population protein was \((46.0 + 39.6) - 47.9 = 37.7\) kg. of protein. Recruitment must make up for this net decrease in order to maintain the average standing crop of \(71.4\) kg. of protein. Under the observed conditions of mortality and growth, recruitment must replace about one-half the average standing crop per year.

References


continuous productivity is to prevail. Recognizing the need for information relating to the influence of physical and biological factors of the environment upon the reproduction of particular species, forest ecologists have undertaken a number of studies since 1908. Nonetheless, for many important North American trees, but little information is yet available concerning the ecology of reproduction (Duncan 1952a).

Tamarack (Larix laricina (Du Roi) K. Koch) is one of the species, the reproductive characteristics of which, have been only superficially explored. It is one of the most widely ranging conifers in North America, extending from Newfoundland and Nova Scotia north and west to the valleys of the Koyukuk and the Yukon in Alaska. From the shores of the Beaufort Sea in northern MacKenzie and from northernmost Quebec where it frequently occurs on well-drained uplands, it extends south to the Atlantic coast of New Jersey, to western Maryland and northern West Virginia. In Minnesota, tamarack reaches its southwestern limit where, as elsewhere in the southern part of its range, it is generally confined to bog forests. Here, it survives in exceptionally hydric situations until, as the sites become more mesic, it is usually overtaken by more shade-tolerant arborescent species (Fig. 1). Where competition does not eliminate it and where favorable moisture conditions permit germination and early survival, however, it thrives on upland sites even in the southern part of its range (Fig. 2). On such favorable sites, it is without doubt the fastest growing conifer in the east (Cheyney 1942).

Ecologically, tamarack plays a significant role. It is a pioneer which, with few exceptions in the Lake States, initiates forest succession on bog lands often following immediately the sedge mat or the sphagnum stages (Conway 1949, Cooper 1913) and in other areas following the bog shrub stage (Cooper 1913, Gates 1942). Although frequently occurring in mixture with black spruce (Picea mariana (Mill.) B.S.P.) or northern white-cedar (Thuja occidentalis L.) tamarack is usually the first to appear and marks the initial change to the forest condition. It is the tree which prepares the way for other, and frequently more valuable, arborescent species although in so doing, it eventually brings about its own elimination.

The present study was undertaken during the summers of 1948, 1949, and 1950 and most of the work was done at the Cloquet Experimental Forest, in the Itasca State Park region, and at Cedar Creek bog and nearby tamarack stands north of St. Paul. Some work was done elsewhere in tamarack stands scattered through various parts of Minnesota, from Ely and Big Falls to St. Cloud. The primary objective was to provide a background of information on some of the most important factors influencing natural reproduction in tamarack between the beginning of seed production and the end of the juvenile stage of seedling.
development. Much remains to be done. Only a few, if any, of the factors affecting reproduction have been thoroughly enough analyzed to obviate the need for further investigation. Information obtained, however, does provide a background against which silvicultural practices aimed at obtaining natural regeneration may be planned (Duncan 1952b).

The Seed

Methods

Cone production was studied by an ocular method using binoculars. The number of cones produced on a single typical branch of at least four levels in each tree was counted, the number of branches at each of these levels was ascertained, and through multiplication, the approximate total production for the entire tree was estimated. To find the number of seeds produced per cone, 10 cones from each of eight trees of ages varying from 30 to 60 years, were examined and the number and condition of the seed recorded. This was also done for all (23) of the cones produced on two 15- or 16-year-old trees.

Quantity of seed disseminated in the Cloquet Forest was ascertained by seed trap (Fig. 3) studies during the fall of 1948. Twelve one-quarter milacre traps were spread through seven pure and mixed tamarack stands. In addition, 12 traps were placed around a single isolated 35-foot tamarack tree during the fall of 1948 at Cloquet in a study of distance and direction of seed dissemination. Three traps were placed in each of the four cardinal compass directions at distances of one, two, and three times tree height from the base of the tree.

To ascertain the significance of rodents as an agent destructive of tamarack seed following dissemination, rodent exclosures covered with half-inch mesh hardware cloth were constructed and placed in the Cloquet Forest adjacent to seed trap locations.

Results and conclusions

Seed production.—Larix is monocious. Solitary staminate strobili are borne terminally on dwarf branches from leafless scaly buds. The buds from which they are produced, are recognizable in some species by the end of October by their greater size (Doyle 1918). When mature, the strobili are globose to sub-globose or oblong bodies. Ovulate strobili are small, red or, less commonly, greenish cones which attain nearly mature size in six to eight weeks. They are erect, more or less oblong in shape with nearly orbicular scales and light-colored bracts extending into elongated green tips. Strobili of both sexes appear with the leaves in late March, April, or early May in Minnesota tamaracks. At St. Paul between 1941 and 1950, the foliage of tamarack first appeared between March 23 and April 24, averaging April 12 (Hodson 1951). The color of unripe cones is consistent for any one tree year after year, but varies among trees from dark red to light green. Between about the first and the middle of August in Minnesota, the cone scales dry out and begin to turn brown.

Good seed years for tamarack occur at five- to six-year intervals according to the U. S. Forest Service (1948). On the basis of the present limited study, good seed years occur in Minnesota at intervals of about four years. Baldwin (1942) suggests that one method of studying periodicity in seed production is "by studying the distribution of age classes in natural, undisturbed forest." Although this may have value for some species, it cannot be used satisfactorily for bog-grown tamarack. While good seed years are essential, of course, for good crops of seedlings, rodents may severely reduce seed supplies after they reach the ground. Furthermore, fluctuating water levels so seriously affect seedling survival that much of the evidence for abundant crops may be obliterated or at least greatly obscured.

Tamarack cones are small by comparison with those of most Lake States conifers. The number of seeds per mature cone varied from about 15 to as many as 48. The average number of seeds in cones taken from mature trees was 26 (26.24 ±0.50) and none had more than 40. In two young trees, cut at 15 and 16 years of age, 28 to 48 seeds were found with an average of 39 (39.34 ±0.36) per cone.

Although about 85 per cent of the seeds pro-

Fig. 3. One of the seed traps used to gather data on seed dissemination. It is divided in half to provide some check on uniformity of distribution and covers exactly one-quarter milacre. Rodents are excluded by half-inch mesh hardware cloth which covers the trap. The bottom is of ½ inch mesh screen wire.
duced by very young trees were well-developed, in mature trees about one-third are not filled. The largest seeds are borne on scales in the central half of the cone. The next lower scales also may produce some large seeds but the much smaller basal scales contain mostly unfilled seeds. Most of the terminal scales of the cone contain small undeveloped seeds, few of which are viable.

The number of cones borne on a particular tamarack tree is influenced primarily by the crown development which in turn is influenced by the competition provided by surrounding trees. After surveying the literature, Nelson (1950) concluded that light is generally considered a very important factor in seed production in conifers, particularly for intolerant species. Its importance to at least one intolerant species is borne out in the present study. Open-grown tamaracks of medium age (50 to 150 years) having large vigorous crowns were usually most productive and bore as many as 20,000 cones in a good seed year (Fig. 4). The heaviest seed-producing tree observed was open-grown and about 85 years of age but was only about 30 feet tall, having had the top broken out of it several years previously. Aside from the missing leader, it had a well-developed crown and was estimated to bear over 20,000 cones. At an average figure of 17 well-developed seeds per cone, such trees may produce over 300,000 good seeds in a single season. Many trees produce over 50,000 in a good year.

Tamarack begins seed production relatively early in life when in a favorable situation. Vigorous isolated bog trees begin to produce in Minnesota at about 15 years of age. Upland tamarack may produce cones as early as the twelfth or thirteenth year. The seed produced on such young tamarack appears to be as viable as that produced on older trees, the number of seeds per cone may be high (about 40) and the per cent of underdeveloped seed may be low (15 per cent). Trees grown under conditions of severe competition in well-stocked stands, however, may not produce seed crops until they have attained ages of 35 to 40 years. This lends support to Mayr's (1925) statement that trees grown in dense stands blossom at a later age than those grown in open stands, a difference which he estimates to average 20 years. Extremely old trees, up to about 250 years, may still produce cones even in light seed years. The limited evidence available on such trees indicates that after about 150 years tamaracks do not produce heavy crops. This is probably the result of crown deterioration which often begins at about this age.

In well-stocked tamarack stands, the dominant and codominant trees produce most of the seeds, the intermediate, oppressed and suppressed bearing few or no cones. In a blowdown of tamarack at Cedar Creek, scattered standing trees having the best top development had the best cone crops. In the same area, many of the trees which were classified as intermediates bore cones, but very few suppressed trees carried any. In an adjacent stand unaffected by the storm, the dominants with much of the crown exposed produced good cone crops whereas suppressed trees bore no cones at all. A larger proportion of the intermediate and suppressed trees in the blowdown area bore cones than trees of comparable crown development in the adjacent stand.

Cones may appear on twigs of various ages but most frequently are borne on two-, three-, or four-year-old wood. On very young trees just coming into production, a few cones may appear on one-year-old wood, that is on wood of the preceding year's formation, although more commonly, they are found on two-year-old wood. On older trees, wood of from five to ten or even more years of age may produce cones. The location of the cones may be dependent, at least in part, upon the available light. Where growth is vigorous, the cones are most frequently found on recent wood (three years old or less). Where growth is very slow, cones are found on older wood. Old cones may be retained up to about five years before falling from the twig.

Seed destruction before dissemination.—Prior to ripening and dissemination, the seeds of tamarack may be destroyed in the cone. Several insects, including an aphid and at least two species of Dip- teran larvae (Cecidomiidae), have been found in the cones. Insofar as could be ascertained, these feed on the succulent cone scales, however, and do not damage the seed directly. There is one species, a Lepidopteran larva belonging either to the

Fig. 4. In good seed years, many branches on open grown trees bear heavy cone crops like this one. In "bumper" years, most branches on such trees produce this sort of crop.
Olethreutidae or to the Tortricidae (Tripp 1951), which does seriously reduce the number of sound seeds produced on certain trees, up to 80 per cent of the cones being infested on some. These larvae feed on the seeds directly leaving simply the empty hull behind. While in few trees were more than five or six seeds eaten in any of the cones examined, these seeds were invariably among the largest and best developed. By the end of the season, this insect had destroyed half the good seeds in three-fourths of the cones on one tree examined. In some years, at least on some trees, therefore, it may become a serious factor in reducing seed supply.

Squirrels and birds may cause some loss of seeds prior to maturity. The red squirrel (Tamiasciurus hudsonicus Erxleben) frequently has been observed cutting cone-bearing twigs from tamaracks before the cones were matured. These are then usually carried to caches. They have also been observed feeding on seeds in the cones well into the winter at Cedar Creek bog (Lawrence 1951). The American red crossbill (Loxia curvirostra pusilla Gloger) and doubtless other seed-eating birds, occasionally feed on tamarack seeds. However, neither rodents nor birds are believed to be very significant factors in seed destruction before dissemination.

Seed dissemination.—In Minnesota, tamarack seeds may begin to be disseminated about three months after pollination, between late August and mid-September, varying with the location and the season. At Cloquet in 1948, seed traps studies revealed that the first seeds fell on September 1. Within the first 20 days of the season (i.e., before September 20) about 65 per cent of the 3409 seed collected had been disseminated; an additional 25 per cent were disseminated within the second 20 days (before October 10); during the next 20 days (before October 31) about 7½ per cent of the total were released; the remaining 2½ per cent fell during the winter (before mid-June when final counts were made). Although a larger number fell during the overwinter period than the 2½ per cent indicated, cutting tests showed that less than 6 per cent of the number released during that time could possibly be viable. These only were included.

The heaviest concentration of seeds disseminated at Cloquet were under more or less open stands where the mature tamaracks were fairly good-sized (four to 10 inches DBH) and had well-developed thrifty crowns. Here the number distributed varied from about 1,500,000 to nearly 2,500,000 per acre in 1948, which was a good seed year. In a moderately heavy, 80-year-old stand of tamarack where crowns were much smaller and less vigorous, the dissemination varied from 500,000 to about 1,200,000 per acre during the same year. In a “bumper” crop year, the evidence, based on seedlings found in the spring of 1948 at Itasca, indicates a probable production of five million or more filled seeds per acre in a medium stocked stand. By comparison with other conifers (Anonymous 1950, Bates 1923, Chapman 1926, Cox 1911, Eyre and LeBarron 1944, Fowells 1944, Haig et al. 1941, Isaac 1943, Jemison and Korstian 1944, LeBarron 1948, Lowdermilk 1925, and Shirley 1941) tamarack is a prolific seed producer.

The distance of dissemination of quantities of seed satisfactory for good stocking of regeneration is small. Heavy seedling stands may be secured up to a distance about equal to the height of the seed trees, fair stands are found up to twice the tree height distant, and a few scattered seedlings may be found at greater ranges. In the seed-trap study around an isolated tree bearing a heavy seed crop, 458 seeds were collected in the quarter mileacre trap immediately beneath the tree. About 10 per cent of that number of seeds was found per equivalent area at a distance equal to the tree’s height, about four per cent at twice the tree’s height, and less than two per cent at a distance equal to three times the tree’s height. Since this tree was open-grown, the distance of dissemination because of unobstructed winds, was undoubtedly appreciably greater than would occur from the edge of a tamarack stand.

Seed destruction following dissemination.—Following dissemination, the consumption of seeds by rodents may be a significant factor in reducing the number present to germinate satisfactorily (Table I). This appears to be particularly true if the seeds are exposed on mineral soil where they can

Table I. Number of seedlings appearing per quarter mileacre plot beneath exclosure and on adjacent area without rodent protection

<table>
<thead>
<tr>
<th>Plot</th>
<th>With exclosure</th>
<th>No exclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter, duff plots</td>
<td>40</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>76</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>20</td>
</tr>
<tr>
<td>Total on litter, duff plots</td>
<td>256</td>
<td>128</td>
</tr>
<tr>
<td>Sphagnum plot</td>
<td>104</td>
<td>21</td>
</tr>
<tr>
<td>Mineral soil plot</td>
<td>58</td>
<td>14</td>
</tr>
<tr>
<td>Total on all plots</td>
<td>418</td>
<td>163</td>
</tr>
</tbody>
</table>
be more readily located than in the litter and duff. Comparison of germination on areas under rodent enclosures during the winter with adjacent areas of equal size without protection, reveals four times as many seedlings established on protected mineral soil as on the unprotected area. Under litter and duff which was undisturbed, seedlings were twice as numerous where protected as where rodent protection was not provided. This difference is highly significant. On Sphagnum, where the effect of the rodent enclosure was to compress the moss and reduce its growth rate, a five to one increase in tamarack germination resulted. Reduction of rodent losses was partially responsible, but probably more important was the improvement of seed-bed conditions otherwise. The increase parallels observations made by Roe (1949) with respect to black spruce germination on compressed Sphagnum.

Although the species of rodents concerned with seed destruction are not definitely known, the red-backed vole (Clethrionomys gapperi gapperi Vigors), the white-footed mouse (Peromyscus leucopus novaboracensis Fisher), and the shrews (Sorex articus laricorum Jackson and Sorex cinereus Kerr.) may be important destructive species. These are common in boggy areas and on bog periphery in Minnesota (Gundersen 1950, Marshall 1951). Both Clethrionomys and Peromyscus are known to feed heavily on seeds (Burt 1946). Moore (1942) has shown that in coastal Oregon Douglas fir, shrews eat not only insects but frequently coniferous tree seed and may be a factor accounting for the dominance of small-seeded species in some areas. Tamarack, being a small-seeded species, is probably less seriously affected by rodents than some of the larger-seeded species with which it is sometimes associated, such as balsam fir.

There is also evidence that between November 1 and mid-June, some seeds may be destroyed by bacterial or fungus attack. Of the seed collected in traps during the overwintering period, some had decayed by the time of collection in June. Since these were in the seed traps during the overwintering period, and consequently were exposed to unnatural conditions, it is not necessarily a good measure of the amount of decay which could be expected in the litter or duff. However, this may be a significant factor in seed loss following dissemination in the fall, at least in certain years and under conditions favorable to the destructive organisms. Baker (1950) believes "these (microbial) losses are not important among sound, uninjured seeds." Rathbun-Gravatt (1931) has shown that for pine at least, decay of unruptured seed may be caused by damping-off fungi, but that this is less serious than the destruction of radicles after they have emerged but before the seedling breaks through the soil.

**Germination**

*Methods*

In several of the field investigations concerned with germination, the objective was to determine the range within which certain environmental factors operate; in others, where variables could be reduced, an effort was made to determine the influence of certain factors on germination under field conditions. The germination factors which were studied in the field include temperature, moisture, oxygen supply, ground cover, and hydrogen-ion concentration. In the laboratory, germination studies were concerned not only with these factors but also with light, tree age at the time of seed production, and time of seed dissemination.

Seeds from two sources were used for the laboratory tests and in those field tests where seeds were sown artificially. One of these collections was made on the Superior National Forest in Minnesota on August 27 and 28, 1940. Following drying and extraction, the seeds were stored at 5°C. in a wax-sealed pint jar from October 11, 1940 until March 4, 1948 at which time they were stratified in moist sand at 5°C. prior to tests made that spring. The second source was collected on the Cloquet Experimental Forest on September 4, 1948. Following extraction, the seeds were placed in cold storage at 5°C. in a wax-sealed pint jar where they remained until removed for stratification.

Surface-soil temperature determinations in the field were made using a glass immersion-type thermometer which was inserted into the surface half-inch of the germinating medium.

In the laboratory, temperature tests were conducted in a refrigerated room which was maintained at 5°C. in order to provide the lower temperatures desired in the test. The apparatus (Fig. 5) included a thermostatic control device for each set of temperature conditions and heating elements for each sand flat. The laboratory test with a 7°C. variation from high to low temperature levels was conducted using seeds from the Superior National Forest. The remaining laboratory temperature tests were conducted using the seeds from the Cloquet Experimental Forest.

Each sand flat in which testing was being undertaken was subjected to alternations of thermostatic settings at 12-hour intervals. The higher temperatures were attained by heating of the coils
in the flats, the lower temperatures by allowing the 5° C. room temperature to bring the flats down to the lower level established by the thermostats. The heating coils were placed 2½ inches below the sand surface and the seeds were covered to a depth of about ¼ inch. Each flat was covered with a sheet of glass to minimize evaporational losses and tap water was added at two- or three-day intervals providing plenty of moisture so that this factor would not reduce germination. The sand flats were constructed of wood and ready drainage was provided.

The influence of light upon germination was studied using seeds from the Superior National Forest collection. After a 63-day stratification period, the seeds were removed on May 7 and about 185 were placed in petri dishes on filter paper for each of five light levels. The light was supplied for 14 hours daily by three 150-watt tungsten lamps and two 100-watt fluorescent day-light lamps suspended 22 inches and 16½ inches respectively above a table. All petri dishes were rotated each day from one position to the next on the table. Temperatures were alternated between about 21° C. or 22° C. during the dark period to 28° C. or 29° C. during the light period. No replications were made. Light was varied from an intensity of approximately 850 foot candles (about one-tenth of full sunlight) by using an unshaded dish, to total darkness; three intermediate levels were obtained by shading with varying numbers of layers of cheesecloth. Photoelectric cell measurements showed these intermediate intensities to be about 340, 160, and 115 foot candles.

In both germination and seedling survival studies, it was necessary to ascertain the moisture level of the surface material of the forest floor. Craib (1929) has pointed out that "moisture expressed as a percentage of dry soil weight is a relative quantity, the significance of which is dependent upon soil density." The moisture equivalent is not too satisfactory a measure of moisture content for organic soils such as were characteristic in this study because of great variability from sample to sample. As early as 1864, Schumacher suggested the desirability of working with soils in place when determining the physical properties, particularly their water relations. In the present study, per cent moisture by volume shows much less fluctuation at the wilting point of tamarack seedlings than does per cent based on dry weight.

Moisture determinations were made using two standard circular soil cans, one inch deep and three inches in diameter with a content of 112 cubic centimeters, for each quarter milacre plot. These were pressed into the surface material to full depth, and were removed including all of the surface material above the level of the rim of the inverted can. The tops were replaced and the can and contents were weighed. After oven-drying for 24 hours at 100° C. to 105° C., they were reweighed. Results were expressed as a per cent by volume and as a per cent by weight. The former was found to be much more consistent than the latter for determining critical levels of moisture when a variety of germinating media, from mineral soil through humus to sphagnum, were being tested. Neither measure was found to be entirely satisfactory for all media.

Results and conclusions

General.—For tamarack, the relationship between number of seedlings emerging from the seedbed and number of seeds disseminated on it varies widely extending from zero per cent to as high as 75 per cent or even more under near optimum laboratory conditions. The point within this range at which field germination actually lies varies with many factors of the environment of which moisture level, oxygen supply, and rodent populations are among the most important. Temperature is seldom, if ever, directly limiting although it does affect speed of germination which may be a significant factor in later survival of the seedlings.

Laboratory tests on fresh, unselected, sound tamarack seeds indicated germination capacities
under favorable temperature and moisture conditions varying from 30 to 60 per cent. A summary of germination data from various sources (U.S.F.S. 1948) for this species indicates that germinative capacity may vary from 10 to 85 per cent with an average of 47 per cent. In the field, however, when germination is expressed on the basis of number of seeds disseminated, these high percentages are not attained. In the spring of 1949 at Cloquet, slightly less than 5 per cent of the seed, all of which were naturally disseminated and none of which were provided rodent protection, germinated successfully. At Cedar Creek in the spring of 1950, artificially seeded fall-sown plots in those situations where at least some germination occurred, showed a 4 per cent average. On a few plots where moisture was definitely limiting, no germination took place. These figures are to be compared with a 44 per cent over-all field germination for jack pine (Pinus banksiana

![Graph](image-url)

**Fig. 7.** Daily germination under various temperature conditions (see Table II, 2nd test). The test was begun on May 22, and 400 seeds were used in each of the five flats.

![Graph](image-url)

**Fig. 6.** Daily germination under various temperature conditions (see Table II, 1st test). The test was begun on May 18, and 800 seeds were used in each of the three flats.
Lamb.) and 26 per cent for black spruce (LeBarron 1944).

Temperature influence.—Under normal conditions, the surface soil in tamarack bogs during the germination period varies from a low of about 10° C. to about 20° C., although higher temperatures up to 28° C., are not infrequently found when the sites are exposed to full sunlight. In the springs of 1948 and 1949, germination generally reached its peak when the surface soils had attained temperatures of 17° C. to 19° C. during the day. However, on sites in deep white-cedar shade, germination occurred at lower temperatures (13° C. to 14° C.; on the more exposed sites, on the other hand, it began at higher temperatures (21° C. to 22° C.). Germination on unshaded sites began earlier (about May 23 to 30 at Cedar Creek and about June 5 to 10 at Cloquet) than on the shaded sites where it began considerably later (about June 8 to 15 at Cedar Creek and June 15 to 25 at Cloquet). These differences in time of germination are undoubtedly the result of temperature differences. White-cedar seeds in the shaded situation (at Cedar Creek) germinated about a week to 10 days earlier than the tamarack.

Field investigations also indicated that seed germination on the sites where higher temperatures prevailed had a much more concentrated germination period than on sites where it remained lower. Under a heavy stand of white-cedar where surface soil temperatures never were recorded as exceeding 19° C., seeds were still germinating as late as August 1. In the warmer, more exposed sites, on the other hand, all germinating seeds emerged before late June.

To determine more precisely the influence of temperature on germination in tamarack, an experiment was designed to test the effects in the laboratory. Since fluctuating temperatures are normal in the natural seedbed, these were used in preference to constant temperatures. Investigations of surface soil temperature variations under natural conditions revealed that daily fluctuations, while quite variable ranging from less than 1° C. to over 10° C., averaged about 3° C. These findings were used as guides in the laboratory tem-

![Graph](image-url)

**Fig. 8.** Daily germination under various temperature conditions (see Table II, 3rd test). The test was begun on August 2, and 400 seeds were used in each of the six flats.
TABLE II. Summary of germination data secured in laboratory temperature tests

<table>
<thead>
<tr>
<th>Test</th>
<th>Temp. range</th>
<th>Germ. cap. %</th>
<th>Peak day</th>
<th>*Days at peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>A...</td>
<td>8°C and 15°C</td>
<td>38.5+</td>
<td>26</td>
<td>206</td>
</tr>
<tr>
<td>B...</td>
<td>13°C and 20°C</td>
<td>45.2</td>
<td>21</td>
<td>252</td>
</tr>
<tr>
<td>C...</td>
<td>18°C and 25°C</td>
<td>45.4</td>
<td>26</td>
<td>278</td>
</tr>
</tbody>
</table>

2nd Test (1950)
Seed source - Cloquet Experimental Forest
400 seeds in each flat
70-day stratification period
Test started May 22

<table>
<thead>
<tr>
<th>Test</th>
<th>Temp. range</th>
<th>Germ. cap. %</th>
<th>Peak day</th>
<th>*Days at peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>D...</td>
<td>14°C and 17°C</td>
<td>30.0+</td>
<td>32-33</td>
<td>360</td>
</tr>
<tr>
<td>E...</td>
<td>17°C and 20°C</td>
<td>37.7</td>
<td>20</td>
<td>285</td>
</tr>
<tr>
<td>F...</td>
<td>20°C and 23°C</td>
<td>38.7</td>
<td>16</td>
<td>269</td>
</tr>
<tr>
<td>G...</td>
<td>18°C and 20°C</td>
<td>41.7</td>
<td>21</td>
<td>245</td>
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<tr>
<td>H...</td>
<td>18°C and 22°C</td>
<td>27.0</td>
<td>16</td>
<td>212</td>
</tr>
</tbody>
</table>

3rd Test (1950)
Seed source - Cloquet Experimental Forest
400 seeds in each flat
53-day stratification period
Test started August 2

<table>
<thead>
<tr>
<th>Test</th>
<th>Temp. range</th>
<th>Germ. cap. %</th>
<th>Peak day</th>
<th>*Days at peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>I...</td>
<td>14°C and 17°C</td>
<td>49.5</td>
<td>19</td>
<td>222</td>
</tr>
<tr>
<td>J...</td>
<td>17°C and 20°C</td>
<td>49.5</td>
<td>13</td>
<td>157</td>
</tr>
<tr>
<td>K...</td>
<td>20°C and 23°C</td>
<td>49.5</td>
<td>11</td>
<td>150</td>
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<tr>
<td>L...</td>
<td>18°C and 20°C</td>
<td>36.7</td>
<td>38</td>
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<tr>
<td>M...</td>
<td>18°C and 22°C</td>
<td>59.7</td>
<td>17</td>
<td>226</td>
</tr>
<tr>
<td>N...</td>
<td>21°C and 22°C</td>
<td>48.5</td>
<td>14</td>
<td>234</td>
</tr>
</tbody>
</table>

The laboratory temperature tests. The results of the tests are shown graphically in Figures 6, 7, and 8 and are summarized in Table II.

The laboratory temperature tests when combined with observations made in the field, lead to certain conclusions as well as to additional questions needing further investigation. The generalizations which appear to be most valid and at the same time to have the most significance follow.

1. Total seed germination probably is not influenced appreciably by temperature variations found in the natural environment. All sites not under water, where field records were maintained, had attained temperatures for the top half-inch of seedbed of at least 17°C on several occasions before mid-July. The laboratory tests indicate that given enough time and favorable moisture conditions, fluctuating temperatures with a high range of only 15°C to 17°C may be expected to provide as good total germination as temperatures with a maximum up to 25°C. Temperatures in Minnesota tamarack bogs do not attain such high levels that total germination is reduced because of temperature effect alone. Seldom do natural seedbed temperatures exceed 25°C which is not limiting. (2) Maximum germination rate may be expected to be relatively early on unshaded sites and may be relatively late in shaded areas. In some years, this is very important in that it may become a limiting factor in subsequent survival. Those seedlings starting late may not obtain sufficient depth of root penetration to survive summer drought. (3) Germination on unshaded sites may be expected to be more concentrated than in shaded locations. Instead of requiring 10 days or even longer for most (75 per cent) of the viable seed to germinate, the same percentage of germination may be secured within a four-day to five-day period. This also usually will help to contribute toward higher ultimate survival of the seedlings.

Some additional interesting relationships may be obtained from the data. With the exception of one test which gave an unaccountably high total (Fig. 8, M), higher germination capacities were attained at alternating temperatures than at constant temperature in tamarack. This appears to be true whether the constant level is an average between the two alternating levels or is at the higher of the two alternating levels. Davis (1939), the U.S.F.S. (1948), and others have found maximum germinative capacity under alternating temperatures for many species. In other plants constant temperatures are satisfactory (Harrington 1921).

Since it is possible that peak germination or a given per cent of germination of a particular lot of seed occurs when a certain number of degree days has been attained, this was computed for all ranges (Table II). The results indicate that simple temperature summation above physiological zero (assumed to be 4°C) does not provide a consistently maintained point at which germination may be expected to take place. The data are very inconsistent and additional experimental work is required to determine what factors influence the amount of heat necessary for germination.

The effect of moisture and oxygen supply.—Moisture is essential, of course, for satisfactory germination and may be limiting when deficient. No satisfactory laboratory experimental study was undertaken to determine what level is required for germination. Probably moisture is seldom limiting during winter months when seed in the duff is...
undergoing after-ripening. Under these conditions, low temperature will prevent germination. In spring, when the temperature has risen to a satisfactory point, moisture content of the seed may have dropped to a level which is limiting.

Field evidence obtained at Cedar Creek bog in the spring of 1948 indicated that moisture deficiency may sometimes be limiting insofar as germination in tamarack is concerned. Here, seed soaked for five days in cold water before being placed in the field, germinated between zero per cent and five per cent at various locations on the surface of relatively dry sandy soils. In moist bog situations in the same general area, on the other hand, germination in similar tests varied from seven per cent to 35 per cent. Rudol. (1950) has concluded tentatively, however, that 14 days of cold soaking is necessary in tamarack and that seven days is insufficient to obtain good response in germination. The five-day treatment, therefore, probably did not provide as good a test as is desirable. Also rodent protection was not provided, and mice or shrews may have been an important limiting factor on the mineral soil plots.

In the spring of 1950 in the Cedar Creek area, similar results were again recorded with fall-planted seeds. On sites where leaf litter was fairly heavy and moisture was limited as well as on dry mineral soils, no germination took place on four plots of 100 seeds each. On sites more favorable from the standpoint of moisture availability, the germination on six plots of 100 seeds each averaged four per cent (from one to nine per cent).

Undisturbed plots adjacent to the seed-trap collections of the fall and winter of 1948-49 at Cloquet, were classified on the basis of moisture determinations made at the height of germination during the middle of June 1949. The precipitation records at Cloquet from the 15th of May to the June samplings reveal about 1.3 inches, or a 30 per cent deficiency, below normal for the period. All plots where moisture content of the surface inch of material was less than 12 per cent by volume were classified arbitrarily as dry sites (Table III). One such plot showed no germination. Five plots with moisture levels between 12 and 22 per cent in the surface inch were classified as intermediate with respect to moisture content and showed an average germination of nearly 4.1 per cent. The remaining six plots with moisture content in the surface inch between 22 and 32 per cent by volume were considered moist sites and showed successful germination of 7.5 per cent of the seeds which fell on them. There is a nearly straight line relationship between germination and moisture content within the limits of these data. Correlation analysis between moisture content of the germination medium at the time of germination and the per cent of seed germinating gives a correlation (r) of .503. These data as well as laboratory experience indicate that higher moisture levels than those found, probably would have produced higher germination, although under conditions of flooding, germination will again drop to zero.

Cooley (1903) in a study of tamarack reproduction in Maine, where annual precipitation exceeded 45 inches and where fogs were common, found abundant reproduction on open mineral soil. She writes, "the best places for germination are those cleared fields open to the sun and covered with low, thin grasses..." Germination on such areas in Minnesota can be expected only in years of particularly favorable moisture conditions and on sites where rodent populations are not high.

A shortage of oxygen resulting from flooding is not infrequently limiting for tamarack. Although some seeds germinate satisfactorily under water (Morinaga 1926), on the basis of both field and laboratory evidence seeds of tamarack do not so long as kept submerged, even though temperature conditions may be favorable. In this respect they resemble the seeds of bald cypress (Taxodium distichum (L.) Richard), another intolerant swamp conifer (Demaree 1933). Other factors being
favorable, within one to three weeks following release from submersion, some tamarack seeds germinated even though they had been submerged in warm stagnant water in the greenhouse at St. Paul for a period of one month or more. There is some field evidence to indicate that the germination following flooding may be less than would have occurred had the flooding not taken place, but this needs controlled experimental study for verification. Baker (1950) suggests that seeds soaked in water swell, the seedcoat may crack and then decay will set in. This may account for reduced germination following release from flooding in tamarack.

Light as an influence.—Although light has been found to affect the germination of a number of species (Nelson 1940, Nelson 1950, Haack 1906), a test of the effect of varying light intensity upon the germination of tamarack seeds following thorough after-ripening and at near optimum temperatures, shows no correlation. The results presented in tabular and graphical form (Table IV and Fig. 9) indicate no consistent trend relating light levels to germination per cent.

The effect of pH level.—Determination of hydrogen-ion concentrations was made in most of the tamarack bogs which were intensively studied. These varied from generally acid bogs at Cloquet (pH 4.5 to pH 6.2) to circumneutral bogs at Itasca (pH 6.9 to pH 7.6). In all of these bogs, enough seeds germinated in good years to provide good seedling stands. Averell and McGrew (1929) found the average pH on tamarack sites in northern Minnesota to be 5.6. Wherry (1922) indicates that tamarack tolerates an "unusually wide" pH range but classifies it as "preferring circumneutral habitats." Baldwin (1942) writes, "the influence of acidity on germination is mostly indirect. . . . In spite of the divergent opinions and theories on the influence of acidity on germination, there is a considerable body of evidence pointing to a favorable effect of mildly acid reactions on seed. . . ." Oosting (1948) believes that "Under ordinary conditions, the hydrogen ions themselves probably have little direct effect upon plants. . . ." It seems probable that pH is seldom if ever a limiting factor insofar as germination of tamarack seeds is concerned.

The influence of ground cover and germination medium.—The microclimate of the seed is determined, at least in part, by the surrounding ground cover which directly influences the amount of sunlight penetrating to the seed's immediate environment. This affects the temperature which in turn indirectly affects the rate of evaporation of moisture available to the seed. Furthermore, the competing ground cover, by consuming moisture, reduces the amount available for germination. Some types of ground cover permit more rapid evaporation from the seed bed than do others which retain moisture to a greater degree. These variations, along with others may materially change the physical factors of the environment, thereby directly affecting germination.

Beneath existing tamarack stands in Minnesota, the ground cover is frequently composed largely of a variety of mosses. Several species of Sphagnum, Mnium, and Plagiothecium are common as are Aulocornium palustre (W. and M.) Schw., Calliergon cordifolium (Hedw.) Kindb., Drepanocladus vernicosus (Lindb.) Warnst., Helodium blandowii (W. and M.) Warnst., and Thuidium delicatum (Hedw.) Hitt. Various species of the sedges belonging to the genus Carex, particularly C. lasiocarpa Ehrh., a relic of the sedge mat stage, C. trisperma Dew., C. leptalea Wahlenb., and C. lacustris Willd., may be fairly abundant. In some tamarack stands, a number of herbaceous plants are also found including Maianthemum canadense Desf., Caltha palustris L., Coptis groenlandica (Oeder) Fern., Sarracenia purpurea L., Mitella nuda L., Potentilla palustris (L.) Scop., Viola spp., Pyrola rotundifolia L., Lysimachia thyrsiflora L., Menyanthes trifoliata L., Galium spp., Linnæa borealis L., and others. Common shrubs include Salix pedicellaris Pursh var. hypo-

![Figure 9](chart.png)
with glauca Fern., Betula pumila L. var. glandulifera Regel, Alnus rugosa (Du Roi) Spreng., Rubus pubescens Raf., Cornus stolonifera Michx., Ledum groenlandicum Oeder, Chamaedaphne calyculata (L.) Moench, and Vaccinium oxycoccus L., among the more important. Other areas in which tamarack seeds were found germinating were covered with a thin litter beneath which lay raw humus. Most frequently in existing stands, needle litter was interspersed with mosses and occasional sedge, herbaceous or shrubby plants.

More seedlings were found on fine moss (primarily Mnium, Drepanocladus, and Helodium) than elsewhere. In one stand in the Itasca area during the early summer of 1948 a study was made of 41 randomly selected plots, each one square link in size (one-millionth acre). Of these, 10 were low lying and wet, with a cover of Mnium and carried a total of three, or 0.3 newly germinated seedlings per plot (later when more oxygen was available with a receding water table, additional seedlings appeared), seven were at an intermediate elevation covered with Sphagnum and carried seven seedlings, or one per plot, seven were at a similar level covered with Helodium blandowii, Calliergon cordifolium, and Thuidium delicatulum and had 69 seedlings, or 9.9 per plot, eight were at a somewhat higher level covered with needles or humus and occasional Mnium affine Bland., with 87 new seedlings, or 10.9 per plot, and nine were Carex knobs which stood several inches above the general ground level having 13 seedlings, or 1.4 per plot.

Adjacent to the 12 seed traps used at Cloquet during the seed dissemination period of 1948-49, 11 per cent of the seed disseminated germinated on non-Sphagnum moss cover. This was over twice the germination secured on Sphagnum (4½ per cent), sedge plots (4 per cent), needle litter plots (1½ per cent), or mineral soil when not protected by a rodent exclusion (4 per cent). The bare mineral soil provided better germination (14½ per cent) than a non-Sphagnum moss cover if rodent losses were eliminated. However, there is likewise a correlation here with moisture level which is probably a determining factor for type of vegetative cover as well as for tamarack seed germination. Most of the ground-covering non-Sphagnum mosses appear to be good indicators, at least in existing tamarack stands, of moisture conditions suitable for satisfactory seed germination.

Sphagnum, although it is probably a good medium for germination because of frequent favorable moisture and temperature conditions near its basal portion, is not satisfactory in the long run because it competes with the growing seedlings for light and because it dries out later in the season. Germination data collected, using it as a medium, are probably lower than actuality, because of the difficulty of locating sprouting seedlings in Sphagnum. This is particularly true in vigorously growing Sphagnum beds. If the growth rate of the Sphagnum is reduced, and particularly if the moss mat is compressed, it may prove to be an ideal germination medium. Schantz-Hansen (1931) also found this true for black spruce.

Age of cone-producing tree as an influence.—Seeds collected from cones of 15- and 16-year-old trees were tested for germinative capacity for comparison with the seed produced by trees 40 years of age and older. Two hundred seeds from each of two young trees gave tests of 27.5 per cent and 31 per cent as compared with seed-trap collections made the same season and treated in exactly the same way following collection, in which 2,663 seeds gave an average germination of 31.2 per cent.

Insofar as seed viability is concerned, therefore, it appears that young trees could be expected to reproduce about as satisfactorily as older trees. However, while the number of seeds produced per cone is relatively high in young trees, the total number of cones borne is very small and older trees with larger crowns are much more satisfactory for regenerative purposes.

The influence of date of dissemination.—Seeds collected from the seed traps during the fall of 1948 at Cloquet were divided into two groups: (1) those disseminated prior to October 11, and (2) those which fell on that date or later. Only seeds which superficially appeared to be sound and filled were used in the test, all cracked, rotting, and obviously unfilled seed having been eliminated. A pronounced difference in total germination was found, those seeds which were disseminated early giving a germination of about 37 per cent compared with one of about 20 per cent for seed disseminated late in the season (Table V). The t test applied to these data indicates a highly significant difference. These differences are not unexpected, particularly when one considers that the best developed seeds are found in the central part of the cone which is the first to open. Seed borne in the basal and terminal scales are frequently unfilled and those which are filled are usually of smaller than average size.

Retention of seed viability in the duff.—Naturally disseminated tamarack seeds ordinarily germinate the spring following dissemination. The field evidence for this statement, however, needs experimental verification. Under only two of the 12 seed traps put out in the fall of 1948 at Cloquet, did any seedlings appear following removal
TABLE V. Differences in germination resulting from tests of seed disseminated prior to October 11 compared with those disseminated October 11 or later at the Cloquet Experimental Forest, fall and winter, 1948

<table>
<thead>
<tr>
<th>Early disseminated seeds</th>
<th>Late disseminated seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds sown</td>
<td>Germinated</td>
</tr>
<tr>
<td>35</td>
<td>12</td>
</tr>
<tr>
<td>80</td>
<td>28</td>
</tr>
<tr>
<td>200</td>
<td>47</td>
</tr>
<tr>
<td>30</td>
<td>14</td>
</tr>
<tr>
<td>100</td>
<td>42</td>
</tr>
<tr>
<td>200</td>
<td>68</td>
</tr>
<tr>
<td>200</td>
<td>69</td>
</tr>
<tr>
<td>300</td>
<td>110</td>
</tr>
<tr>
<td>135</td>
<td>59</td>
</tr>
<tr>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>200</td>
<td>131</td>
</tr>
<tr>
<td>125</td>
<td>52</td>
</tr>
</tbody>
</table>

1,717 640 37.3 946 192 20.3

The next spring. The three found on these trap locations may have been from seeds which reached the ground surface by accident during collection from the traps. Still better evidence is provided by the failure of an appreciable number of seedlings to appear on the Itasca plots during the spring of 1949, the second spring following the very heavy seed crop of 1947. The seed crop in 1948, although very small by comparison with that of 1947, was large enough to provide some reproduction. In spite of this, the first year seedlings found on the Itasca plots in the spring of 1949 were less than two per cent of the number found in the spring of 1948 (Table VI). This ratio is probably not far from the cone-crop ratio of the two years.

THE SEEDLING

Methods

The plots used throughout the seedling investigations in this study were one-quarter milacre in size. Such a plot measures five links, 39.6 inches, or 1.006 meters on each side. Larger plots could not be inspected thoroughly enough to find small seedlings when first germinated without destroying them, particularly where ground cover was heavy or where seedlings were very abundant. All seedlings on each study plot were marked using small wooden medical applicators 6½ inches long. Where necessary to distinguish several different classifications of seedlings on one plot, the tips of the applicators were painted using various colors.

Inasmuch as it was not possible to visit all plots at frequent intervals, a large proportion of the loss of seedlings on the various plots could not be assigned satisfactorily to a definite cause. As a matter of fact, only about 10 per cent of the loss was assigned specifically. Certain assumptions could have been made on many of the others based on circumstantial evidence, but such uncertain evidence has been excluded from the data.

In an effort to determine the direct influence of light upon seedling survival, a series of shade frames (Fig. 10) were constructed and placed over third-year seedlings in the Iron Springs bog just north of Itasca State Park. This bog is spring-fed and well-drained. The shade frames were four feet square and were designed to satisfactorily shade the entire quarter milacre plot. Screen wire of one to three layers, heavy muslin, and a combination of the muslin and screen wire tacked to the frames, provided shade in varying degrees.

[Fig. 10. Three of the four-foot square shade frames used in the light intensity study undertaken at Iron Springs bog at Itasca State Park. Heavy muslin or varying numbers of layers of screen or both, were used to provide shade.]
on each plot, as well as on the five control plots on 12 occasions representing various dates, times of day, and sky conditions through the summer. At the same time, seedling counts were made, and the cause of mortality, when it could be assigned, was recorded. The frames were removed September 26.

**Results and conclusions**

**General.**—The early seedling stage is probably the most critical time in the establishment of a stand of tamarack. Mortality during the first three years under severe conditions may reduce a stand of half a million new seedlings per acre to only scattered individuals incapable of providing reasonable stocking. The following Itasca data have shown that losses during the first three years following a good seed year may be extremely high. Of 1,630 new seedlings on nine plots, about 30 per cent survived the first summer. Of those alive at the end of the first summer, half survived the following winter; by the end of the second growing season, the survival based on original germination was only six per cent. Of those still living at the end of the second summer 70 per cent survived the winter; during the third summer, survival for the year was reduced to about 60 per cent. Thus, of the original 1,630 new seedlings on the plots, only 53 or about 3½ per cent lived to the end of the third growing season.

Survival at the end of the third summer varies widely with individual logs. At Iron Springs, where water levels are very constant in a well-drained, spring-fed area, survival at the end of the third summer was high, nearly 14 per cent of 571 original seedlings. On the LaSalle Trail plots, the 203 new seedlings had all died by the end of the second growing season. Since only about five per cent of the disseminated seeds germinate, it can be calculated that approximately 32,000 seeds were probably distributed over all the Itasca plots. On this basis one seed in 1,600 resulted in a surviving seedling at the end of the third summer.

Douglas fir seedling survival, as shown in a study made by Isaac (1938) of the 1928 crop in western Washington, averaged about 17 per cent at the end of 1930. The 1929 crop had a survival of five per cent three years later. At the end of the third growing season in this species, survival was from 1½ to five times that found in tamarack. In the investigations by Haig, *et al.* (1941) in the northern Idaho region, western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), which is comparable to tamarack in seed size, showed a survival of about 18 per cent of the original seedlings at the end of the third year. In the same study at the end of the three-year period, western white pine (*Pinus monticola* Doug.) survival was 45 per cent. Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.) was 40 per cent, western larch (*Larix occidentalis*, Nutt.) was 39 per cent, grand fir (*Abies grandis* (Dougl.) Lind.) was 50 per cent, and western redcedar (*Thuja plicata* Donn.) was 40 per cent. In central Idaho on grazed areas, Sparhawk (1918) has shown that ponderosa pine (*Pinus ponderosa* Laws.) and Douglas fir seedlings have a survival at the end of the third year of about 7½ per cent. In the same study, lodgepole pine (*Pinus contorta* Doug.) showed a survival of about 25 per cent at the end of the third year.

These comparisons with other species indicate that tamarack has more severe mortality during the first three years following germination than other conifers for which data are available. If reproduction is to be successful, the causes of this mortality must be analyzed and removed wherever possible in silvicultural practice.

**Seedling survival in the succulent stage.**—Baker (1950) distinguishes between two periods in the critical time of seedling establishment, first the succulent stage and later the juvenile stage. The first of these continues for from five to six weeks in tamarack grown beneath an overstory of older trees and is terminated by the hardening of the hypocotyl. Mortality during this stage was nearly 40 per cent of 705 seedlings studied on 52 plots at Itasca, Cloquet, and Cedar Creek. During this stage, over half of the dying seedlings for which cause of mortality could be assigned definitely showed symptoms of damping-off.

Davis, *et al.* (1938) describe four types of damping-off, “pre-emergence damping-off,” “post-emergence damping-off,” “root rot,” and “top damping-off,” on which the only type definitely found in this study of tamarack was the second, post-emergence damping-off. This is typical of the succulent stage and is marked by characteristic constriction of the hypocotyl just above the germinating medium followed by toppling of the seedling. Neither sun scald nor wind injury symptoms (Hartley, *et al.* 1918), which are similar in general appearance, occurred among the seedlings on the sites studied. The specific organisms causing the damping-off, however, were not identified. There is very limited evidence to indicate that mortality from damping-off may be most severe in circum-neutral bogs and less serious on the acid sites. On the basis of knowledge common to forest nursery practice, this is to be expected.

It is not improbable that some loss, perhaps
considerable loss, in tamarack is the result of pre-emergence damping-off. Such losses may destroy two-thirds of the seedlings in coniferous nurseries in some years (Hartley, et al. 1918). Hartley (1921) has found a high correlation between the number of seedlings emerging and the percentage of subsequent loss resulting from ordinary damping-off for two species of western firs. In tamarack also, pre-emergence damping-off may account, in part, for the low germination characteristics of the species in the natural environment, since ordinary damping-off is a common cause of loss. However, damping-off mortality before the seedling appears above the ground was not analyzed in the present study.

Other important causes of loss found in the succulent stage are mechanical injury, drowning, and drought. Mechanical injury refers to trampling or breaking of the hypocotyl by animals including man. On the Itasca plots, such losses were sustained from man, deer, and porcupines and undoubtedly also from other mammals who chanced to walk over the plots.

On the basis of very limited evidence, it appears that young tamarack seedlings in the succulent stage cannot survive more than about a week of complete submergence under water. If only the roots are submerged, even succulent seedlings can withstand floods of one week's duration or longer.

On many of the plots, some seeds germinated after mid-July. Few of the resulting seedlings survived and by all odds the most important cause of mortality among them was drought. The depth of root penetration of tamarack seedlings in the succulent stage rarely exceeds three-quarters of an inch and particularly after the first of August, this surface layer may dry out almost completely.

An additional source of loss which proved to be of little importance on the plots included in the period of this study, was defoliation by insects including the larva of the larch sawfly (Pristiphora erichsonii (Hartig)). It seems probable, however, that in epidemic attacks of this insect when older trees are defoliated, the feeding larvae may fall to the ground and there consume all or most of the tamarack seedlings on the area.

Seedling survival in the juvenile stage.—The juvenile stage of seedling development begins with the hardening of the hypocotyl and continues for an indefinite period until the seedling may be considered established (Baker 1950). In tamarack, a particular seedling may be "established" in three years, or perhaps even in two, if it is grown in favorable conditions of soil, light, and moisture. On the other hand, tamarack seedlings grown under a well-stocked overstory of the same species will not become established, even in four or five years or more.

During this study in which many tamarack stands in various parts of Minnesota were inspected, only one seedling over four years of age was found in reasonably well-stocked stands. That lone seedling was five years old and died in its sixth year. Very few seedlings four years of age were found although a large population of three-year seedlings appearing after the bumper seed crop of 1947 survived to the end of the summer of 1950 in favorable areas at Itasca State Park. On the other hand, in many areas where the tamarack overstory was scattered or even where a fairly heavy cover of shrubs existed without a tamarack overstory, seedling tamarack of many ages were to be found and satisfactory stands were being established.

Light influence.—During the early succulent stage of development the tamarack seedling depends, at least in major part, upon food stored in the seed for sustenance. In the latter part of the succulent stage and following entrance upon the juvenile stage, however, when the seedling must manufacture its own food, light becomes the dominating or master factor. While light deficiency may not be a direct cause of death resulting from the seedling's inability to maintain its photosynthetic activity above the compensation point, it frequently is a contributing factor which weakens the seedling to causes of mortality not directly ascribable to light.

Light conditions within the tamarack stands intensively studied were quite variable because of stocking variations (Table VII). The lowest average intensities encountered in pure tamarack without an understory of shrubs were about 5½ per cent of full sunlight. These were found in mature heavy stands on good sites. Where black spruce or balsam fir were intermixed with tamarack, average intensities as low as three to 3½ per cent were encountered. In those stands which had an overstory sufficiently open to permit the entrance of spruce and other shrubs, the ground level intensity was further decreased to a minimum of about 1½ per cent of that in the open. The well-stocked stands of pure tamarack having little or no shrubby understory usually have light intensities between six and 10 per cent whereas it is only the stands in which holes in the canopy are found that exceed 15 per cent.

The only study concerned with the compensation point of tamarack seedlings known to the writer is that of Burns (1923) in which seedlings were exposed to three hours of electric light and the results were reduced to an expression in terms
of full sunlight on the basis of total thermal energy. This work indicated that the compensation point in a test of seven, 18- to 24-inch tall, potted tamarack seedlings is 9.8 per cent of sunlight at noon on December 22 in Vermont. Converted to summer conditions in Minnesota, this is about five per cent of full sunlight. If these measurements are representative for tamarack seedlings of this type, such seedlings can successfully maintain photosynthesis above the compensation point in most, if not all, pure tamarack stands without an understory occurring in Minnesota. However, in the heavier stands there is little residual photosynthetic capacity, and even moderate injury probably will result in mortality.

Tolerance has been defined by the Society of American Foresters (1950) as "the capacity of a tree to develop and grow in the shade of, and in competition with, other trees." An alternative definition is also offered as follows: "a general term for the relative ability of a species to survive a deficiency of an essential growth requirement, such as light, moisture or nutrient supply." Shirley (1943) recommends that the term be used in the second sense and that the specific type of tolerance be stated when it is used, i.e., shade tolerance, tolerance of low nitrogen supply, drought tolerance, etc. This provides a more precise usage than the first definition quoted and therefore is superior, at least for scientific purposes.

Tamarack is quite universally conceded to be a very intolerant species (Baker 1949), in the sense of the first definition given above. Cheyney (1942) under his discussion of the species with reference to its light requirements writes "... (it) is probably the most intolerant tree in the east." Seedling tamaracks are able to withstand drought and flooding more satisfactorily if grown in good light conditions than where light intensity is low. Survival of drought is largely dependent upon the depth of rooting which in seedlings beyond the succulent stage appears to be dependent upon the amount of light received. Likewise, seedlings grown under full sunlight appear to be better able to withstand flooding than seedlings grown in light intensities of only 10 to 20 per cent of full light. These relationships will be discussed in greater detail under the sections dealing with drought and flooding.

A study of the influence of light upon third-year seedling survival was undertaken at Iron Springs bog just north of Itasca State Park. Light intensity readings on the plots, the type of cover used, survival percentages, and other pertinent data are shown in Table VIII. Survival plotted over light intensity is also shown in graphical form (Fig. 11). These data indicate a pronounced drop in survival at an intensity of 200 to 300 foot-candles, which is a little over two or three per cent of the intensity of full sunlight on bright, clear days during the summer in Minnesota. However, there is some question as to the precise cause of this sudden downward trend in the curve. Since the four plots having lowest survival are the plots covered with muslin, these are the plots on which humidity was increased by reduced air movement and rate of evaporation. If these plots are eliminated there is still a general downward trend with decreasing light intensity but no sharp descent at the 200 foot-candle level.

The shade frame plots were intentionally located in an area where water levels were relatively constant. Therefore drought mortality as well as

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**Table VII. Summary of light intensities at seedling level in stands at Cloquet and Itasca between mid-June and mid-September. All intensities are expressed in foot-candles and were taken with a Norwood Director Model B incident light exposure meter.**

<table>
<thead>
<tr>
<th>Sky condition</th>
<th>Location</th>
<th>Full light intensity (in the open) average</th>
<th>Average intensity in all stands</th>
<th>Number of stands</th>
<th>Number of readings</th>
<th>Stand average as per cent of average in open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clear</td>
<td>Itasca</td>
<td>8300</td>
<td>990</td>
<td>8</td>
<td>112</td>
<td>1 [9], 6 [1/2], 29 [13]</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>8510</td>
<td>1165</td>
<td>10</td>
<td>45 [2]</td>
<td>2 1/2 [21 1/2], 8 [8]</td>
</tr>
<tr>
<td>Cloudy</td>
<td>Itasca</td>
<td>3720</td>
<td>430</td>
<td>7</td>
<td>48 [2 1/2]</td>
<td>5 [12], 20 1/2 [12]</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>2460</td>
<td>435</td>
<td>10</td>
<td>69 [2]</td>
<td>6 [27 1/2], 27 1/2 [16 1/2]</td>
</tr>
<tr>
<td>All days</td>
<td>Itasca</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Sky condition</th>
<th>Location</th>
<th>Full light intensity (in the open) average</th>
<th>Average intensity in all stands</th>
<th>Number of stands</th>
<th>Number of readings</th>
<th>Stand average as per cent of average in open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clear</td>
<td>Itasca</td>
<td>8300</td>
<td>990</td>
<td>8</td>
<td>112</td>
<td>1 [9], 6 [1/2], 29 [13]</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>8510</td>
<td>1165</td>
<td>10</td>
<td>45 [2]</td>
<td>2 1/2 [21 1/2], 8 [8]</td>
</tr>
<tr>
<td>Cloudy</td>
<td>Itasca</td>
<td>3720</td>
<td>430</td>
<td>7</td>
<td>48 [2 1/2]</td>
<td>5 [12], 20 1/2 [12]</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>2460</td>
<td>435</td>
<td>10</td>
<td>69 [2]</td>
<td>6 [27 1/2], 27 1/2 [16 1/2]</td>
</tr>
<tr>
<td>All days</td>
<td>Itasca</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
<tr>
<td></td>
<td>Cloquet</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
<td>. . .</td>
</tr>
</tbody>
</table>

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The above data indicates that tamarack is able to tolerate a reduction in light intensity to 20 per cent of full light without a significant reduction in survival. This is in contrast to the results obtained by Cheyney (1942) who found that tamarack seedlings were unable to survive at an intensity of 10 per cent of full light. The reasons for this discrepancy are not clear, but may be related to differences in site conditions, particularly moisture and nutrient supply. Further studies are needed to clarify this point.
October, 1954
FACTORS AFFECTING THE NATURAL REGENERATION OF TAMARACK

Table VIII. Summary of data gathered on 13 plots at different levels of light intensity at Iron Springs bog, showing average, maximum, and minimum light intensities and seedling survival for each.

<table>
<thead>
<tr>
<th>Average light intensity*</th>
<th>Maximum intensity* (average of four readings)</th>
<th>Minimum intensity* (average of four readings)</th>
<th>Number of light observations</th>
<th>Seedlings present on June 23</th>
<th>Seedlings present on Sept 26</th>
<th>Per cent survival</th>
<th>Type of cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>1120</td>
<td>2960</td>
<td>335</td>
<td>48</td>
<td>29</td>
<td>28</td>
<td>97</td>
<td>1 screen</td>
</tr>
<tr>
<td>908</td>
<td>1000</td>
<td>405</td>
<td>48</td>
<td>21</td>
<td>19</td>
<td>90</td>
<td>control</td>
</tr>
<tr>
<td>849</td>
<td>2430</td>
<td>440</td>
<td>48</td>
<td>90</td>
<td>82</td>
<td>91</td>
<td>control</td>
</tr>
<tr>
<td>790</td>
<td>1845</td>
<td>250</td>
<td>48</td>
<td>29</td>
<td>22</td>
<td>76</td>
<td>control</td>
</tr>
<tr>
<td>775</td>
<td>2600</td>
<td>170</td>
<td>48</td>
<td>17</td>
<td>14</td>
<td>82</td>
<td>control</td>
</tr>
<tr>
<td>569</td>
<td>1075</td>
<td>305</td>
<td>36</td>
<td>14</td>
<td>14</td>
<td>100</td>
<td>control</td>
</tr>
<tr>
<td>426</td>
<td>1275</td>
<td>90</td>
<td>48</td>
<td>35</td>
<td>30</td>
<td>86</td>
<td>2 screens</td>
</tr>
<tr>
<td>377</td>
<td>945</td>
<td>85</td>
<td>48</td>
<td>22</td>
<td>18</td>
<td>82</td>
<td>2 screens</td>
</tr>
<tr>
<td>244</td>
<td>740</td>
<td>20</td>
<td>48</td>
<td>25</td>
<td>9</td>
<td>41</td>
<td>1 muslin, 1 screen</td>
</tr>
<tr>
<td>130</td>
<td>410</td>
<td>50</td>
<td>48</td>
<td>25</td>
<td>19</td>
<td>76</td>
<td>4 screens</td>
</tr>
<tr>
<td>101</td>
<td>230</td>
<td>55</td>
<td>48</td>
<td>87</td>
<td>42</td>
<td>48</td>
<td>1 muslin</td>
</tr>
<tr>
<td>62</td>
<td>190</td>
<td>25</td>
<td>40</td>
<td>46</td>
<td>29</td>
<td>63</td>
<td>1 muslin</td>
</tr>
<tr>
<td>41</td>
<td>125</td>
<td>15</td>
<td>48</td>
<td>28</td>
<td>5</td>
<td>18</td>
<td>1 muslin, 1 screen</td>
</tr>
</tbody>
</table>

*In foot-candles.

Fig. 11. Survival of third-year tamarack seedlings from June 23 to September 26 under various light intensities at Iron Springs bog, Itasca State Park. Numbers beside points indicate number of seedlings present at the beginning of the period for each intensity.

Flood losses were eliminated, leaving insects and damping-off as the major causes of mortality. The two most important causes of death in third-year seedlings had been eliminated but the importance of damping-off was increased. Bates (1925), in studying a variety of first-year coniferous seedlings, also found an increase in damping-off losses with a decrease in light intensity. In his study, instead of using shading and natural light, artificial light was used, its intensity being determined by the distance of the seedlings from the source. Damping-off was an important cause of loss among those seedlings farthest from the light even on sand which had been "peculiarly free" of damping-off when well-insolated.

The amount of mortality resulting directly from
light reduction over a three-month period beginning at the end of June is probably less serious than a similar reduction for the entire year. Wiesner (1907) has pointed out that for all forest species, the minimum light requirement is relatively high at the time of bursting of the buds. For European larch (Larix decidua Mill.), he found this starting minimum for foliage to be half of full light. Decreased light early in the season, therefore, may be most significant to seedling survival in tamarack. Being a deciduous species, however, the shading beneath a tamarack overstory is much less severe than shading beneath an overstory of other conifers. One might expect appreciably higher mortality of tamarack seedlings beneath an overstory including black spruce or white-cedar, for example, than beneath a stand of pure tamarack.

Shirley (1935) points out that although failure of some forest species to succeed themselves is frequently attributed to failure to grow in the reduced light intensity, probably more precisely the major difference between shade tolerant and intolerant is the length of time which they can survive light intensities too low for growth. Tamarack seedlings appear to be able to survive from three to six years under an overstory of the same species. The shading test undertaken in this study on third-year seedlings for only three months extends over too short period to provide conclusive data. Additional experimental study is required to determine the significance of light as a direct factor in seedling survival. Certainly as a contributing factor, it is of great importance as will be shown.

The effect of drought.—A major cause of mortality among first-year seedlings after they have passed the succulent stage and a cause of considerable importance among older juveniles is moisture deficiency. Even bog species, such as tamarack, are subject to serious losses from drought. As has been pointed out in previous discussion, germination occurs only on sites where moisture levels are above about 12 per cent by volume. Under moisture conditions above 22 per cent but short of saturation, appreciably better germination may be expected. Occasionally, because of flooding, the most satisfactory germination occurs on the higher portions of a particular area, on knolls several inches above the general bog level. In late summer, these dry out most readily and in some years it may be found that the sites on which germination was most successful are those on which seedling mortality is highest.

Many writers (Livingston and Koketsu 1920, Conrad and Veihmeyer 1929) have pointed out that plant survival under drought conditions depends upon ability to push new absorbing root surfaces into regions where moisture has not been exhausted. The rapid exhaustion of moisture in the immediate vicinity of seedling rootlets both by absorption and by surface evaporation, and the inability of capillary action to replace it at a rate fast enough to meet plant needs, frequently renders good growing conditions, particularly with respect to light, essential to survival. This has been very well demonstrated by Haig (1936) in his study of mortality of seedlings of western white pine and associated species. Western larch, in this study, showed 93 per cent drought mortality among residual seedlings in full shade plots but only two per cent and four per cent in part-shade and full-sun conditions respectively. After averaging mortality among all of the species studied, Haig found the lowest rate, five per cent, occurred among residual seedlings in partial shade. In full sunlight where dry, hot conditions prevailed, rapid and deep seedling root penetration kept drought mortality to 16 per cent. In full shade, where shallow surface soil drying was accompanied by shallow root penetration, drought mortality rose to 61 per cent average for all species studied.

Superficial evaporation of the moisture from the forest floor is a major factor in the survival of first-year tamarack seedlings and also of older seedlings grown in shaded situations. The loss of moisture at greater depths resulting from tree root competition is of little or no significance at least in the juvenile stage of tamarack development. It may be of some significance later on, although even then, in the bog environment usually occupied by this species in Minnesota, deep competition is of less significance than for many upland species. Except in prolonged drought periods, water tables probably rarely recede beneath the reach of mature root systems. This has been found true for swamp-grown black spruce (Shirley 1934). Probably the major reason that seedling mortality is lower on Mnium-covered sites, for instance, than on litter-occupied areas is the higher level of moisture retained during critical periods in the surface soil beneath the moss.

The rate of root development in tamarack is slow, in part because it grows from small seeds, and the stored food available to the seedling for rapid root elongation is very limited. Of the first-year seedlings inspected in a series of examinations of individuals removed from older tamarack stands in the latter part of the first summer, none had root systems penetrating to a depth exceeding 1 1/2 inches and the average was less than one inch. The tops of such seedlings were usually longer than their roots. Western larch seedlings grown in full shade had a minimum root penetration of
0.5 inch and a maximum of 1.8 inches in late August. In full sunlight, corresponding figures were 6.1 inches and 13.4 inches, respectively (Haig 1936).

The moisture content of the surface inch of the forest floor was measured in the present study with special reference to the ability of first-year tamarack seedlings to survive late summer droughts. Variations through the season on the several sites studied ranged from two per cent to over 60 per cent by volume or from about 30 per cent to over 1200 per cent by weight in bog soils. The highest moisture contents appear in the very light mosses such as Sphagnum where tamarack seeds sometimes germinate. With few exceptions, moisture levels during the first two to 2½ months of the summer were satisfactory for seedling growth, ranging from 15 to 35 per cent by volume. During late August and September in many years, however, the levels may be expected to drop appreciably to ranges between 10 and 25 per cent by volume, or during critical periods, even lower. On the basis of limited field evidence it appears that shade-grown first-year tamarack seedlings during late August or early September drought periods, fail to survive moisture contents by volume in the surface inch of material below eight to nine per cent. In the humus soils typical beneath tamarack stands, this level is about 100 to 110 per cent by weight. On mineral soil (loamy sand) plots, shade-grown tamarack seedlings in their first year showed no drought mortality when moisture content by volume descended to 13 per cent which was about 11 per cent by weight.

Three-year-old seedlings because of deeper root penetration frequently exceeding three inches, can withstand reductions of moisture levels in the surface inch of material to about four per cent by volume or from 45 to 65 per cent by weight in organic soils. This level was never reached on the plots studied in the field except upon sites so dry that no tamarack seeds germinated on the area in the first place. It was attained in greenhouse flats where samples of the forest floor including tamarack seedlings were removed for study.

Additional experimental evidence obtained from seedling studies in the greenhouse indicates that first-year seedlings produced in full sunlight in organic soils brought in from tamarack bogs also will survive moisture level in the surface inch down to three to four per cent by volume. Such seedlings have a much lower top-root ratio than do seedlings of equal age grown in the shade of a tamarack overstory. While the root length of such seedlings is not quite as great as that of shade-grown three-year-old seedlings, it does approach them more closely than might be expected (Fig. 12).

Hofmann (1918), in a study of western larch on four areas in northern Idaho, found 22 per cent seedling establishment in the shade and 70 per cent in the open. In a study involving eight coniferous species, Bates (1925) concludes that root development suffers most severely from light deficiency, predisposing the seedlings to mortality from drought and nutrient deficiency.

In sterile sand, where because of nutrient deficiency, the first-year full-sun seedling roots are less well-developed than in the organic soils (Fig. 12) but still much better developed than those of forest-grown seedlings on organic soils, much lower levels of moisture in the surface material can be sustained. General mortality occurs only when the surface inch drops to a moisture level of less than one per cent by volume. Presumably, the difference between this medium and organic soils is the result of tighter packing of the mineral soil about the seedling root system and a smaller percentage at hygroscopic water, thereby rendering more of the moisture present available to the seedling.

The effect of flooding.—During the summer of 1949, extremely heavy rainfall in July caused a mid-summer flooding of some of the bogs being studied both at Cloquet and at Itasca. The inundation of many of the plots under observation caused heavy mortality among seedlings in the juvenile stage. In this respect tamarack resembles bald cypress (Demaree 1933) in that neither conifer, even though both are frequently found in aquatic environments, can withstand flooding of much duration as seedlings. Flooding is not uncommon in tamarack stands.

The field evidence from the Cloquet Forest indicates that first-year seedlings grown beneath existing stands will be killed by complete submergence for a period of approximately one week to 10 days. Partial submergence covering about half
of the top with complete submergence of the roots for a similar period of time may or may not kill similar seedlings immediately. By the end of the summer, however, most seedlings so covered die. Submergence of only the roots for this period results in little, if any, mortality. At Itasca second-year shade-grown seedlings subjected to complete submergence for about three weeks all died. The submerged portions of similar seedlings partially inundated for the same period on these plots turned brown. By the end of the summer all such seedlings were also dead.

To obtain additional verification of the influence of flooding upon seedlings, sections of the forest floor containing three-year-old seedlings were transplanted in August of 1950 from the Iron Springs area at Itasca to the St. Paul greenhouse where they were subjected to flooding for a period of three weeks (Table IX). Also, first-year seedlings grown in full sunlight in the greenhouse on the same soils were subjected to a similar test for a four-week period (Table X). The results indicate that, as was true in the drought tests, three-year-old seedlings grown in the shade of older tamarack stands are no better able to withstand severe conditions than are one-year-old seedlings grown in full sunlight. Seedlings grown in full light appear to be much more capable of withstanding flooding than do seedlings of the same age grown in the shade of a tamarack overstory.

Miscellaneous influences.—Fire may be a factor in regeneration. Cutover tamarack stands examined in the course of the study had occasionally been broadcast-burned to reduce the slash following cutting. These were still completely barren of tree reproduction several years later. Light fires burning through existing stands, on the other hand, actually encouraged natural reproduction by reducing the overstory and by reducing the severity of ground competitors. In two stands examined which recently had been burned lightly, moist pockets had not been charred, and in these pockets first-year tamarack seedlings showed vigorous growth. Many of the trees in the overstory as well as the shrub cover beneath had been partially or completely killed. On an adjacent area with a more or less complete overstory and a heavy shrub cover of Ledum, not a single surviving seedling was found.

Most tamarack seedlings beyond the succulent stage have ectotrophic mycorrhizae. In one stand examined at Itasca, some first-year seedlings had mycorrhizal roots whereas others did not. No noticeable differences in the thrift of the two classes of seedlings was found.

Browsing has not been found on tamarack seedlings in the present study and appears to be a factor of little or no importance at the present time in the areas studied. DeBoer (1947), in a survey of deer damage to forest reproduction in heavily browsed forest areas in Wisconsin, found comparatively little injury in tamarack. Some injury by snowshoe hares was recorded in his study in addition to limited deer damage.

**Vegetative Reproduction**

Layering as a means of regeneration among conifers is not uncommon, particularly in the genera *Picea* and *Abies* (Cooper 1911). Mayr (1925) indicates that *Larix* also reproduces by this method. Cooper points out that layering occurs more frequently with increasing latitude and altitude. The findings in Minnesota relative to layering in tamarack, therefore, may be conservative since the region lies at the southwestern limit of its range. This form of reproduction may be more common toward its northern limits.

Throughout the study seedling tamaracks were found to produce roots quite readily along the stem as *Sphagnum* covered the lower portion. However, only one tree definitely produced by layering was found in the course of this study. This was in an open bog containing a heavy growth of *Chamaedaphne* and of *Sphagnum*. The rapid-growing *Sphagnum* had completely covered the lower portion of the scattered black spruces and tamaracks. Many small spruce trees obviously had originated by layering, forming groups around the older trees in the center. Similar arrangement of tamaracks in groups was not found. The evidence supports the presumption usually made, that
at least in Minnesota, vegetative reproduction in tamarack is of no significance.

The Reproductive Ecology Having Silvicultural Implications

If tamarack is to be managed successfully on a sustained yield basis, the practicing forester must recognize and give due consideration to its ecological characteristics, particularly with respect to natural regeneration. The biology of any species determines the framework within which economic management must operate.

As has been indicated, tamarack is very intolerant of shade, perhaps as much so as any tree native to the region. Even the seedlings are seriously affected by light deficiency. The species, however, is relatively tolerant of root submergence. These two characteristics result in its confinement primarily to wet lands in the southern part of its range where it cannot compete with the large variety of semi-tolerant or tolerant species characteristic on the uplands. On the bog lands, however, competition is limited to a few species. At the northward extensions of its range, on the other hand, where competing species are less abundant, it appears on the upland. Even in the southernmost portions of its range, this may occur if competition is very limited and if moisture conditions are suitable for germination. In any part of its range, the first essential to satisfactory regeneration is abundant light.

Tamarack differs from bald cypress in the juvenile stages. In that species, Mattoon (1916) has shown that the seeds and seedlings demand a very high degree of soil moisture for satisfactory development. He believes that in cypress, the confinement of the species to swamps may result not only from inability to compete on better sites but that the necessities for satisfactory reproduction, principally a super-abundant water supply, are also involved. Tamarack appears not to be limited to bogs because of exceptionally high moisture requirements during the reproductive stage although germination may be restricted by early season drought.

Satisfactory regeneration, however, has been shown to involve a relatively constant water level. Both drought and flooding are serious causes of mortality among seedlings and in spite of the fact that provision of abundant light will help to reduce loss from these causes, it will not eliminate them. The control of water levels is frequently impossible. However, successful steps have been taken by foresters in Europe and more recently in the United States to increase growth rate in existing stands through drainage (Averell and McGrew 1929, Hoene 1951, LeBarron and Neetzel 1942, and others). It is possible that at least in some areas, a limited amount of effort directed toward maintenance of consistent water levels could be economically justified to attain natural reproduction of tamarack.

The third major requirement for successful tamarack regeneration is a satisfactory seed source. If the stand of reproduction is to be well-stocked, vigorous trees of seed-bearing age (preferably 50 to 150 years) having well-developed crowns must be found within one to two times their height of all portions of the area to be stocked. Fulfillment of these requirements—abundant light, reasonably consistent water levels, and a satisfactory seed source—will usually assure natural tamarack regeneration.

One additional consideration, attention to which will help to relieve the environmental resistance faced by tamarack in the reproductive process, is the reduction of rodent populations. Such action may be necessary only on certain areas where, and in particular years when, populations are high. Even with peak rodent populations, however, it is possible that in heavy seed years on bog soils where the small seeds of tamarack are not easily found, a satisfactory stand may be established.

Summary

Tamarack (Larix laricina), a native conifer widely distributed in North America, has received but little attention with respect to its ecological characteristics. During the summers of 1948, 1949, and 1950, studies undertaken in Minnesota were directed toward a determination of some of the more important factors affecting its reproduction.

Good seed crops, which occurred at intervals of about four years in greatest abundance on 50- to 150-year-old trees with well-developed crowns, produced one to two million filled seeds per acre in stands of medium stocking. Most of the good seeds were disseminated during September and October and satisfactory regeneration was seldom secured beyond two tree-heights distant from the source. Seed destruction may be caused in significant quantities before dissemination by a seed-eating Lepidopteran larva and after dissemination by various rodents which may be particularly destructive on bare mineral soil surfaces.

Field germination in tamarack was low by comparison with seed-flat germination tests, averaging only four or five per cent. On exposed sites where temperatures were relatively high, germination started earlier and was more concentrated than on shaded sites, although total germination did not vary between them because of temperature differences. Tamarack seeds will not germinate under
water and prolonged spring flooding may result in reduced germination. Moisture deficiency frequently limited field germination, and considerable improvement was recorded with increasing moisture content from about 10 to 35 per cent by volume of the germination medium. Under a fine moss cover (i.e., 

\[ \text{Mnium, Helodium, and Drepanocladus} \]

maximum field germination in existing stands was secured, although compressed \[ \text{Sphagnum} \] and mineral soil protected from rodents gave better results. Light did not influence germination nor does \[ \text{pH} \] appear to be a seriously limiting factor since tamarack occurs on sites ranging at least from \[ \text{pH} \] 4.5 to \[ \text{pH} \] 7.5. Young trees bore seeds which germinated as well as those from older trees. There was a highly significant decrease in germination among seeds collected after mid-October when compared with those collected earlier. Viable seeds did not lay over in the duff to the second year in appreciable quantities if at all.

Only about \( \frac{3}{2} \) per cent of new tamarack seedlings survived to the end of the third summer, a very low percentage when compared with other North American conifers for which data are available. During the succulent stage of seedling development which lasts for from five to six weeks, damping-off was the principal cause of mortality, although mechanical injury, drought, drowning, and insects also reduced survival. In the juvenile stage immediately following, light deficiency, drought and drowning were major causes of loss. No seedlings surviving beyond the sixth year were found in well-stocked, existing stands during the course of the study.

Light intensities in pure tamarack stands, lacking a shrub understory, varied from about \( \frac{5}{2} \) per cent to more than 25 per cent of full light in the open. Lower intensities occur where black spruce or balsam fir are in mixture or where a shrubby understory exists. Damping-off, drought losses, and flooding mortality may be expected to increase with reductions in light intensity, particularly at the lower levels. First-year, forest-grown seedlings, with a root penetration averaging only about an inch, did not survive moisture contents in the surface inch below about nine per cent by volume. Seedlings of equal age grown in full light as well as three-year-old forest-grown seedlings, both of which may have root penetrations of \( \frac{2}{2} \) to \( \frac{3}{2} \) inches, withstood reductions to about four per cent. Complete or partial top submergence by flooding for a week or more killed first-year, forest-grown seedlings which were beyond the succulent stage. First-year seedlings grown in full sunlight and shade-grown three-year-old seedlings showed 90 per cent or greater mortality following three to four weeks of submersion.

Severe fires appear to completely eliminate tamarack regeneration for many years but light burning may be beneficial by reducing competition for light. Most tamarack seedlings had mycorrhizal roots but first-year seedlings lacking mycorrhizae were not retarded. Browsing by mammals as a cause of loss in tamarack was of minor importance.

Although reproduction by layering does occur in tamarack, it is so uncommon as to be of little practical significance.

To obtain satisfactory natural regeneration, certain biological requirements of the species must be met. These are: 1) abundant light; 2) a relatively constant water level; and 3) a satisfactory source of seed.

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