

The Development of Poplar Clones Suited to Low Latitudes

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The possibility of growing poplar in relatively low latitudes is being examined especially because of the increasing interest in planting this tree in the Southern Hemisphere. The practice of planting poplar has been built up mainly in Europe and extends south Sicily to about latitude 37° N. Centres of active development in the Southern Hemisphere in South America, New Zealand, Australia and South Africa are for the most part in latitudes which are lower than this. The great success achieved in Italy (SCHREINER 1959, F. A. O. 1958) by the use of Euramericana hybrids derived from various combinations of the American *Populus deltoides* and the European *Populus nigra* has led to a good deal of speculation as to where such clones can be used successfully elsewhere. Preliminary trials in latitudes of less than 30° particularly in South Africa, Australia and South America have shown that the vegetative growth rhythm of many such clones becomes disordered in these lower latitudes. The sensitivity of many poplar species to the photo-period regime is well known and in particular has been examined by PAULEY and PERRY (1954), and VAARTAJA (1959). From these studies the poor performance of poplar clones which are derived from parents adapted to a high latitude, in a low latitude is well known and understood. With clones adapted to the long photo-periods of higher latitudes, bud dormancy occurs early in the growing season in the short days of low latitude sites. This leads to a consequent limitation to height growth which is soon accompanied by a similar restriction in diameter growth.

Associated with this behaviour is the complementary thermal requirement which photo-period sensitive clones always seem to possess. This need is for a period of relatively low temperature such as is associated with a substantial number of winter frosts, without which the threshold temperature for bud burst and growth in spring is much higher than if the necessary winter low temperature preconditioning has been experienced. The effect of low temperature in preconditioning vegetative and other cyclic responses is widespread and well known in practice as in the vernalisation response of winter varieties of cereals.

The disorganisation of growth rhythm expressed particularly by late spring bud burst and subsequent early seasonal dormancy leads in many clones to poor and entirely unsatisfactory growth in latitudes lower than 30°. The effect is not the same in all clones. It is evidently related to a considerable extent to the latitude of origin of the parents of the particular clone. This variation is illustrated by the growth records in a nursery in latitude 24° S at Itaporanga, Sao Paulo, Brazil, where the average height growth at the

end of one year in five clones in comparable circumstances is as follows (Table 1).

The vast variation in response represents the difference between complete failure and successful growth at Itaporanga. It illustrates the variation in growth responses which results from different clones. Similar response has been obtained in latitude 29° S in Grafton, New South Wales, Australia (PRYOR, 1964) and this is illustrated by the following Table 2 in which some Euramericana and other clones and species including some from the Tacamahaca are included showing a like range of growth response.

Table 2.

Clone	Ht. m. (3 yrs)
<i>trichocarpa</i> X <i>tacamahaca</i>	Dead
<i>candicans</i>	1
"oxford"	2
<i>nigra</i> "thevestina"	2
<i>robusta</i>	3
<i>monilifera</i>	4
1455	5.5
1154	6
<i>nigra italica</i>	6
1488	7.5
<i>deltoides</i> "angulata"	7.5
"semi-evergreen"	10

It is apparent that the clones at present available which are suitable for use in lower latitudes are very strictly limited. In latitudes below 30° clones derived from the species *P. deltoides* and the clone which is related to *Populus nigra* var. *italica*, known as Chilean Semi-evergreen (called "Persistente" in Chile) are the only ones amongst the Aigeiros as far as is known which can be depended on fully in these localities. While it is clear that where there is a photoperiod response in growth cycles there is in general a complementary need for low temperature preconditioning for normal bud burst, it is not yet clear to what extent, if at all, planting at higher altitudes, when suitable sites are available, will permit an extension to a latitude lower than those which will accommodate satisfactory growth for any given clone at altitudes near sea level. There is some evidence that *Populus angulata* ceases to grow satisfactorily in less than 27° south in Northern Zululand in South Africa at an altitude near sea level whereas from the evidence of one year's growth, clones from *P. deltoides* thrive at 3,000 feet in latitude 24° south in Brazil. It may be that there is some degree of interaction between altitude and latitude in determining, at least for *P. deltoides*, the geographical limit towards the Equator, for successful growth. It is possible too that there is in some clones at least, variation caused by rainfall fluctuation since it appears a photoperiod induced dormancy may on occasions be broken by heavy irrigation or rainfall. Since there is considerable value in finding clones which can be grown in low latitudes it is therefore desirable to explore any means by which this can be achieved.

Table 1.

Clone	Ht. cms
<i>gelrica</i>	20
<i>robusta</i>	75
1214	120
1455	200
<i>P. deltoides</i>	500

Variation in *Populus deltoides*

It seems that in the *Aigeiros* group, *Populus deltoides* extends to the lowest latitudes. It certainly occurs a little south of San Antonio in Texas and also at Wharton near the coast of Texas on the Colorado River, at latitude 28° N. The taxonomy is somewhat confused and the populations which are regarded by some as the same species extend north more or less to the Canadian border. Without discussing the systematic status of these Black Poplar populations it is clear there is gradual variation from south to north which may or may not be interrupted by some discontinuities in variation. From PAULEY and PERRY's work (*ibid*) it is apparent that the whole population is very sensitive to day length influence; those which occur in higher latitudes being unable to thrive if planted in lower latitudes and those from low latitudes though growing well early in the season in high latitudes being damaged or killed back by winter temperatures later.

PAULEY and PERRY present evidence to show that the growth rhythms are closely related to latitude of origin and the performance when planted in any one locality is related especially to latitudinal provenance. It is apparent therefore from both theoretical consideration and from the general evidence so far available that selections from *Populus deltoides* from low latitudes in the United States, particularly from Texas, will provide material which will thrive in similar latitudes elsewhere. What is not known yet is whether day length response in those populations occurring naturally at the southern limit of Cottonwood distribution in latitudes from 28°–30° N is of consequence if the material is shifted to a still lower latitude.

One small plantation near Mexico City, latitude 19° N, and ornamental trees planted in Lima, Peru at 12° S suggest that in clones of this type still shorter day length may no longer be a critical factor in growth rhythms. It is possible that by selection from the most southerly North American material clones will be forthcoming which will thrive in still lower latitudes than that of origin and which will not be surpassed by any other form.

The Chilean Semi-evergreen Poplar

The origin of this clone is obscure. It is known to have been in Chile for a long time, probably since well before 1900, and it may have been introduced very much earlier than this from Spain and not have had its origin in South America at all. The Semi-evergreen is a male clone and is closely related to *Populus nigra* var. *italica*, particularly in the fastigate character. In the past it was quite extensively planted in Chile and the wood was found to be indistinguishable in use from *Populus nigra* var. *italica* which itself is considered of first quality, particularly for peeling or sawing.

The special interest in this clone is in its growth rhythm behaviour. It appears to be day-length neutral and also to have no thermal preconditioning requirement. The threshold temperature at which flushing occurs is somewhat lower than that for many clones in cultivation which are temperature sensitive even when they have been conditioned by a cold winter. In most localities it becomes dormant also considerably later in the season than other clones (*Figure 4*). The onset of dormancy appears to be directly related to the ambient temperature. Once dormant, cuttings may taken at any time of the year and placed in a warm greenhouse where they will readily commence growth at once (*Figure 2*).

A question of importance is whether the semi-evergreen habit is due only to a delay in leaf abscission. This would lead to the persistence of the leaves late into the season and be of minor importance. However, if it reflects later growth than in the case of clones with earlier leaf loss it would be of much wider significance.

The latter is found to be the case for the semi-evergreen parent and likewise as *Figure 1* shows for the Semi-evergreen hybrids in comparison with some other Euramericana clones. In clones with "Semi-evergreen" parentage not only do the leaves persist on the trees longer but height growth extension continues later in the season. The same is true of diameter growth where tests have been made.

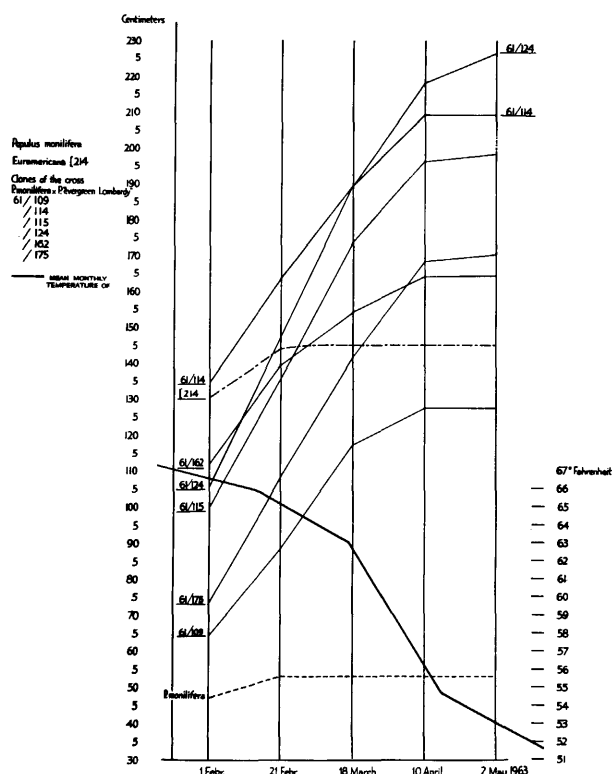


Figure 1. — Seasonal trend in height growth in hybrid poplar clones, Canberra 1962/63.



Figure 2. — Left: *P. monilifera* × Chilean Semi-evergreen after 4 weeks in a heated greenhouse in early winter. — Right: I 154 under similar conditions without having had low-temperature preconditioning.

Hybrids with the Chilean Semi-evergreen Clone

One hundred and thirty-nine seedlings were obtained from a cross between Chilean Semi-evergreen (male) and *monilifera* (female). Some of these died before scoring but the

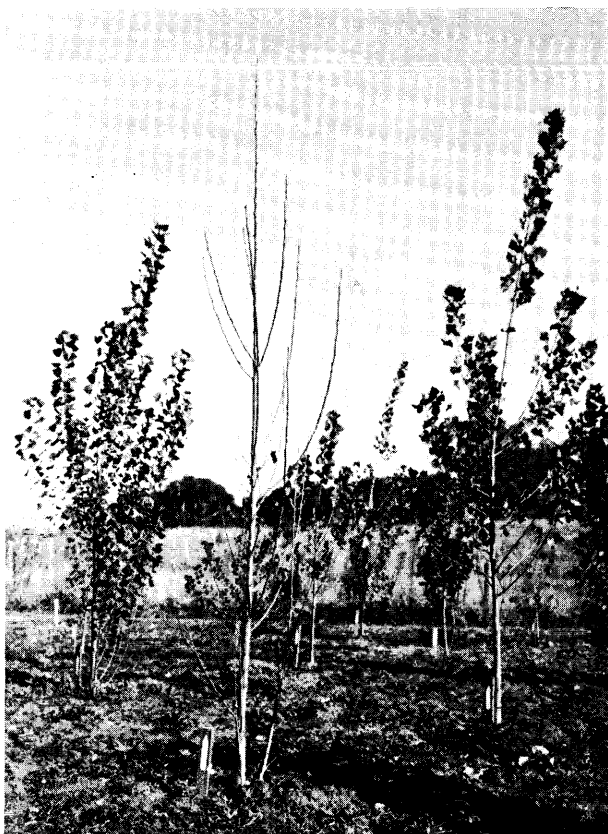


Figure 3. — Seedlings from the cross *P. monilifera* × *P. Chilean Semi-evergreen*. — Centre: An individual fully deciduous as the *monilifera* parent. — Left and right: *Evergreen* types with persistent foliage in winter.



Figure 4. — *Chilean Semi-evergreen* (on left) at Itaporanga, Sao Paolo, Brazil, still substantially in leaf in early July, 1964. Restricted growth of *gelrica* is indicated by the left hand of the figure.

remainder of the small progeny has given some interesting results.

An assessment was made of leaf persistence at the end of March, that is, at the time at which the *monilifera* parent had shed its leaves. The results were 55 semi-evergreen and 58 deciduous, giving close agreement with a 1:1 ratio. At this date about one quarter of the progeny was still in active height growth as was the semi-evergreen parent. When an assessment was made of leaf persistence in mid-winter in June, about one third of the progeny was classed

as Semi-evergreen and had most of the leaves still persisting like the semi-evergreen parent, although all height growth had ceased.

Even though the progeny size is small and there are some fluctuations in numbers of Semi-evergreen according to the time of assessment, the approach to simple ratios suggests that there may be simple genetic control of this character — probably by a single gene.

Nothing is known of the genetic makeup of either parent and for the moment it is a matter for speculation as to the mode of inheritance of the character. However, if the difference is due to a single gene, it is worthwhile considering some of the evolutionary implications, particularly dominance modification, which may be involved.

It should be noted that the evergreen habit because of the associated reduced resistance to low temperature, is probably a deleterious condition in most of the areas where *Populus nigra* occurs naturally. It is undoubtedly so in the areas where partially or fully fastigiate forms of the species occur, such as in central Anatolia, where in those possessing it there is little doubt that this habit confers an advantage in avoiding snow loading and consequently reducing snow break in winter.

Assuming a single gene effect, the first question is whether the Chilean Semi-evergreen is heterozygous (S, s) or homozygous (s, s) for this character. If it is homozygous, it must be recessive and this would imply that the female parental clone, designated *Populus monilifera* in Australia, is heterozygous for the semi-evergreen character.

The fact that no semi-evergreen types have been reported in the *Aigeiros* group other than the Chilean Semi-evergreen and this too in spite of the fact that large numbers of seedlings have now been raised and established widely in Italy in situations where at least as seedlings the Semi-evergreen would have a selective advantage suggests that if the gene is present it is very rare. The alternative hypothesis is that the semi-evergreen parent is heterozygous, semi-evergreen being dominant to the deciduous habit, and the *monilifera* parent is homozygous recessive. On this basis one can proceed to further speculation as to its origin. It must have arisen either as a seedling mutant or as a chimera. Evidence suggests that a somatic mutation in an individual of *Populus nigra* var. *italica* was the most likely origin of this useful character because in other respects the Semi-evergreen closely resembles the *Populus nigra* var. *italica* phenotype. In many species chimeras can be clonally propagated. In fact several horticultural varieties have originated in this way.

The performance of the hybrids *monilifera* × *Semi-evergreen* is interesting in that those which are assessed as evergreen at the time when the *monilifera* parent has lost all its leaves, which is within a few days of the clone *Populus nigra* var. *italica* losing its leaves, retain their leaves and continue to grow for varying periods (Figure 3). This phenotypic variation among the semi-evergreens is compatible with the hypothesis of a single dominant gene and is explicable on the basis of segregation of modifying genes. Data from intercrosses between semi-evergreen offspring should provide unequivocal evidence relating to the inheritance of the character.

A few individuals continue to hold their leaves late into the season and some still later than the Semi-evergreen parent, whereas others cease growth and shed their leaves before leaf fall in the Semi-evergreen parent.

The time of flushing is likewise variable. The Semi-evergreen was in 1964 about 3 weeks earlier than *monilifera* in

Canberra. Most of the *monilifera* × *Semi-evergreen* hybrids which were themselves semi-evergreen, flushed at the same time but a few were even earlier while others were as late as the *monilifera* parent.

The hybrids which were deciduous at the same time as the *monilifera* parent displayed a similar but not identical pattern. Some (although not a majority) flushed late as with the *monilifera* parent but many were as early as the bulk of the *Semi-evergreen* phenotypes and a few were as early as the earliest of these (Table 3).

Table 3. — Flushing of Separate Seedlings of the Hybrid Combination *monilifera* × *Semi-evergreen* 1964.

	Date				
	13. 9. 64	20. 9. 64	27. 9. 64	4. 10. 64	11. 10. 64
<i>Semi-evergreen</i>					
Phenotype	7	24	5	2	1
Deciduous					
“ <i>monilifera</i> -like”					
Phenotype	6	31	31	19	2
Flushing of <i>Semi-evergreen</i> 20/9/64					
Flushing of <i>monilifera</i> 11/10/64					

It therefore seems that time of spring flushing is to some degree independent of the feature of foliage persistence in autumn but if variation patterns are due to the presence of modifiers the establishment of the basis for control of the differences must await further study.

The growth of Chilean *Semi-evergreen* is faster in height than most other clones but it tends to be slower, in any given climate, in total diameter growth than clones otherwise adapted to the particular situation. In latitude 29° S for example in diameter growth it appears to be rather less than *P. angulata* and in latitude 35° S it is usually less than that of I 154 or I 488 although accurate comparisons have not been made. The particular interest in this form is that experiment to date suggests it may be possible to incorporate the evergreen habit and its associated longer growing period into other black poplars with great advantage in producing new clones which will be suitable for quite low latitudes.

Future Prospects for developing Clones suitable for Low Latitudes

It is obvious that one of the first steps is to determine the extent to which clones of *Populus deltoides* are suitable for low latitudes and the limits to which they can be successfully grown at different altitudes as one proceeds towards the Equator. It is likely that a selection programme of this kind will lead to very considerable benefits (MAISENHEDER, 1961). It is observed, however, in latitudes of about 29° S that even *P. deltoides* still becomes dormant when the air temperature and soil moisture content are still above those at which growth occurs during the earlier part of the season and in which the Chilean *Semi-evergreen* still continues to grow. If the semi-evergreen character with its longer growing period can be added by breeding to the general *deltoides* phenotype it seems very likely that even higher yields will be obtained than that possible with the most suitable selections of *P. deltoides*. If the semi-evergreen habit is determined by a single dominant gene this will be simple to manipulate.

A complication may arise from the rust susceptibility of the *Semi-evergreen* which has been sufficient to lead to

its exclusion now from common use in Chile. It seems probable however that this susceptibility could be separated from the evergreen habit in recombinants with *P. deltoides* since rust resistance is general in the latter.

Breeding tests are proceeding to see to what extent improvements are possible, and it seems clear that there is a good chance of producing clones which will thrive in latitudes below 30°.

Summary

The suitability of Poplar for use as a timber crop under conditions of intense cultivation has led to an examination of the possibility of planting clones of the genus in latitudes lower than those in which it is commonly grown at present.

The main limitation to successful growth in latitudes less than 30° is the disorganisation in growth expressed as early dormancy and late flushing because of an unsuitable photoperiod regime. Well-known clones commonly used in high latitudes in Europe such as *gelrica* and *robusta* fail almost completely in latitude 30°, and the widely used forms I 214 and I 455 and similar Euramerica clones are either unsatisfactory or perform substantially below their maximum in the same area.

There is a good prospect for developing clones suitable for low latitudes in two ways. Firstly, by selection from southern provenances of *Populus deltoides* which extends to latitudes substantially below 30° in Texas in the United States of America and secondly by hybridizing *Aigeiros* poplars with the Chilean *Semi-evergreen* clone, progeny from which has a substantial proportion of individuals displaying the semi-evergreen habit which is apparently associated with independence to daylength control.

Some possibilities for the nature of the genetic constitution of the *Semi-evergreen* are suggested and an estimate is made of the extent to which improvements may be possible by its use.

Résumé

Titre de l'article: *Clones de peupliers adaptés aux basses latitudes.*

Il existe un besoin réel pour de nouveaux clones de peupliers qui puissent prospérer sous des latitudes plus basses que celles sous lesquelles cette espèce est communément plantée. On peut penser obtenir des résultats intéressants pour des latitudes inférieures à 30° soit en sélectionnant des clones dans des provenances méridionales de *Populus deltoides*, soit en hybridant des peupliers de la section *Aigeiros* avec des peupliers chiliens à feuilles semi-persistantes, cette hybridation étant suivie de sélection.

Certaines suggestions sont faites sur la nature de la constitution génétique des peupliers à feuilles semi-persistantes et sur les possibilités d'utiliser ces clones comme parents dans des programmes d'amélioration.

Zusammenfassung

Titel der Arbeit: *Über die Entwicklung von für niedrige Breitengrade geeigneten Pappelklonen.*

Es besteht ein Mangel an Pappelklonen, die in niedrigeren Breiten erfolgreich angebaut werden können, als da, wo sie jetzt gewöhnlich genutzt werden. Man hat eine aussichtsreiche Möglichkeit in Breiten unter 30° entweder in der Selektion südlicher Provenienzen von *Populus deltoides* oder in der Bastardierung von *Aigeiros*-Pappeln mit der chilenischen halb-immergrünen Pappel und anschließender Selektion.

Möglichkeiten hinsichtlich der genetischen Konstitution der halb-immergrünen Pappel und der künftigen Verwendung als Elter für Züchtungszwecke werden erörtert.

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Karyotype Analysis of Sitka Spruce, *Picea sitchensis* (Bong.) Carr.¹⁾

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Introduction

Sitka spruce, *Picea sitchensis* (BONG.) CARR., occurs in a narrow coastal belt on the west coast of North America, ranging from Mendocino County, California (41° N latitude) to Kodiak Island and the Kenai Peninsula, Alaska (61° N). It is an important timber tree, both in its natural range and as an exotic in northwest Europe.

In a series of reports, the author has attempted to describe the pattern of natural variation in development of Sitka spruce; emphasis was given to basic developmental characters and phenological responses that cause genetic variation in height growth (BURLEY, 1964; 1965 a; b; c). The underlying cause of this variation should be sought in the nucleus; differences in growth characteristics may be a reflection of differences in chromosome number, size or morphology. The purposes of the research described in this paper were to determine practical methods of chromosome analysis for Sitka spruce, to establish the basic karyotype of the species, and to investigate the variation in karyotype between ten selected provenances representing the natural range of distribution.

Literature review

The haploid chromosome number in the genus *Picea* has been reported as 12 for over 20 species (MIYAKE, 1903; SAX and SAX, 1933; SEITZ, 1951; DARLINGTON and WYLIE, 1955; MEHRA and KHOSHOO, 1956; LITTLE and PAULEY, 1958; GUSTAFSSON, 1960; SANTAMOUR, 1960; KHOSHOO, 1961; MORGENSTERN, 1962; PACKER, 1964). Studies of meiotic material confirm the basic haploid number as 12 in Norway spruce, *Picea abies* (*Picea excelsa*) (MIYAKE, 1903; ANDERSSON, 1947 a, b, 1948). Reports of basic numbers other than 12 are rare. KIELLANDER (1950) found triploid, tetraploid and mixoploid seedlings among nursery stock of Norway spruce and he induced polyploidy with colchicine. Chromosome numbers between 24 and 70 were found in embryos and dwarf plants of Norway spruce by ILLIES (1958); she believed this was due to pathological polysomy rather than endomitotic polyploidy. TOROK and WHITE (1960) reported that somatic tumor cells of white spruce, *Picea glauca*, contained 22 chromo-

somes, but RISSE (1964) used similar material and concluded that the diploid number was stable at $2n = 24$.

DARLINGTON and WYLIE (1955) cited THOMAS as authority for the diploid number of 24 chromosomes in Sitka spruce. The same number was observed by VABRE (1954); she postulated that differences in length and shape of chromosomes may assist in the classification of species but she gave no measurements for Sitka spruce. In a study of the unusual hybrid, *Tsuga-Picea hookeriana* (*Picea sitchensis* × *Tsuga heterophylla*) she again found a basic number of 24, but believed that one chromosome is doubled or 'polysomatic' (VABRE-DURRIEU, 1954).

In view of the similarity in chromosome number, chromosome size and morphology become of greater significance in comparative karyotypic studies. Previous reports agree that, in all species of spruce, nine chromosomes are isobrachial and three heterobrachial, but they have not specified the brachial indices (ratio of short arm length to long arm length), and are therefore purely subjective. For example, in the most recent and detailed analysis of spruce chromosomes, MORGENSTERN (1962) considered that both *Picea rubens* and *Picea mariana* have three heterobrachials in the haploid complement, but his ideograms suggest that possibly five chromosomes in *Picea mariana* are heterobrachial. The usual limits of the brachial index are 0.50—0.75 for heterobrachials and 0.75—1.0 for isobrachials. The use of the index in identifying chromosomes and describing karyotypes is of more value than qualitative terminology, particularly when the index is accompanied by statistical analysis of the variation in arm length (e. g. SAYLOR, 1961; SIMAK, 1962; HENEEN, 1962; MOORE and GREGORY, 1963). It is of particular importance in the case of coniferous genera, in which species differentiation is generally recognized to have occurred by individual gene mutations rather than by gross changes in chromosomal structure (SAX and SAX, 1933).

Secondary constrictions have been reported for only three species of spruce. SANTAMOUR (1960) observed secondary constrictions on two chromosomes in *Picea jezoensis hondoensis*, a species closely allied to Sitka spruce (WRIGHT, 1955). Three chromosomes in the haploid complement of *Picea smithiana* were shown to possess secondary constrictions (MEHRA and KHOSHOO, 1956). MORGENSTERN (1962) observed secondary constrictions in *Picea rubens* and *Picea mariana* but found that they could neither be consistently identified nor separated from other achromatic areas. Similar conclusions were reached for pines (SAYLOR, 1961) and firs (MERGEN and BURLEY, 1964).

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