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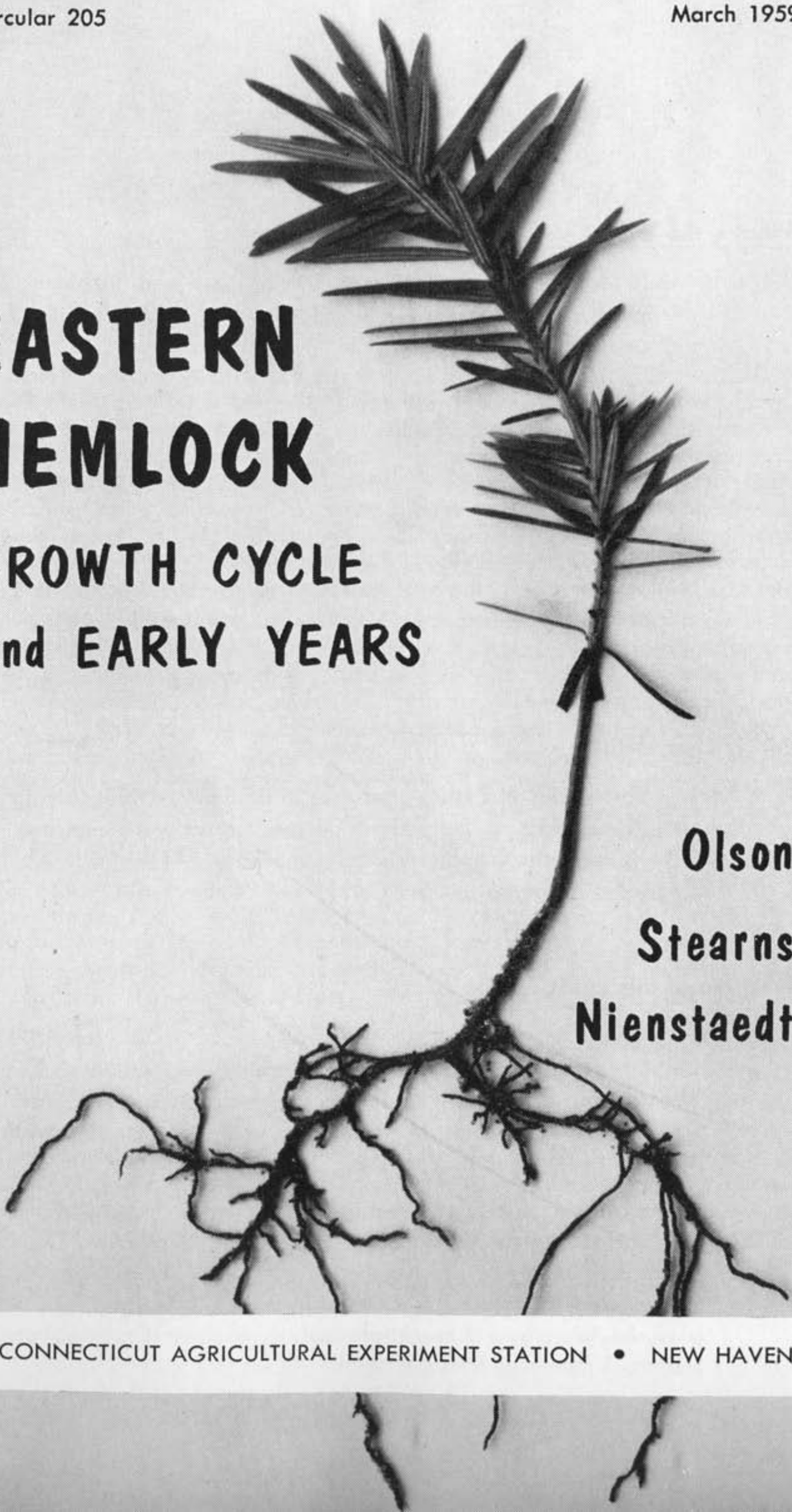
EASTERN HEMLOCK
GROWTH CYCLE and EARLY YEARS



Olson
Stearns
Nienstaedt

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION • NEW HAVEN

Foreword

What's the story?

If you would like to experiment, and have some interest in trees, you may enjoy "looking over our shoulder" as we ask hemlock seeds and seedlings some questions:

How do seeds and seedlings from one source respond to different light and temperature conditions?

How do seeds and seedlings from many geographic sources behave under uniform conditions?

Finally, from these answers — from this new knowledge of how hemlock grows — can we see how to overcome some of the difficulties that have long beset those who grow hemlock, whether for the forest or the front yard?

For further details

These lines of inquiry, with scientific detail, a bibliography, and acknowledgments of help given by many others, are explored more fully in Bulletin 620 of this Station, "Eastern Hemlock Seeds and Seedlings: Response to Photoperiod and Temperature."

Who made this study?

When the experimental work was performed, Dr. Jerry S. Olson and Dr. Hans Nienstaedt were members of the Station staff in the Departments of Forestry and Genetics, respectively; Dr. Forest W. Stearns was a member of the Forestry Department staff while on sabbatic leave from Purdue University in 1956.

As of the date of this publication Dr. Olson is employed at the Oak Ridge National Laboratory, Oak Ridge, Tennessee; Dr. Nienstaedt is in charge of the Northern Institute of Forest Genetics, Lake States Forest Experiment Station, Rhinelander, Wisconsin; Dr. Stearns is at the Waterways Experiment Station, Souhern Forest Experiment Station, Vicksburg, Mississippi.

EASTERN HEMLOCK

GROWTH CYCLE AND EARLY YEARS

Jerry S. Olson **Forest W. Stearns** **Hans Nienstaedt**

INTRODUCTION

Because of the significance of the eastern hemlock for forest ecology and its intangible and economic values, the species has been studied intensively at this Station for the past 6 years. The present report covers mainly the results of laboratory and greenhouse experiments. By using seed from selected sources, and controlling growing conditions with respect to light, temperature, and nutrient, it has been possible to estimate the separate and combined effects of these factors on seeds and seedlings. The early stages of growth are especially critical for the establishment and survival of hemlock. Knowledge of the factors that regulate the growth of the young plants should also help us to understand the growth of the tree throughout its life.

Indeed, the growth responses by hemlock were so striking as to arouse interest in its physiology. This is one of the first plants to show response of *seeds* to duration of light and dark (photoperiodism) during germination. Photoperiod also had a strong influence on breaking *bud* dormancy and forcing growing plants back into dormancy. Day and night temperature, chilling, and nutrient also had important effects on growth, and modified the response of seeds and seedlings to light.

THE LIFE CYCLE OF EASTERN HEMLOCK, *Tsuga canadensis* (L.) Carrière

The life cycle consists of a vegetative or sporophytic stage, during which the tree grows, and a sexual or gametophytic stage during which male and female cells are produced; these cells unite to start a new sporophyte generation. The sporophytic (tree) stage may extend over several hundred years, with the tree producing sexual structures periodically; the sexual stage is completed within a few months.

Development of Cone and Seed

The nucleus of each cell of the parent tree or sporophyte has *two* sets of 12 chromosomes. During the sexual stage, male and female strobili or "flowers" are developed in specialized buds. Within each of these strobili certain cells divide so that the resulting cells have nuclei with only *one* set of 12 chromosomes. These are the first cells of the male and female gametophyte, from which the embryo develops, as described below. The sequence, based on observations by Echols and others, and by ourselves during this study, traces the progress of development from the time the strobilate buds are formed, through the gametophytic stages, and finally to the fully developed seed. Dates are approximate for New Haven, Connecticut.

1. Buds for male and female strobili are developed the preceding summer on the parent tree (Figure 1).

2. After remaining inactive until late March, certain cells in the male strobili undergo meiosis, or reduction division, to produce the male gametophyte cells, each with one set of 12 chromosomes. As the buds swell in April and early May, these cells develop into mature pollen grains.

In early May, the female gametophyte is produced within the female strobilus by reduction division of certain cells inside the ovule (Figure 1). During the following two months, the cells of this gametophyte divide to form (a) one or more unfertilized egg cells which may later be fertilized by a nucleus from a pollen cell, and (b) other cells from which the endosperm develops. All cells of the female gametophyte have one set of 12 chromosomes per nucleus. Two ovules lie on each scale of the miniature cone and are exposed to air when the cone scales spread during the second week in May (Figure 3B).

Surrounding the female gametophytic cells are two layers of tissue previously derived from the cone scale of the parent tree, the nucellus and integument. The wing is also derived from the cone scale. Seed and wing are initially attached to the cone scale (Figure 3D-F) but later become freed from it.

3. After pollen is carried to the young cone by wind about the second week in May, it sends out a pollen tube (Figure 2C) which, over a period of about 6 weeks, grows into the ovule. Two 12-chromosome nuclei are produced from the original nucleus of the pollen grain and are then drawn into the ovule. One of these joins the nucleus of an egg cell of the female gametophyte to constitute a fertilized egg cell (Figure 2D) whose nucleus then has two sets of 12 chromosomes which carry the genetic contributions of both parents to the new generation. The remaining cells of the female gametophyte, which still have only 12 chromosomes per nucleus, develop into the endosperm which nourishes the growing embryo before and during germination.

4. After fertilization in late June, and continuing during July and August, the fertilized egg develops into the embryo. Embryo and endosperm grow at the expense of the nucellus which persists only as a remnant, the endosperm membrane. The integument gives rise to the outer and inner seed coats which enlarge as endosperm and embryo develop (Figures 2C-E).

5. By September, cone and seed are mature but they are still green, wet, and oily. By early October much of the excess moisture has been lost, the color has changed from green to tan and finally to brown, and the cones begin to open (Figure 3G, H). Most of the seed is shed during the first few periods of dry windy weather thereafter. Some seed may hang in the cones through the winter and be dispersed more gradually, but much of this is sterile seed which developed without an embryo.

At maturity, the embryo is a white cylindrical structure about 3 mm. long and .5 to .7 mm. in diameter (Figure 4B). The embryo (Figure 4A) extends almost the full length of the seed, but its diameter is only about one-third that of the seed. At the end of the seed which bears the wing, the embryo has incisions which separate the seed leaves or cotyledons (normally three, occasionally four or more, rarely two) below which is the hypocotyl. At the other end, a small notch divides the true root from the stem portion of the hypocotyl.

New seed is partially dormant and incapable of rapid germination in the autumn when shed. This dormancy is normally overcome by winter chilling. Thus seed can germinate rapidly in the spring as soon as the temperature

FIGURE 1. LIFE CYCLE OF TSUGA CANADENSIS

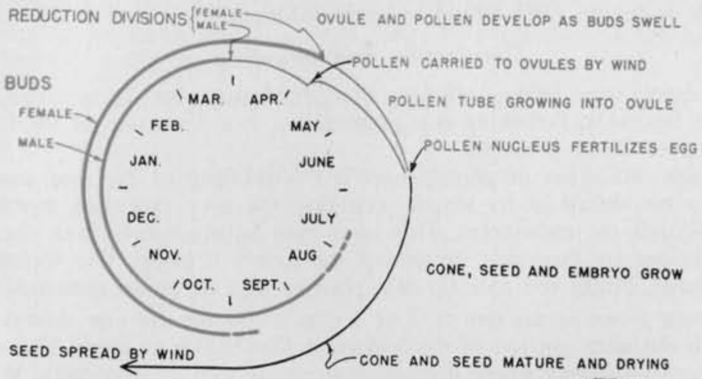
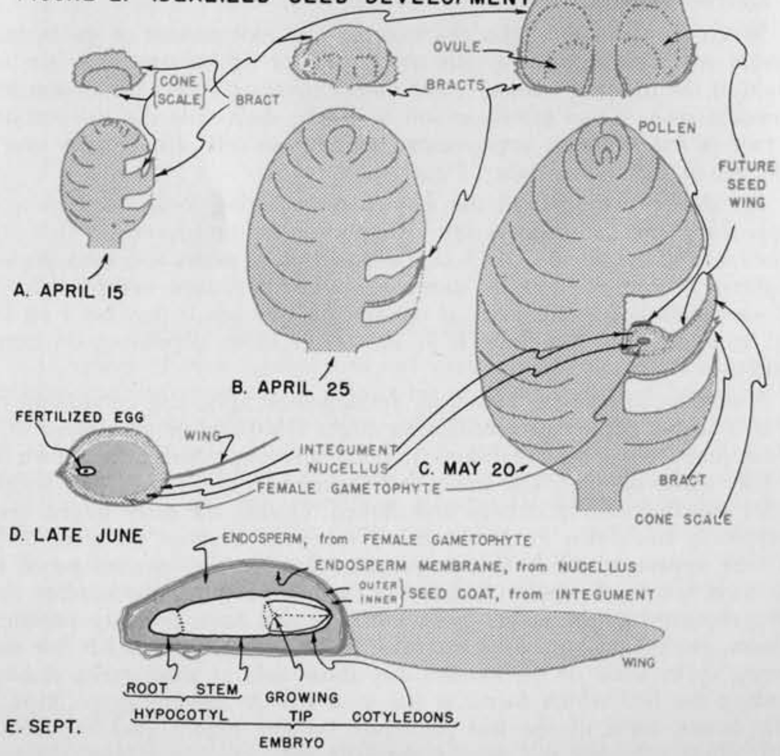


FIGURE 2. IDEALIZED SEED DEVELOPMENT



Figures 1 and 2. Green represents parent sporophytic (tree) stages (Figure 1) and tissue (Figure 2); red, gametophytic (sexual) stages and tissues after reduction divisions; black, successive stages of the new sporophyte terminating with the fully developed embryo.

again becomes warm enough to permit growth. Over the years the sporophyte passes through seedling, sapling, and mature tree stages. When about 15 years old, or much later in some cases, the tree produces strobili and another sexual cycle is begun. (We would welcome information on earlier flowering.)

Germination and Growth

The description below assumes that conditions for germination and growth are favorable. Following this presentation is a discussion of the factors which regulate these processes.

The first indication of germination is the splitting of the seed coat for one-half to two-thirds of its length, exposing the grey reticulate membrane which surrounds the endosperm. This layer may bulge slightly from the gap. If all conditions are favorable, growth of the root will begin. The appearance of the pointed, bright red root tip is a positive sign of active germination.

The root grows at the rate of 2 or 3 mm. a day for the first several days after which the stem portion of the hypocotyl also begins to grow. The entire structure curves abruptly where it emerges from the seed (Figure 6A). Within the seed, digestion of the food reserves proceeds as the endosperm softens and becomes liquified.

When grown in the light, much of the true root portion of the hypocotyl is bright red. The pigmented cells cover the root tip densely while the older portion of the root has a loose, rather shaggy covering of the same filamentous, pigmented cells. When grown in soil or in the dark, only the tip portion of the root is red although unpigmented filamentous cells are present over the remainder of the root surface (Figure 6A).

An abrupt change from the filamentous covering to a green shiny epidermis marks the transition to the stem portion of the hypocotyl. This region reaches its full length of 2 or 3 cm. within 1 to 3 weeks and then begins to straighten (Figure 4H, I). It shows a marked curvature toward light. The root also continues to elongate; at the end of a month it may be 2 to 4 cm. long; at the end of 3 months, 6 to 10 cm. or more, depending on nutrient conditions.

Normally there is a pause in development after the cotyledons open and it is at this point that germination might arbitrarily be considered to end. At the junction of the cotyledons lies the growing point from which stem and later leaves develop. The leaves first appear as a tiny tuft of pale yellowish needles which gradually enlarge and darken. During the early stages, needles are typically laid down in threes around the stem at about the same level so that they appear whorled. This is indicated by the high percentage of seedlings with 3, 6, or 9 needles (Table 1). The stem between the needles (internode) elongates as the leaves grow. On later and faster-growing portions of the stem, grouping by three's is less evident. Toward the end of the first annual growing cycle, some of the needles may show only as short green stubs surrounding the bud which forms at the stem tip. As growth slows down and finally ceases, some of the leaf primordia become highly modified into bud scales. These surround and protect the primordia which will give rise to the next year's growth. Early buds on vigorous shoots occasionally put out a second flush of growth but normally late summer buds will not resume growth unless the buds are chilled for a month or more at temperatures slightly above freezing. In nature such chilling takes place during the late autumn months

and, by the time the chilling requirement is completed, temperatures will usually have become too low to permit a resumption of growth until the following spring when rising temperatures permit the initiation of another cycle of growth; this is terminated by formation of buds later in the summer. Only by keeping successive annual growth cycles in adjustment to the local climate can hemlock attain maturity.

Table 1. Frequency distribution of needles and stem length in relation to daylength

Needles above cotyledons	*Hours of light and darkness* Day 8 Night 16	Day 12 Night 12	Day 16 Night 8	Stem length above cotyledons	*Hours of light and darkness* Day 8 Night 16	Day 12 Night 12	Day 16[1] Night 8
No.	*Percentage of seedlings*			*Mm.*	*Percentage of seedlings*		
0	4	6	....	0	14	19	....
1	....	3	....	1	37	40	....
2	1	1	....	2	26	24	8
3	42	57	....	3	16	8	13
4	6	....	....	4	7	5	31
5	7	1	....	5	....	4	18
6	39	27	2	6	....	....	16
7	....	....	8	7	....	....	10
8	....	1	5	8	....	....	5
9	....	4	44				
10	....	....	10				
11	....	....	10				
12	....	....	10				
13	....	....	11				
14	....	....	2				

[1]Mean stem elongation for five seed sources on 16-hour day, 8-hour night: No. 34, Quebec, 2.93 mm.; No. 24, Maine, 4.46 mm.; No. 7, Connecticut, 4.71 mm.; No. 50, Indiana, 4.54 mm.; No. 17, Tennessee, 6.60 mm.

Factors Regulating Germination and Growth

Adjustment of seed germination and stem growth to climate is regulated mainly by sensitive responses to temperature and the length of day and night. Separate and combined effects of these variables were estimated in a long series of experiments. Hemlock seeds from various parts of the species' range were germinated and, in some cases, grown for a year or more under controlled conditions of light and temperature in growth chambers. Some experiments included 2-year-old wild seedlings brought indoors to controlled conditons.

This experimental approach not only permitted the separation of effects which would be confounded with one another outdoors; it permitted a reduction in variability due to other factors which affect germination or growth in the field. The observations below bring out the principal results of these experiments.

Control of germination

Stratification[1] was the most important factor affecting the course of germination. Stratified seed (upper curves, Figure 5) germinated much better

[1]Chilling at temperatures between 32° and 44° markedly hastens the germination of *moistened* hemlock seeds and the opening of buds. In this paper the chilling of moistened seed, by whatever means accomplished, will be referred to hereafter as "stratification." The term "chilling" will be applied to plants which have already formed buds.

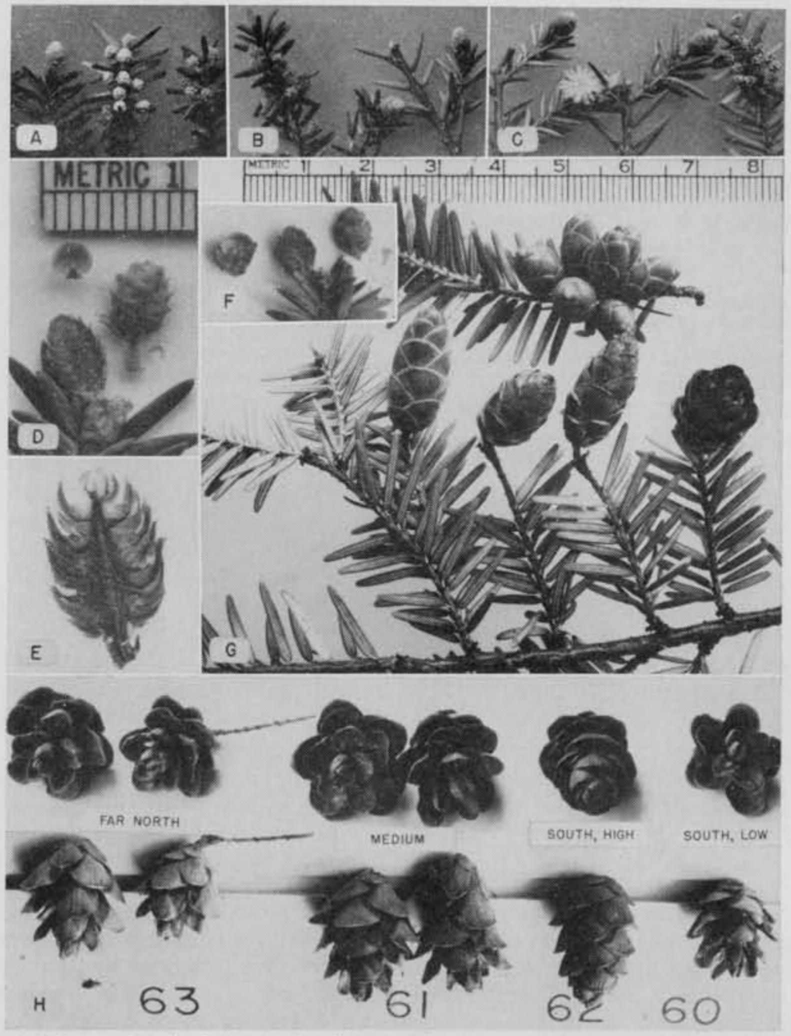


Fig. 3. Eastern hemlock cone development.

A-C. Three stages in opening of male and female strobili, described by Nienstaedt and Kriebel (35); A, May 7, pollen beginning to shed; B, May 9, cones slightly open and receptive to pollen; C, May 15, cones closed and developing. Note rosette of light-colored new needles.

D. May 8 (before pollination); tips of cone scales just showing behind pointed bracts; note faint outline of ovules and wings on detached cone scale.

E. May 23. Cross section of young cone shortly after pollination. Note rounded ovules. Compare with diagramatic sketch, Fig. 2C.

F. June 4 (after pollination but before fertilization); cone scales have grown out over bracts; seeds and wings are separating from cone scale as they grow.

G. Late September, mature cones; those unopened are still green in color; those with spreading scales have turned tan; size depends on mutual competition.

H. Brown cones in October. Note that smallest cones are from extreme northern and southern locations: 60. Grayson, Ala., 800′; 62. Robbinsville, N. C., 4600′; 61. Cheshire, Conn.; 63. Mont Tremblant, Quebec.

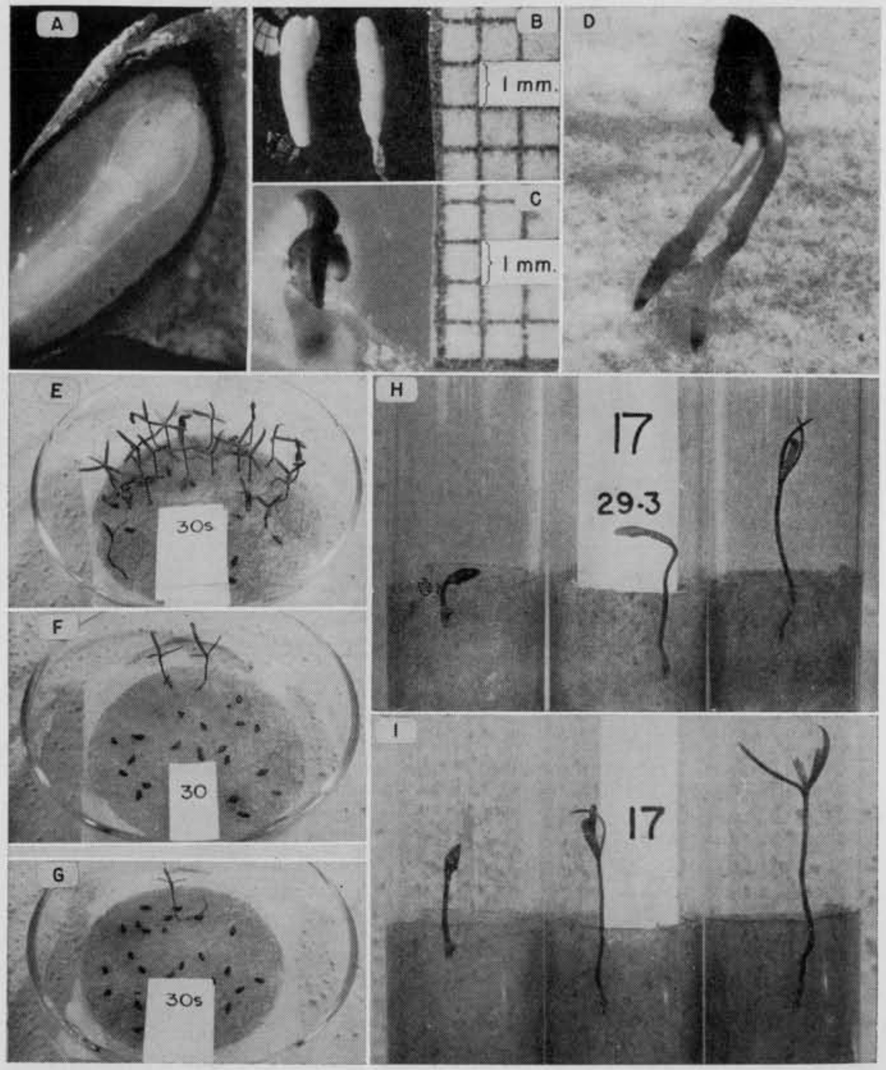


Fig. 4. Hemlock germination.

A. Cross-section of embryo surrounded by oily endosperm, endosperm membrane layer and brown seed coats. See Figure 2E.

B. Embryos excised from seed.

C. Excised embryo on agar showing three dwarfed cotyledons surrouding rudimentary epicotyl. Root tip (in agar) shows as a dark blur; such embryos lived only a short time.

D. Rare example of two embryos developed in a single seed.

E,F. Higher germination of stratified seed (30s) compared with unstratified seed (30) at 62° under 16 hours of light.

G. Poor germination of stratified seed (30s) at 80°; unstratified seed failed to germinate at 80° and is not shown.

H,I. Growth of seedlings during a 1-week period at several early stages of development.

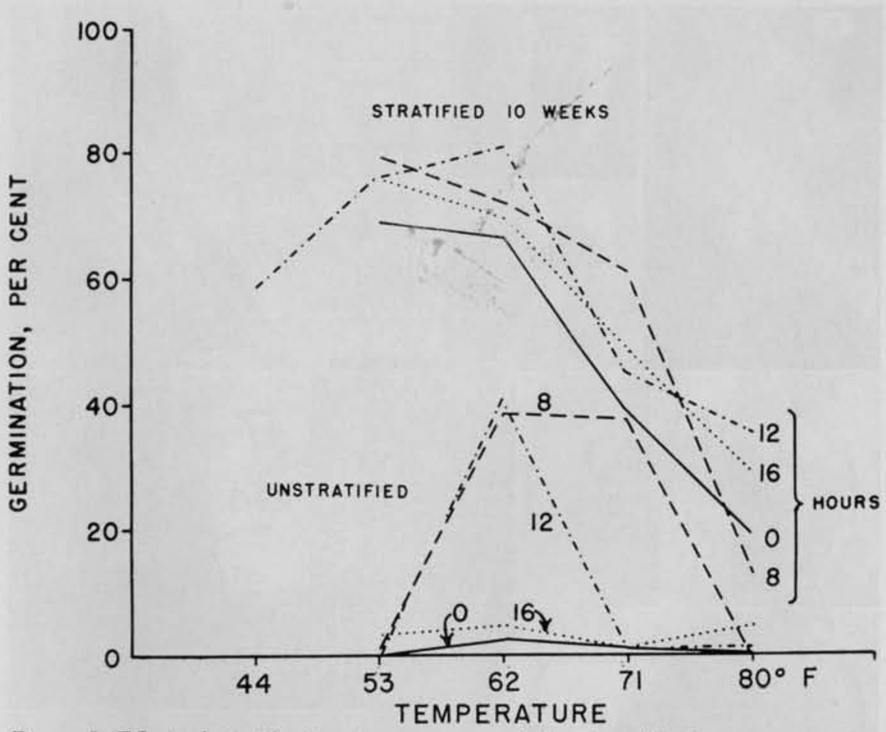


Figure 5. Effect of stratification, temperature, and duration of light on germination of hemlock seed, 7 weeks after start of test. Numbers indicate hours of light in each 24-hour day.

than unstratified seed (lower curves) at temperatures[2] ranging from 53° to 80°, put percentage germination as of 7 weeks decreased as temperature increased. The duration of exposure to light had little effect on the germination of stratified seed although there appeared to be a tendency for somewhat better germination at 80° on the longer light periods.

Unstratified seed germinated poorly under 0 and 16 hours of light at all temperatures. There was, however, a marked improvement in germination at 62° under 8 and 12 hours of light and at 71° under 8 hours of light, indicating that under these conditions a favorable duration of light (photoperiod) compensates for the lack of stratification.

A constant temperature of 62° was generally satisfactory for the germination of stratified or unstratified seed of all sources but it was found that temperatures which fluctuated between about 70° during the day to 55° at night were also favorable. Constant temperatures of 55° or below tended to slow down germination; above 70°, to depress germination levels.

Seeds from different sources did not respond the same to these factors (Table 2). Unstratified southern seed showed a much stronger stimulation by photoperiod than northern seed. This geographic difference may also reflect a lesser requirement of southern seed for stratification, thereby adapting it to milder winters. Stratified Tennessee seed germinated best at temperatures above

[2]All temperatures are in degrees Fahrenheit.

62°; Indiana seed between 53° and 62°; and Connecticut, Maine and Quebec seed at 53° or below, as might be expected if the life cycle of trees from different regions had become adapted to the climate of the region from which they came. Just as crop varieties have been selected by man for different climates, a widespread native species like eastern hemlock evidently contains different genetic types which have undergone a natural selection; this helps to explain its adaptation to diverse regions.

Table 2. Genetic variation in germination response as of 7 weeks

	Seed source				
Environmental factor	Tennessee 17	Indiana 50	Connecticut 9	Maine 24	Quebec 34
Stimulation by 8- or 12-hour photoperiod (unstratified seed at 62°)	high	medium	medium	low	low
Temperature with high germination (stratified seed)	above 62°	53° to 62°	53° or below		

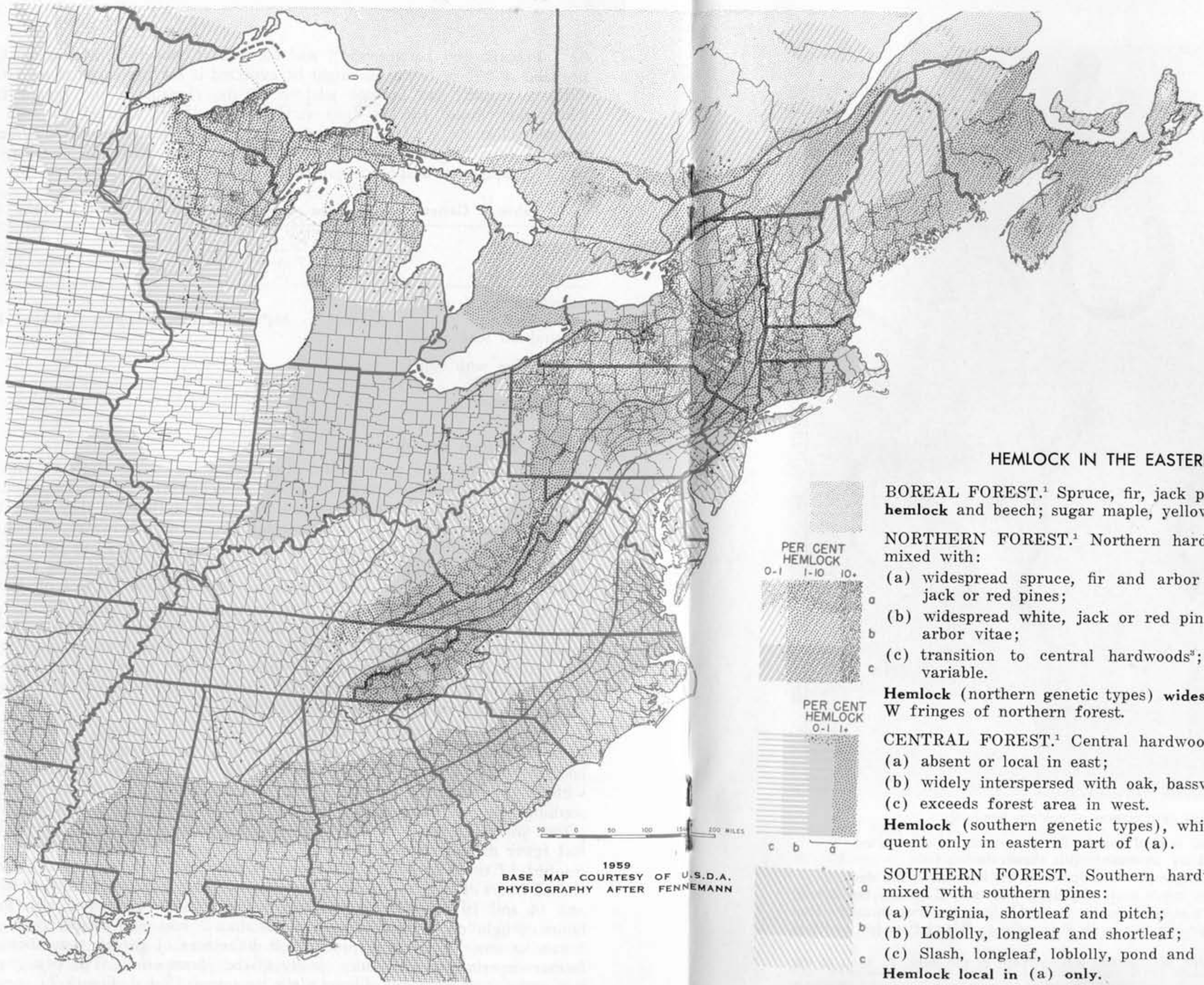
Control of stem growth

Temperature and photoperiod also have a regulating effect on seedling growth. Seedlings which have completed their growth and formed buds in late summer will ordinarily not break dormancy until after they have been chilled[3] for a month or more at temperatures below 40°. However, if unchilled plants are subjected to daylengths of 16 hours or more, they can be forced to break dormancy without chilling, although more slowly than if they had been chilled. Hence photoperiod can compensate to some extent for lack of chilling.

Once dormancy is broken a constant temperature of about 60° is quite favorable for growth but, as in germination, the effects of much higher or lower constant temperatures are adverse; below 50° growth slows down, above 80° plants are stunted. Also, as in germination, it was found that temperatures which fluctuated between 80° and 90° during the daytime and 60°, or even somewhat lower, at night, were also favorable.

Photoperiodic effects are shown in Table 1 by differences in the number of needles formed above the cotyledons and by stem elongation under 8, 12, and 16 hours of light. Under 8-hour daylength some seedlings formed buds without producing any needles above the cotyledons (Figure 6H) and no seedlings put out more than 6 needles. More needles were formed on a few plants under 12 hours of light, but under a 16-hour daylength no seedling had fewer than 6 needles and most had 9 (Figure 6I, Table 1). Several developed 12 or more before growth was stopped by bud formation. Under 8 and 12 hours of light no seedling grew more than 5 mm. above the cotyledons and 14 and 19 per cent, respectively, made no stem growth at all. On 16 hours of light no seedling elongated less than 2 mm. and 49 per cent grew 5 mm. or more. Even more pronounced differences in growth were shown in further experiments with more closely spaced photoperiods. The best growth was under a 20-hour day, 4-hour night treatment (Pot d, Figure 7); growth was markedly reduced if the dark period was longer than 8 to 9 hours.

[3]See footnote, page 7.



HEMLOCK IN THE EASTERN FOREST

BOREAL FOREST.[1] Spruce, fir, jack pine, paper birch; **lacks hemlock** and beech; sugar maple, yellow birch rare or absent.

NORTHERN FOREST.[1] Northern hardwoods[2], alternating or mixed with:

(a) widespread spruce, fir and arbor vitae; variable white, jack or red pines;

(b) widespread white, jack or red pine; variable spruce, fir, arbor vitae;

(c) transition to central hardwoods[3]; with species in (b) variable.

Hemlock (northern genetic types) **widespread** except in N and W fringes of northern forest.

CENTRAL FOREST.[1] Central hardwoods[3]; prairie:

(a) absent or local in east;

(b) widely interspersed with oak, basswood;

(c) exceeds forest area in west.

Hemlock (southern genetic types), white and pitch pine frequent only in eastern part of (a).

SOUTHERN FOREST. Southern hardwoods[4], alternating or mixed with southern pines:

(a) Virginia, shortleaf and pitch;

(b) Loblolly, longleaf and shortleaf;

(c) Slash, longleaf, loblolly, pond and sand.

Hemlock local in (a) only.

[1]Southern phases of spruce-fir forests occur at high elevations in the southern Appalachians.

[2]Northern hardwoods: northern genetic types of sugar maple, beech, yellow birch, red oak, and basswood.

[3]Central hardwoods: white, red, black, scarlet, chestnut, and other oaks, hickories, tulip tree, and southern types of sugar maple, beech, and others.

[4]Southern hardwoods: many of the hardwoods in (3) plus southern red and additional oaks, extensive black and red gum, magnolia, and others.

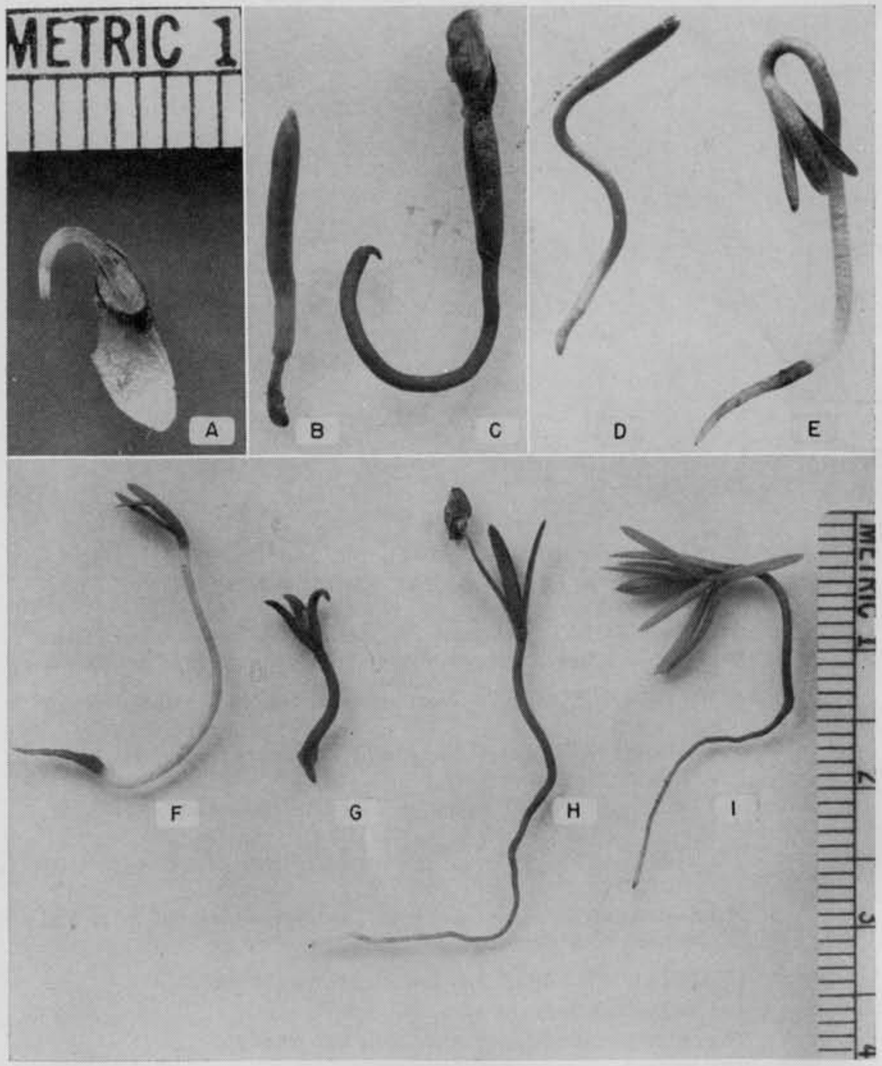


Fig. 6 . Normal and abnormal germination of eastern hemlock.

A. Germination in darkness; normal except for persistence of seed wing.
B-G. Abnormalities induced by treatment with chemicals.
B, C. *Urea*, .5 per cent damages the root tip: B in the light, C in the dark.
D, E. *Thiourea*, .3 per cent, stunts roots slightly in the dark, E, (color tan instead of normal pink); more strongly in the light, D. Stronger concentrations lead to more severe damage like that in B. Pale color in E and F is for seedlings grown in darkness.
F, G. *Coumarin*, .05 per cent, also shows less damage in the dark, F, than in the light, G.
H, I. More advanced stages of normal growth. H, effect of short (8-hour) days with no growth beyond cotyledons; I, of long (16-hour) days with several whorls of needles showing beyond the cotyledons.

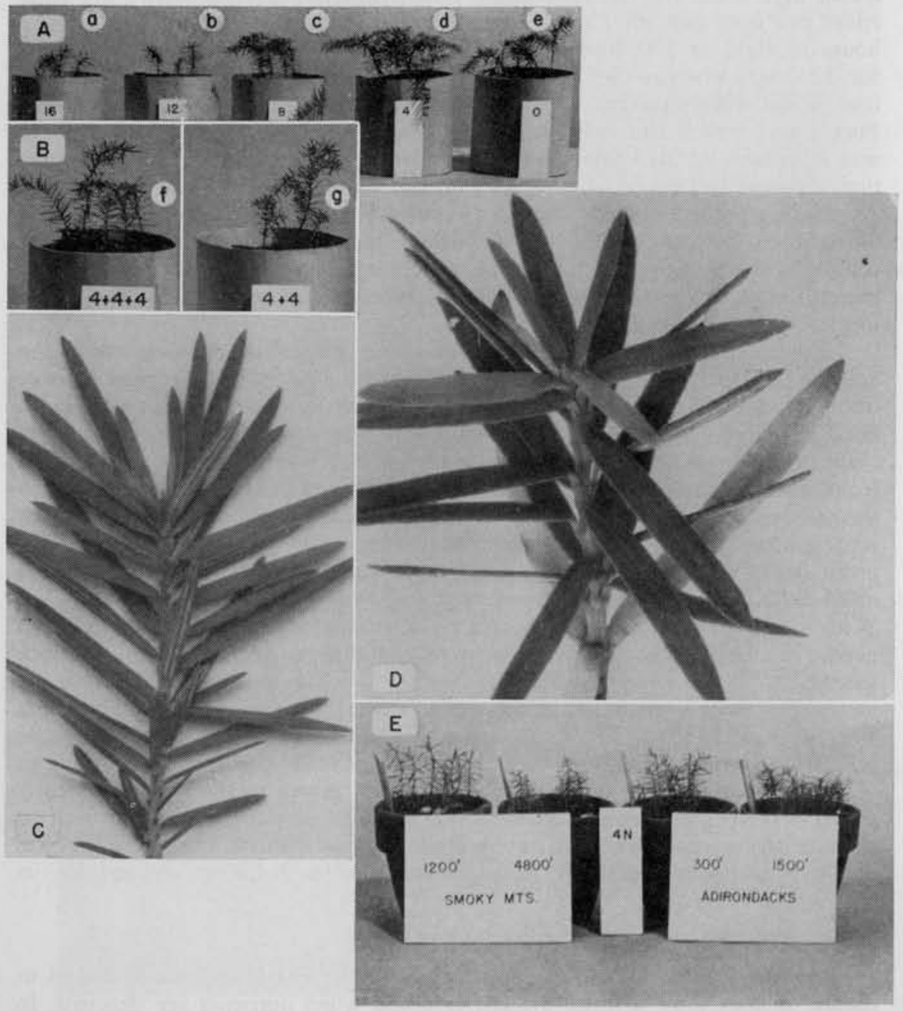


Figure 7. Stem growth and bud formation.

A. Effects of photoperiod. Short nights lead to better growth than long nights. Numbers indicate hours of continuous darkness per 24-hour cycle.
B. Daily interruption of long dark periods by dim light permits plants to grow like those under a long day, short night regime (pots 4½" wide as in A).
C. Plant still elongating. There is no terminal bud; leaves near the apex show all gradations in length.
D. Terminal bud on dormant plant. Gradation to small needles no longer present.
E. Effect of latitude and altitude of seed source on amount of elongation of plants on a favorable 20-hour day, 4-hour night (4N) cycle.

Breaking a long dark period into two or more *short* dark periods with a dim light (too low for appreciable photosynthesis) has essentially the same effect as a *long day, short night.* Pots b and g, Figures 7A and B, both had 12 hours of light at 300 foot candles daily; Pot b was in continuous darkness for 12 hours whereas the 12-hour dark period for Pot g was interrupted for four hours with incandescent light below 10 foot candles (4+4). Similarly Pots a and f each had 8 hours of light daily at 300 foot candles but Pot a was in continuous darkness for 16 hours; the dark period for Pot f was interrupted twice for 2 hours (4+4+4) with the same dim illumination as in Pot g. As in many other biological effects of light, this suggests that the total duration of light or darkness throughout a 24-hour period is less important in controlling growth than the *manner* in which light and total darkness are distributed over the period, and that the duration of darkness probably has more importance than the duration of light.

Seed source also had a marked effect on the timing of bud formation and hence on the amount of growth that can be attained in any given season. Table 1 also gives the mean length of stem for five seed sources under 16-hour daylength, and shows that seedlings of Tennessee parentage had more than twice as much elongation as seedlings of Quebec parentage; seedlings from intermediate latitudes fell between these extremes. Much larger experiments have shown the same kind of relation among seedlings from 30 sources, representing a wide sampling over the entire range of the species. For any given daylength and temperature condition, northern types consistently tended to go dormant earlier and to make less growth than southern types (Figure 7E). Within any given latitude, mountain types tended to go dormant earlier than nearby lowland types. Thus northern or mountain types of eastern hemlock seem best adapted to early termination of growth and hardening off where the growing season is short; southern types, especially those from lowland areas with long growing seasons, seem adapted to more prolonged growth and fuller utilization of the season. However, as a result of tardy hardening off, seedlings of southern origin may suffer frost injury when grown in the north. Evidently nature has selected genetic types whose patterns of stem growth, as well as of seed germination, are in harmony with the local climate. Such physiological diversity within a seemingly homogeneous species helps to account for its wide climatic range.

Nutrient deficiency

Although hemlock can do quite well on nutrient levels usually found in nature, it does show a quite marked response when nutrients are deficient. In the experiments shown in Figure 8, some hemlock seeds which had already begun to germinate were placed between fiberglass sheets and the vertical walls of plastic boxes and provided with distilled water or nutrient solution. All plants on complete nutrient solution developed good roots and tops and were dark green, but under 12 hours of light, early bud formation caused premature cessation of top growth (Figure 8T). Under 16 hours of light (8U) plants made far more top growth than is usual in soil; conditions of photoperiod and nutrient were nearly ideal. Plants in Figures 8V and 8W, also on a 16-hour photoperiod, were provided with a nutrient solution that was complete except for reduced quantities of nitrogen. The series 8U, V, W, clearly shows the effects of decreasing even one of the major nutrient elements. Plants in Figure 8X, supplied only with distilled water, had very limited top and

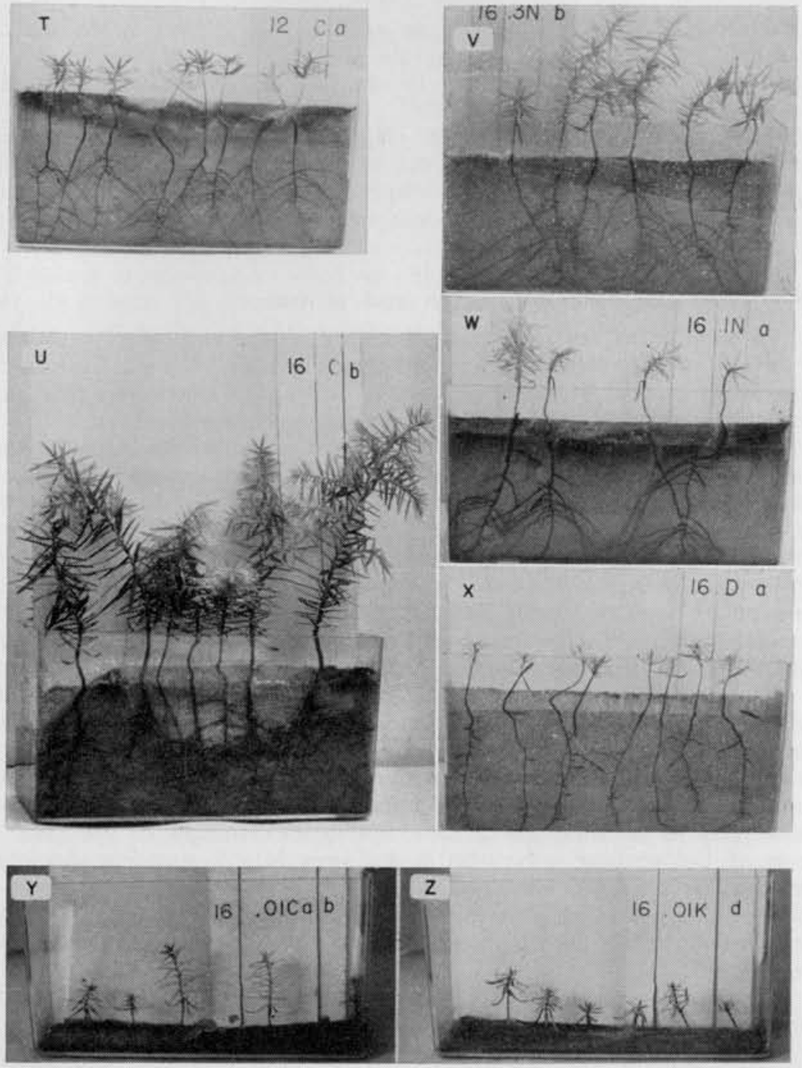


Figure 8. Effects of nutrients on first-year growth of hemlock.

T,U. Plants supplied with complete nutrient solution, (C); T on a 12-hour photoperiod, U on a 16-hour.

V,W. All plants on a 16-hour photoperiod. Nutrient solutions complete except for nitrogen (N) which was reduced to 30 per cent of complete in V and 10 per cent of complete in W.

X. Plants on a 16-hour photoperiod supplied only with distilled water (D).

Y,Z. Plants on a 16-hour photoperiod. Nutrient solutions complete except that calcium (Ca) in Y and potassium (K) in Z were reduced to 1 per cent of the level in complete nutrient solutions. Calcium deficiency indicated by terminal rosette of dark, short needles, and somewhat variable stunting; potassium deficiency by general stunting, chlorosis, and gradual shortening of younger needles.

root growth; these were subsisting on nutrient carried over in the seed and on minor impurities introduced in the fiberglass or from the air. Natural nutritional conditions undoubtedly lie somewhere between the extremes of this series.

Plants from another experiment (Figure 8Y, Z) illustrate the deficiency symptoms resulting from lowering the amounts of calcium and potassium to 1 per cent of the levels in complete nutrient solutions. Deficiencies of either of these elements, and to a less extent of certain others, hasten the onset of dormancy and stunt growth.

Other factors affecting germination and survival

In addition to the factors just discussed, others may affect germination or survival of the seedling during its first few months. Adverse situations are most likely to exist when germination is delayed, or when seed falls on an unfavorable seed bed, or under a combination of these conditions.

Moisture is essential for germination and growth of seedlings. Naturally shaded seedbeds are usually sufficiently moist in early spring. At this time temperatures are most favorable for germination, and for the rapid development of a root system and partial hardening of stem tissues. A seedling established under these conditions is usually able to survive.

If, due to lack of stratification, incomplete stratification, or other causes, germination is delayed until later in the spring, the probability of survival is greatly reduced. Temperatures will then be too high for good germination and even shaded seedbeds may have become somewhat dried out. Development of the root and shoot are consequently retarded; stem tissues are still succulent and are particularly susceptible to attack by damping-off fungi during warm, humid periods. On open seedbeds[4] temperature and moisture conditions unfavorable for germination and seedling growth occur much earlier than on shaded seedbeds. Under full sunlight, temperatures at the surface of litter or humus may be high enough to cause heat lesions, collapse of the stem, and death of the seedling, especially if the stem is still succulent. Sometimes germination is delayed until autumn and the seedling is not hardened off sufficiently to withstand frost injury; germination may also be delayed until the following spring. Such long delays expose the seed to destruction by many agencies.

Sometimes seed is buried so deeply in the litter of the forest floor that the seedling cannot force its way through.

Seedlings may be stunted or killed when daylight intensity falls below about 100 foot candles, as under very dense coniferous shade. Seedlings established on more open seedbeds respond vigorously to light of much higher intensity.

Insects may infest seeds while in the cone, and insects, birds, and other animals often consume large quantities of seed on the ground, or damage or destroy seedlings.

In nature the hazards to survival are often very great but are, in large measure, compensated for by abundant seed crops which are produced at intervals of 2 or 3 years. In nursery propagation many of the natural hazards can be avoided but certain others are introduced; these can be largely nullified by proper conduct of the nursery operation.

[4]Nursery seedbeds, a special kind of open seedbed, are discussed on page 21.

THE GROWING OF HEMLOCK

As with domestic plants and animals, the best trees require both superior heredity and a favorable environment. These factors are particularly important in the propagation of trees because of their long life span; they apply both to trees for forest growth and for ornamental purposes although the methods used and the permissible costs differ greatly.

In much of northeastern United States, hemlock can usually be introduced by planting on sites where natural seedling establishment may be difficult, or on extensive areas where a natural seed supply has been eliminated by fire or other disturbance. The demand for forest nursery stock has kept ahead of the supply in recent years in Connecticut; over half a million nursery trees are also currently being grown for ornamentals. Probably this species would now be planted even more widely if growers were not plagued by unpredictable behavior in the nursery.

Large-scale production will be primarily from seed because it is cheap and permits the growing of large amounts of stock. If the trees are to be grown for timber production, progeny from seed from superior stands of unusually tall, straight trees with narrow crowns, little trunk taper, and light branches will increase the chances of passing on these desirable characteristics to future generations; likewise stand degeneracy can result if seed is consistently collected from poor individuals.

For ornamental plantings, trees with special characteristics such as compactness, unique branching habits, and leaf size and color are desired. Occasional trees with these features often occur in nature or in nurseries as sports or mutants[6]; rarely do they produce seed progeny similar to themselves. Hence they usually must be propagated vegetatively[7] by grafts, or by rooted cuttings, which will have the same characteristics as the parent stock. Our own experience and that of Mr. E. C. Childs, Norfolk, Connecticut, and of others cited in the footnotes indicates that improved rooting of hemlock is obtained through the use of hormone powders or solutions, and that success appears to vary markedly with the horticultural type being propagated, and with the season.

Seed Collection and Storage

Seed should preferably come from areas with a climate like that prevailing where the trees are to be grown so that they will be well adapted to it. If seed is purchased, remember that its age and source have a bearing on germination and development.

Cones are most readily collected from the tops of trees felled in normal cutting operations in late September of a good seed year. If the trees cannot be felled, small quantities of cones can be collected by using special sectional ladders and a pole pruner. Cones collected just as they are turning tan will open readily in the sun or in a dry room. They should be spread out in thin layers for a week or two and stirred occasionally so that they will dry quickly

6 For a discussion of horticultural varieties and forms see articles by J. C. Swartley in the Cornell Plantations, Vol. 2, pp. 3-6, 1945 and in American Nurseryman Vol. 83, No. 7, pp. 7-10; No. 8, pp. 11-13, 1946.

7 Additional references on vegetative propagation: Doran, W. L., American Nurseryman, vol. 74, pp. 18-19, 1941. Journal of Forestry, vol. 50, pp. 126-129, 1952; Thimann, K. V. and Behnke, J., Maria Moors Cabot Foundation Publ. No. 1, Harvard Forest, Petersham, Mass., 1947.

and not become contaminated by molds which tend to develop on damp cones. Green cones are not only subject to molds but are often very hard to open; difficulty of opening may be partially overcome by subjecting cones to repeated cycles of drying at 100°, alternated with moistening.

Care in excluding or removing leafy twigs makes cleaning easier. Seeds can be de-winged by rubbing them by hand or by machine. They should be cleaned as thoroughly as possible by a fan or special blower adjusted to winnow out hollow seed and fine debris. Low viability that is commonly reported for hemlock may be due to the difficulty of separating the poor seed from the good in cleaning.

Our experience shows that seed can be stored for 2 to 4 years in jars or plastic bags in a refrigerator running at a few degrees above freezing, but different lots of seed, even from the same locality, varied considerably in their retention of viability so that periodic testing is necessary. Temperatures below freezing have been used successfully (26° for eastern hemlock at the nursery of the Connecticut Park and Forest Commission at Voluntown and 0° for western hemlock at the Boyce Thompson Institute, Yonkers, New York).

Stratification hastens the breaking of seed dormancy and permits the rapid germination of hemlock and many other seeds. Germination of unstratified hemlock seed is usually greatly delayed. Seed from northern sources may require longer stratification than that from southern sources.

Wind-dispersed seed or seed sown in the autumn in the nursery is naturally stratified and is ready for quick germination in the spring. Here the stratification process is subject to little control and losses due to rodents, birds, fungi, and other causes may run very high. Where possible, it is better practice to stratify during the winter under conditions that permit at least some degree of control, and to sow the seed early in the spring. The best method of stratifying large amounts of seed is to place them in thin layers, alternating with damp sand or peat moss, in flats which are kept for 2 to 3 months in a cold room or refrigerator maintained at a temperature above freezing and below 40°. A method which is often used but which is less subject to control is to rodent-proof the flats, place them on well-drained ground, and cover them with enough straw to keep the temperature within the desired range. The temperature of the seeds should be checked occasionally, and straw added or removed as needed; a maximum-minimum thermometer is helpful.

Seed Testing

Seeds may be cut open with a razor blade or finger nail to provide an estimate of the percentage of filled, firm, oily seeds with embryos. Since the percentage germination is usually less than such tests indicate, actual germination tests are desirable for estimating rate of sowing. These may be made by placing duplicate or triplicate lots of 50 seeds each in glass or plastic dishes on absorbent tissue that is kept moist enough so that a little water oozes off the tissue when the dish is tilted. The tissue should be kept moist during the tests.

If the seed has already been stratified, the dishes should be placed where the temperature can be maintained at 62° ±8°. This may be in a suitable unheated room or in a closed box fitted with a lead heating cable and a household thermostat for maintaining the desired temperature range. Light is not essential for successful germination of stratified seed.

If the seed has not been stratified, the dishes of seed prepared for germination can be placed in a refrigerator for 2 to 3 months, prior to testing.

If for any reason seed cannot be stratified, germination tests in the prepared dishes can still be made, but it will be necessary to maintain a more rigid control of both light and temperature. Optimum conditions are 8 to 12 hours of light, equivalent to natural daylight under fall and winter conditions, alternating with 16 to 12 hours of total darkness, with corresponding alternating temperatures of about 70° and 55°, respectively. If natural daylight is not suitable, fluorescent or incandescent lights controlled by a time switch set for 8 hours of light can be substituted.

Continuous temperatures in the upper 70's are definitely unfavorable for hemlock germination.

Nursery Practice

Nursery work begins with the establishment of the seedbed where the seedlings may either be left for 2 or 3 years and directly planted into the field, or be transplanted after the second year and left in transplant beds for 1 or 2 years. Usually 3-year seedlings (3-0) or 3-year transplants (2-1) are sufficiently well rooted and of suitable size for out-planting.

Of the several nursery operations, the establishment and care of seedbeds is the most critical. Availability of labor and ease of working up the beds offer some advantages for fall sowing and some seed beds will undoubtedly be put in at this time. However, fall-sown beds are subject to losses from causes which are not easily controlled, and it is probably better to shape the beds in the fall when the ground works easily but to delay sowing until spring. If fall sowing is planned, small lots of seed from crops of previous years can be stratified for testing in a refrigerator for 2 to 3 months, beginning in June or July, and tested for germination in September and October in time to serve as a guide to the amount of seed to sow in November or early December. (Note — All dates given are for southern New England.) If seed is collected in the same year it is to be sown, a germination test without stratifying can be made if the test is started promptly. If there is any delay, only a cutting test can be made.

For spring sowing, the suggested procedure is to place enough seed for testing in stratification about November 1, and withdraw it for germination tests about January 1. By February 1, germination should be sufficiently well along to indicate the amount of seed to be stratified for the main planting. If this is stratified about February 1, it should then be ready for field sowing between April 1 and 15.

When seed is stratified too long, it is likely to start germinating while still in stratification. Because such seed is quite susceptible to drying out and to mechanical injury, it is not satisfactory for routine nursery work. However, seeds already germinated during stratification get off to an unusually rapid start after planting. With careful handling, small lots of such seed can be used advantageously in experimental work and in making sowings in woodland where a fast start is necessary for good establishment before the soil dries out in the spring. Another way of getting pregerminated seed for such uses is merely to take seed that has been stratified for the normal period and leave it at 60° for about a week before planting.

Seedbed soil should be loose and friable so that it does not cake, and the surfaces of beds should be convex and elevated several inches to provide good drainage. A common practice is to cover fall-sown beds immediately with a pine needle mulch which is removed about April 1st and replaced with lath or tobacco shade tent cloth supported a foot above the bed surface.

Spring sown beds are immediately covered with the cloth. During the first season, the surface of the beds should never be allowed to dry out.

Seed which is sown after May 1, even if stratified, may not germinate that spring if soil temperatures are too high. Some of it may germinate in the fall, often so late that the tender seedlings are killed by frost; some may not germinate until the following spring. After the ground freezes at the end of the first and second years, it is usually desirable to mulch with needles or salt hay to prevent heaving during the winter and following spring. During the second and third years the beds are usually left uncovered but should be watered thoroughly during periods of drouth.

For very special lots of hemlock seedlings or cuttings, the growth of several normal growing seasons can be compressed into a shorter period. If, after the growth for a year has been completed and the buds have formed, the stock is chilled for 4 to 6 weeks below 40°, it can then be moved back to the growth room or greenhouse under favorable temperature and light conditions with the expectancy that buds will break dormancy and the trees again resume growth without the long over-winter delay.

The Use of Chemicals

Thiourea and several other chemicals stimulate hemlock seed germination under certain conditions. However, there is also a danger of damaging the embryos unless the right concentration and appropriate rinsing are used. Since the desired germination can be obtained without chemicals, the practice is not yet recommended for routine use.

Essentially the same conclusion was reached regarding the use of various fungicides to prevent superficial molds because of the risk of delaying germination. If preliminary tests indicate serious contamination, products like Tersan or Arasan (50 per cent active) as dust or in 0.5 to 3.0 per cent solutions may be tried out, preferably on a small scale at first.

Inherently good seed usually survives superficial contamination with molds on the seed coat if other conditions are favorable for rapid germination. If seed is infected internally, it is probably not viable and no treatment is effective.

During the first few months of life, seedlings in the nursery are very subject to damping off by the fungus *Rhizoctonia.* A treatment of the beds in early September to a depth of 6 inches with formaldehyde at the rate of 2 quarts of 2 per cent solution per square foot should fully sterilize the soil and kill the weed seed to a depth of 1 foot. *Two weeks should elapse between treatment and sowing, longer if temperature is below 50°. After the first week the top 6 inches of soil should be turned over several times.* September treatment permits sowing either in the late fall or the following spring.

After the seed has germinated, damping off by *Rhizoctonia* can be quite well controlled by treating the soil with 8-hydroxyquinoline sulfate, 1:2000 or 2/3 teaspoonful per gallon of water, applied at the rate of 1 pint per square foot two or more times during the season; more frequent treatments may be needed during humid weather while the stems are green and soft. *Rhizoctonia* may also attack the small active roots of older hemlock trees and cause wilting and sometimes death, especially during dry periods. Further injury to the roots can be checked by the same treatment if diagnosis is made in time.

Nutrition

Hemlock seedlings can survive at a low level of nutrition. However, experiments and nursery experience have demonstrated that growth can be increased several-fold by maintenance of nutrition at moderate levels. Maintenance of high levels of nutrition, or the continuance of fertilization and watering into the late summer or fall season are to be avoided because plants will continue growth too late in the season and will not be sufficiently hardened off before cold weather sets in. This is particularly true for plants from southern sources which tend to keep growing late in the fall.

Experience at this Station has repeatedly demonstrated that over-fertilization of larger hemlocks, and many other plants in commercial nurseries and home plantings, increases their susceptibility to *Rhizoctonia* as a root-destroying fungus. If the roots are not too severely injured, the plants will recover if the soil is treated with 8-hydroxyquinoline sulfate, but it is better to lessen the probability of infection by keeping nutrition at a moderate level than to have to treat a heavily infected plant.

SUMMARY

The development of hemlock cones requires a little over one year from the time the flower buds are formed until the seed is shed. Seed is produced in some abundance at intervals of 2 or 3 years.

Seed retains good viability for at least 2 years if stored dry in sealed containers in a refrigerator operating at about 35°.

Stratification, i.e. the chilling of moistened seed, is essential for rapid germination. In nature, or in fall-sown nursery beds, seed is stratified and ready for quick germination the following spring, but losses from rodents and other causes may be very high. A better practice is to stratify seed artificially during the winter and sow as early as possible in the spring while air temperatures are below 60°. Under these conditions a high percentage of viable seed will germinate within 20 days.

Germination of spring-sown *unstratified* seed may be greatly delayed. This exposes seed and seedlings to serious loss from many causes.

Hemlock seeds will germinate, though quite slowly, at temperatures as low as 45° but germination levels are lowered by temperatures constantly in the upper 70's. Best results are obtained when temperatures fluctuate between about 70° during daytime and about 55° at night.

Light seems to have little effect on the germination of stratified seed but at favorable temperaures 8 to 12 hours of light daily improves germination of otherwise sluggish unstratified seed.

In nature seedlings form buds in late summer, are chilled during the winter, and start new growth early the next spring. If seedlings are brought into a greenhouse in the early fall before they have been chilled, they will not

break dormancy and start new growth unless they are subjected to daylengths of 16 hours or more.

The growth of several normal growing seasons can be compressed. Plants which have already formed their buds in late summer are subjected to temperatures below 40° for 4 to 6 weeks and then placed in a greenhouse at a temperature of 60° ±8°; the plants soon resume growth.

For maximum growth, seedlings require 16 to 20 hours of light daily. Breaking a 12- to 16-hour night with one or more periods of dim incandescent light of several hours duration will result in about as much growth as 16 to 20 hours of daylight.

Temperatures which vary between 80° to 90° during the day and 50° to 60° at night, or constant temperatures in the range of 55° to 70°, are very favorable for seedling growth. Plants are stunted at constant temperatures above 90°; their growth is slowed down at constant temperatures below 50°.

Seedlings from northern or high altitude sources tend to become dormant early and so produce less growth than seedlings from southern or low altitude sources. The latter may continue to grow too late in the fall and be frost killed. It is best to get seed from sources of approximately the same climatic region as the place where the trees are to be grown.

Seedlings will grow quite satisfactorily at the moderate levels of nutrition typical in nature but not if certain elements are grossly deficient. Over-fertilization may lead to root rot or damping-off, or may unduly prolong the period of active growth, with consequent winter injury.

The light intensity required for photosynthesis to exceed respiration is below 100 foot candles but established seedlings respond vigorously to light of much higher intensity.

Moisture is essential for germination and early seedling growth. Even after the root system is established, moisture is important for optimal growth.

Although the requirements for germination and early growth are quite critical, hemlock is unusually well adapted to natural establishment under forest cover. Seeds fall to the ground about mid-October and many are soon stratified. In this condition they remain dormant during the winter and are ready to germinate and grow at the relatively low temperatures of early spring when seed beds are almost always moist. Root systems are consequently well advanced and stems are partially hardened off before late spring when conditions are less favorable.

Hemlock seedlings are truly shade-tolerant plants. Their ability to survive in deep shade, then to thrive in bright light when the canopy opens, makes hemlock a formidable contender for a prominent place in our mixed forests.

The frequently erratic behavior of hemlock when planted in the open is due, in large measure, to lack of the favorable conditions natural to the forest.