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A summary of meiotic investigations in conifers

Meiosstudier hos barrträd

by

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Introduction

The studies of meiosis in conifers have varied considerably concerning purpose and design of investigation. To facilitate a survey of these investigations we found it worthwhile to classify them regarding the general outline of study according to the following:

1. Microsporogenesis
2. Megasporogenesis
3. Chromosome number
4. Irregularities
   A. Inherited
   B. Environmentally conditioned
   C. Artificially induced
5. Meiosis in hybrids
6. Meiosis in polyploids

Most of the references treating the entire meiosis or only part of it have been listed in Tables 1—6 according to the scheme presented above. Several of the reports could be included in more than one of the tables, however, for simplicity they are mostly included only once. The purpose of the present communication is to give a brief review of the recent meiotic investigations in conifers.

Pollen mother cell(s) will be abbreviated by PMC and megaspore mother cell(s) by MMC. The names of the species used in the references will be used in this communication.

Microsporogenesis

Mostly the appearance of the meiotic stages in conifers (MERGEN and LESTER 1961, MERGEN *et al.* 1963, KANTOR and CHIRA 1965, EKBERG *et al.* 1968) agrees with that of other higher plants. However, one important difference exists, namely the long duration and the diffuse appearance of diplotene which is typical for PMC of *Larix* (EKBERG *et al.* 1968). This is connected with the dormancy during this stage.

A classification of the pattern of meiotic development in PMC based on literature data was carried out by ERIKSSON (1968 B) who distinguished the following three types:

1. Meiosis is started and completed during autumn. Genera or species belonging to this group are *Cedrus*, *Cryptomeria*, *Juniperus chinensis*, *J. horizontalis*, *J. virginiana*, and *Taxus*.
2. Meiosis is started during autumn and completed during spring. Microsporogenesis in *Larix* mostly follows this pattern.
3. Meiosis is started and completed during spring. This pattern is followed by *Abies*, *Athrotaxis*, *Cunninghamia*, *Juniperus communis*, *J. rigida*, *Keteleeria*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga*, *Thuja* and *Tsuga*. Megasporogenesis in *Larix* and *Taxus* also follows this pattern of development.

It is interesting to note that different pattern of development exists within a genus as is the case in *Juniperus*. Furthermore differences between microsporogenesis and megasporogenesis within a genus have been observed in *Larix* and *Taxus*.

The total duration of meiosis has only been reported in some cases. It varies from a few days in *Picea abies* (ANDERSSON 1969) and *Pinus* (SAYLOR 1962) to around half a year as reported for PMC of *Larix decidua* and *L. leptolepis* by ERIKSSON (1968 B). In contrast to this the entire meiosis in the MMC in *Larix* is completed within one or two weeks (ERIKSSON 1968 B and unpublished).

A presentation of the extension in time of different phases of meiosis in PMC of different species belonging to the genera *Abies* and *Pinus* was published by CHIRA (1965 B) and KANTOR and CHIRA (1965). From the diagrams presented by the authors it is evident that meiosis in different species starts and ends at quite different occasions. All trees studied by CHIRA were growing in the Arboretum at Mlynany, Slovakia. Thus many species were cultivated

Table 1. Investigations of the entire or part of the microsporogenesis in conifers.

Species	Special type of study	Reference
Abies balsamea, Juniperus, Pinus maritima, P. silvestris, Thuja occidentalis		Hofmeister 1848
Abies nobilis glauca, A. sachalinensis		Mergen and Lester 1961
Araucaria Bidwillii		Lopriore 1905
Araucaria brasiliensis		Burlingame 1913
Araucaria columnaris		Hodcent 1963
Cryptomeria japonica		Singh and Chatterjee 1963
Cunninghamia sinensis		Miyake 1911
Juniperus communis		Norén 1907
Juniperus communis		Nichols 1910
Juniperus communis, J. virginiana		Ottley 1909
Keteleeria evelyniana		Wang 1948
Larix Americana, L. europaea	spindle formation	Timberlake 1900
Larix dahurica		Prosina 1928
Larix decidua	spindle formation	Allen 1903
Larix decidua		Barner and Christiansen 1960
Larix decidua, L. Kaempferi, L. eurolepis, Tsuga canadensis	chiasma formation	Sax, H. J. 1933
Larix decidua, L. leptolepis, L. sibirica	irregularities (polyspory)	Ekberg *et al.* 1968
Larix europaea		Strasburger 1895
Larix europaea	spindle formation	Devisé 1922
Larix europaea		Saxton 1929
Larix leptolepis		Ishikawa 1902
Larix		Belajeff 1894
Pinus austriaca, P. Laricio, P. strobus, Thuja occidentalis		Lewis 1908
Pinus austriaca, P. montana, P. recinosa, P. rigida, P. strobus		Ferguson 1904
Pinus echinata, P. taeda		Mergen *et al.* 1963
Pinus elliottii, P. roxburghii	chiasma frequency	Kedharnath and Upadhaya 1967
Pinus laricio, P. silvestris		Coulter and Chamberlain 1901
Pinus pinceana		Diaz Luna 1962
Pinus silvestris		Vogel 1936
Pinus (18 different species)	extension in time of meiosis	Chira 1963
Pinus (25 different species)	extension in time of meiosis	Chira 1965 B
Pseudotsuga Menziesii		Barner and Christiansen 1962
Pseudotsuga taxifolia	bivalent identification	Zenke 1953
Taxus baccata, T. canadensis		Dark 1932
Taxus canadensis		Dupler 1917
Taxus		Hawker 1930
Taxus		Keen 1958
Tetraclinis articulata		Saxton 1913
Torreya californica		Robertson 1904

outside their native range of distribution which might influence their pattern of meiotic development.

The maximum extension in time of pachytene, diplotene, diakinesis—telophase II for meiosis in PMC of *Larix decidua*, *L. leptolepis*, and *L. sibirica* growing in the Stockholm region was presented by Eriksson (1968 A). The following characteristics for the three species were given by Eriksson (1968 B):

"1. Diplotene is reached early in *L. sibirica*. The initiation of further development from diplotene takes place early, even during autumn in *L. sibirica*.
2. Diplotene is reached relatively early in *L. decidua*. The initiation of further development from diplotene takes place late in *L. decidua*.
3. Diplotene is reached relatively late in *L. leptolepis*. The initiation of further development from diplotene takes place somewhat earlier in *L. leptolepis* than in *L. decidua*."

Megasporogenesis

Throughout the years megasporogenesis has been studied to a small extent. During the sixties only a few hints about this phase of development have been published. Singh and Chatterjee (1963) who studied *Cryptomeria japonica* reported that only one of the dyad cells underwent the second meiotic division. Eriksson (1968 B) claimed that there was a great variation in stage of development within a female strobilus of *Larix decidua*.

Table 2. Investigations of the entire or part of the megasporogenesis in conifers

Species	Reference
Cryptomeria japonica	Singh and Chatterjee 1963
Cunninghamia sinensis	Miyake 1911
Juniperus communis	Norén 1907
Juniperus communis, J. virginiana	Ottley 1909
Juniperus communis	Nichols 1910
Keteleeria evelyniana	Wang 1948
Larix europaea	Saxton 1930
Larix sibirica	Juel 1900
Pinus austriaca, P. montana, P. resinosa, P. rigida, P. strobus	Ferguson 1904
Pinus Laricio	Coulter and Chamberlain 1901
Taxus canadensis	Dupler 1917
Torreya californica	Robertson 1904

Table 3. Meiotic investigations concerning chromosome number or chromosome morphology

Species	Type of study	Reference
Abies cephalonica, A. Nordmanniana, Cedrus libanotica, Juniperus chinensis, J. communis, J. rigida, J. virginiana, Larix decidua, L. eurolepis, L. Kaempferi, Picea Abies, P. mariana, Pinus Banksiana, P. Jeffreyi, P. nigra, P. Strobus, P. Thunbergiana, Pseudolarix amabilis, Taxus cuspidata, T. Hunnewelliana, T. media, Thuja Standishii, Tsuga canadense, T. caroliniana, T. diversifolia	chromosome number	Sax and Sax 1933
Agathis australis, Dacrydium biforme, D. bidwillii. D. colensoi, D. cupressinum, D. intermedium, D. kirkii, D. laxifolium, Libocedrus bidwillii, L. plumosa, Phyllocladus alpinus, Ph. glaucus, Ph. trichomanoides, Podocarpus acutifolius, P. dacrydioides, P. ferrugineus, P. hallii, P. nivalis, P. spicatus, P. totara	chromosome number	Hair and Beuzenberg 1958 B
Cephalotaxus drupacea, Podocarpus gracilior, P. latifolius, P. macrophyllus	chromosome number	Mehra and Khoshoo 1956 B
Juniperus bermudeana, J. phoenicea, J. virginiana, Pinus merkusii	chromosome number	Mehra and Khoshoo 1956 A
Pinus radiata	karyotype	Pederick 1967
Pinus silvestris	chromosome number	Blackman 1898
Podocarpus macrophyllus	chromosome number	Tahara 1941
Pseudotsuga menziesii	chromosome number	Christiansen 1963

Inherited irregularities

CHANDLER and MAVRODINEAU (1965) studied the meiosis in PMC of *Larix laricina* trees which had produced only poor seeds. The meiotic division was irregular showing high numbers of univalents which caused an irregular distribution of chromosomes to the poles during anaphase I. This caused the formation of nuclei and microspores of varying size. The number of pollen formed from each PMC ranged between one and ten. A final decision whether environmental or inherited factors were responsible for the irregularities was not given.

A detailed description of meiosis in three asyndetic pines (*Pinus silvestris*) was published by RUNQUIST (1968). The asyndesis in these pines might be regarded as weak since the average number of bivalents per PMC varied between 7.68 and 9.60. According to RUNQUIST the pairing of the chromosomes was originally normal. During pachytene it became weaker in some cases. Besides the formation of univalents other types of irregularity were reported. Those consisted of stickiness, ring chromosomes, precocious and delayed centromere division, micronuclei, fragmentation and bridge formation as well as polyspory. The average number of micronuclei per tetrad varied between 0.18 and 0.49 whereas the corresponding range for micronuclei per dyad was 0.16—0.86. For a prediction of the pollen sterility the percentage of affected cells would be more informative than the average number of micronuclei per dyad or tetrad. Those percentages varied between 13 and 54.

The irregularities observed by SAYLOR (1962), SAYLOR and SMITH (1966) and PEDERICK (1968) will be presented in connection with a discussion of their meiotic investigations in interspecific hybrids.

Table 4 A. Reports concerning inherited meiotic irregularities in conifers

Species	Study of	Reference
Cephalotaxus drupacea	translocation	Sugihara 1940
Cephalotaxus drupacea	inherited irregularity	Khoshoo 1957 A
Cephalotaxus drupacea	inherited irregularity	Khoshoo 1957 B
Larix decidua, L. laricina, L. leptolepis	inherited or environmentally conditioned irregularity	Chandler and Mavrodineau 1965
Picea abies	asyndesis and stickiness	Andersson 1947 A
Picea abies	asyndesis	Andersson 1947 B
Pinus radiata	inversions	Pederick 1968
Pinus silvestris	inherited irregularity	Aass 1957
Pinus silvestris	asyndesis	Runquist 1968
Taxus cuspidata	translocation	Matsuura and Suto 1935

Climatically conditioned irregularities

During the recent decade a great interest has been focused on the climatically conditioned—especially low temperature induced—meiotic irregularities as is revealed in Tab. 1. This is mainly due to the fact that meiotic irregularities might lead to gamete lethality which in turn might reduce the seed-setting. Already during the thirties VOGEL (1936) carried out the first investigation to evaluate whether or not meiotic irregularities were responsible for the poor seed-setting in some French provenances of *Pinus silvestris* growing at Chorin, Germany. This was followed by the investigations on *Picea abies* of ANDERSSON (1954, 1965, 1969), which were started during the forties.

ANDERSSON (1969) studied the amount of damage in PMC of various meiotic stages from different trial plots in Sweden and Austria. Furthermore, he transported twigs from one level to another within a locality in order to get information about the temperature influence on the amount of irregularity. The most elucidating information was obtained from the material at Sälen

Table 4 B. Reports o f environmentally conditioned irregularities in conifers

Species	Type of study	Reference
Abies alba, A. concolor, A. grandis, A. koreana, A. nordmanniana, A. pinsapo	low temperature induced irregularity	Kantor and Chira 1965
Cryptomeria japonica	high ,, ,, ,,	Iwakawa and Chiba 1952
Larix decidua	low ,, ,, ,,	Christiansen 1960
Larix decidua, L. leptolepis, L. sibirica	,, ,, ,, ,,	Ekberg and Eriksson 1967
,,	,, ,, ,, ,,	Eriksson *et al.* 1967
,,	,, ,, ,, ,,	Eriksson 1968 A
,,	,, ,, ,, ,,	Eriksson 1968 B
Picea abies	,, ,, ,, ,,	Andersson 1954
,,	,, ,, ,, ,,	Andersson 1965
,,	,, ,, ,, ,,	Andersson 1969
Picea excelsa	high ,, ,, ,,	Chira 1965 A
Pinus edulis	low ,, ,, ,,	Chira 1967
Taxus baccata	low and high temperature induced irregularity	Chira 1964

(N W Dalecarlia, Sweden) where observations were made at 350, 590, and 775 metres above sea level. Following transfer from the 350 metre level to the 590 or 775 metre level the percentage of irregularity was in most cases decreased compared to that obtained at the 350 metre level. Conversely the amount of irregularity increased following transfer to the 350 metre level. This increase could be attributed to the fact that the lowest temperatures were observed at the 350 metre level. Based on these data ANDERSSON concluded that there is a positive relation between sub-zero temperatures and the percentage of irregular PMC. It was clearly shown that most of the irregularities were induced during the stages diakinesis—A I and M II—A II. In some cases more than 50 per cent of the PMC of the stages M I—A I carried irregularities. Aberrations were also observed during T I, interphase, and T II which was interpreted as due to induction during preceding stages. The various types of irregularity appearing during different meiotic stages were illustrated by microphotographs. Stickiness was the dominating category.

In contrast to the observations at Sälen the amount of irregularity at Yttermalung and Svanvik was low or completely lacking. At Svanvik the PMC passed meiosis during favourable temperature conditions. At Yttermalung meiosis was also to the greatest extent passed when the temperature was above 0°C which probably explains the low percentage of irregularity from this locality.

The material in Austria was exposed to extremely large daily temperature fluctuations, in some cases ranging from −5°C during the night to +38°C during daytime. It is expected that such temperature conditions are unfavourable for a proper pollen formation. Irregularities might be induced by low temperatures as well as by high ones (see also CHIRA 1965 A). In agreement with expectation the percentages of irregularity were in several cases high, amounting to more than 50 per cent.

The first investigation showing frost damage in *Larix* emanates from CHRISTIANSEN (1960) who daily followed the meiotic development in the PMC of two trees of *Larix decidua.* He described various types of irregularity such as stickiness, fusion and pycnosis. Interestingly enough the temperature during the meiotic division was not lower than −2.3°C, which means that such a temperature might provoke irregularities in *Larix decidua.* Unfortunately no quantitative estimation of the amount of irregularity was presented by CHRISTIANSEN.

The critical temperature for induction of irregularities varies from species to species. Thus three hours' exposure to +3° C caused irregularities in PMC of *Pinus edulis* as reported by CHIRA (1967). The cells in the heterotypic prophase were damaged to 20 per cent by +2—+4° C. The most common irregularity was the formation of 3—4 nuclei of varying size during the interphase. CHIRA (1967) claimed that M I—A I and M II—A II were highly sensitive to low temperature. For *Taxus baccata* CHIRA (1964) reported that three days at -4°C caused damage during prophase I—telephase I but to a lesser extent during the second meiotic division. For *Pinus nigra* and *Pinus silvestris* CHIRA (1963) obtained pollen sterility amounting to 100 and 87 per cent respectively, which he interpreted as being due to a 15-day period of temperatures below 0° C during the sensitive part of the meiotic division. In *Abies koreana* a complete pollen sterility was provoked by -2.1° C during metaphase I—telophase II according to KANTOR and CHIRA (1965). However, the data presented suggest that also temperatures above 0° C might be responsible for induction of irregularities in different *Abies* species.

In *Larix decidua, L. leptolepis,* and *L. sibirica* EKBERG and ERIKSSON (1967), EKBERG *et al.* (1968), ERIKSSON (1968 A and B) have studied the influence of low temperature on PMC. Furthermore they have tried to evaluate the differences between various phases of meiosis regarding sensitivity to low temperature. This was made possible by examining the meiotic development in the same cells as were used for estimating the amount of irregularity. ERIKSSON concluded that the resting stages (the dormant phase of diplotene and the interphase) were insensitive whereas stages in active division were highly sensitive to low temperatures. Such low temperatures as -25—-30° C did not provoke any irregularities in the dormant diplotene PMC.

ERIKSSON (1968) suggested the following scheme for classification of the irregularities:

1. Chromosomal irregularities
   a. stickiness
   b. fragmentation
2. Irregularities in cell division
   a. spindle abnormalities
   b. polyspory
   c. univalents
   d. monads, dyads, triads.

Micronuclei and degeneration can arise as a consequence of (1) or (2).

Microphotographs illustrating the various categories were presented by ERIKSSON (1968 B).

The main purpose of the classification of the irregularities as made by ERIKSSON (1968 B) was to facilitate the examination and the understanding of the factors responsible for the origin of the irregularity.

The most common types of irregularity were stickiness, polyspory and degeneration. The origin and development of polyspory was described with the aid of photomicrographs in the report of EKBERG *et al.* (1968).

ERIKSSON (1968 B) constructed models which might be regarded as attempts to show quantitative relations between low temperatures and sensitive cells on one hand and irregularities on the other hand. Good agreement for such relations was observed in several cases.

The prerequisites for a proper pollen formation were summarized in the following way by ERIKSSON (1968 B):

"1. Reaching of diplotene before frost appears during autumn.
2. Stability of the resting diplotene stage to short temperature fluctuations around 0° C (−5—+5° C).
3. Rapid reaching of the tetrad stage when development from diplotene is initiated."

Linear relationships between percentage of irregularities during meiosis and pollen sterility were obtained by ERIKSSON (1968 B). This should be taken into consideration when the crossings in the seed orchards are planned.

Summarizing this chapter it can be stated that the critical temperature responsible for induction of irregularities ranges from about −2—−4°C in *Picea abies* (ANDERSSON 1969) to a few degrees above 0° C as is the case in *Pinus edulis* (CHIRA 1967). As the species studied are native in quite different climatic regions it is probable that the temperature limit for starting and ceasing of certain essential physiological processes varies from species to species. This in turn means that various types of irregularity are induced at different temperatures in species more or less generatively adapted to different climatic conditions.

Artificially induced irregularities

During the two last decades an increased interest in the effect of radiation upon conifers has taken place (*cf.* ERIKSSON *et al.* 1966). However, the information concerning radiation induced irregularities during meiosis is limited.

MERGEN and JOHANSEN (1963) reported about the effect of chronic gamma irradiation upon PMC of *Pinus rigida.* The irregularities occurred in low frequencies at daily dose rates up to 7—10 R/day whereupon a steep increase of the frequency of irregularities appeared. Another constant level (around 80 %) of the frequency seemed to exist in the dose range of 17—56 R/day. Fragmentation and chromosomal bridges were the irregularities reported.

Table 4 C. R eports concerning artifically induced meiotic irregularities in conifers

Species	Type of study	Reference
Cryptomeria japonica	Irregularities following heat treatment	Chiba and Watanabe 1952
Larix decidua	” ” chloroform treatment	Němec 1910
Larix leptolepis	” ” colchicine treatment	Illies 1956
Larix leptolepis	” ” γ-irradiation	Eriksson *et al.* 1966
Pinus rigida	” ” ”	Mergen 1963
Pinus rigida	” ” ”	Mergen and Johansen 1963

Following semiacute irradition (45—500 rad) of PMC in the diplotene stage in *Larix leptolepis* ERIKSSON *et al.* (1966) reported an almost linear increase of the frequency of irregularities. However, a sigmoidal increase could not be excluded. Almost all cells carried irregularities at the highest dose level. Bridges and fragments constituted the dominating categories of irregularity. The irradiation also provoked the formation of giant (probably diploid) pollen grains at a higher rate than in the control material.

Meiosis in hybrids

Meiotic investigations in hybrids are mostly undertaken to evaluate species relationships or pattern of evolution. The most comprehensive study within this research line emanates from SAYLOR (1962, 1967), SAYLOR and SMITH (1966), who investigated the meiosis in around 50 species or interspecific hybrids in *Pinus*. The percentages of irregular cells ranged between 0.46 and 7.13 per cent in the pure species and between 0 and 47.24 per cent in the interspecific hybrids. However, the percentages were low mostly, not exceeding 5 per cent. The irregularities encountered were: precocious disjunction, univalents, lagging chromosomes, fragments, inversion bridges, and micronuclei. All types were documented by convincing and instructive microphotographs. To obtain a basis for comparison between the amount of irregularity in species and hybrids SAYLOR and SMITH (1966) calculated an irregularity index. This was done by constructing a frequency distribution for each of the types of irregularity mentioned above and by calculating an average based on the ranking for each category of irregularity of the individ-

Table 5. Meiotic investigations in interspecific hybrids of conifers

Species	Type of study	Reference
Athrotaxus cupressoides, A. laxifolia, A. selaginoides	Investigation of species relationship	Gulline 1952
Larix decidua, L. eurolepis, L. Kaempferi	chiasma frequency	Sax H. J. 1932
Juniperus horizontalis, J. virginiana	meiosis in presumed hybrids	Ross and Duncan 1949
Pinus densiflora × P. Thunbergii	meiosis in a presumed hybrid	Hirayoshi *et al.* 1943
Pinus Griffithii × P. strobus, P. Holfordiana × P. parviflora, P. parviflora P. parviflora × P. strobus	meiosis in hybrids	Sax, K. 1960
Pinus nigra × P. silvestris	meiosis in a presumed hybrid	Vidaković 1958
Pinus sp. and hybrids	meiosis in pure species and hybrids	Saylor 1962
,,	,,	Saylor and Smith 1966
,,	,,	Saylor 1967
Podocarpus hallii × P. nivalis	chromosome pairing	Hair and Beuzenberg 1958 A

ual trees. The irregularity index varied between 1.54 and 4.60 in the pure species and 1.00—8.71 in the interspecific hybrids. The study of the irregularity index clearly revealed that the amount of irregularity on an average was at a higher level in the hybrids than in the pure species. However, no differences between species and hybrids were noted for fragments and heterozygous inversions.

The overwhelming majority of trees were shown to be heterozygous for paracentric inversions which is in line with the data reported by PEDERICK (1968) who studied the occurrence of paracentric inversions in 12 trees of *Pinus radiata* and 4 fullsib *P. radiata* × *P. attenuata* hybrids. All trees examined were shown to be heterozygous for paracentric inversions. In similarity with the data of SAYLOR and SMITH (1966) the inverted segments were small. The small size of the inversions might according to SAYLOR and SMITH (1966) be explained by the localization of the inversions to the distal region of the chromosomes or the localization of crossing-over to these regions.

As some of the species have been growing isolated from other pines for a long time SAYLOR and SMITH (1966) pointed out that hybridity could not explain the heterozygosity for paracentric inversions in those species (*Pinus pinea* and *P. resinosa*).

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Table 6. Meiotic investigations in polyploid conifers

Species	Type of study	Reference
Larix dahurica	meiosis in a triploid tree	Manžos and Pozdnjakov 1960
Larix decidua	meiosis in a tetraploid tree	Christiansen 1950
Larix decidua × L. occidentalis	meiosis in a triploid tree	Syrach Larsen and Westergaard 1938
Larix decidua × L. occidentalis	meiosis in a triploid tree	Knaben 1953

LITERATURE CITED

AASS, I. 1957. En cytologisk analyse av Skjåkfurua. (A cytological analysis of Scots pine (Pinus silvestris L.) from Skjåk, Norway.) — Medd. Norske Skogforsøksvesen 14: 93—109.

ALLEN, C. E. 1903. The early stages of spindle-formation in the pollen-mother-cells of Larix. — Ann. Botany 17: 281—312.

ANDERSSON, E. 1947 A. A case of asyndesis in *Picea abies*. — Hereditas 33: 301—347.

— 1947 B. Pollen and seed setting studies of an asyndetic spruce and some normal spruces; and a progeny test of spruces. — Svensk Papperstid. 50: 74—83, 113—117, 146—152, 177—179.

— 1954. Några data om pollenvariationen och pollenfertiliteten hos gran och tall. — Ibid. 57: 242—255, 654—676.

— 1965. Cone and seed studies in Norway spruce (*Picea abies* (L.) Karst.). — Stud. For. Suec. 23: 1—214.

— 1969. Meiosstörningar i pollenmoderceller hos gran (*Picea abies*). — Manuscript.

BARNER, H. and CHRISTIANSEN, H. 1960. The formation of pollen, the pollination mechanism, and the determination of the most favourable time for controlled pollination in Larix. — Silvae Genet. 9: 1—11.

— 1962. The formation of pollen, the pollination mechanism, and the determination of the most favourable time for controlled pollination in *Pseudotsuga Menziesii*. — Ibid. 11: 4: 89—102.

BELAJEFF, W. 1894. Zur Kenntniss der Karyokinesis bei den Pflanzen. — Flora 79: 430—445.

BLACKMAN, V. H. 1898. On the cytological features of fertilization and related phenomena in *Pinus silvestris* L. — Phil. Transact. Roy. Soc. Ser. B 190: 395—426.

BURLINGAME, L. L. 1913. The morphology of *Araucaria brasiliensis*. I. The staminate cone and male gametophyte. — Botan. Gaz. 55: 97—114.

CHANDLER, C. and MAVRODINEAU, S. 1965. Meiosis in Larix laricina Koch. — Contrib. Boyce Thompson Inst. 23: 67—76.

CHIBA, Sh. and WATANABE, M. 1952. Abnormal pollen groins of *Cryptomeria japonica* D. DON produced by heat treatment. — Rept. Gov. Forest Expt. Sta. 64: 13—20.

CHIRA, E. 1963. (K otázke sterility pel' u u borovice sosny a borovice čiernej.) The pollen sterility of Scots and black pines (Pinus silvestris L. and P. nigra Arnold). — Lesnický Časopis 9: 821—826.

— 1964. Vplyv teploty na priebeh meiózy pel' oých materských buniek Taxus baccata L. (Einfluss der Temperatur auf den Verlauf der Meiosis der Pollenmutterzellen von Taxus baccata L.). — Biólogia 19: 235—244.

— 1965 A. On some biological questions concerning Picea excelsa (Lam.) Link. pollen. — Ibid. 20: 641—653.

— 1965 B. Vývoj pel' u borovice sosny a niektorých introdukovaných borovíc (The pollen development of Scotch pine and some other introduced pines). — Lesnický Časopis 11: 595—604.

— 1967. Pollen grains of Pinus edulis with more than the haploid number of chromosomes. — Silvae Genet. 16: 14—18.

CHRISTIANSEN, H. 1950. A tetraploid *Larix decidua* Miller. — Kgl. Danske Videnskab. Selskab Biol. Medd. 18: 1—8.

— 1960. On the effec t of low temperature on meiosis and pollen fertility in Larix decidua Mill. — Silvae Genet. 9: 72—78.

— 1963. On the chromosomes of Pseudotsuga macrocarpa and Pseudotsuga menziesii. — Ibid. 12: 124—126.

COULTER, J. M. and CHAMBERLAIN, C. J. 1901. Morphology of spermatophytes. — D. Appleton & Co., New York, 189 pp.

DARK, S. O. S. 1932. Chromosomes of *Taxus, Sequoia, Cryptomeria* and *Thuya*. — Ann. Botany 46: 965—977.

DEVISÉ, R. 1922. La figure achromatique et la plaque cellulaire dans les microsporocytes du "Larix europaea". — Cellule 32: 247—309.

DIAZ LUNA, C. L. 1962. Estudio cromosomico de Pinus pinceana Gordon. — Boletin tecnico no 4, Instituto nacional de investigaciones forestales 27 pp.

DUPLER, A. W. 1917. The gametophytes of Taxus canadensis Marsch. Contributions from the Hull botanical laboratory 234. — Botan. Gaz. 64: 115—136.

EKBERG, I. and ERIKSSON, G. 1967. Development and fertility of pollen in three species of *Larix*. — Hereditas 57: 303—311.

— ERIKSSON, G. and ŠULÍKOVÁ, Z. 1968. Meiosis and pollen formation in Larix. — Ibid. 59: 427—438.

ERIKSSON, G. 1968 A. Meiosis and pollen formation in Larix. — Thesis, 18 pp.

— 1968 B. Temperature response of pollen mother cells in *Larix* and its importance for pollen formation. — Stud. For. Suec. 63: 1—131.

— EKBERG, I., EHRENBERG, L. and BEVILACQUA, B. 1966. Genetic changes induced by semi-acute γ-irradition of pollen mother cells in *Larix leptolepis* (SIEB et ZUCC.) Gord. — Hereditas 55: 213—226.

— ŠULÍKOVÁ, Z. and EKBERG, I. 1967. Varför är frösättningen hos lärk så låg? — Sveriges Skogsvårdsförbunds Tidskr. 65: 691—697.

FERGUSON, M. C. 1904. Contributions to the knowledge of the life history of Pinus with special reference to sporogenesis, the development of the gametophytes and fertilization. — Proc. Wash. Acad. Sci. 6: 1—202.

GULLINE, H. F. 1952. The cytology of Athrotaxis. — Papers Proc. Roy. Soc. Tasmania 86: 131—136.

HAIR, J. B. and BEUZENBERG, E. J. 1958 A. Chromosomal evolution in the Podocarpaceae. — Nature 181: 1584—1586.

— and BEUZENBERG, E. J. 1958 B. Contributions to a chromosome atlas of the New Zealand flora-1. — New Zealand J. Sci. 1: 4: 617—628.

HAWKER, L. E. 1930. *Microsporogenesis in Taxus.* — Ann. Botany 44: 535—539.

HIRAYOSHI, I. NAKAMURA, Y. and KANO, T. 1943. Cytological and genetic studies on forest plants. II. Chromosome conjugation in pollen mother cells and pollen fertility of *Aiguro-matu* (*Pinus densi-Thunbergii* Uyeki). — Seiken Zihô 2: 90—96.

HODCENT, E. 1963. Étude cytologique de la formation des grains de pollen à partir de leurs cellules mères chez *Araucaria columnaris* (Forster). — C. R. Acad. Sc. Paris. 257: 489—492.

HOFMEISTER, W. 1848. Ueber die Entwicklung des Pollens. — Botan. Zeitung 6: 425—434, 649—674.

ILLIES, Z. M. 1956. Veränderungen der Pollengrösse bei Lärche nach Blütenbehandlung mit Colchicin. — Z. Forstgenetik Forstpflanzenzücht. 5: 112—115.

ISHIKAWA, C. 1902. Ueber die Chromosomenreduction bei *Larix leptolepis* Gord. — Beih. Botan. Centralblatt 11: 6—7.

IWAKAWA, M. and CHIBA, Sh. 1952. Abnormal pollen grains of *Cryptomeria* and *Pinus* occurred in natural conditions. — Rept. Gov. Forest Expt. Sta. 64: 1—9.

JUEL, H. O. 1900. Beiträge zur Kenntniss der Tetradentheilung. — Jahrb. Wiss. Botan. 35: 626—659.

KANTOR, J. and CHIRA, E. 1965. Mikrosporogenéza u niektorých druhov Abies. (Microsporogenesis at some species of Abies.) — Sborník Vysoké Školy Zemědělské v Brně, 3: 179—185.

KEDHARNATH, S. and UPADHAYA, L. P. 1967. Chiasma frequency in Pinus roxburghii Sarg. and P. elliottii Engelm. — Silvae Genet. 16: 112—113.

KEEN, R. A. 1958. A study of the genus Taxus. — Dissertation Abstr. 18:1196—1197.

KHOSHOO, T. N. 1957 A. Cytology of conifers. III. Partial failure of meiotic spindle in *Cephalotaxus drupacea* var. *pedunculata.* — Cytologia 22: 80—89.

— 1957 B. Meiosis in *Cephalotaxus drupacea* var. *pedunculata.* — Current Sci. 26: 118—120.

KNABEN, G. 1953. En cytologisk analyse av diploid og triploid Larix. — Blyttia 11: 105—115.

LEWIS, I. M. 1908. The behaviour of the chromosomes in Pinus and Thuja. — Ann. Botany 22: 529—556.

LOPRIORE, G. 1905. Über die Vielkernigkeit der Pollenkörner und Pollenschläuche von *Araucaria Bidwillii* Hook. — Ber. Deut. Botan. Ges. 23: 335—346.

MANŽOS, A. M., and POZDNJAKOV, L. K. 1960. Triploidnaja forma listvennicy daurskoj v centralnoj Jakutii. (A triploid form of Larix dahurica from Central Yakutia.) — Dokl. Akad. Nauk SSSR 130: 437—439.

MATSUURA, H. and SUTÔ, T. 1935. Contributions to the idiogram study in phanerogamous plants. I. — J. Fac. Sci. Hokkaido Imp. Univ. Ser. V: 33—75.

MEHRA, P. N. and KHOSHOO, T. N. 1956 A. Cytology of conifers. I.—J. Genetics 54: 1: 165—180.

— and KHOSHOO, T. N. 1956 B. Cytology of conifers. II.—Ibid. 54: 1: 181—185.

MERGEN, F. 1963. Evaluation of spontaneous, chemical, and radiation-induced mutations in *Pinaceae*. — Proc. World Consultation Forest Genet. Tree Improvement, Vol. I., Stockholm, Sweden 23—30 Aug. 1963. FAO/FORGEN 63 1/1. 29 pp.

— and JOHANSEN, S. T. 1963. Effect of ionizing radiation on microsporogenesis in Pinus rigida Mill. — Radiation Botany 3: 321—331.

— and LESTER, D. 1961. Microsporogenesis in Abies. — Silvae Genet. 10: 146—156.

— STAIRS, G. R. and SNYDER, E. B. 1963. Microsporogenesis in *Pinus echinata* and *Pinus taeda*. — Ibid. 12: 127—129.

MIYAKE, K. 1911. The development of the gametophytes and embryogeny in Cunninghamia sinensis. — Botan. Zentralblatt 27: 1—25.

NĚMEC, B. 1910. Über den Einfluss des Chloroformierens auf die Pollenbildung. — Das Problem der Befruchtungsvorgänge und andere zytologische Fragen. Verl. Gebr. Bornträger, Berlin. Pp. 192—223.

NICHOLS, G. E. 1910. A morphological study of Juniperus communis var. depressa. — Botan. Zentralblatt 25: 201—241.

NORÉN, C. O. 1907. Zur Entwicklungsgeschichte des Juniperus communis. — Uppsala Univ. Årsskr. 1907. Matematik och naturvetenskap 1: 1—64.

OTTLEY, A. M. 1909. The development of the gametophytes and fertilization in *Juniperus communis* and *Juniperus virginiana*. — Botan.Gaz. 48: 31—46.

PEDERICK, L. A. 1967. The Structure and Identification of the Chromosomes of Pinus radiata D. Don. — Silvae Genet. 16: 69—77.

— 1968. Chromosome Inversions in Pinus radiata. — Ibid. 17: 22—26.

PROSINA, M. N. 1928. Verhalten der Chondriosomen bei der Pollenentwicklung von *Larix dahurica* Turcz. — Z. Zellforsch. Mikroskop. Anat. 7: 114—134.

ROBERTSON, A. 1904. Spore formation in Torreya californica. — New Phytologist 3: 133—148.

ROSS, J. G. and DUNCAN, R. E. 1949. Cytological evidences of hybridization between Juniperus virginiana and J. horizontalis. — Bull. Torrey Botan. Club 76: 414—429.

RUNQUIST, E. W. 1968. Meiotic investigation in Pinus silvestris (L.). — Hereditas 60: 77—128.

SAX, H. J. 1932. Chromosome pairing in Larix species. — J. Arnold Arboretum 13: 368—374.

— 1933. Chiasma formation in *Larix* and *Tsuga*. — Genetics 18: 121—128.

SAX, K. 1960. Meiosis in interspecific pine hybrids. — Forest Sci. 6: 135—138.

— and SAX, H. J. 1933. Chromosome number and morphology in the conifers. — J. Arnold Arboretum 14: 356—375.

SAXTON, W. T. 1913. Contributions to the life-history of *Tetraclinis articulata* Masters, with some notes on the phylogeny of the Cupressoideae and Callitroideae. — Ann. Botany 27: 577—605.

— 1929. Notes on conifers. II. Some points in the morphology of Larix europaea D. C. — Ibid. 43: 609—631.

— 1930. Notes on conifers. III. Further points in the morphology of Larix europaea D. C. — Ibid. 44: 161—165.

SAYLOR, L. C. 1962. Chromosome behaviour and morphology in species and interspecific hybrids of *Pinus*. — Thesis 128 pp.

— 1967. Variability of chromosome structure and behaviour in southern pine hybrids. — Proceedings of the Ninth Southern Conference on Forest Tree Improvement held at Knoxville, Tennessee, U.S.A., June 8—9, 1967. Pp. 95—100.

— and SMITH, B. W. 1966. Meiotic irregularity in species and interspecific hybrid in Pinus. — Am. J. Botany 53: 453—468.

SINGH, H. and CHATTERJEE, J. 1963. A contribution to the life history of *Cryptomeria japonica* D. Don. — Phytomorphology 13: 429—445.

STRASBURGER, E. 1895. Karyokinetische Probleme. — Jahrb. Wiss. Botan. 28: 151—204.

SUGIHARA, Y. 1940. On the multipartite chromosome-ring in *Cephalotaxus drupacea* Sieb. et Zucc. — Sci. Rept. Tôhoku Imp. Univ. 4th Ser. 15: 13—18.

SYRACH LARSEN, C. and WESTERGAARD, M. 1938. Contributions to the cytogenetics of forest trees. I. A triploid hybrid between *Larix decidua* Miller and *Larix occidentalis* Nutt. — J. Genet. 36: 523—530.

TAHARA, M. 1941. Embryogeny of *Podocarpus macrophyllus* and *Podocarpus nagi.* — Sci. Rept. Tôhoku Imp. Univ., 4th Ser. Biol. 16: 91—98.

TIMBERLAKE, H. G. 1900. The development and function of the cell plate in higher plants. — Botan. Gaz. 30: 73—99.

VIDAKOVIĆ, M. 1958. Investigations on the intermediate type between the Austrian and the Scots pine. — Silvae Genet. 7: 12—19.

VOGEL, G. 1936. Die männliche Haploid-Generation von *Pinus silvestris* und ihre Beziehung zur Hohlkornbildung. — Thesis, 52 pp.

WANG, F. H. 1948. Life history of Keteleeria. I. Strobili, development of the gametophytes and fertilization in Keteleeria evelyniana. — Am. J. Botany 35: 21—27.

ZENKE, U. 1953. Untersuchungen über den Ablauf der Meiosis bei Pseudotsuga taxifolia Britton. — Silvae Genet. 3: 96—102.

Sammanfattning

Meiosstudier hos barrträd

Meiosstudierna hos barrträden har varierat avsevärt beträffande syfte och utformning av undersökningarna. För att åstadkomma största möjliga överskådlighet har dessa undersökningar klassificerats på följande vis:

1. Mikrosporbildning (tabell 1)
2. Makrosporbildning (tabell 2)
3. Kromosomtal (tabell 3)
4. Oregelbundenheter
   A. Ärftliga (tabell 4 A)
   B. Miljöbetingade (tabell 4 B)
   C. Artificiellt inducerade (tabell 4 C)
5. Meiosstudier hos hybrider (tabell 5)
6. Meiosstudier hos polyploider (tabell 6)

I uppsatsen ges en kortfattad presentation av de resultat som kommit fram under 1960-talet inom ovanstående ämnesområden.