2. Cone yield depends clearly on the disposition of the female clone, the influence of the male parent being insignificant. According to their tendency of keeping or dropping cones two types of clones can be distinguished:
   type I: cone development is corresponding to the annual variations of the plantation means.
   type II: cone development is relatively constant every year.
   There were significant clone specific differences in the tendency to keep or drop cones.
3. The seed yield per cone rnay be used as unit of reference for evaluating the mating disposition of the clones in quantitative terms. The number of the total seeds per cone is determined by the female parent, but the relation between full and empty seeds in a cone depends on the compatibility with the male parent.
4. Quantity and quality of pollen decide upon the number of ovules in a cone which will develop. Therefore, in a seed orchard with insufficient pollen production only poor seed yields are to be expected.
5. With a few exceptions most of the examined pine clones showed a high self-sterility.
6. Mating disposition of a clone rnay differ according to its utilization as female or male partner.
7. The female parent determines also the thousand seed weight, which rnay vary in a certain margin. Between the TSW and the number of corns per cone exist negative correlations.
8. The probable seed yield of a seed orchard can be forecast with acceptable reliability, if flowering behaviour, cone drop, total seed yield as well as mating disposition of the clones are known.

Key words: Seed orchard, progeny test, flowering behaviour, clones, cone set, seed yield, thousand seed weight.

Abstract

In three seed orchards of Pinus sylvestris L. five years observations on the flowering, cone set and seed crop behaviour of clones in controlled and free pollinations as well as in selfings yielded valuable aspects to the estimation of presumable seed productions in seed orchards.

The age of the grafted trees will influence the flowering capacity, the disposition of the clone rnay regulate the degree of the male or female florescence.

Clone specific reactions could be observed in respect to cone set, seed yield per cone and thousand seed weights. These characters are determined by the female crossing partner. The male partner or influences by climatic conditions (years of pollinations) will only take effect within a clone specific range set by the female. But quantity and quality of the used pollen will decide upon the number of ovules which rnay develop. Self-sterility or incompatibility in the crossing partners show in an increased amount of empty seeds per cone. The relation between full and empty seeds can be used as unit of reference for evaluating the mating dispoeition of the clones. The mating disposition of a clone rnay differ according to it's utilization as female or male parent.

The probable seed yield of a seed orchard can be forecast with acceptable reliability, if flowering behaviour, cone set and total seed yield as well as the mating disposition of the clones are known.

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Male Meiosis in Sitka Spruce, Picea sitchensis (Bong.) Carr.

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Introduction

It is only recently that there has been a growing interest in the process of meiosis in Conifers (see ANDERSON *et* al. 1969). Although the course of meiosis is similar to that found in other higher plants, there are two features, clumping ob chromosomes around the nucleolus at prophase-I and diffuse diplotene, which are typical of some conifer genera but are not general features of meiosis in all higher plants.

The ability to study meiasis is essential for any crop plant since defects in the process rnay often give rise to reduced fertility. In this respect we were particularly anxious to study meiosis in Sitka spruce for, in addition to its importance as a timber crop (FLETCHER and FAULKNER, 1972) some provenances also contain supernumerary chromoso-

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mes (Moir and Fox, 1972). Supernumerary chromosomes, in some plant species, may have dramatic effects on meiosis such as the regulation of pairing between homologous and homoeologous chromosomes, the formation of chiasmata in regions normally protected from recombination and the production of univalents chromosomes (see Jones, 1975 for review of supernumerary chromosomes.)

Sitka spruce does not reproduce until about 20 years old. This fact in combination with the occurrence of reproductive buds in the crown of the tree (Allen and Owens 1972) makes Sitka spruce a difficult subject in which to study meiosis. However, in combination with work on bud differentiation in this species (Moir and Fox, 1975) we have been able to follow the whole process of male meiosis and both the quantitative and qualitative aspects of meiosis are dealt with in the present Communication. Unfortunately, supernumerary chromosomes were not present in the trees employed but these studies constitute a necessary basis on which to plan further work.

Material and Methods

Male buds were collected from four 41 year old trees, (A, B, H and K) growing at Roseisle Forest, Elgin (Samuel *et al.* 1972) in the spring of 1973 and 1974. Microsporophylls were dissected out and squashed directly, without fixation, in 2% lacto-propionic orcein. Preparations of pollen mother cells (P. M. C.'s) and microspores suitable for photography were produced by this method. In some cases the technique was altered for premeiotic tissues. Buds were fixed in 10% phosphate-buffered formalin for 2½ hours, washed in distilled water for 24 hours, then fixation continued in Carnoy's fluid (6 parts alcohol, 3 parts chloroform, 1 part acetic acid) for a further 24 hours. This was followed by hydrolysis and staining by the Feulgen technique. The date of collection and "external" and "internal" length of buds (Moir and Fox, 1975) were all carefully recorded prior to fixation and squashing.

Results

Qualitative

Premeiotic sporogenous cells are thin-walled, compact and polyhedral in shape. They have darkly staining cytoplasm and a large granular nucleus, often with two large nucleoli *(Fig. 1)*. Prior to leptotene the cells enlarge to approximately four times the diameter of the smallest tapetal cell. The tapetal cells undergo mitosis *(Fig. 2)*. Formation of a reticulate nucleus marks the initiation of leptotene. The highly attenuated single strands are often evenly distributed throughout the nucleus but sometimes they tend to cling in a tangled mass filling only a portion of the nucleus *(Fig. 3)*. Small chromomeres can be seen along the length of the strands and over 40 chromocentres may be counted in some nuclei. The microsporophyll contents are still gelatinous at this stage but later when the microsporophylls burst more easily, cells with both single and double strands *(Fig. 4)* can be seen. This is due to the synapsis of homologues and marks the beginning of zygotene. Pairing of homologous chromosomes is accompanied by increased chromosome tangling and a movement of the nucleus to one side of the cell. At this stage of late zygotene *(Fig. 5)* short unpaired regions may still be observed where chromosome loops are not included in the general mass of chromatic material. In other parts intimate pairing of chromomeres can also be seen. Often during this stage up to five nucleoli are present in each cell and a high percentage of tapetal cells is in mitosis. Chromosome contraction continues and the cell enters pachytene *(Fig. 6)*. The chromomeres appear to swell and make the strands distinctly broader and more beaded. Maximum packing of chromosomes to form a tight ball occurs at this stage and the number of tapetal cells undergoing mitosis diminishes rapidly.

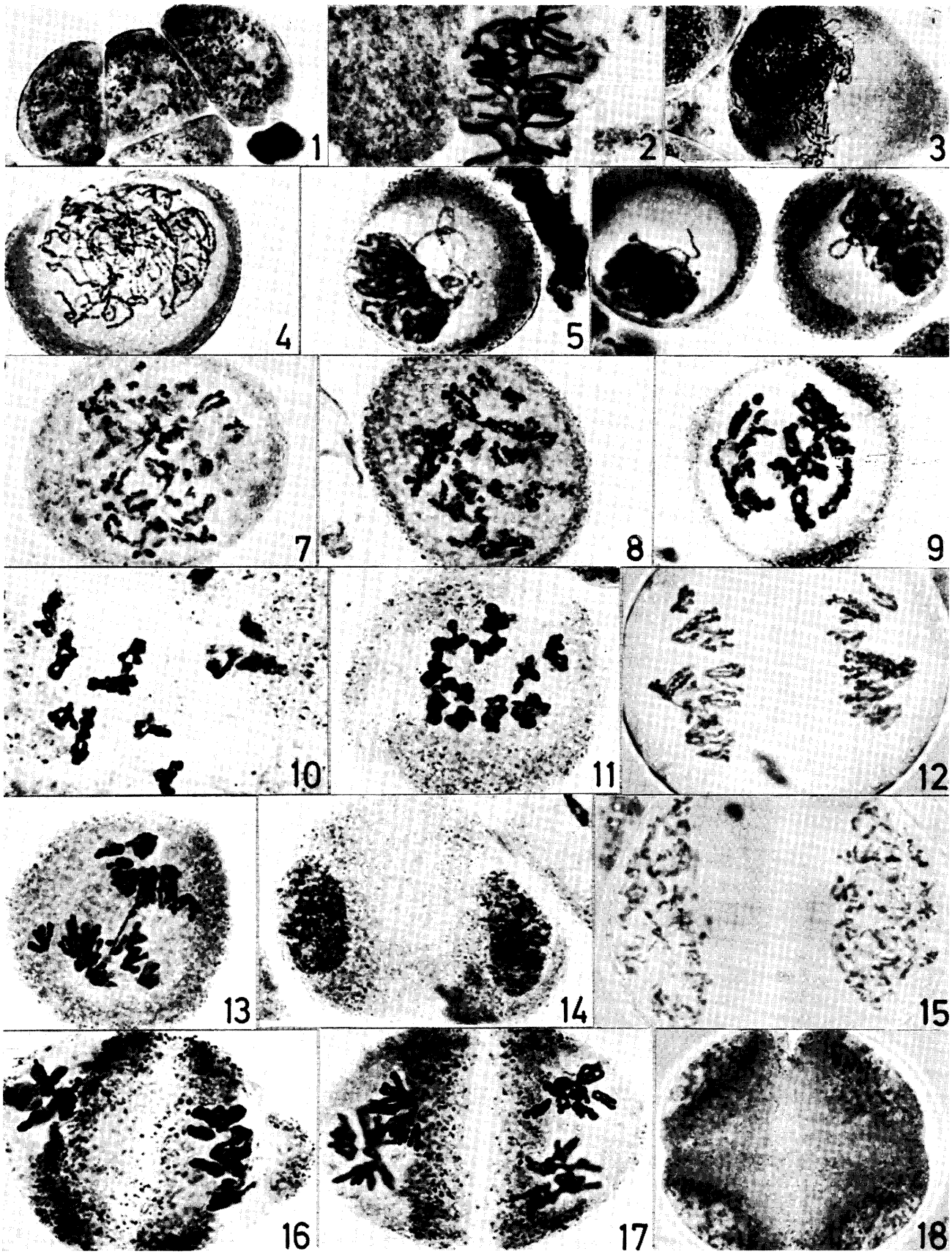
Early diplotene *(Fig. 7)* is characterised by diffuse staining as the bivalents become dispersed throughout the enlarged nucleus. As diplotene progresses the bivalents shorten and thicken and achromatic segments *(Fig. 8)* become increasingly obvious. Only in late diplotene *(Fig. 9)* is it possible to recognise a few individual bivalents with their repulsed homologues and binding chiasmata. Even during diakinesis it is difficult to study in detail the number and localisation of chiasmata because of the pattern of coiling in the homologues and the persistent achromatic regions *(Fig. 10)*. As metaphase-I approaches the nucleoli disperse and the nuclear membrane breaks down. Although very occasionally it is possible to count the number of bivalents on the equatorial plate, usually at this stage the bivalents are in the form of a sticky mass *(Fig. 11)*. However, in both *Figs. 9* and *10* the general features of chiasma distribution can be seen with up to five chiasmata per bivalent and no obvious pattern of localisation.

As the chromosomes separate at anaphase-I, centromere locations can be seen. In this study, all observed positions were more or less metacentric although some members of the complement are known to be acrocentric (Moir and Fox, 1972). Sister chromatids are splayed and on occasions even the chromatid tips appear to be split in two with a thickening at the end of each strand *(Fig. 12)*. Subchromatid bridges are occasionally seen *(Fig. 13)*. Chromosome despiralisation, typical of telophase, and entry into cytokinesis follow in rapid succession. The appearance of the interkinesis nuclei *(Fig. 14)* closely resembles that of the premeiotic nuclei. No cytokinesis takes place after the first meiotic division although there is a lightly stained area of cytoplasm between the two daughter nuclei. This region persists until the end of meiosis. Following a brief interkinesis the chromatin again contracts in preparation for the second division. Initially, individual chromosomes of prophase-II cannot be recognised because of their segmented appearance resulting from the presence of achromatic regions *(Fig. 15)*. Very occasionally the two spindles inside the metaphase-II are orientated at right angles to each other *(Fig. 16)* though more often *(Fig. 17)* they are orientated in such a way as to give rise eventually to a tetrad of cells lying in the same plane. Before being enclosed in microspore cell walls, the four granular interphase nuclei move to the circumference of the cell *(Fig. 18)*.

Quantitative

Meiosis fell naturally into five periods, each being demarked by buds in one cell division phase for a long period (pre-leptotene, 1; tetrads, 4; pollen, 5) or passing through two (leptotene — pachytene, 2) or more (diplotene — telophase-II, 3) phases in rapid succession.

The relationship of "external" bud length to meiotic stage over the two seasons is presented in *Figs. 19* and *20*. *Fig. 19* revealed bimodal distributions in three periods, 2, 3 and 5. This was particularly emphasised in period 3. In the 1974 material *(Fig. 20)* there was only a slight suggestion of bimodality in periods 1 and 2. In both seasons when buds reached 5—6 mm "external" length they entered meiosis. However, the peak frequency of period 2 (leptotene-



Figures 1—18. — Male meiosis in Sitka spruce. Magnification ×800. *Fig. 1.* — Pre-leptotene sporogenous cells. *Fig. 2.* — Metaphase of tapetal mitosis. *Fig. 3.* — Leptotene. Note chromocentres and excentric placement of chromosome mass. *Fig. 4.* — Early zygotene. *Fig. 5* — Late zygotene. Unpaired regions still visible. *Fig. 6.* — Pachytene. Chromomeric organisation can be seen in paired homologues projecting from the chromosome mass. *Fig. 7.* — Early diplotene. Note diffuse regions. *Fig. 8.* — Mid-diplotene. Achromatic regions still visible. *Fig. 9.* — Late diplotene. Chiasmata can now be seen clearly in the fully-condensed bivalents. *Fig. 10.* — Diakinesis. *Fig. 11.* — Metaphase-I. *Fig. 12.* — Anaphase-I. *Fig. 13.* — Anaphase-I showing sub-chromatid-type bridge between the two groups of half-bivalents. *Fig. 14.* — Interkinesis. Note the absence of cell plate formation but the presence of a region of pale-staining cytoplasm between the two daughter nuclei. *Fig. 15.* — Prophase-II. *Fig. 16.* — Metaphase-II. The axes of the two spindles are placed at right angles to each other. *Fig. 17.* — Metaphase-II. The axes of the two spindles are more or less parallel. *Fig. 18.* — Post-meiotic interphase with cell plate formation just beginning.

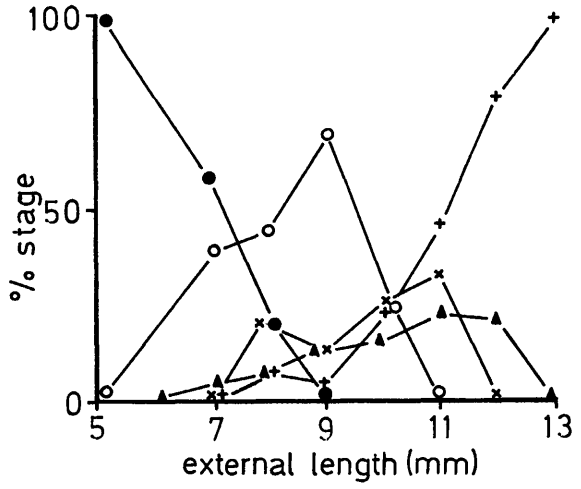


Figure 19. — The relationship between "external" bud length and meiotic stage for buds collected in 1973. ● — pre-leptotene, ⊙ — leptotene-pachytene, X — diplotene-telophase-II, ▲ — tetrads, + — pollen.

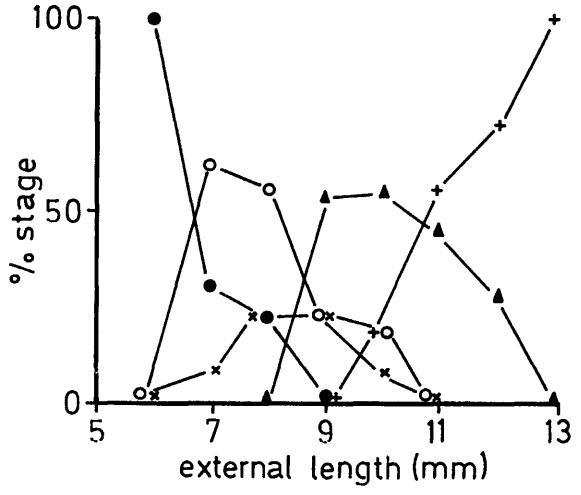


Figure 20. — The relationship between "external" bud length and meiotic stage for buds collected in 1974. ● — pre-leptotene, ○ — leptotene-pachytene, X — diplotene-telophase-II, ▲ — tetrads, + — pollen.

pachytene) was reached at a bud length of about 7 mm in 1974 but 9 mm in 1973. Period 3 (diplotene-telophase-II) was found mostly in buds of 8—11 mm in 1973 and 8—9 mm in 1974. The peak in period 4 (tetrads) was also found at a smaller bud size in the 1974 season. Although pollen was found in buds as small as 7 mm in 1973, in both years all buds contained pollen by the time they had reached 13 mm in length.

Figs. 21 and *22* show the comparison of "internal" bud length (the length of the bud with the scales removed) with meiotic stage. In 1973 all curves except that for period 3 were bimodal. However, the 1974 data *(Fig. 22)* showed no evidence of bimodality. There is good agreement between the two years in spite of the occurrence of bimodality in some curves for 1973. In all cases the modes (or the larger modes, where two exist) correspond closely.

Figs. 23 and *24* show the relationship between meiotic stage of the buds and date of collection. Again bimodal curves are frequently seen in the 1973 data *(Fig. 23)* but not the 1974 data *(Fig. 24)*. Also there is a close agreement between the data derived from different years.

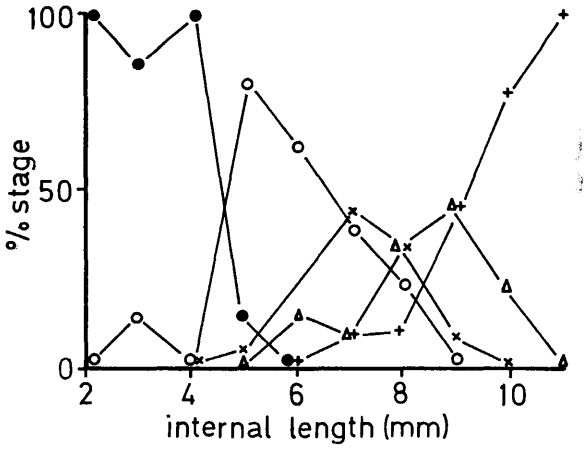


Figure 21. — The relationship between "internal" bud length and meiotic stage for buds collected in 1973. ● — pre-leptotene, ○ — leptotene-pachytene, X-diplotene-telophase-II, ▲ — tetrads, + — pollen.

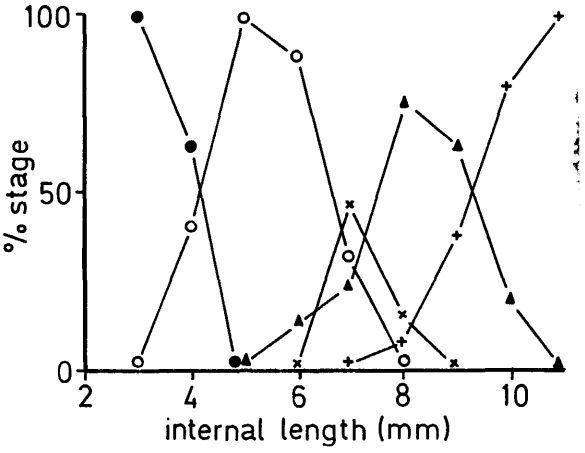


Figure 22. — The relationship between "internal" bud length and meiotic stage for buds collected in 1974. ● — pre-leptotene, ⊙ — leptotene-pachytene, X — diplotene-telophase-II, ▲ — tetrads, + — pollen.

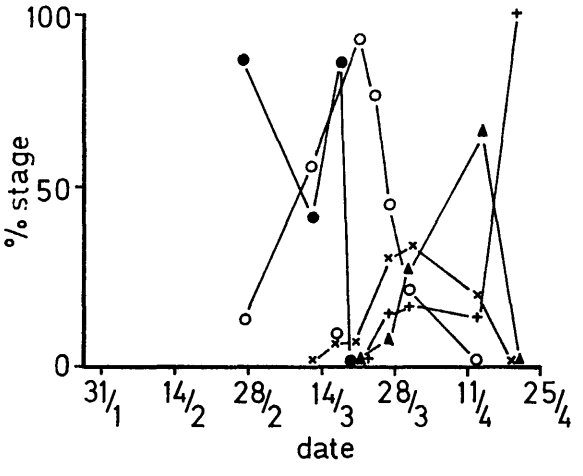


Figure 23. — The relationship between meiotic stage and date of collection for buds collected in 1973. ● — pre-leptotene, ○ — leptotene-pachytene, X — diplotene-telophase-II, ▲ — tetrads, + — pollen.

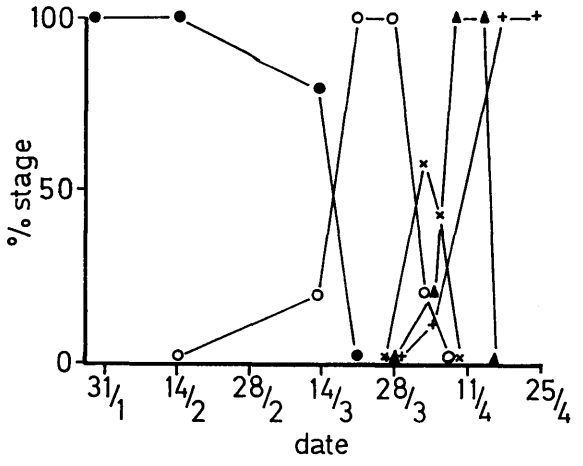


Figure 24. — The relationship between meiotic stage and date of collection for buds collected in 1974. ● — pre-leptotene, ○ — leptotene-pachytene, X — diplotene-telophase-II, ▲ — tetrads, + — pollen.

Synchrony of meiosis

Synchrony of meiotic stage was a common feature of development of the male buds. However, this was not absolute and a detailed study of this phenomenon was carried out using nine buds in various stages of meiosis. Four microsporangia from each of the three regions — base, middle and tip — were used to assess the degree of synchrony in these buds. When asynchrony is observed between regions it is always the tip which is more advanced than the base, with the middle region intermediate in its state of development. Where there appears to be synchrony between all regions (e.g. leptotene and zygotene) it is probably due to that particular meiotic stage being of long duration. On the other hand when a range of stages is found in one area (e.g. diplotene — telophase-II) these stages are probably of very short duration.

Until late diplotene all microsporangia within a region were in synchrony. Then in one region it was possible to find a microsporangium mostly in late diplotene (range early diplotene — anaphase-I) and another in diakinesis — metaphase-I (range diplotene-interkinesis). This was observed in the middle region of one bud and the tip of a second. In the base of one bud there were microsporangia in metaphase-I (range diplotene — interkinesis) and interkinesis (range metaphase-I — metaphase-II). However, in the middle region of another bud, all four microsporangia were in metaphase-I — anaphase-I. When prophase-II — metaphase-II (range interkinesis — telophase-II) was observed in a sporangium of the middle region, another was found to be in metaphase-II — anaphase-II (range telophase-I — telophase-II). Those in a basal region varied from metaphase-II (range metaphase-I — telophase-II) to telophase-II (range interkinesis to post-meiotic interphase). Metaphase-II (range interkinesis — interphase) and interphase (range metaphase II — interphase) were the extremes observed in tip microsporangia. The final stage when microsporangia were seen to differ was observed in a middle region where interphase (range anaphase-II — partitioning tetrads) and tetrads (telophase-II — tetrads) were present. Subsequentliy, irrespective of region, all four microsporangia appeared to be synchronous in develomental stage.

Discussion

Chromosome clumping and a diffuse diplotene stage are both present in Sitka spruce, in common with many other conifer species. Chromosome clumping has been recorded in the following conifers: *Torreya california, Juniperus communis, Cunninghamia sinensis, Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata* and *Abies sacchalinensis* and *A. nobilis glauca* (Robertson, 1904; Nichols, 1909; Miyake, 1910; Owens and Molder, 1971; Mergen and Lester, 1971). According to Ekberg *et al.* (1968), at leptotene the chromosomes of *Larix decidua, L. leptolepis* and *L. sibirica* form a dense clump but by pachytene they are well spread out. However, in *Pinus echinata, P. taeda, P. sibirica* and *Picea abies,* the chromosomes do not clump at all in the initial stages of meiotic prophase. Evidence on *Thuja plicata gracilis* presented by Simak *et al.* (1974), contrary to the findings of Owens and Molder (1971), would suggest that this species is in the same category as *Pinus.* Swanson (1958) p. 64, noted clumping in *Lilium* and termed it "synizesis". It occurred in leptotene and could persist until pachytene. Of course, if clumping occurs at leptotene it precedes chromosome synapsis. However, Allen and Owens (1972) p. 47 claim that in Douglas fir clumping is only evident in cells where synapsis is already underway. Moens (1973) speculates that "the clumping of chromosomes around the nucleolus during synapsis is a form of chromosome polarisation analogous to the organisation of chromosomes at the nuclear envelope or chromocentre in other plants and in some animals". In other words it may be an adaptive feature which aids syapsis. Our observations on Sitka spruce show that while clumping is present at leptotene it is most marked and the chromosome mass most excentrically placed at pachytene i.e. a stage following completion of synapsis.

Diffuse diplotene occurs in several *Larix* species (Ekberg *et al.* 1968); Owens and Molder, 1971, *Pseudotsuga* (Owens and Molder, 1971) and, in the text though not in the figures, in the paper on *Abies* by Mergen and Lester (1961). Bivalents are so diffuse and pale-staining that the cell may seem initially to be pre-leptotene, but as chromosome contraction continues they take on the appearance of diplotene in conifers which show no diffuse stage, i.e. dark-staining bivalents with many achromatic regions. Sitka spruce resembles *Larix, Pseudotsuga* and *Abies* in showing both diffuse diplotene and achromatic regions. However, in contrast to *Larix,* Sitka spruce does not overwinter in this diffuse diplotene stage, both starting and ending meiosis in the Spring. The significance of diffuse diplotene in Sitka spruce therefore cannot be that it is an adaptation to meiotic overwintering *(contra* Ekberg *et al.* 1968).

In *Pinus* (Ekberg *et al.* 1972; Mergen *et al.* 1963) the metaphase I bivalents often form a "sticky" clump similar to that shown in *Fig. 11* for Sitka spruce. Usually no cell wall formation takes place in conifers until the entire process of meiosis is complete but there may be an ephemeral cell plate at interkinesis in *Juniperus* (Nicholls, 1909) or a lighter-staining region of cytoplasm between daughter nuclei in *Picea* (Anderson, 1947; and see *Fig. 14).*

Meiosis in the pollen mother cells of conifers may follow one of three patterns (Anderson *et al.* 1969), (i) Meiosis starts and is completed during autumn, (ii) Meiosis starts in autumn but is completed during spring, (iii) Meiosis starts and is completed during spring. Anderson noted that species within a single genus and even meiosis in the male and female strobili of the same species may fall into different categories. Sitka spruce clearly falls into the third category, both starting and completing meiosis in the spring.

The data contained in *Figs. 19, 21* and *23* relate to buds collected in 1973 while the data in *Figs. 20, 22* and *24* relate to buds collected in 1974. In comparing data from the two years (see Results) one main generalisation can be made: the 1973 data often show bimodality for the frequency of meiotic stages when related both to bud length and date of collection, while the 1974 data do not show this trend. We think that the tendency to biomodality present in the 1973 data may be a consequence of either of two differences in the bud collections in the two years. The 1973 buds (see Moir and Fox, 1975) were not selected in a random fashion. Early in the season the most advanced buds tended to be selected while later in the season the least advanced buds were favoured. In 1974 bud collection was entirely random. Also the 1973 data are heterogenous in that buds were collected from four different trees and pooled. We already know (Moir and Fox, 1975) that bud size varies with its position in the crown of the tree and it would not be surprising if this parameter varied between trees, especially since some of the Roseisle trees may derive from different provenances (Samuel *et al.* 1972). In 1974 buds were only collected from tree B.

In spite of this obvious difference between the two years there is still good agreement between them. Indeed, either bud size or date of collection (at least for the Roseisle site) can now be used as excellent indicators of the meiotic state of male buds.

Moir and Fox (1975) have shown that male buds undergo a growth spurt which in 1974 was initiated between 13th and 20th March, depending on the position of the male buds in the crown. It can be seen from *Fig. 24* that this growth spurt corresponds very closely with the entry of cells into leptotene. The considerable increase in tissue mass which occurs as the tapetal cells divide and the P.M.C.'s grow in volume must account for much of the early part of this spurt in growth.

Sitka spruce shows good synchrony in meiotic development between buds and also between sporangia within buds, and within sporangia. While similar degrees of synchrony are found in some other conifers e.g. *Pseudotsuga* (Allen and Owens, 1971 p. 46), in other cases e.g. *Torreya* (Robertson, 1904) synchrony is less marked. The developmental pattern in Sitka spruce male strobili, with the most advanced meiotic stages in sporangia at the tip, is also found in *Juniperus* (Nichols, 1909) but Wang (1948) found that the opposite was true in *Keteleeria*. *Fig. 24*, which relates meiotic development to date of collection, allows rough estimates to be made of the length of time taken for some parts of meiosis and microsporogenesis. Taking the mid-point of the ascending limbs of the curves contained in *Fig. 24* as the time when 50% of the P.M.C. population had passed into the next meiotic stage, the following estimates can be derived. Beginning of leptotene to the end of pachytene — 14 days; beginning of diplotene to the end of telophase-II — 7.7 days; beginning of post-meiotic interphase to beginning of pollen formation — 4.5 days. Thus the total duration of the microscopically recognisable stages of meiosis was about 22 days.

Acknowledgements

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Summary

1. Male meiosis was investigated in four 41 year old trees of Sitka spruce at Roseisle Forest, Elgin.

2. The microscopic appearance of meiosis in this species is similar to that recorded for other conifers in showing chromosome clumping in the prophase of the first meiotic division, diffuse early diplotene and achromatic regions at late diplotene and prophase of the second meiotic division.

3. Meiosis starts and ends in spring. In 1974 leptotene was initiated between 13th and 20th March and cells took an average of 22 days to complete meiosis.

4. There is considerable synchrony for meiotic development both between and within the buds of one tree. Where asynchrony can be seen within a bud the tip microsporangia are more advanced than those at the base.

5. Meiotic stage is closely correlated with "external" and "internal" bud length, and with date of collection.

6. Time of meiotic initiation coincides with the growth spurt previously recorded for male buds.

Key words: Sitka spruce, meiosis, developmental synchrony, chromosome clumping.

Zusammenfassung

Im Frühjahr 1973 wurde im Roseisle Forest, Elgin, Schottland, an vier 41 Jahre alten *Picea sitchensis* (Bong.) Carr. der Ablauf der Meiose während der Pollenbildung untersucht. Hierbei wurde festgestellt, daß die Vorgänge ähnlich denjenigen sind, wie sie bei anderen Koniferenarten beobachtet werden konnten. Die Meiosis beginnt und endet im Frühjahr. Im Jahre 1974 wurde das Leptotän zwischen dem 13. und 20. März eingeleitet und die Meiose innerhalb von 22 Tagen beendet. Innerhalb eines Baumes verlaufen die Teilungsvorgänge vorwiegend synchron.

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