Bud differentiation in Sitka Spruce, Picea sitchensis (Bong.) Carr.

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Introduction

In spite of the commercial importance of Sitka spruce (Fletcher and Faulkner, 1972) there is no detailed report of sexual differentiation and the time course of meiosis in this cpecies. However such studies have been frequent in other spruces.

Fraser (1962, 1966) and Eis (1967) both found that, with the outer bud scales removed, male strobili of ***Ficea mariana*** and ***Picea abies*** could be recognised in late July though microsporophylls and microsporangia could not be discerned until mid — or late August. ***Picea mariana*** female strobili are similar to male strobili until late September when bracts and ovuliferous scales develop (Fraser, 1966). In ***Picea glauca,*** according to Nienstaedt and Teich's (1971) review, some buds produce bracts and ovuliferous scales as early as mid-August. Varnell and Romberger (1967) noted that by late summer ***Picea abies*** male strobili are smooth hemispheres while embryonic vegetative shoots and female strobili are paraboloidal. The vegetative and female buds, with the outer scales removed, remain superficially similar until winter when ovuliferous scales begin to appear. The apical meristems of these two also remain relatively conspicuous and unchanged throughout winter but the male meristem declines and almost disappears in autumn. Ovule outline, though the tissue is undifferentiated, can be seen during February. Externally, bud type can be recognised before January in all ***Picea*** species except ***sitchensis*** where the buds are very small at this time (A. Fletcher, personal communication).

In this report we show that bud morphology can be used to recognise the type of differentiation while the buds are still less than 8 mm in length.

Materials and Methods

General observations on the morphological changes taking place in the buds were made in the early months of 1973 using material derived from four 41 year old trees at Roseisle Forest, Elgin (Samuel ***et al.,*** 1972). In addition, male and vegetative buds were collected from different parts of these trees and their lengths measured before and after the bud scales had been removed ("external" and "internal" bud measurements respectively).

In the following season (1974) the same procedure was repeated using buds from tree B. Also during this season buds from tree A were tagged. Three regions of the crown were selected, the upper crown (vegetative — female sector), the mid-crown (predominantly male sector) and the lower crown (vegetative — male sector). Ten tagged buds in each sector were measured periodically. Thus development of specific buds was recorded throughout the season to a stage at which bud type could be stated accurately.

During the winter and spring of 1973 branches were collected from the Roseisle trees and kept in buckets of water in the laboratory. No special treatment was applied to them. Morphological development of the buds was compared with that of buds freshly collected from the trees.

Results and Discussion

General observations

In January buds are undifferentiated and all are very small and pyramidal. With the brown outer scales removed the remaining structure is flat-topped and the central axis is sometimes exposed at the tip of the spirally-arranged transparent primordial leaves or sporophylls. Often this "internal" bud does not entirely fill the volume enclosed by the bud scales. The patterns of sporophyll scales and leaf primordia are initially alike, being broadly V-shaped. By early February it is possible to recognise male buds for, during the initial stages of elongation they become shaped like a short, fat cigar. Longitudinal bud sections in mid-February reveal the female strobilus to be tapered and to fill the outer scales enclosure. The "internal" vegetative bud is flat-topped and fills only part of the enclosure, while the male has a rounded strobilus which may or may not fill the enclosure. At this stage the pattern of sporophyll scales in male and female strobili can be distinguished from the pattern of leaf primordia in vegetative buds since each scale is fan-shaped as opposed to pointed. Initial appearance of ovule and sac formation is also present in some buds. These differences are shown diagrammatically in ***Fig.*** 1.

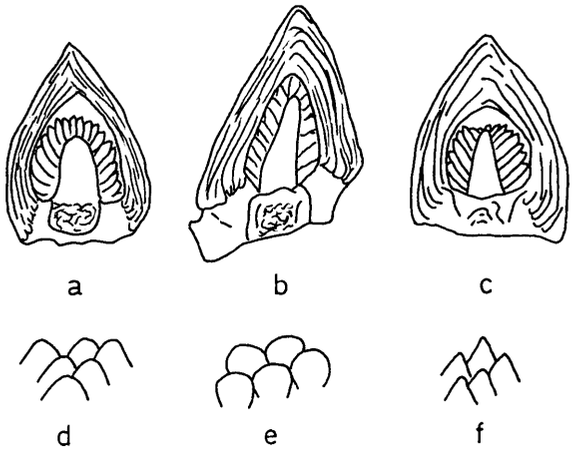

Fig. 1. — Bud differentiation in Sitka spruce. Longitudinal sections of young male bud (a), young female bud (b) and young vegetative bud (c). Note the bud shape and the space between the "internai" bud and outer bud scales in (a) and (c), and the mammary apex in (c). d–f Scaie and leaf patterns of internal buds. Very young bud before differentiation (d), sporophyll scale pattern (e) and leaf primordia pattern (f).

In early March the male buds (***Figs.*** 2—5) were large and more rounded with fewer layers of brown scales surrounding the well-developed microsporophylls of the strobilus. The jelly-like spore suspension was not yet easily extractable from the sacs. Female buds, in contrast, still had many layers of scales around the strobili. By the latter half of

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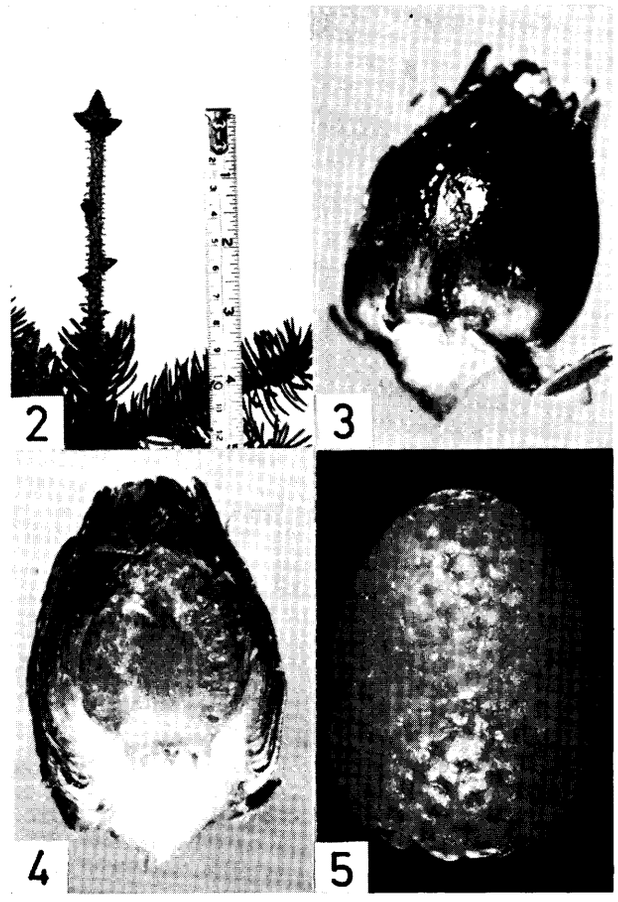
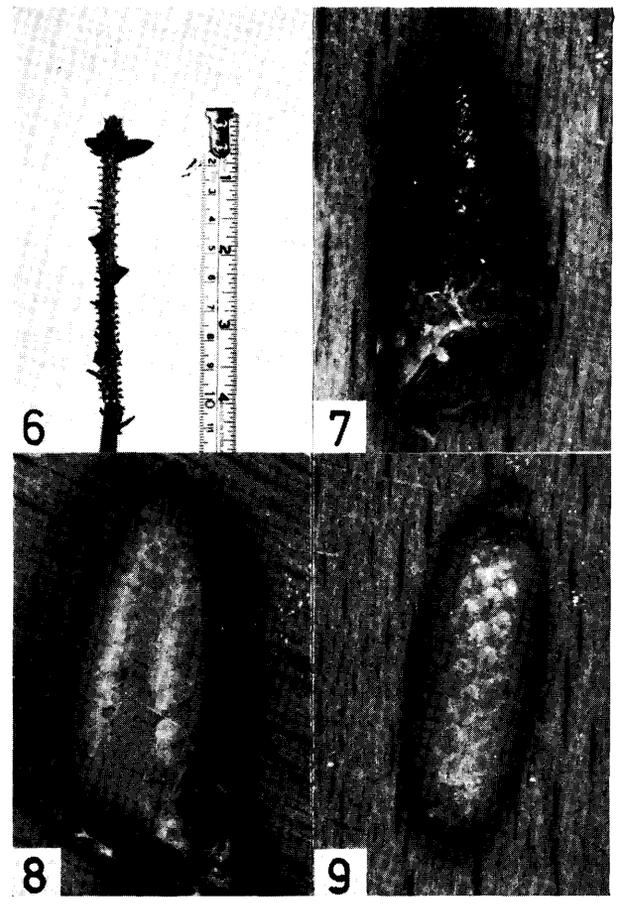


Figs. 2—5. — Male buds in mid-March.
Fig. 2. Arrangement of buds on branch (needles removed). *Fig. 3.* One bud enlarged to show the cigarshape magnification ×5. *Fig. 4.* Longitudinal section of the same bud. Strobilus fills the space enclosed by the outer bud scales magnification ×5. *Fig. 5.* Bud with outer scales removed to reveal the fan-shaped sporophyll scale pattern magnification ×10.



Figs. 6—9. — Female buds in mid-April.
Fig. 6. Position of buds on the branch (needles removed). *Fig. 7.* Single bud in process of elongation magnification ×35. *Fig. 8.* Longitudinal section of a bud. A thin layer of outer scales covers the large strobilus magnification ×35. *Fig. 9.* But with outer scales removed. The fanshaped sporophyll scales are starting to curl at the edges magnification ×35.

March the microsphorophylls were swollen with a more fluid spore suspension. Occasionally a bud was seen with bud scales shed to expose a deep pink strobilus. Only the fan-shaped tip of the sporophyllous scales were pigmented. By April the "internal" vegetative buds *(Figs. 6—8)* had begun to alter from being flat-topped to being rounded then pointed. This was due to the process of leaf primordial elongation. As yet the bracts of female strobili were small and hidden and often the axes of the strobili were as long as the strobili themselves *(Figs. 9—12).* In mid-April there was a sudden burst of elongation and all vegetative buds were pointed by this time, there being no gap between the "internal" bud and the outer bud scales. By the end of April all buds were greatly enlarged, the greatest difference being in the vegetative ones which were elongating rapidly. Pollen was shed in mid-May. Pinkish-green female cones were held erect with their ovuliferous scales curled back on themselves. Vegetative buds began flushing. Early in June the male cones dropped off the trees and the female cones, by now greatly enlarged, started to bend over.

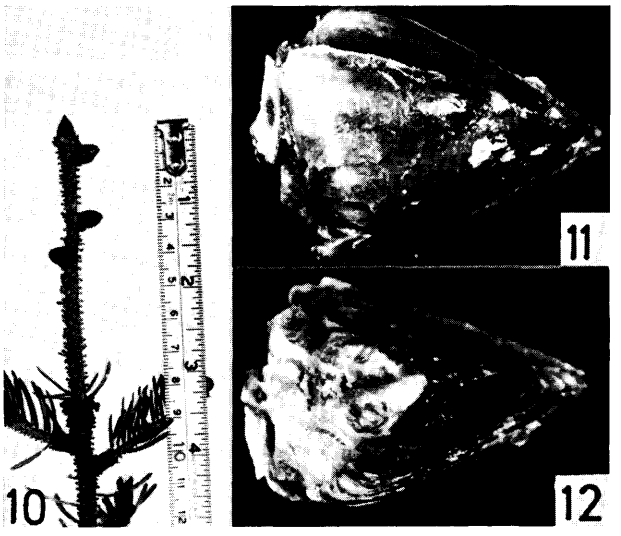
Buds forced in the laboratory were morphologically similar in external development to those observed *in situ.* However, if male buds had not shed pollen within 20 days of collection, the strobili disintegrated within the bud scales.

(ii) *Quantitative results*

The relationship of "external" and "internal" bud length to date, obtained from collected material, is presented in *Figs. 13 and 14.* The method of bud selection differed between the two years. Initially, in 1973, the buds that were more advanced and therefore recognisably male were selected. Latterly, when pollen had begun to be shed, late-developers were chosen. In 1974 buds were chosen at random.

Until March 21st in the 1974 season, male and vegetative buds had similar external measurements but after that date there was a distinct difference between them as the male elongated rapidly. The marked increase in vegetative bud growth did not occur until a month later. By comparing internal measurements from the first date of sampling, February 13th, it can be seen that the two bud types already differed. For five weeks the vegetative buds did not alter while the male buds gradually increased in length. After March 21st both male and female vegetative buds developed rapidly.

Results derived from the 1974 tagged buds are given in *Figs. 15 and 16.* Data from the lower and upper crowns are displaced respectively to left and right of the actual date of collection to prevent overlaps. In the upper, mid- and lower crowns the random tagging had included 4, 4 and 6 vegetative buds and 6, 6 and 4 male buds respectively in



Figs. 10—12. — Vegetative buds in mid-April. *Fig. 10.* Buds on a branch (needles removed). *Fig. 11.* Enlarged single bud showing pyramidal shape magnification ×5. *Fig. 12.* Longitudinal section of a bud showing the very small "internal" bud encased in a think layer of scales magnification ×5.

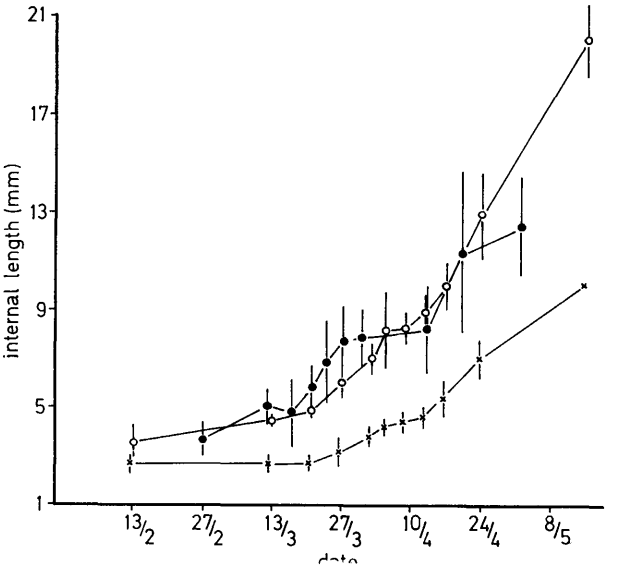


Fig. 14. — Relationship between male and vegetative "internal" bud length and date. Data obtained from same source as *Fig. 13* and the symbols used are identical to those used in that figure.

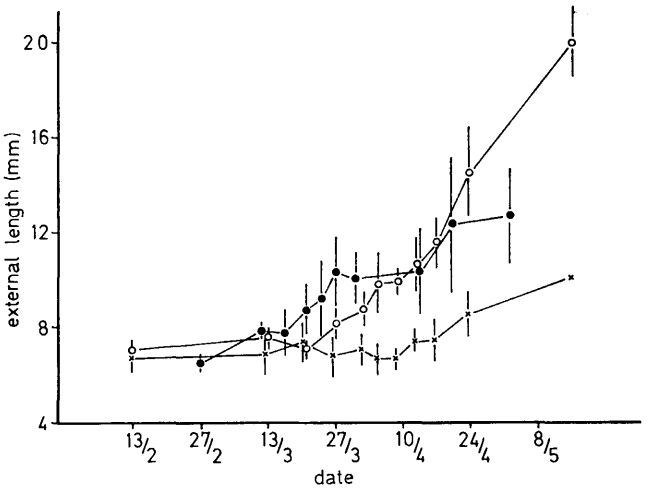


Fig. 13. — Relationship between male and vegetative "external" bud length and date. The data were obtained from buds collected over two seasons from four trees. o — male (1974); ● — male (1973); x — vegetative (1974). Symbols and vertical bars indicate means and standard errors respectively.

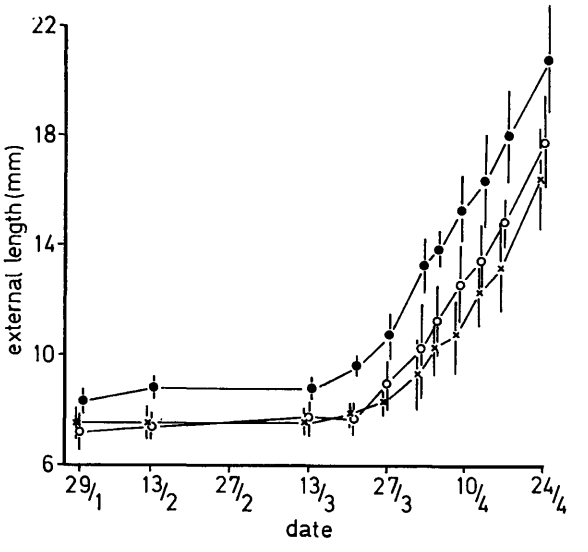


Fig. 15. — Relationship between male "external" bud length and date for buds in different parts of the crown. ● — upper crown; o — mid-crown; x — lower crown. Symbols and vertical bars indicate means and standard errors respectively.

each sector. Unfortunately no female buds had been included.

Prior to March 21st male buds in the upper crown were longer than those in the other two regions but following that date a difference became apparent in the bud size of these regions too. On March 27th mean bud size decreased in the order upper, mid-, lower. This is one of six possible permutations and was found on all subsequent collection dates. The probability of this result being obtained by chance is $(1/6)^7 = 3.57 \times 10^{-6}$. Thus the increase in bud length as one ascends the tree is obviously a real phenomenon. Visible increase in bud length occurred in the upper crown approximately 8 and 11 days respectively prior to that in the mid- and lower crowns. Although the elevations of the three lines in *Fig. 15* differed, their slopes did not. This implies that once development is initiated it proceeds at the same rate, irrespective of where in the tree the bud is situated.

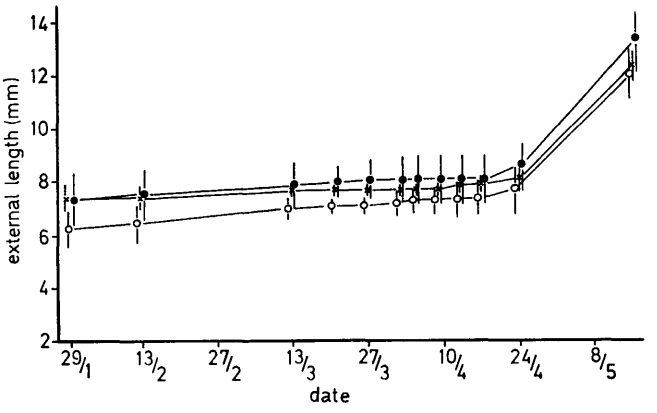


Fig. 16. — Relationship between vegetative "external" bud length and date for buds in different parts of the crown. ● — upper crown; x — mid-crown; ○ — lower crown. Symbols and vertical bars indicate means and standard errors respectively.

Regular variation in the size of vegetative buds, similar to that found for male buds, is demonstrated in *Fig. 16*. On February 2nd the mean length decreased in the sequence upper, mid-, lower and this permutation was found on each of the ten succeeding sampling dates. The probability of this result being obtained by chance is $(1/6)^{11} = 3.4 \times 10^{-9}$. In comparison with male buds, all vegetative buds began elongating on or about the same date, April 17th, in preparation for flushing.

Picea sitchensis clearly differs from other spruces both in the size that vegetative and sexual buds reach before the winter and in the time that sexual and vegetative differentiation can be recognised. While in other spruces this differentiation is obvious before January, *Picea sitchensis* buds are extremely small (7 mm "external" length) at this stage and show no obvious differentiation. Observations of the internal morphology of buds reported here show that the type of differentiation can be recognised by mid-February. However, based on external morphology, this distinction cannot be made until mid — late March when there is a spurt of growth in the sexual buds preceding that which occurs in the vegetative buds. Finally, this work has also shown that bud size for both sexual and vegetative buds is strongly influenced by the level at which they occur in the crown. The higher a bud is placed in the crown, the greater its size. At present we offer no comment on the possible significance of this observation.

Acknowledgements

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Summary

1. Observations on bud growth and differentiation were made on four 41-year old trees of *Picea sitchensis* growing at Roseisle Forest, Elgin, Scotland in 1973. In 1974 further studies were made on two of those trees.

2. In January the buds of *Picea sitchensis* are very small (about 6 mm long) and do not show obvious sexual differentiation.

3. By early February male buds can be recognised by a slight elongation to become cigar-shaped instead of pyramidal.

4. In mid-February female buds are distinguishable by the strobilus being tapered and filling the space enclosed by the bud scales in contrast to the leaf primordia of vegetative buds which are flat-topped and do not fill this enclosure. The scale pattern also differnetiates it from the vegetative bud.

5. External measurements of bud length show that male and vegetative buds cannot be distinguished on this basis until mid — to late March when the male buds have a spurt of growth.

6. The growth spurt of vegetative buds does not occur until mid — to late April.

7. Both male and vegetative buds are bigger the higher they occur in the crown.

Key words: Sitka spruce, bud differentiation, bud growth.

Zusammenfassung

An vier 41jährigen Sitka-Fichten *(Picea sitchensis* (Bong.) Carr.) wurden in den Jahren 1973 und 1974 im Roseisle Forest, Elgin, Schottland, Untersuchungen zur morphologischen Veränderung der Knospen im Frühjahr durchgeführt. Hierbei waren im Januar noch keine äußeren Veränderungen gegenüber dem Winterzustand zu erkennen und auch keine Unterscheidung bezüglich des Geschlechts möglich. Anfangs Februar werden die männlichen Blütenknospen länger. Ab Mitte Februar sind die weiblichen Blütenknospen zu erkennen. Erst Mitte bis Ende April beginnt das Wachstum der vegetativen Knospen. Männliche und vegetative Knospen sind in höheren Kronenregionen stärker ausgebildet.

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Some observations of the Flower biology of Ekebergia capensis Sparrm. (Syn. E. senegalensis A. Juss.)

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Introduction

The species *Ekebergia senegalensis* A. Juss. is recorded in the Flora of West Tropical Africa (Keay 1958), Nigerian Trees (Keay *et al.* 1964) and in Savanna trees of Nigeria (Hopkins *et al.* 1966). Its distribution is stated as stretching from Senegal to Sudan and Uganda. Another closely related species *E. capensis* Sparrm. which occurs naturally in the South African Cape, spreads upwards into Uganda.

Recent intensive taxonomic studies of the two species by White and Uzoechina between 1971—72 (to be published) reveal that *E. senegalensis* and *E. capensis* should be merged into a single species. *Ekerbergia capensis* Sparrm. which is the earlier name is thus retained for the two species. *E. senegalensis* is thus sunk under *E. capensis*.

After dissections and examinations of hundreds of flowers sampled from herbarium specimens collected from the