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TIMING OF MICROSPOROGENESIS IN TREES WITH REFERENCE TO CLIMATIC ADAPTATION A REVIEW

MIKROSPOROGENEESIN AJOITUS JA PUULAJIEN ILMASTOLLINEN SOPEUTUMINEN

Alpo Luomajoki

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Seloste

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To be presented, with the permission of the Faculty of Science of the University of Helsinki, for public criticism in the Auditorium of the Department of Botany, Unioninkatu 44, Helsinki, on the 20th of March 1987 at 12 o'clock noon.

In addition to this paper, the thesis includes three other publications by the author. These are referred to in the text by their Roman numerals:

I. Temperature and dates of male meiosis in trees. Hereditas 97:167–178. 1982.

II. The tetrad phase of microsporogenesis in trees with reference to the annual cycle. Hereditas 101:179–197. 1984.

III. The latitudinal and yearly variation in the timing of microsporogenesis in Alnus, Betula and Corylus. Hereditas 104:231–243. 1986.

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LUOMAJOKI, A. 1986. Timing of microsporogenesis in trees with reference to climatic adaptation. Seloste: Mikrosporogeneesin ajoitus ja puulajien ilmastollinen sopeutuminen. Acta For. Fenn. 196: 1–33.

The timing of the tetrad phase of microsporogenesis in sixteen trees species was studied. The tetrad phase of microsporogenesis in conifers and in *Populus tremula* L. was reached from late March to early June including the yearly and the latitudinal variation. The tetrad phase in Betulaceae was reached in late July to mid-August. The microsporogenesis in Betulaceae species differed in ecophysiological terms from the other species studied in that the timing in Betulaceae was rather daylength-dependent than heat sum-correlated. In conifers and in Populus the timing of tetrad phase correlated with heat sums accumulated and did not correlate with day length or any kind of thermal threshold. This difference was, however, judged to be associated to seasonal adaptive strategies rather than to taxonomic relationships.

Kuudentoista puulajin mikrosporogeneesin ajoitusta tutkittiin. Havupuilla sekä haavalla mikrosporogeneesin tetradivaihe saavutettiin maaliskuun lopun ja kesäkuun alun välillä vuosittainen ja latitudinaalinen vaihtelu mukaan lukien. Koivuilla, lepillä ja pähkinäpensaalla tetradivaihe saavutettiin vastaavasti heinäkuun lopun ja elokuun keskivaiheen välillä. Ekofysiologisesti koivukasvien heimon puut erosivat muista puulajeista siinä, että meioosin ajoitus osoittautui enemmän päivänpituuden kuin lämpösumman säätelemiseksi. Havupuilla ja haavalla tetradivaiheen saavuttaminen korreloi kertyneiden lämpösummien, mutta ei päivänpituuden tai minkään määrätyn lämpökynnyksen kanssa. Tätä eroa kahden lajiryhmän välillä ei voi kuitenkaan katsoa lajien sukulaissuhteista johtuvaksi, vaan se ilmentää ilmastollista sopeutumista, joka edellyttää eri säätelykeinoja eri vuodenaikoina.

Key words: Annual cycle, heat sum, meiosis, photoperiod, tetrad phase
ODC 181.8

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PREFACE

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Application of some terms

Active period. The period when a tree is not dormant (Sarvas 1972).

Adaptation. Evolutionary changes to improve a population's adjustment to local environmental conditions.

Autonomity. Here means that pollen mother cells (PMCs), due to histological isolation, are less rigorously under the regulation of the parent plant than the more integral parts of it.

Autumn dormancy. Precedes winter dormancy; the period when chilling is effective. Sarvas (1974) used this term.

Base period unit-sum. The p.u.-sum that is cumulated in the spring during the winter dormancy state of the tree. Base p.u.'s are a source of error in measurement of the active period since the zero point is not generally known.

Degree day (d.d.). A linear heat sum unit based on daily mean temperature minus base temperature. A base temperature of +5 °C was adapted, so the d.d. sum grows daily by ($\bar{t}$ −5) d.d.'s.

Dyad. When cytokinesis takes place (prematurely) at interkinesis and makes the PMCs 2-celled. Abnormal 2-celled microspores (2n) after telophase II are also called dyads.

Growing season. The part of the year during which the daily mean temperature stays above +5 °C.

Heat sum. Number of any defined units cumulated under the joint effect of time and temperature.

Interaction. Here means that the more the heat-sum requirement is satisfied, the smaller is the critical night length requirement for the termination of growth. This condition is also called the joint effect.

Interphase. Used frequently as a synonym of the interkinesis, i.e. the phase between reduction and somatic divisions.

Period unit. Progress in development within one hour at 10 °C is equivalent to 5 period units according to Sarvas (1972). This regression is limited to the active period. The period unit is here considered in this context as a heat sum unit, even if Sarvas (1972) did not so consider it. He pointed out that no threshold is used in p.u.'s as in conventional heat sums.

Point event. For practical purposes any stage of meiosis can be identified as having reached a given stage or not. In general, events that can be characterized dichotomously are called point events.

Stamen. All leaves producing microspores including the stamens of angiosperms and the microsporophylls of conifers are here called stamens.

Sunhours. The length of day according to the almanac, i.e. according to the upper edge of the sun. It is longer than the astronomical day length.

Temperature sum. Identical to heat sum.

Winter dormancy. The period, between autumn dormancy and active period, when a tree is hardiest against unfavourable environment. In meiosis, it is a period of standstill in visible chromosomal movements and, apparently, little cytological development.

Zero point. The onset of either the active period or winter dormancy. While this concept is somewhat theoretical, it means the relatively rapid physiological change from one major phase of the annual cycle to another. Sarvas (1974) considered the onset of winter dormancy as the zero point of the entire annual cycle.

1. INTRODUCTION

1.1. Background to the study

The annual cycle of trees growing in cool temperate regions consists of similar main periods both in the generative and the vegetative cycles. The corresponding reactions with the environment may differ in detail, but the severe conditions in the northern climate always demands protection against the adverse effects of the cold period.

Broadly, development and growth in the spring have to start flexibly, within close limits. That is, they must begin after the frost period but without wasting too much of the short growing season. Towards the end of the growing season growth and differentation must terminate so as to prepare trees to the chilling period and to aquirement of winter hardiness. The length of the winter dormancy has great adaptative value in appropriately closing the circle for the onset of a new active period.

One of the prequisites for a functional annual cycle regulation in trees is the maintenance of synchrony with the seasons despite variability in the length of growing seasons in terms of temperature sums (Sarvas 1972).

Microsporogenesis in trees usually covers nearly one full cycle, but in various tree genera the relevant stages of microsporogenesis are located quite differently in relation to the annual cycle. At least in conifers (Andersson et al. 1969) the course of microsporogenesis always includes a winter dormancy period and, therefore, fractions of two active periods before and after the dormancy. Four different patterns are known from cold to temperate climates (see Andersson et al. 1969). The behavior of trees in the tropics is different (Wycherley 1973).

The principal events during the microsprogenesis are the initiation and growth of the male buds, generation and growth of the sporogenous tissue, pre-meiotic maturation of the PMCs, meiosis, the tetrad stage, androgenesis and anthesis. Only the period from maturation of the PMCs to the tetrad stage is considered here, with the emphasis being on the timing of the tetrad stage.

The meiotic stages of tree species have been described (usually with photomicrographs) by many authors. For example meiosis in *Larix* has been studied by Ekberg and Eriksson (1967), Ekberg et al. (1968), Eriksson (1968), Eriksson et al. (1970b), Hall and Brown (1976) and by Owens and Molder (1979b); in *Picea* by Eriksson et al. (1970a), Moir and Fox (1976), Owens and Molder (1979a, 1980) and by Singh and Owens (1981); in *Pinus* by Runquist (1968), Willemse (1971a, b, c), Ekberg et al. (1972), Ho and Owens (1974) and by Owens et al. (1981); and in *Populus* by Ekberg et al. (1967). Details of meiosis in several tree species with diffuse phases can be found in a paper by Owens and Molder (1971) while most of the older literature on meiosis in conifers was reviewed by Andersson et al. (1969). There is, therefore, no compelling reason for describing the relatively well-known progress of meiosis in the present context.

Early attempts to construct a model of the development of perennial plants during the growing season already utilized heat sums (reviewed by Koski and Selkäinaho 1982). A still more demanding attempt to find a quantitative basis for such a model throughout the year, was made by Sarvas (1972, 1974).

One of the basic ideas in Sarvas' (1972, 1974) studies was to control the experiments in such a way that the most important factor, temperature, could be studied separately. This was possible only with certain limitations (I). The second idea was to draw attention to the whole population of objects under investigation and to treat it statistically. For example, in meiosis, attention was earlier directed to the various phases themselves. Short phases, however, emerged only sporadically, in small percentages. This caused uncertainity about the real timing. Statistically satisfactory results are achieved when the population of cells is halved, i.e. when a phase is cumulatively 50 % completed (I).

It is evident that only large materials are

valid in a statistically oriented study. Owing to Sarvas' premature death in 1974 he had not the opportunity to test his model with a sufficiently large material. Rather, the data published (Sarvas 1972, 1974) are solitary examples of the timing of events during the annual cycle.

Extension of the study outside Sarvas' examples also calls for the consideration of the light factor. In nature this can be accomplished by simply observing the variation of day length, e.g., from an almanac. Mature trees cannot be taken indoors for forcing experiments, and it should be noted that such forcing also involves monitoring of the arbitrary temperature.

Skjelvåg (1981) pointed out that the effects of temperature, day length, bright sunshine and water stress on development rate were all non-linear (see also Fritts 1960). He also found that appraisal of such effects should be restricted to short periods, so that a plants physiological state remains stable. This stability, the homogeneity condition, has been studied mathematically by J. Sarvas (1977).

The non-linear regression of the development rate of microsporogenesis required for this author's studies was available. Measurements of the progress of meiosis and the opening of catkins permitted the calculation of the regression of rate of development of the "active period" (Sarvas 1972). He considered that this regression had universal applicability with respect to development during the "active period". However, it is safer to use a regression that is derived from the observation of closely related events.

Homogeneity of development of generative development might be better than that of vegetative growth. The difference in cycles comes visible in so called inversion (Bos 1933). That is, the mutual succession of events relative to growth and flowering can in some year be the opposite to that in preceding year. In other words, the two cycles are somewhat independent.

There is reason to believe that during the generative cycle, especially in the microsporogenesis, development is considerably more homogeneous than in vegetative growth. The histological isolation alone is a significant point. After mid-leptotene, the meiosis progresses in relative isolation (Heslop-Harrison 1966, Linskens 1966, Reznickova and Bogdanov 1972, Takegami et al. 1981). Finally, at the end of the development period, pollen leaves the parent plant (Kupila-Ahvenniemi et al. 1978).

While there is some reciprocity between the pollen mother cells (PMCs) and the tapetum (Willemse 1971c, Stieglitz 1973), it may be safely assumed that the PMCs are much less under the active regulation of the parent plant than the more integral parts of the plant. So no effects of thermoperiodism (e.g. Went 1944, 1945, 1948, Lang 1963, Skjelvåg 1981) have been detected under meiosis. The PMCs are also histologically rather independent in that already at an early stage they hold all the nutrients they need for further development.

It has also been shown that the temperature of soil (i.e. of roots) has no effect on the timing of anthesis in trees (Huikari and Paarlahti 1967, Hammond and Seeley 1978) while soil temperatures can seriously affect growth (Ottonson 1958, Balvoll and Bremer 1965, Wit and Brouwer 1968), however, sometimes only height growth is affected (Huikari and Paarlahti 1967).

Flowering is mostly restricted to mature trees. Therefore, there are no complications of the large range of various physiological ages involved into vegetative development from a tiny plant to a mature tree. After the isolation between the PMCs in meiosis and the rest of the plant is fully developed, temperature (incl. direct radiation) becomes the decisive factor for determining the progress and rate of development. For example, light effects received by leaves or the stem, probably can not reach PMCs at an advanced stage of microsporogenesis owing to isolation of the PMCs.

The timing of microsporogenesis follows several patterns (see Andersson et al. 1969, for conifers), and considerable parts of the year can be covered by just observing microsporogenesis in various tree genera. Thus springtime development can be investigated by observing the many species of *Abies*, *Picea*, *Pinus* and *Populus*) in which meiosis takes place in the spring. Similarly, development during summer can be traced through meiosis in Betulaceae species, and progress of meiosis in *Larix* species can be observed in the autumn and towards the onset of the winter.

The period of winter dormancy can not be studied so directly. However, the pattern of the onset of dormancy can, in theory, be traced as late as the following spring (see Sarvas 1974). The differences in time and in heat sums between the beginning of the cumulation of heat sums in the spring and between the end of winter dormancy should also to be considered. The existence of this kind of deviation is called the zero point problem (II). While dormancy effects are mostly a nuisance in the study of development during the early active period, these effects can at times be utilized for indirect conclusions about the pattern of dormancy in different climatic and adaptive conditions.

1.2. Aim of the investigation

Knowledge of the generative annual cycle of trees is still scant and most of it is not comparable in physioecological terms. The following questions particularly need more detailed answers: How does the timing of male meiosis differ in the species growing in the cool northern region? Is there close similarity in the timing of meiosis of related tree species? Are there latitudinal differences in the timing of meiosis, and are they similar in all tree species? What are the likely physioecological reasons for such differences? How can the timing of meiosis be numerically simulated in various species when taking into account differences between years?

Broadening our scope towards more general questions it is natural to ask: Is the timing system found in microsporogenesis of trees unique, or can similarities be found in other organisms? How accurate is the simulation of development rate and progress of development with different heat sum systems? What are the relative lengths of meioses in various tree species? What is the length of the tetrad phase in various species and how does this correlate with the length of the preceding meiosis?

Our northern climate makes Finland a priviledged area for the study of marginal populations near or at the timber line. Is the phenological variation found in northern marginal populations of trees similar to that in populations of southern Finland? Are the adaptive forces in the generative cycle comparable to those in the vegetative cycle? What is the position and significance of dormancy in microsporogenesis? Can an optically observable phase shift be found that is the precise equivalent to a major physiological change, such as the onset or the release of dormancy period?

The aim of this study is to answer the questions above by studying microsporogenesis of mature trees in nature at various localities in Finland. Especially the tetrad phase of meiosis is used as an efficient microphenological timing indicator.

2. MATERIAL AND METHODS

The material for this study was collected from 51 stands. On the basis of this material only in some species could the timing of microsporogenesis be studied on a nationwide scale. Most species could be studied only locally owing to their restricted distribution. Finland is geographically rather narrow for efficient research of east-west correlations, but latitudinal variation can be studied within Finland quite successfully. In *Betula pubescens* Ehrh., *Picea abies* (L.) Karsten and *Pinus sylvestris* L. the material extends over a range of at least 900 km (Fig. 1).

Eight of the 16 species studied are autochthonous, while the *Abies* and *Larix* species studied, and *Pinus cembra* L. and *P. peuce* Griseb. are introduced species in Finland (Table 1). The microsporogeneses of 125 species/stand/year – combinations were studied during the period 1964 to 1973 and 1983, not including the meioses studied for preliminary orientation. The study of 10–50 samples or 4 000–20 000 PMCs was needed to follow the progress of one or several stages of each microsporogenesis (II, III). Including preparative microscopy, nearly one and half million PMCs were inspected. There are many ways of handling the material when making preparations for observations with the microscope. The orcein squash methods used were described by Luomajoki (1977, I, III).

The temperatures had to be followed constantly. Indoors, bi-metal probes were connected to multichannel printers. Outside thermographs were used at treetop level and checked twice a day. Thermograph data were read and converted to a library of bi-hourly heat-sum data. This made possible the quick conversion of calendar time into period unit heat sums and vice versa for each of the stands studied.

Ready identification rather than the investigation of stages was the aim when inspecting the PMCs. To speed up the work on the microscope, the zygotene phase was not separately identified but included in the leptotene. While there are many optically observable

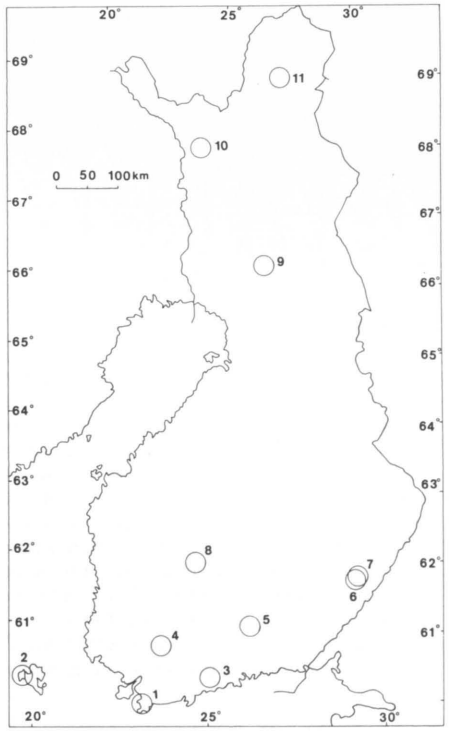

Fig. 1. The localities where microsporogenesis materials were collected. One to seventeen experimental stands (see Table 1) were studied at each locality. These places were in latitudinal order: 1. Bromarv (60°02'; annexed in 1977 to Tenhola parish), 2. Eckerö (60°11'), 3. Tuusula (60°21'), 4. Jokioinen (60°49'), 5. Heinola (61°07'), 6. Punkaharju (61°48'), 7. Kerimäki (61°51'), 8. Vilppula (62°03'), 9. Rovaniemi mlk (66°21'), 10. Kittilä (68°01') and 11. Inari (69°04'). The distance between localities 1 and 11 is ca. 1 050 km. Localities 1–8 were grouped together as southern Finland and localities 9–11 as northern Finland.

Table 1. Latitude and origin of the sample stands.

Species	Site, plot	Latitude (N.L.)	Origin
CONIFERAE			
Abies balsamea	Punkaharju 292	61°49'	Canada, New Brunswick, St. John
A. lasiocarpa	Punkaharju 353	61°49'	Canada, British Columbia, Shushwap Lake
A. sibirica	Punkaharju 45	61°49'	Unknown
Larix decidua	Punkaharju 27	61°48'	France, (Briancon)[1]
L. gmelinii	Punkaharju 9	61°48'	USSR, Sakhalin
L. russica	Punkaharju 8	61°48'	USSR, (Raivola)[1]
	Punkaharju 49	61°49'	Unknown (USSR)
	Rovaniemi 26[4]	66°21'	Unknown (USSR)
	Tuusula 48	60°21'	USSR, (Raivola)[1]
	Vilppula 16	62°04'	Unknown (USSR)
Picea abies	Bromarv I[2]	60°02'	Local
	Heinola 565	61°08'	Local
	Jokioinen I	60°49'	Local
	Kittilä IV	68°01'	Local
	Punkaharju LII[2]	61°49'	Finland, Lammi
	Rovaniemi XVIII	66°21'	Local
	Tuusula XXXIV	60°21'	Local
Pinus cembra	Punkaharju 100	61°49'	Unknown
P. peuce	Punkaharju 306	61°48'	Bulgaria, Pirn Mts.
	Tuusula 111	60°21'	Bulgaria, Rino Planino
P. sylvestris	Bromarv II	60°02'	Local
	Bromarv III	60°03'	Local
	Eckerö I	60°11'	Local
	Heinola 566	61°07'	Local
	Kittilä I	68°02'	Local
	Kittilä II	68°02'	Local
	Punkaharju XLV	61°49'	Local
	Rovaniemi XXVII	66°21'	Local
	Rovaniemi XXIX	66°21'	Local
	Tuusula XXXII	60°21'	Local
	Vilppula 2a	62°04'	Local
DICOTYLEDONS			
Alnus glutinosa	Tuusula 3	60°22'	Local
A. incana	Inari, Toivoniemi[3]	69°04'	Local
	Kerimäki 540[2]	61°52'	Local
	Punkaharju LXII	61°48'	Local
	Tuusula XLI	60°20'	Local
Betula pendula	Bromarv VI	60°03'	Local
	Kerimäki 543[2]	61°48'	Local
	Punkaharju LIV	61°49'	Local
	Rovaniemi XXVIII	66°21'	Local
	Vilppula V	62°04'	Local
B. pubescens	Inari, Toivoniemi[3]	69°04'	Local
	Punkaharju XIV	61°49'	Local
	Punkaharju L[2]	61°49'	Local
	Punkaharju LX	61°49'	Local
	Rovaniemi XVII	66°21'	Local
	Tuusula 12	60°22'	Local
	Vilppula 153	62°03'	Local
Corylus avellana	Bromarv V	60°03'	Local
	Punkaharju[3]	61°49'	Finland, Bromarv
Populus tremula	Tuusula XXXIII	60°20'	Local

1) Not autochthonous. Exact origin unknown.

2) The stand was cut down: Bromarv I in 1975–76, Kerimäki 540 in 1973–77, Kerimäki 543 in 1978, Punkaharju L in 1974–75, Punkaharju LII in 1975–76.

3) Not a regular, numbered plot. The numbered plots are sample stands of Dept. Silviculture, Finnish Forest Research Institute.

4) The stand was damaged by storm in 1982.

premeiotic changes in the PMCs, the onset of the leptotene stage was in this investigation associated with the moment when the polarized chromosome strands first became visible.

The beginning of each stage in meiosis is a point event (Sarvas 1972), i.e. the stage is either completed, or it is not, and so the onset of stages makes for good reference points for precise observations in a phenological study.

The observations of PMCs at various stages were arranged on probability paper and the statistically unbiased reference points of 50 % of the PMCs at each individual stage were obtained (I, II). The beginning of the tetrad stage (50 % of the PMCs at that stage) was observed in every microsporogenesis studied. This point event was used for a comparison of the timing in the various species studied and for comparing development in one species in different years. With the aid of two other point events (50 % of the PMCs in leptotene and 50 % of the tetrads disintegrated) the length of meiosis and that of the tetrad stage could be measured (III). Short periods within meiosis were appraised and compared earlier (Luomajoki 1977).

3. RESULTS

3.1. Patterns in the timing of meiosis in species

The timing of the microsporogenesis could be accurately determined in 16 tree species and ascertained in four further species. The earliest developers in the spring were those species in which meiosis already began in the autumn of the previous year, the same year the initiation of the male organs took place. They include all *Larix* species studied (and *Pseudotsuga menziesii* (Mirb.) Franco, preliminary, unpublished). The timing pattern of meiosis in these exotics was found to be largely the same as in other countries in which they have been studied except for *Larix gmelinii* (Rupr.) Kuzeneva. So *Larix decidua* Miller and *L. russica* (Endl.) Sabine ex Trautv. (= *L. sibirica* Ledeb.) overwintered at diplotene (*Pseudotsuga* at pachytene) while the dormancy in *L. gmelinii* was interrupted prematurely, already in November in two known cases (I). The dormancy of *L. gmelinii* is thus not of proper dimensions for a climate that prevails in Finland, but rather to a much more continental climate.

The final phases of meiosis of the above species passed quickly in the spring, and these species were the first to reach the tetrad stage. This took place at small period unit sums and usually at a time when no degree days were yet cumulated. Attainment of the tetrad stage was not closely related to calendar time, but followed the period unit sums cumulated, albeit loosely (II).

It was evident that these species did not require a high threshold temperature or a specific daylength for completion of their development to the tetrad stage. Unlike *Larix* (or *Pseudotsuga*) the meiosis in *Populus tremula* L. began in the spring from an archesporial stage (II). The tetrad stage was reached in March or April at temperature sums of closely the same order as those for *Larix*, but relative to this species the length of meiosis in *Populus* was found to be short.

There are no conifers with anything like the short meiosis found in *Populus*. So there was a gap of several weeks (or about 1000 p.u.'s) before *Abies* species reached the tetrad stage in late April or, more often, in early May. Perhaps due to close kinship of the species, the timing in *Abies balsamea* Miller, *A. lasiocarpa* (Hooker) Nutt., *A. sibirica* Ledeb. and *A. veitchii* Lindl. (preliminary result in the latter species) was nearly identical (II). These species are also known for naturally producing offspring form mutual crosses, so overlapping timing also extends to antheses.

Picea abies followed the *Abies* species so closely that the difference was not significant in terms of heat sums. The temperature sums at reaching the tetrad stage in *Picea* were consistent in different years and also all over Finland. This indicates a good correspondence between the stage of development and between heat sums measured. In calendar time the corresponding time span extended throughout May, with a few recorded cases in late April and early June (II).

Pinus sylvestris succeeded *Picea* at a considerable distance in terms of heat sums, i.e. on a biological time scale. The distance in calendar time was not so large owing to prevailing higher average temperatures, and the tetrad stage was reached between late May to the middle of June. The heat sums varied considerably, especially in relation to latitude. This suggests a discrepancy between the total heat sums cumulated and the actual development in the active period (II). Preliminary (unpublished) results suggest that *Quercus robur* L. reaches the tetrad stage on a par with *Pinus sylvestris*, and *Juniperus communis* L. reaches it a little later (II).

As could be expected the exotic *Pinus* species were slow to reach the tetrad stage. This happened at considerably higher heat sums than in Scots pine, but the difference in calendar time was not so large (II).

After the pine meioses there followed a relatively long time span with no completed meioses at all. By the time the species in Betulaceae were found to reach the tetrad stage from late July to mid-August, a major difference had taken place in all aspects of the

timing of the meiosis. Not only was the latitudinal succession different, the nationwide range was also smaller while the local distribution was larger than in Conifers (or *Populus*). A good fit in terms of heat sums had changed to a regularity in calendar time. The similarity between *Alnus glutinosa* (L.) Gaertner, *Alnus incana* (L.) Moench, both *Betula* species and *Corylus avellana* L. was such that no significant differences between the species studied could be demonstrated (III).

3.2. Latitudinal correlations

The number of localities and observations permitted the calculation of latitudinal correlations for five species (both *Betula* species, *Larix russica*, *Picea* and *Pinus sylvestris*). Calculation of such correlations was, however, not sensible for *Larix russica*, the origin of seed of this exotic being more or less the same at the various localities in Finland (II). Thus no clinal trends were expected to appear and, accordingly, there was no significant latitudinal correlation in *Larix russica* in terms of heat sums.

There was no latitudinal heat-sum-related correlation in *Picea abies*, either. In this species the populations studied were all local, except for the stand at Punkaharju, the origin of which is Lammi, Finland. A separate test at Punkaharju with six provenances supported the lack of latitudinal correlation within Finland in respect to this phenological parameter (II).

Pinus sylvestris revealed a significant latitudinal correlation in respect to p.u. heat sums, the northern sums being smaller. The stability of the correlation varied, however. The correlations in 1967 and 1968 were highly significant but were not significant in 1969 (II). This latitudinal correlation could not be taken for a proof that the initial stages of male generative development in the north were actually shorter. It was found that the actual development period in *Pinus* in the spring was shorter than the period of accumulation of period units. This contributes to the variability of the p.u. sums, which was far larger in *Pinus* than in *Picea* (II).

Also, the average distributions measured from p.u. sums were in *Pinus* far larger than those measured from the probability paper, while the two types of measurement agreed well in *Picea*. This dissimilarity between the two species can be taken as a difference in the variability of the tree populations or as a difference in the relative position of the zero point with respect to the onset of accumulation of p.u. heat sums (II). The latter condition means latitudinal variation in the termination of the winter dormancy relative to heat sum accumulation, i.e. the safety margin against late frosts has to be larger in the south.

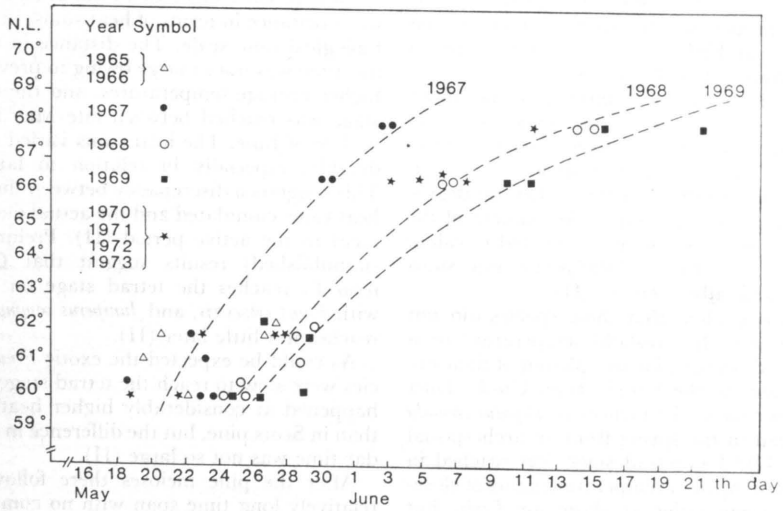

Fig. 2. Date of onset of the tetrad phase in *Pinus sylvestris* in relation to latitude, or the temporal variation at the end of male meiosis. Effects of altitudes (33–330 m) have been ignored. The broken curved lines that illustrate the progress of meiosis in 1967–69 within Finland have been drawn by interpolation (II: Fig. 2).

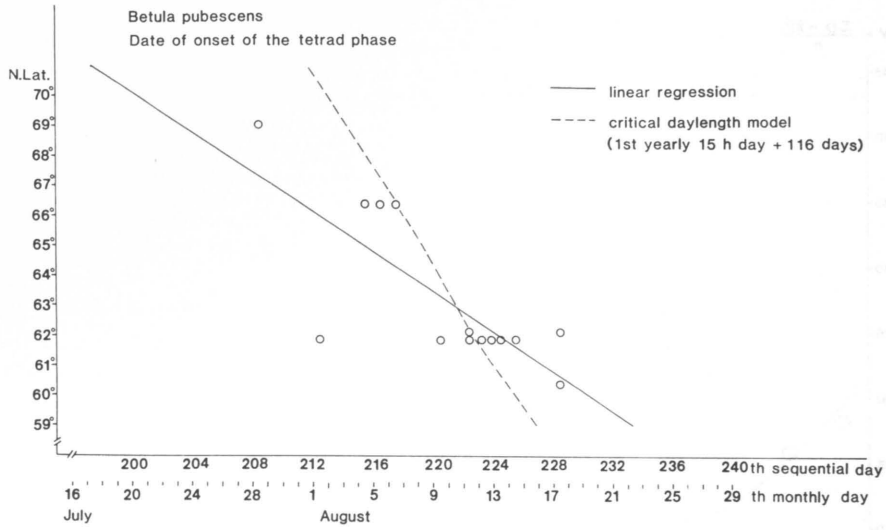

Fig. 3. Date of onset of the tetrad stage in relation to latitude in *Betula pubescens*. The figure was compiled according to the sequential day scale; the monthly day scale is valid in non-leap years. The years involved were 1964, 1966–67, 1970–71 and 1983 (only 1964 was a leap year). Effects of altitudes (45 - 170 m) on geographic relationships have been ignored. Of the species studied, *B. pubescens* has the widest latitudinal distribution in Finland. The linear regression fitted into the observations (Y = 137.448 − 0.33715 X) exaggerates the timing of the tetrad phase at latitudinal extremes. Also shown is the critical day length model: impulse at 15 hours of daylight and 116 days of subsequent development. - The leftmost two observations originate from 1983, an exceptionally early year (III: Fig. 4).

In each of the three conifer species discussed above the latitudinal correlations with respect to calendar time were similar in that the southernmost stands developed first and the northernmost last. The correlation was most accentuated in *Picea* in which the observed ranges of dates in the north and in the south were far apart. Also in *Pinus* (Fig. 2) the correlation was distinct (II).

In both *Betula* species studied the heat sums accumulated in the north were considerably smaller than those accumulated in the south. While this correlation was most accentuated, the heat sums in Betulaceae seemed to have far less connection to the developmental stage of microsporogenesis than, for example, in conifers. Considering that the northernmost stands of *Betula* species developed first, and the southernmost last (Fig. 3), the modest role of heat sums is even more evident. The latitudinal order of development is thus exactly the opposite to that observed in conifers (III).

While the timing of conifer meioses was only weakly connected to calendar time, the timing of meiosis in *Betula* seemed to be quite accurately predictable simply in terms of calendar time. It was also possible to simulate the latitudinal relationship observed by assuming that the timing of microsporogenesis in

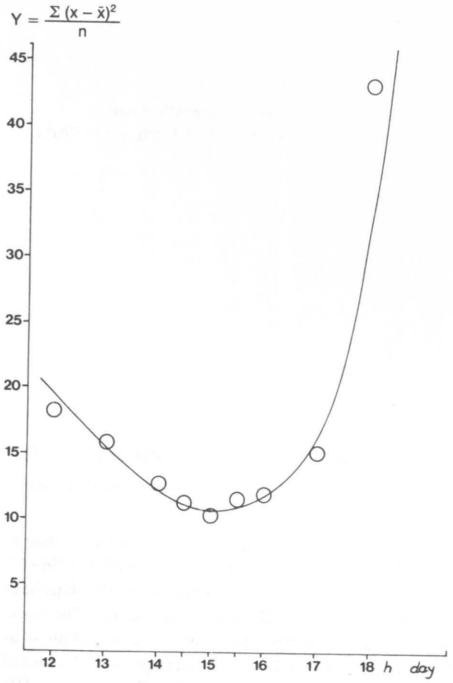

Fig. 4. The method used for finding the hypothetical critical day length that best fits the observed *Betula* data. At each latitude, day lengths in the spring from 12 to 18 hours (measured from the upper edge of the sun) were considered (at half-hour increments near the optimum). In the figure,

X = day length

$$Y = \frac{\Sigma (x - \bar{x})^2}{n}$$

where

x = the time in days from the first day of given length (12 to 18 hours) to each observation of 50 % of the PMCs of *Betula* at the tetrad stage

$\bar{x}$ = mean of each series relevant to a given day length

n = number of observations (= 27)

The best fit (the lowest sum of squared deviations) was obtained at a day length of 15 hours (see also III).

Betula was initiated by a single critical day length (Fig. 4) in the spring (actually the length of night is critical). Thus, a hypothetical critical day length of 15 hours (according to the upper edge of the sun) and 116 days of subsequent development predicted the onset of the tetrad stage so accurately that it was difficult to improve the model further by introducing the plausible modifying effect of the heat sum. The model in its simple form leads to average errors of only 2.6 days in *Betula pubescens* and 1.8 days in *Betula pendula* (III).

As well as critical day lengths, the duration of daytime can also influence the development in plants. It was calculated, however, that combining sunhours to heat sums produced far less accuracy in prediction of the timing than the simple critical day length method.

3.3. Lengths of meiosis and tetrad stage

Time is not a meaningful measure for the length of meiosis or its subphases, except at stable temperatures. Comparison of two or more measurements presupposes the same temperatures throughout or a method for simulating progress of meiosis at variable temperatures. The period unit system was adopted in this study. Even so, it was impossible to measure the total length of meiosis in *Larix* (or *Pseudotsuga*) other than in calendar time. The durations of these meioses are of the order of six months, and incommensurable amounts of the active period as well as autumn and winter dormancies are included.

A good approximation of the duration of meiosis, i.e. the period from the onset of leptotene to the onset of the tetrad stage (50 % of the PMCs in the stages), was obtained in nine species. However, the entire meiosis has been accurately measured in nature only in *Picea*. For most species the length of leptotene and zygotene phases had to be extrapolated using the assumption of proportionality to *Picea* meiosis – an imperfect method, because the very beginning of meiosis in quite variable. It was also found that deficient proportionality was partly caused by the fact conifers had relatively longer interkinesis than the other tree species (Luomajoki 1977). The results are preliminary but reveal the right orders of size.

Populus tremula has the shortest meiosis of all species studied. The progress from an archaesporical stage to tetrads took in nature only 423 p.u.'s at its shortest. In an (unpublished) forcing experiment the period leptotene to tetrads was actually measured, and the result of 535 p.u.'s (in the laboratory) corresponds to slightly under 400 p.u.'s in nature. This includes a correction of −33 % from the laboratory result to compensate for the estimated effect of direct radiation.

The length of meiosis was considerably longer in the other species studied. The estimated figures are given with the direct radiation correction included (Table 2). The figures are thus fully comparable with laboratory conditions, the progress of development being in one hour, e.g., 5.00 p.u.'s at 10 °C and 16.18 p.u.'s at 20 °C. The length of meiosis in *Picea* is, then, about two times that of *Populus*, and in *Pinus sylvestris* the length of meiosis in nearly four times the shortest meiosis.

Table 2. Length of meiosis and tetrad phase.

Species	Length of meiosis in p.u.'s [1]	Length of tetrad phase	
		Absolute value in p.u.'s [1]	Percent of the length of meiosis
CONIFERAE			
Abies balsamea	950	–	–
A. lasiocarpa	1 050	–	–
A. sibirica	–	650	–
Larix spp.	2)	155	2)
Picea abies	1 100	320	29
Pinus cembra	–	660	–
P. peuce	–	660	–
P. sylvestris	1 950	555	28
DICOTYLEDONS			
Alnus incana	1 400	620	44
Betula pendula	1 320	1 030	78
B. pubescens	1 480	1 065	72
Corylus avellana	1 860	1 100	59

1) With direct radiation correction (see Luomajoki 1977).

2) Impossible to express in simple terms owing to dormancy phases included to the meiosis.

Details in II, III

The length of the tetrad stage could be measured in eleven species, but the results in *Larix decidua* and *L. sibirica* were almost identical, and were therefore combined. There was no difficulty in observing both ends of tetrad stage, i.e. cytokinesis and rupture of the callose wall. However, both incidents are rather subsceptible to high and low temperatures, and so the variation of the measurements is high. The figures for *Larix* are quite short for an application of this type of measurement in nature. However, eight measurements were performed to reduce the effect of errors. The most thoroughly studied species was *Pinus sylvestris* with no fewer than 23 measurements (II, III).

The tetrad phase was shortest in both *Larix* species, where the average was 155 p.u.'s including the direct radiation correction (Table 2). The next shortest tetrad stage was measured in *Picea*, 320 p.u.'s (correction included). This is 29 % of the length of the preceding meiosis in *Picea*. Even taking into account the variability of the data, it is safe to say that the tetrad phase is generally longer in Betulaceae than in conifers, both in terms of heat sums and in relation to the length of meiosis (III).

3.4. Adaptation and variability of the populations

In this material no differences were found in the heat sums for *Picea* at tetrad stage at different latitudes. Nor were there differences in the timing of the six provenances studied at Punkaharju. The adaptation of the early generative cycle in *Picea* seems to be small in the south - north direction. The longitudinal component of adaptation could not be studied.

The latitudinal differences were obvious in

Pinus sylvestris. There was, however, no evidence of the adaptation of the generative cycle itself. The differences found were judged to be located rather in the relative length of the winter dormancy rather than in the active period. At least there is a variable amount of p.u.'s included in the heat sums that are not associated with the period under study, the active period. This was apparent when a comparison was made between the variation of heat sums in *Picea* and *Pinus*, the variation being unduly high in *Pinus*. The latitudinal correlations in *Pinus* also varied between years 1967, 1968 and 1969 indicating not only different location of the zero point in different years but also an unequal balance latitudinally in the location of the zero point in different years (II).

The estimated length of the initial development in the generative cycle seems to be of a similar magnitude than the smallest heat sums measured for *Pinus* in the north. This suggests an almost immediate onset of development in the north in some years (but not every year). This is contrary to the development pattern in the south, which includes a lengthy margin against late frosts. The indirect methods used for finding the zero point were backward tracing of p.u. sums graphically, calculating an average of p.u. sums from the date (April 15) onwards (when the first morphological changes were seen in the PMCs according to other authors) and a (unpublished) forcing experiment at two stable temperatures. The corresponding estimates were 2 700–2 800, 2 753 and 3 035 p.u.'s. The last estimate is rather high, but the zero point can preliminarly be located at ca. 2 800 p.u.'s (in air temperature p.u.'s) before onset of the tetrad stage, i.e. in mid-April on average (II).

In *Betula* species, the latitudinal temporal correlations were practically the opposite of those observed in conifers. The best simulation of the timing of *Betula* species was achieved by using a single critical day length as a basis for calculations. This simple solution permits no conclusions about adaptiveness of the species studied. In terms of careful taxonomic scrutiny, *Betula* species do vary within Finland but this fact does not seem to influence the basic strategy of the timing of meiosis. As all Betulaceae species studied behaved very similarly, it is unlikely that varieties within species had different reactions with respect to the timing of meiosis.

The variability of *Picea* and *Pinus* populations at tetrad stage in terms of variation of heat sums was, within each species, almost uniform over the whole country. While the total variation in *Picea* in northern Finland was slightly smaller and that in *Pinus* larger than in southern Finland, the differences were not significant. A phenological indicator does thus not furnish any evidence of the decrease of variability in the northern populations or between northern populations of the two tree species (II). In *Betula pendula* the variation of heat sums was almost the same in the south as in the north. In *B. pubescens*, however, the variation in the north was considerably higher than in the south. The greater latitudinal spread of the northern subarea in comparison with the southern (2°43' vs. 2°01') may contribute to the larger variation. Because the temperature factor has far less influence on the timing in *Betula* than in conifers, emphasis can not be placed on this difference in heat sums. The variability in *Betula* in calendar time seems equally large throughout the whole country. Phenological indicators do not therefore support the hypothesis that variability of *Betula* populations in the north is smaller than in the south of Finland (III).

A comparison of the variability at the individual or small population level with the variability at the national level was possible in *Picea* and *Pinus*. Both parameters for *Picea* being of the same order, *Picea* populations can not be expected to vary much. The large difference in *Pinus* between the two parameters is partly due to zero point effects, i.e. inaccuracy of the plain p.u. sums that were cumulated during a period longer than that actually under study. It is, however, likely that the larger figures at the national level are also otherwise influenced, i.e. by variability of *Pinus* populations in a large geographic scale.

4. DISCUSSION

4.1. The annual cycle

4.1.1. Temperature and light as factors in the annual cycle

Many of the complexities found in the regulation of growth are evidently absent from the regulation of microsporogenesis when advanced as far as meiosis. The effects of environmental factors like water, temperature and light must still be considered, however. Sufficient moisture is the prequisite for the disappearance of water stress and so for the normal progress of microsporogenesis. For example, in the tropics meiosis can commence when the drought-maintained dormancy has been broken by rain (Mes 1957, Alvim 1960, Reddy and Narayan 1974, Browning 1977).

In the laboratory, the water deficit can also hamper forcing experiments with cut branches. In the northern cold and temperate zones, however, water stress is seldom strong enough in nature to interfere with the progress of microsporogenesis. During the present study no effects of water deficit were observed in nature.

Temperature is a factor that has to be considered throughout the annual cycle (e.g., Sarvas 1972, 1974, Fuchigami et al. 1982). Temperatures are also significant when other factors, such as the light factor, influence development. A partial exception in this connection being impulse-type effects of light that are involved with the somewhat temperature - compensated circadian rhythms (Mayer 1966, cf. Bünning 1961, Hamner 1963, Hillman 1976). While temperatures control rate of development they also contribute in the synchronization of the annual cycle (Sarvas 1974). The effects of temperature are known only to a limited extent, and the effect of temperature on development rate is one of the most neglected fields of study. Within meiosis the effect of low and high temperatures on karyokinesis and cytokinesis have been studied more thoroughly (review by Andersson et al. 1969; Michaelis 1926, Stow 1927, Andersson 1980).

Unlike temperature, light seems not to have affect on the timing of the generative cycle throughout the year. However, there are many kinds of light effects, and there is still no certainity which of these effects are involved in the annual cycle of trees. Besides the impulse-type effects mentioned, the sheer amount of radiation, relative changes in duration of daylight, relation between red and far-red radiation etc. may also be significant. The later part of the active period is known to be receptive to effects of light (e.g., Wareing 1956, Smithberg and Weiser 1968, Roche 1970, Anderson 1974, Fuchigami et al. 1982, Koski and Selkäinaho 1982) and during the chilling period trees may still be sensitive to certain other light effects than the inevitable short day (long night).

4.1.2. Dormancy

There is little current unanimity about the subphases involved in dormancy, of their extension in relation to each other, about relevant physiological needs, not to mention the incoherent terminology (cf. Perry 1971, Sarvas 1974, Kwolek and Woolhouse 1981, Fuchigami et al. 1982, Hänninen 1986). Following Sarvas (1974) dormancy in trees consists of two of the three main periods of the annual cycle. Autumn dormancy (or the chilling period) prepares a tree for full hardiness which is reached by the subsequent winter dormancy. Synchronization of the whole annual cycle, or prevention of accumulation of cycle deviations generated by annual environmental variation, is effected by a definite chilling requirement. In practice synchronization is tied to a quite restricted span of time (Sarvas 1974).

The most radical conceptual difference between Sarvas (1974) and most other authors (cf. e.g. Perry 1971, Fuchigami et al. 1982, Cannell and Smith 1983) is that Sarvas (1974) considers the most frost resistant phase (winter dormancy) to be attained first after the chilling requirement (autumn dor-

mancy) is fulfilled while others think deep rest is broken and frost resistance is reduced by the time the chilling requirement is fulfilled. In this case the chilling period has to be considered as more protracted, and as a less effective potential synchronizer. Incidentally, the idea of annual synchronization by a chilling requirement works according to Sarvas (1974) and Hänninen et al. (1985).

Dormancy often lasts for more than six months in Finland, and the latter part of dormancy, i.e. the winter dormancy, can alone be that long. Dormancy in *Larix* PMCs, nearly tantamount to the diplotene stage, is a good example of the protracted dormancy period. In winter 1969 - 1970, an average duration of 190 days in diplotene was measured in an individual tree of *Larix russica* at Punkaharju (I). The duration of dormancy is not the same in different *Larix* species and the duration also varies between years and localities. The duration of dormancy even varies slightly between adjacent trees of the same species (see table in I).

The length of dormancy is one of the most crucial characteristics of the adaptability of a species to a specific climate. *Larix gmelinii* is an exotic that vegetatively grows comparatively well in Finland, but in which male meiosis regularly fails. In 1969 the diplotene phase lasted only 39 days ending in mid-November, before onset of the real winter. In autochthonous stands of *L. gmelinii* in Siberia, the length of winter dormancy (or diplotene) must be sufficient to ensure success of the latter part of meiosis and it actually extends over the whole winter in those conditions.

Durations of developmental periods in nature are actually never fully comparable on a temporal scale, and this is also true with dormancy. Quantifying the duration of dormancy should be attempted (Sarvas 1974). However, experiences of such quantifying of dormancy in nature are not sufficient. This is not so in quantifying the early stages of active period in which p.u. heat sums have been applied almost routinely (Sarvas 1972, Luomajoki 1977 I, II, Chung 1981).

Quantifying meiosis during dormancy would be advantageous not only because this period lasts so long in calendar time, but because dormancy involves so much in terms of the adaptability of species. So most of the latitudinal variation observed in the timing of meiosis of *Pinus sylvestris* has to fall in the winter dormancy because in the early stages of the active period no signs of a sufficiently large adaptation were found to explain the considerable differences observed in the heat sums (II). The knowledge of quantifying dormancy is still tentative, and limiting of the subphases of dormancy so problematical that quantifying dormancy within meiosis has not been attempted in this study.

The need for chilling is known to exist in northern tree species (Perry and Wu 1960, Nienstaedt 1967, Kobayashi et al. 1982, Cannell and Smith 1983). Northern trees also retain their needs for chilling when moved to the south, and this often affects flowering and especially fruiting (Brenner 1912, Svedelius 1924, Zeller 1973).

Chilling requirements can be substituted for unnaturally high temperatures and long days (cf. Nienstaedt 1967, Simak et al. 1974, Kwolek and Woolhouse 1981) but the possible effects of natural light variations on chilling requirement is still an open question (Cannell and Smith 1983).

Dormancy is currently understood as another physiologically mobile period (Barr 1978, Kupila- Ahvenniemi et al. 1978, Tyurina 1979) and not as a state of standstill, except for a lack of any conspicuous stages with chromosomal movements in meiosis.

4.1.3. Parallel development in plants and insects

The development in a host tree and in an insect pest in spring is usually well synchronized (cf. Eidt and Little 1968). Especially the hatching of eggs of certain insects coincides well with bud burst in trees (Graf 1974, Wickman 1976), so egg development of insects is well adapted to local climatic conditions. Wickman (1976) found both the bud burst in *Abies concolor* (Gordon et Glendenning) Lindley and the egg hatch in Douglas-fir tussock moth to be closely related to accumulated degree-days.

According to J. Sarvas (1977) the physiological clocks of synchronized developmental processes are identical. Close synchrony with the host observed in development is an advantage to the pest, and the quite different developmental events, in buds of a tree, and in insect eggs seem able to adopt practically identical development rates.

Both the generative cycle in trees (Sarvas 1972) and reproduction of insects (Shelford 1927, Saarenmaa 1985) seem also to share the same sigmoid character of the development rate on temperature (Robertson 1973, Skjelvåg 1981), even if the temperature ranges are often different. According to Lumme (1982) temperature is the principal factor in spring also for *Drosophila littoralis* Meigen, while day length controls reproduction later in the summer. The terms of development in trees (e.g., Basset et al. 1961) and insects seem thus surprisingly similar not only in host-pest relationships, but universally.

4.1.4. Development rate and temperature

The effect of temperature on development rate has been studied mostly within applied sciences such as agriculture and forestry. Crop maturation prognoses for the canning industry (Balvoll and Bremer 1965) are usually based on the simple linear degree-day method (Ottonson 1958). While degree-days may serve well in agriculture, they are usually inadequate for physiological studies (cf. Robertson 1973). Shortcomings of the degree-day system have been somewhat lessened by calculated corrections involving both minimum and maximum threshold temperatures (Abrami 1972). Even so, degree-day methods can only satisfy limited needs. They are too coarse for short developmental phases. Further, in the long run threshold temperatures may shift (Wang 1960, Williams 1974). The degree-day system also involves the idea of compensation questionable in that no high temperatures exceeding the threshold are considered if the daily average does not exceed the threshold (Sarvas 1967). Hourly data are thus superior to daily values in certain studies.

The study of development rate was advanced when more suitable objects of study than vegetative growth were identified. Meiosis (Wilson 1959, Sarvas 1972) was an appropriate choice because regulatory functions of the plant or other environmental factors were less involved than in growth. So far, there are only two studies with really comprehensive temperature ranges, but considering the form of the curvilinear regression Wilson's (1959) and Sarvas' (1972) results agree quite well within the range 0–21 °C. At higher temperatures than 21 °C the similarity vanishes rapidly. However, Wilson (1959) had no accurate statistical basis for limiting the onset or the end of meiosis. The unavoidable errors in the estimates of the duration of *Endymion* meiosis must increase when dealing with the shortest periods, i.e. those measured at the highest temperatures.

Development at high temperatures should evidently be studied repeatedly, especially as neither of the studies mentioned show any retardation in development rate at high temperatures. Retarded development at high temperatures is plausible considering experiences from other experiments on development, e.g. spore germination (Waggoner and Parlange 1974). Relevant curvilinear regressions with an optimum and subsequent retardations have also been studied theoretically in the light of thermodynamics. Such regressions can be generated, e.g. based on the assumption of inactivation of control enzymes at low and high temperatures (Sharpe and De Michele 1977). Within species, especially in maize and in some fish species, tolerance of extreme temperatures was found to be better in heterozygotes than in homozygotes (reviewed by Stern and Roche 1974).

The development in the generative cycle may, however, be more homogenenous than could be expected at first thought. Development rates in *Populus tremula* (Sarvas 1972) and *Endymion nonscriptus* (L.) Garcke (Wilson 1959) seem to behave in very similar manner at least at low and medium temperatures up to 21 °C, i.e. at plausible springtime temperatures in nature, despite the fact the species studied belong to distant plant categories.

4.2. Limitations of the methods

4.2.1. Measuring subphases of microsporogenesis

The method of counting the frequencies of cells at various stages in a sample and then calculating the relative durations of the stages, assuming reciprocity between ob-

served frequencies and durations of individual stages, is known from the study of mitosis (e.g., Brown 1950, Mäkinen 1963). The mitotic division of cells is largely continuous at root tips, which are the usual objects of study when mitosis is concerned. The problem involved is rhythmicity or daily differences in division rate (Mäkinen 1963, Bevilacqua 1965, Hillman 1976) which can bias the estimates of stage durations.

The frequency method has also been applied to the study of the duration of individual stages of meiosis (Beatty and Beatty 1953, Hsu and Peterson 1981). However, the generation of new cells is not continuous in meiosis. On the contrary, the meiotic process can be described as a single wave of divisions with more or less variation as a stochastic element. A frequency-based estimate of stage durations is thus biased in favor of the stage that represents the mean of the progress at a moment. This temporal bias can be relieved by taking frequent samples at even intervals, but temperature should be kept stable to ascertain equality of intervals. An advantage of the frequency method is that large amounts of cells can be counted easily and, purely arithmetically, the method gives well-defined estimates.

PMCs can be inspected only once and so it is impossible to continuously follow development in an individual anther (or locule) not to mention an individual PMC. However, in cereals, progress of meiosis has been followed using previously aquired knowledge of the synchrony of progress of meiosis between spikelets, flowers and the three anthers of a flower (Lindgren et al. 1969, Bennett et al. 1971, 1972, 1973). The precision achieved depends on the accuracy of the synchrony in relation to developmental stage of the object of study. The synchrony is somewhat better in the beginning of the meiosis, however, the large differences often reported are only apparent (Luomajoki 1977, 1985). An obvious advantage of the method is that it does not call for large materials. Repeated study of the same species has also improved the original estimates of the duration of meiosis (cf. Roupakias and Kaltsikes 1977a, b).

The third method available is the one used in this author's studies, and it originates from Sarvas (1972). The two other methods described were impractical in the study of conifers, for which the last mentioned method was designed. Sarvas' (1972) method is the only one in which statistical parameters are used all the way, and accordingly this fact has to be considered in sampling, in microscopy as well as in calculating the results. Sarvas' (1972) method calls for relatively large materials, but it can be applied in nature as well as in laboratory and it also gives estimates concerning the variation involved.

4.2.2. Observation of the temperature

One prequisite of the present study was the continuous measurement of temperatures at each locality at tree-top level. This was found necessary owing to the microclimatic variation. However, effects of direct radiation could be taken in account only formally. This was possible owing to comparative seasonal measurements by Sarvas (1972) both in atmosphere and in buds of an adjacent tree.

The effects of direct radiation distort the lengths of developmental phases so that the same periods often appear shorter in nature than in the laboratory. However, the phases themselves are equally long at comparable temperatures both in nature and the laboratory. The routine corrections applied restore the approximate balance between measurements in the two surroundings. This parallels earlier findings that the duration of meiosis at each temperature is the same in nature and in the laboratory, and equal also in vivo and in vitro (Ito and Stern 1967).

Even though effects of direct radiation are the most severe inaccuracy in measurement of developmental intervals in heat sums in nature, it is useful to point out that this shortcoming does not considerably mar the most obvious benefit of the p.u. -system, i.e. the synchronization of the time and the heat sum scales so that the right sequence of events is always maintained even on a reduced thermal scale. This means that phenological observations made with the aid of the p.u. -system are particularly accurate in temporal scale, even though shortcomings mentioned occur in measurement of developmental intervals in heat sums. On the other hand, the measurement by thermographs at each locality is expensive, and more perfect

methods were rejected on purely economical grounds.

A possible source of error lies in the age of trees under study. It has been found that young trees usually develop earlier in the spring than mature trees, at least vegetatively (Nienstaedt 1974), while age differences in mature trees are not significant (Morris et al. 1957). There are no comparable clear-cut experiences about the timing of the flowering in old and young trees. However, in the present studies only mature stands were studied, and so this hypothetical source of error was avoided.

4.2.3. The observable and the unobservable

It is tempting to draw physiological conclusions from the visual obsevations made. Archesporic PMCs are fully developed in the male buds of many conifer species already in late autumn, not to mention the species in which meiosis actually begins in the autumn. It is only natural to think that the onset of meiosis in the spring is a reliable sign of the breaking of winter dormancy and start of the active period.

Sarvas (1972) considered the onset of meiosis both in *Picea abies* and *Pinus sylvestris* as probable locations of the zero point, i.e. the onset of the active period. In *Picea*, however, Sarvas (1972) did not mean the onset of the leptotene phase but an earlier phase of microsporogenesis when the first signs of contraction of chromatin in the nuclei of PMCs were observed. From tables on the length of winter dormancy it can be determined that Sarvas (1974) placed the zero point in *Pinus* approximately at the onset of leptotene.

The hypothesis concerning the location of the beginning of the active period at the onset of meiosis is not supported by this author (II). In *Picea* development in the active period has to start considerably earlier than the meiosis itself, and probably earlier than any cytological changes are visible on the light microscope. In *Pinus* this temporal difference is much more pronounced and the initial phase of submicroscopic development is still longer (II). However, a correspondence between the first changes in PMCs and tapetum visible on the transmission electron microscope (Kupila-Ahvenniemi 1966) in spring and the onset of the active period, is plausible, and the author (II) gave support to this location of the zero point by indirect evidence given by heat-sum calculations.

The onset of the diakinesis stage in the meiosis of *Larix* is a far more reliable indicator of a change into the physiology of active period. However, there is no reason to think that major physiological changes are simultaneous (cf. Sarvas 1972) with phase changes easily observable under the light microscope. In theory, an earlier onset of development first allows large enough changes to be visible under the light microscope (II).

4.2.4. Cold tolerance of stages in microsporogenesis

The reservations outlined above concerning conclusions about physiological activity should also be extended to the interpretation of meiotic irregularities caused by extremities of the environment. It is well known that irregularities typical to each meiotic phase are present and that the abundance of irregularities visible at each phase vary (Eriksson 1968), even in the same conditions. This often leads to direct conclusions about sensitivity of the individual stages (Eriksson 1968, Andersson 1980), and the stages from diakinesis to anaphase I and from metaphase II to telophase II were found the most sensitive. However, it can be expected that damage caused earlier, even as early as in the premeiotic phase, may only become visible much later.

It is also obvious that irregularities are better visible during the more kinetic phase of meiosis (Luomajoki 1977), for example bridges in the anaphases which could well be caused by damage during the earlier phases. However, it is known that severe damage to PMCs leads to their rapid death (Luomajoki 1977, Andersson 1980) and so severe damage can not be latent for lengthy periods.

The cold tolerance of PMCs has been estimated by following ambient temperatures during sensitive stages of succesful and destroyed meioses. The critical temperatures are around −10 °C, or even lower, both for *Larix* (Luomajoki 1977) and *Picea* (Andersson 1980). With reference to these observations of critical temperatures the significance of the

length of exposure to cold is not very well known, but it is plausible that most of minimums recorded have been effective for at least a number of hours. Also, the speed of the change in temperature may, in extreme conditions, be significant (Biel et al. 1955, Andersson 1980).

In controlled experiments the effects of cold can be more precisely appraised. Michaelis (1926) came to the conclusion that a temperature of only −4 °C caused a multitude of irregularities in meiosis of *Epilobium* leading to irregular pollen. Contrary to findings by Eriksson (1968) and Andersson (1980), Michaelis (1926) found the prophase (incl. diakinesis) in PMCs of *Epilobium* more sensitive to cold than the later stages, often thought to be the most sensitive. However, there is unanimity about the excellent frost resistance of the dormancy-adapted diplotene stage in *Larix* (Eriksson 1968, Luomajoki 1977). Similarly, the dormancy-adapted pachytene stage in *Pseudotsuga* (Owens and Molder 1971) is frost resistant, and healthy pollen is known to form even in Finland, where this species is also exotic.

4.3. Adaptation and variability

4.3.1. The latitudinal and longitudinal components of variation

Latitudinal and longitudinal variation in *Picea abies* and *Pinus sylvestris* have been assessed by morphological measurements (e.g., Ruby 1967) and by observing phenological characteristics (e.g., Wright and Bull 1963). Both the latitudinal and the longitudinal variation within Europe correlate with a change in climate.

Owing to the direction of mountain ranges from west to east and to the effects of glaciation, including the time factor, the clinal changes in Europe along the latitudinal or the longitudinal gradient are not as explicit as might be expected. For example the patterns of change in *Picea* and *Pinus* are different. The patterns of change may be accentuated in one direction and be lacking in the other direction, while local variation is often high (Wrigh and Bull 1963, Karrfalt et al. 1975, Steiner 1979).

Latitudinal clinal variation in *Pinus sylvestris* has been frequently reported (see review by Eriksson 1982 and also Wright and Bull 1963, Hiltunen et al. 1975, Chung 1981, Mikola 1982). In *Picea abies* there seems to be far less latitudinal variation (Langlet 1960, Lundkvist 1979, Krutzsch cit. by Eriksson 1982), at least within Scandinavia. On the other hand, longitudinal variation in *Picea* seems to be quite strong within certain latitudes (Langlet 1967, Krutzsch cit. by Eriksson 1982). The author's observations (II) fit earlier findings well. No experiments with different provenances of *Pinus* were made by the author, but there was significant latitudinal correlation in the heat sums required for the onset of the tetrad stage. No such correlation existed in *Picea*, and a limited test also failed to reveal any significant differences in the six provenances (II). The latitudinal invariability found in *Picea* may be associated with its well-known capacity to tolerate even extreme transfers in south-north direction while Scots pine is quite intolerant in this respect (Langlet 1967).

4.3.2. Retaining of variability

Northern populations of tree species in Finland at the latitude of ca. 68° or higher can be considered marginal. For example, owing to their frequent inability to produce mature seed. These marginal populations were once believed to be practically homozygous (Sarvas 1970b, cf. Stern and Roche 1974) but much variability has been later found. As phenotypic variation correlates with heterozygoty (e.g., Stern and Roche 1974, Knowles 1979) variability of populations can be used in assessing heterozygoty of outcrossing populations. Isozyme variation has also been used for studying genetic variability. This latter approach has shown that there is plenty of genetic variability of allozymes in *Picea abies* and this means that the marginal populations have retained a high level of heterozygoty (Tigerstedt 1973, Tigerstedt et al. 1979).

Sarvas (1970a) reported that phenological variation in northern Finland is smaller than

in southern Finland, while Rozhdestvenskii (1981) found enlarged phenological variation in meiosis of *Picea obovata* Ledeb. in Salekhard, Siberia. Andersson (1965) and Ryynänen (1982) pointed out there is lot of variability in the maturation of Norway spruce and, respectively, Scots pine seeds in the marginal populations.

As far as phenological variation reflects genetic variability, the views of retained variability in the northern populations can be confirmed by the considerable variation observed in the timing of meiosis (II). Lack of latitudinal variation in *Picea* and high heterozygoty in the north may both be explained by the mainly unidirectional gene flow from south to north. This follows from prevailing southwestern winds and the fact that male flowering in Norway spruce and in Scots pine is later than female flowering (Sarvas 1962, 1968) on average. Gene flow is directed from late flowering (southern) individuals to early flowering (northern) individuals (Koski 1970, Tigerstedt et al. 1979, Chung 1981). This condition should retard the tendency of the northern populations to develop earlier flowering and shorter active period. However, this conclusion does not assist an understanding of the dissimilar latitudinal characteristics of Norway spruce and Scots pine.

4.3.3. Adaptive forces and variability of cycle intervals

A stochastic model consisting of normally distributed variables has become indispensable for understanding the life cycle of insects. Owing to hard selection the reproduction of certain *Drosophila* species is forced into certain seasonal limits owing to the probability of spring and autumn frosts (Lumme 1982). Otherwise, the length of the reproduction period of the flies would certainly increase.

The development of trees contains similar stochastic elements. In trees, also, there should be populations of individuals normally distributed with respect to early and late development. Because the temporal distance of generations is much larger in trees than in flies, the effects of such selection are not instantly apparent in trees. Selection may in fact affect differently the vegetative and generative cycles of trees. Selection must be harder on the vegetative cycle where the survival of a tree is concerned. On the other hand the adaptative forces must influence the generative cycle of the tree less critically because only the success of an annual reproduction is concerned, not the survival of the individual. There may thus be a connection between the surprisingly large variation found in the north and the plausible weak adaptative forces in the generative cycle (cf. Stern and Roche 1974). Because trees are long-lived, a limited success in reproduction, e.g. every tenth year or even more rarely, may be sufficient. It is a well-known fact that the marginal populations of conifers in northern Finland produce good seed crops only infrequently (Renvall 1912, Koski and Tallqvist 1978). Andersson (1965) considered the generative cycle of *Picea abies* to be rather ill-adapted to the climate of northern Sweden.

The maturation of conifer seed is one of the better known aspects of annual cycle variation with respect to the warmth (or the temperature sum) of the local summer (Sarvas 1970a). Considering variation in the maturation of seed at the population level, complete maturation of the seed crop is not self-evident even in central Finland. Northwards, the probability of such an event falls rapidly (Ryynänen 1982).

Sarvas (1972) investigated the distribution of the passing of a certain developmental phase in young *Picea abies* female cones. In terms of p.u. sums the distribution at that stage can be considered about normal. Sarvas (1974) also found the chilling requirement of *Betula pubescens* seeds to be normally distributed. Perry (1971) also emphasized the variation in chilling requirement within a species.

While only a few accurate observations have been made concerning the distribution of events in the annual cycle of trees, it is pertinent to consider all events of the annual cycle to be basically normally distributed. If an event is normally distributed, the subsequent events should also have a similar distribution. If not, the reason for the difference should be carefully considered. Damage to PMCs restricted in a part of the population owing to spring frosts (Luomajoki 1977, II) and non-continuances in appearance of potential chilling temperatures (Sarvas 1970b,

1974) may both affect the distribution of events. Accordingly, narrowing of a distribution (Luomajoki 1977) probably with a shift of the mean (II), or fracturation of the distribution into parcels (Sarvas 1974) have been observed.

4.4. The timing of meiosis and the time of flowering

The time of the onset of meiosis in different species and the subsequent time of flowering do not always correlate well. Not only are the meioses of unequal lengths in different species, but also overwintering of PMCs prior to meiosis, in meiosis or after meiosis can render the timing of microsporogeneses in various species comparable only during a limited part of the process. The onset of the tetrad stage and the flowering time of species generally correlate much better.

Comparing eleven tree species in which the tetrad stage is reached in the spring (II) the succession of flowering is the same as the succession of the completion of meiosis. However, *Populus tremula* in which the completion of meiosis occurred at the same time or slightly later than in *Larix decidua* and *L. russica*, flowers perceptibly earlier than the two *Larix* species.

In *Alnus*, *Betula* and *Corylus* overwintering at the microspore stage weakens the considerable synchrony found in species at the tetrad stage (III) so that flowering time in the different genera does not coincide. Within genera, the synchrony is better and there is still some overlapping at anthesis.

4.5. Lengths of meiosis and of tetrad stage

The length of meiosis is here considered as the duration of the interval from the beginning of leptotene to the end of telophase II and can be given in any temporal units. However, the rate of progress in meiosis is highly temperature-dependent. The stable temperature involved should thus be announced. It is impossible to define the duration of meiosis at variable temperatures in a dependable way in temporal units.

However, after estimating the regression of development rate on temperature, the length of an interval at any stable temperature or at variable temperatures can be given by a single figure of a specialized unit. For generative development in trees such a regression is available (Sarvas 1972), and this is the period unit system used in the present study. Such methods are rare in botany, but in the study of egg and pupal development of insects, similar methods have been used several times (Shelford 1927, Messenger and Flitters 1958, 1959). In insects, the regression is also curvilinear, but the main difference with respect to trees lies in the often narrower range of permissible temperatures between thresholds of 100 % mortality. On the other hand, reproduction of certain insects, including meiosis, can take place under snow cover at temperatures hardly exceeding 0 °C (Hågvar 1976). As far trees are concerned, the effects of highly fluctuating temperatures on the development rate are not fully known (cf. Ryan 1941), so estimates of the duration of intervals under such conditions can only be approximate.

In the present investigation, a range of lengths of meiosis in trees from 535 to 1950 p.u.'s (in laboratory) was observed. This is equivalent to durations of 33 to 120 hours at 20 °C. There is very little information available on duration of meiosis in trees and it is also impossible to unambiquously assess the duration of meiosis if a dormant phase is included in the course of meiosis (e.g., in *Larix* and *Pseudotsuga*). However, description of meiosis in *Populus alba* (Pospišil 1966) permits the conclusion that meiosis in that species is very short, probably considerably shorter than that in *Populus tremula* which was measured as 535 p.u.'s.

A short meiosis is plausibly a characteristic of genus *Populus*. The estimates for two *Abies* species and *Picea abies* range from 950 to 1 100 p.u.'s, and the estimates for *Alnus incana* and two *Betula* species range from 1 320 to 1 480 p.u.'s. These figures suggest that the duration of meiosis is of the same order in closely related species. This is also the case in cereals, the length of meiosis being 630–825 p.u.'s in several diploid cereals and 3 100–4 270 p.u.'s in two *Lilium* species (calculated from figures by Bennett 1977). The duration of meiosis in *Lilium* is thus relatively very long, that of *Beta* and *Vicia* (see Bennett 1977) being of the shortest kind (at ca. 320 p.u.'s) and so roughly equivalent to *Populus alba*, and also to a moss, *Ceratodon purpureus* (Luomajoki 1985).

The length of the tetrad phase can be measured in similar terms as that of meiosis. However, the duration of the tetrad phase is generally quite short in comparison to meiosis and is, therefore, more difficult to measure accurately. A range from 155 to 1100 p.u.'s was measured in trees, the shortest tetrad phase by far being found in *Larix* and the longest in *Corylus*. This range is equivalent to 9.6 to 68 hours at 20 °C.

There are still fewer observations of the length of the tetrad phase in trees than of the length of meiosis. However, there are several measurements from cereals. The figures given by Roupakias and Kaltsikes (1977a, b), for 18 cultivars of rye, wheat and triticale are surprisingly invariable ranging in terms of p.u.'s from 115 to 144 p.u.'s (7.1 to 8.9 hours at 20 °C). In fact, the lengths of the preceding meioses varied more (27.5 to 47.9 hours), and there was apparently no accurate correlation between the lengths of meiosis and those of the tetrad phase. The relative length of the tetrad phase, however, can be typical in different plant categoria, being 15.0 to 28.0 % of the preceding meiosis in various cereals (Roupakias and Kaltsikes 1977a, b), 30.4 % in maize (Hsu and Peterson 1981), 28.6 and 28.9 % in Scots pine and Norway spruce (II), respectively, and from 44.3 to 78.1 % in four species of Betulaceae (III). A very accurate correlation between the length of meiosis and the length of tetrad phase is probably not possible considering the sensitivity of sytokinesis to low and high temperatures (II).

SUMMARY

The timing of the onset of the tetrad phase of microsporogenesis in sixteen tree species growing in natural conditions in Finland was studied by calendar days and by period unit and degree-day heat sums. Latitudinal variation and variation between successive years could be studied in four of the species. The timing of three to twelve stages of male meiosis in eleven of the species was also studied. The length of meiosis was evaluated in nine of the species and that of tetrad phase in eleven species.

The tetrad phase of microsporogenesis in the conifers studied and in *Populus tremula* L. was reached in the spring, i.e. from late March to early June including the yearly and the latitudinal variation. The tetrad phase in Betulaceae was reached from late July to mid-August incl. the latitudinal variation.

The microsporogenesis in Betulaceae species was found to differ in ecophysiological terms from the other species studied in that the timing in Betulaceae was rather day-length-dependent than heat sum-correlated. In conifers and in Populus the timing of the tetrad phase correlated well with accumulated heat sums and did not correlate with day length or any kind of thermal threshold. This difference was judged to be associated to seasonal adaptive strategies rather than to taxonomic relationships.

In addition to the Betulaceae species studied, pronounced latitudinal differences in accumulated heat sums were found in *Pinus sylvestris* L. Similar differences could not be found in *Picea abies* (L.) Karsten. The adaptivity of the early generative period seems low. The difference between *Pinus* and *Picea* was thus accounted for unequal durations of winter dormancy in *Pinus*, leading to unequal margins against late frosts in the south and in the north. The phenological variation measured in the north was roughly equal to that in the south. This indicates that genetical variation is probably retained in the northern marginal populations.

The microsporogenesis in exotics (eight of the sixteen species) was well adapted to local Finnish climate, the exception being *Larix gmelinii* (Rupr.) Kuzeneva, in which male meiosis regularly took place prematurely leading to destruction of the pollen mother cells by frost. This condition can be accounted for by an inherently too short winter dormancy in *L. gmelinii* for the Finnish conditions.

The length of meiosis in the tree species studied varied so that the longest measured (in *Pinus sylvestris*) was 3.6 times that of the shortest (in *Populus*). The length of the tetrad stage varied also, the longest (in *Corylus avellana* L.) being 7.1 times the shortest (in *Larix*). There was no apparent correlation between the length of the preceding meiosis and between the length of the tetrad stage, but a taxonomic trend is visible in that the lengths of the tetrad stage in Betulaceae are the longest both in terms of heat sums and as percentages of the preceding meioses.

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SELOSTE

MIKROSPOROGENEESIN AJOITUS JA PUULAJIEN ILMASTOLLINEN SOPEUTUMINEN

Kuudentoista puulajin mikrosporogeneesin ajoitusta tutkittiin Suomessa pitäen tetradivaiheen alkamista vertailukohtana. Ajoitusta selvitettiin kalenteriajassa sekä kahdella lämpöasteikolla: tehoisa lämpösumma Σ (t-5) ja period unit -summa (katso Sarvas 1972). Latitudinaalista vaihtelua sekä vuosien välistä vaihtelua voitiin tutkia neljässä puulajissa. Yhdessätoista puulajissa voitiin selvittää meioosin vaiheiden ajoitusta: kolmesta kahteentoista vaiheeseen puulajin mukaan. Meioosin pituus saatiin arvioiduksi yhdeksällä lajilla ja tetradivaiheen pituus yhdellätoista lajilla.

Havupuilla sekä haavalla mikrosporogeneesin tetradivaihe saavutettiin maaliskuun lopun ja kesäkuun alun välillä latitudinaalinen ja vuosittainen vaihtelu mukaan lukien. Koivuilla, lepillä ja pähkinäpensaalla tetradivaihe saavutettiin vastaavasti heinäkuun lopun ja elokuun keskivaiheen välillä.

Ekofysiologisesti koivukasvien heimon puut erosivat muista tutkituista puulajeista siinä, että meioosin ajoitus osoittautui enemmän päivänpituuden kuin lämpösumman säätelemäksi. Tästä syystä meioosi oli Pohjois-Suomessa jonkin verran aiemmin kuin Etelä-Suomessa. Havupuilla ja haavalla tetradivaiheen saavuttaminen korreloi kertyneiden lämpösummien, mutta ei päivän pituuden eikä minkään määrätyn lämpökynnyksen kanssa. Näillä lajeilla meioosi oli pohjoisessa huomattavasti myöhemmin kuin etelässä. Tätä eroa kahden lajiryhmän välillä ei voi kuitenkaan katsoa lajien sukulaissuhteesta johtuvaksi, vaan se ilmentää ilmastollista sopeutumista, joka edellyttää eri säätelykeinoja eri vuodenaikoina.

Koivukasvien ohella myös kotimaisella männyllä havaittiin huomattavia eroja tetradivaiheeseen mennessä kertyneissä lämpösummissa eri leveysasteilla. Kuusella ei ollut vastaavaa latitudinaalista vaihtelua. Koska puiden generatiivisen syklin alkuosan adaptiivisuus vaikuttaa alhaiselta, kuusen ja männyn eron voi selittää männyn talvihorroksen suhteellisilla pituuseroilla. Näin ollen pohjoisessa on paljon pienempi marginaali kevähalloja vastaan kuin etelässä, jossa generatiivinen kehitys alkaa lämpösumma-asteikolla mitaten suhteellisesti myöhemmin. Pohjois-Suomessa fenologinen vaihtelu oli suurin piirtein samansuuruista kuin Etelä-Suomessa. Tästä päätellen myös geneettinen variaatio säilyy pohjoisissa marginaalipopulaatioissa.

Tutkituista kahdeksasta vierasperäisestä puulajista seitsemän lajin mikrosporogeneesi oli sopeutunut Suomen ilmastoon. Dahurian lehtikuusen hedemeioosi epäonnistui säännöllisesti liian lyhyen talvihorroksen vuoksi. Meioosin jälkiosa, jonka olisi pitänyt osua maalis-huhtikuulle, alkoi ennenaikaisesti ennen sydäntalvea, jopa edellisen vuoden marraskuussa.

Puiden meioosin pituus (leptoteenin alusta telofaasi II:n loppuun) vaihteli siten, että männyn meioosi oli noin 3,6 kertaa haavan meioosia pidempi. Tetradivaiheen pituus vaihteli vieläkin enemmän: pähkinäpensaan tetradivaihe oli noin 7,1 kertaa pidempi kuin lehtikuusilajeilla. Edeltävän meioosin ja sitä seuraavan tetradivaiheen pituuksilla ei ollut riippuvuussuhdetta. Koivukasvien heimossa tetradivaiheen pituus oli kuitenkin suurin sekä lämpösummana että suhteellisesti (prosentteina) meioosin pituuteen nähden.

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