# Heat Tolerance of Tree Seedlings

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THE ability of a tree to withstand fire depends on both its fire resistance and its heat tolerance. Fire resistance is the ability of a tree to survive the passage of a fire and is mainly determined by the tree's size, its bark thickness, and the spatial distribution of its foliage. Heat tolerance is the ability of a tree's organs and tissues to withstand elevated temperatures. It determines immediate physiological effects of heat rising from a fire and, together with fire resistance, ultimate ecological effects.

Knowledge of the reaction of crowns to heat is essential for effective vegetation management employing fire, but direct observation of temperatures and tissues in mature tree crowns is difficult and the heat produced by a prescribed fire cannot be sufficiently controlled for experimental purposes. Structurally, the most heat-susceptible portions of tree crowns closely resemble seedlings: Both are composed of slender, thin-barked, foliage-bearing stems and twigs. Their reaction to heat is probably similar also. The convenient size and accessibility of seedlings adds to their being a logical choice for test material.

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Plants probably react differently to heat depending on whether they are physiologically active or dormant. Heat tolerance likely is analogous to frost hardiness (Levitt, 1951), dormant material being more tolerant or hardy. If dormancy, a seasonal phenomenon, has an effect on heat tolerance, it could be of practical significance in vegetation management employing fire. But, for such management to be effective, not only must the benefits be known, but also any shortcomings and how they can be minimized. Knowledge of heat tolerance will aid in developing guides for safe and efficaceous use of fire and may also aid in selecting species adapted to exposed sites.

The experiments reported here were undertaken to investigate the heat tolerance of tree seedlings and to determine how it varies with species, degree of physiological activity, and method of heat application.

## LITERATURE REVIEW

Heat tolerance varies with stage of development and plant-part and is discussed under the headings Seeds, Roots, Stems, Leaves, and Seedling Tops.

### SEEDS

Seeds are probably the most heat-tolerant stage in the life-cycle of a plant. Dry seeds of several Australian species withstood 110°C for 4 hours (Beadle, 1940), and some hard seeds survived 70 minutes in boiling water. Beaufait (1960) found that jack pine (*Pinus banksiana* Lamb.) seeds, enclosed by a serotinous cone, were not only extremely well protected from heat but also were heat tolerant. Heating cones at 482°C for 30 seconds had no adverse effect on germination and seeds unprotected by cone scales did not decrease significantly in viability until the wings ashed and the seed coats cracked.

Ben Zeev and Zamenhof (1962) studied the effects of heating on the germination of radish (*Raphanus sativus* L.) seeds. Heating them at atmospheric pressure for 16 minutes at 90°C resulted in a 30 percent drop in germination, and at 100°C in complete mortality. However, if the treatment was preceded by heating at 55 to 60°C for 3 hours, then the general heat tolerance was increased in the order of 10°C. If seeds were pre-heated and then heated in a vacuum for 16 minutes, general tolerances were increased 40°C. Thus the pre-heating and vacuum gave 80 percent germination at 125°C, 50 percent at 135°C, and zero at 140°C.

Using simpler heating methods, Stone and Juhren (1951) found an exposure of 5 minutes at 100°C assisted germination of seeds of the chaparral species *Rhus ovata* Wats. Whittaker and Gimingham (1962) found that seeds of heather (*Calluna vulgaris* (L.) Hull.) treated with air between 40 and 80°C for 1 minute showed increases in both numbers germinating and rate of germination. At 120°C, treatments exceeding 30 seconds depressed germination, and this effect became pronounced at 160°C for 20 seconds. An exposure of 200°C, or charring even if accompanied only by non-lethal temperatures, killed heather seeds.

## Roots

According to Hare (1961) roots apparently have received little study relative to lethal temperatures. He reports that the tolerance of seedling roots of loblolly pine (*Pinus taeda* L.) determined by Ursic (1961) varied considerably, but 54°C for 5 minutes, or 50°C for 30 minutes, or 48°C for 2 hours, were generally lethal. From these results, roots appear to be the part of a plant most susceptible to heat injury.

## Stems

Using a controlled temperature water bath, Lorenz (1939) investigated heat tolerance of the cortical parenchyma tissues of five forest trees and found lethal combinations of temperature and time to range between 57°C and 59°C for durations of 30 minutes up to 66°C to 69°C for 1 minute. The writer (Kayll, 1963) investigated tolerance of Scots pine (*Pinus sylvestris* L.) seedling cambium by applying controlled temperature air and found that exposures of 60°C for 2 to 4 minutes, or 65°C for less than 2 minutes, were lethal.

## Leaves

Using a hot water bath, Shirley (1936) found that needles of northern conifers could withstand only 49°C for 2 hours and using similar methods, Nelson (1952) determined average lethal temperatures and durations of 64°C for 3 seconds, 61°C for 5, 60°C for 31, and 52°C for 11 minutes. Both authors found small differences between species. Jameson (1961), however, found significant differences between the heat tolerance of grass and tree tissues and a seasonal variation in tolerance related to moisture conditions of the plant and its environment.

### Seedling Tops

Apparently little has been done on the effect of applying lethal and sub-lethal temperatures to seedling tops. Shirley (1936) found that when immersed in water, tops were unaffected by 44.3°C for 5 hours. He also found killing temperatures were higher in air than in water, and higher in dry air than in moist.

The author (Kayll, 1963) noted that immersing test material in heated water prevents heat dissipation whereas using heated air applied to a restricted area of a stem does not. Estimates of heat tolerance determined using heated air may therefore be higher and have greater relevance in terms of fire in th natural environment.

## MATERIALS AND METHODS

Physiologically dormant and active tree seedlings were treated with heated air applied to individual stem sections and to whole seedling tops. A visual evaluation of physiological condition was supplemented by determning relative turgidity. Viability of stem sections was determined using a vital stain, and of wholly treated seedling tops by observing growth and development. The results were evaluated and summarized according to the individual reactions of the test material.

### Test Material

Seedlings 1 to 5 years old and 40 to 80 cm tall of six tree species, Scots pine, eastern white pine (*P. strobus* L.), American beech (*Fagus grandifolia* Ehrh.), Norway spruce (*Picea abies* L.), Japanese larch (*Larix leptolepis* [Seib. and Zucc.] Gord.) and European larch

(*L. decidua* Mill.) were used in the local application of heat to seedling stems, and the last three species were used in the general application of heat to seedling tops. In all, approximately 700 seedlings were used. Their general characteristics and the year the experiments were conducted are presented in Table 1.

TABLE 1. CHARACTERISTICS OF SEEDLINGS

| Species | Date of Experiment | Age Years | Avg. Ht. cm | Avg. Butt Diameter mm | Bark Thickness mm |
|---|---|---|---|---|---|
| Scots pine | 1961 | 1 | 45 | 8 | $<1$ |
| Eastern white pine | 1962 | 5 | 40 | 5 | $<1$ |
| American beech | 1964 | 3 | 40 | 3.5 | $<0.5$ |
| | 1965 | 4 | 43 | 3.5 | $<0.5$ |
| Norway spruce | 1964 | 3 | 47 | 10 | $<1$ |
| | 1966 | 4 | 62 | 12.5 | $<1$ |
| Japanese larch | 1964 | 3 | 67 | 10 | $<1$ |
| European larch | 1966 | 5 | 76 | 13 | $<1$ |
| | 1967 | 5 | 80 | 13 | $<1$ |

"Relative turgidity" was used as an index of activity or dormancy to supplement the subjective evaluation of test material. This measure has been found useful by Bannister (1964) in ascertaining the activity or dormancy of heather and by Bier (1959) in determining the susceptibility of certain plant tissues to disease.

The expression of relative turgidity is a percentage, based on the formula:

$$RT = \frac{FWC}{TWC} \times 100, \text{ where}$$

FWC = field water content = fresh weight minus oven-dry weight

TWC = turgid water content = water-saturated weight minus oven-dry weight.

Relative turgidity of the test material was determined in the manner prescribed by Bannister (1964). Immediately before each heat treatment, terminal and upper lateral shoots 4 to 5 cm long were clipped from each seedling and put in stoppered glass tubes. After weighing, shoots were transferred to polyethylene tubes containing .5 cm of distilled water and kept in cool dark storage for 24 hours. Shoots were blotted dry and re-weighed in their original tubes and then oven-dried at 95 °C for 24 hours, and a final weight determined.

### Local Application of Heat to Stems

An apparatus was designed and constructed (Kayll, 1963) which directed heated air of known temperature against a restricted area of a seedling's stem surface for specified periods of time. Air was forced through a steel pipe 2.5 cm in diameter and heated by either a Bunsen burner or an electric resistance-coil element connected through a rheostat. The temperature of the air coming out of the pipe was controlled by adjusting the Bunsen burner or the rheostat.

Temperatures of the applied air and on the surface of the stem were measured with 22-gauge, butt-welded, chromel-alumel thermocouples and read directly on indicating pyrometers. Applied temperatures ranged from 45 °C to 117 °C, and durations from 15 seconds to 10 minutes. Because several instruments and calibrations were used over the course of the experiments, steps between applied temperatures varied slightly. Five or six replicates of each treatment were randomly applied.

Sections 5 to 6 cm long were marked on the central stem of a seedling and section diameter and bark thickness noted. Depending on seedling height, at least three and at most six sections were heated. One additional section was kept as a control. A thermocouple was attached with a spring clip, the exact location of the thermocouple weld marked on the bark, and the appropriate predetermined treatment applied, starting with the uppermost section.

### Viability

Immediately following completion of the locally applied heat, each stem was cut into sections, split, and immersed in a 1 percent aqueous solution of 2,3,5 triphenyl-2H-tetrazolium chloride (TTC). After 24 hours in cool dark storage, the cambium was examined by peeling back the bark and noting the colour. Dead cambium remains a natural, neutral shade; living cambium colours deeply (Kayll, 1963).

## General Application of Heat to Seedling Tops

An apparatus was designed and constructed which enabled heated air to be applied for specified durations to the aerial parts of a seedling. A steel frame 100 cm high on a 60 cm equilateral triangle base was made and covered with polystyrene 2.5 cm thick. Air heated by electric elements and rising through a flexible hose 10 cm in diameter entered the "shroud" in a bottom corner. Hinged pieces of polystyrene jammed against the lower stem and outer edges of the shroud fully closed it during each test. Temperatures were monitored in five locations on each seedling using 20-gauge butt-welded chromel-alumel thermocouples and recorded automatically on a potentiometric recorder. Locations monitored were the terminal bud, two lateral branch ends on opposite sides of the seedling, and two lateral branches at approximately the mid-point of each branch. Average temperatures for the five locations for all treatments on Japanese larch ranged from 51 to 63°C, for European larch from 50 to 67°C, and for Norway spruce from 43 to 52°C. Six durations of 1.0, 1.5, 2.0, 2.5, 3.0 and 3.5 minutes, and six replicates, were used.

Thermocouples were attached to the seedlings and their locations marked with small twists of wire. In each treatment, an instrumented seedling was put in the shroud and closed off. After 15 seconds, when a temperature equilibrium had been reached, timing of the treatment duration was begun.

## Viability

Following the general application of heat, the potted plants were kept in a heated greenhouse where periodic observations were taken of ensuing growth and development of both individual stems where thermocouples had been attached, and of the seedling as a whole. Since none of the seedlings died, a treatment was considered lethal if the particular plant part (terminal bud, lateral bud, or portion of a lateral branch) failed to flush and grow or, if already flushed, aborted.

## Evaluation of Effects

Results were evaluated by plotting viability and mortality for each test. The resultant graphs were used to estimate combinations of temperature and time resulting in approximately 50 percent mortality. This value was used as an estimate of heat tolerance because of the highly variable individual responses of test material and because it was considered a seedling could survive such treatment. Lorenz (1939) used a similar value in estimating the heat tolerance of cortical parenchyma tissues.

## RESULTS

From the experiments in which heat was applied locally to seedling stems, the average combinations of temperature and duration which killed approximately one-half of the underlying cambium are portrayed in Figure 1. The main result of these experiments was that dormant seedlings were generally more tolerant of heat than active seedlings (by 30 to 35°C for the same duration of heating). Estimated responses for each species are presented in Figure 2 and can be summarized as follows:

(a) Norway spruce was generally more heat tolerant than Japanese and European larch.
(b) The two larch species had about the same heat tolerance.
(c) In the active condition, heat tolerance was relatively low and about the same for both larches, eastern white and Scots pine, and American beech. Active Norway spruce was slightly more heat tolerant than these species.
(d) For applications of heated air for 1 minute, dormant Norway spruce was most heat tolerant (108°C), dormant Japanese and European larch were next (93°C), active Norway spruce was next (78°C), followed by active Japanese larch (70°C), active European larch (64°C), active American beech (62°C and 60°C) and active eastern white pine (60°C).

In the general application of heat to seedling tops as a whole:

(i) No seedlings were killed by the treatments, but most of the Norway spruce were almost completely defoliated.
(ii) The terminal buds of leader and lateral branches of Norway spruce withstood heat better than those of the two larch species.

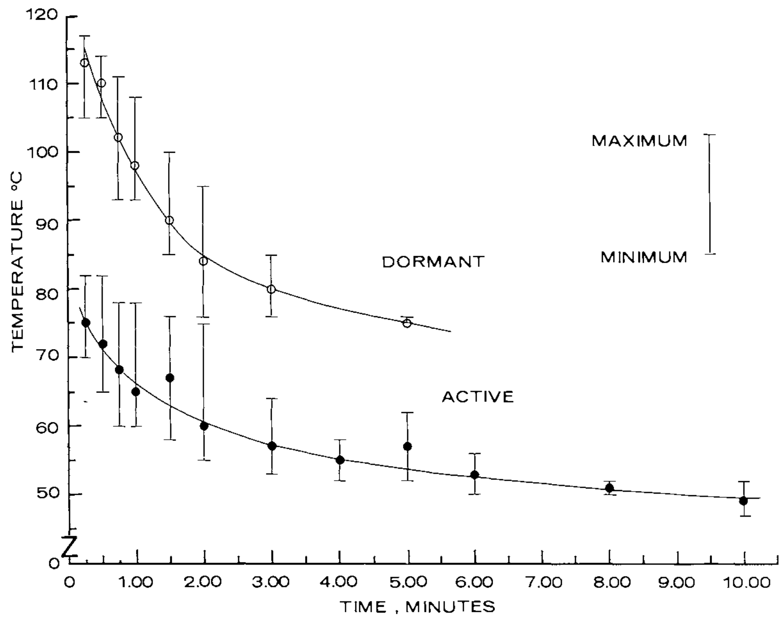


Fig. 1. Average heat tolerance of dormant and active tree seedling.

(iii) Dormant Norway spruce again showed a greater heat tolerance (65 °C) for 1 minute down to 55 °C for 3 minutes) than the two larch species (55 to 59°C and 52 to 54°C for the same durations) but the difference was less than that determined by the local heat application.

(iv) Active European larch was least tolerant (52 °C for 1 minute down to 48 °C for 3 minutes), but active Norway spruce with an apparent tolerance of 62 °C for 3 minutes was unlike all other results.

Six weeks after treatment, Japanese larch (and European larch to a lesser degree) exhibited three peculiarities:

1. Primary needles on the mid-section of the central stem grew more profusely than normal and secondary needles on the lateral branches less than normal (Fig. 3).

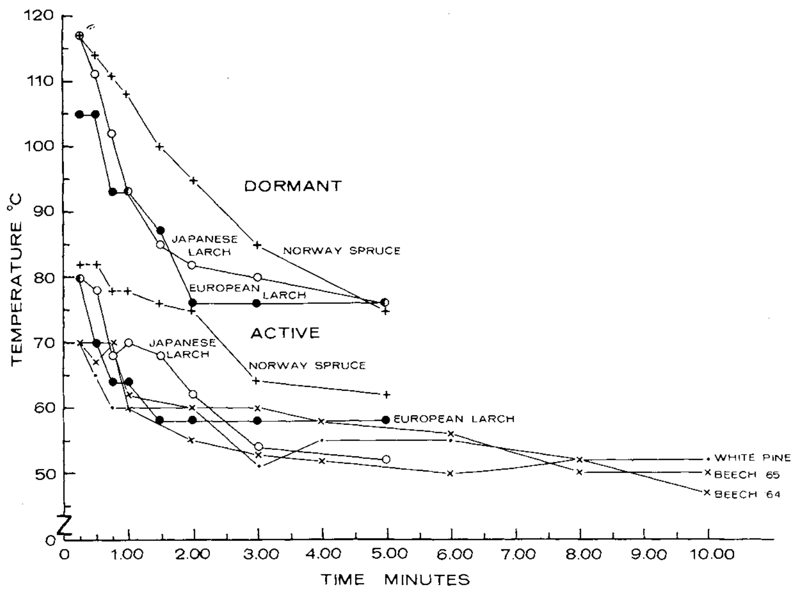


FIG. 2. Average heat tolerance determined from local application of heat to seedling stems.

2. In the few instances where the lowermost branches and needles of the seedling could not be accommodated in the heating enclosure, they grew more profusely than the completely unheated controls.
3. Many more primary needles were produced on the heated seedlings than on the unheated controls.

## DISCUSSION

In the experiments conducted at Aberdeen, Scotland (Kayll, 1964), the expression of relative turgidity was a helpful supplement in distinguishing seedlings in the active or dormant state. Dormant Norway spruce and Japanese larch seedlings had an average relative turgidity of 80 percent and active plants 91 to 94 percent. With

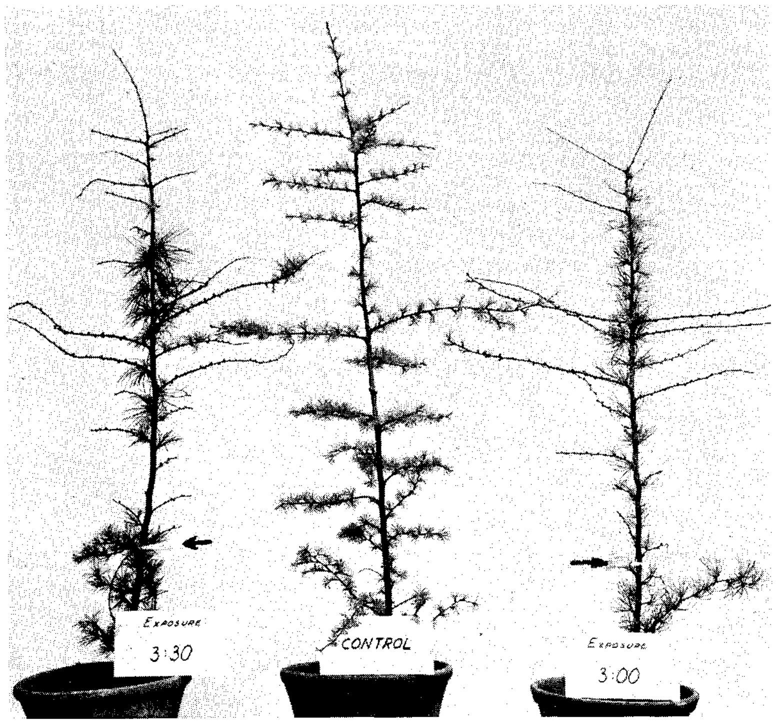


FIG. 3. Condition and appearance of Japanese larch seedlings after being subjected to hot air (51 to 63 C, average 57 C) for the durations (minutes) shown. The arrow indicates the location of the bottom edge of the heat shroud.

later experiments conducted at Chalk River, Ontario, dormant seedlings of European larch had an average relative turgidity of 78 percent and active seedlings 84 percent. But for concurrent tests with Norway spruce, relative turgidities were 93 percent for "active" and 91 percent for "dormant". The latter result is unlike those from the other tests and reasons for this are not completely understood. All of the Chalk River, Ontario seedlings were brought indoors in a dormant state and put either in a heated greenhouse to promote activity, or in a cold room to maintain dormancy. A few days before heat treatments, the seedlings kept in the cold room had to be moved to the greenhouse for the tests. Outward appearances to the contrary, this short time may have been sufficient to break dormancy. It has been found (Macklon, 1962; Jarvis and Jarvis, 1963) that plants of the same species grown under dissimiliar environmental conditions can exhibit different relationships between relative turgidity and other measures of a plant's water balance. This environmental effect might account for the variation between Norway spruce grown in Scotland and Ontario, but tends to restrict the use of relative turgidity to a local comparison of physiological activity. However, since heat tests using the Norway spruce gave dissimilar but not wholly contradictory results, the writer feels that relative turgidity remains a useful supplement in distinguishing between seedlings in an active or dormant state.

The essential value in determining that heat tolerance of tree seedlings and relating it to mature tree crowns is to enable estimates of mortality likely to result from using prescribed fire. To the practicing forester the purpose of a prescribed fire in part dictates its required characteristics. He may therefore not only need to know the intensity of prescribed fire which causes total mortality, but also the maximum intensity which does not destroy the overstory. Since none of the seedlings died in the experiments, but severe defoliation did occur, the estimate of 50 percent mortality on an individual test basis seems correctly chosen as a maximum which can be safely tolerated. Thus the crown of a tree or canopy of a stand could probably suffer damage to that extent and survive.

As determined from local application of heat to their stems, physiologically active seedlings could withstand from 60 to 78°C applied for 1 minute. These tolerances are about the same as those determined by Lorenz (1939) for five North American tree species. His results showed temperatures between 65 and 69°C were lethal if applied for 1 minute and he also found little variation between species. In the dormant state, however, the writer found seedlings were able to tolerate between 93 and 108°C for the same duration. Relating this greater tolerance to mature crowns, its importance to the silviculturist lies in the possibility of minimizing heat damage by prescribing fire in either early spring or late autumn.

When describing forest fires, Uggla (1957) observed air temperatures in spruce crowns above a fire to be in the range of 20 to 80°C, and usually of short durations. These temperatures are generally below the critical limits presented above, but he indicated that portions of crowns were killed. He attributed the damage to smoke, perhaps correctly, but the writer feels similar effects could be produced by excessive transpiration and drying of the crown. The question is open to further study and should be included in pilot studies of the effects and consequences of prescribed fire.

The heat tolerance of seedling tops wholly subjected to heat was less than the tolerance determined by local application to sections of a stem. For durations of 1 minute, temperatures of 51 to 65°C were lethal for both dormant and active plants. The rule of dormant material being more tolerant of heat than active material was seemingly upset by the reaction of active Norway spruce. However, the writer feels these results could be the consequence of a variation in the test material which was not recognized at the time of treatment. Heat tolerance of active Norway spruce determined for the seedling top as a whole should logically be close to that of active European larch.

Estimates of tolerance to applied heat determined from the general heating of seedling tops were less than those determined by locally-applied heat. Similarly, the differences between species were less. These relationships probably arise from the test material being unable to dissipate heat in the heating chamber and the possible additive effect of desiccation. Also, in the local application of heat, bark thickness must be considered. Temperatures given are those applied externally to stems having bark less than 1 mm thick, but even this thickness (contrary to a previous statement, Kayll, 1963) will reduce the temperature achieved at the cambium, particularly for short durations. The effect cannot be large, however, because American beech, with its thin bark ($<0.5$ mm) reacted in the same range of temperature-durations as did the other species.

Heating apparently stimulated physiological processes in the two larch species and caused the prolific production of primary needles on the central stem. The stimulation seemed to affect the plant as a whole rather than only a part, because in the few instances where the lowermost stems and needles on a treated plant were not subjected to heat, they also grew more profusely. These effects have probably little importance or use in considerations of seedling or mature crown heat tolerance, but could possibly cause malformations in growth and development.

Critical temperatures and their durations influencing plant survival on exposed sites will be those which occur when the plant is most susceptible to heat damage, i.e. when it is actively growing. In this case, the lower tolerances determined in the application of heat to seedling shoots as a whole must be considered. Survival of a tree's crown over prescribed fire is more controllable in that the time of burning can be selected to take advantage of the higher heat tolerance of dormant material. Furthermore, since the temperature of the heated air above a fire fluctuates rapidly, heat is soon dissipated, and the greater heat tolerance indicated from the local application of heat to stems can be utilized as the critical limit.

Ensuing studies should establish definite relationships between tolerance of seedlings to applied heat determined in the laboratory and tolerance to heat of crowns of mature trees subjected to prescribed fire. By incorporating knowledge of the factors governing the intensity of prescribed fire and temperatures produced in the overstory crown, effective and efficient management prescriptions can be developed. It seems most likely that the greater heat tolerance of dormant than of active material can be utilized in burning prescriptions. It is less likely that advantage can be taken of the smaller differences in heat tolerance between species since sufficiently precise control of prescribed fire is not practicable.

## SUMMARY

Heat tolerance of physiologically active and dormant tree seedlings was determined by applying controlled-temperature air for specified durations to restricted areas on seedling stems, and by putting whole seedling tops in a hot air shroud. Subjective evaluations of dormancy and activity were supplemented by estimates of relative turgidity, dormant material having a low relative turgidity and vice versa. Dormant seedlings were generally 30 to 35°C more

## Appendix

*Combinations of air temperature, °C and duration causing mortality in 50 per cent of tests.*

A. Local application of heat to seedling stems.

| Test Material | Duration, minutes :15 | :30 | :45 | 1:00 | 1:30 | 2:00 | 3:00 | 4:00 | 5:00 | 6:00 | 8:00 | 10:00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dormant: | | | | | | | | | | | | |
| Norway spruce | 117 | 114 | 111 | 108 | 100 | 95 | 85 | — | 75 | — | — | — |
| Japanese larch | >117 | 111 | 102 | 93 | 85 | 82 | 80 | — | 76 | — | — | — |
| European larch | <105 | <105 | < 93 | < 93 | < 87 | <76 | <76 | — | <76 | — | — | — |
| Average | 113 | 110 | 102 | 98 | 90 | 84 | 80 | — | 75 | | | |
| Active: | | | | | | | | | | | | |
| Norway spruce | > 82 | > 82 | 78 | 78 | 76 | 75 | 64 | — | 62 | — | — | — |
| Japanese larch | 80 | 78 | 68 | 70 | 68 | 62 | 54 | — | 52 | — | — | — |
| European larch | 80 | 70 | < 64 | < 64 | < 58 | <58 | <58 | — | <58 | — | — | — |
| American beech '64 | > 70 | 70 | 70 | 60 | — | 55 | 53 | 52 | — | 50 | 52 | 47 |
| American beech '65 | > 70 | 67 | 70 | 62 | — | 60 | 60 | 58 | — | 56 | 50 | 50 |
| Scots pine | — | — | — | — | — | 55 | — | — | — | — | — | — |
| Eastern white pine | > 70 | 65 | 60 | 60 | — | 60 | 53 | 55 | — | 55 | 52 | 52 |
| Average | 75 | 72 | 68 | 65 | 67 | 60 | 57 | 55 | 57 | 53 | 51 | 49 |

B. General application of heat to seedling tops.

| | 1:00 | 1:30 | 2:00 | 2:30 | 3:00 | 3:30 |
|---|---|---|---|---|---|---|
| Dormant: | | | | | | |
| Norway spruce | 65 | 58 | 57 | 56 | 55 | 55 |
| Japanese larch | 59 | 56 | 55 | 54 | 54 | 53 |
| European larch | 55 | 54 | 53 | 53 | 52 | 52 |
| Active: | | | | | | |
| Norway spruce | — | — | — | — | 62 | 55 |
| European larch | 52 | 50 | 49 | 48 | 48 | 47 |

heat tolerant for the same exposure time than active seedlings; Norway spruce was more heat tolerant than Japanese and European larch, which in turn were more tolerant than American beech, eastern white pine and Scots pine.

Using an estimate of 50 percent mortality on an individual test basis, temperature tolerances for 1 minute durations determined by the local application of heat to stems were: dormant Norway spruce 108°C, dormant Japanese and European larch 93°C, active Norway spruce 78°C, active Japanese larch 70°C, active European larch, 64°C, and active American beech and eastern white pine about 62°C. When whole seedling tops were heated, the limits were much lower, ranging from 65 down to 52°C.

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