécondation chez cette espèce s'accompagne de perte de vigueur. Les résultats préliminaires des études de descendances dérivant d'autofécondations ou de sujets apparentés, sont rapportés pour fournier un guide pour le choix des arbres à placer en vergers à graines ou parcelles d'amélioration génétique. Les faits montrent qu'en comparaison à des croisements non apparentés, l'autofécondation ne provoque pas d'excès d'avortement de cônes et n'a pas d'effet significatif sur le nombre de graines par cônes. Les effets sur la germination sont variables. Il résulte de ceci que les proportions relatives entre descendants consanguins et non apparentés on pu être normalement maintenues.

Sous de bonnes conditions de pépinière, la survie des plantes issues d'autofécondation et des croisements non apparentés a éte à la fois élevée et comparable. En conditions difficiles de pépinière, la survie a été inférieure pour les deux catégories mais les autofécondés ont eu un taux de survie inférieur à celui des non apparentés. Les autofécondés n'ont atteint que 65 à 80% de la hauteur des non apparentés dans la pépinière, ainsi d'ailleurs qu'après un an en forêt. Ensuite, la perte de vigueur liée à la consanguinité est devenue beaucoup plus sévère. Après 14 ans en forêt dans la seule famille disponible, les plantes issues d'autofécondation mesuraient seulement 42% de la hauteur et 29% du diamètre des non apparentés comparables. Il est donc prudent de réduire la consanguinité dans les vergers à graines de *Séquoia sempervirens.*

#### Zusammenfassung

Die Polyploidie bei *Sequoia sempervirens* regt die Frage nach der Möglichkeit einer Inzuchtdepression an. Wir berichten über vorläufige Ergebnisse von Untersuchungen an Selbstungsfamilien und verwandten Fremdungsfamilien als Anleitung bei der Selektion von Bäumen für Samen- und Zuchtplantagen. Die Ergebnisse zeigen, daß Selbstung im Vergleich zur Fremdung zusätzlich keine Verkümmerung von Zapfen hervorruft, die Anzahl der Samen pro Zapfen nicht beeinflußt und einen variablen Einfluß auf die Keimung ausübt. Die durch Inzucht und Fremdung hervorgebrachten Nachkommen unterscheiden sich wenig in diesen Merkmalen.

Unter günstigen Anzuchtbedingungen überleben Selbstungs- und Fremdungsnachkommen gleich gut. Unter schwierigen Anzuchtbedingungen ist die Überlebensrate für beide Gruppen niedriger, und zwar geringer für Selbstungsnachkommen als für Fremdungsnachkommen. Die Inzuchtdepression scheint im Anschluß an die Zeit in der Baumschule noch ausgeprägter zu werden. Die Selbstungsnachkommen erreichen durchweg nur 65 bis 80% der Höhe von Fremdungsnachkommen, sowohl in der Baumschule als auch nach einem Jahr im Feld. Nach 14 Jahren im Feld erreichen die Selbstungsnachkommen der einzigen zur Verfügung stehenden Familie im Durchschnitt nur 42% der Höhe und 29% des Durchmessers der verwandten Fremdungsnachkommen. Es erscheint daher ratsam, in Samenplantagen von *Sequoia sempervirens* Inzucht zu vermeiden.

#### Introduction

Most conifers thus far investigated exhibit inbreeding depression with respect to seed set, germination, early survival, and early growth, when offspring resulting from self-pollinations are compared to those from outcross-pollinations (Pawsey 1964; Dogra 1967; Franklin 1970; Koski 1973; Bishir and Pepper 1977). This had led to the general recommendations that inbred trees should not be included in woodproduction plantations, and that the creation of such inbreds should be minimized by excluding close relatives from seed-orchards (Libby 1976).

The genetic improvement of redwood *(Sequoia sempervirens* (D. Don.) Endl.) has recently progressed to the seed-orchard and breeding stage in California (Libby and McCutchan 1978) and in France (AFOCEL 1979). Although some of the data reported below are conflicting, suggesting the need for more experiments, the overall picture suggests that a high proportion of inbred-producing pollinations will result in plantable seedlings, and it further indicates that redwood then suffers substantial inbreeding depression as a growing tree. Therefore, steps should be taken to avoid mating relatives when breeding redwood seedlings for wood-production purposes.

Except for a few domesticated cultivars, redwood and *Fitzroya* (Hair 1968) are the only conifers known to have a polyploid genome (Sax and Sax 1933; Hair and Beuzenberg 1958; Khoshoo 1959; Fozdar and Libby 1968). Observations of meiosis led Stebbins (1948) to the opinion that redwood is of auto-allopolyploid origin, and the karyotype of Saylor and Simons (1970) supports this hypothesis.

Species with polyploid genomes often do not experience severe inbreeding depression (Stebbins 1957). Allopolyploids are thought to be sheltered from inbreeding depression due to their ability to fix heterozygosity. In autopolyploids, the mixed pairing configurations of multiple homologous chromosomes greatly slows the rate of increase in homozygosity with inbreeding (Markert, Shaklee and Whitt 1975). Thus, in either case, polyploidy was expected to moderate inbreeding depression in redwood. Prior to the work reported below, inbreeding depression had not been documented in redwood.

#### Materials

Data from three different experiments are now available to us, and have been compiled for this paper.

In 1963, during preliminary work to gain experience with redwood control-pollination, one tree of unknown origin, growing 15 km east of Berkeley at UC's Russell Reservation, was selfed and outcrossed. The resulting offspring were outplanted in 1965, along with open-pollinated sibs.

In 1978, three unselected mature clones, also growing at Russell Reservation, were selfed and outcrossed. Wind-pollinated seeds, and seeds from strobili protected from pollination, were collected when the control-pollinations were harvested. These three clones all originated from seed trees in the same stand, about 30 km inland near the Mad River in Humboldt County, California. Seedlings from the control-crosses were outplanted in 1979.

As part of a larger redwood breeding program (Libby and McCutchan 1978), 10 select clones of Humboldt County origin were selfed and outcrossed. Of these, 5 were pollinated in 1977, all 10 in 1978, and 9 in 1979. Most pollinations were performed on recently-rooted cuttings growing in large clay pots in a greenhouse and/or lathhouse. A few were performed on cuttings rooted earlier and growing in soil. The year and location of the pollinations have proved to be more important than the select or non-select origin of the clones, and, where appropriate, the data are so reported.

For the purposes of this paper, seeds and plants derived from self-pollinations are referred to as "selfs"; those from control-crosses among different trees as "outcrosses"; those from unbagged wind-pollinated strobili as "opens"; and those from bagged but unpollinated strobili as "bagged controls".

#### Specific Methods, Results and Discussions

*Cone Abortion.* In *Pinus* and *Juniperus,* pollination failure greatly increases the frequency of seed-cone abortion. However, in *Abies, Pseudotsuga* and *Picea,* unpollinated conelets develop in essentially the same way and same frequency as pollinated ones (Sweet 1973).

Sausage-casing bags were used to exclude pollen in all three experiments. In 1963, pollen was delivered by a hypodermic needle; in 1977—79, by a camel's-hair brush inserted through a small hole punched in the bag. This procedure was also followed for the bagged unpollinated controls, but without pollen in the needle or on the brush. The holes were taped shut seconds after the needle or brush was withdrawn. Each pollination was performed at least twice during the period when the bagged female strobili were receptive. Current-year pollen was used in all crosses.

Self-pollination could affect cone development in several ways. Self pollen may fail to adhere to the micropyle, it may fail to germinate, or it may be unable to penetrate the nucellus. If it is effective in fertilization, it may subsequently affect cone development differently from outcross

*Table 1.* — Cone abortion in seven frequently-pollinated redwood clones.

| | Females well-rooted in soil | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | No pollen | | | Self pollen | | | | Outcross pollen | | | |
| Clone identity | S3 | ARC 154 | ARC 28 | 10 | S3 | ARC 154 | ARC 28 | 10 | S3 | ARC 154 | ARC 28 |
| Number of bagged strobili | 106 | 49 | 10 | 122 | 38 | 127 | 13 | 112 | 23 | 180 | 11 |
| % abortion | 5% | 12% | 100% | 2% | 13% | 28% | 31% | 0% | 9% | 13% | 27% |
| Number of bags | 2 | 6 | 2 | 1 | 2 | 8 | 1 | 2 | 2 | 9 | 2 |
| Bags with no abortions | 0 | 4 | 0 | 0 | 0 | 5 | 0 | 2 | 0 | 3 | 0 |

| | Females recently rooted -- pots in lathhouse or greenhouse | | | | | |
|---|---|---|---|---|---|---|
| | Self pollen | | | Outcross pollen | | |
| Clone identity | R37 | R41 | R17 | R37 | R41 | R17 |
| Number of bagged strobili | 34 | 23 | 18 | 3 | 52 | 126 |
| % abortion | 3% | 18% | 67% | 0% | 33% | 51% |
| Number of bags | 5 | 3 | 2 | 1 | 6 | 6 |
| Bags with no abortions | 4 | 1 | 0 | 1 | 3 | 3 |

pollen. Pollen was excluded from some bags to test whether the effect of self pollen might be similar to the effect of no pollen.

As of late 1979, our combined data from all relevant crosses gave the following somewhat surprising results: Pollen was excluded from 251 bagged strobili on 9 females, and 19% of these developing strobili aborted. Self pollen was applied to 437 strobili on 13 females, and 17% aborted. Unrelated pollens were applied to 789 strobili on 15 females, and 27% aborted.

In general, pollination priorities were for outcrosses first; then, for selfs if bagged strobili were in excess of the number thought needed for outcrosses; and finally, for unpollinated controls. This created opposite biases. Of the strobili-bearing branches that were bagged, the most promising were used for outcrosses and the least promising were used as bagged controls. However, on the (perhaps weaker) females that produced few female strobili, most or all of these were used for outcrosses.

In order to reduce the second bias, data for the seven clones most used as females are presented in *Table 1*. In six of these, self-pollination was associated with a higher percent abortion than was outcrossing. However, the differences are generally small, and could be due to the differences in pollination priority.

It was our impression that the clonal identity of the female is important. It may be noted that, within each of the two groups of clones in *Table 1*, the rank-order of the clones is the same for each type of pollen. For most of the clones, pollinations were made on more than one member of the clone, and in more than one location. Careful inspection of these data indicated to us that the location or history of the individual plant (ramet) contributes little to differences in cone abortion.

The abortion histories of different bags on the same tree were frequently very different. For instance, for 8 self-pollinated bags on ARC 154, all cones completed development in 5 of the bags, 1 of 36 strobili aborted in 1 bag, but 27 of 30 and 7 of 7 strobili aborted in the other 2 bags. Thus, in ARC 154, regardless of the pollen applied (or not), many branchlets developed all of their cones while others aborted most of them *(Table 1)*. By contrast, clone S3 aborted a small percentage of its strobili in each of its 6 bags.

These data suggest that selfing has little or no effect on cone abortion. Furthermore, exclusion of pollen does not consistently change frequency of cone abortion.

*Number of seeds per cone.* Material recovered from a redwood cone exhibits all stages of seed development, from seedless wings to fully-developed seeds. In counting seeds, we included both partially- and fully-developed seeds, but excluded rudimentary seeds and other bits of detritus. *Table 2* presents data from the eleven clones we have both selfed and outcrossed to date.

Unbagged open-pollinated cones generally contained similar numbers of seeds per cone as bagged outcrossed cones from the same 6 clones, indicating little effect of bagging and other manipulation.

In 1963, bagged unpollinated cones on 3 clones produced substantially fewer seeds per cone than did open-pollinated and control-pollinated strobili on the nearby clone 10, which unfortunately had no bagged controls (Linhart and Libby 1967). This led us to suspect that pollination affected the development of redwood seed structures. However, in more recent work, in two additional clones with sufficient data (S3 and ARC 154), excluding pollen from bagged strobili had little or no effect on the number of seeds produced per cone.

Clone 10, when selfed in 1963, produced less than 64% of the seeds per outcrossed or open-pollinated cone collected from the same tree in the same year. This led us to believe that selfing, like pollen exclusion, might reduce seed yield per cone. However, it now appears that the 1963 data were unusual in these respects. Of the ten other clones selfed and outcrossed during 1977—79, five produced more seeds per cone when selfed, and the numbers of seeds per cone were generally similar among selfs and outcrosses within each clone.

Number of seeds per redwood cone is related to cone size, which in turn is related to the history and condition of the cone-bearing branch (Linhart and Libby 1967). In the experiments summarized in *Table 2*, recently-rooted cuttings grown in pots in the greenhouse and lathhouse tended to produce more seeds per cone than trees or cuttings well rooted in soil. There also appears to be an important clonal component, with ARC 154 and ARC 28 (the world's two tallest trees) consistently producing the fewest seeds per cone, and R49 producing the most.

*Percent germination.* Tests we have performed indicate that stratification does not increase seed germination in redwood. We soaked the seeds overnight in aerated water, which does speed germination, but did not otherwise pretreat the seeds in these experiments. Soaked seeds from a given collection were placed on the surface of a light potting soil in one or more small clay pots, and covered with a thin layer of soil. The pots were randomly placed on a mist bench in a greenhouse. Germination begins in redwood within a week and often continues for a month or more. We counted a seed as germinated when the cotyledons had emerged from the soil.

It is known from the work of Hansen and Muelder (1963) that nearly all redwood seeds with healthy embryos will germinate. The seeds used in different germination runs from the same cross were unselected samples, and thus should have had similar numbers of germinable seeds. However, the first germination run of the 1978 crosses had significantly lower germination than the other three runs of those crosses, and data from that first run is excluded from *Figures 1, 2 and 3.* The poorer germination in this first 1978 run apparently was the result of pre-emergence mortality due to drying and/or to damping-off, problems that were largely corrected in later runs.

We routinely set all seeds from the unpollinated controls to germinate, and have set over 12, 000 such seeds from 10 clones. Thus far, no seed from a strobilus protected from pollen has germinated.

Koski (1973) reviewed the evidence for, and possible causes of, embryonic lethals. With respect to selfing, he stated: "A dominating feature in the numerous controlled self-pollination experiments with conifers is the very pro-

*Table 2.* — Average numbers of seeds per cone produced by eleven clones that were both selfed and outcrossed.

Females well-rooted in soil

| | Open pollinated | | | | | | No pollen | |
|---|---|---|---|---|---|---|---|---|
| Clone identity | S1 | S3 | S6 | ARC 154 | ARC 28 | 10 | S3 | ARC 154 |
| Number of cones | 16 | 68 | 31 | 49 | 31 | 50 | 101 | 43 |
| Seeds per cone | 92 | 76 | 81 | 55 | 48 | 85 | 68 | 61 |

| | Self pollen | | | | | | Outcross pollen | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clone identity | S1 | S3 | S6 | ARC 154 | ARC 28 | 10 | S1 | S3 | S6 | ARC 154 | ARC 28 | 10 |
| Number of cones | 9 | 33 | 3 | 92 | 9 | 120 | 29 | 21 | 10 | 171 | 8 | 112 |
| Seeds per cone | 95 | 69 | 83 | 67 | 58 | 54 | 92 | 58 | 91 | 54 | 34 | 89 |

Females recently rooted -- pots in lathhouse or greenhouse

| | Self pollen | | | | | Outcross pollen | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Clone identity | R17 | R22 | R37 | R41 | R49 | R17 | R22 | R37 | R41 | R49 |
| Number of cones | 6 | 5 | 33 | 19 | 10 | 35 | 57 | 3 | 35 | 14 |
| seeds per cone | 96 | 84 | 95 | 81 | 128 | 97 | 102 | 99 | 107 | 121 |

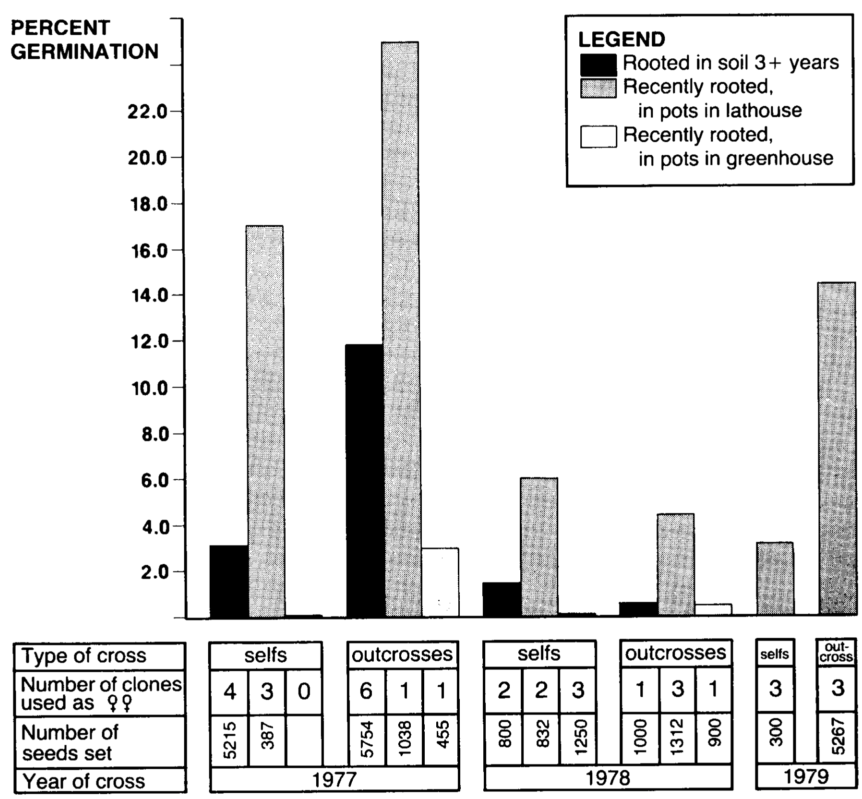



*Figure 1.* — Percent germination of selfs and outcrosses from three years' pollinations, by location of female parent.

nounced decrease in the proportion of filled seeds compared with the results for cross pollination or open pollination". YABLOKOV (1960) noted that redwood set almost no seed capable of germination on selfing, but that the germination capacity was increased up to 50% on artificial cross-pollinations. In our 1963, 1977 and 1979 experiments, the average percent germination of the selfs was significantly ($p < .001$) lower than the average for the outcrosses. However, in 1978, the reverse was true, with significance levels of .01 and .001 for clones rooted in soil, and grown in the lathhouse, respectively *(Figure 1)*.

LINHART and LIBBY (1967) reported large differences in germination, depending on whether the cones were ripened on the tree or on detached branches. We and others (MUELDER and HANSEN 1961) have also observed very different average germination from open-pollinated redwoods growing in different locations. In our experiments, the same clones were not located in the greenhouse,the lathhouse, and the field, nor were they always employed in each year's crosses. But they do provide some evidence that the nutritional status and location of the mother tree influences the percentage of germinable seeds *(Figure 1)*. Seeds from recently-rooted females in the lathhouse consistently germinated better than seeds from other clones rooted earlier and growing in field conditions. Seeds from cones that initiated and developed in the unusual daylength and temperature conditions of the greenhouse consistently germinated the poorest.

An analysis by female clones *(Figure 2)* indicates large differences in average germination among clones, and large clonal differences in the relative germination of selfs and outcrosses. Among select clones, R37 and perhaps ARC 154 had higher germination of selfs than of outcrosses, with R37 being unusually self-compatible in both 1977 and 1978. Thus far, open- and control-pollinated cones from ARC 28 have yielded over 800 seeds, none of which have germinated.

PAWSEY (1964), KOSKI (1973), and others have also reported considerable differences among clones in both absolute and relative numbers of filled or germinating seeds per cone in selfs and outcrosses.

These preliminary data also indicate that pollen parent and year of pollen collection can be of importance *(Figure 3)*. Pollen of R37 in particular indicates the importance of collection year, as used on R17, ARC 154, and R22.

Comparisons of open-pollinated families to the selfs and outcrosses with respect to germination *(Figure 2)* are probably not very useful. Redwoods have been planted near all of the mother trees, but these scattered neighbors are unlikely to form a pollen cloud similar to one in a forest. It is expected, therefore, that pollination might be limiting in such open-pollinations.

Overall, the impression from the germination data is one of great variability, with many inbred seeds (from various clones and with various histories) germinating successfully. Differences among both self and outcross families have important implications for seed-orchard management.

*Nursery survival.* When the cotyledons of a germinating seedling extended to a horizontal position, it was transplanted into a 10-cubic-inch leach tube filled with light potting soil. Two weeks later, the tubes were transferred from the mist bench to (in 1977 and early 1978) an unmisted greenhouse, and two weeks after that began receiving liquid fertilizer (10:8:7 NPK + micronutrients) at 2-week intervals.

During April and May, 1978, most of the seedlings of the December 1977 germination run became infected with a root rot identified as *Phytopthora* (by Prof. R. RAABE, Dept. Plant Pathology, UC Berkeley), and substantial mortality occurred. To abate this problem and avoid further seedling mortality, these seedlings received a Truban soil drench and were moved to the cooler drier conditions in a lath-

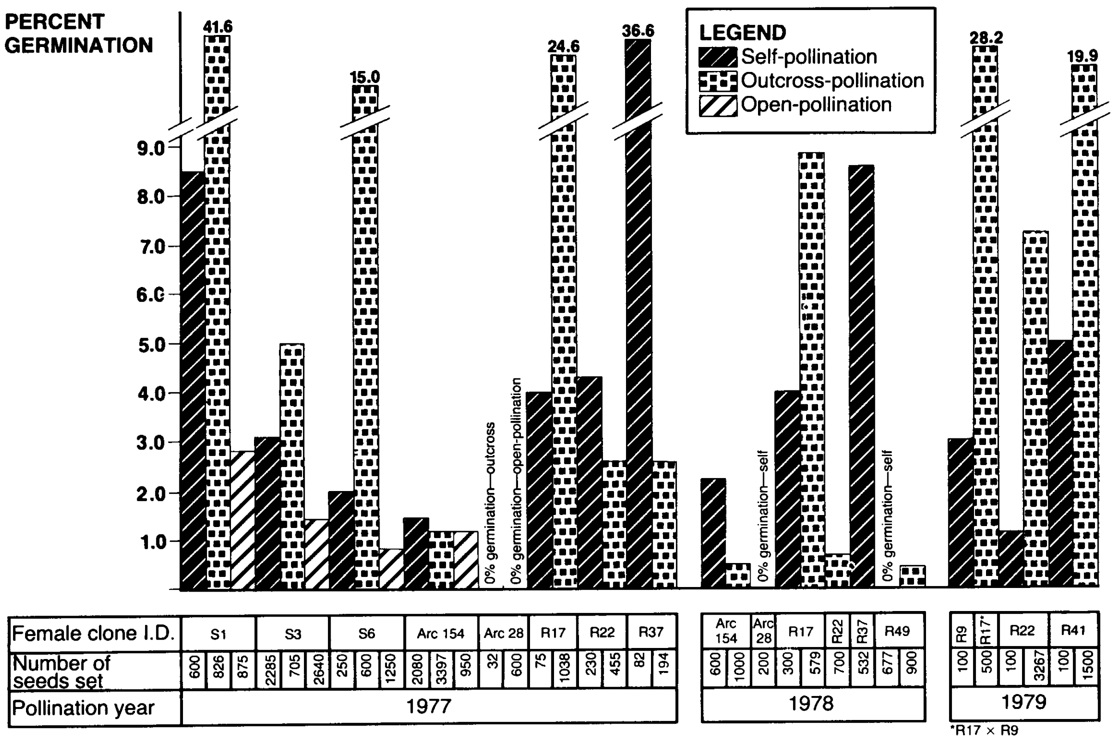
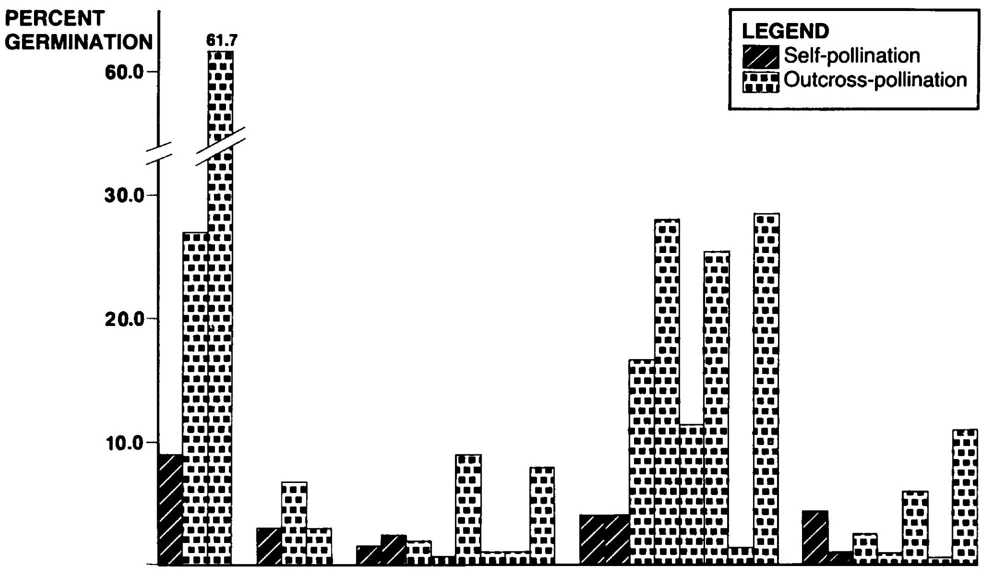



*Figure 2.* — Percent germination of selfs, outcrosses and opens from three years' pollinations, by female clone.

house; all subsequent seedlings were moved from the mist bench directly to the lathhouse.

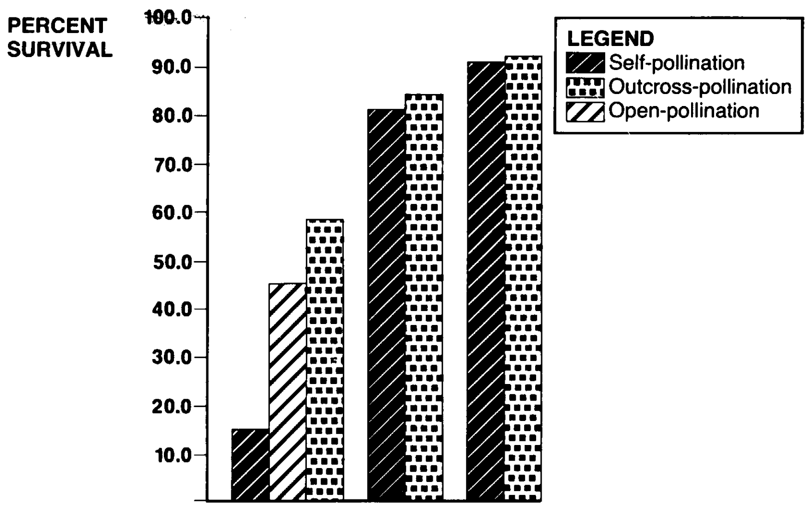
Differences in post-germination nursery survival were not consistently associated with location of the female parent, and *Figure 4* combines data from all locations.

Among seedlings from the 1977 germination run, the outcrosses survived significantly better than the selfs ($p < .001$). Set to germinate in June, a second sample of most of these same families survived much better, and the survival of the selfs was essentially equal to that of the outcrosses.




| Mother | Father | Year | Number of seeds set |
|---|---|---|---|
| S1 | S1 | 1977 | 600 |
| | Arc 154 | 1977 | 476 |
| | S6 | 1977 | 360 |
| S3 | S3 | 1977 | 2285 |
| | S1 | 1977 | 405 |
| | T6 | 1977 | 300 |
| Arc 154 | Arc 154 | 1977 | 2080 |
| | | 1978 | 600 |
| | Arc 28 | 1977 | 1448 |
| | | 1978 | 400 |
| | | 1979 | 43 |
| | R37 | 1977 | 1949 |
| | | 1978 | 600 |
| | | 1979 | 669 |
| R17 | R17 | 1977 | 75 |
| | | 1978 | 300 |
| | R9 | 1978 | 279 |
| | | 1979 | 500 |
| | R19 | 1977 | 78 |
| | R23 | 1977 | 960 |
| | R37 | 1978 | 300 |
| | | 1979 | 500 |
| R22 | R22 | 1977 | 230 |
| | | 1979 | 100 |
| | R2 | 1977 | 455 |
| | R9 | 1978 | 400 |
| | | 1979 | 2500 |
| | R37 | 1978 | 300 |
| | | 1978 | 767 |

*Figure 3.* — Percent germination of selfs and outcrosses from five females, by male and year of pollen collection. T6 (mated to S3) is a clone that produced this pollen on a rooted cutting grown in greenhouse conditions at a chronological age of 18 months.




| Nursery run | Dec. 1977 | | | Jun. 78 | | Dec.78-Jun. 79 | |
|---|---|---|---|---|---|---|---|
| Number of families | 7 | 4 | 11 | 6 | 9 | 2 | 7 |
| Number of seedlings | 62 | 33 | 216 | 135 | 564 | 29 | 72 |

*Figure 4.* — Percent nursery survival of selfs and outcrosses from two pollination years. The December 1977 (including opens) and June 1978 runs are samples of the same families, grown under conditions of high and low root-rot incidence, respectively. The four germination runs of the 1978 pollinations, all grown in favorable conditions, are combined in the two right-hand bars.

*Table 3.* — Nursery height, and First-year Plantation Survival and Height of Plants Outplanted in 1979

| | Location | Gill Nursery | | Simpson Plantation | | | Masonite Plantation I[1]) | | | Masonite Plantation II—V | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Number Measured | Average Ht.-cm. | Number Planted | Survival % | Average Ht.-cm. | Number Planted | Survival % | Average Ht.-cm. | Number Planted | Survival % | Average Ht.-cm. |
| | Date | | Jan '79 | Mar '79 | Aug '79 | Aug '79 | Mar '79 | Aug '79 | Aug '79 | Mar '79 | Aug '79 | Aug '79 |
| | Outcrosses[2]) | | | | | | | | | | | |
| | S6 × S3 | 36 | 10.0 | 17 | 71% | 16.6 | 3 | 67% | 19.5 | 16 | 13% | 15.7 |
| | S3 × S1 | 11 | 9.3 | 6 | 100% | 15.6 | 2 | 100% | 12.0 | 3 | 0% | — |
| | S1 × S6 | 22 | 15.6 | 11 | 82% | 14.6 | 2 | 100% | 16.5 | 9 | 56% | 23.0 |
| | S1 × ARC 154 | 31 | 12.8 | 16 | 81% | 14.2 | 3 | 100% | 9.3 | 12 | 8% | 25.0 |
| | Selfs | | | | | | | | | | | |
| | S1 self | 39 | 9.4 | 20 | 90% | 11.5 | 4 | 75% | 9.7 | 14 | 21% | 12.7 |
| | S3 self | 53 | 7.9 | 26 | 88% | 12.8 | 3 | 67% | 13.0 | 23 | 13% | 14.0 |
| | S6 self | 2 | 6.0 | 0 | — | — | 2 | 50% | 5.0 | 0 | — | — |
| | ARC 154 self | 6 | 4.6 | 3 | 33% | 12.0 | 1 | 100% | 3.0 | 2 | 0% | — |
| | Select Family & Standard Clones | | | | | | | | | | | |
| | Clone H7 | 10 | 13.1 | 5 | 60% | 11.5 | 1 | 100% | 10.0 | 4 | 25% | 9.0 |
| | Clone T4 | 10 | 11.9 | 5 | 60% | 17.7 | 1 | 0% | — | 4 | 0% | — |
| | R17 × R23 | 10 | 13.9 | 5 | 100% | 17.5 | 1 | 100% | 23.0 | 4 | 75% | 12.7 |
| | Clone T6 | 10 | 10.1 | 5 | 100% | 16.8 | 1 | 100% | 12.0 | 4 | 0% | — |
| | Clone T9 | 10 | 8.8 | 5 | 100% | 11.5 | 1 | 100% | 8.0 | 4 | 25% | 11.0 |
| | Averages | | | | | | | | | | | |
| a | R17 × R23 | 10 | 13.9 | 5 | 100% | 17.5 | 1 | 100% | 23.0 | 4 | 75% | 12.7 |
| b | Unsel. Outcr. | 69 | 11.6 | 34 | 79% | 15.8 | 7 | 89% | 16.0 | 28 | 29% | 20.3 |
| c | S1 × ARC 154 | 31 | 12.8 | 16 | 81% | 14.2 | 3 | 100% | 9.3 | 12 | 8% | 25.0 |
| d | Std. Clones | 40 | 11.0 | 20 | 80% | 14.6 | 4 | 75% | 10.0 | 16 | 13% | 10.0 |
| e | Unsel. Selfs | 94 | 8.5 | 46 | 89% | 12.3 | 9 | 67% | 10.0 | 37 | 16% | 13.4 |
| f | ARC 154 Self | 6 | 4.6 | 3 | 33% | 12.0 | 1 | 100% | 3.0 | 2 | 0% | — |
| | p value of b versus e < .001 | | | | N.S. | < .01 | | N.S. | N.S. | | N.S. | ≈ .05 |

[1]) Block I at the Masonite Plantation is presented separately from Blocks II—V due to poorer growing conditions and heavy mortality in Blocks II—V . . . see text.

[2]) ARC 154 is a clone of the world's tallest tree. S1, S2 and S6 are random seed-trees used as parents of the "unselected" selfs and outcrosses. R17 & R 23 are outstanding redwoods from the same area as ARC 154 and S1—S6.

Survival was again high and similar among seedlings from different families in the four germination runs (combined in *Figure 4)* of the 1978 crosses.

Seedlings from open-pollinations were kept only from the December 1977 germinants. Their survival was marginally similar ($p = .06$) to that of controlled outcrosses of the same female parents, and like the outcrosses, it was substantially and significantly ($p < .001$) better than that of the selfs.

Pawsey (1964) and Koski (1973) both cited examples of large differences in nursery survival between selfs and outcrosses under stress conditions, and much smaller differences under favorable conditions. Our results are consistent with this pattern.

*Nursery height.* Most of the seedlings from the 1977 crosses among select parents were hedged as cutting donors near the end of the year, making height measurements inappropriate. However, 10 blocks of plants, mostly from unselected mother clones (S1, S3 & S6), were used for further growth studies. Each block was organized as a single rack of leach tubes approximately two months after the seedlings were transplanted to the tubes. Each block contained 25 plants: 10 seedling selfs, 10 seedling outcrosses related to the selfs, 1 ramet each of 4 "standard clones" (of similar size to the seedlings), and 1 seedling of the select cross R17 × R23. All seedlings came from the June 1978 germination run *(Figure 4).* The "standard clones" are four unrelated juvenile clones that we include in many of our redwood experiments. The blocks were arranged in one of two experimental layouts: in rows 1, 2, 4 & 5, selfs alternated with outcrosses, such that one of the outcross parents was the same as the parent of the adjacent self; or, 10 selfs were in rows 1 & 2, and 10 outcrosses related to the selfs were in rows 4 and 5. The 3rd row was occupied by the four standard clones, and the seedling of (R17 × R23) occupied the center position of each block. Mortality during the nursery phase was replaced by a random plant of the same family or clone, germinated or rooted at about the same time as the plant that died, and growing nearby in similar conditions. The experiment was grown in a lathhouse, and the plants were fertilized every 14 days until they were hardened-off for winter.

Pawsey (1964), Koski (1973) and others have noted small (often not significant) differences in growth between selfs and outcrosses during the first year under nursery conditions. Yablokov (1960) noted that redwood outcross seedlings grew more rapidly and vigorously than did selfs, without quantifying the difference.

In our experiments, between-plant competition for light did not become intense until late in the season, and the relative performances of the selfs and the outcrosses were similar in the two experimental layouts. *Table 3* lists the height performance in the nursery of each family and standard clone, and summarizes by group. On the average, the outcrosses grew tallest during the nursery period, the standard clones were intermediate, and the selfs grew the least. The most sensitive comparison is between the heights of the three unselect-outcross families (S1 × S6, S6 × S3 & S3 × S1) and these same three parents selfed. These selfs grew only 73% as tall as these outcrosses ($p < .001$).

It may be noted that, in the nursery, parent S1 produced the tallest selfs on the average, and it also combined well with S6 and ARC 154 as the female parent. It also appears that ARC 154 does not produce very tall seedlings when selfed.

*Early survival: 1979 plantations.* The plants described in the section on nursery height, above, were outplanted on two redwood sites in northern California in March 1979, during a favorable period of rainy weather. Five blocks were planted at each site. The trees in each block were planted in the same arrangement as existed in the leach-tube rack in the nursery, at a spacing of 3 meters between trees.

The northern site, on Simpson Timber Co. land in northern coastal Humboldt County near Korbel, is located at 185 meters elevation of a flat deep alluvial soil next to the Mad River, approximately 14 km inland from the ocean. The site was cleanly prepared, but weeds densely invaded and frequently overtopped the planted redwoods. The redwoods were irrigated and weeded as judged necessary during the first summer.

The southern site, on Masonite Corp. land in central Mendocino County near Philo, is on a relatively xeric side-ridge at 480 meters elevation, approximately 21 km inland. The site was generally clean following clearing of pole-sized radiata pine. Invading weeds, though present, were small and scattered on Blocks II—V. Weed growth was greatest on Block I, where general conditions for growth were clearly best. These trees were given supplemental water only once during the hot dry summer.

Browsing by deer or small mammals was not a significant problem at either plantation, although the negative growth of a few families or clones that may be noted in *Table 3* is usually due to mild browsing of a few plants.

Survival was recorded at both plantations in late August, 1979 *(Table 3).* Survival was relatively high at the Simpson plantation, and the difference between the unselect selfs and unselect outcrosses is not statisically significant. At the Masonite plantation, Blocks II—V are located on an exposed, hot dry slope. These suffered much greater mortality than Block I, which is on a more mesic, north-facing slope. Under the more difficult conditions at the Masonite site, the selfs and the rooted cuttings generally did not survive as well as the adjacent outcrossess. These differences, however are not statistically significant. The relative survival performance at the Simpson and Masonite sites of the selfs and outcrosses does continue the pattern of nursery survival under favorable and stress conditions.

It is tempting to note the high survival of the only select family (R17 × R23) with some enthusiasm.

*Early height: 1979 plantations.* Heights were also measured in late August, part-way through the first growing season in the plantations.

At Simpson, the nursery pattern of height was largely maintained, although families with smaller trees frequently grew relatively more (or were browsed less) during this establishment period than families with larger trees. At Masonite, with fewer survivors, the pattern is less consistent. But, in both Block I and Blocks II—V, the outcrosses remain taller than their selfed relatives.

In the sensitive comparison between unselect outcrosses and the selfs of the same parents, these selfs were only 78% as tall as these outcrosses at Simpon, 62% as tall in Block I at Masonite, and 66% as tall in Blocks II—V at Masonite. These differences are statistically significant for Simpson ($p < .01$) and for Blocks II—V at Masonite ($P \approx .05$), but not for Block I at Masonite. There is a tendency in these unselect families for the relatively few survivors in Masonite Blocks II—V to be the larger plants.

*First- eleventh- and fourteenth-year survival, form and size: 1965 plantation.* In December 1965, 28 seedlings from the 1963 crosses were planted near the top of a northeast-facing ridge on Simpson Timber Co. land about 14 km east of Korbel, at elevation 380 meters. They were planted in 7 rows and 4 columns at 3-meter spacing, alternating between selfs and outcrosses (or opens), such that every self is surrounded by outcrosses (or opens) and every outcross (or open) is surrounded by selfs *(Figure 5)*. All came from the same tree, tree 10 at Russell Reservation. They were observed and measured in 1966, 1976 and 1979, at ages 3, 13 and 16 years from germination, for survival and height. In

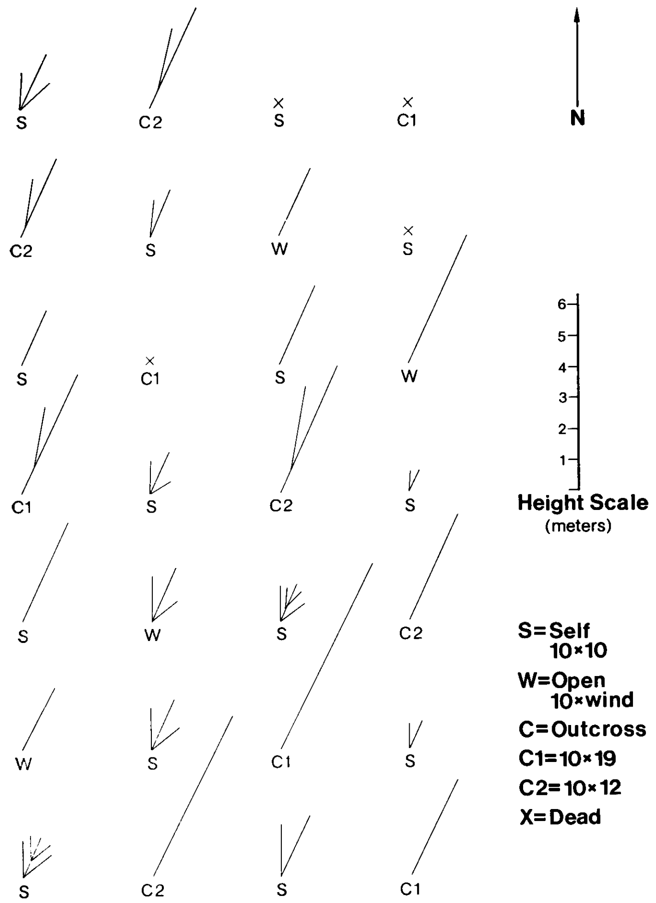



*Figure 5.* — Graphic presentation of the 1965 outplanting of selfs, opens and outcrosses from clone 10, as of 1979. Heights are drawn to scale, and size and location of forks are as indicated. (The main stems are drawn at an apparent angle for clarity, and the trees are in fact growing vertically.)

addition, data on diameter (at 2 decimeters) and stem forking were taken in 1979.

Survival of these trees has been remarkably high, particularly given that survival on two adjacent plantations of seedlings, mature rooted cuttings and grafts of redwood planted at the same time has been less than 50%. All 28 of these seedlings survived the establishment year. Ten years later, two outcrosses and two selfs had died, and no further mortality had occurred as of August 1979.

In all three measurement years, outcross family 10 × 19 was tallest *(Table 4)*. In 1966, the open-pollinated family was second tallest, and was taller than the average of the two outcross families. But by 1976 and 1979, the second outcross family had become taller than the opens. In all three measurement years, the self family was shortest.

The difference in average height between outcrosses and selfs in 1966 is not statistically significant, whereas in both 1976 and 1979 the differences are highly significant ($p < .001$). Note that the differences between families as expressed in 1966 are not just being maintained, nor do the same relative growth rates prevail in these families over time. In 1966, the selfs were 75% the average height of the outcrosses, but in 1976 and 1979 they were only 43% and 42% average outcross height. By 1976 and 1979, the differences in height and form were so obvious that it was usually apparent by casual observation which trees were the selfs.

Stem diameters of outcrosses were significantly greater ($p < .001$) than those of selfs. As was the case for height, by 1979 the opens more closely resembled the selfs with respect to diameter than they resembled the outcrosses.

On the average, selfs had significantly ($p \approx .05$) more main stems (low forks) than did outcrosses or opens. These data are graphically presented for all trees in the experiment, with heights to scale, in *Figure 5*. We are uncertain whether the multiple stems on the selfs were due to the inbred condition *per se*, or due to greater opportunity for deer browsing and subsequent sprouting on the relatively shorter selfs. Note in *Figure 5* that only one of the short open-pollinated seedlings is forked, while all but one of the short selfs is forked.

## General Discussion and Conclusions

The experiments reported above are small, generally somewhat unbalanced, and *ad-hoc* in nature. More extensive investigations are in progress, or are planned. The data are presented now because redwood breeding programs are in progress, creating a need to evaluate the probable importance of inbreeding depression.

Selfing does not seem to affect cone abortion, except perhaps under unusual conditions. While the number of seeds that develop per cone is substantially affected by the condi-

*Table 4.* — Height in first and eleventh years plus height, diameter and forking in fourteenth year after planting.

| Data year | 1965 Number Planted | 1966 n[1] | 1966 Average Height (m) | 1976 n | 1976 Average Height (m) | 1979 n | 1979 Average Height (m) | 1979 Average Diameter (cm)[2] | 1979 Average number of main stems |
|---|---|---|---|---|---|---|---|---|---|
| Outcross families | | | | | | | | | |
| 10 x 19 | 5 | 5 | 0.15 | 3 | 3.4 | 3 | 4.7 | 8.5 | 1.3 |
| 10 x 12 | 5 | 5 | 0.09 | 5 | 2.8 | 5 | 4.1 | 7.3 | 1.6 |
| Open-pollinated family | | | | | | | | | |
| 10 x wind | 4 | 4 | 0.13 | 4 | 1.7 | 4 | 2.7 | 3.5 | 1.5 |
| Self family | | | | | | | | | |
| 10 x 10 | 14 | 14 | 0.09 | 12 | 1.3 | 12 | 1.8 | 2.2 | 2.3 |

1) Number still alive that year. 2) Diameter at 2 decimeters above ground.

tion of the female plant, selfing does not consistently reduce the number developed in the cones of a given female. Thus, two mechanisms that might reduce the percentage of inbred seeds in wild stands or in open-pollinated seed-orchards do not appear to operate in redwood.

We have no information on the competitive relationship of self and unrelated pollen when such a mixture effects pollinations. Competitive fertilization favoring unrelated pollen would be another mechanism for reducing inbreds under open-pollinated conditions, and research on this question is needed.

Percent germination of redwood seed varies enormously, and the factors affecting this variation are not well understood. Pollination is clearly necessary. It appears that the health of the cone-bearing tree and the health of the embryo are both important. Germination of self seed was significantly and substantially less than germination of related outcross seed in some of our experiments, but in others the reverse was true. Overall, a substantial percentage of self seed does germinate- on the order of 50% or more of the percentage of outcross seed. From this it may be predicted that, if pollinations producing inbred seeds are frequent at the source of seed used in a nursery, then substantial numbers of inbred seeds will germinate in the nursery.

The relative early survival of selfs and outcrosses seems to depend very much on the environmental conditions. Under conditions of stress (disease and drought in the experiments reported above), where substantial mortality occurs among both outcrosses and selfs, relatively more outcrosses survive. However, when conditions are such that a high percentage of outcrosses survive, a similar percentage of selfs survive. This difference in relative performance under favorable and stress conditions has been noted in other inbreeding studies (ALLARD and HANSCHE 1964). Thus, we must caution that, in a well-run nursery and in well-established plantations, there will be very little reduction in the percentage of inbred redwoods due to inbreeding-related mortality.

Selfs grew to about 3/4 the height of related outcrosses in the nursery. While this difference is significant and substantial, it may not be enough to allow the nursery to cull a high proportion of the inbreds while keeping most of the outcrosses.

Thus, it seems likely that if some proportion of seeds delivered to a well-run nursery are inbred, a somewhat smaller proportion of trees in well-established plantations from that nursery will be inbred.

Data from our 1965 and 1979 plantations indicate that the size differences noted in the 1978 nursery are largely maintained among the first-year survivors in these three plantations. Data for later performance of inbred redwoods are at present restricted to our 1965 plantation, which contains offspring of only one female tree. Experience with various diploid conifers indicates that differences between selfs and outcrosses increase under conditions of competition, and increase even more when the crowns close. Our 1965 plantation has experienced modest competition from weeds and brush, and the crowns were just beginning to touch in 1979. The average height of the selfs has changed from 75% that of the outcrosses in 1966 to only 42% that of the outcrosses in 1979.

Data from a few open-pollinated families were included as possible and appropriate. In general, the performance of the open families was intermediate between that of the selfs and outcrosses. This lends some support to the reasonable hypothesis that many open-pollinated families are mixtures of selfs, milder forms of inbreds from crosses among relatives, and outcrosses. Tree 10, used in the 1963 crosses, is a planted tree. It is possible that some or even many of the nearby planted redwoods that may have donated pollen to wind-pollinated strobili are related to tree 10, but this is not known. Trees S1, S3 and S6, used in the 1977 crosses, are very unlikely to have received pollen from other trees of their distant native stand. Thus, the marginally poorer nursery survival of their open-pollinated families may be explained by the inclusion of selfs within these families, or possibly by maladapted wide crosses. Since trees S1, S3 and S6 are all from the same native stand, crosses among them may produce some milder levels of inbreeding, thus causing an underestimation of the difference between their selfs and "outcrosses" in this experiment. It may also help to explain the relatively better performance of family R17 × R23, which is surely a cross between unrelated trees from the same region.

It is important to note that there is considerable variability between and within selfed families (PAWSEY 1964; KARKI 1973). Thus, there are some vigorous healthy selfs in families showing inbreeding depression, and some self families (such as R37 × R37) apparently perform, on the average, as well or better than their outcrossed relatives. Such unusual inbreds may be of considerable use in a redwood breeding program.

Although inbreeding depression in redwood is variable, both with respect to developmental stage and among families, it appears to be substantial with respect to growth in plantations. The presence of such severe inbreeding depression in redwood is contrary to expectations based on redwood's hexaploid genome. Polyploidy in redwood does not seem to protect the species from the detrimental effects of inbreeding. The reasons for this are not clear. It is possible that redwood has a diploidized genome, behaving essentially as if it had 33 independent pairs of chromosomes with unique genes on each. However, this seems unlikely in view of the multiple and unbalanced multivalent meiotic pairing configurations in redwood (STEBBINS 1948; unpublished observations by c. i. m.).

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**Literature Cited**

AFOCEL: Micropropagation d'Arbres forestiers. Etudes et Recherches No. 12 - 6/79. Assoc. Foret-Cellulose, Domaine de l'Etancon, 77370 Nangis. France. (1979). — ALLARD, R. W. and P. E. HANSCHE: Some parameters of population variability and their implications in plant breeding. Adv. in Agronomy 16: 281—325 (1964). — BISHIR, J. and W. PEPPER: Estimation of number of embryonic lethal alleles in conifers. I. Self-pollinated seed. Silvae Genetica 26: 50—54 (1977). — DOGRA, P.: Seed sterility and disturbances in embryogeny in conifers with particular reference to seed testing and tree breeding in *Pinaceae*. Studia Forestalia Suecica (Royal College of Forestry) Stockholm. 97 pp. (1967). — FOZDAR, B. and W. J. LIBBY: Chromosomes of *Sequoia sempervirens:* 8-hydroxyquinoline — castor oil pretreatment foor improving preparation. Stain Tech. 43: 97—100 (1968). — FRANKLIN, E. C.: Survey of mutant forms and inbreeding depression in species of the family *Pinaceae*. SE For. Expt. Sta. USDA For. Ser. Res. Pap. SE-61. 21 pp. (1970). — HAIR, J. B.: The chromosomes of the *Cupressaceae*. 1. *Tetraclineae* and *Actinostrobeae*. N. Z. J. Bot. 6: 277—84 (1968). — HAIR, J. B. and E. J. BEUZENBURG: Chromosomal evolution in the *Podocarpaceae*. Nature, *181*: 1584—86 (1958). — HANSEN, J. H. and D. W. MUELDER: Testing of redwood seed for silvicultural research by x-ray photography. For. Sci. (4): 470—476 (1963). — KHOSHOO, T. N.: Polyploidy in gymnosperms. Evolution 13: 24—39. (1959). — KOSKI, V.: On self-pollination, genetic load, and subsequent inbreeding in some conifers. Comm. Inst. For. Fenn. 78 (10): 1—40 (1973). — LIBBY, W. J.: Closing remarks and summary. IUFRO Joint Meeting on Advanced-Generation Breeding. Bordeaux. 181—88. (1976). — LIBBY, W. J., Y. T. KIANG and Y. B. LINHART: Controlpollination seeds from cuttings of coast redwood Silvae Genetica 21: 17—20 (1972). — LIBBY, W. J. and B. G. MCCUTCHAN: "Taming" the redwood. Am. Forests 84 (8): 18—23; 37—39 (1978). — LINHART, Y. B. and W. J. LIBBY: Successful controlled pollination on detached cuttings of coast redwood. Silvae Genetica 16: 168—72 (1967). — MARKERT, C. L., J. B. SHAKLEE and G. S. WHITT: Evolution of a gene. Science 189: 102—14 (1975). — MEHRA, P. N. and T. N. KHOSHOO: Cytology of conifers. Jour. Genet. 54: 165—80 (1956). — MUELDER, D. W. and J. H. HANSEN: Biotic factors in natural regeneration of *Sequoia sempervirens*. IUFRO 13th Cong. Vienna Proc. PT 2. Vol. 1 (24—4/1) 5 pp. (1961). — PAWSEY, C. K.: Inbreeding radiata pine. Aust. For. and Tim. Bur. Leaflet 87, 31 pp. (1964). — SAX, K. and H. J. SAX: Chromosome number and morphology in conifers. Jour. Arn. Arb. 14: 356—75 (1933). — SAYLOR, L. C. and H. A. SIMONS: Karyology of *Sequoia sempervirens*: Karyotype and accessory chromosomes. Cytologia 35: 294—303 (1970). — STEBBINS, G. L.: The chromosomes and relationships of *Metasequoia* and *Sequoia*. Science 108: 95—98 (1948). — STEBBINS, G. L.: Self-fertilization and population variability in the higher plants. Am. Naturalist 91: 337—54 (1957). — SWEET, G. B.: Shedding of reproductive structures in forest trees. *In:* Shedding of plant parts. *Ed.* T. T. KOZLOWSKI. Acad. Press. NY. pp. 341—82. (1973). — THOMAS, G. and K. K. CHING: A. comparative karyotype analysis of *Pseudotsuga menziesii* and *P. wilsoniana*. Silvae Genetica 17: 138—42 (1968). — YABLOKOV, A. S.: Wide hybridization in silviculture and greenbelt work. survey and prospects. p. 60. *In:* Wide hybridization of plants. *Ed.* N. V. TSITSIN. Proc. Conf. on wide hybridization of Plants and Animals. Acad. of Sciences of the U.S.S.R., 1962 Translation for NSF, Washington D. C. by the Israel program for Sci, Trans. (1960).

# Height growth of some interracial hybrids of norway spruce using selected trees of a north and a central european provenance with special regard to between-plot-competition[1])

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### Summary

7 crossings between selected trees of the provenances Sundmo (Sweden) and Westerhof (Germany) were done in 1954. Field trials were established in 1959 using these interracial hybrid progenies together with the open pollinated progenies of the parent trees (10 at a total). Height growth has been measured at different ages (from 5 to 17 years).

The results showed a superiority of the open pollinated progenies from Westerhof (W-progenies) at all locations and at all ages, while the open pollinated progenies from Sundmo (S-progenies) are inferior, and the hybrid progenies are of approximately intermediate height growth. From age 5 to age 17 the hybrid progenies increased their relative height growth from about 60% up to 80% compared to that of the W- progenies (= 100%). Thus the increment of height growth was higher than would be expected from exactly intermediate growth patterns of the hybrid progenies. A trend of an increasing increment of height growth was found, which at the age 17 was still evident. In the field trials at high elevation this trend was very strong. Here the increment of height growth of the hybrid progenies reached or even surpassed that of the W-progenies.

The results were in close agreement with those of Swedish investigations. It seems that interracial hybrids may be of some interest for sites at high elevations.


*Key words:* Norway spruce, interracial hybrids, height growth

[1]) Some sections of this paper have been partially given as a lecture at the IUFRO-Norway-Spruce-Meeting in Bucharest/Romania 1979.

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### Zusammenfassung

Sieben Kreuzungen zwischen selektierten Bäumen der Provenienz Sundmo (Schweden) und Westerhof (Deutschland) wurden 1954 durchgeführt. 1959 wurden Feldversuche angelegt mit diesen Zwischen-Rassen-Hybridnachkommenschaften zusammen mit den freiabgeblühten Nachkommenschaften der Elternbäume (insgesamt 10). Die Höhen wurden im Alter von 5 bis 17 Jahren gemessen.

Die Ergebnisse zeigten eine Uberlegenheit der freiabgeblühten Nachkommenschaft von Westerhof (W-Nachkommenschaft) auf allen Standorten in jedem Alter, während die freiabgeblühten Nachkommenschaften von Sundmo (S-Nachkommenschaften) unterlegen waren und die Hybridnachkommenschaften annäherungsweise intermediäres Höhenwachstum zeigten. Im Alter von 5 bis 17 Jahren steigerten die Hybridnachkommenschaften ihr relatives Höhenwachstum von rund 60 auf 80% im Vergleich zu dem Höhenwachstum der W-Nachkommenschaften (= 100%). Daraus ergab sich, daß der Höhenzuwachs der Hybridnachkommenschaften größer war als der, der bei exakter intermediärer Vererbung der Anlage Höhenwachstum erwartet werden konnte. Ein Trend des zunehmenden Höhenzuwachses bei den Hybridnachkommenschaften wurde gefunden, der im Alter 17 noch anhielt. Gerade in den Feldversuchen der hohen Höhenlage war dieser Trend sehr deutlich. Hier erreichte der Höhenzuwachs der Hybridnachkommenschaften den der Westerhöfer Nachkommenschaften oder übertraf diese sogar.

Die Ergebnisse stimmten gut mit denen schwedischer Untersuchungen überein. Es scheint, daß die Zwischen-Rassen-Hybriden für Standorte in Höhenlagen Bedeutung haben können.


### Introduction

Scandinavian and german forest tree breeders have been doing interracial hybridization in Norway spruce *(Picea*