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GROWTH OF SPRUCE SEEDLINGS UNDER LONG PHOTOPERIODS

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(Project P-385)

by

D. A. Fraser[1]

INTRODUCTION

Experimental control of plant growth is proving of practical value in an ever-increasing variety of plants. In one year it is now possible to grow several generations of cereal plants under controlled light and temperatures. This is of especial value in breeding new varieties of rust-resistant wheat. In nurseries, supplementary illumination in chrysanthemum beds extends the vegetative period and allows the grower to produce flowers when the market values are high owing to lack of flowers on plants growing under natural daylight conditions (Ditchman 1958, Post 1942). Went's (1957) book "Experimental Control of Plant Growth" brought up to date a decade of research with "phytotrons" and evaluated their importance in understanding the physical factors influencing plant growth.

Botanists have used long photoperiods to produce experimental material in the greenhouse and growth chamber during the winter months when natural photoperiods are short in the temperate zones (Fraser 1957, 1958b, Senn 1957). The effect of photoperiod on growth and dormancy in woody plants has been explored by various workers starting with Garner and Allard in 1920 who worked on sumac as well as herbaceous plants; many recent studies have been made of a wide group of hardwoods and conifers (Downs 1958, Wareing 1950a, 1950b, 1956, Watt 1961).

The present investigation summarizes growth responses of seedlings of black, white, and red spruce (*Picea mariana* (Mill.) BSP., *P. glauca* (Moench) Voss, and *P. rubens* Sarg.) to extended photoperiods in the growth chamber, greenhouse, and nursery. It is a part of a project on the physiology of flowering of spruce.

MATERIALS AND METHODS

Seeds of black and white spruce of local origin were stratified in wet vermiculite at 34° F. in September, 1957. One month later the seeds were planted in loamy sand at 70° F. Germination occurred within a fortnight. The seedlings were potted in 3-inch pots in early November and repotted into 5- and 6-inch pots in February and October, 1958, respectively. Cultures in the main growth chamber and greenhouse experiments received 10 cc. weekly of Hoaglund's No. 2 nutrient solution (Curtis and Clark 1950) from November, 1957.

One group of black spruce seedlings was grown for two years under 24-hour (continuous light) and 16-hour photoperiods from a combination of eight 8-foot, daylight, slim line tubes and six 200-watt incandescent bulbs. This arrangement resulted in a range from approximately 300 foot candles at the 4-foot distance where the seedlings were started, to 1,000 foot candles at the 1-foot distance which was reached by the tops of the black spruce seedlings under the 24-hour photoperiod at the end of 18 months. These two photoperiods were used in a growth chamber with two compartments where an air temperature cycle of 78° F. "day" and a 56° F. "night" was adopted because this temperature cycle approximated that of the summer (June-August) of 1955 at Chalk River, which was conducive to the formation of flower primordia (Fraser 1958a). The temperature

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TABLE 1. OUTLINE OF GROWTH RESPONSES TO LIGHT AND TEMPERATURE TREATMENTS IN BLACK SPRUCE SEEDLINGS

1st Treatment		Response	2nd Treatment			Response	3rd Treatment	Response	4th Treatment	Response
PP* No. Hrs.* Lt.*/Dk.*	TP* °F. Day/Night		Mo*	PP	TP					
16/8	70/70	TB* formed after 2-3 Mo. and G ceased.	1	16/8	34	G* resumed temporarily under original PP and TP	Planted in outside nursery	Natural G cycle	24/0 PP June-Aug.	Increased G
16/8	78/56								Sunlight only	Natural G
24/0	70/70	G continuous and rapid for at least 2 years	Several	16/8	78/56	G ceased TB formed	½ Hr. 107° F.	Loss of new needles. G temporarily resumed under 16/8 PP-78/56 TP.		
24/0	78/56						1 Mo. 34° F.	G temporarily resumed under 16/8 PP-78/56 TP		
							24/0 PP 78/56 TP	G resumed and continuous		
							Planted in outside nursery	Natural G cycle	24/0 PP June-Aug.	Increased G
									Sunlight only	Natural G
			Several	24/0	70/70	G continued	½ Hr. 107° F. 24/0 PP 78/56 TP	Loss of new needles. Slight reduction in rate of G		
				24/0	78/56		Planted in outside nursery	Natural G cycle	24/0 PP June-Aug.	Increased G
									Sunlight only	Natural G

* Abbreviations used in table.
Dk-Dark, G-Growth. Hrs-Hours, Lt-Light, Mo-Month, PP-Photoperiod, TB-Terminal Bud, TP-Thermoperiod.

TABLE 2. OUTLINE OF GROWTH RESPONSES TO LIGHT AND TEMPERATURE TREATMENTS IN WHITE SPRUCE SEEDLINGS

1st Treatment		Response	2nd Treatment			Response	3rd Treatment	Response	4th Treatment	Response
PP* No. Hrs.* Lt.*/Dk.*	TP* °F. Day/Night		Mo*	PP	TP					
16/8	70/70	TB* formed after 2-3 Mo and G ceased	1	16/8	34	G* resumed temporarily under original PP and TP	Planted in outside nursery	Natural G cycle	24/0 PP June-Aug.	Increased G
16/8	78/56								Sunlight only	Natural G
24/0	70/70	TB formed after 1-1½ years G slow. G continuous but slow for at least 2 years if additional nitrogen supplied	Several	16/8	78/56	TB formed G ceased	Planted in outside nursery	Natural G cycle	24/0 PP June-Aug.	Increased G
24/0	78/56								Sunlight only	Natural G

* Abbreviations used in table.
Dk-Dark, G-Growth, Hrs-Hours, Lt-Light, Mo-Month, PP-Photoperiod, TB-Terminal Bud, TP-Thermoperiod.

change from the high of the "day" to the low of the "night" and *vice versa* was gradual, extending over a 4-hour period. Thus at 6 a.m. air temperatures started to increase from 56° F. by approximately 6° F. each hour, until 78° F. was reached at 10 a.m. The temperature reversal began at 6 p.m. and continued until the air temperature of 56° F. was reached at 10 p.m.

A second growth chamber with constant temperature of 70° F. was also used. Here an illumination of 300 foot candles at seedling level was attained for 16 hours (with a bank of 200-watt incandescent bulbs); during the remaining 8 hours the seedlings received approximately 25 foot candles (from two 25-watt bulbs).

One hundred black spruce seedlings were used in these experiments; 30 in the 78°/56° F. temperature cycle and 70 in the 70° F. temperature cycle. Poor germination and establishment limited the number of white spruce seedlings to 13, which were located in the 70° F. growth chamber in October, 1957. Experiments with several dozen white spruce were continued the following year in both growth chambers.

Acclimatization experiments with black spruce (15 seedlings per experiment) included transfer of seedlings from the 24-hour to the 16-hour photoperiod in the 78°/56° F. growth chamber, and between both growth chambers and a cold room at 34° F. Effects of an extended photoperiod on growth of seedlings were also explored in the greenhouse where a combination of fluorescent tubes and incandescent bulbs, similar to those in the 78°/56° F. growth chamber, was switched on from dusk to dawn to give a 24-hour photoperiod. The greenhouse temperature was regulated at 70° F. minimum, but during the summer afternoons higher temperatures (up to 90° F.) were reached for short periods. Additional light was supplied in the nursery as well to test its effect under natural conditions.

Sections of the growing points and stems of black spruce seedlings exposed to the 16- and 24-hour photoperiods in the growth chamber were made on a sliding microtome. Their anatomical condition was recorded by photomicrographs.

OBSERVATIONS AND RESULTS

An outline of the growth responses to light and temperature treatments described in detail in this section, has been prepared for black and white spruce seedlings (Tables 1 and 2). These tables summarize data contained in growth curves shown in Figures 1, 3 and 5.

Growth Responses of Seedlings to Extended Photoperiod in Growth Chambers

Following germination, the seedlings grew to a height of approximately one inch during the first few months, (Fig. 1). In black spruce the rate of apical growth increased at the end of the fourth month in the seedlings grown at the 78°/56° F. temperature cycle and continuous "high" light intensity, and after the fifth month in those grown at 70°/70° F. temperature and 16-hour "high" light and 8-hour "low" light intensity. By the eighth month, apical growth attained a rate of about 2½ inches per month for the seedlings in the 78°/56° F. temperature under continuous "high" light intensity and slightly less for the other temperature-light regime. At that time the air temperature was increased to 106° F. for 30 minutes. This caused the new needles on the black spruce seedlings to die, and the growth rate of these seedlings decreased. The tops of the plants eventually approached the lights in both growth chambers and excessive heat from these lights affected their apices. Because the effect of root binding appeared about the same time, the experiment was terminated after 26 months.

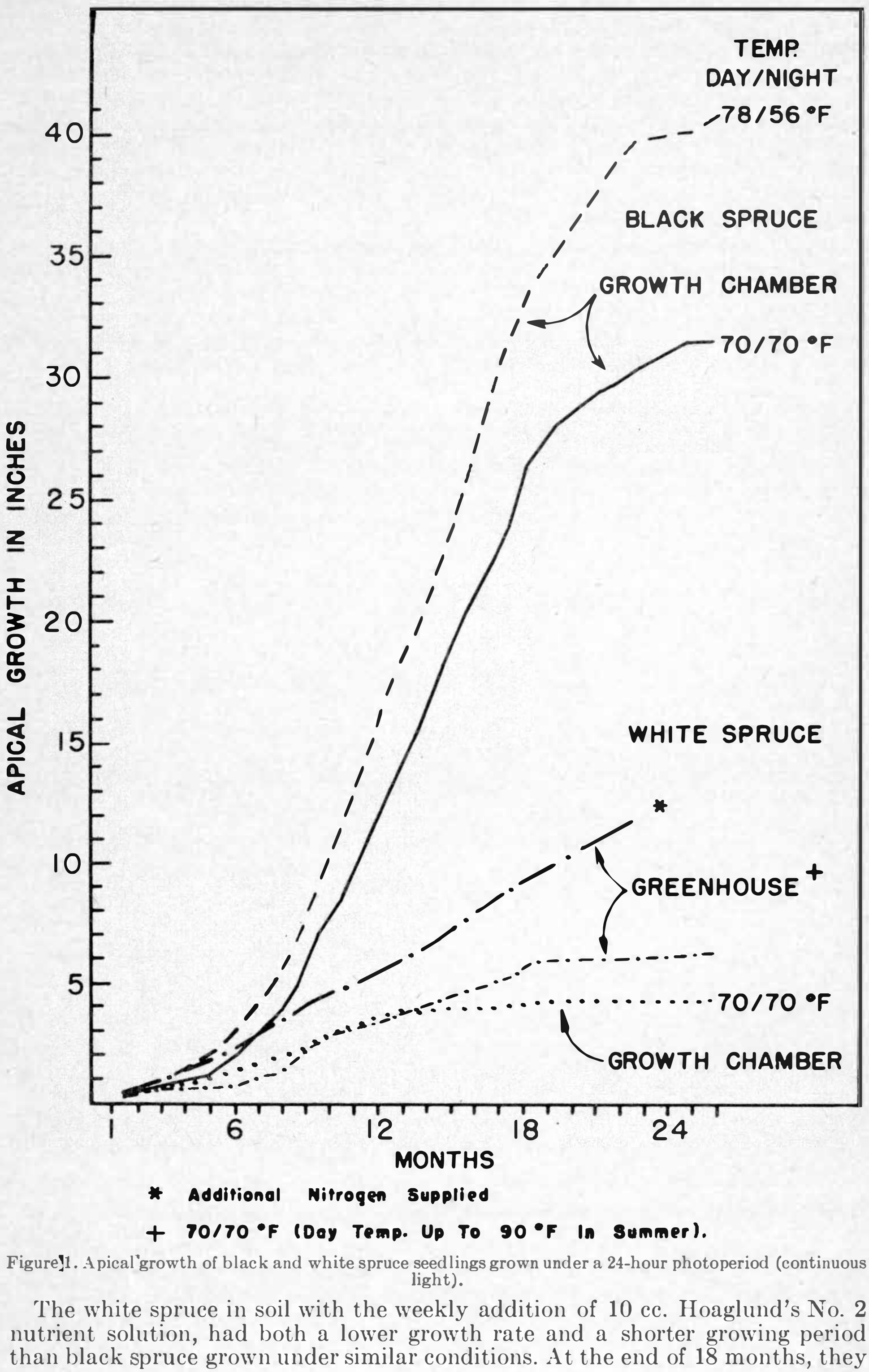

Figure 1. Apical growth of black and white spruce seedlings grown under a 24-hour photoperiod (continuous light).

The white spruce in soil with the weekly addition of 10 cc. Hoaglund's No. 2 nutrient solution, had both a lower growth rate and a shorter growing period than black spruce grown under similar conditions. At the end of 18 months, they averaged only 4 inches in height compared with the 27 inches produced by the black spruce growing under the same conditions (Fig. 1). After this period, the white spruce seedlings growing under continuous light formed a terminal bud and went into dormancy which lasted until the end of the experiment. This dormancy did not occur in white spruce seedlings grown under continuous light in the greenhouse with the weekly addition of 10 cc. of a commercial fertilizer with high nitrogen content. However, even these white spruce attained a height of only 10 inches in 18 months compared with 27 inches for black spruce seedlings under similar greenhouse conditions.

The average dry weight of various parts of two black and two white spruce seedlings grown for 24 months under continuous light in the same growth chamber was obtained by bringing them to constant weight in an oven at 215° F. The material was then ashed at 1100° F. for at least 4 hours in a muffle furnace to obtain ash weights. That the increase of growth of black spruce was accompanied by an equivalent increase in dry matter is evident from Tables 3 and 4.

TABLE 3. MEAN OVEN DRY WEIGHT (ODW) AND ASH WEIGHT (AW) IN GMS, OF VARIOUS PARTS OF TWO BLACK AND TWO WHITE SPRUCE SEEDLINGS GROWN UNDER 24-HOUR PHOTOPERIOD IN A GROWTH CHAMBER FOR TWO YEARS. DATA REPRESENT AVERAGES OF TOTAL WEIGHTS.

	Needles	Buds	Wood	Bark	Branches	Roots	Total
Black Spruce							
ODW	27.5	1.4	50.2	12.0	12.5	54.2	157.8
AW	1.4	0.03	0.3	0.5	0.4	1.6	4.2
% Ash	5.	2.	1.	4.	3.	3.	3.
White Spruce							
ODW	1.60	0.18	0.66	0.61	0.46	1.37	4.9
AW	0.15	0.01	0.01	0.04	0.03	0.05	0.29
% Ash	9.	7.	1.	6.	7.	4.	6.

TABLE 4. AVERAGE HEIGHT, DIAMETER OF TRUNK BASE, AND NUMBERS OF NEEDLES AND BUDS ON TWO BLACK AND TWO WHITE SPRUCE SEEDLINGS GROWN FOR TWO YEARS UNDER A 24-HOUR PHOTOPERIOD IN THE GROWTH CHAMBER. DATA REPRESENT AVERAGES OF TOTAL COUNTS.

	Height	Diameter of trunk base	Number of needles	Number of buds
Black spruce	49″	0.7″	32,000	550
White spruce	8″	0.2″	2,100	75

The relative size and form of these trees at 79 weeks of age is shown in Figure 4. A few black spruce seedlings did not maintain a straight monopodial form. In these plants the growing point formed a terminal bud after 12 months of growth while the upper whorl of lateral branches continued to grow and compete for apical dominance, giving rise to a shorter plant with a larger proportion of side branches.

Acclimatization Experiments with Black Spruce Seedlings

The black spruce seedlings grown under the 24-hour photoperiod were used in successive experiments to study apical growth in that species. Four nine-month-old seedlings about 10 inches high (from the growth chamber at 78°/56° F.) were planted outside in the nursery in June, 1958. These seedlings formed a terminal bud, survived the following winter and grew 5 inches during May-July, 1959 (Fig. 3).

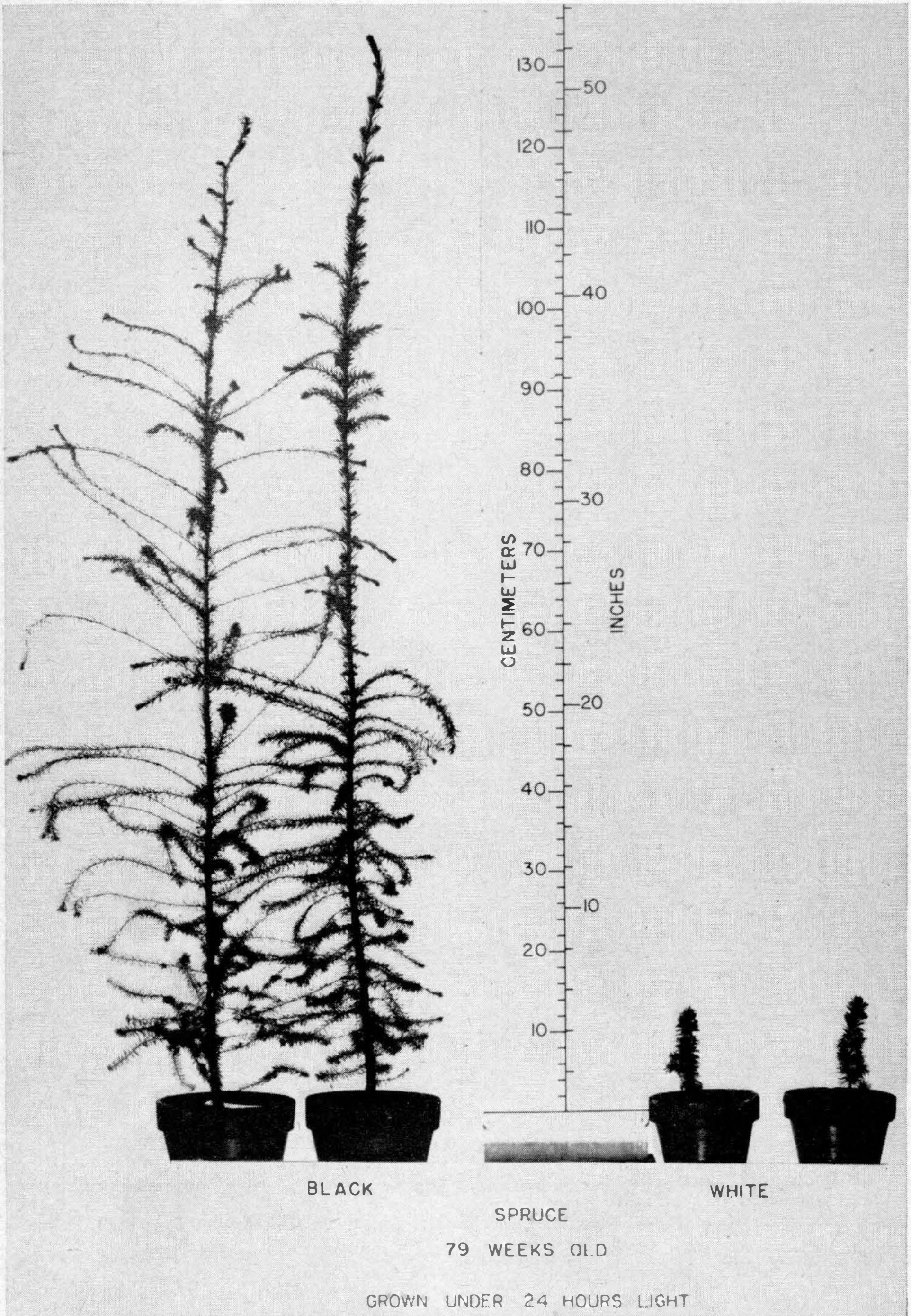

Figure 2. Black and white spruce seedlings grown under a 24-hour photoperiod (continuous light) at 70° F. for 79 weeks.

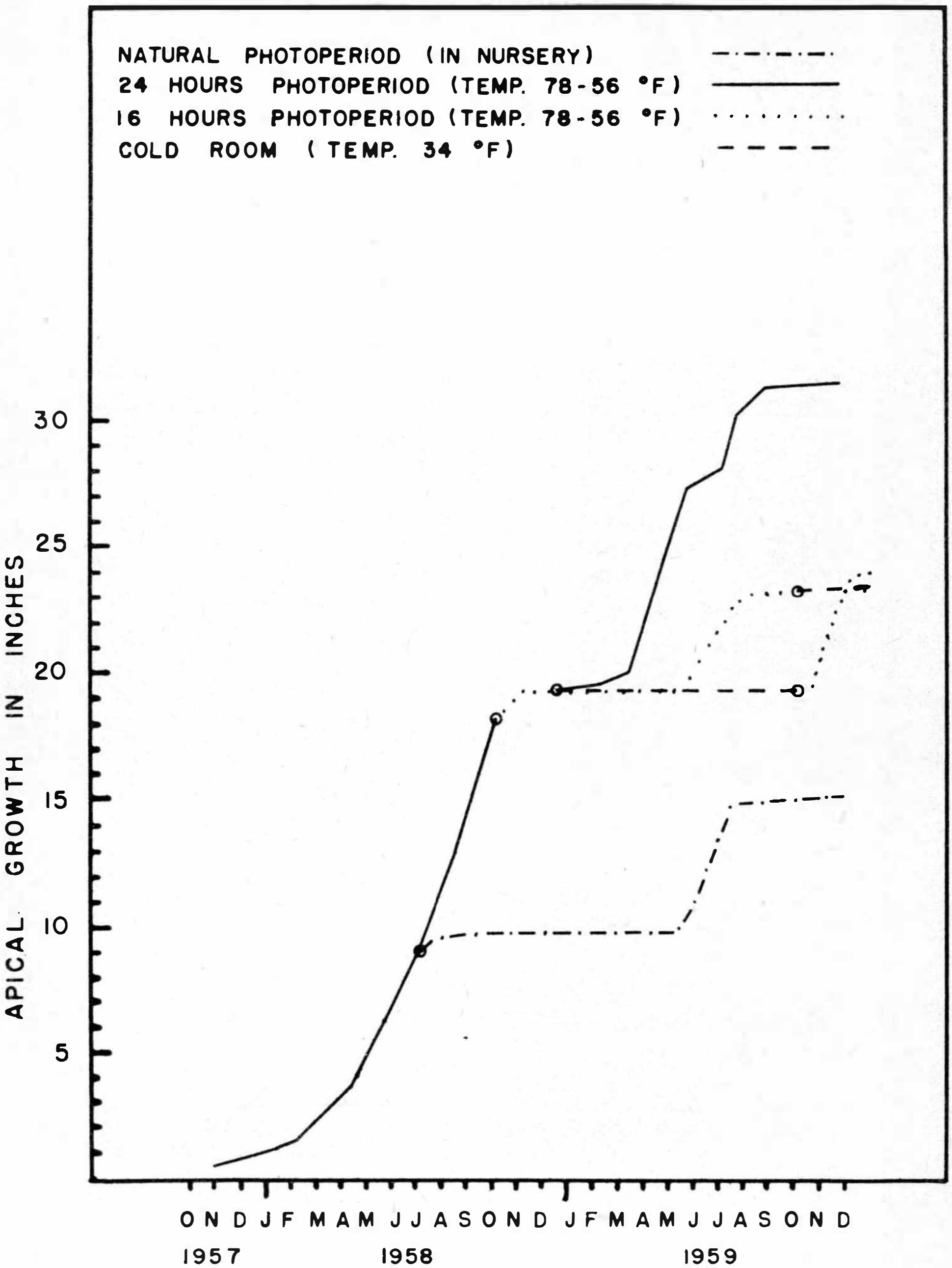

Figure 3. Apical growth of black spruce seedlings under 16-hour (dotted line) and 24-hour (solid line) photoperiods and under natural conditions (dot-dash line). Defoliation of trees in growth chamber, May 1959, broke the dormancy of terminal buds in 16-hour photoperiod trees (dotted line), and slowed the rapidly growing 24-hour photoperiod (continuous light) trees (solid line).

Another group of 12 seedlings, 20 inches high, was selected after one year under the 24-hour photoperiod at 78°/56° F. and moved to a 16-hour photoperiod (still at 78°/56° F.) in October, 1958. These seedlings formed a terminal bud and ceased apical growth (Fig. 3). Longitudinal sections of the black spruce apices formed under the 24- and 16-hour photoperiods are shown in Figure 4. The apex in the actively growing seedlings under the 24-hour photoperiod was narrow, with numerous needles in various stages of development distributed from its base along the main axis. The apex of the black spruce formed after growth ceased under the 16-hour photoperiod comprised a terminal bud with rudimentary needles arranged along the flanks of the bud and their surrounding bud scales. The stem of the 24-hour photoperiod black spruce had no differentiation into "spring" and "summer" wood, whereas that of the seedlings moved from the 24-hour to the 16-hour photoperiod formed a narrower band of wood, which appeared to be associated with the formation of the terminal buds. After two months in a dormant state in the 16-hour photoperiod, those black spruce seedlings were divided into three lots (Fig. 3):

(a) One lot was transferred back to the 24-hour photoperiod at 78°/56° F.
(b) One lot remained under the 16-hour photoperiod at 78°/56° F.
(c) One lot was moved to a 16-hour photoperiod in a cold room at 34° F.

The seedlings transferred from the 16-hour photoperiod to the 24-hour one resumed growth, slowly at first, then after three months the original rate of apical growth maintained during their first year was regained.

The seedlings in the 16-hour photoperiod at 78°/56° F. remained dormant. However, owing to a mechanical difficulty with the temperature control on May 30, 1959, the temperature within the growth chambers rose for $\frac{1}{2}$ hour from 56° F. to 106° F. This temperature increase killed the new needles on both the 16-hour and 24-hour photoperiod trees. This loss lead to an interesting reaction. Following defoliation, the dormant seedlings under the 16-hour photoperiod renewed apical growth for a period of two to three months. When the needles on the new shoots were well-developed, a terminal resting bud was produced and the plants became dormant again. The seedlings under the 24-hour photoperiod reduced their growth rate noticeably, but apical growth regained its previous rate as new needles appeared.

The seedlings transferred into the 16-hour photoperiod at 34° F. remained dormant. When they were moved back to the 16-hour photoperiod at 78°/56° F. in November 1959, they renewed apical growth for three months and then again formed a terminal resting bud.

Growth Responses of Seedlings to Extended Photoperiod in the Nursery

In May, 1959, 26 each of black and white spruce seedlings which had been subjected to two 4-month growth cycles in the growth chamber at 70° F. with a month-long rest period between, and 26 red spruce seedlings which had been subjected to one 4-month growth cycle in the greenhouse, were planted in three plots of the outside nursery. Two of these plots received supplementary illumination of 300 foot candles from fluorescent tubes so that they were exposed to a 24-hour photoperiod from mid-June to the end of August. The third plot had the natural photoperiod. Apical growth on these seedlings was measured periodically (Fig. 5). A 't' test (Cox 1952) indicated that apical growth of all species under light was greater than that of untreated seedlings at the 1 per cent level of significance. The onset of cool fall weather would eventually limit the amount and continuation of growth induced by the long photoperiod. When continuous light was maintained throughout September over seedlings growing outside, they did not become frost hardy and were damaged or killed by freezing temperatures when winter approached. Failure to achieve frost hardiness in red oak (*Quercus rubra* L.) and other species receiving long photoperiods from external illumination has been previously noted (Fraser 1952, Kramer 1937, Matzke 1936).

16-HOUR 24-HOUR

Figure 4. Photomicrographs of shoot apices of black spruce seedlings ormed under 16- and 24-hour (continuous light) photoperiods. The 16-hour apex has formed a dormant terminal bud whereas the apex under continuous light is in an active state of growth. X50.

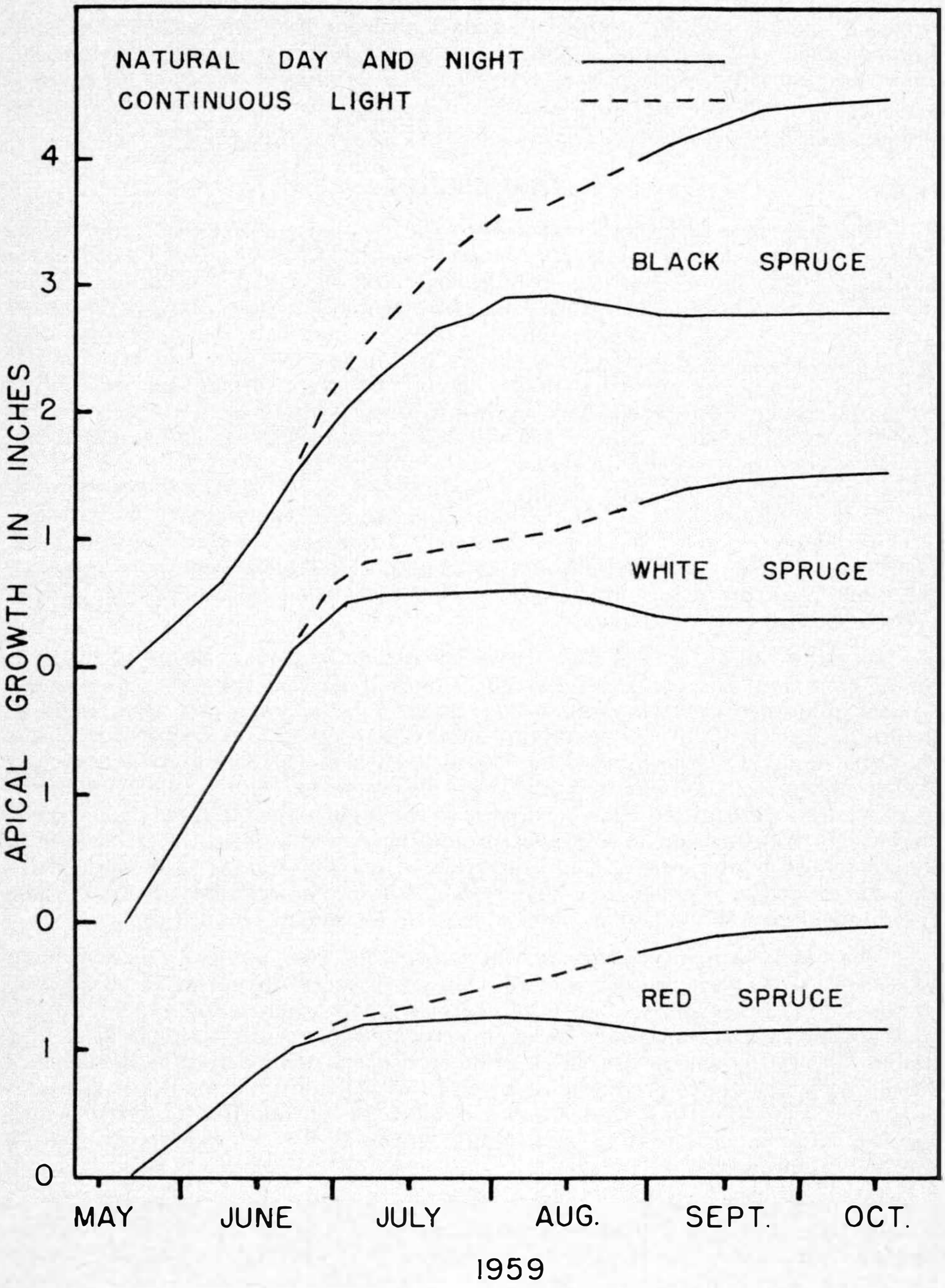

Figure 5. Increased growth (dash line) of black, white, and red spruce nursery seedlings stimulated by a 24-hour photoperiod (continuous light), compared to growth (solid line) under natural conditions.

Following the success of experiments to increase growth of spruce seedlings by extended photoperiods, a series of 150 watt reflector flood lamps were installed over part of a plantation of 400 ten-year-old white and 50 black spruce. These lights gave about 150 foot candles illumination during the night period from mid-June until the end of August, 1960. Apical growth of these illuminated trees was increased almost 100 per cent over the controls receiving the natural photoperiod. This increase was occasioned by growth continuing into September. There was a similar significant increase in radial growth of the illuminated trees.

DISCUSSION

The difference of growth response to the 24-hour photoperiod (continuous light) in the black and white spruce seedlings is apparent. The black spruce seedlings appear more responsive to supplementary light. An inhibitor, initiating the onset of dormancy and the formation of a terminal bud, is probably elaborated in the needles under the 16-hour photoperiod and then translocated to the stem apex. This is evidenced by the breakage of dormancy of the black spruce seedlings under the 16-hour photoperiod which had their needles killed by excessive heat; dormancy set in again when new needles were formed. Black and white spruce seedlings with dormancy induced by a decreasing day length in late summer, can have this dormancy broken by a two-month exposure to a temperature of 34° F., followed by an exposure to a 16-hour photoperiod at 70° F. At the low temperatures, the inhibitor may not be elaborated in the needles and thus the inhibitor already present in the buds would gradually disappear. On this assumption, it takes six weeks or so for the inhibitor to be elaborated again and translocated to the buds when the plants are moved from the coldroom to the 16-hour photoperiod in the growth chambers.

Wareing (1956) stated that leaves of *Betula pubescens* Ehrh. maintained under short days have an inhibitory effect on bud growth. He grew plants under various photoperiods with buds either shielded or not shielded from light to determine the locale of the postulated inhibitor of growth. His observation was that the removal of the inhibitor is not in itself sufficient to induce bud-break; direct exposure of the buds to long days is also required. Thus while some inhibitory effect is transmitted from the leaves to the buds under short-day conditions, there is no transmission of a growth promoting stimulus from the leaves under long-days. In white spruce, small amounts of an inhibitor are still apparently elaborated in the needles even under the 24-hour photoperiod to prevent the rapid apical growth evident in black spruce under similar conditions.

The black spruce seedlings produced over 30 times more dry matter than white spruce. Yet the relative mineral content of the white spruce seedlings was double that of black spruce. This is not surprising, for whereas the mineral uptake in black spruce was continually being incorporated into a proportionately greater amount of new tissue, the uptake in white spruce was being deposited in the older tissues since new tissue production was very slow. In addition, the black spruce as compared with the white spruce had a much higher proportion of xylem which has less mineral content than bark. White spruce is also more demanding in its mineral requirements.

Seedlings grown under continuous light in the greenhouse during the winter months survived when planted outside the following spring. These seedlings assumed then the seasonal periodicity of growth of plants grown under natural conditions. This technique has been used successfully to establish small plantations for future tree physiology experiments.

Apical growth of spruce seedlings and young trees growing in the nursery can also be significantly accelerated by the addition of supplementary light to lengthen the photoperiod to 24 hours. Approximately 30 per cent more growth was produced under these modified conditions for the seedlings and up to 100 per cent in young trees. However, it is necessary to discontinue the supplementary illumination about ten days before the first autumn frost, so that the seedlings may develop frost hardiness stimulated by the naturally shortened photoperiod. Increased growth in nursery stock including black and white spruce, was recently reported by Watt (1961) who extended the photoperiod (to 20 hours) with supplementary incandescent lighting at an intensity of 25 foot-candles at ground level. In addition he has obtained a significant reduction in the per cent of cull of seedlings grown for transplanting.

SUMMARY

Black and white spruce seedlings were grown for two years in growth chambers under extended photoperiods. Under continuous incandescent light, the black spruce grew 30 inches whereas the white spruce grew only 5 inches. Black spruce seedlings grown under continuous light in the laboratory during the winter were successfully transferred to an outside nursery in the spring and assumed there the normal seasonal periodicity of growth. Black spruce plants that were grown completely under a 24-hour photoperiod formed a terminal bud when transferred to a 16-hour photoperiod. The dormancy of this bud was broken when the needles were killed by high temperatures; apical growth continued then until new needles were formed. The mechanisms controlling apical growth are discussed. Apical growth of black, white, and red spruce seedlings in the nursery was significantly increased by a 24-hour photoperiod effected through supplementary illumination during the summer months.

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