die Epikotyllänge und das Überstehen der ersten Vegetationsperiode festgestellt bzw. gemessen. Im Mai 1972 wurden die Pflanzen in gleicher Blockanordnung verschult. Nach dem ersten Jahr zeigte sich eine allgemeine Tendenz zu klinaler Variation beim Austreiben, bei der Knospenbildung, bei der Nadelfarbe und der Epikotyllänge. Insbesondere nach der zweiten Vegetationsperiode ergaben sich deutliche Zusammenhänge bei der Knospenbildung, Epikotyllänge und Gesamthöhe jeweils bezogen auf den Herkunftsort einer Provenienz. Die genetische Varianz war zwischen den Nachkommenschaften größer als zwischen den Einzelbäumen.

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Female Sterility in Douglas-fir

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Introduction

In 1967, controlled pollinations were made on three young Douglas fir, Pseudotsuga *menziesii* (MIRB.) FRANCO which were located in a natural stand some 100 km southeast of Cowichan Lake on southern Vancouver Island, British Columbia. The trees were bagged at the beginning of April and pollinated May 9th, the pollen used for the crosses coming from single trees on the coastal mainland of the province, Oregon, Arizona and New Mexico. Cones were collected at the beginning of September together with wind-pollinated samples from each of the trees. There had been little damage from cone insects and the seed was extracted without any difficulty. It was then found that the more than 3500 seeds from tree 618 were all undeveloped and flat so that not one seed could be sown. The seeds from the other two trees, were perfectly normal with yields of 45.0 and 68.4 seeds per cone respectively and later produced 28.2 and 37.0 healthy genninants per cone in the nursery. The difference between normal fully formed seed and the typical flat seed from tree 618 is shown in *Figure* 1.

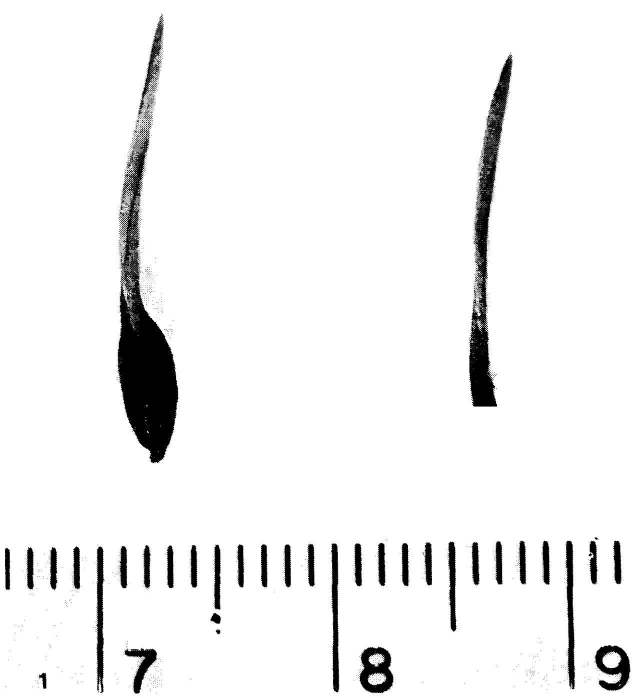

Figure 1. — Normal seed compared with flat undeveloped seed.

Seed Development on Clone 618

As this was the first occasion that this phenomenon had been observed in the course of extensive pollinations with Douglas fir, tree 618 was propagated to ascertain whether the clone would produce similar flat seed when grown in a different environment. Scions were accordingly removed and grafted at Lake Cowichan in 1968, the two surviving

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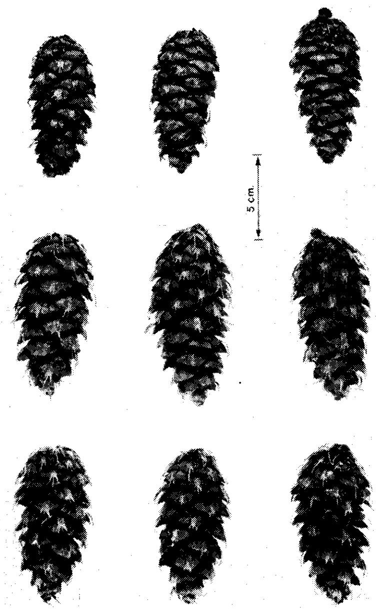

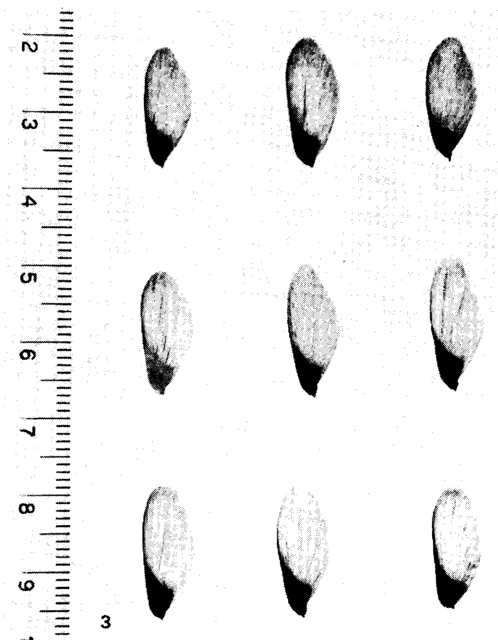

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Figure 2 and 3. — Cones and seed from tree 618 and the two ramets.

ramets 1 and 2 producing male and female strobili eight years later. No controlled pollinations were made but 103 and 91 cones respectively were collected from the two ramets in the autumn. There had been little damage from cone insects and the seed was extracted without difficulty. It was found that all of the more than 5000 seeds were undeveloped and flat. *Figures 2 and 3* show, from top to bottom, the cones and seeds from the 1967 collection of tree 618 followed by those made on ramets 1 and 2 respectively in 1976. Male strobili were also collected from the two ramets in the autumn, these were normal in appearance with regular sporophylls. Small amounts of pollen were found in the sporophylls and these were examined under a microscope. The pollen appeared normal but some pollinations will have to be made as soon as possible to check whether the clone is also male sterile. Both ramets are vigorous and *Figure 4,* taken in autumn 1976, shows ramets 1 in the foreground and 2 on the left, their heights and diameters being 10.5 m and 17.7 cm and 10.75 m and 15.8 cm respectively.

Conclusions

In such a study, it is important to make a clear distinction between incompatibility and sterility in plants. ALLARD (1960) has pointed out that in the former, both pollen and ovules are functional and lack of viable seed results from some physiological hindrance to fertilization. Sterility, however, is characterized by nonfunctional gametes caused by chromosomal aberrations, gene action or cytoplasmic influences that either cause abortion or upset development. There is no question that tree 618 belongs to the latter category as the ovules are not functional and it is, therefore, female sterile. Both male and female sterility in crop plants have been extensively studied and indeed been used to advantage in certain crosses. Relatively few detailed studies have, however, been made with conifers, ANDERSSON (1947) being the first to investigate microsporogenesis in an asyndetic Norway spruce *(Picea abies* (L.) KARST). This tree however was not completely male sterile, as a few viable seeds were produced. JONSSON (1973) later investigated megasporogenesis in a clone of this spruce. She considered that irregularities during meiosis in the embryo sac mother cells could have more serious consequences than meiotic irregularities in the pollen mother cells owing to the much larger number of pollen grains compared with the number of ovules. As far as is known, the incidence of total ovular sterility has not been previously reported in Douglas fir. It must not be confused, however, with the development of fully formed but empty seeds in this species as a result of either lack of pollination or in some cases self pollination.

In the most recent account of the life history of Douglas fir, ALLEN and OWENS (1972) have pointed out that the ovule and female gametophyte of this species showed few irregu-

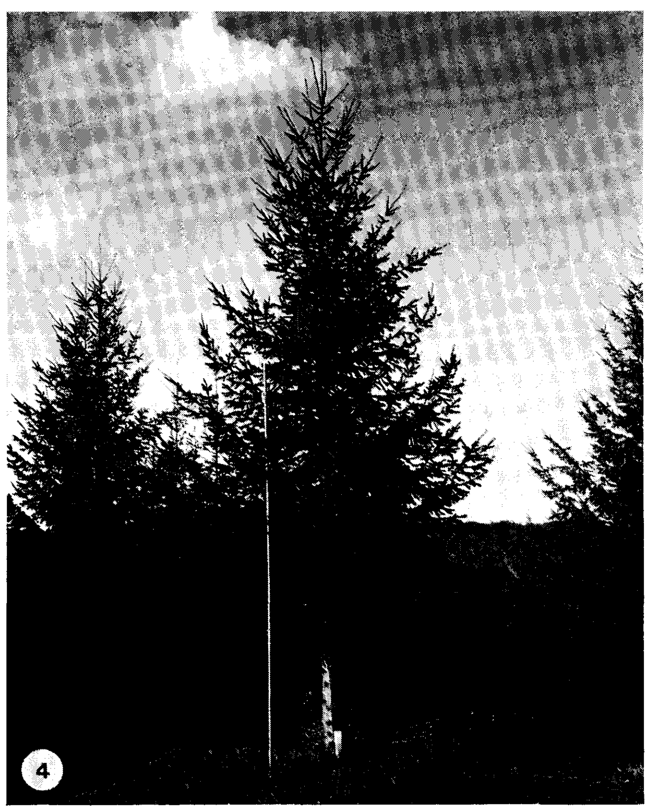

Figure 4. — Ramets 1 and 3, clone 618.

larities that would affect seed production. It may be that female sterility is not of common occurrence in Douglas fir but the fact that it can occur makes close examination of the seed from individual trees established in seed orchards an essential part of any seed production program. On the positive side, the clones of any male and/or female sterile trees should be established as could be of considerable value in future breeding research.

Summary

In 1967, three 20 year old Douglas fir in southern Vancouver Island were control pollinated. The seeds from the cones of two of the trees were normal and yielded healthy seedlings, all the seeds from the third tree, however, were undeveloped and flat. Scions from this tree were grafted in 1968 at Cowichan Lake, located some 100 km to the northwest on Vancouver Island. In 1976, cones were collected from the two surviving ramets and all the seeds were likewise undeveloped and flat. It is considered that this tree is female sterile. The importance of female sterility in seed orchards and future breeding is discussed.

Key words: Ovules, clone, incompatibility, sterility, microsporogenesis, megasporogenesis, asyndetic.

Zusammenfassung

Im Jahre 1967 wurden drei 20jährige Douglasien kontrolliert bestäubt. Von zwei dieser Bäume konnten normale Samen geerntet und daraus Pflanzen angezogen werden. Dagegen hatte der dritte Baum nur taube Samen. Im Jahre 1968 wurde dieser Baum abgepfropft und die Pfropflinge an anderer Stelle, d. h. einige 100 km entfernt ausgepflanzt, so daß im Jahre 1976 erneut Zapfen und Samen zur Verfügung standen. Auch diese waren unbefruchtet. Es wird daraus geschlossen, daß dieser Baum weiblich steril ist. Das Ergebnis wird im Zusammenhang mit Samenplantagen-Problemen diskutiert.

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Embryo Development and Yield of Seed in Larix

By J. P. HALL and I. R. BROWN*

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Introduction

There are two major categories of factors influencing formation of empty seed in *Larix* (a) those which act between pollination and fertilization and (b) those which act after fertilization. Between pollination and fertilization, failure can occur if pollen does not reach or does not germinate on the nucellus. After fertilization, failure can occur if the pro-embryo fails to grow out of the archegonia or if the young embryo fails to develop at a later stage.

HAKANSSON (1960) stated that seed sterility in Larch arises from "failure of fertilization and developmental disturbances leading to embryo lethality". He described the appearance of unfertilized ovules and degenerating embryos and attributed the occurrence of all empty seed to these factors but did not quantify their proportionate contribution. In *Pinus* it has been reported that hybridity barriers result in death of hybrid embryos (HAGMAN and MIKKOLA (1963), DOGRA (1967) and KRIEBEL (1970)). It is possible that the low yield of seed per cone in hybrid crosses in *Larix* are a result of hybridity barriers but there is no indication of this from the literature.

As part of an investigation in the yield of seed in *Larix* in North-east Scotland it was decided to study the development of the female gametophyte to determine the proportionate contribution of the above factors to the production of empty seed. According to HALL and BROWN (1976) approximately one fifth to one third of the ovules remain unpollinated after controlled pollination and this must account for at least that proportion of the empty seed in the final harvest. The study reported here concerns the development in both pollinated and unpollinated ovules of known parentage. The development of hybrid embryos and intraspecific embryos was also compared.

Development of the embryo in Larix

Briefly to summarise the literature, the sequence of events during the development of the embryo is as follows.

The stigmatic flap collapses 7 to 10 days after pollination and the pollen is ingested into the micropyle and embedded on the micropylar side of the collapsed tissue (DOYLE and O'LEARY 1935). The pollen then swells with "the pollen tube forming a bulge of the intine up to one-fifth of the pollen diameter" (BARNER and CHRISTIANSEN 1960). After 5 to 7 weeks the nucellus enlarges, partly filling the micropylar canal and exudes a fluid which dissolves the material holding the pollen grains on the under side of the stigmatic flap. The fluid appears to retract, bringing the pollen grains with it until they come to the top of the nucellus (BARNER and CHRISTIANSEN 1960). The pollen grains do not release the male gametes unless, and until, they come in direct contact with the nucellus.

The germinated pollen grains discharge two male gametes enclosed in a membrane which make their way through the nucellus and penetrate the archegonia at the neck cells.

Four to six archegonia develop and are fully formed about 44 days after pollination occurs (SMOLSKA 1927).

Development of the fertilized zygote can be conventiently divided into two stages (a) Pro-embryo development from fertilization to elongation of the suspensors and (b) Early embryo and embryo enlargement and the formation of the mature embryo.

(a) *Pro-embryo development* During the first mitosis after fertilization the zygote nucleus becomes elongated;

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