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Further studies on meiosis and pollen formation in *Larix*

Fortsatta studier av meiosen och pollenbildningen hos lärk

by

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ABSTRACT

The meiotic development in pollen mother cells of *Larix decidua, L. leptolepis* and *L. sibirica* growing at different localities in Sweden was studied. The percentage of completely damaged buds as well as the pollen sterility was estimated.

The reaching of diplotene took place earlier in *L. sibirica* than in *L. decidua* and *L. leptolepis.* The second phase of high frost sensitivity (diakinesis — telophase II, except for the interphase) in the PMC appeared in the sequence *L. sibirica* — *L. leptolepis* — *L. decidua.* Differences within a species from locality to locality regarding the initiation of further development from diplotene could be attributed to differences in temperature conditions at the different growth localities. The same was true for the induction of completely damaged buds.

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1. Introduction

The importance of the generative fitness in larch for the possibilities of cultivating larch in Sweden was pointed out by Eriksson (1968 *a*). The reasons for the frequently poor seed setting in larch were summarized by Eriksson (1968 *a*) according to the following:

»1. Failure of fertilization
2. Disturbances in development causing embryonic lethality».

So far we have confined our investigations to point 1. Therefore, only questions related to this point will be treated in this communication.

Failure of fertilization might be due to:

A. Insufficient pollination
B. Lethality of the gametes
C. Imperfect development of the pollen tube

From the literature it is well documented that there is a positive correlation between a low amount of pollen and the frequency of empty seeds (Kurdiani, 1912; Tyszkiewicz, 1931; Rubner & Svoboda, 1944). Recently Eriksson *et al.* (1969) have pointed out that poor seed setting in larch might be due to the fact that the dispersal of pollen is of short duration. Furthermore, only a limited number of ovules were assumed to be receptive (cf. Barner & Christiansen, 1960) during the period of pollen dispersal. These assumptions were supported by empirical data from a detailed analysis of the seed quality of individual cones. This examination showed that the percentage of filled seeds reached a maximum in a certain part of a cone. Sometimes the maximum was observed close to the base of the cone. In other cones the maximum appeared in the central part or close to the apex of the cone. This means that the regions of the cones showing high percentages of filled seeds had contained receptive ovules during the time for pollen dissemination. Conversely in those regions in which the percentage of empty seeds was high, most of the ovules had not been receptive during the period of pollen dispersal.

If this is of universal applicability has yet to be confirmed in a similar and extended analysis of the seed quality in individual cones harvested different years.

It seems as if there is a disharmony between the duration of the receptiveness of ovules and the duration of the dispersal of pollen. As a consequence of this the percentage of filled seeds from trees in seed orchards is not expected to be high nor even moderate. This in turn means that it is necessary to compensate for the lack of pollen which appears before and subsequent to the period of dissemination of pollen. Otherwise the ovules which are receptive during those periods will not take part in any fertilization.

It was stressed by Eriksson *et al.* (1969) that this pattern of flowering biology might be advantageous for the continued existence of a species. On the other hand it is a great disadvantage in silviculture especially in the seed orchards. Unfortunately this has to a great extent been disregarded.

The influence of gamete lethality upon the seed setting in larch has been discussed in a series of publications (Ekberg & Eriksson, 1967; Eriksson *et al.*, 1967; Ekberg *et al.*, 1968; Eriksson, 1968 *a* and *b;* Eriksson *et al.*, 1969). The gamete lethality might be due to genetic factors or unfavourable environmental conditions during gamete formation. Both types of lethality have been shown to appear in conifers (cf. the summary of meiotic investigations published by Andersson *et al.*, 1969).

A low self fertility has frequently been regarded as a reason for the poor seed setting in larch (cf. Eriksson, 1968 *b* and lit.cit.). Whether the low seed setting following self pollination originates from inhibition of the growth of the pollen tube has not been proved.

The present communication constitutes a continuation of the papers listed above. The main purpose was to study the pattern of meiotic development in pollen mother cells (PMC) of larch clones cultivated at two or three different localities. Differences in pattern of development for an individual clone from one locality to another will reveal the influence of environmental conditions on meiosis in the PMC. We also intended to investigate differences in pattern of meiotic development between the three species involved, *Larix decidua, L. leptolepis* and *L. sibirica.* Similarly it was of interest to analyse a possible variability within a species. On the basis of the pattern of meiotic development, the percentage of completely damaged buds, and the pollen sterility of various clones growing at different localities we hope to be able to suggest localities for cultivation of larch in order to obtain a good pollen quality and a sufficient pollen quantity.

2. Materials and methods

The grafts involved in the present investigation are the same as listed in Tables 2—5 (p. 16—19) in the paper by Eriksson (1968 *b*). To facilitate the reading of the present paper an appendix showing the growth localities of all the investigated clones has been enclosed. In the appendix the diagrams showing the meiotic development of individual clones are also indicated. The latitudes, the longitudes and the altitudes of the growth localities were presented in Table 1 (p. 15) of the paper referred to above. The growth localities are illustrated in the map in Fig. 1.

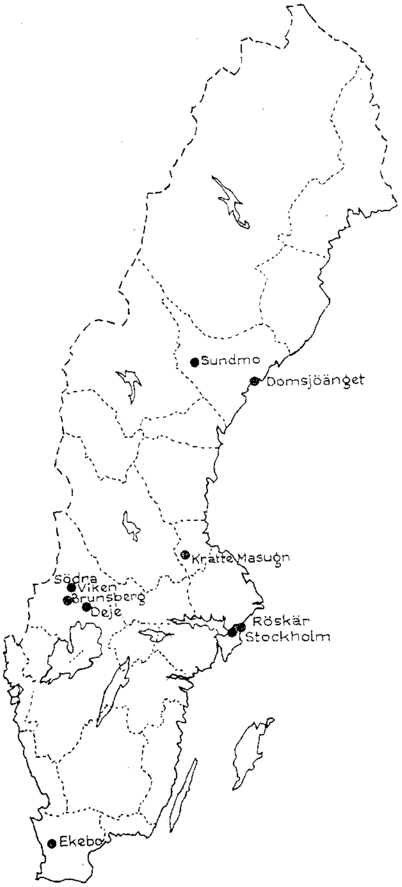


Fig. 1. The growth localities for the grafts of *Larix decidua*, *L. leptolepis* and *L. sibirica* studied in the present communication.

If possible at least ten male buds were fixed in acetic alcohol (1: 3) at each sampling. Some grafts did not contain generative buds in sufficient amounts and had to be omitted from the investigation. The interval between the fixations was determined in advance and planned in such a way as to cover the entire development from diplotene to tetrads. Owing to the temperature conditions the plan had to be revised to a certain extent. In the Stockholm region almost daily fixations were made during the active phase of the meiotic development. The dates for fixation will be evident from the diagrams below (Fig 2—24 and 34—71).

If possible the stage of development was determined in ten different buds for each graft and fixation occasion. However, in several cases completely damaged buds, i.e. buds lacking regular PMC occurred, which means that the determination of the meiotic stage had to be carried out in less than ten buds. The percentages of completely damaged buds are illustrated in the diagrams showing the pattern of meiotic development. As previously stated (Eriksson, 1968 *b*) the cells in the completely damaged buds will not give rise to any pollen formation. This means that the completely damaged buds will not contribute to the pollen sterility.

The temperature measurements were performed as described by Eriksson (1968 *b*, p. 17). Similarly the estimation of the pollen sterility was carried out according to Eriksson (1968 *b*, p. 20).

3. Pattern of meiotic development

3.1. Larix decidua

About 375,000 PMC have been classified with respect to meiotic stage in this species. The pattern of development in the PMC for the various clones is illustrated in Fig. 2—24. As is evident from these figures any common characteristic of the pattern of the meiotic development can hardly be observed.

3.1.1. Reaching of diplotene

Most of the grafts showed that the PMC to a great extent were still in pachytene at the start of the investigation during October 1967. The clones E 1001, R 1002, R 1003 at Deje, E 2006 at Broknäs as well as clone IS 520 at Sundmo constitute the only exceptions in this respect. In most of the clones all PMC had reached the diplotene stage on 3 November. Whether or not this was true for the PMC at Sundmo cannot be stated as no fixation was carried out between 25 October and 24 November.

It can be stated that the reaching of the diplotene stage took place relatively independent of the temperature conditions. It might be expected that the onset of meiosis is determined by a photoperiodic response.

3.1.2. Completion of meiosis

Ekebo and Deje

The results obtained from the clones studied at two or more localities clearly reveal that the initiation of further development from diplotene takes place at different occasions dependent on the locality. This is well illustrated for clone L 2001. At Ekebo diplotene was to a relatively great extent passed on 17 February whereas the initiation of further development from diplotene did not take place until the second part of March at Deje. All clones studied at Ekebo and Deje reveal the same type of difference in pattern of development. The smallest difference was noted for clone E 2002 in which more than 90 per cent of the PMC remained in diplotene until 9 March at Ekebo. Subsequent to this a relatively rapid development to the tetrad stage took place. Unfortunately the meiotic development could not be determined accurately for all the clones involved owing to the high percentage of

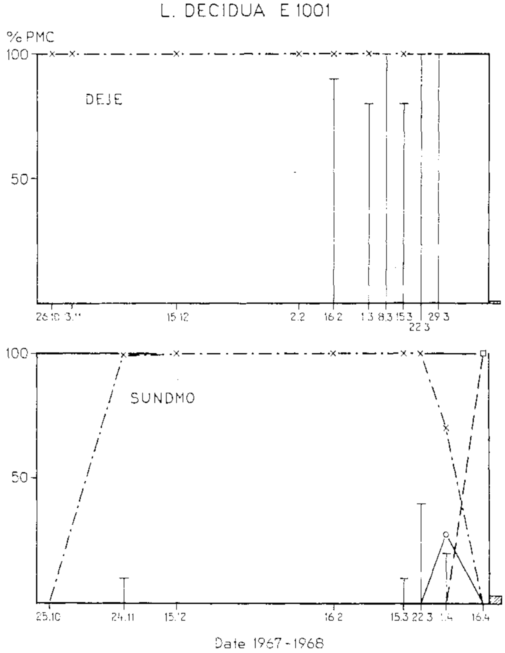


Fig. 2. The meiotic development in the PMC of clone E 1001, *L. decidua* growing at Deje and Sundmo.

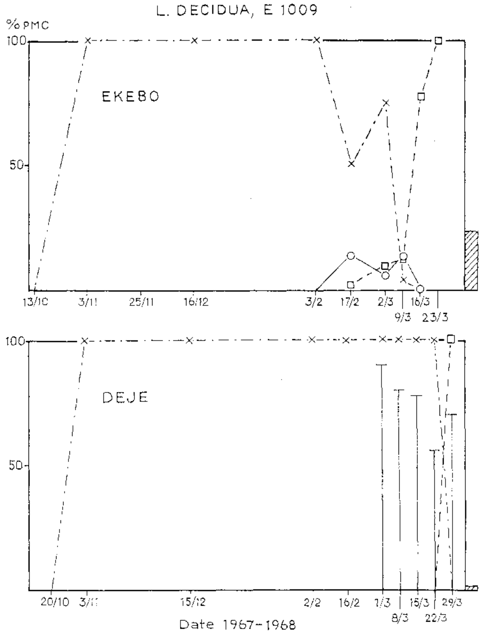


Fig. 3. The meiotic development in the PMC of clone E 1009, *L. decidua* growing at Ekebo and **Deje.**

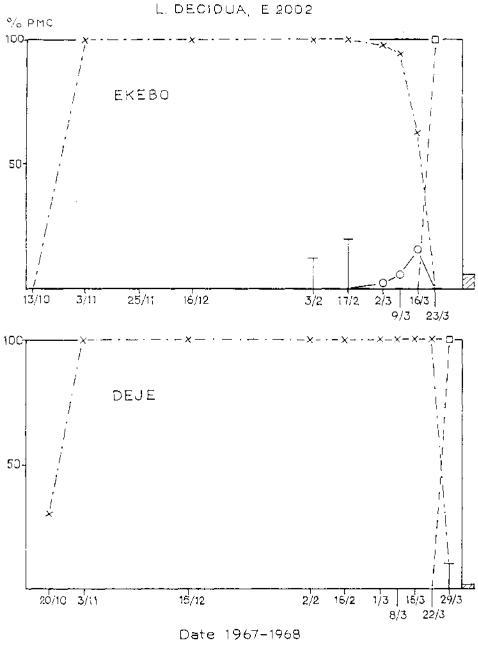


Fig. 4. The meiotic development in the PMC of clone E 2002, *L. decidua* growing at Ekebo and Deje.

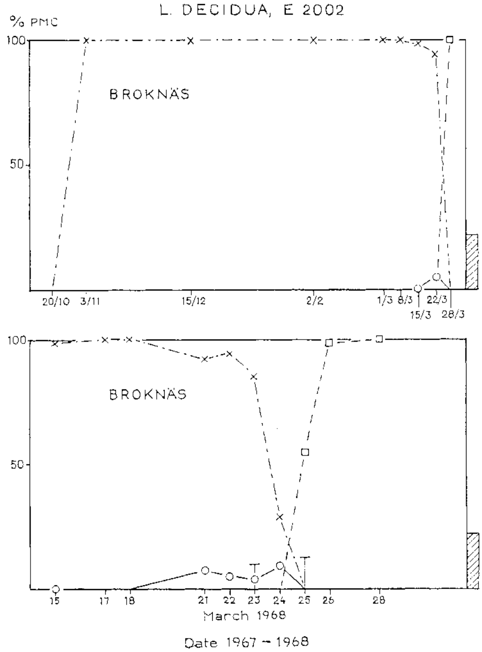


Fig. 5. The meiotic development in the PMC of clone E 2002, *L. decidua* growing at Broknäs. The end of the meiotic development is shown separately.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, ☐ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

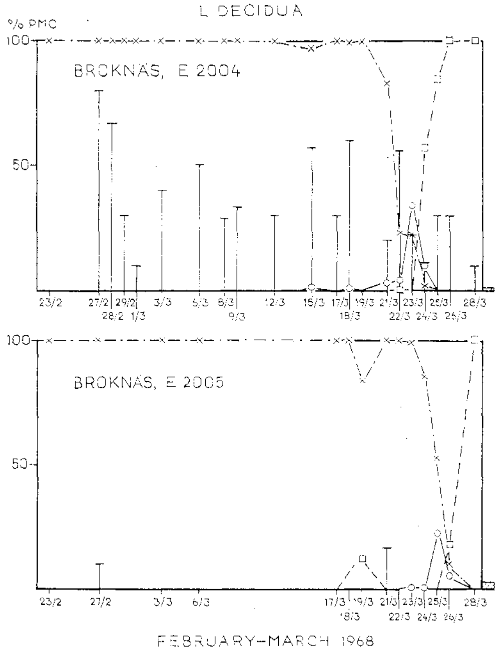


Fig. 6. The end of the meiotic development in the PMC of the clones E 2004 and E 2005, *L. decidua* growing at Broknäs.

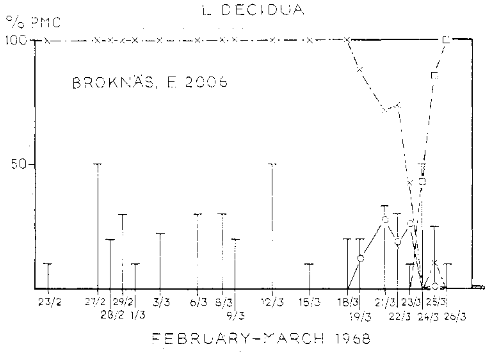


Fig. 7. The end of the meiotic development in the PMC of clone E 2006, *L. decidua* growing at Broknäs.

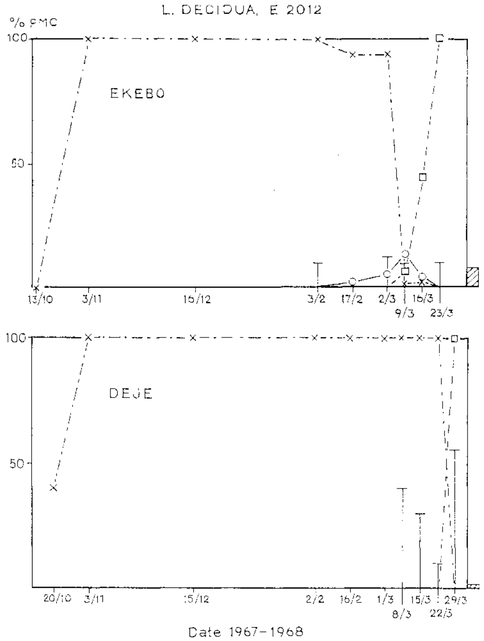


Fig. 8. The meiotic development in the PMC of clone E 2012, *L. decidua* growing at Ekebo and Deje.

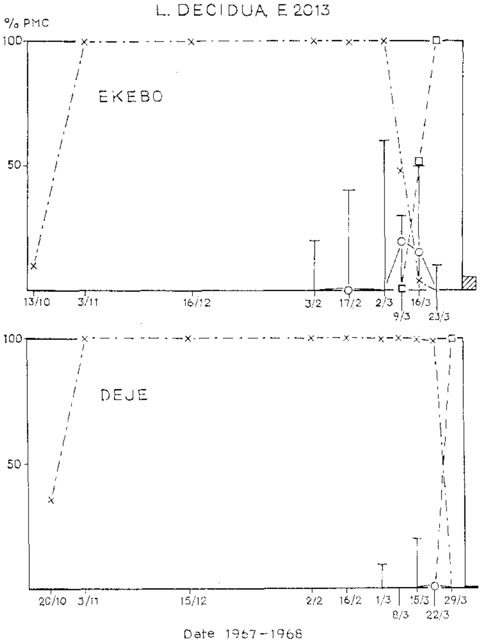


Fig. 9. The meiotic development in the PMC of clone E 2013, *L. decidua* growing at Ekebo and Deje.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, ☐ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

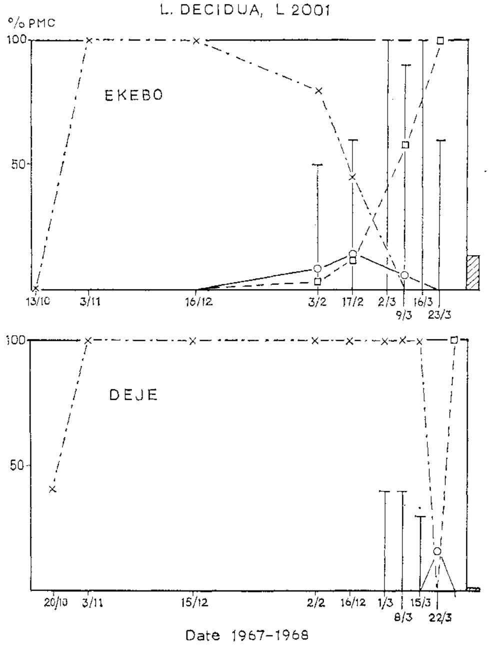


Fig. 10. The meiotic development in the PMC of clone L 2001, *L. decidua* growing at Ekebo and Deje.

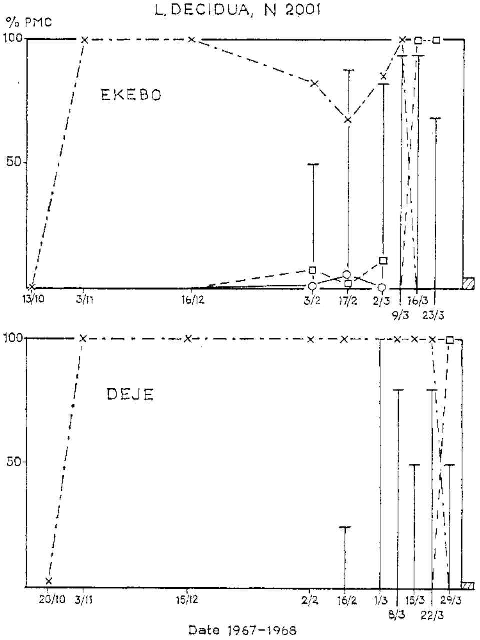


Fig. 11. The meiotic development in the PMC of clone N 2001, *L. decidua* growing at Ekebo and Deje.

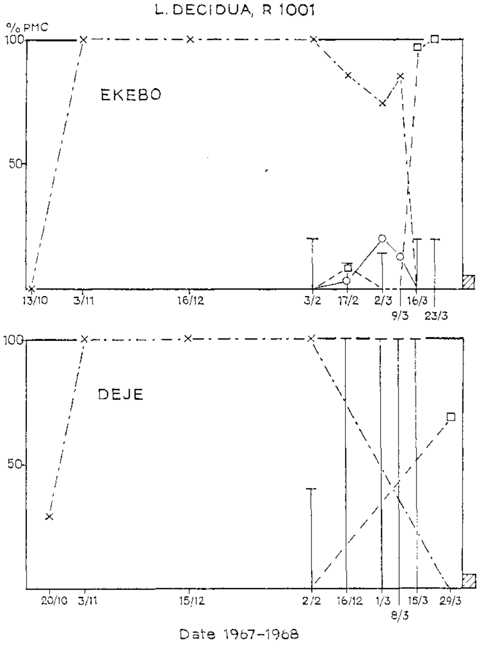


Fig. 12. The meiotic development in the PMC of clone R 1001, *L. decidua* growing at Ekebo and Deje.

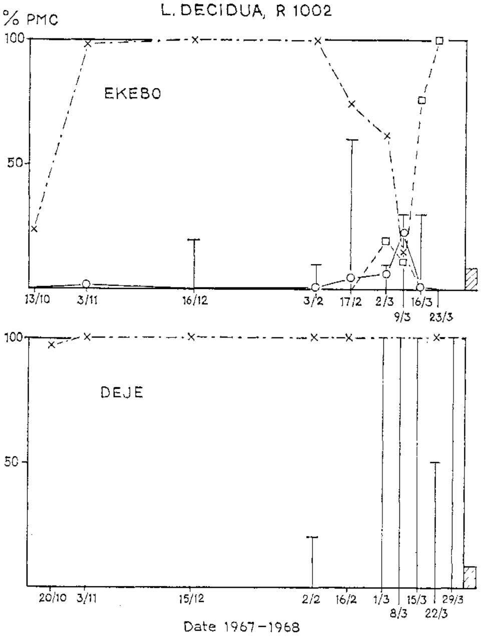


Fig. 13. The meiotic development in the PMC of clone R 1002, *L. decidua* growing at Ekebo and Deje.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

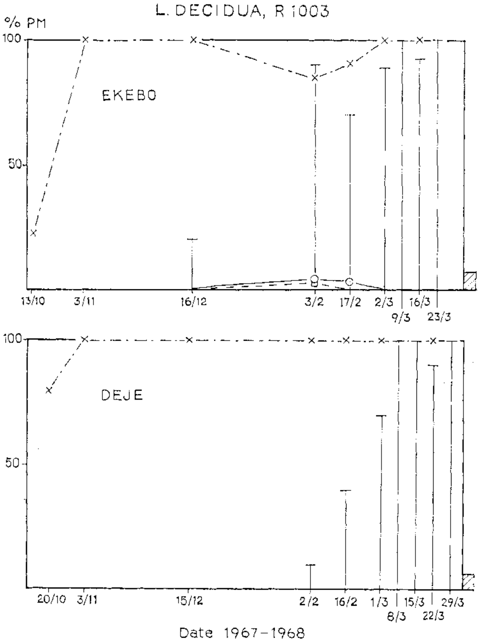


Fig. 14. The meiotic development in the PMC of clone R 1003, *L. decidua* growing at Ekebo and Deje.

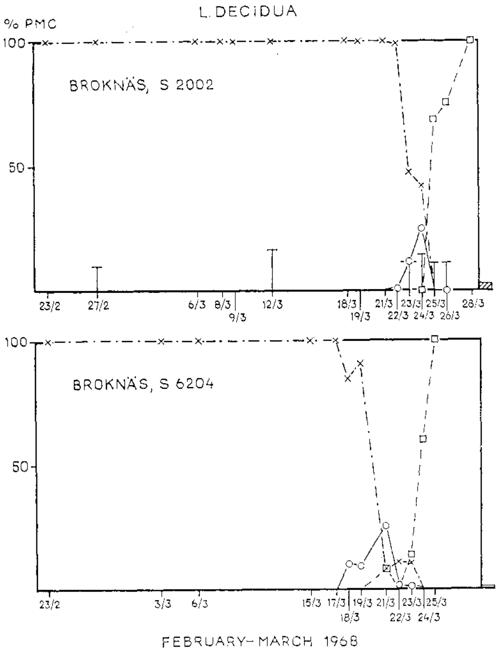


Fig. 15. The end of the meiotic development in the PMC of the clones S 2002 and S 6204, *L. decidua* growing at Broknäs.

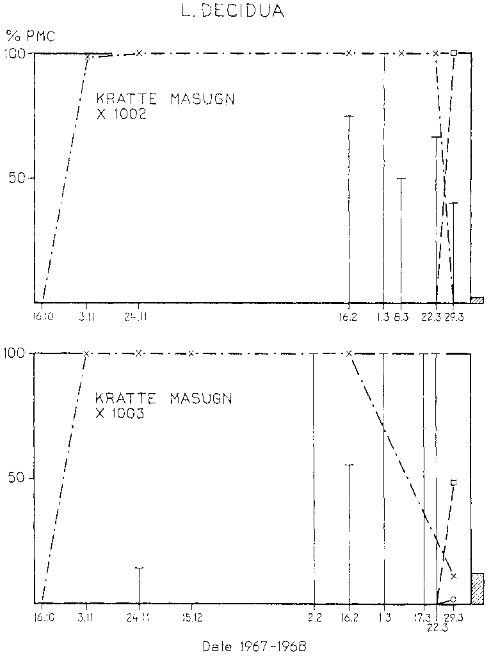


Fig. 16. The meiotic development in the PMC of the clones X 1002 and X 1003, *L. decidua* growing at Kratte Masugn.

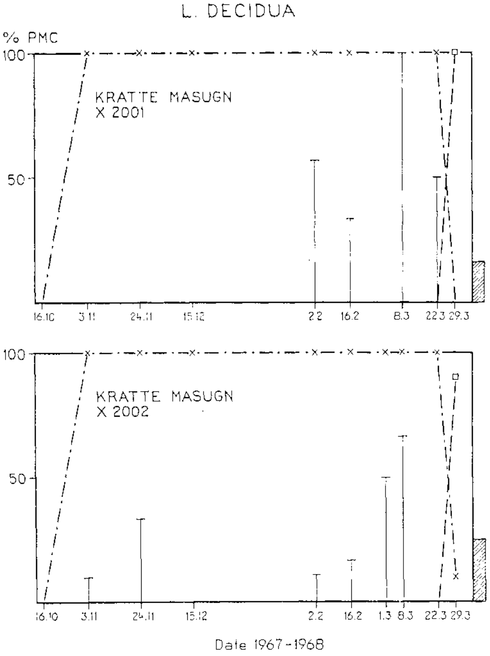


Fig. 17. The meiotic development in the PMC of the clones X 2001 and X 2002, *L. decidua* growing at Kratte Masugn.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

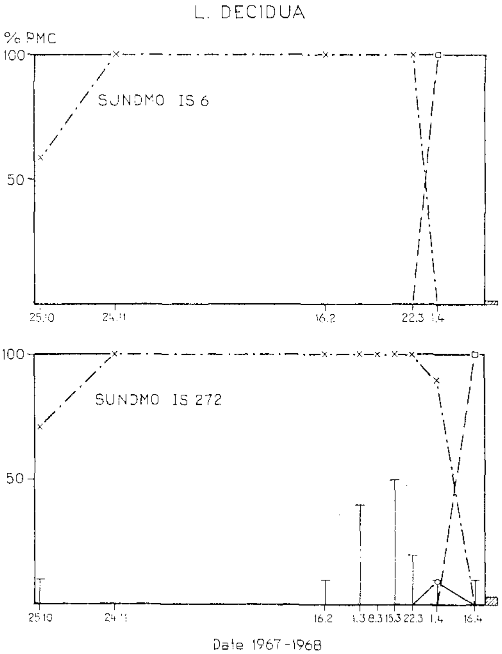


Fig. 18. The meiotic development in the PMC of the clones IS 6 and IS 272. *L. decidua* growing at Sundmo.

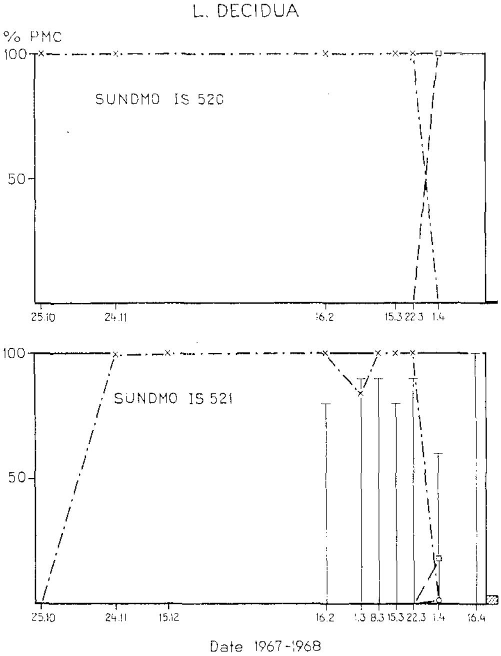


Fig. 19. The meiotic development in the PMC of the clones IS 520 and IS 521, *L. decidua* growing at Sundmo.

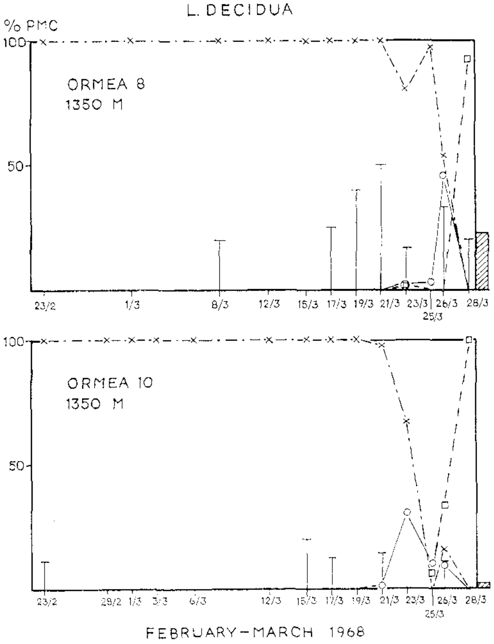


Fig. 20. The end of the meiotic development in the PMC of the clones Ormea 8 and Ormea 10, *L. decidua* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

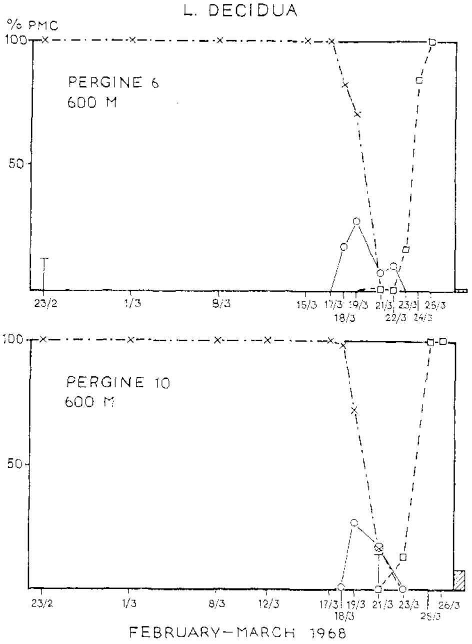


Fig. 21. The end of the meiotic development in the PMC of the clones Pergine 6 and Pergine 10, *L. decidua* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

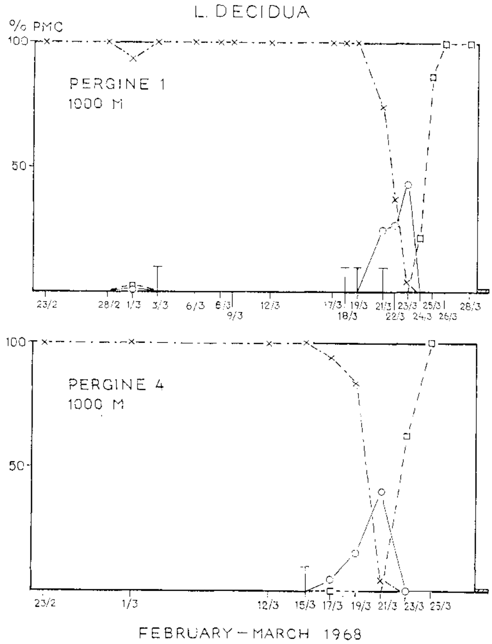


Fig. 22. The end of the meiotic development in the PMC of the clones Pergine 1 and Pergine 4, *L. decidua* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

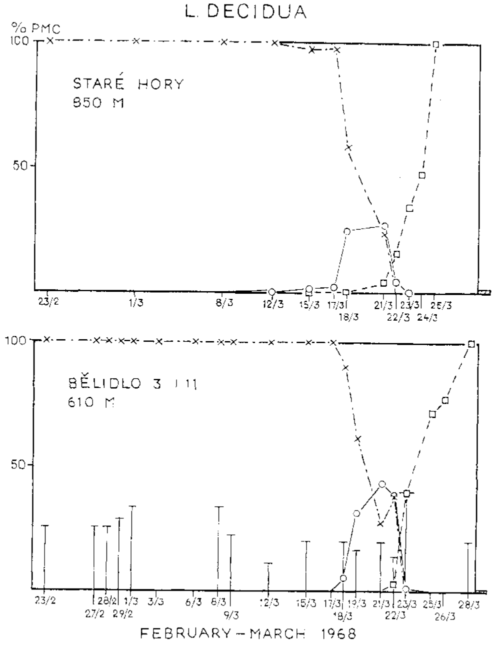


Fig. 23. The end of the meiotic development in the PMC of the clones Staré Hory and Bělidlo, *L. decidua* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

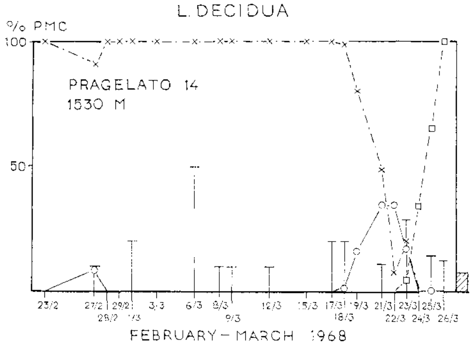
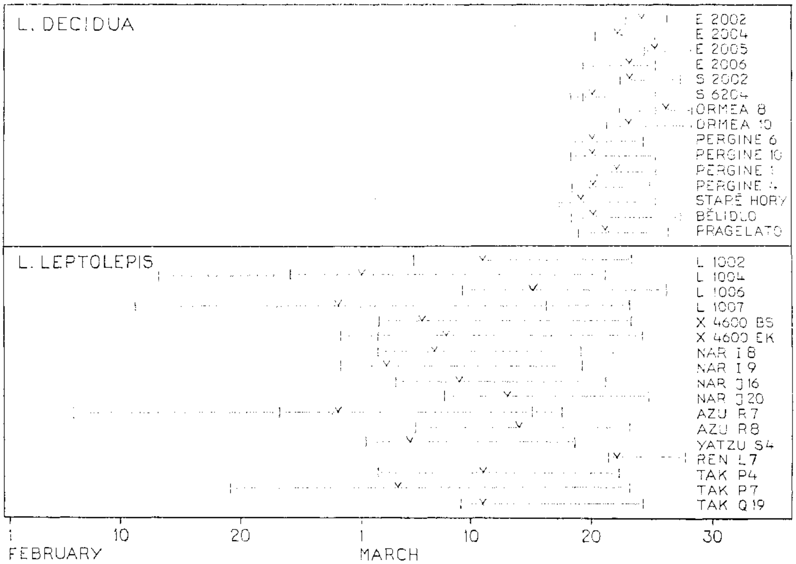


Fig. 24. The end of the meiotic development in the PMC of clone Pragelato 14, *L. decidua* growing at Grabbtorp. The altitude at the origin of growth of the clone is indicated.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.



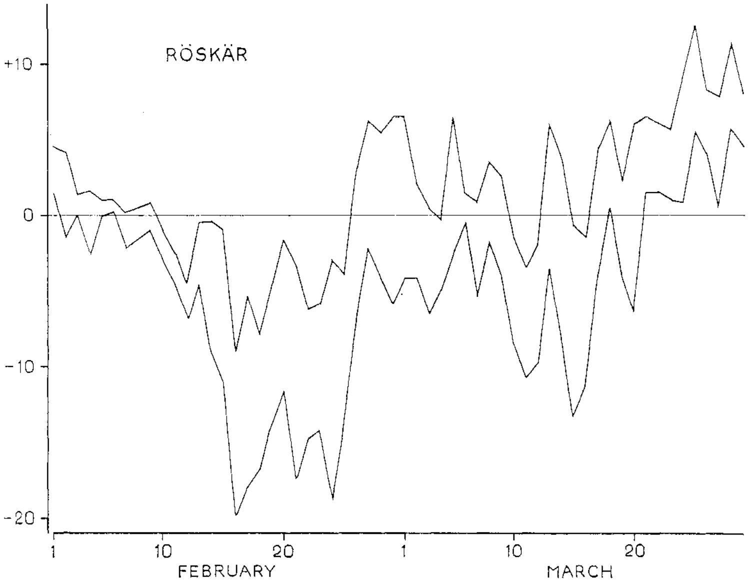


Fig. 32. *(above)* The extension in time for the development of the PMC from 90 % in the diplotene stage to 90 % in the tetrad stage for the European and Japanese larch clones growing at Broknäs and Grabbtorp. In case of fluctuation about 90 % this has been indicated in the diagram by the dashed lines. The date for passing of diplotene by 50 % of the PMC is indicated by the arrows.

Fig. 33. *(below)* Maximum and minimum temperature curves from 1 February to 28 March at Röskär.

previous investigations it was known that diplotene PMC are insensitive to temperatures as low as −30° C. However, from Fig. 9 it seems as if the irregularities causing the formation of completely damaged buds were induced during diplotene. Based on previous data this could not be true. Rather it was probable that the initiation of further development from diplotene took place during the beginning of February and the cells became damaged owing to exposure to low temperatures at the end of February before they had reached the insensitive tetrad stage. According to this interpretation of the origin of completely damaged buds the first date for passing of diplotene has been masked. This phenomenon has also appeared in other clones growing at other localities. Another explanation for the origin of completely damaged buds might be that large temperature fluctuations could bring about irregularities. This could not be tested in the present material as daily fixations were not made. The occurrence of completely damaged buds during diplotene might also be due to a viral infection.

If the temperature curves for Karlstad are examined it may be observed that the minimum temperature was below 0° C almost all the time from 15 December until the second part of March. The maximum temperature on the other hand was above 0° C on several occasions. However, it is probable that these periods were too short to be able to initiate the further development from diplotene. In all clones studied at Deje except for clone L 2001 (Fig. 2—4 and 8—14) the PMC remained in diplotene until the last week of March. During this week the maximum as well as the minimum temperatures were above 0° C. Therefore, no frost damage could be induced during this week. As seen from the diagrams (Fig. 2—4 and 8—14) for the clones growing at Deje the percentages of completely damaged buds were frequently high. The reason for the occurrence of completely damaged buds during diplotene in most of the clones growing at Deje (E 1001, E 1009, N 2001, R 1001, R 1002 and R 1003, and to a certain extent for E 2012, E 2013 and L 2001) is probably the same as suggested for clone E 2013 at Ekebo. Thus, it must be assumed that the initiation of the further development from diplotene probably took place partly during February and early March. Furthermore it must be assumed that all the post diplotene cells became damaged before reaching the frost insensitive tetrad stage. It must be pointed out that the temperature conditions at Deje might differ somewhat from the situation at Karlstad. Therefore, it is hardly possible to give an exact estimate of the date for passing of diplotene in the PMC and its implication for the induction of irregularities.

completely damaged buds (cf. E 1001, R 1001, R 1002 and R 1003 at Deje; N 2001 and R 1003 at Ekebo).

The differences in pattern of development from one locality to another within individual clones must be attributed to differences in environmental conditions at the two localities. Therefore, it is of interest to analyse the observed meiotic pattern in relation to the temperature curves for the meteorological stations in the neighbourhood of Ekebo and Deje (Svalöv and Karlstad respectively, Fig. 25 and 27).

At Ekebo there was alternating cold and mild weather during the winter. The initiation of further development from diplotene took place during the end of January — beginning of February (clones E 1009, E 2012, L 2001, R 1003 and probably also R 1002) or during the end of February — beginning of March (clones E 2002 and E 2013). Clone R 1002 constitutes an exception as diplotene was passed to a small extent already on 3 November. Based on previous experience (Eriksson, 1968 *b*) this should constitute an extremely extraordinary observation the reliability of which must be questioned. Although great care has been taken to avoid contamination, there are a few possibilities that it has taken place. On the other hand it may be pointed out that the completely damaged buds revealed on 16 December give some support to the early passing of diplotene in this case.

For those clones in which the development from diplotene started during the period of mild weather beginning in the middle of January and lasting until 10 February it would have been advantageous if the meiosis had been completed during the same period to avoid exposure to low temperatures during the end of February and beginning of March. However, in none of the clones was the meiosis completed until the second part of March. Owing to the exposure of the sensitive cells to low temperature the percentage of completely damaged buds was high (cf. clones L 2001, N 2001, R 1003). Clone E 1009 constitutes an extreme exception to this as no completely damaged buds were observed in this clone. This could partly be explained by the fact that the development from diplotene to tetrads took place to a great extent during the days in the beginning of March when the temperature conditions were favourable (5—9 March).

Independently of the date for passing of diplotene the development from diplotene to tetrads took place to the greatest extent during favourable conditions in clones E 2002, E 2012, E 2013 and R 1001 growing at Ekebo (cf. Fig. 4, 8, 9, 12 and 25). Therefore, the percentages of completely damaged buds were expected to be low. Low percentages were observed for all clones except for E 2013. From

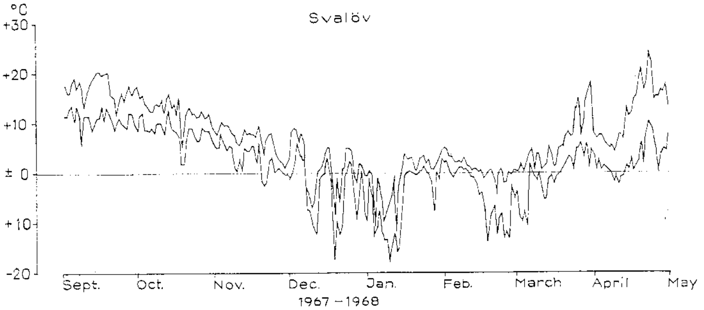


Fig. 25. Maximum and minimum temperature curves during September 1967—April 1968 at Svalöv.

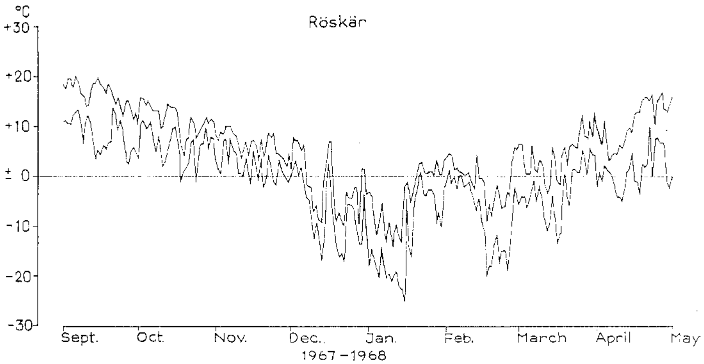


Fig. 26. Maximum and minimum temperature curves during September 1967—April 1968 at Röskär.

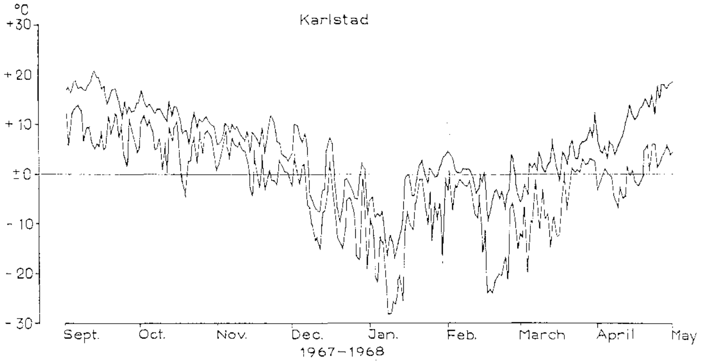


Fig. 27. Maximum and minimum temperature curves during September 1967—April 1968 at Karlstad.

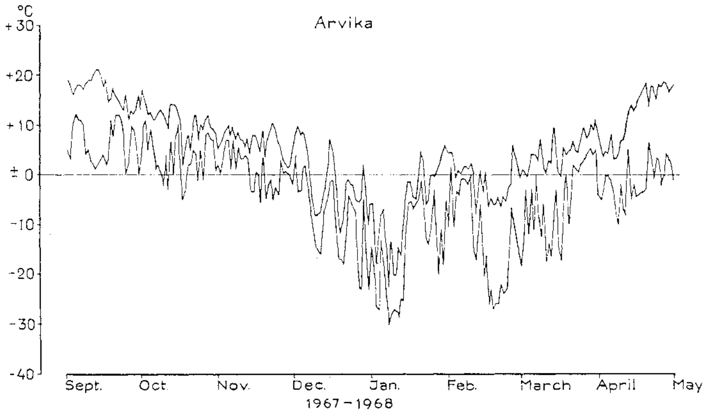


Fig. 28. Maximum and minimum temperature curves during September 1967—April 1968 at Arvika.

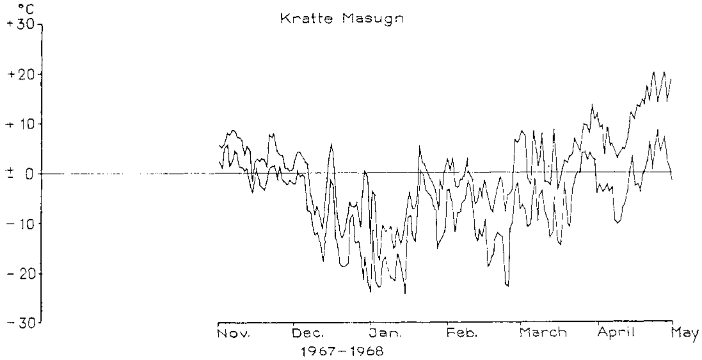


Fig. 29. Maximum and minimum temperature curves during November 1967—April 1968 at Kratte Masugn.

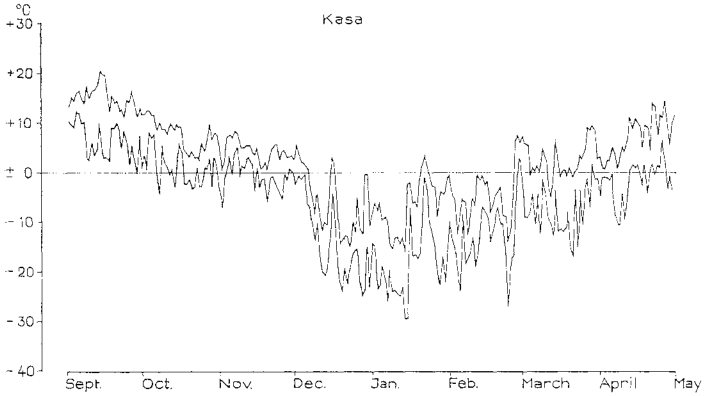


Fig. 30. Maximum and minimum temperature curves during September 1967—April 1968 at Kasa.

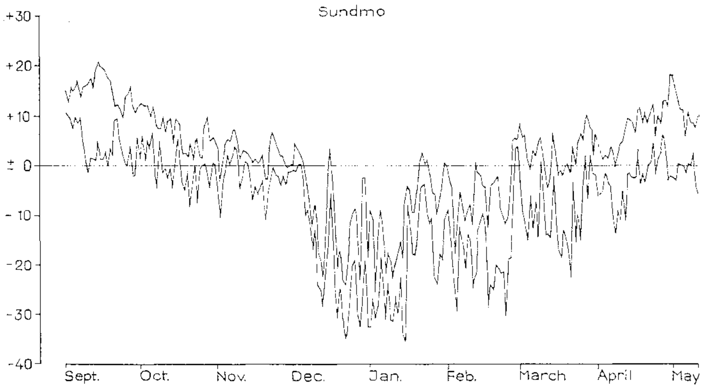


Fig. 31. Maximum and minimum temperature curves from 1 September 1967 to 10 May 1968 at Sundmo.

Both at Ekebo and Deje the percentage of sterile pollen grains was low. This might seem surprising. However, as stated on page 8 the development of the PMC in the completely damaged buds has ceased. Therefore, those PMC will not contribute to the pollen sterility.

Broknäs and Grabbtorp

The fixations were carried out at shorter intervals at these two plantations than at the other localities. The intervals were chosen according to the temperature conditions. During days when the temperature was below 0° C no development was expected to take place. Therefore, fixations on such days were omitted. As soon as the temperature passed 0° C by a few degrees fixations were performed again. The relatively short fixation intervals made a relatively detailed study of the meiotic pattern possible. Owing to this only the end of the meiotic development is illustrated in the diagrams (Fig. 6—7, 15 and 20—24, see also Fig. 5).

There is a common characteristic in all the clones studied at Broknäs and Grabbtorp, viz. the late initiation of further development from diplotene. Thus, there was hardly any passing of the diplotene stage before 15 March. Therefore, the seemingly high maximum temperatures at the end of February were not able to provoke any initiation. This means that the diplotene cells are rather resistant to temperature fluctuations (—5° — +5° C) of short duration with regard to initiation of further development from diplotene.

In Fig. 32 (p. 16) the extension in time for the development from 90 per cent of the PMC in the diplotene stage to 90 per cent in the tetrad stage is illustrated. The date for passing of diplotene by 50 per cent of the PMC is also demonstrated in Fig. 32. From this figure it might seem that the clones are relatively similar with regard to development from diplotene to the tetrad stage. The date for passing of diplotene by 50 per cent of the PMC did not differ more than seven days (19 March for Staré Hory and 26 March for Ormea 8). However, if the temperatures offered to the grafts during this period are analysed it might be observed that the temperature sum — either based on the area limited by the line for 0° C and the minimum temperature curve above 0° C or the corresponding area limited by the maximum temperature curve — varies considerably. Such temperature sums should be calculated from a day shortly before the first observed passing of diplotene. In the present case 17 March was selected. As there was a sharp decline of the diplotene stage it might be justified to end the calculation on the date for 50 per cent passing of diplotene. For the two extreme grafts, the temperature sums (maximum temperature) amounted to 12.0 and 60.5 degrees × days respectively. Therefore, the apparently great similarity in pattern of reaction might be more complex than it seems to be. The variability observed is probably due to differences in temperature response of the clones. It is worth mentioning that the first pronounced initiation of further development from diplotene took place on 18—19 March (clones Pergine 4, 6 and 10, Staré Hory and Bělidlo 3 I 11 as well as E 2006 and S 6204 at Broknäs). At that time the minimum temperature curve had not passed 0° C since the beginning of February. It is hardly probable that the minimum temperature of +0.5° C observed on 18 March could be responsible for the initiation. Whether the maximum temperature is the deciding factor for initiation cannot be determined. The fact that no passing of diplotene was observed at the end of February to the beginning of March although the maximum temperature was high could be explained by the almost immediate induction of irregularities in the post diplotene PMC in the clones showing moderate percentages of completely damaged buds. As only a few clones behaved in this manner this explanation cannot be of general importance.

A discussion of the influence of the origin of the clones on the temperature response of their PMC cannot be carried out until observations have been made during several seasons.

For the most part the percentage of completely damaged buds was low. However, in some clones the percentage was moderately high

(E 2004, E 2006, Bělidlo 3 I 11 Fig. 6—7 and 23). It should be pointed out that in the clones of Pergine origin completely damaged buds were almost lacking. The great difference in this respect between the clones within the E 2000-series at Broknäs is worth mentioning. As those clones originate from the same plantation in the province of Östergötland a relatively great agreement between the clones was expected.

Like the situation in many other clones the completely damaged buds appeared during the diplotene stage. This can be explained in the same way as for clone E 2013 at Ekebo (cf. p. 8).

Owing to the presence of favourable temperature conditions during the development from diakinesis — telophase II, the pollen sterility was low in all clones. The highest percentage (23 %) was observed in clone Ormea 8.

Kratte Masugn

Before the results are discussed it ought to be pointed out that the number of generative buds was rather limited in the four clones tested at this locality. This might bias the pattern of meiotic development, especially if the percentage of completely damaged buds is high as was the case for clone X 1003.

As seen from Fig. 29 the curve for the minimum temperature was almost uninterruptedly below 0° C from the end of November until 25 March. As a consequence of this the initiation of further development from diplotene probably took place subsequent to 24 March (cf. Fig. 16—17). The tetrad stage was still not completely reached in two of the clones on 29 March.

In similarity with the situation in many other clones growing at other localities completely damaged buds occurred at a relatively high frequency before any passing of diplotene had been observed. The same interpretation as given for clone E 2013 growing at Deje (cf. p. 18) will also be given for this observation in the clones growing at Kratte Masugn.

Owing to the favourable temperature conditions during the period 25—29 March when the development from diplotene to tetrads to the greatest extent took place in those PMC which gave rise to any pollen formation, the pollen quality was expected to be low. The actual observations agreed well with this expectation.

Sundmo

At this locality two of the clones (IS 6 and IS 520) showed almost identical patterns of development. The passing of diplotene and the reaching of the tetrad stage took place simultaneously. Furthermore, no completely damaged buds were observed in these two clones. It must be assumed that the development from diplotene to tetrads was rapid and perhaps took place within one day, either on 26 March or 28 March when both the maximum and the minimum temperature were above 0° C. Otherwise it must be assumed that the PMC of these two clones (IS 6 and IS 520) are insensitive to low temperature since the minimum temperature was below 0° C on all other days during the period 22 March — 1 April.

Also the clones E 1001 and IS 272 revealed a favourable pattern of development and a relatively low percentage of completely damaged buds. The latter observation was somewhat unexpected as the minimum temperature from 1 April to 16 April was below 0° C. At least the pollen sterility was expected to be higher than observed.

It seems as if the mild weather on 27—28 February was responsible for the initiation of further development from diplotene in clone IS 521. It might be assumed that the PMC which passed diplotene at that time became damaged before reaching the tetrad stage. On the other hand the percentage of completely damaged buds was high already on 16 February, which suggests a still earlier passing of diplotene than assumed above.

3.2. Larix leptolepis

About 340,000 PMC have been classified with respect to meiotic stage in this species. The pattern of development in the PMC of the individual clones is illustrated in Fig. 34—48. Like the situation in *Larix decidua* any common characteristic in the pattern of the meiotic development can hardly be observed in the Japanese larch.

3.2.1. Reaching of diplotene

Most of the grafts showed that the PMC to a great extent were still in pachytene at the start of the investigation during October 1967 (cf. Fig. 34—35, 38—41). The clones M 3018 at Brunsberg, L 2005, L 2006 and N 2005 at Ekebo constitute exceptions as they had reached diplotene to a great extent at that time. In most of the clones all PMC had reached the diplotene stage on 3 November. As with *L. decidua,* it can be stated that the reaching of the diplotene stage took place relatively independent of the temperature conditions.

3.2.2. Completion of meiosis

Ekebo and Värmland

Only two of the Japanese larch clones in Värmland (M 2002 and M 2003) could also be studied at Ekebo. In both clones there was a pronounced difference between the pattern of meiotic development at Ekebo on one hand and Deje and Södra Viken on the other. Thus, diplotene was completely passed on 17 February at Ekebo whereas the first passing of diplotene was observed on 22 March at Deje (Fig. 41). It can once more be stated that the difference in pattern of meiotic development from locality to locality within the same clone must be attributed to the difference in environmental conditions at the two localities.

From the temperature curves at Svalöv it is evident that the mild weather appearing in the end of January to the beginning of February is responsible for the initiation of the further development from diplotene in clones M 2002 and M 2003 at Ekebo. The same is true for all other Japanese larch clones studied at Ekebo (F 1001, L 1001, L 2005, M 2001 and N 2005). In clones F 1001, L 1001 and M 2002 diplotene was almost completely passed on 3 February whereas diplotene did not disappear until 17 February in clones L 2005, L 2006, M 2001 and M 2003. Whether or not there is a difference regarding the passing of diplotene in the two groups of clones is difficult to decide owing to the long interval between the fixations at Ekebo (from 16 December 1967 to 3 February 1968).

The percentage of completely damaged buds was in most clones low or completely absent. This is probably due to the fact that the tetrad stage was reached to a great extent on 17 February (clones F 1001, L 1001, L 2005, M 2001, M 2002 and M 2003) before the period of low minimum temperatures at the end of February and beginning of March. On the other hand it is probable that some of the PMC in sensitive stages were exposed to low temperatures as the pollen sterility in some of the clones was relatively high (clones F 1001 and M 2001). In clone N 2005 the tetrad stage was not completely reached until 23 March, which means that the sensitive stages appeared during the period of low temperature in the end of February to the beginning of March. This caused the induction of irregularities to a great extent. This is especially evident from the high pollen sterility in this particular clone.

As the four clones studied in Värmland were growing at three different localities it is impossible to determine if the difference in passing of diplotene observed in clones L 8 at Brunsberg and M 2002 at Södra Viken really is due to an intrinsic difference or a climatically conditioned one. In the first mentioned clone diplotene was completely passed on 22 March whereas only 7 per cent of the PMC had passed diplotene at Södra Viken on that date.

All four clones show one common characteristic, viz. the presence of relatively high percentages of completely damaged buds during March before any passing of the diplotene stage had been observed. The reason for the occurrence of this characteristic has been discussed so frequently for the European larch clones that the reader is referred to the discussion on p. 18. The PMC which had not started their development from diplotene until the minimum temperature curve had passed over 0° C on 21 March had the opportunity to complete the meiosis under favourable conditions at the end of March (cf. the temperature curves for Karlstad and Arvika, Fig. 27—28).

Broknäs, Ernvik and Grabbtorp

Like the situation for the European larch clones cultivated at these localities a relatively detailed information concerning the meiotic development in the PMC of the Japanese larch clones could be obtained owing to the short intervals between the fixations (especially during March).

A comparison of the data in Fig. 32—33 reveals that four different categories of clones could be distinguished concerning the development from diplotene to the tetrad stage. The first group consisted of clones L 1004 and L 1007 at Broknäs and Azu R 7 and Tak P 7 at Grabbtorp in which the development started before the period of mild weather at the end of February. The initiation of further development from diplotene in these clones probably took place in connection with the mild weather around 1 February. As can be seen from Fig. 36—37, 45 and 47 mostly no more than 10—20 per cent of the PMC had passed diplotene during the period ending on 27 February. This was also expected since the temperature was below 0° C during the period 10—25 February.

The next group of clones — L 1002 and X 4600 at Broknäs, X 4600 at Ernvik, Nar I 8, Nar I 9, Nar J 16, Azu R 8, Yatsu S 4 and Tak P 4 at Grabbtorp — started their development from diplotene to tetrads during the period of maximum temperatures of around +6° C at the turn of the month February—March.

A third category of clones—L 1006 at Broknäs, Nar J 20 and Tak Q 19 at Grabbtorp — could be distinguished. These clones did not

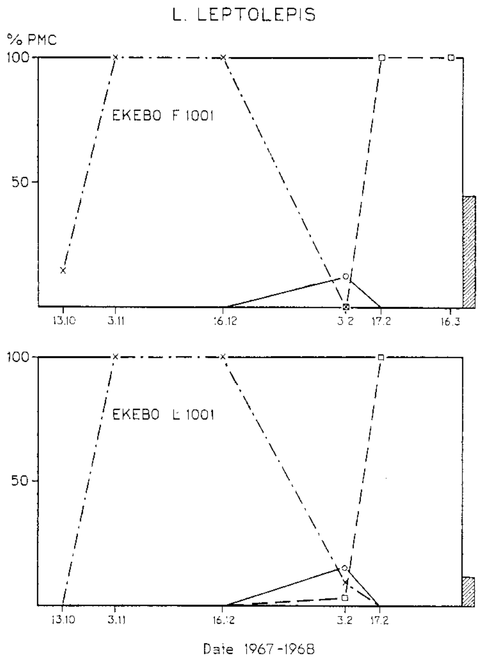


Fig. 34. The meiotic development in the PMC of the clones F 1001 and L 1001, *L. leptolepis* growing at Ekebo.

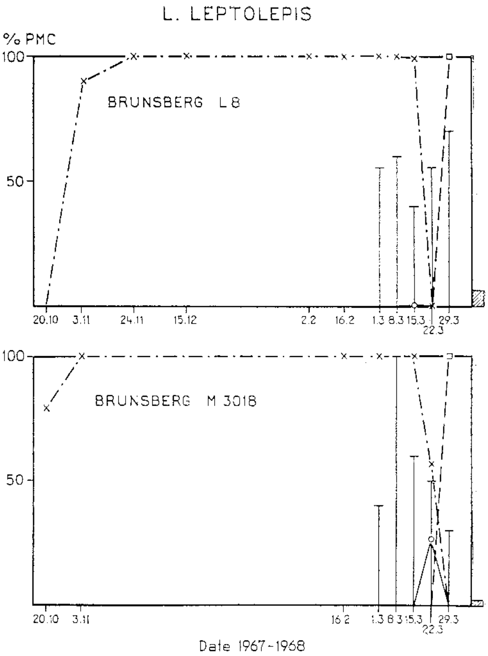


Fig. 35. The meiotic development in the PMC of the clones L 8 and M 3018, *L. leptolepis* growing at Brunsberg.

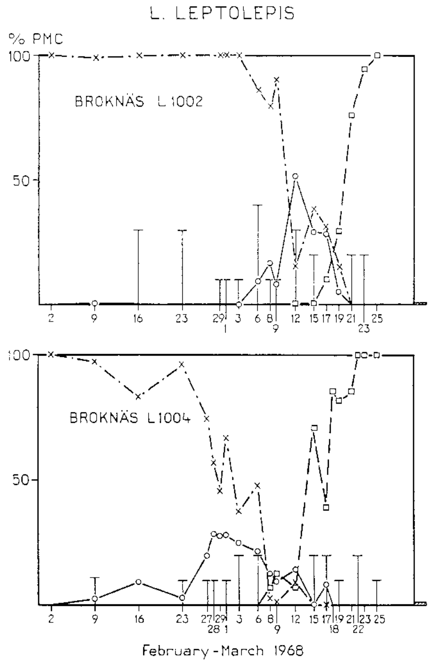


Fig. 36. The end of the meiotic development in the PMC of the clones L 1002 and L 1004, *L. leptolepis* growing at Broknäs.

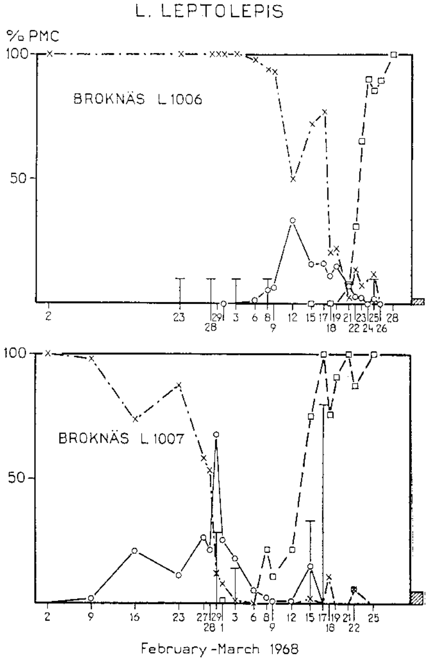


Fig. 37. The end of the meiotic development in the PMC of the clones L 1006 and and L 1007, *L. leptolepis* growing at Broknäs.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

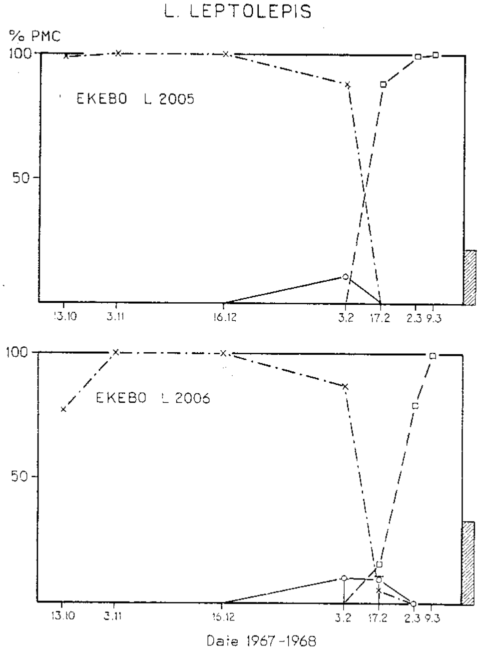


Fig. 38. The meiotic development in the PMC of the clones L 2005 and L 2006, *L. leptolepis* growing at Ekebo.

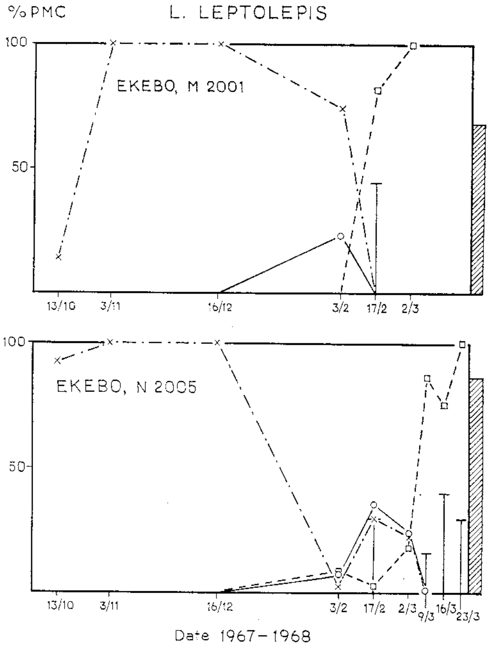


Fig. 39. The meiotic development in the PMC of the clones M 2001 and N 2005, *L. leptolepis* growing at Ekebo.

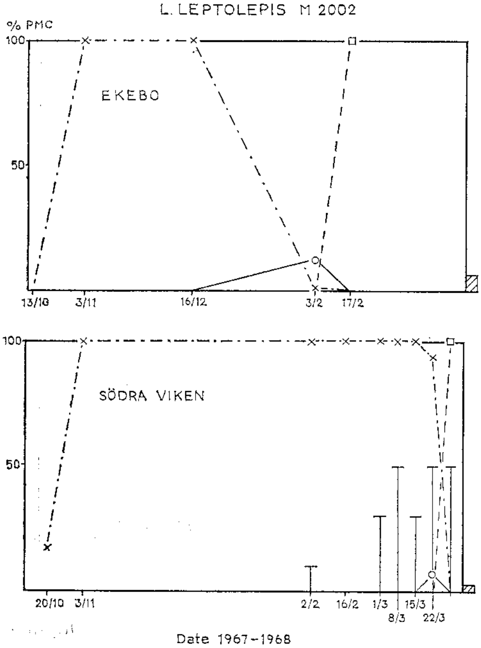


Fig. 40. The meiotic development in the PMC of clone M 2002, *L. leptolepis* growing at Ekebo and Södra Viken.

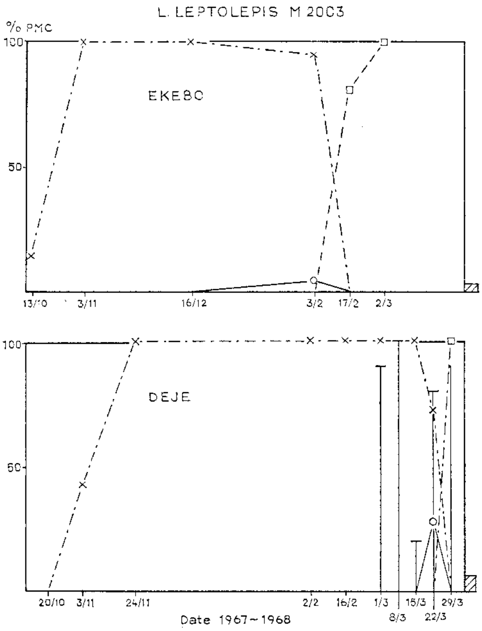


Fig. 41. The meiotic development in the PMC of clone M 2003, *L. leptolepis* growing at Ekebo and Deje.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

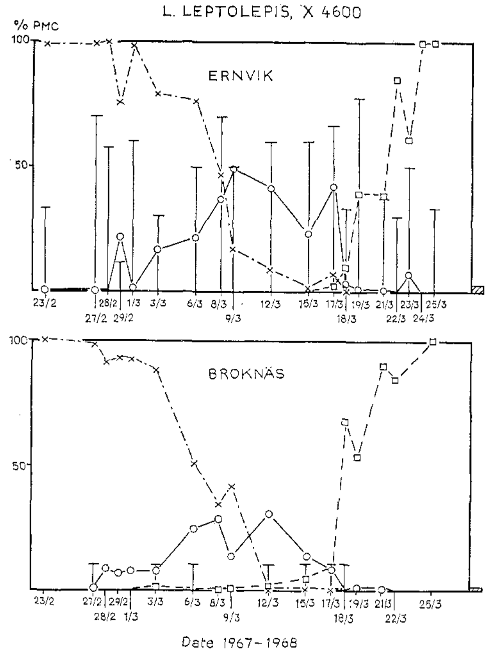


Fig. 42. The end of the meiotic development in the PMC of clone X 4600, *L. leptolepis* growing at Broknäs and Ernvik.

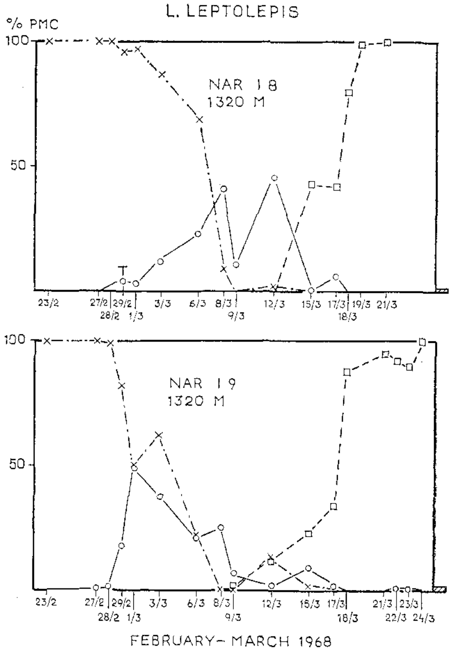


Fig. 43. The end of the meiotic development in the PMC of the clones Nar I 8 and Nar I 9, *L. leptolepis* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

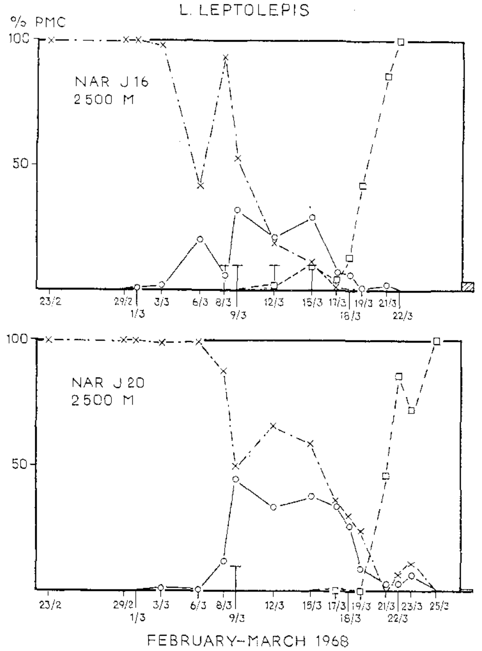


Fig. 44. The end of the meiotic development in the PMC of the clones Nar J 16 and Nar J 20, *L. leptolepis* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

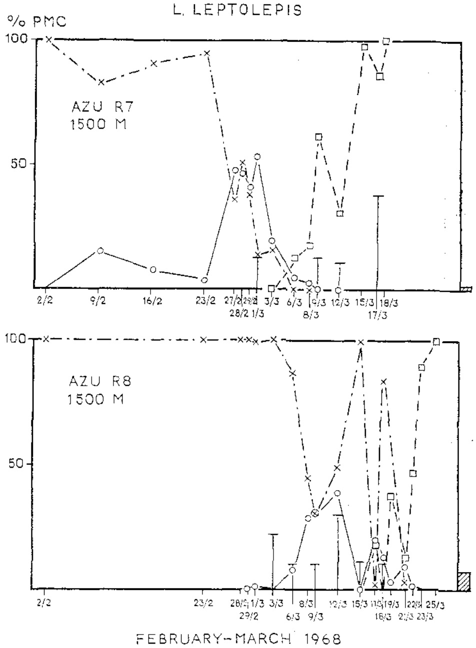


Fig. 45. The end of the meiotic development in the PMC of the clones Azu R 7 and Azu R 8, *L. leptolepis* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

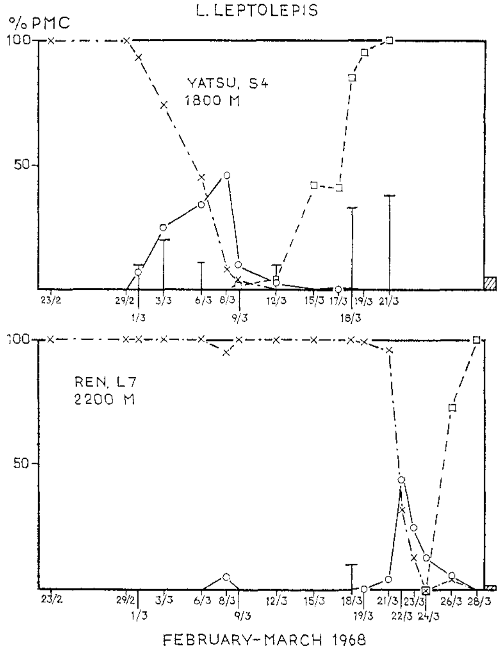


Fig. 46. The end of the meiotic development in the PMC of the clones Yatsu S 4 and Ren L 7, *L. leptolepis* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

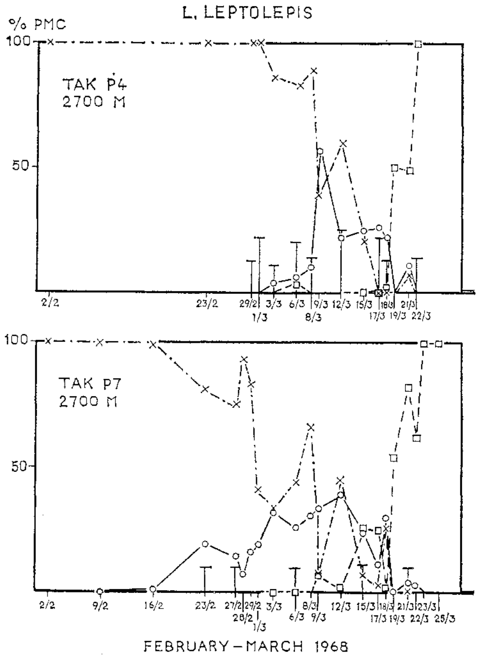


Fig. 47. The end of the meiotic development in the PMC of the clones Tak P 4 and Tak P 7, *L. leptolepis* growing at Grabbtorp. The altitudes at the origin of growth of the clones are indicated.

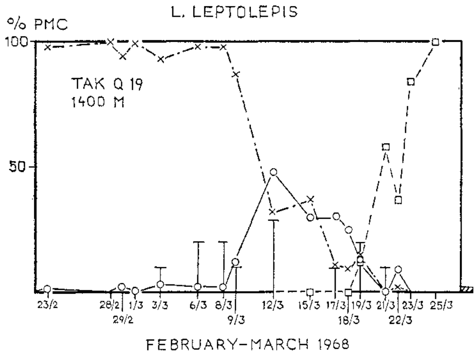


Fig. 48. The end of the meiotic development in the PMC of clone Tak Q 19, *L. leptolepis* growing at Grabbtorp. The altitude at the origin of growth of the clone is indicated.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

respond as fast as the clones of the second group to the previously mentioned period of high (+6° C) maximum temperature.

Clone Ren L7 at Grabbtorp did not start the development from diplotene to tetrads to any great extent until the minimum temperature was above 0° C. This clone resembled the European larch clones in this respect (see Fig. 32).

The reason for the difference in pattern of meiotic development between the four groups is probably that the individual clones respond to different temperatures. With the exception of clone Ren L 7 it is evident that a minimum temperature below 0° C does not constitute any obstacle for an onset and a continuing of the development from diplotene to tetrads in the clones of Japanese larch studied at Broknäs, Ernvik and Grabbtorp. On the other hand it is probable that this development ceases below a certain temperature limit as stated by Christiansen (1960) for European larch but continues as soon as sufficiently high temperatures (+2° — +5° C) again are offered to the PMC. Whether or not temperature fluctuations around 0° C have any influence upon the initiation of further development cannot be determined on material cultivated outdoors. For such an evaluation it will be necessary to expose the PMC to changing temperatures and constant temperatures under strictly controlled conditions.

The percentage of completely damaged buds was in most of the clones low or equal to zero. Clone X 4600 at Ernvik and clone L 1002 at Broknäs constitute exceptions to this as the average percentage in these clones amounted to 49.0 and 16.0 respectively. The situation in clone X 4600 needs a special comment as there was a pronounced difference between the percentage of completely damaged buds at Ernvik and Broknäs. As seen from Fig. 42 the disappearance of diplotene took place in almost the same way at the two localities. On the other hand it might be observed that the percentage of PMC in the stages diakinesis — anaphase I was higher at Ernvik than at Broknäs during the period with low minimum temperatures from 10 March until 17 March. This could partly explain the difference observed. The temperature might be another contributing factor as the exposure to frost must be regarded as higher at Ernvik than at Broknäs. This focuses the attention on the importance of having temperature readings at the plantations, which in this investigation could not be carried out owing to the fact that too limited economic resources were placed at our disposal. In this connection it is worth mentioning that experiments have been in progress in which the temperature within the generative buds were registrered continuously. The data from that investigation will be presented in the future.

The percentages of sterile pollen grains were low in all clones, in no case exceeding 10 per cent. A detailed investigation of the occurrence of irregularities in the PMC of the Japanese larch clones growing at Grabbtorp has been undertaken. The data from that investigation will be discussed in another context. Therefore, it will only be stated here that the low percentages of completely damaged buds and sterile pollen suggest that the PMC in active division are relatively resistant to short exposures to low temperatures down to about −10° C.

3.3. Larix sibirica

About 350,000 PMC have been classified with respect to meiotic stage in this species. The pattern of meiotic development in the PMC of the individual clones is illustrated in Fig. 49—70. The breakage of dormancy in the PMC and the further initiation of development from diplotene during the autumn of 1967 was discussed in a previous paper by Eriksson (1968 *b*). Therefore, mainly the passing of diplotene during the winter will be discussed in the present communication. At first the data from the different localities will be presented individually. When this has been carried out a comparison of the pattern of development in clones growing at more than one locality will be undertaken.

Before this can be done it is necessary to point out that in the paper by Eriksson (1968 *b*) a passing of diplotene was indicated by arrows in the diagrams showing the temperature curves. As this passing frequently consisted of a few cells out of approx. 2000 PMC, they will not in all cases be observed in the diagrams of the present communication where only 100 PMC from each bud were classified with respect to meiotic stage. This explains the apparent discrepancy between the data in the present communication and the data of the previous paper (Eriksson, 1968 *b*).

3.3.1. Completion of meiosis

Ekebo

All clones studied showed an early passing of diplotene, sometimes already during the autumn of 1967 (clones E 1005, W 2001 and W 5002, Fig 50, 53 and 58). However, only in clone E 1005 was the passing accentuated. Thus, even tetrads were observed on 16 December. In spite of the early passing of diplotene in this clone the development did not accelerate until the end of February.

Two more types of developmental pattern might be distinguished at this locality. The first of those two groups consisted of clones E 2011, W 2001 and W 5002, in which diplotene was almost completely passed on 3 February. It is probable that the mild weather during the second part of January is responsible for the passing of diplotene in these clones. The high percentages of completely damaged buds as well as the pollen sterility indicate that not all PMC had reached the tetrad stage, escaping the exposure to the low minimum temperatures appearing during the second part of February (cf. Fig. 25).

In the third group of clones (U 1001 and W 5001), the main passing of the diplotene stage took place subsequent to 3 February. In the two clones belonging to this group the percentage of completely damaged buds was relatively high. The pollen sterility was also high in clone W 5001. The reason for these high percentages can be explained in the same way as for the clones in the previous groups, i.e. most of the PMC did not escape from exposure to low minimum temperatures appearing during the second part of February and the beginning of March.

Ernvik

Some passing of the diplotene stage was detected on 23 January (cf. Fig. 6 in Eriksson, 1968 *b*). However, any pronounced development from diplotene was not observed until the beginning of February in clones E 1004, E 1005, W 5002, W 5006 and W 5007. The reaching of the tetrad stage was a relatively slow process which lasted until 22—24 March. This means that the sensitive PMC at several occasions were exposed to low minimum temperatures, especially from 16—25 February. In spite of this, the percentage of completely damaged buds was relatively low. Except for clone W 5006 the pollen sterility was relatively moderate in these clones. Especially astonishing is the situation in clone W 5007, in which completely damaged buds were absent and the pollen sterility was as low as 11.1 per cent although this clone showed the highest percentage of sensitive cells at the minimum of the temperature curve (16—25 February). These data suggest that this clone either is highly insensitive to low temperature or that the pollen sterility is underestimated. The need for a reliable method for determination of the pollen sterility has been pointed out previously (Eriksson, 1968 *b*).

Another temperature response of the diplotene PMC was revealed in clone E 1002. In this case any pronounced passing of the diplotene stage did not take place until the end of February at a time when the

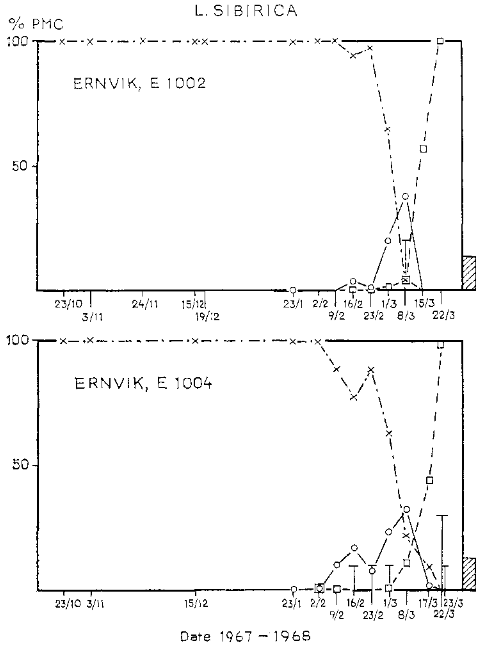


Fig. 49. The meiotic development in the PMC of the clones E 1002 and E 1004, *L. sibirica* growing at Ernvik.

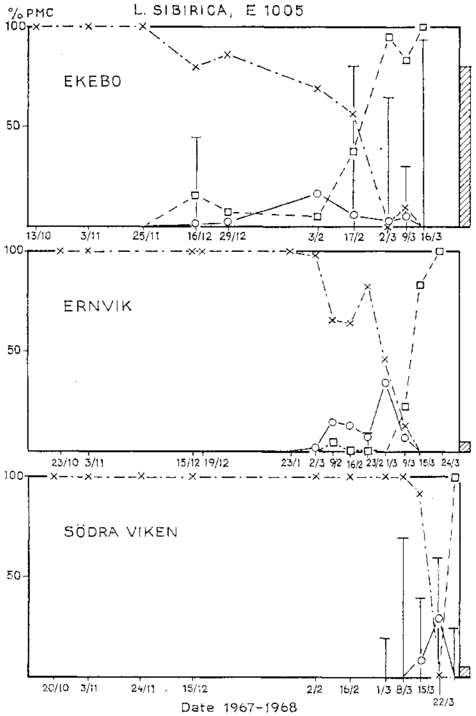


Fig. 50. The meiotic development in the PMC of clone E 1005, *L. sibirica* growing at Ekebo, Ernvik and Södra Viken.

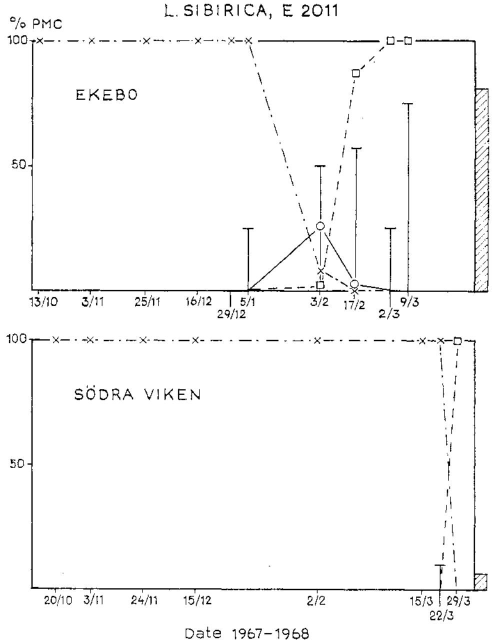


Fig. 51. The meiotic development in the PMC of clone E 2011, *L. sibirica* growing at Ekebo and Södra Viken.

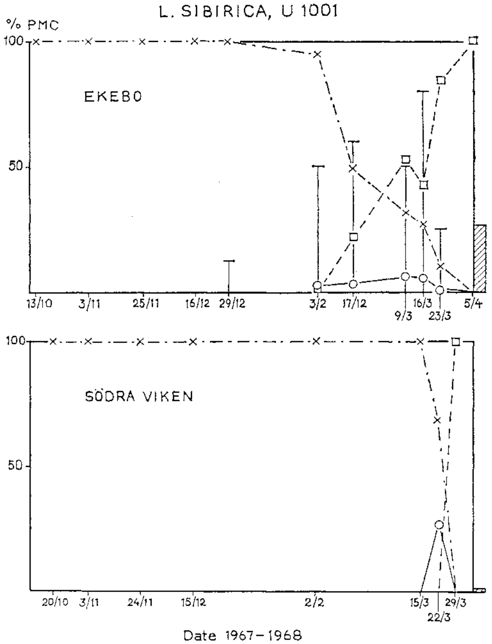


Fig. 52. The meiotic development in the PMC of clone U 1001, *L. sibirica* growing at Ekebo and Södra Viken.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

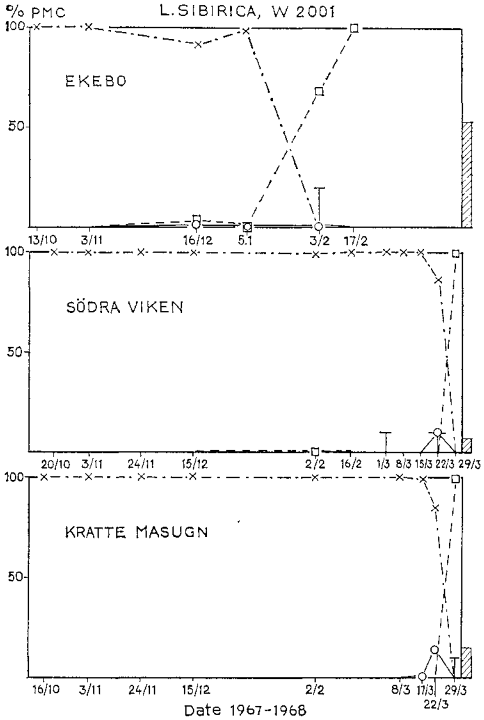


Fig. 53. The meiotic development in the PMC of clone W 2001, *L. sibirica* growing at Ekebo, Södra Viken and Kratte Masugn.

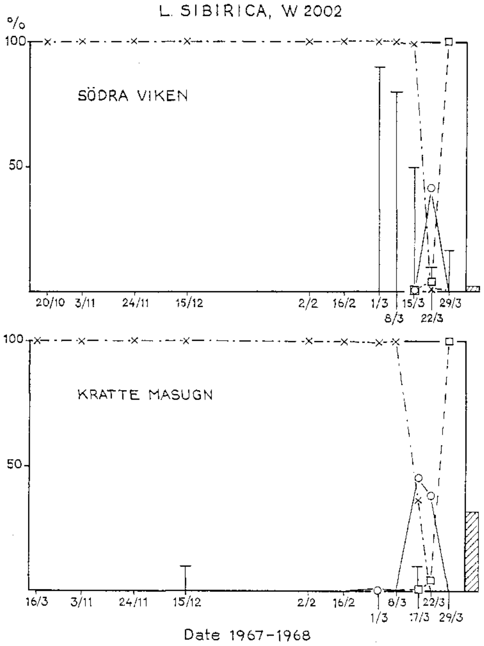


Fig. 54. The meiotic development in the PMC of clone W 2002, *L. sibirica* growing at Södra Viken and Kratte Masugn.

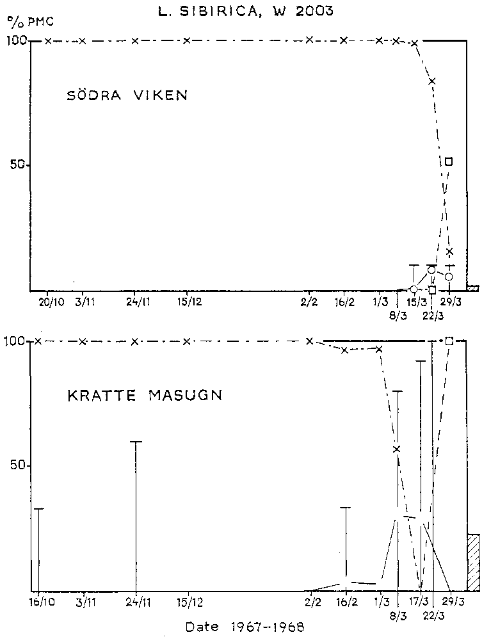


Fig. 55. The meiotic development in the PMC of clone W 2003, *L. sibirica* growing at Södra Viken and Kratte Masugn.

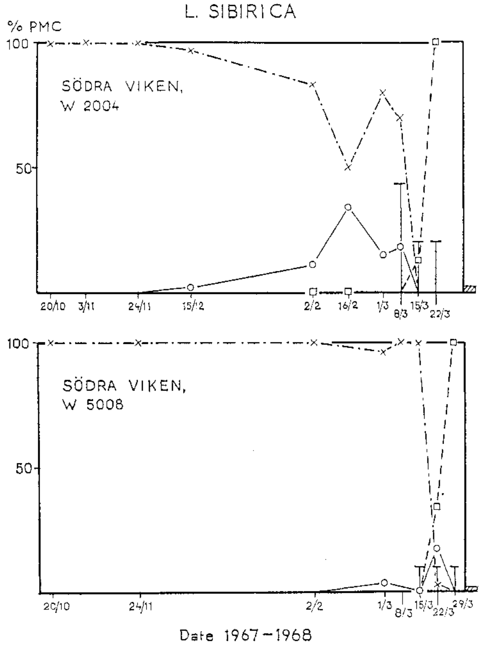


Fig. 56. The meiotic development in the PMC of the clones W 2004 and W 5008, *L. sibirica* growing at Södra Viken.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

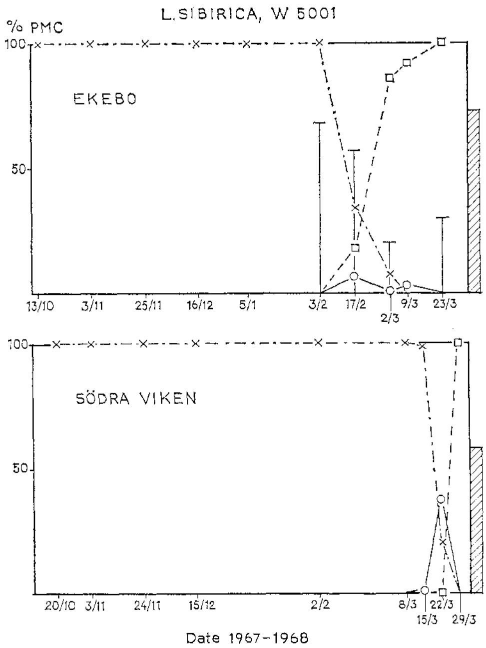


Fig. 57. The meiotic development in the PMC of clone W 5001, *L. sibirica* growing at Ekebo and Södra Viken.

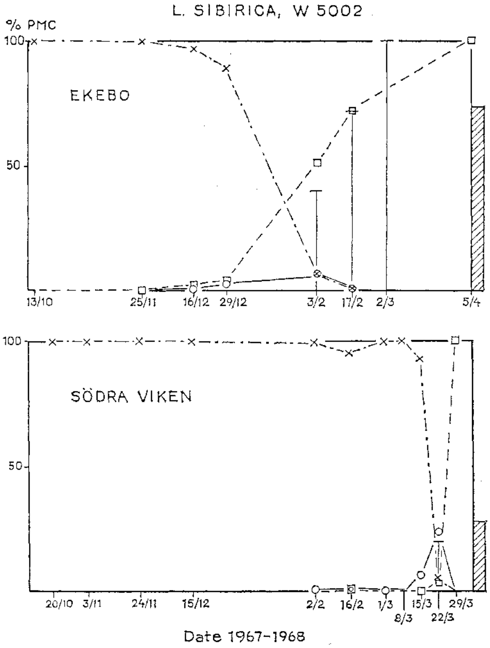


Fig. 58. The meiotic development in the PMC of clone W 5002, *L. sibirica* growing at Ekebo and Södra Viken.

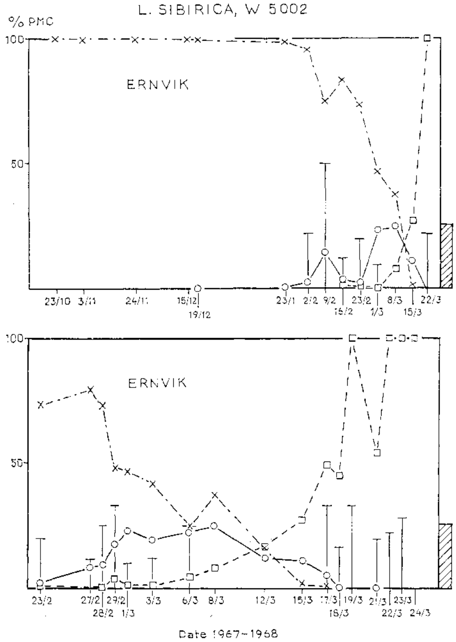


Fig. 59. The meiotic development in the PMC of clone W 5002, *L. sibirica* growing at Ernvik. The end of the meiotic development is shown separately.

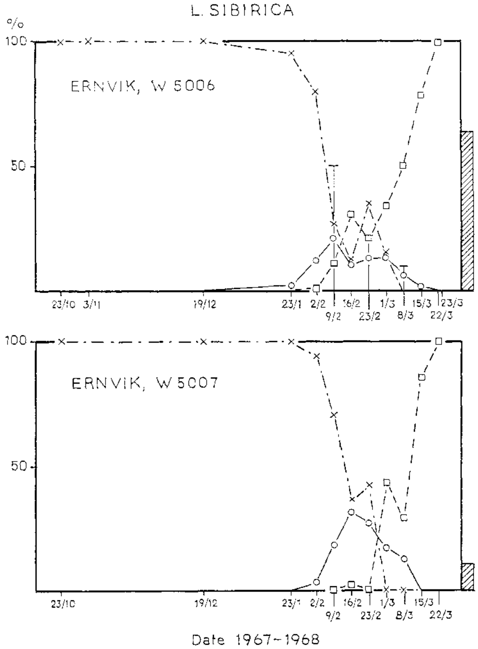


Fig. 60. The meiotic development in the PMC of the clones W 5006 and W 5007, *L. sibirica* growing at Ernvik.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, ☐ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

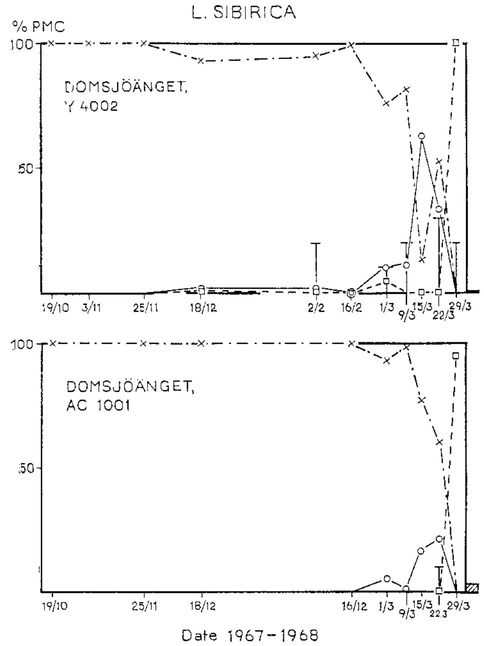


Fig. 61. The meiotic development in the PMC of the clones Y 4002 and AC 1001, *L. sibirica* growing at Domsjöänget.

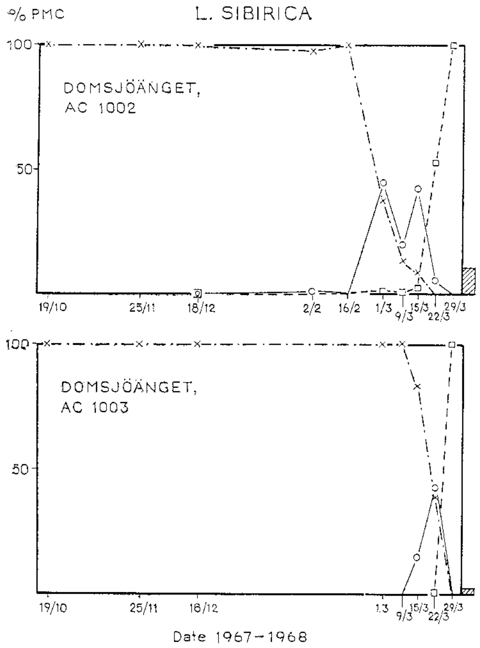


Fig. 64. The meiotic development in the PMC of the clones AC 1002 and AC 1003, *L. sibirica* growing at Domsjöänget.

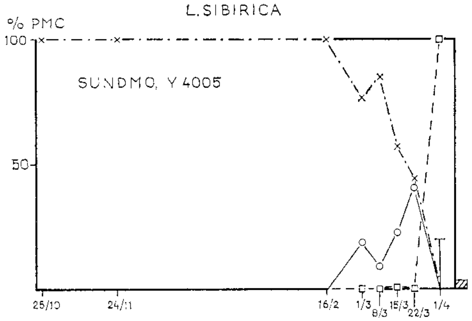


Fig. 62. The meiotic development in the PMC of clone Y 4005, *L. sibirica* growing at Sundmo.

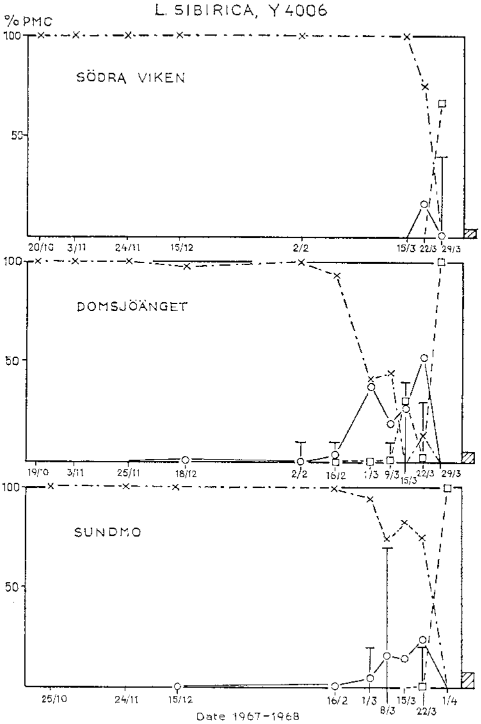


Fig. 63. The meiotic development in the PMC of clone Y 4006, *L. sibirica* growing at Södra Viken, Domsjöänget and Sundmo.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

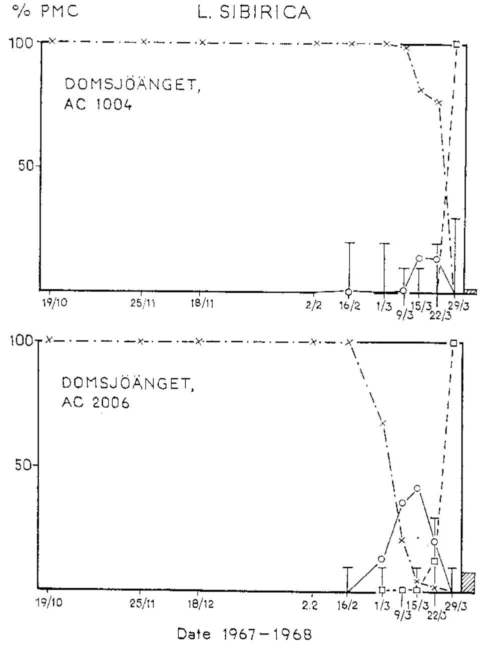


Fig. 65. The meiotic development in the PMC of the clones AC 1004 and AC 2006, *L. sibirica* growing at Domsjöänget.

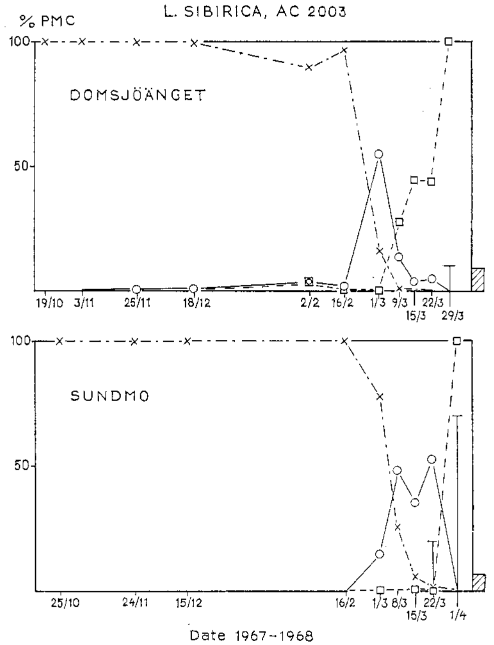


Fig. 66. The meiotic development in the PMC of clone AC 2003, *L. sibirica* growing at Domsjöänget and Sundmo.

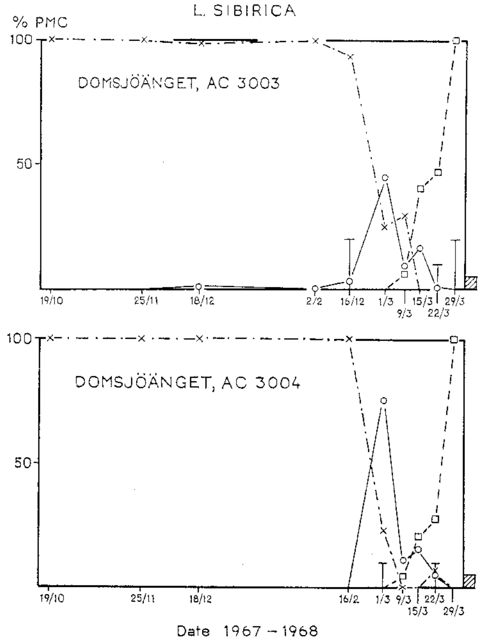


Fig. 67. The meiotic development in the PMC of the clones AC 3003 and AC 3004, *L. sibirica* growing at Domsjöänget.

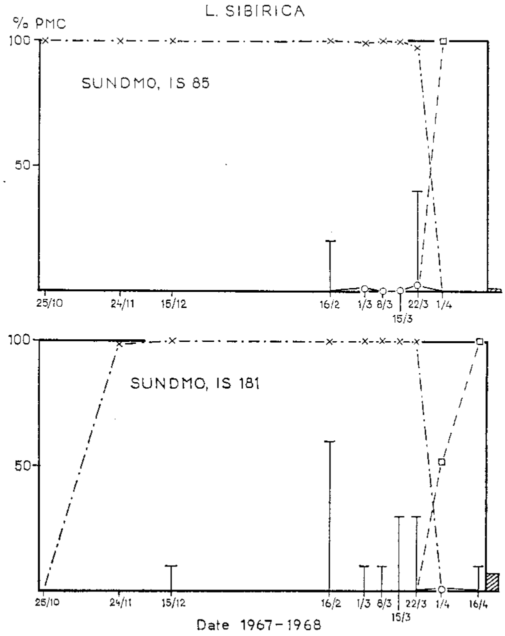


Fig. 68. The meiotic development in the PMC of the clones IS 85 and IS 181, *L. sibirica* growing at Sundmo.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, ☐ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

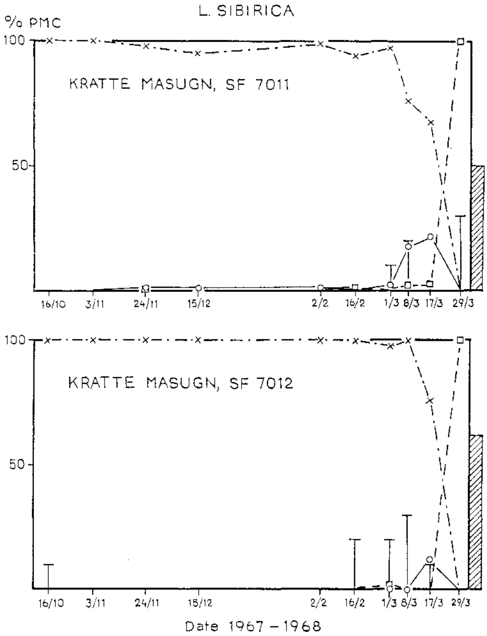


Fig. 69. The meiotic development in the PMC of the clones SF 7011 and SF 7012, *L. sibirica* growing at Kratte Masugn.

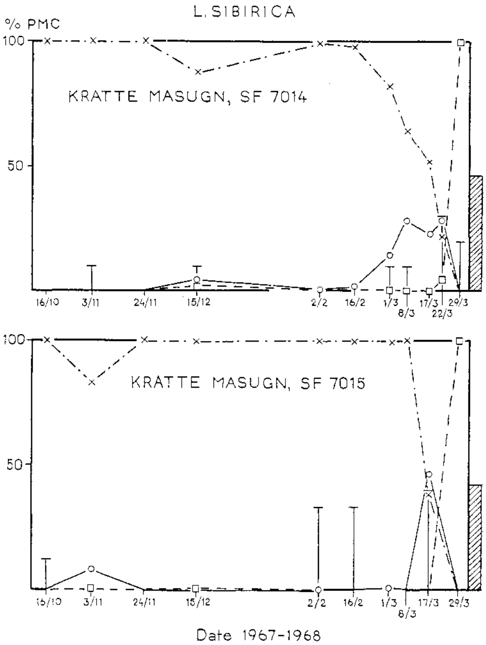


Fig. 70. The meiotic development in the PMC of the clones SF 7014 and SF 7015, *L. sibirica* growing at Kratte Masugn.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The columns shown as straight lines refer to the percentage of completely damaged buds. The hatched columns refer to the pollen sterility.

maximum temperature amounted to about +6° C. Compared to the situation in the clones belonging to the first group, the development from diplotene to tetrads took place under favourable temperature conditions. As a consequence of this the percentage of completely damaged buds was low. This was also the case for the pollen sterility.

Södra Viken

Diplotene was passed to a small extent during December 1967 at this locality (cf. Fig. 7 p. 27 in Eriksson, 1968 *b*). However, for the most part no pronounced passing of diplotene was observed until the second part of March. Clone W 2004 constitutes an exception to this as 3 per cent of the PMC had passed diplotene on 15 December.

Concerning the passing of diplotene three groups of clones might be distinguished. The first group consisting of one clone only (W 2004) in which diplotene was completely passed on 15 March. In clones

E 1005, W 2002, W 5001, W 5002 and W 5008 diplotene was passed to the greatest extent between 15 March and 22 March. These clones constitute the second group. Finally clones E 2011, U 1001, W 2001, W 2003 and Y 4006 were referred to a third group of clones. In these clones the passing of diplotene took place to the greatest extent between 22 March and 29 March. It might be mentioned that diplotene was not completely passed on 29 March in clone W 2003.

During the period 15—21 March, the minimum temperature was below 0° C every day except for 21 March (+ 1.9° C). Therefore, it is probable that the maximum temperature is of some importance for the initiation of further development from diplotene in the clones belonging to the second group. As the sensitive PMC of these clones were exposed to low temperatures on several occasions during the period 15—22 March (16 March −17° C, 19 March −10.2° C) it was expected that some frost damage had been induced in those clones. In all clones belonging to the second group except for clone W 5008 either the pollen sterility or the percentage of completely damaged buds was high. In clone W 5008 the sensitive PMC might not have appeared until 21—22 March when the minimum temperature was above 0° C.

During the period 22—29 March the minimum temperature was above 0° C all the time. Therefore, in these clones the development from the diplotene stage to the tetrad stage could take place during favourable temperature conditions. As a consequence of this both the pollen sterility and the percentage of completely damaged buds were low.

In spite of the exposure of sensitive PMC to low temperatures for a considerable time in clone W 2004 (cf. Fig. 56 and Fig. 28) the pollen sterility was low. The percentage of completely damaged buds was also mostly low except on 8 March when it amounted to 43 per cent. Therefore it might be suggested that the PMC in the stages diakinesis — telophase II are relatively insensitive to exposure to low temperatures.

Kratte Masugn

The clones growing at this locality have reacted in a quite heterogeneous way concerning the development from diplotene to tetrads. In three of the clones of Finnish provenance (SF 7011, SF 7014 and SF 7015) diplotene was passed to a small extent already during November—December 1967. However, a pronounced passing of diplotene was not observed until March 1968 or possibly during the end of

February in clone SF 7014. This clone constitutes the one of the extreme cases where diplotene was passed early and the tetrad stage was reached late.

The other extreme case was observed in clone W 2001 where the development from diplotene to tetrads to the greatest extent took place during the week starting on 22 March. The type of meiotic development revealed by clone W 2001 was favourable as the temperature during this period was close to 0° C or above.

The PMC in sensitive stages in the other clones did not escape the exposure to low temperature as might be observed if the data in Fig. 54—55 and 69—70 are compared with the temperature curves in Fig. 29. As a consequence of this the pollen sterility was relatively high in clones W 2002, W 2003, SF 7011, SF 7012, SF 7014 and SF 7015. A high percentage of completely damaged buds was noted for clone W 2003.

Domsjöänget

In similarity with the situation at many other localities diplotene was passed during November—December 1967 to a small extent in some of the clones at this locality (cf. Fig. 9 p. 28 in Eriksson, 1968 *b*). However, any pronounced development from diplotene was not observed until 2 March.

Concerning the passing of diplotene two groups of clones might be distinguished, the first consisting of clones Y 4006, AC 1002, AC 2003, AC 2006, AC 3003 and AC 3004 whereas clones AC 1001, AC 1003 and AC 1004 might be referred to another group. Finally clone Y 4002 was regarded as intermediate owing to the fluctuation in the percentage of PMC in the diplotene stage.

If the temperature curves in Fig. 30 are examined it will be seen that there was a period of mild weather at the very end of February. The clones belonging to the first group responded to the high temperatures of this mild weather by starting their development from diplotene.

In the clones belonging to the second group the PMC did not respond to the mild weather referred to above. Instead the development from diplotene to tetrads took place to the greatest extent during the second part of March.

Independent of the date for starting the development from diplotene the complete reaching of the tetrad stage did not take place until 29 March. This means that the sensitive cells in the two groups of clones were exposed to low temperatures for considerably different times.

However, there is no conspicuous difference between the two groups regarding the pollen sterility or the percentage of completely damaged buds both being relatively low in the two groups of clones. This is somewhat astonishing as low temperatures (down to –10° C) appeared frequently during the three first weeks of March. At that time the percentage of sensitive cells was relatively high in some clones (see for example Fig. 64, clone AC 1002). Therefore, it seems as if the PMC in the stages diakinesis — telophase II are relatively insensitive to low temperatures (down to –10° C) if the exposure is of short duration. This was the case at Kasa where the temperature during the three first weeks of March fluctuated from low during the night to 0° C or higher during the day.

Sundmo

Only a limited passing of the diplotene stage took place during the autumn (cf. Fig. 11 p. 29 in Eriksson, 1968 *b*). Regarding the passing of diplotene two groups might be distinguished. In the first group (clones Y 4005, Y 4006 and AC 2003) the development from diplotene started during, or subsequent to, the period of mild weather at the very end of February. As the tetrad stage was not reached until 1 April this means that the stages diakinesis — telophase II were exposed to low temperatures (cf. Fig. 62, 63, 66 and 31) during this phase of development. In spite of this the percentage of completely damaged buds was mostly low. The same was also true for the pollen sterility. In similarity with the situation at Domsjöänget, it must be suggested that the stages diakinesis — telophase II are relatively insensitive to short exposures to low temperature.

In the second group (clones IS 85 and IS 181) diplotene was passed during the last week of March. The completely damaged buds observed before any passing of the diplotene stage took place in clone IS 181 could partly be explained as originating from induction of irregularities during the pachytene stage. In similarity with the situation in the previous group of clones the pollen sterility was low, not exceeding 10 per cent.

Clones growing at more than one locality

Among the ten clones (E 1005, E 2011, U 1001, W 2001, W 2002, W 2003, W 5001, W 5002, Y 4006 and AC 2003) only one (W 2002) did not show any difference in pattern of the meiotic development at the two localities where it was studied. In this connection it is also

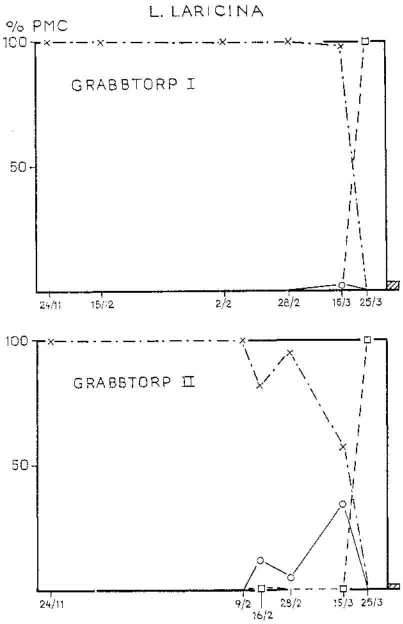


Fig. 71.
The meiotic development of the PMC from two grafts of *Larix laricina* growing at Grabbtorp.

× = % PMC in diplotene, ○ = % PMC in diakinesis — anaphase I, □ = % PMC which have reached the tetrad stage. The hatched columns refer to the pollen sterility.

worth mentioning that there was no difference in pattern of meiotic development in clone W 2001 between Kratte Masugn and Södra Viken. The temperature conditions at Arvika and Kratte Masugn are relatively similar (cf. Fig. 28—29) which explains the absence of a difference in meiotic development. On the other hand it should be noted that there was a difference in meiotic development in clone W 2003 which also was growing at Södra Viken and Kratte Masugn. This suggests that the temperature response of clones W 2001 and W 2002 on one hand and W 2003 on the other differ somewhat.

The difference in pattern of meiotic development was frequently conspicuous where Ekebo constituted one of the growth localities. (Clone W 2001, Fig. 53, is a good example of this.) This was also expected as there was a pronounced difference in temperature conditions at Ekebo on one hand and the rest of the localities on the other.

As a consequence of the difference in pattern of meiotic development from one locality to another there was frequently a difference regarding the percentage of completely damaged buds. The reason for the occurrence of completely damaged buds was discussed in connection with the discussion of the temperature response at the different localities.

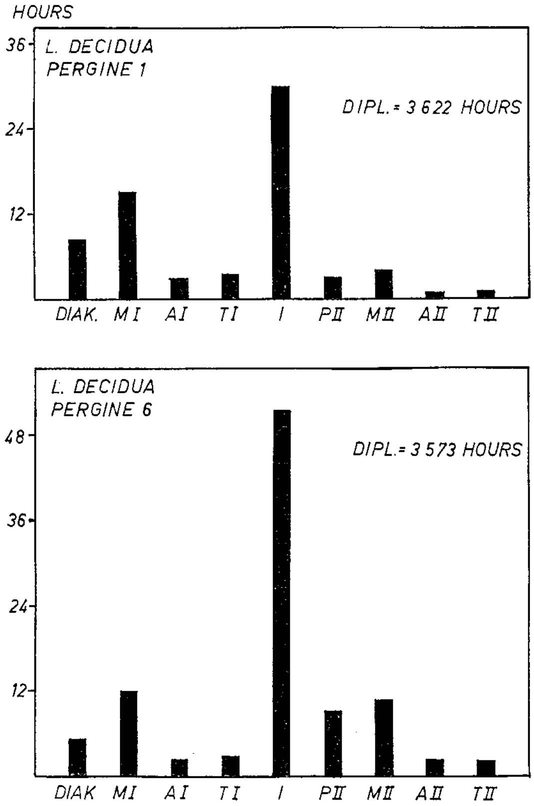


Fig. 72. The duration of the stages diakinesis — telophase II in two European larch clones studied 1967—1968 at Grabbtorp.

3.4. Larix laricina

Only two grafts growing at Grabbtorp were examined. As seen from Fig. 71 they behaved in different ways. In one of the grafts the development from diplotene to tetrads took place during the period 15 March—25 March whereas diplotene was passed to some extent already in middle of February in the other graft. In spite of the exposure of the sensitive PMC to low temperatures at several occasions during the period 9 February—25 March no completely damaged buds were observed. The pollen sterility was low. Therefore, it seems as if these *Larix laricina* grafts are highly resistant to exposure to low temperature.

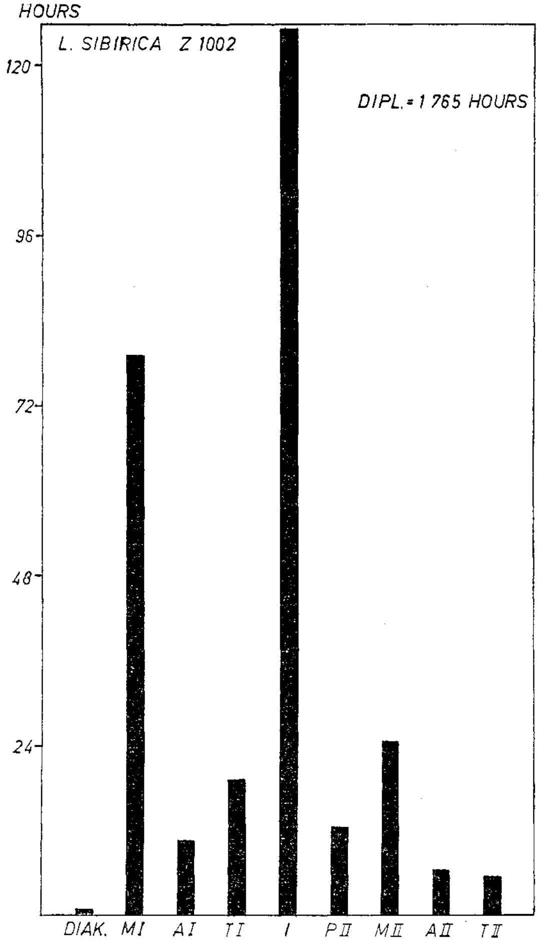


Fig. 73. The duration of the stages diakinesis — telophase II in clone Z 1002, *L. sibirica* studied 1966—1967 in Stockholm.

3.5. Duration of individual meiotic stages

The duration of individual meiotic stages is of importance for the probability of inducing irregularities. The longer the duration of a sensitive stage the higher is the probability that irregularities will be induced. However, it must be remembered that the duration of any stage is dependent on the temperature conditions during the appearance of the particular stage. Thus, the development could stop during a certain stage which means that the duration of that particular stage will be exaggerated. Therefore, we would only like to demonstrate extreme cases regarding the time lapse for the development from diplotene to tetrads. The calculation of the duration was made in the same way as suggested by Lindgren *et al.* (1969).

In the two European larch grafts illustrated in Fig. 72, the duration of diplotene amounted to around 150 days whereas this duration in the Siberian larch clone illustrated in Fig. 73 did not last for more than 75 days. In spite of this difference it is revealed in both Fig. 72 and Fig. 73 that among the other stages interphase is of longest duration followed by metaphase I. Anaphase II and telophase II are seen to be of shortest duration in the three clones investigated. This agreement from clone to clone regarding the relative duration of individual meiotic stages is worth pointing out, especially as the clones in Fig. 72 were investigated during 1967—1968 whereas clone Z 1002 (Fig. 73) was investigated 1966—1967. The relatively long duration of metaphase I is interesting to note as this stage was shown to be highly sensitive to exposure to low temperature (Eriksson, 1968 *b*).

Generally it could be stated that it is meaningless to study the duration of individual stages unless the temperature conditions are kept constant.

4. Species characteristics

In this chapter the differences in pattern of development between the species will be discussed. As we are interested in the probabilities for induction of frost damage it is of interest to construct parameters which are informative regarding these probabilities. According to Eriksson (1968 *b*) there are two phases of high sensitivity to low temperature, the first constituted by the development up to the insensitive diplotene stage, and the second constituted by the stages diakinesis — telophase II except for the interphase. This means that the reaching of the diplotene stage is of interest for predicting the probability of the occurrence of frost damage. Concerning the second phase of high sensitivity the development of 90 per cent of the PMC from diplotene to 90 per cent in the tetrad stage would be elucidating. However, the fixation intervals were too long to allow such a calculation at most of the localities. Only at Broknäs, Ernvik and Grabbtorp is this calculation justified. The extension in time for this development could mostly be read off in the diagrams without any difficulty. Another way of estimating the point of time for the presence of many frost sensitive PMC is to determine the date for passing of diplotene by 50 per cent of the PMC. This could also be read off in the diagrams. In case of fluctuations around 50 per cent of PMC in diplotene an average percentage was calculated for several fixation occasions and this average value was connected with a percentage from a later fixation occasion and the 50 per cent value was read off on this last line.

4.1. First phase of frost sensitivity

As stated above this phase ends by the reaching of the diplotene stage. Although the dates for the first fixation varied from locality to locality it might be of interest to determine the percentage of PMC in the diplotene stage during October. The data from this estimation are illustrated in Fig. 74. As seen from this figure there is a conspicuous difference between *L. sibirica* on one hand and *L. decidua* and *L. leptolepis* on the other hand. In only one of the Siberian larch clones diplotene was not reached to 100 per cent during October, viz.

clone IS 181 growing at Sundmo. The long fixation intervals during the autumn as well as the fact that the first fixation was not simultaneously performed at the different localities exclude the possibility for an evaluation of a possible difference between *L. decidua* and *L. leptolepis* regarding reaching of the diplotene stage.

It can be stated that the probability for inducing irregularities during the autumn will be higher in *L. decidua* and *L. leptolepis* than in *L. sibirica.*

4.2. Second phase of frost sensitivity

In Fig. 75 the average date for passing of diplotene by 50 per cent of the PMC for the species under investigation is demonstrated. From this diagram it is clearly seen that diplotene is passed earlier in *L. sibirica* than in *L. decidua.* This is true for all localities. The most pronounced difference was observed at Ekebo. At Kratte Masugn the difference was least conspicuous.

L. leptolepis was shown to be intermediate in the Stockholm region and Värmland, whereas it seemed to be the first species to pass diplotene at Ekebo. At Ekebo fixations of the Siberian larch were performed to some extent on 29 December and 5 January which was not the case for the Japanese larch. This means that the fixation interval at that time of the year was considerably longer in *L. leptolepis* than in *L. sibirica.* The pattern of development in the Japanese larch clones F 1001, L 1001, N 2005 and M 2002 should be compared with the Siberian larch clones E 2011 and W 2001. Although it might be assumed that the pattern of development is almost identical in these clones the dates for passing of diplotene by 50 per cent of the PMC differ owing to the difference in fixation intervals. In the Japanese larch clones listed above, 10 January was observed as the date for passing of diplotene by 50 per cent of the PMC, whereas 20 January was the corresponding date for the Siberian larch clones listed above. As a consequence of this we get the impression that the Japanese larch should be the first to pass diplotene at Ekebo. Rather it is probable that the dates for *L. leptolepis* and *L. sibirica* do not differ too much at Ekebo. This is supported by the fact that the average date for reaching of the tetrad stage by 50 per cent of the PMC was the same in both species (15 February).

A discussion of the local influence on the date for passing of diplotene will be omitted in this context as it was discussed in connection with the presentation of the meiotic pattern of development at individual localities. Furthermore, it might be stated in this connec-

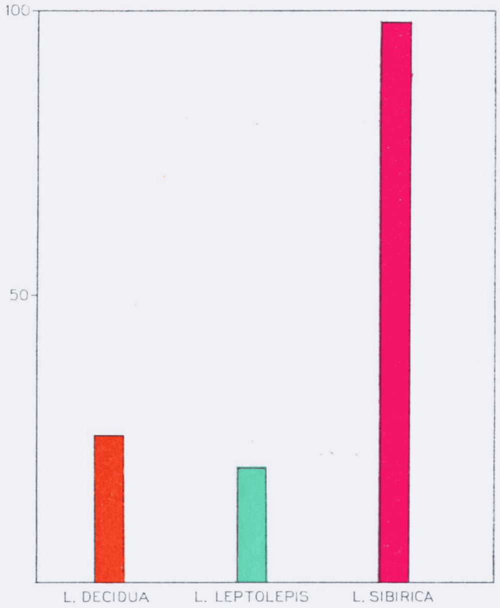


Fig. 74. The average percentage of PMC of *L. decidua*, *L. leptolepis* and *L. sibirica* which had reached the diplotene stage during October 1967.

Fig. 75. See p. 52.

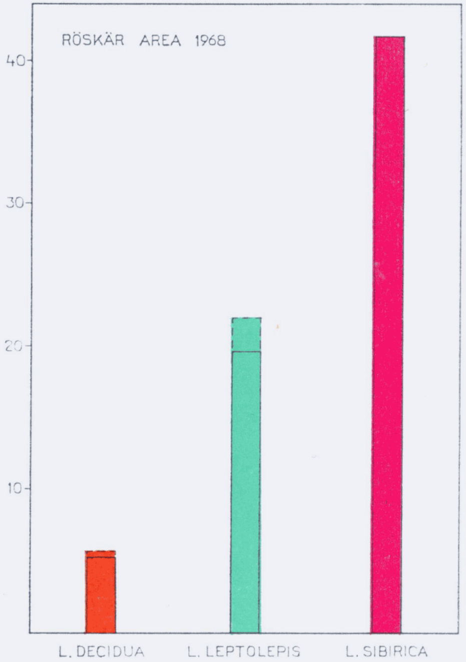


Fig. 76. The average number of days for the development of the PMC from 90 % in the diplotene stage to 90 % in the tetrad stage for the clones growing in Röskär area (Broknäs, Ernvik, Grabbtorp). The dashed parts of the columns refer to the dashed lines in Fig. 32.

tion that a scheme like the one in Fig. 75 ought to be constructed during a series of years before a general discussion of the influence of the climatic conditions upon the pollen formation at a particular locality could be carried out.

Based on the data presented in Fig. 75 it could be concluded that the probability for induction of frost damage vill increase in the sequence *L. decidua* — *L. leptolepis* — *L. sibirica* presuming that the frost sensitivity is the same in the PMC of all three species. This is probably not true as Eriksson (1968 *b*) showed that *L. sibirica* was much less sensitive for induction of frost damage than *L. decidua* when all types of irregularity besides the polyspory were considered. As polyspory hardly appeared in *L. decidua* and *L. leptolepis* a reverse relationship might exist for this particular irregularity.

For the clones growing at Broknäs, Ernvik and Grabbtorp the extension in time for the development of 90 per cent in the diplotene stage to 90 per cent in the tetrad stage was determined. A comparison of the data in Fig. 32 reveals that there is a pronounced difference between the two species *L. decidua* and *L. leptolepis*. The average duration of this development for the different species is demonstrated in Fig. 76. The data in this figure indicate that the species differ considerably concerning the duration of the second phase of high sensitivity. In contrast to the situation during 1968 this phase of development was shorter in *L. sibirica* than in *L. decidua* during 1966 (Ekberg & Eriksson, 1967). The variations from year to year suggest that the date for the initiation of further development from diplotene is of decisive importance for the duration of the second phase of high frost sensitivity in the PMC. During a year like 1968 the probability for occurrence of frost damage in the PMC will increase in the sequence *L. decidua* — *L. leptolepis* — *L. sibirica* under the assumption that they are of equal frost sensitivity. Another year a reverse situation might exist. Therefore, it must once more be stressed that the meiotic pattern of development ought to be tested during a sequence of years to allow general statements.

5. The fitness of a locality regarding pollen production

The pollen sterility was frequently low in *L. decidua* and *L. leptolepis* which might suggest good possibilities for a satisfactory seed setting. However, it must be remembered that not only the pollen quality but also the pollen quantity are of importance for a proper seed setting (cf. p. 5—6). That the pollen quantity is not satisfactory for many of the European larch clones growing at Deje is evident from Fig. 2—3, and 12—14. As an example it might be mentioned that no less than 97.5 per cent of the buds from the four last fixation occasions were completely damaged in clone R 1003 growing at Deje.

To obtain general information about the importance of completely damaged buds for the pollen quantity an average percentage was calculated from the four next to last fixation occasions. For the clones growing at Broknäs, Ernvik and Grabbtorp the average percentage was based on all fixation occasions during the same period of time. Also in this case the last fixation occasion was excluded from the calculation. The reason for this was that it was observed that the percentage of completely damaged buds was low at the last fixation occasion owing to the fact that the completely damaged buds at that time of the year were of such an appearance that they resembled one year old buds and therefore they were not fixed (cf. Eriksson, 1968 *b*). If the last fixation occasion was not excluded from the calculation it would have caused an underestimation of the percentage of completely damaged buds.

In Fig. 77 the average percentage of completely damaged buds and the pollen sterility observed during 1968 is demonstrated. Regarding the pollen production this diagram should be used as a starting point for a selection of localities. To allow a recommendation of a certain locality both columns in the diagram should be low. Especially important is of course the column showing the pollen sterility but the column showing the percentage of completely damaged buds must not be neglected. For the year 1968 the following localities could be regarded as satisfactory concerning the pollen production:

Stockholm region	*L. decidua, L. leptolepis, L. sibirica*
Värmland	*L. sibirica*
Domsjöänget	*L. sibirica*
Sundmo	*L. sibirica*

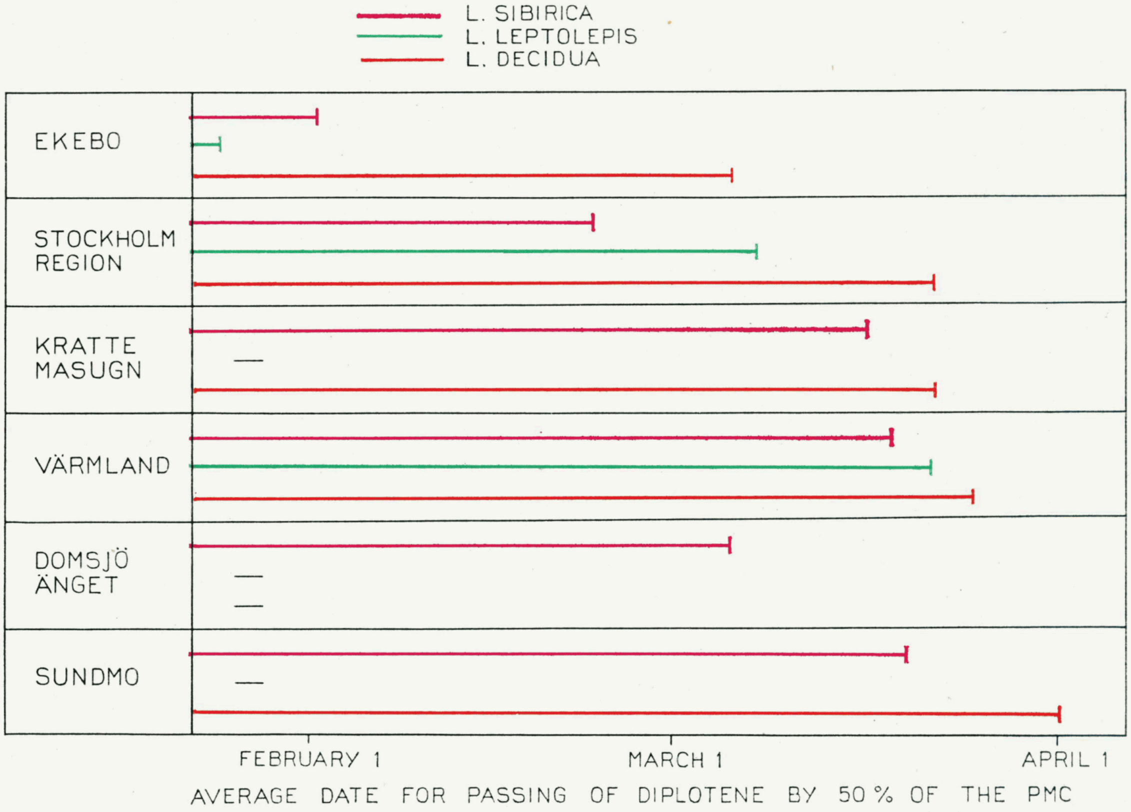


Fig. 75. The average date for passing of the diplotene stage by 50 % of the PMC of *L. decidua*, *L. leptolepis* and *L. sibirica* growing at different localities.

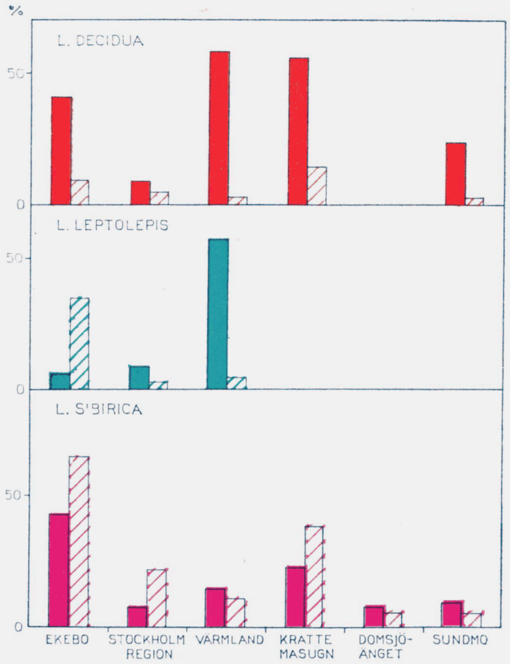


Fig. 77. The average percentage of completely damaged buds (stained columns) and the pollen sterility (hatched columns) 1968 in *L. decidua*, *L. leptolepis* and *L. sibirica* growing at different localities. Concerning the calculation of the percentage of completely damaged buds compare for text.

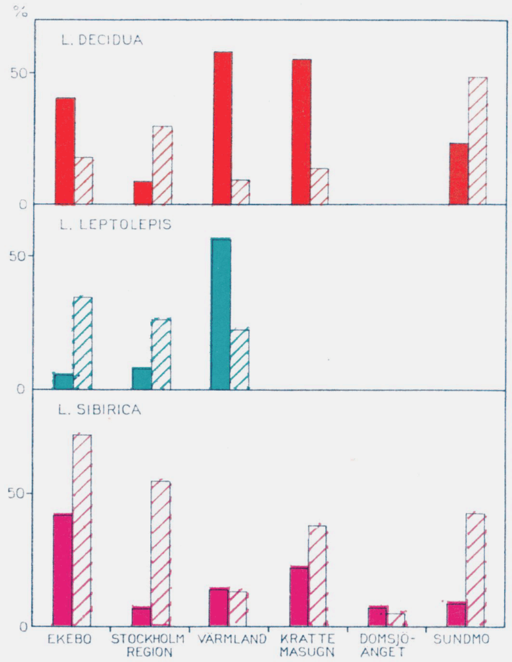


Fig. 78. The average percentage of completely damaged buds (stained columns) and the pollen sterility (hatched columns) 1966—1968 in *L. decidua*, *L. leptolepis* and *L. sibirica* growing at different localities. Concerning the calculation of the percentages compare for text.

It must be stressed that this holds for 1968 and the recommendation must not be overestimated. Another year, with another temperature climate, the situation might be drastically changed. As an example it might be mentioned that the pollen sterility in *L. decidua* and *L. sibirica* growing at Röskär 1966 amounted to around 90 per cent. Simultaneously the meiosis in the PMC of *L. leptolepis* was completely collapsed (Ekberg & Eriksson, 1967). That year it is quite clear that the Stockholm region could not be recommended concerning pollen production in any of the larch species.

Any determination of the perçentage of completely damaged buds in the same way as made for 1968 has not been performed earlier. The pollen sterility on the other hand was determined for most localities during 1967. In Fig. 78 the average percentage for the pollen sterility of two or three years is demonstrated. The percentages of completely damaged buds are the same as in Fig. 77. A comparison of the data in Fig. 77 and 78 reveals that a selection of localities for a good pollen production based on the data in Fig. 78 is different from the suggestions based on Fig. 77 only. From Fig. 78 it is seen that only the Siberian larch could be expected to have a satisfactory pollen production, viz. at Domsjöänget and in Värmland. The low percentages at Domsjöänget could be due to the fact that observations from one year only (1968) were made at this locality. For *L. decidua* and *L. leptolepis* hardly any of the localities could be recommended. However, the extremely high pollen sterility during 1966 in *L. decidua* and *L. leptolepis* in the Stockholm region contributes considerably to the moderate pollen sterility seen for these two species in Fig. 78.

Based on all data so far obtained it could be stated that an optimistic view of the possibilities for a pollen production in *Larix* is not justified. Rather it is necessary to select certain localities for certain species. Furthermore, it will be necessary to select clones with a favourable meiotic pattern of development regarding the pollen formation.

Owing to the climatic conditions at Ekebo during the winter with fluctuations around 0° C on several occasions it might be suggested that a selection of generatively well adapted larch clones should preferably be carried out at this locality. The clones which do not pass diplotene until the winter is passed in spite of the fluctuations at this locality will have good opportunities for a proper pollen formation. Such clones will probably react in a similar way at other localities as well. Conversely poorly adapted clones at Ekebo might react in an unfavourable way at other localities too. As examples it might be mentioned that the initiation of the further development from diplotene partly took place before 3 February at Ekebo in the European larch clones L 2001, N 2001 and R 1003. Except for clone L 2001 the percentage of completely damaged buds in these clones was extremely high at Deje too (Fig. 10—11 and 14).

The discussion carried out above does not hold if the temperature is not the determining factor for the initiation of the further development from diplotene. Eriksson (1968 *b*) pointed out that the influence of the day length on the initiation should not be neglected. At Ekebo where diplotene was passed to some extent before 3 February the day length amounts to less than ten hours at that time of the year. In the native regions for *L. decidua* the day length is somewhat longer when the temperatures (+3° — +5° C) responsible for the initiation of the further development from diplotene appear. Therefore, the day length can hardly have any influence on the initiation. A final evaluation of this question has to be carried out following experiments under controlled photoperiodic and thermoperiodic conditions.

The last question to be discussed concerns the existence of clones showing a favourable pattern of development at Ekebo. Among the European larch clones E 2002 showed such a meiotic pattern. As a consequence of this the percentage of completely damaged buds and the percentage of sterile pollen grains were low. The same situation was observed at Deje and Broknäs which confirms the statement that Ekebo should be used as a test locality in order to obtain a satisfactory pollen production. Unfortunately, clone E 2002 was the only European larch clone showing this favourable pattern of meiotic development.

Among the Japanese and Siberian larch clones hardly any clone could be regarded as completely satisfactory. The Japanese larch clones L 2005 and L 2006 (Fig. 38) could possibly be accepted. It is possible that the frequent temperature fluctuations around 0° C at Ekebo during January are too extreme to allow any of the Siberian larch clones to react in a favourable way.

6. Summary

In the present paper the meiotic development in the pollen mother cells (PMC) of the three larch species *Larix decidua, L. leptolepis* and *L. sibirica* was studied. The grafts included in the investigation were growing at different localities in Sweden (Fig. 1). Emphasis was paid to the analysis of the influence on the temperature upon the meiotic development and induction of completely damaged buds.

The diplotene stage was completely reached in most of the Siberian larch grafts at the start of the investigation during October 1967 whereas the percentage of PMC in diplotene in *L. decidua* and *L. leptolepis* amounted to 25 and 20 per cent respectively at that time. Based on this observation it could be stated that the probability for inducing irregularities during the autumn will be higher in *L. decidua* and *L. leptolepis* than in *L. sibirica.*

Concerning the second phase of high temperature sensitivity (i.e. the stages diakinesis—telophase II except for the interphase) the data for all species and localities have been summarized in Fig. 75 in which the average date for passing of the diplotene stage by 50 per cent of the PMC is demonstrated. From this diagram it is clearly seen that diplotene is passed earlier in *L. sibirica* than in *L. decidua* at all localities. The most conspicuous difference between the two species in this respect was observed at Ekebo. The Japanese larch was intermediate to *L. decidua* and *L. sibirica* in Värmland and in the Stockholm region whereas there was no difference between *L. leptolepis* and *L. sibirica* at Ekebo.

The average date for passing of diplotene by 50 per cent of the PMC differed considerably within the species from locality to locality. This must be attributed to differences in temperature conditions at the different localities.

Based on the data presented in Fig. 75 it could be concluded that the probability for induction of frost damage will increase in the sequence *L. decidua—L. leptolepis—L. sibirica* assuming the frost sensitivity to be the same in the diakinesis—telophase II PMC of all three species.

Based on the percentage of completely damaged buds and the pollen sterility during 1968 the following localities could be regarded as satisfactory concerning the pollen production:

Stockholm region	*L. decidua, L. leptolepis, L. sibirica*
Värmland	*L. sibirica*
Domsjöänget	*L. sibirica*
Sundmo	*L. sibirica*

It was stressed that this situation might be drastically changed another year.

The advantage of using Ekebo as a test locality concerning a satisfactory pollen production in larch species was pointed out.

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Sammanfattning

Fortsatta studier av meiosen och pollenbildningen hos lärk

I det föreliggande arbetet har utvecklingsförloppet hos pollenmodercellerna (PMC) i de tre lärkarterna *Larix decidua, L. leptolepis* samt *L. sibirica* studerats. Vilka kloner som studerades på olika lokaler i Sverige (se Fig. 1) framgår av tabellerna i appendix. Speciell vikt lades på analysen av temperaturinflytandet på utvecklingsförloppet samt induktionen av fullständigt skadade knoppar. Dylika knoppar innehåller uteslutande skadade PMC.

Artskillnader beträffande meiosförloppet

Eftersom vi i våra undersökningar är intresserade av sannolikheten för uppkomst av skador är det av intresse att konstruera parametrar som ger värdefulla upplysningar rörande sannolikheten för induktion av skador. Enligt Eriksson (1968 *b*) finns det två faser av stor temperaturkänslighet hos PMC av lärk. Den första utgörs av utvecklingen fram till det känsliga diplotenstadiet medan den andra fasen utgörs av stadierna diakines — telofas II om man undantar interfasen. Detta innebär att uppnåendet av diplotenstadiet är av intresse för förutsägelser angående uppkomst av frostskador. Beträffande den andra fasen av hög känslighet skulle utvecklingen från 90 % av PMC i diploten till 90 % av PMC i tetradstadiet vara upplysande.

Första frostkänsliga fasen. Även om tidpunkten för den första fixeringen varierade från lokal till lokal var det av intresse att bestämma procenttalet PMC i diploten under oktober månad 1967. Resultaten från denna bestämning har sammanfattats i Fig. 74. Såsom framgår av denna figur är det en markant skillnad mellan den sibiriska lärken å den ena sidan samt den europeiska och japanska lärken å den andra sidan. Endast hos en sibirisk lärkklon var diplotenstadiet inte fullständigt uppnått under oktober 1967, nämligen hos klon IS 181 från Sundmo.

Det kan konstateras att sannolikheten för induktion av höstskador är större hos europeisk och japansk lärk än hos sibirisk lärk.

Andra frostkänsliga fasen. I Fig. 75 har genomsnittsdatum för femtioprocentig passering av diplotenstadiet hos de olika arterna angivits separat för de olika lokalerna. Av Fig. 75 framgår det tydligt att diplotenstadiet passeras tidigare hos *L. sibirica* än hos *L. decidua.*

Detta gäller för samtliga lokaler. Den mest markanta skillnaden observerades vid Ekebo, medan skillnaden var minst vid Kratte Masugn. Den japanska lärken visade sig vara intermediär i stockholmsregionen och i Värmland. Däremot var det troligen ingen skillnad mellan japansk och sibirisk lärk vid Ekebo beträffande femtioprocentig passering av diploten.

Med ledning av de data som presenterats i Fig. 75 kan det fastslås att sannolikheten för induktion av frostskador ökar i följande ordning: *L. decidua* — *L. leptolepis* — *L. sibirica*. Detta gäller under den förutsättningen att frostkänsligheten är densamma hos PMC av alla tre arterna.

Eftersom fixeringar togs nästan dagligen under slutskedet av meiosförloppet hos de kloner som växte vid Broknäs, Ernvik och Grabbtorp kunde utvecklingsförloppet bäst följas hos dessa kloner. För de europeiska och japanska lärkkloner som växte på dessa lokaler har utsträckningen i tiden för utvecklingen från 90 % av PMC i diploten till 90 % av PMC i tetradstadiet återgivits i Fig. 32. Denna figur avslöjar att det är en markant skillnad mellan *L. decidua* och *L. leptolepis*. Den genomsnittliga tiden för denna utveckling har åskådliggjorts i Fig. 76. Resultaten i denna figur bekräftar den tidigare rangordningen beträffande sannolikheten för uppkomst av frostskador hos de undersökta lärkarterna. Det betonades dock att situationen kunde vara helt omkastad ett annat år. Initieringsdatum för den fortsatta utvecklingen från diploten är av stor betydelse för utsträckningen i tiden av den andra fasen av hög frostkänslighet.

En lokals lämplighet beträffande pollenproduktionen

Pollensteriliteten var ofta låg hos *L. decidua* och *L. leptolepis* vilket kunde antyda att det fanns goda möjligheter för en tillfredsställande frösättning. Man måste emellertid komma ihåg att inte bara pollenkvaliteten är av betydelse för frösättningen. Pollenkvantiteten var ofta otillfredsställande hos den europeiska lärken vid Deje, vilket framgår av Fig. 2—3 och 12—14.

I Fig. 77 har det genomsnittliga procenttalet av fullständigt skadade knoppar (beträffande beräkningen se sid. 51) och den genomsnittliga pollensteriliteten under 1968 åskådliggjorts för de olika arterna och lokalerna. Båda kolumnerna i Fig. 77 skall vara låga för att man skall kunna rekommendera en lokal beträffande pollenproduktionen. På basis av resultaten från 1968 skulle man kunna komma fram till följande rekommendation:

Lokal	Art
Stockholmsregionen	*L. decidua, L. leptolepis, L. sibirica*
Värmland	*L. sibirica*
Domsjöänget	*L. sibirica*
Sundmo	*L. sibirica*

Det poängterades att förhållandena kan vara helt annorlunda ett annat år varför denna rekommendation inte får överskattas. Detta framgår av Fig. 78 där den genomsnittliga pollensteriliteten för 1—3 år har beräknats. Med ledning av de data som presenterats i Fig. 78 kan man endast rekommendera Värmland och Domsjöänget beträffande den sibiriska lärken. Däremot har inte någon av lokalerna varit helt tillfredsställande då det gäller pollenproduktionen hos den europeiska och japanska lärken. Det bör i detta sammanhang betonas att utvecklingsförloppet bör studeras under en följd av år för att man skall kunna komma fram till allmänna rekommendationer.

På grund av att temperaturväxlingar omkring 0° C förekommer ofta under vintern vid Ekebo skulle denna lokal vara lämplig som testlokal beträffande den generativa anpassningen på hansidan. Kloner som inte passerar diploten förrän vintern är förbi trots temperaturväxlingarna kommer att ha goda förutsättningar för en god pollenproduktion inte bara vid Ekebo utan även vid andra lokaler.

Meiosstadiernas varaktighet

Endast ett par exempel på enskilda meiosstadiers varaktighet presenterades i Fig. 72—73. Trots att den totala varaktigheten av utvecklingen diakines — telofas II skilde sig väsentligt hos de undersökta klonerna visade sig interfasen vara den längsta av dessa stadier följd av metafas I. Anafas II och telofas II visade sig vara de mest kortvariga stadierna. Det betonades att det är meningslöst att studera varaktigheten av enskilda stadier såvida detta inte sker vid en bestämd temperatur.

Appendix

Table 1. Compilation of the clones of *L. decidua* investigated at different localities 1967—68.

L. decidua	Figure	Broknäs	Deje	Ekebo	Grabbtorp	Kratte Masugn	Sundmo
E 1001	2		×				×
E 1009	3		×	×			
E 2002	4—5	×	×	×			
E 2004	6	×					
E 2005	6	×					
E 2006	7	×					
E 2012	8		×	×			
E 2013	9		×	×			
L 2001	10		×	×			
N 2001	11		×	×			
R 1001	12		×	×			
R 1002	13		×	×			
R 1003	14		×	×			
S 2002	15	×					
S 6204	15	×					
X 1002	16					×	
X 1003	16					×	
X 2001	17					×	
X 2002	17					×	
IS 6	18						×
IS 272	18						×
IS 520	19						×
IS 521	19						×
Bělidlo 3 I 11	23				×		
Ormea 8	20				×		
Ormea 10	20				×		
Pergine 1	22				×		
Pergine 4	22				×		
Pergine 6	21				×		
Pergine 10	21				×		
Pragelato 14	24				×		
Staré Hory 114	23				×		

Table 2. Compilation of the clones of *L. leptolepis* investigated at different localities 1967—68.

L. leptolepis	Figure	Broknäs	Brunsberg	Ekebo	Ernvik	Grabbtorp
F 1001	34			×		
L 1001	34			×		
L 8	35		×			
L 1002	36	×				
L 1004	36	×				
L 1006	37	×				
L 1007	37	×				
L 2005	38			×		
L 2006	38			×		
M 2001	39			×		
M 2002	40		× *a*	×		
M 2003	41		× *b*	×		
M 3018	35		×			

Table 2. (continued)

L. leptolepis	Figure	Broknäs	Brunsberg	Ekebo	Ernvik	Grabbtorp
N 2005	39			×		
X 4600	42	×			×	
Azu R 7	45					×
Azu R 8	45					×
Nar I 8	43					×
Nar I 9	43					×
Nar J 16	44					×
Nar J 20	44					×
Ren L 7	46					×
Tak P 4	47					×
Tak P 7	47					×
Tak Q 19	48					×
Yatsu S 4	46					×

a Södra Viken *b* Deje

Table 3. Compilation of the clones of *L. sibirica* investigated at different localities 1967—68.

L. sibirica	Figure	Domsjö-änget	Ekebo	Ernvik	Kratte Masugn	Södra Viken	Sundmo
E 1002	49			×			
E 1004	49			×			
E 1005	50		×	×		×	
E 2011	51		×			×	
U 1001	52		×			×	
W 2001	53		×		×	×	
W 2002	54				×	×	
W 2003	55				×	×	
W 2004	56					×	
W 5001	57		×			×	
W 5002	58—59		×	×		×	
W 5006	60			×			
W 5007	60			×			
W 5008	56					×	
Y 4002	61	×					
Y 4005	62						×
Y 4006	63	×				×	×
AC 1001	61	×					
AC 1002	64	×					
AC 1003	64	×					
AC 1004	65	×					
AC 2003	66	×					×
AC 2006	65	×					
AC 3003	67	×					
AC 3004	67	×					
IS 85	68						×
IS 181	68						×
SF 7011	69				×		
SF 7012	69				×		
SF 7014	70				×		
SF 7015	70				×		

Electronic version

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