EFFECTS OF NATURAL DAYLENGTH AND NUTRITION ON THE CESSATION OF CAMBIAL ACTIVITY IN YOUNG PLANTS OF PICEA ABIES

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ABSTRACT

The cessation of activity in the cambial zone of Picea abies under natural conditions has been estimated over several years. To assess the effect of photoperiod, experiments in controlled environments were combined with investigations of plants grown under field conditions.

A direct effect of photoperiod, with a critical night length different from the night length causing termination of shoot growth, is established.

In Trondheim (63^{o} 25' N) cambial activity normally stops between 10th and 20th of September. Night lengths and light conditions under changing weather in August have been studied in an attempt to estimate the approximate date of photoperiodical induction and the critical night length for cessation of cambial activity.

It appears that other factors such as mineral nutrition and light intensity can have a modifying effect on the reaction leading to termination of activity in the cambial region.

Keywords: Photoperiod, natural daylength, cambium, nitrogen, *Picea abies*.

INTRODUCTION

It is a common opinion that termination of growth in plants is necessary to obtain full resistance to winter stress, such as frost, dessication, fungus attack and metabolic disturbances.

Young coniferous plants living entirely in a layer near soil or snow surfaces can be exposed to the most critical conditions. The ability of young plants to survive the winter season is important when a species such as spruce, Picea abies, is colonizing new areas, and can in this way be a main limitation to the distribution of spruce in northern regions or at higher altitudes.

Nursery plants, often growing on large open areas, can be strongly affected by winter stress. A typical example is a nursery near Trondheim which lost a million plants in the extreme winter of 1972.

Planting of spruce is extensively used in Norwegian forestry. Plants of southern origin are often moved to the north. Over a long range of time seeds have also been imported from southerly parts of Europe. It is important then to understand the ecophysiological potentials of such plants in a northern climate.

The cambial zone seems to be one of the last places to stop growing in the spruce plants during the autumn. Thus our studies have been focused on the conditions decisive for the time of final termination of activity in the cambial zone.

It has been known for a long time that photoperiod can affect cambial growth. At our institute Ness (1966) performed experiments involving covering of plants in the field. A 12 hour night length given from July 15th, induced 4-5 weeks earlier cessation of cambial activity than under the natural light conditions.

In many previous physiological investigations such long nights, even up to 16 h, have been applied. This has, however, little relevance to the natural situation in the field. As an example I could mention that at our latitude because of the twilight effect 12 hour nights do not occur until the first days of October, - a time at which the first frost could already have been observed. Growth termination and attainment of a certain degree of hardiness should take place well before this.

The literature gives no clear answer as to whether growth cessation in the cambium is only a regular, secondary event following photoperiodic induction of termination of shoot length growth, or if a certain night length later on in the summer or autumn directly induces the stop of cambial activity.

If the latter is the case, at which time in late summer does it occur, and what is the corresponding natural night length?

METHODS

Young plants, usually 4-5 years old were used. They could easily be covered in field experiments or grown in pots for culture in climate cabinets. Two Vötsch Ecophyt cabinets were used in some experiments.

In the study of cambial activity a section is cut from the main shoot from last year, thus representing two year old wood. It is fixed in formaldehyde-acetic acid-ethanol and later on sectioned on a microtome, stained with phloroglucinol and examined under a microscope.

An index for description of growth cessation was worked out with numbers from 0-4 representing different stages of growth and differentiation. (Bjørnseth 1977)

As an example: The index number 2 implies that the most recent 1-2 cell layers have a distinct appearance of latewood, that is a rectangular shape when seen in cross section, but with lignification not completed. Quite newly formed cells generally could be seen along the border of the xylem. Index 4 represents an entirely terminated year ring. The cells are fully differentiated even in the outer layer of xylem, and the transition to cambium/phloem is really sharp and easy to observe.

Our criterium for full cessation of activity in the cambial zone thus includes terminated wall growth and differentiation of the most recent xylem cells.

RESULTS

1. Photoperiod

Some of the investigations done in Trondheim over a period of years, will be referred to in the following:

a) Field experiments with photoperiods given after the termination of shoot length growth and bud-set demonstrated that short nights or long nights with a 1 h light break postponed the time of cambial growth cessation.

b) In an experiment in cooperation with Ingegerd Dormling at The Phytotron in Stockholm plants were raised from seeds for 11 weeks and then given photoperiods inducing termination of length growth. Dormling (1977) estimated the critical night length to 4-5 h. After the shoot growth stopped, the night length was increased by 2 h.

Studies of the cambial zone after 4-8 weeks at such photoperiod showed that 7 h nights induced only a preliminary growth reduction. A zone of latewood was produced, but after some weeks new layers of earlywood were gradually formed and the appearance of a xylem region similar to a false ring was evident.

So in this case obviously, a 7 h night length was not sufficient to stop cambial activity.

A supplementary experiment in climate cabinets later on verified that 7 h night had no permanent effect, but that 9 h nights gave total cessation of activity.

c) In 1976 potted plants were moved from outdoor conditions to the climate cabinet on the 6th of August and kept there at 20^{o}C and 5½ h nights, a night length longer than the critical night length of shoot growth, but presumedly shorter than nights inducing cambial growth cessation.

It appeared then that the cambium kept a sustained slow growth for weeks. Samples taken in December, 3 months after growth cessation under natural photoperiods, showed growth still continuing and a 54% increase in diameter, compared to plants which stopped growing at the normal time in September.

From this set of experiments it may be concluded that at least young spruce plants have a specific night length requirement for induction of growth cessation in the cambium.

It is interesting in this connection to carry out observations under natural conditions. From a series of investigations in Trondheim, located 63° 25' N, we have estimated that the cessation of cambial activity normally takes place around the 10th-20th of September. As shown in figure 1, there are certain differences between years and between provenances.

CESSATION OF CAMBIAL ACTIVITY AT NATURAL NIGHT LENGTH TRONDHEIM (63° 26' N)

1964	9/9	19/9	25/9
K 1	66 %	100 %	
F 1	0	100 %	
Ber 13-15	0	33 %	100 %
1966	**3/9**	**12/9**	**16/9**
K 1	30 %	42 %	100 %
1969			
K 3	cessation 10/9 - 17/9		
1976		**10/9**	**20/9**
B 2		63 %	100 %
1977	**7/9**	**16/9**	**20/9**
B 3	0 %	55 %	85 %
1978	**7/9**		
B 3	ca. 100 %		

Figure 1. Observations of time of growth cessation in the cambial zone. Percent of plants showing termination of growth and differentiation. Provenances: B South Norway, F Southern coast of Norway, K Trondheim region, Ber Berchtesgaden, altitude 1300-1500 m.

The question arises then as to when induction has been taken place under the natural light conditions in these years.

As with other physical factors it is a matter of reaction time. In a climate cabinet experiment with a 12 h night, a reaction time of about 4 weeks was found. This is also confirmed by some covering experiments in the field

In this way the night length conditions around the middle of August turned out to be interesting. It may be asked how precise the photoperiod is as a signal, and what effect changing weather conditions have?

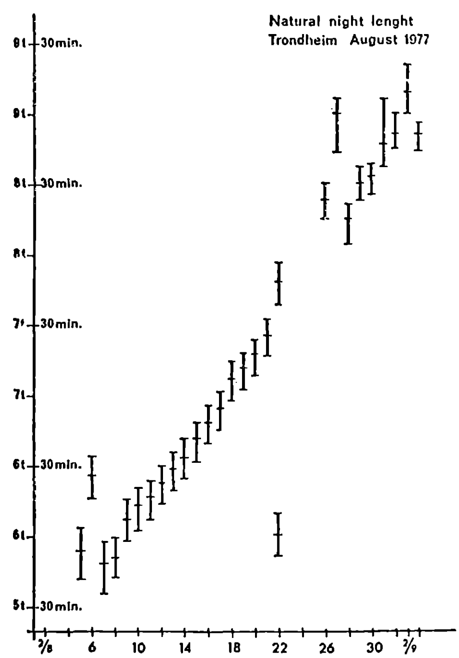
We do not know exactly which low intensity of natural light the plants of Norwegian ecotypes react to as night.

With results from photoperiodic experiments by I. Dormling (1977) in mind, I have chosen to register each day between passing the light intensities 0,5, 1,0, 1,5 and 2,0 $\mu E\ cm^{-2}\ sec^{-1}$.

1,5 $\mu E\ cm^{-2}\ sec^{-1}$ is comparable to 75 lux. A Lhambda Instrument Corp. quanta photometer connected to a recorder has been used. The changing night lengths the last 3 weeks of August were followed over the last 4 years.

Fig. 2 illustrates the situation in 1977. In this period there were many fine days with clear sky.

Figure 2. Measurements of natural night lengths in August 1977. Three different light intensities are indicated as possible distinctions between day and night in a photoperiodic sense.



If we choose 1.5 µE cm^{-2} $sec.^{-1}$ as a limit between day and night, 6 h night occurs on 9th of August, 7 h night on the 18th, and 8 h night around 24th of August.

Measurements under thick clouds on rainy days have shown nearly 1 h longer nights than under clear sky. Thus a certain critical night length could be passed up to 7-8 days earlier in bad weather conditions. In this way meteorological conditions can give a maximal variation in night length, which makes precision in time measurements of about 1 week.

The ability of the plants to react precisely to the photoperiodic signal is, however, a much more complicated matter.

During some days in 1978 a few concurrent measurements were done in Trondheim and a place 60 km southeast of Oslo at 59° 40' N, a latitude difference of nearly 4 degrees.

With clear sky the difference in night length between these two localities seemed to be about 54 min. This means that on the southern locality the 7 h night may be passed 9 days earlier than in Trondheim. This must be taken as an example of change in time of photoperiodic induction, when moving plants from south to north or vice versa.

In recent attempts to estimate the critical night length for cessation of cambial activity the following strategy has been applied.

At certain intervals in August potted plants are moved from outdoors to climate cabinets with constant non-inducing night length. Cross sections are studied in late September. Plants photoperiodically induced when they were kept outdoors, are then supposed to have stopped growing.

In other experiments plants are moved to climate cabinets at the date they have been exposed to e.g. 6 h, 7 h or 8 h nights, and this night length is kept constant in the cabinet. The results vary slightly from year to year, but in summary they show that around 18th - 23th of August is likely to be the time for photoperiodic induction, corresponding to a critical night length of about 7½-8h measured at the 1,5 µE cm^{-2} sec^{-1} level.

Such experiments, however, raise new problems as to presentation time, - that is how many inducing nights are necessary to obtain full response. The effect of light intensity, the quality of light in twilight compared to the light sources in the climate cabinet, a possible reversion of the induction by following non-inducing nights are also of vital interest in this connection.

Such investigations are in progress.

2. Other factors.

One could naturally expect that other factors, which influence growth in general, would also affect the reaction time from induction to the end of activity in the cambial zone. Nutrition, light and temperature should be taken into account. The water balance of the plants, on the other side, could easily be kept optimal by watering, but under natural conditions water supply may certainly be an important factor.

In a postgraduate thesis Aasved (1979) investigated the effect of nitrogen supply on the cambial activity. He cultured young spruce plants in nutrient solutions comparing two doses of nitrogen and a destilled water control. The cultures were kept outdoors under natural light.

As illustrated in figure 3 it appeared that increased

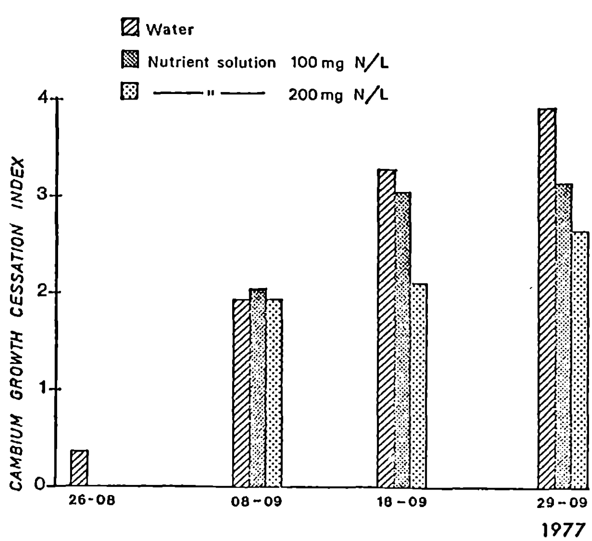


Figure 3. The effect of different nitrogen supply on growth cessation in the cambial zone. (Redrawn from Aasved (1979).)

nitrogen supply prolonged the cambial growth activity, giving growth cessation at a later date.

This observation is interesting since people at Norwegian forest nurseries are still discussing if N fertilizing late in the season will lead to winter damage.

At present another student is working on the effect of photosynthetic light as another kind of nutritional factor. Different kinds of shading are used to see how reduced photosynthesis may affect the cambial growth.

Preliminary results indicate that reduced photosynthetic production delayed the growth termination as we define it. It is reasonable to see this as an effect on growth and differentiation of the secondary walls in the last formed xylem cells.

A similar effect was observed in one of my former experiments, where low temperature clearly gave reduced differentiation.

CONCLUSION

In summary it must be pointed out that our work has been done on quite young plants.

It seems evident that passing a certain night length about 7½ - 8 h which in Trondheim normally occurs some days later than the middle of August, gives our spruce plants an impulse leading to growth cessation in the cambial zone.

Provenance differences in critical night length are to be expected similar to those shown by Dormling (1977) for shoot length growth.

When the induction has been perceived, other environmental factors such as mineral nutrition, light and temperature have an influence on the growth processes so that the time of growth cessation may be affected to a certain extent.

How close a correlation there may be between the time of growth cessation and the attainment of winter hardiness, remains to be established.

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