Acknowledgements

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Summary

A half-diallel progeny test of ***Eucalyptus grandis*** was raised, planted and assessed in the field at ages 6 and 15 months after planting. The 15 parent trees involved were selected in evenaged stands in the Republic of South Africa. The objectives were to investigate the relative magnitude of genetic variances, and phenotypic and genetic correlations of several traits. Results indicated the importance of additive as well as non-additive variances. The magnitude of the latter raised the question of possible allelic or linkage disequilibrium that could have arisen due to intermating of divergent genotypes in the exotic plantations. High correlations illustrated the possibility of simultaneous improvement of several characteristics in a selective breeding programme.

Key words: Eucalyptus grandis, half-diallel, progeny test, variance components, correlations.

Zusammenfassung

Bei der Prüfung der Nachkommenschaften aus einem Kreuzungsdiallel mit 15 ausgewählten Einzelbäumen von ***Eucalyptus grandis*** (HILL) MAIDEN war im Alter von 6 bzw. 15 Monaten der Sämlinge deutlich additive und nicht additive Varianz festzustellen. Die Untersuchungsergebnisse zeigen, daß in einem solchen Auslesezüchtungsprogramm Möglichkeiten zur Verbesserung verschiedener Eigenschaften gegeben sind.

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Microsporogenesis, pollination and potential yield of seed of Larix in NE Scotland

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Introduction

It is widely known that the yield of seed from Larch seed orchards is poor. KIELLANDER (1966) suggested that thirty percent germination could be considered normal in European Larch, ***Larix decidua*** (MILL.) and Japanese Larch, ***L. kaempferi*** (SARG.) and MESSER (1956) found that the percentage of empty seeds in ***L. decidua*** ranged from 59.8% to 80.1%. Similar yields of seed from controlled hybrid crusses by the authors have resulted in 20 or fewer full seed per cone which is one third or less of the potential yield.

Seed production in seed orchards is affected by a variety of factors and failure at, or prior to, fertilization, due to either maternal, paternal or environmental effects, with subsequent disturbances in embryogeny is known to have an important effect on yield of seed (SARVAS 1962, MATTHEWS 1963, ANDERSON 1965 and ERIKSSON *et al.* 1972). Failure at this stage may be due to variation in quality and/or quantity of pollen leading to non-fertilization or be due to genetic and/or environmental factors which cause early failure of the zygote. Swedish workers have shown that low seed yield may be due to unfavourable climatic conditions during microsporogenesis (ERIKSSON 1968, ERIKSSON *et al.* 1972). In Larch, microsporogenesis takes place between October and March (EKBERG *et al.* 1968). Low temperatures during the active stages of meiosis appear to result in chromosomal irregularities, disturbances of cell division and non-functioning pollen. Disturbance of meiosis due to low temperatures has been reported to occur in many conifers for example in ***Abies sachalinensis*** (MAST.) MERGEN and LESTER 1961, ***Picea abies*** L. (KARST), ANDERSON 1965, *Pinus edulis* (ENGEL.) VOSS, CHIRA 1967 and ***Larix laricina*** (K. KOCH), CHANDLER and MAVRODINEAU 1965. In some species abnormally high temperatures are also known to disturb meiosis as reported for ***Picea abies,*** CHIRA 1965 and ***Taxus baccata*** L., CHIRA 1964. Because of the reported detrimental effects of local climate on microsporogenesis in Sweden it is felt that the location of seed orchards for the production of forest tree seed is an important consideration (ERIKSSON *et al.* 1972).

Winter temperatures in North-east Scotland are not as low as in Sweden but temperatures below the critical level

of —2.5° C can occur. An analysis of temperature data for the 5 years prior to this study for areas near Newton showed that each year between December and March periods of 10 to 14 days with frost occurred. Monthly minimum temperatures of —10° C to —14° C occurred in January and February and temperatures of —6° C to 9° C in December to March (HMSO 1969—1973). As a first step in a general investigation of factors affecting seed yields in Larch, a study was untertaken during the winter of 1973—74 to determine the effects of local climate on microsporogenesis at two sites in North-east Scotland. Additional studies on pollen viability, estimated by fluorescent staining and distribution of pollen within strobili were also carried out.

The two sites were in Morayshire, North-east Scotland, at Newton Nursery and in Teindland Forest. The seed orchard at Newton is approximately 6.4 km. from exposed coastline and is 24 m. above mean sea level. The second site at Teindland Forest is 9.7 km. inland and 107 m. ASL with a more continental climate than at Newton. The two sites are at about 13 km. apart. At both sites grafted clones of *L. decidua* and *L. kaempferi* were used for the microsporogenesis study. The pollen collection and distribution study was carried out at Newton nursery.

Methods

Male strobili were collected at weekly intervals from 20 October 1973 to 27 March 1974. The following grafted clones were sampled at Newton only, *L. decidua*, E-6 and E-120 and *L. kaempferi*, J-5, J-12, J-42, J-50 and J-52. At Teindland twelve year old progeny from crosses between some of these clones were sampled: *L. decidua* × *kaempferi*, E-6 × J-42 and E-120 × J-42; *L. kaempferi* × *kaempferi*, J-12 × J-52, J-50 × J-52 and J-12 × J-50. The following clones of Danish Provenance were sampled at both locations, *L. decidua*, E-9000, E-9004 and E-9011, *L. kaempferi*, J-9005 and J-9007.

The strobili were fixed in a mixture of Ethanol : Propionic Acid (3 : 1) saturated with Ferric Acetate and stored at —12° C. For staining the strobili were soaked in a solution of alcoholic carmine for 96 hours. The pollen mother cells were dissected from 10 or more microsporangia and squashed in 45% acetic acid. The pollen mother cells (PMC's) were then examined microscopically to determine the course of development of meiosis and to detect any abnormalities that might occur during microsporogenesis.

Weather stations consisting of Stevenson screens containing a thermohygrograph and a maximum — minimum thermometer were established at both locations. The station at Newton was approximately 2 m. above the ground within the area of male flowering of the parent clones. The station at Teindland was about 5m. above the ground and within the lower crowns of the progeny. Daily temperature records were kept during the winter of 1973—74 at both locations.

Pollen was collected from twigs which had large numbers of flowers. The twigs were collected from six clones of each species before anthesis and laid out for the pollen to shed on sheets of dry paper. Air temperature in the extraction area was maintained at 18—21° C and relative Humidity at 70—90%. The pollen was cleaned of foreign matter and stored at 4° C in a desiccator with calcium chloride. Collections of *L. kaempferi* took place between 1 and 17 March and *L. decidua* between 18 and 28 March.

Pollen viability was estimated by staining pollen with fluorescein diacetate and examining it under a microscope according to methods outlined by Paton and Jones (1975). Approximately 600 pollen grains from 12 random samples were examined for each pollen mixture.

Female strobili were isolated in clear tubes of cellulose nitrate, sealed with foam plastic at each end and pollinated with pollen guns consisting of a pollen agitator and bellows. In order to detect and count pollen grains in the ovules it was found necessary to stain the grains before application. The pollen was stained with a 0.5% aqueous solution of methylene blue and redried over calcium chloride. Female strobili on clones *L. decidua* E-1102 and *L. kaempferi* J-12 were each pollinated with stained pollen three times during the receptive period of the strobili. Pollinations were done in late March and strobili collected in mid-May after the micropyles had closed. The strobili were partially frozen and the floral bracts broken off individually and examined under a wide-field dissecting microscope. The occurrence and number of pollen grains in each ovule was determined.

Results

The results of the examination of the pollen mother cells are shown in *Figures 1* and *2*. The temperature data consisting of the daily maxima and minima are shown graphically in *Figures 3* and *4*. The occurrence of pollen grains in the female strobili is shown in *Table 1* and the distribution of pollen grains within the strobili is shown in *Figure 5*.

(i) *Meiosis in grafted clones (Newton) and their progeny (Teindland)*

According to previous work in Sweden it is known that there are three distinct periods of meiosis in relation to temperature sensitivity;

(a) the temperature — sensitive pre-diplotene (Interphase I to Diplotene) stages;

(b) the temperature — insensitive Diplotene period, and

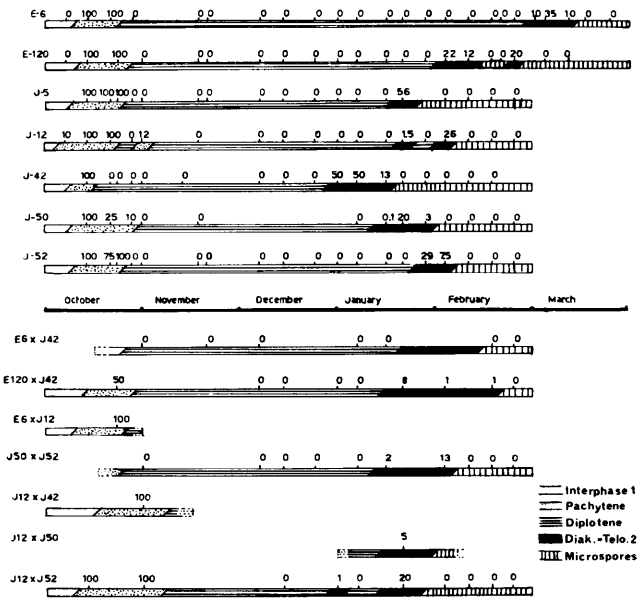

Figure 1. — Times of occurrence of various stages of meiosis in PMC from Interphase I to Microspores.
Vertical lines indicate sampling points and the figures show the percentage of cells in temperature-sensitive stages. Since the sampling interval was approximately one week, boundaries between different stages were, of necessity, arbitrary. The parent clones were located at Newton (top half), the progeny at Teindland (botton half).

(c) the temperature — sensitive post-Diplotene to Tetrad (Diakinesis to Telophase I and Prophase II to Telophase II) stages. (Interphase II is considered to be insensitive to low temperatures.)

The pre- Diplotene stages in the parent clones occurred over a two week period during the middle of October with little variation in time of occurrence among clones *(Figure 1).*

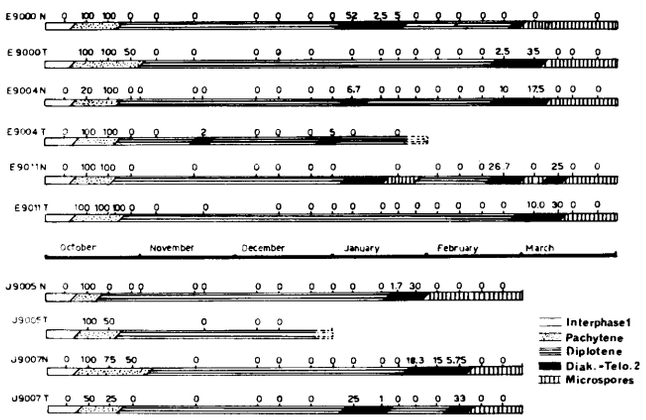

Figure 2. — Percentage of pollen mother cells in temperature sensitive stages for clones of *Larix* at Newton (N) and Teindland (T) during 1973—74.

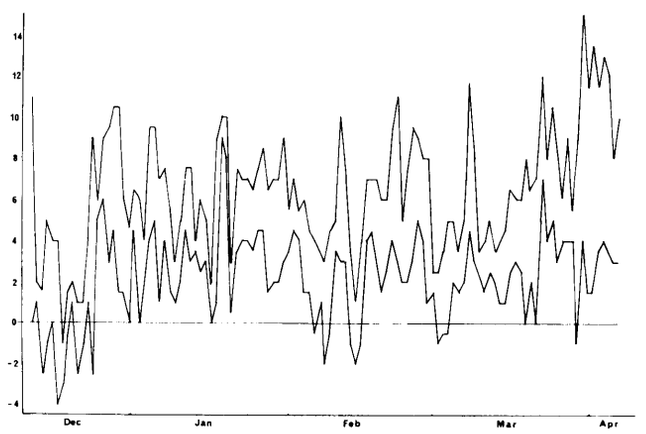

Figure 3. — Maximum and minimum daily temperatures at Newton 6 December 1973 to 4 April 1974.

In the progeny these stages occurred in mid and late October. Results from Teindland were incomplete because the trees produced few flowers. Diplotene lasted for 8—10 weeks in *L. kaempferi* and about 14 weeks in *L. decidua.* The post-Diplotene stages, Diakinesis to Telophase II were completed during a two to three week period in each clone. The earliest clone which completed these stages was J-42. Clones J-5, J-12, J-50 and J-52 all passed through these stages about two weeks later. In *L. decidua* the post-Diplotene stages occurred in late February and early March, after the *L. kaempferi* clones had completed meiosis.

Data for the progeny were scarce but they show that the post-Diplotene stages in the inter-specific crosses, E-6 × J-42 and E-120 × J-42 occurred between the dates of the corresponding stages in the parents. The intra-specific crosses, J-50 × J-52, J-12 × J-52 and J-12 × J-52 passed through the post-Diplotene stages at approximately the same time as did their parents. On any given date usually less than 30% of the PMC's sampled were in the stages of Diakinesis to Telophase II, the maximum number of cells in these stages was 56% found in clone J-5 on 20 January. This is in contrast to the pre-Diplotene stages which occur almost simultaneously, with all or nearly all the PMC's in sensitive stages at the same time.

(ii) *Meiosis in grafted clones of L. decidua and L. kaempferi at two sites.*

The pre-Diplotene stages occurred during mid and late

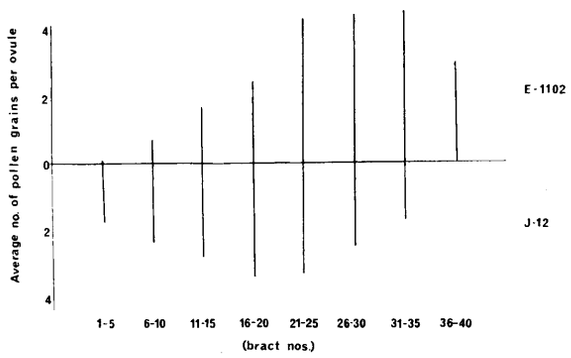

Figure 5. — Average numbers of pollen grains per ovule in *L. decidua,* clone E-1102 and *L. kaempferi,* clone J-12. Averages are for 30 ovules — 5 bracts numbered from the bottom each containing 2 ovules and for 3 strobili.

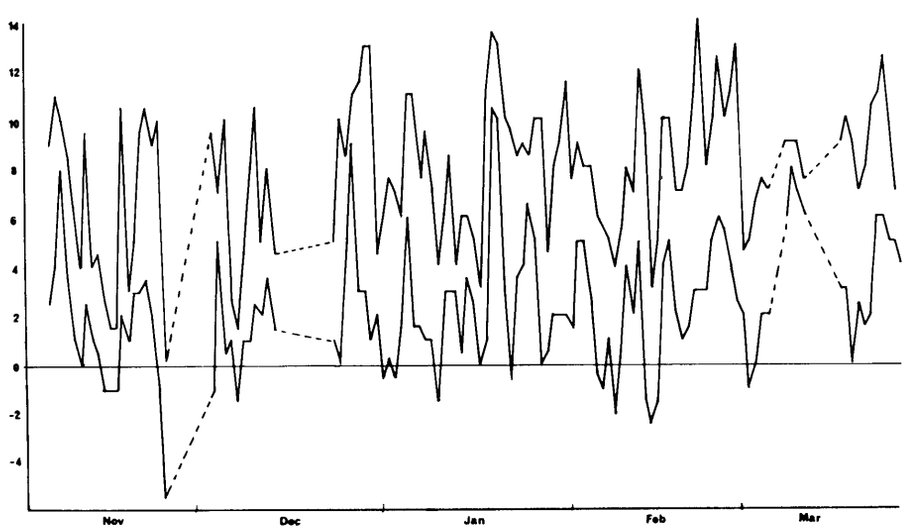

Figure 4. — Maximum and minimum daily temperatures at Teindland 10 November 1973 to 28 March 1974 (Broken lines indicates missing data).

Table 1. — Occurrence and number of pollen grains in strobili after controlled pollination.

	Clone E-1102	Clone J-12
Percent of ovules with 1 or more pollen grains	66.4	79.5
Average number of pollen grains per ovule in ovules with 1 or more pollen grains	4.1	3.1

October for both species at both sites. Clone J-9007 at Newton was an exception in that this stage was not completed until some time in early November. The period over which Diplotene occurred was variable between clones and sites. In all *L. decidua* clones at Newton and in one of these clones at Teindland some PMC's entered the post-Diplotene stages at various times from mid November to late December-early January. All cells however, had completed Diplotene by late February or early March. One of the *L. kaempferi* at Teindland had PMC's which entered post-Diplotene stages in early January and others which did not complete this phase until mid February. In the *L. kaempferi* clones for which complete data were available, all PMC's entered post-Diplotene stages in late January to early February.

Given that data was not complete for all clones due to the shortage of flowers it appears that there were no significant differences in microspore development between sites. But, as before, there appear differences between species, in that *L. kaempferi* entered the final stages of microsporogenesis earlier than *L. decidua*. These clones differed from the older clones and their progenies in the variable times of occurrence of post-Diplotene stages.

The stages between formation of microspores and anthesis proceded normally.

(iii) *Temperature records from the two sites.*

Freezing temperatures at Newton occurred during the first two weeks of December, in mid February for six nights and again during the first three nights in March (Fig. 3—4). Temperatures below —2.5° C only occurred during five nights in December. Maximum temperatures during the day were 5° C or greater through most of the period between 23 December and the end of February.

At Teindland, frosts occurred on several occasions during the winter, however, temperatures below —2.5° C occurred only on 25 November and on 13 February. Maximum temperatures of 5° C or greater occurred frequently from mid December to early March.

Mean daily temperatures (not shown) varied from 0° to 10° C througouth the winter and there was little difference between the two locations.

(iv) *Pollen viability*

The viability of pollen grains of each species as estimated by fluorescent staining was:

(a) *L. decidua* mean 84% max. 90% min. 80%
(b) *L. kaempferi* mean 91% max. 97% min. 82%

(v) *Occurrence and distribution of pollen within the strobilus following controlled pollination*

The percentage of ovules pollinated and the average number of pollen grains in the micropyle was higher in clone E-1102 than in clone J-12 *(Table 1)*. The distribution of pollen grains within the female strobilus of clone J-12 shows that ovules in the middle part of the strobilus had more pollen than those at the bottom or the top *(Figure 5)*. In clone E-1102 larger numbers of pollen grains were found in the top third of the strobilus.

Discussion

The general pattern of meiosis in clones of both species was similar to that previously described (Eriksson 1968). The pollen mother cells passed from Interphase I to Diplotene during October and early November. The high percentages of cells in Pachytene shown in *Figure 1* reflect the fact that nearly all PMC's went through this stage simultaneously in any particular microstrobilus.

Diplotene lasted for about 2 months in *L. kaempferi* and about 3 months in *L. decidua*. Eriksson (1968) reported that Diplotene in Sweden was of approximately the same length. Diplotene was interrupted during the winter in 3 clones of *L. decidua* and in one of *L. kaempferi* when PMC's in a few of the microstrobili passed from Diplotene to the Tetrad stage.

Eriksson (1968) also found interruptions in Diplotene in 2 of the 3 clones of *L. decidua* he studied. Interruptions in Diplotene were preceded by mean daily temperatures in the range of 2—7° C. These temperatures occurred frequently throughout the winter and probably, did not stimulate the PMC's to pass from Diplotene to the post-Diplotene stages. Only a small proportion of the microstrobili contained PMC's which passed Diplotene and the PMC's in the remainder of the microstrobili completed meiosis later in the year.

The post-Diplotene stages were completed within a 3 week period in both species while in the hybrids up to four weeks was required for completion. This is in contrast to the case in Sweden where a more extended post-Diplotene period was observed, lasting, in some cases up to 8 weeks in *L. decidua* (Eriksson 1968). At any given sampling date a small proportion of the PMC's were in post-Diplotene stages — a maximum of 56% was recorded in clone *L. kaempferi* — 5 sampled on 20 January. Similar results have been reported for Sweden (Eriksson 1968).

There was very little difference in the development of meiosis within the same clones at the two sites. The site at Teindland had greater extremes of maximum and minimum temperatures but there was very little difference between the mean daily temperatures at the two sites.

Temperatures below 0° occurred rarely and only once when there were any PMC's in the post-Diplotene stages. The temperatures dropped to —2.5° C on 13 February while some PMC's were in the post-Diplotene stages in the hybrid clone E-120 × J-42. No chromosomal irregularities however were observed in any of the PMC's. In Sweden, PMC's in post-Diplotene stages and below freezing temperatures frequently occurred together and chromosomal irregularities were observed shortly after, which were believed to result in almost complete pollen sterility in some clones (Eriksson 1968).

Low temperatures during pollen mitosis are also believed to cause chromosomal irregularities (Ekberg *et al.* 1968), however none were observed in any of the clones at either site investigated in north-east Scotland. Eriksson *et al.* (1966) reported that 0.5% of pollen grains were "giant pollen grains" (double the average volume) under normal

conditions and about the same proportion was observed in this study.

Since winter minimum temperatures in North-east Scotland are not nearly as low as those in Sweden it is not surprising that no chromosomal irregularities were observed if a causal relationship does exist.

Our findings did not demonstrate a causal relationship between the different stages of meiosis and the air temperature in the crowns where meiosis was occurring. If the PMC's in Diplotene need a "cold period" to break dormancy as suggested by ERIKSSON (1968) then the low frequency of such periods in North-east Scotland would suggest a longer Diplotene than in Sweden which is not the case. If short fluctuations of temperature around 0° C did indeed stimulate post-Diplotene stages, it would have been expected that the PMC's of Larch in North-east Scotland would pass through Diplotene and complete meiosis during the winter. This, of course, did not happen. If, as has been suggested by Swedish workers, meiosis is controlled by air temperatures it is surprising that the timing of meiosis is broadly similar in both areas where temperatures are very different. It seems reasonable to suggest that the timing of meiosis might be controlled by photoperiod which is broadly similar in Sweden and North-east Scotland.

In assessing the possibility of the occurrence of damage to pollen in a seed orchard several factors must be considered. At any given time in any given clone there is only a proportion of PMC's in the temperature sensitive post-Diplotene stages. There is variation in the time of meiosis within a single strobilus as well as among strobili on the same branch, within the crown and among ramets of the same clone (ERIKSSON 1968). There is a point at which the highest proportion of PMC's are undergoing meiosis and this point is different for each clone. Results from this and other similar studies indicate that the temperature sensitive periods Diakinesis to Telophase I, and Prophase II to Telophase II, are of very short duration compared to the stages Interphase II and Tetrad, which are much less susceptible to damage from low temperatures. Thus the probability that an entire clone (much less several clones) would be rendered pollen sterile due to low temperatures must be considered as the product of several probabilities — the probability of temperatures below 2 or 3° C; the probability of the PMC's in that clone being in post-Diplotene stages and the probability of those stages being the temperature sensitive ones discussed above. It can be seen that the final probability of the pollen crop in any given year being significantly affected is extremely small. It must also be stressed that some of the more common temperature-induced irregularities in the chromosomes may heal and viable pollen be produced (ERIKSSON 1968).

Results of the pollen viability test indicate that viability was high. The fluorochromatic reaction is a test of the integrity of the plasmalemma of the vegetative cell which is thought to be closely related to the ability of the pollen grain to fertilise an archegonium (HESLOP-HARRISON, J. and HESLOP-HARRISON, Y. 1970). Thus, a positive reaction is not a certain measure of viability, but a negative reaction almost certainly indicates a non-viable pollen grain.

Ovules containing one or more pollen grains were found mostly in the mid-portion of the strobili (where nearly all of the ovules were pollinated with one or more pollen grains). Since the estimated pollen viability is high a high proportion of ovules will contain a viable pollen grain. The proportion of ovules pollinated with at least one viable pollen grains is the product of the percentage of ovules pollinated and the probabality of one viable pollen grain in that ovule. This has been calculated for combinations of one, two and three pollen grains per ovule. The probability of one or more viable pollen grains per ovule in those which receive more than three pollen grains is so close to 1.00 as to make calculations for these combinations unnecessary. The estimated proportion of pollinated ovules in each species is shown in *Table 2*. In clone J-12 ovules with 1 or more pollen grains had an average of 3.10 pollen grains per ovule; in clone E-1102 the corresponding figure was 4.13.

The effect of pollen viability was quite small and only reduced the potential number of fertilized ovules by 1.7 and 2.5 percent for J-12 and E-1102 respectively. At this stage of development it could be expected that 77.8 and 63.9 percent of ovules in the two clones would contain at least one viable pollen grain. The results also indicate that a relatively high proportion of non-viable pollen would be needed in order to affect the number of ovules pollinated with one viable pollen grain when the average number of pollen grains per ovule is two or more.

Under conditions of artificial pollination the effect of pollen viability is small. If there were fewer pollen grains present, for instance, with wind pollinations then pollen viability would have a greater effect.

Summary

The general pattern of meiosis in *L. decidua* and *L. kaempferi* was similar to that described previously with Diplotene beginning in October and early November and lasting for 2—3 months and meiosis being completed in the early spring over a period of 1—4 weeks. The occurrence of meiosis on the hybrid progeny was intermediate between the times of meiosis in the parent trees, and in non-hybrids meiosis occured at the same time as the parents. No disturbance in meiosis attributable to low temperatures was observed.

It is perhaps surprising that Larch, originating from countries with continental climates, should not suffer some disturbance of meiosis in the variable winter climate of

Table 2. — Percent of Ovules Pollinated with at least 1 Viable Pollen Grain in Clones J-12, E-1102.

	Percent of ovules with 1, 2, 3 and 4+ pollen grains*		Probability of 1 viable PG present in ovules with more than one pollen grain**		Percent of ovules with 1 or more viabe pollen grains	
	J-12	E-1102	J-12	E-1102	J-12	E-1102
% w. 1 PG	16.4	13.1	.91	.84	14.9	11.0
2	16.4	9.3	.99	.97	16.2	9.0
3	17.9	12.6	1.00	.99	17.9	12.5
4+	28.8	31.4	1.00	1.00	28.8	31.4
Total	79.5	66.4	—	—	77.8	63.9

* Determined by examination of ovules under dissecting microscope.
** Calculated from the results of the fluorescent staining.

North-east Scotland at as least as great a degree as was reported from Sweden. Although minimum winter temperatures were mainly above the reported threshold of —2.5° C, warm winter periods did not appear to stimulate the progress of meiosis as has been reported in Sweden. It should be noted that the winter of 1973—74 was considerably milder than normal. The fact that meiosis in parent clones at Newton and their progenies at Teindland was comparable indicates that genetic control and photoperiodic control of meiosis is stronger than any temperature effects experienced in North-east Scotland.

A relatively high proportion of ovules were pollinated with viable pollen and the viability of pollen had a very small effect on the potential yield of seed in controlled crosses.

The low yield of seed in hybrid larch seed orchards was not attributable to temperature conditions during microsporogenesis and work is continuing on the post-pollination stages to determine the causes of empty seed.

Key words: Meiosis, Winter temperatures, *Larix decidua* Mill., *Larix kaempferi* (Lamb.) Carr.

Zusammenfassung

Zur Erzielung möglichst hoher Samenerträge in sog. Samenplantagen wird den klimatischen Bedingungen des Standortes großes Gewicht beigemessen. In der vorliegenden Arbeit wurde zu diesem Problem untersucht, inwieweit die inneren Vorgänge bei der Ausbildung männlicher und weiblicher Blüten von *Larix decidua* und *Larix kaempferi* auf Temperaturänderungen reagieren bzw. ihren Rhythmus ändern. An Hand von wöchentlich entnommenen Blütenknospen von Lärchenklonen unterschiedlicher Herkunft und deren Nachkommenschaften, in der Zeit von Ende Oktober — Anfang November 1973 bis zum 27. März 1974, konnte festgestellt werden, daß der Ablauf der Meiose etwa Anfang November beginnt und bis in das zeitige Frühjahr hineinreicht, wobei Hybridnachkommen bezüglich der einzelnen Phasen intermediär zu den Elternarten zeitliche Verschiebungen aufweisen. Auf den Versuchsstandorten in Schottland konnte nicht nachgewiesen werden, daß die Vorgänge bei der Blütenbildung wesentlich durch die Temperatur beeinflußt werden, so daß auch niedrige Samenerträge dort nicht auf Temperaturstörungen zurückzuführen sind.

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Spontaneous chlorophyll mutations in Bombax L.

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Introduction

Spontaneous chlorophyll mutations have been reported in several temperate tree species (McKay, 1956; Franklin, 1970) but so far in few tropical ones (Posnette, 1950; Venkatesh a. Sharma, 1974). The present note records the occurrence of such mutations in *Bombax ceiba* L. (n = 36, 46, 48) and *B. insignis* Schott et Endl. (n = 36), two tropical broadleaved forest tree species which constitute India's principal industrial matchwood resource and hence are included in a genetic improvement programme at this Institute (Venkatesh, 1974). As per the standard procedure adopted in such forest tree improvement work, phenotypically superior plus trees (so far of only *B. ceiba)* have been selected and assembled as grafts in clonal banks and seed orchards (Venkatesh a. Arya, 1973).

Material

The present study is based on progenies raised from time to time at the Institute's forest genetics nursery and mostly from open pollinated seeds of individual tree or clone origin.

Observations

Initially when one-parent progenies were raised out of some *B. ceiba* trees chosen at random on the New Forest estate, some seedlings with yellow-green mottled cotyledons had been noticed in certain of the families. Iodine test