EFFECTS OF SOIL TEMPERATURE ON TREE SEEDLING GROWTH IN CONTROLLED ENVIRONMENTS

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RONALD LEE HENINGER

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presented by

Ronald Lee Heninger

has been accepted towards fulfillment
of the requirements for

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Major professor

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ABSTRACT

EFFECTS OF SOIL TEMPERATURE
ON TREE SEEDLING GROWTH IN CONTROLLED
ENVIRONMENTS

By

Ronald Lee Heninger

The effect of soil temperature on shoot and root development was examined for white spruce (Picea glauca (Monench) Voss), jack pine (Pinus banksiana Lamb.), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), paper birch (Betula papyrifera Marsh.), tree-of-heaven (Ailanthus altissima (Mill.) Swingle), and Siberian elm (Ulmus pumila L.). Seedlings were raised in controlled environment chambers in which soil temperatures were controlled by immersing large (40 x 4.7 cm) glass cylindrical containers in constant-temperature water baths. Soil temperature parameters were 15°, 19°, 23°, 27°, and 31°C (±0.1°C) with soil moisture at or near field capacity. Other environmental factors were held constant at levels which simulate natural conditions and have been previously reported in the literature as providing good growth. Air temperature was held constant, day and night, at 22°C at the surface of the tubes. Relative humidity ranged between 60 and 70 percent. Day length was 14 hours with illumination at the surface of the plants between 4100 and 5000 ft-c. The soil was treated with Captan solution to control damping-off disease and a complete nutrient solution was applied as needed to the plants.

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Seedlings were raised from seed of known origin in two stages: (1) they were germinated and grown for the first two weeks in a small growth chamber without control of soil temperature, and (2) transferred to the large chamber where soil temperature was controlled by immersion in a constant-temperature water bath for the remaining six weeks. The test soil was a Kalamazoo loamy sand (Ap horizon) collected from a forest nursery on the campus.

Water baths were constructed of exterior plywood with inside dimensions of 110 x 76 x 42 cm. The exterior was insulated with a 2 cm thick Styrafoam panel.

Temperature was controlled by a thermoregulator, with a sensitivity of 0.01°C, connected to a electronic relay. This arrangement maintained water temperature to within ±0.1°C and soil temperature was in equilibrium with the water temperature.

At the end of the 8 week growing period the soil was carefully washed from the roots. Measurements were made on (1) shoots: height, diameter, and dry weight; (2) roots: tap root penetration, maximum depth, lateral extension, volume, mycorrhizae, and dry weights; and (3) weekly heights and diameters. Since soil temperature was the only criterion for classifying the data, a one-way analysis of variance was used to analyze the data by species. Duncan's multiple range test was utilized to determine which soil temperature range was most significant.

Soil temperature had a pronounced effect of seedling growth. All species showed a significant effect of soil temperature on shoot and root growth. White spruce, jack pine and tree-of-heaven showed a single optimum soil temperature for both shoot and root development. White spruce and t

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spruce and tree-of-heaven had optimal growth at 19°C soil temperature. Jack pine growth was optimum at 27°C soil temperature. Douglas-fir and paper birch showed good development over a range of soil temperatures. Douglas-fir seedlings responded similarly to soil temperatures between 15° and 27°C. Paper birch grew well between soil temperatures of 19° and 31°C. Best shoot development occurred at the 31°C soil temperature, while root development was favored at 23°C soil temperature. Siberian elm growth was slightly better at the higher soil temperature, 27°C.

Results of the one-way analysis of variance show conclusively that soil temperatures have a significant affect on the development of seedlings grown in containers. Significant differences were shown for almost every measured parameter.

Results from this study may be helpful in designing future semi-controlled greenhouse parameters for raising planting stock in containers. The data presented suggests that seedlings of these test species had good shoot and root development between 19° and 23°C soil temperature. Therefore, in general, a soil temperature range between 19° and 23°C would be recommended for growing various forest tree seedlings in controlled environments.

Seedlings raised in this study, 8 weeks of age, compare favorably to one-year-old seedlings raised in conventional forest nurseries. Thus, with intensive culture, one year's biomass was produced in 8 weeks.

EFFECTS OF SOIL TEMPERATURE
ON TREE SEEDLING GROWTH IN CONTROLLED
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By

Ronald Lee Heninger

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CHAPTER I

INTRODUCTION

Growing tree seedlings in nursery seed beds for bare rooted field planting may be partially phased out of forestry practice. There is already some reorientation in the temperate regions by public agencies and private nurseries toward the production of planting stock in containers grown under controlled or semi-controlled environments.

The use of plastic greenhouses has already resulted in increased seed germination, seedling survival, growth rates and shortened rotation cycles (Arnott, 1971; and Uhorskai, 1970). Thus the use of containerized planting systems will reduce the acreages necessary to produce the number of seedlings required for planting in any one season. This procedure will bring about reduced labor and mechanical equipment needs in the production of seedlings for afforestation and reforestation (Scarratt, 1972).

A major problem in the use of container grown seedlings is the need to provide for adequate root development (Harris, 1968; and White and Schneider, 1972). Ideally, the root system should have developed to the point where good soil-root contact is made at the time of outplanting. Without proper root development subsequent survival and growth may be hampered.

There are many climatic and edaphic factors which may influence root development. Environmental effects on root development have been indirectly measured by a direct measure of the above-ground parameters.

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The amount of shoot growth is considered to be a good indication of how well the plant is adapted to the growing medium and therefore measures the efficiency of the root system in assimilating nutrients and water.

Of the environmental factors, soil temperature has generally been overlooked in studies of plant development, partly because of the difficulty in controlling soil temperature and evaluating its effects. However, with the development of controlled-temperature greenhouses and plant growth chambers, it becomes feasible to study these effects and possibly to separate the temperature effect from the effects of other environmental factors.

In most pot and greenhouse studies the soil temperature comes to equilibrium with the ambient air temperature. However, in nature only the surface few millimeters of the soil are in equilibrium with the surrounding air. This problem can easily be overcome by immersing pots in a constant-temperature water bath so that the relationship between soil temperature and other environmental factors and plant growth can be investigated.

The objective of this study is to examine the effects of soil temperature on the growth of several conifers and hardwoods, while holding other environmental parameters constant in a controlled environmental chamber.

The results obtained should prove helpful in providing soil temperature regimes for the production of container grown planting stock.

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CHAPTER II

LITERATURE REVIEW

This review is primarily concerned with the growing of tree seedlings in controlled environments with special emphasis on finding optimum temperature for growth. Since temperature affects many aspects of plant growth, attention has also been given to temperature as it effects physiological processes in the root system.

Nielsen and Humphries (1966) in an excellent review have summarized much of the information on soil temperature as it relates to agricultural crops. Walker (1969) has designed a very sophisticated chamber for determining optimum soil temperatures and root behavior of maize seedlings. Richards, Hagen and McCalla (1952) summarize knowledge on soil temperature as a biological factor. Detailed reviews on special phases include one on resistance to extreme temperatures by Levitt (1972).

Hellmers (1962) was the first researcher to really attack the problem from the tree species point-of-view and synthesizes the findings in several of the important earlier papers.

Temperature and Root Development

The factors determining whether or not a root will grow, and thus how a root system will develop, are complex and involve genetic and environmental interactions. The view has been expressed that heredity determines the type of root system tree seedlings will have (Sutton, 1969). However, the great variability in root form within species points to the

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to the strong influence of the environment (Fraser and Gardiner, 1967, and Merritt, 1968).

Various combinations of soil factors have been suggested as being important in determining root behavior of trees (Bilan, 1968), but in general it is difficult to improve on the views of Goff (1877, cited by Lutz et al., 1937): "... a certain degree of warmth, moisture, and oxygen are indispenable to the development of roots, and ... when these are present, the rapidity of growth and the number of branches are dependent upon the amount of available plant food". Other important factors involved in the environmental control of root growth include: soil texture (Biswell, 1935), soil structure, soil depth, soil fauna and flora, nursery and planting treatments and influence acting on aerial parts of the plant. Romberger (1963), summing up the present position, noted the general agreement that root growth is inhibited by soil temperatures that are too high or too low, by water stress, or by oxygen deficiency in the root zone. He concluded that very little is known about endogenous control of root growth when environmental factors in the root zone are not limiting.

Observations and studies to determine temperature effects on plant growth have been conducted for hundreds of years. Temperature is an important environmental factor in tree growth, but relatively few common management practices can affect temperature. Temperature has always been a difficult factor to evaluate because it has an indirect effect on growth through its influence upon practically every other factor that affects growth directly (Hellmers, 1962; Kramer and Kozlowski, 1960; Nielsen and Humphries, 1966; Went, 1943, 1953 and 1957).

Soil temperature is correlated with other environmental factors and its effects are not easy to distinguish in the field. However, during the last

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the last decade, attempts have been made to assess its effects, independently of air temperature, on tree growth and to apply the results in the field.

Determination of the temperature requirements of different species for maximum tree growth is one of the problem areas. Obviously, information on optimum temperatures can be obtained only from trees grown under controlled temperature conditions (Hellmers, 1967 and Went, 1957). Field studies of forest vegetation have contributed little to the knowledge of this subject because, in the field, as temperature approaches the optimum other factors may gradually become limiting and there is no sharp change in the growth pattern.

Bilan (1966) investigated the effect of low temperature on root elongation in loblolly pine (Pinus taeda L.) seedlings. He found that low temperature is a limiting factor in root growth during the dormant season. Both number of growing root tips and rate of root elongation diminished gradually with decreasing minimum temperatures down to 1.7°C.

While low temperature is a limiting factor in the dormant season, Krugman and Stone (1966) concluded that seedlings of ponderosa pine (Pinus ponderosa Laws.) required cold nights (6°C) as a prerequisite for high root regenerating potential during the growing season.

Leibundgut and Dafis (1964) investigated the effect of soil temperature on the growth of Scots (Pinus sylvestris L.) and Austrian pine (Pinus nigra Arnold). They concluded that the threshold temperature for root growth was equal to 12°C and that root growth commenced 16 to 18 days before shoot growth. Root growth was closely related to soil temperature throughout the growing season. Straub (1966) found similar results for aspen (Populus) seedlings whereby shoot growth lagged 5 to

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19 days behind root growth. However, total root growth appeared to be related to shoot development which varied with temperature and photoperiod.

Lavarenne (1968) states that root growth of English white oak (Q. robur) grown in a controlled environmental chamber from May to August was regular and continuous, whereas that of shoots was rhythmic.

Root growth of forest tree species during the dormant season is of great importance in the practice of forestry. Field planting of seedlings is recommended during those periods of the dormant season which would assure adequate root regeneration before the commencement of shoot growth and increased transpiration.

Water and Mineral Nutrition - Temperature Interaction

Uptake of water and nutrients by plants is affected by soil temperature. Entry of water into plant roots is a passive process. Experimental results show that diffusion of labelled water into plant tissue follows Fick's second law of diffusion, whereby water apparently diffuses equally well throughout all the tissues, both the apoplast and the symplast (Salisbury and Ross, 1969).

Kramer (1940 and 1969) concluded that "the principal cause of reduced intake of water by transpiring plants in cold soils is the physical effect of increased resistance to water movement across the living cells of the root". He suggested that the additive effects of temperature on viscosity of water and permeability of protoplasm decreased uptake of water at 5°C to a quarter of that at 25°C. He concluded that species differ in the reaction of their protoplasm to low temperature. Tree species vary greatly in their ability to take up water at

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water at low soil temperatures, white pine (Pinus strobus L.), for instance, being much more efficient in this regard than loblolly pine (Kramer, 1942; and Kozlowski, 1943). Kozlowski (1955) suggested that such species differences may be significant in determining their natural ranges.

In ponderosa pine seedling grown under controlled conditions, soil temperature and moisture accounted for most of the variation in root growth (Stone, 1967). Greatest root growth occurred when soil was watered to field capacity for all temperature treatments.

Miller (1970) working with jack pine (Pinus banksiana Lamb.) found that the influence of temperature was most pronounced when soil water was not limiting. The soil moisture X temperature interaction was highly significant for every growth parameter measured. Growth response differences were greatly diminished when seedlings were subjected to soil water stress.

Soil temperature can affect the mineral nutrition of plants by changing the concentration of soluble nutrients in the soil, or affecting the ability of the plant to absorb and use nutrients. Uptake of ions depends on energy supplied by the oxidation of carbohydrates and this process is retarded in cold soils. Entry of ions into the free space (intercellular space) is not temperature-dependent because it takes place largely by diffusion. Bowen (1970) working with Pinus radiata D. Don found that increasing soil temperature from 15° to 25°C approximately doubled phosphorus uptake. This was primarily due to the increase in length and number of lateral roots. Therefore, when soil temperature restricts growth of roots it will restrict the absorption of nutrients.

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Meyer and Tukey (1967) examined Forsythia intermedia and Taxus media under various root temperatures and varing nutrient applications during the dormant season. Roots of both species grew appreciably while the above-ground parts were dormant. Fertilizer applied to roots during dormant season increased the nutrient content of the above-ground parts of dormant plants. Good and Tukey (1969) in their experiment with Ligustrum ibolium and Euonymus alatus found that radioactive phosphorus was absorbed by the roots and translocated to the dormant shoots at all three temperatures tested: 1.7°, 7.2° and 12.8°C. Thus, in temperate regions fall applications of mineral nutrients during the dormant season have advantages over spring applications because plants can absorb these in preparation for the spring flush of growth. Ashby (1960) found that uptake of phosphorus and potassium by American basswood (Tilia americana L.) was greatest per unit plant dry weight at the lowest root temperature studied, 10°C.

Temperature affects ion uptake and transport through the plant similarly because both are energy-dependent processes, and are much slower at lower temperatures. Slowing down translocation may have a two-fold effect; it may decrease the transport of minerals to the shoot and it may also prevent or retard carbohydrates from reaching the root system where it is essential for continued root growth and for absorption of nutrients (Nielsen and Humphries, 1966). Thus, the root system is a sink for carbohydrate; and its growth is regulated to a large degree by the activity of the assimilatory system. Because the root depends on the shoot for carbohydrate, and the shoot depends on the root for water and mineral nutrients, the growth of both is closely integrated.

The rate of chemical reactions in the soil, such as the equilibrium exchangeable and non-exchangeable forms of potassium, is approx

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approximately doubled with every 10°C rise in temperature. Nutrients such as N, P, S, and Ca in soil organic matter are released when temperature favors microbial decomposition.

Soil temperature is particularly important for newly planted stock. Trees planted into cold soil in the spring may transpire far more water than they are able to take up, particularly if the soil is also poorly aerated. New roots do not develop, and old roots do not function effectively. Subsequent recovery is further jeopardized because of the associated inadequacy of mineral uptake.

Light - Temperature Interaction

There is evidence that at higher light intensities optimum temperatures for growth are higher (Brix, 1967). For Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with light intensities of 450 and 1000 foot-candles the temperature for maximum net photosynthesis was 10° and 20°C respectively.

Increased light energy brought about increased rate of root elongation which in turn increased the rate at which water became available to the roots of ponderosa pine (Stone, 1967). Barney (1951) found that 120 to 295 ft-c was the threshold intensity required for growth of loblolly pine seedlings and that growth increased with an increase in light intensity up to 5330 ft-c which gave the best average root growth. It is important to remember that the application of growth chamber results at low light intensities to greenhouse and field conditions under natural sunlight may give different results.

The effect of photoperiod on plant growth is widely known (Downs, 1962). The effect of temperature and photoperiod on loblolly pine has

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been reviewed by Kramer (1957). Manipulation of light and temperature can also induce seedling dormancy and develop cold hardiness before outplanting. Whether this is necessary or not depends on the what, where and when of planting. Blue spruce (Picea pungens Engelm.) and ponderosa pine can be hardened by 6 weeks of short photoperiod at growing temperatures followed by 6 weeks of short photoperiod plus 0° to 5°C temperature (Tinus, 1970).

Light provides energy for photosynthesis, and trees differ in their ability to utilize light. At low light intensities more light means more photosynthesis which means increased growth. A point is reached at which an increase in light intensity doesn't result in increased photosynthesis; the tree is "light-saturated". There is no value in providing additional light if a plant is light-saturated, in fact it may result in chlorophyll breakdown (Ronco, 1970).

Root Maturation - Soil Temperature Interaction

Soil temperature also affects rate of root maturation. Relatively low temperatures retard growth and maturation, whereas relatively high temperatures accelerate both processes, also roots grown at low temperatures appear "typically white, succulent, and relatively large in diameter, with few scattered laterals" (Richards, Hogan and McCalla, 1952). Barney (1947), however, found that root tips of loblolly pine seedlings differed very little in appearance whether developed at 5° or 30°C.

The optimum root temperature may differ with stage of development, e.g., optimum root temperature may change as the plant ages. This has been found to be true for several agricultural crops (oats, turnips, peas, and barley; Nielsen and Humphries, 1966) but has not been examined to any extent in woody species.

Methods of Soil Temperature Studies

The various facets of temperature important to plant growth include: day, night, summer, and winter temperature of both soil and air. Temperature differences between day and night also can be a controlling factor in tree growth.

Growth occurs over a wide range of temperatures and somewhere within this range there are temperature conditions which promote optimum growth. However, growth *per se* is a complex process and the optimum temperature condition need not, and probably does not, coincide with the optimum for all or any of the component processes that together produce growth. The relationship between root temperature and shoot growth is also complex, and precise experiments in controlled environments are necessary to analyse the interactions between the important environmental variables like radiation, temperature and mineral nutrition. These environmental factors also affect the basic physiological and biochemical processes which are very important to growth and development.

Controlled environments have been used to study various phases of tree physiology since the seventeenth century when Van Helmont first grew a willow tree in a pot and measured the amount of material removed from the soil. However, it was not until 1949 that Went, at the Earhart Plant Research Laboratory, was able to examine the non-lethal effects of temperature on entire woody plants such as tree seedlings (Went, 1957). In the growth of plants there are three cardinal temperature points. These are the lethal maximum temperature, the lethal minimum temperature, and the optimum temperature.

The maximum and minimum cardinal points of temperature for seedling survival have been extensively studied, (Kramer and Kozlowski, 1960). One significant unsolved problem in this area is how plants develop resistance mechanisms to hot and freezing temperatures (Levitt, 1972).

Few field trials have been conducted on the effects of soil temperature and plant response. Stephens (1965a) looked at the effects of nitrogen, soil temperature and soil moisture on the height growth of white spruce (Picea glauca (Monench.) Voss) seedlings. Soil temperature and moisture were regulated by choice of mulch or living ground cover. Soil temperature alone had little effect on height growth. However, a significant interaction between soil temperature and soil moisture was found. The cool-moist treatment favored the most growth. No actual temperature measurements were reported.

Height growth of one-year-old yellow poplar (Liriodendron tulipifera L.) seedlings increased with soil temperature and moisture during the first growing season after transplanting (Stephens, 1965b). Mulches were again used to both reduce evaporation and warm or cool the soil in comparison to bare uncovered soil. A highly significant positive regression equation was calculated for height growth upon soil temperatures up to 36°C.

Bilan (1960) tried to improve the root development of loblolly pine seedlings under various cover and light conditions. He reported that in protected plots (mulch, sod, or shaded) more than half of the root growth was in the uppermost 8-cm soil layer, and over 70 percent of root weight was in the top 15-cm layer. This may have been the result of improved moisture conditions and reduced temperature extremes. Root length of laterals was also increased on the protected plots.

O. Rlov (1967) investigated Scots pine in four pine forest types. In the Pinetum-Myrtillosum type the duration of root growth is determined mainly by soil temperature. In the wetter Pinetum-Polytrichosum and two Pine-Sphagnum types the duration of root growth is determined almost exclusively by soil aeration.

Lyford and Wilson (1966) have developed a "rhizotron" which can be located in the forest itself to allow the study of roots attached to mature trees. The rhizotron consists of a shed-like building built over a bulldozed trench. Roots are severed with a clean cut and wrapped with moist soil, and the soil, in turn, is wrapped in aluminum foil or plastic sheeting to prevent drying. New tips develop from the woody root within 2-3 weeks. These new roots are placed in a tray with moist soil for observation, measurement, or experiment. Their preliminary observations suggest that the red maple (Acer rubrum L.) root habit is fairly consistent over a broad range of soil texture and fertility if the soil is maintained at near optimum moisture conditions. Soil temperature, controlled by electric space heaters, had a pronounced effect on root growth rates. Roots in unheated trays showed day-to-day variation in temperature and growth rate that closely paralleled the variation in daily mean outside air temperature. Roots in trays with controlled temperatures grew at essentially constant rates, independent of outside air temperature. Roots grew faster as the temperature was increased up to 25°C. The optimum temperature for root growth in the trays seemed to be about 12° to 15°C. Advantages of this technique are that tree roots may be produced year around, at will, by using a modification of a naturally occurring process, and these roots seem to grow at a normal rate and with a normal habit.

Several studies on soil surface temperatures of cutover lands (Hallin, 1968; Hermann, 1963) have related temperature regimes to harvesting and various planting techniques. Thermal properties and surface temperatures of seedbeds were examined by Cochran (1969). Heat flux density and the thermal properties of the soil controlled soil surface temperature variation. Slope, aspect, shade, water content, evaporation rates, wind, surface roughness and color all influenced either the soil heat flux density, the thermal properties, or both. The studies prompted Stone and Norberg (1971) to suggest that agricultural engineers help in designing seedbeds and equipment to control temperatures for improved root growth capacity. Soil temperature controlling systems are now being developed as an important needed improvement in forest nursery practice.

Growing Tree Seedlings in Controlled Environments

Maximum tree growth is often achieved when root and shoot temperatures are different. In most controlled environment studies, root and shoot temperatures were approximately the same. Therefore, the influence of root temperature on the growth of the whole plant could not be easily assessed. Furthermore, in actual field situations the temperature of roots, except those very near the surface, fluctuates less than the temperature of the shoots. Therefore, results from pot and field experiments are often difficult to reconcile because root temperatures in pots are likely to rise much above those in the field. In general, the optimum temperature for root growth is less than for tops (Nielsen and Humphries, 1966) and roots tolerate a narrower temperature range than shoots. More precise control of soil temperature in pots has been obtained by immersing the pot in a controlled-temperature water bath (Steinbrenner and Rediske, 1964).

Trees respond to temperatures in a variety of ways. Published reports can be grouped into five general categories of situations in which temperatures may influence the growth of tree seedlings under controlled environmental conditions. These are:

Controlling Factors of Growth

Day-Night Air Temperature Differential

Daily Air Temperatures

Night Air Temperatures

Daily Heat Sun

Soil-Air Temperature Differential

Frequently the day-night temperature differential is most important (Table 1).

Table 1. Day-night temperature differentials were the most influential in growing tree seedlings under controlled environments.

Species	Best Day Temperature	Best Night Temperature	Authority
Loblolly pine	30°C	17°C	Kramer (1957)
	23	7	Hellmers (1962)
Red fir	17	4	Hellmers (1966b)
Coastal redwood	19	15	Hellmers (1966a)
Douglas-fir	17	7	Hellmers and Sundahl (1959)
Blue spruce	19	16	Tinus (1971)
Northern red oak	30	17	Kramer (1958)

Day air temperature was influential in growing some tree seedlings in controlled environments (Table 2).

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Table 2. Day temperature was the most important factor in the growth of tree seedlings under controlled conditions.

Species	Best Day Temperature	Nighttime Range	Authority
Ponderosa pine	25°c	13-25°C	Tinus (1971)
	23	7-31	Larson (1967)
Red pine	20	10-30	Kozlowski (1968)
Redwood	23	7-23	Hellmers and Sundahl (1959)
Douglas-fir	24	8-28	Brix (1971)
Western hemlock	18	8-28	Brix (1971)
Norway spruce	20	10-25	Dormling, et al (1968)

Conversely, in some experiments night air temperature was the most influential factor in growing tree seedlings (Table 3).

Table 3. Night air temperature was the most important factor in the growth of tree seedlings under controlled conditions.

Species	Best Night Temperature	Daytime Range	Authority
Digger pine	17°C	17-30°C	Hellmers (1962)
Ponderosa pine	25	10-25	Schubert and Baron (1965)
Engelmann spruce	23	15-35	Hellmers, et al (1970)

The daily heat sum was significant in some trials, i.e. a cool day can be compensated for by a warm night and vice versa (Table 4).

Table 4. Daily heat sum had the most influence on growth of tree seedlings, grown under controlled conditions.

Species	Best heat sum (Degree-hrs. per day)	Authority
Jeffery pine	350	Hellmers (1963)
Erectcone pine	475	Hellmers and Ashby (1958)
Eastern hemlock	500	Olson, et al (1959)
Red oak (1 yr. seedling)	580	Larson (1970)
Red and white oak (Freshly germinated seedlings)	1032	Larson (1971)

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In most of the above cited studies soil temperature did not differ from the ambient air temperature. However, except for the surface centimeter, under natural day conditions the soil temperature is generally cooler than the air above it, and at night the converse is usually true. The fifth category has taken this natural factor into account. The growth of tree seedlings in some experiments were most influenced by soil and air temperatures, Table 5.

Table 5. Soil and air temperature has most influenced the growth of these tree seedlings while grown under controlled environments.

Species	Soil Temperature	Air Temperature Day	Air Temperature Night	Authority
Ponderosa pine	21°C	28°C	18°C	Steinbrenner and Rediske (1964)
	23	15	15	Larson (1967)
Douglas-fir	21	28	18	Steinbrenner and Rediske (1964)
	20	30	--	Cleary and Waring (1969)
	20	24	24	Lavender and Overton (1972)
Red Oak	24	24	24	Larson (1970)

From these studies it is obvious great variation exists between species. It is important to note that these investigations did not include all possible temperature combinations. Only the best temperature results have been included in the tables. One may wish to interpolate these results to approach an optimum, but caution must be used because other factors (light, moisture, etc.) may become limiting.

Most of these experiments were preformed in growth chambers or greenhouses under a particular set of environmental conditions. These conditions varied for each experiment and may help to explain why a species appears in different categories. The working hypothesis also differed for these experiments, for example ponderosa pine was investigated by four researchers. Steinbrenner and Rediske (1964) studied the growth response of ponderosa pine and Douglas-fir seedlings to controlled high and low levels of: (1) air temperature, (2) humidity, (3) light intensity, (4) soil temperature, (5) soil region, (6) soil quality, (7) soil moisture and (8) soil nitrogen. The main effects of each variable was examined by the split-plot design used. The results indicate that high soil temperature (21°C) was the most effective factor in increasing root length but was less effective than high air temperature and light in increasing root weights. Therefore, high soil temperature in combination with high day and night temperature and high light intensity gave the best root development. This study helps point out the complex interaction existing between root development and the environmental factors which affect the basic physiological and biochemical processes involved in root development.

Schubert and Baron (1965) measured root responses on seedlings lifted at monthly intervals throughout the year from several forest nurseries after they were allowed to grow for one month in soil containers set in thermostatically controlled water baths maintained at 10°, 15°, 20°, and 25°C. Root growth response of transplants was greatest in number of root elongations at 20°C and highest in total length at 25°C. The best soil temperature depended on the parameter measured. The same study investigated the effects of nursery air temperature. The root productivity cycle at a nursery with warm nights differed markedly from that at a nursery with cold nights, although their daily air temperatures were similar. Therefore, differences in root response of seedlings appears to be directly related to night temperatures and not to day temperatures. A night temperature greater than 5°C and averaging 10°

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Larson (1967) designed a study to test the effect of: (1) constant air and soil temperature regimes, and (2) day and night temperature regimes on the initial development of ponderosa pine seedling from three provenances. His results indicate that roots grew best in 15°C air and 23°C soil, while height growth was best in 23°C air and soil for all seed sources.

Tinus (1971) tried to optimize light intensity, air temperature, rooting media, and nutrition as they would be used in a production greenhouse. He expanded the work done by Larson (1967) and used the same ecotype. Dry weight curves were much different, probably because of the differences in light intensity, ambient air temperature, and length of treatment. Tinus reports that optimum growth varied with the growth parameter; height growth = 25°C, caliper = 23°C, dry weight = 20°C, and that optimum night temperature was 25°C.

Each experiment was done under a specified set of environmental conditions and differed in various ways including: greenhouse versus growth chamber, potting media, light intensity, soil moisture, air and soil temperature ranges, soil fertility, length of treatment, seedlings from seed or transplants and growth parameters measured. Therefore, it is quite possible to have a species appear in several of the categories in which temperature influences the growth of seedlings.

In a similar manner, five researchers studied the effects of temperature on the growth of Douglas-fir. Experimental conditions and investigation techniques varied between them. Thus, different conclusions were reached by each investigator.

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With respect to genetic variation no evidence has been reported to show a difference in optimum temperature conditions for different seed sources of the same species (Larson, 1967). It is quite possible that such differences do exist.

Much of the experimental work on forest tree species and soil temperature effects has been conducted on conifers and little attention has been given to hardwood species. This may be because more conifers are used in reforestation in the regions where these tests have been conducted. However, Nightingale (1935) studied the effect of temperature on growth, anatomy and metabolism of apple (Malus) and peach (Prunus) roots. Studies conducted in a water bath indicate that 18°C was the optimum for both species over a temperature range of 7° to 35°C.

When growing plants in a confined area, such as a controlled environmental chamber, one should be cognizant of other factors which may influence growth. One of the most recent limitations discovered has been that under many conditions CO_2 concentrations limit photosynthesis more than does low light intensity. CO_2 is present in the atmosphere at only 320 ppm and is the source of all carbon for plants. Researchers have found that when the atmosphere is enriched with CO_2, plants show a marked increase in growth. Accordingly, horticulturists have found growth responses of 30 to 100 percent when CO_2 was present at 700 and 2000 ppm respectively in the greenhouse (Tinus, 1970). Yeatman (1970) has verified a positive growth response to CO_2 additives to the atmosphere for white spruce, Norway spruce (Picea abies (L.) Karst.), jack pine and Scotch pine. Tinus (1972) has found that quadrupling CO_2 in the greenhouse yields a 50 percent increase in dry weight or better for blue spruce and ponderosa pine. Roots increased slightly over shoots on a dry weight basis.

Important Environmental Conditions Gained from Literature and Used in Present Study

Pertinent experimental parameters derived from the literature were used in this study. In general, the soil temperature ranges chosen were similar to previous studies, except that the upper ranges were extended to bracket the optimum temperature regimes. While a 4°C interval between air temperature treatments was commonly used by other workers, it appears that soil temperature has not been examined as closely as it should be, because soil temperature was not generally separated from air temperature.

An experimental way to accurately control soil temperature is by immersing the potting container in a thermostatically controlled water bath.

The importance of light intensity, relative humidity (Steinbrenner and Rediske, 1964), soil moisture, and air temperature have been examined; however, in most cases interactions have not been adequately tested. Optimum or near optimum parameters as reported from previous studies were incorporated into the present study, i.e., high light intensity (4000 to 5000 ft-c), relative humidity (65 percent), soil moisture (field capacity, 0.1 to 0.3 atm., for coarse textured soils), and ambient air temperature (22°C).

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CHAPTER III

MATERIALS AND METHODS

This study was conducted in controlled environmental facilities of the Department of Forestry, Michigan State University.[1] Seedlings of jack pine, white spruce, Douglas-fir, tree-of-heaven, paper birch and Siberian elm were grown in large glass tubes for 8 weeks. A pilot study revealed that roots had reached the bottom of the glass container in 8 weeks; therefore, to prevent root bounding an 8 week growth period was decided upon. Seedlings were raised in two stages: (1) they were germinated and grown for the first two weeks in a small growth chamber without control of soil temperature, and (2) transferred to the large chamber where soil temperature was controlled by immersion in a constant-temperature water bath for the remaining six weeks. Ambient air conditions remained constant at 22°C while soil temperatures were varied as the principal environmental factor under study.

Glass Tube Preparation

Large glass tubes (40 cm long x 4.7 cm diameter) were selected as an adequate container for this study. These glass tubes provided good heat conduction and were watertight. A system to provide for proper soil aeration consisted of a 3 cm layer of P-gravel (2 to 5 mm diameter) at the bottom of the tube in which a hollow glass rod was inserted and

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[1] See Appendix A for physical characteristics of plant growth chambers.

extended above the tube's surface. This provided good aeration and allowed excess water to be drawn out if over watering occurred (Figure 1).

A thin layer of cheese cloth was placed between the gravel and the soil column. Tubes were weighed, filled to within one inch of the tube's surface with soil (Kalamazoo loamy sand) and reweighed. This weighing procedure permitted accurate gravimetric control of watering. Tubes were watered and allowed to dry out in order to settle the soils before seeding. A total of 72 tubes were included in each soil temperature treatment.

Soils

The soil selected was the surface horizon (Ap, 0-15 cm) of a Typic Hapludalfs (Kalamazoo series) collected from a seedbed at the Tree Research Center on the Michigan State University campus. Two weeks before soil collection, the nursery seedbed was covered with a plastic tarp and the soil was fumigated with methyl bromide. This treatment has been a standard practice in forest nurseries in controlling pathogenic organisms and weeds (Howe and Clifford, 1962; White and Potter, 1963). The soil was air-dried, rolled, and sieved through a two-mm mesh sieve prior to filling the glass tubes.

Particle size analysis was determined by the Bouyoucos Hydrometer method. Chemical analysis of the soil samples was made in the Soils Testing Lab, Crops and Soil Sciences Department, Michigan State University. The results of these analyses are outlined below:

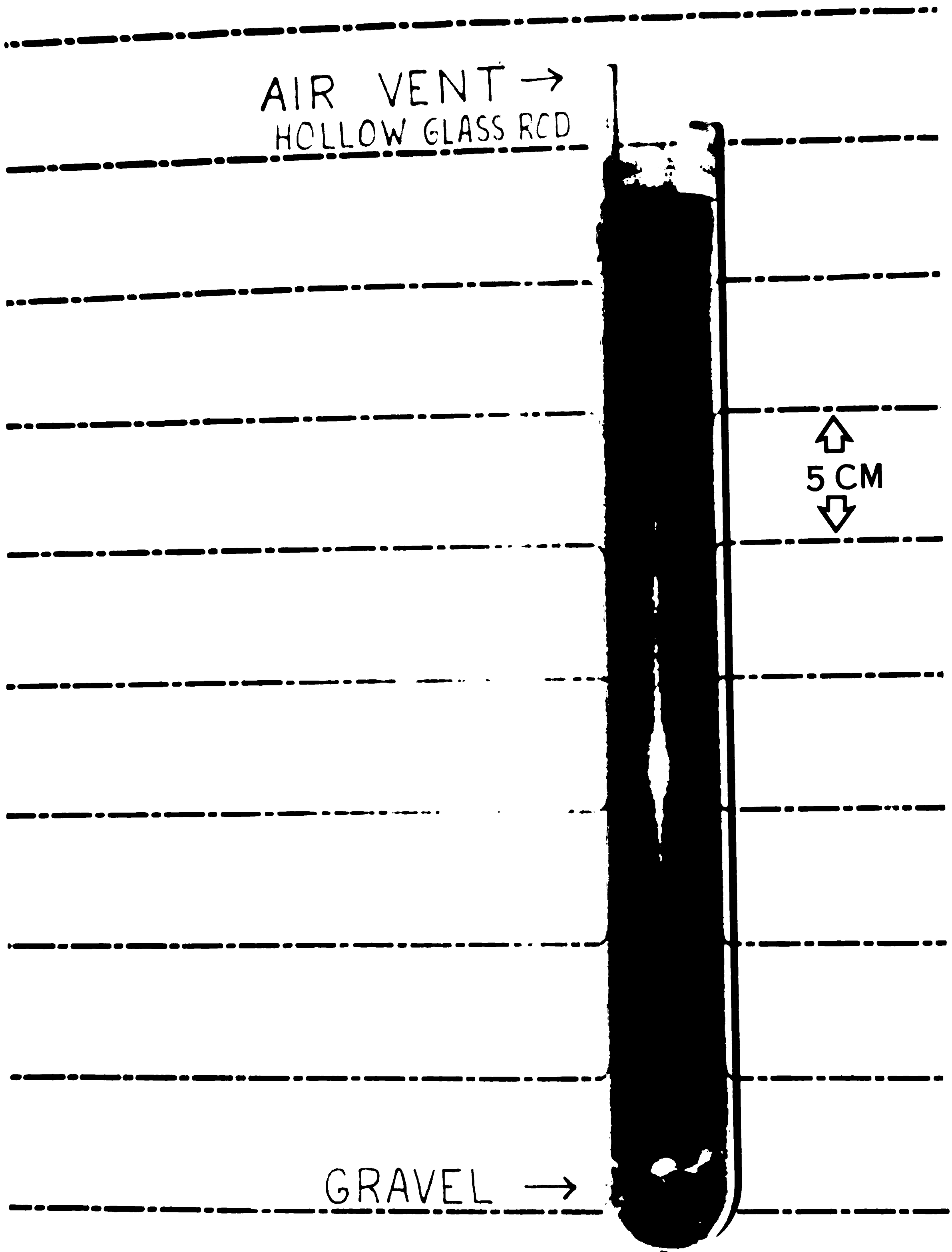

Figure 1. Glass tube (40 x 4.7 cm) used to provide a deep watertight container for growing seedlings.

Physical Properties

Sand	Silt (Percent)	Clay	Texture Class	Bulk Density (soil in tubes) gcm^{-3}
81	10	9	Loamy sand	1.38

Chemical Properties

NO_3-N	P	K (ppm)	Ca	Mg	C %	Organic* Matter %	pH
8.2	2.4	65.3	311	36.5	0.74	1.27	5.4

*O.M. = C x 1.72

Moisture holding capacity was determined for a range of tensions between field capacity and wilting point. A standard Pressure Plate Extractor (Model 1200) was used to determine moisture retention at low tensions. High tension moisture retention values were obtained with the pressure membrance apparatus. This equipment simulates the force required to extract water from the soil matrix. Soil moisture tension data are shown in Figure 2.

Field capacity of the potting soil is approximately 10 percent moisture on a weight basis (14 percent by volume). Soil moisture is not a variable in this study, but was constant for all soil temperature treatments. Stone (1967) found that greatest root growth occurred when soil was watered to field capacity. Thus, in this study soils were

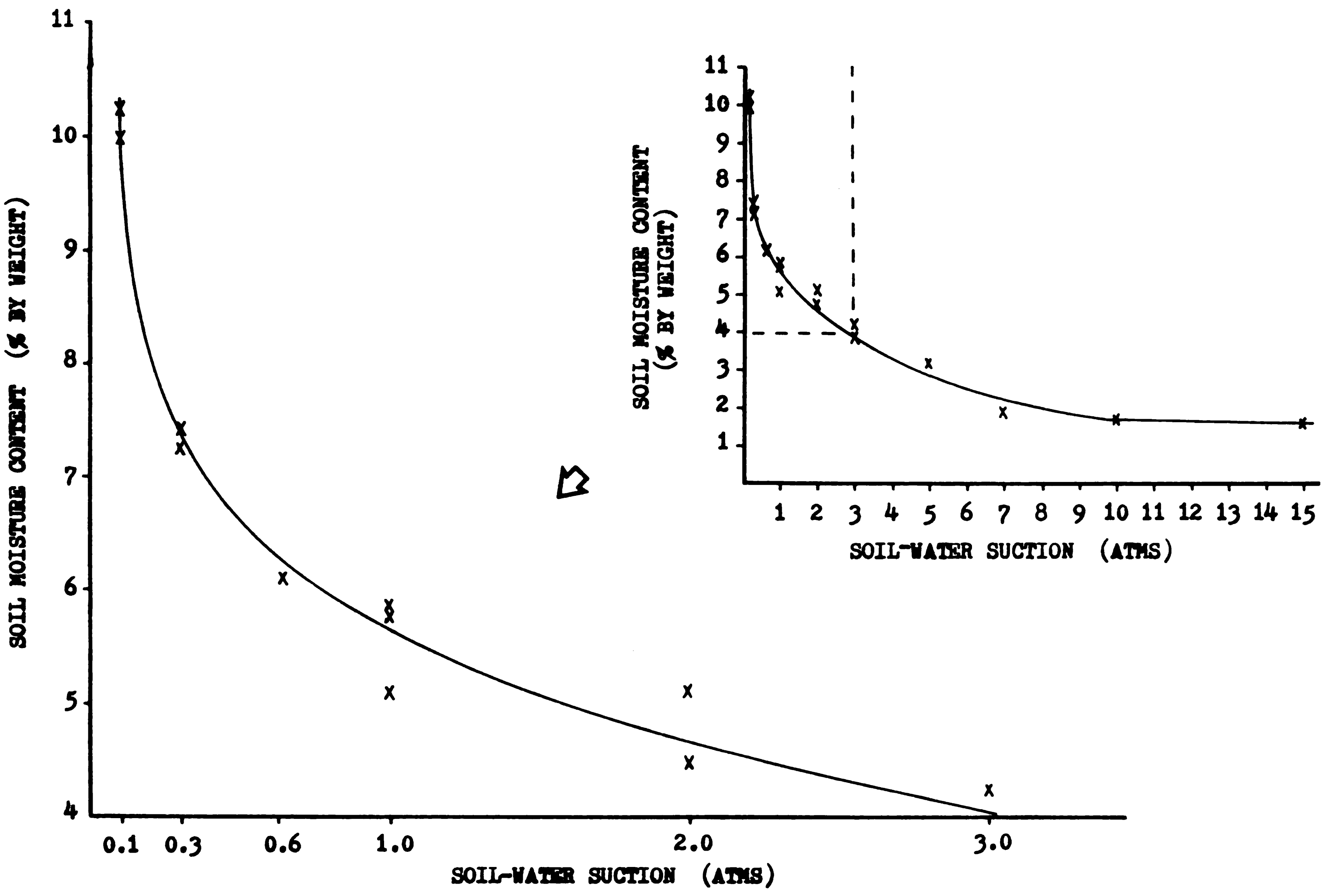

Figure 2. Soil moisture retention curves for loamy sand soil used to grow seedlings.

watered to field capacity and allowed to dry to half field capacity (5 percent moisture by weight) before rewatering. Watering was controlled by weighing the entire container on a top-loading balance until the proper weight was attained (Figure 3). Following this procedure the tubes required watering once a week in the early stages of development; however, larger plants required more frequent watering toward the end of the growing period.

Species Selection

Species were selected on the basis of their potential use in forest revegetation and the plants ability to be influenced by fluctuating environmental parameters. The conifers selected were: jack pine, white spruce and Douglas-fir. Douglas-fir has been used successfully by other authors to study the effect of soil temperatures (Brix, 1971; Hellmers and Sundahl, 1959; Larender and Overton, 1972; and Steinbrenner and Rediske, 1964). White spruce has not been investigated for the effects of soil temperature under controlled environmental conditions. However, Stephens (1965a) has examined the effect of various mulches in regulating soil temperature on the height growth of white spruce. Jack pine has been examined by Miller (1970) where soil moisture times day-night temperature interaction was highly significant for every growth parameter measured. However, in all but two of these studies soil temperature, *per se*, was not evaluated independently of air temperature.

As noted, not much research has been conducted on hardwood soil temperature relationships. Northern red oak (*Quercus rubra* L.) has been studied but since these large seeded oaks have large amounts of stored

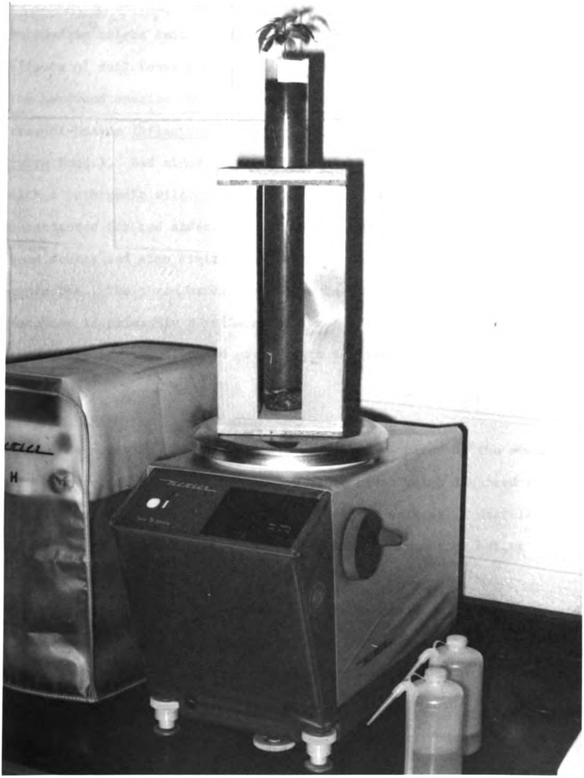

Figure 3. Soil moisture was controlled by measuring weight loss on a top-loading balance. Distilled water was added to bring weight to field capacity.

energy in the endosperm, it is hard to evaluate the effects of the environment on the seedlings produced at a young age. It was therefore, decided to select small seeded hardwoods so that the environmental effects of soil temperature could be evaluated with greater precision. The hardwood species chosen were: paper birch (Betula papyrifera Marsh.), tree-of-heaven (Ailanthus altissima (Mill.) Swingle) and red alder (Alnus rubra Bong.). Red alder, however was later dropped because of problems with a pathogenic wilt. Siberian elm (Ulmus pumila L.) was then substituted for red alder, but because of difficulties in locating a seed source and time limitations, not all test combinations were conducted. The three hardwoods tested have small seeds, and the growth response is primarily a reflection of the environmental factors under which they are grown. Seed source data is given in Appendix B.

Seeding Procedure

Germination tests run on all seed lots resulted in the sowing of six seeds of each species except for paper birch which required twelve seeds. Seeds were pretreated before sowing by soaking in distilled water for 48 hours at 4.4°C. All seeds had 80 percent or better germination.

Seeds were individually placed into each tube with a forceps and covered so that about a third of the seed coat was exposed to the surface. The tubes were then covered with a plastic film to maintain high humidity during germination.

Tubes were placed in a small controlled environmental chamber while the seeds germinated. The controlled environmental chamber was set at a constant air temperature of 22° (±1°C). Relative humidity was kept at 60 to 70 percent. The photoperiod was a 14 hour day. Illumination was kept constant during the day period at 1100 ft-c at the soil surface. As germination proceeded, dates were recorded and when seeds had germinated this was considered day number one of the 8-week growth period.

The plants remained in the controlled environmental chamber for a two week period after germination. This two week pretreatment was found necessary to insure good establishment and survival, because during a pilot study seed germination was adversely affected by the high and low soil temperature treatments. Germination at "normal" soil temperatures allowed the plants to become well adjusted before temperature treatments were applied. At the end of the second week seedlings were thinned to two plants per tube and placed in the constant-temperature water bath in the larger growth chamber.

For the balance of the growth period soil temperature effects on seedling growth were studied.

Growth Chamber and Constant-Temperature Water Bath Characteristics

The plant growth chambers used in this study are designed for precise control of temperature and humidity. These units are completely self contained (Appendix A).

The constant-temperature water baths were constructed of 1.9 cm exterior plywood with inside dimensions of 110 x 76 x 42 cm. The boards were pretreated with "Cuprinal Copex" wood preservative before assembly. All corners and joints were glued with U.S. Plywood Resorcinal Waterproof Glue (with powder catalyst) before joining with screws. After assembling they were sealed with a marine-epoxy paint. To prevent any leakage the inside was lined with a single piece of 6 mil polyethylene sheeting. The exterior was insulated with a 2-cm thick Styrafoam panel (Figure 4A). Distilled water was used to prevent lime deposits.

Temperature was controlled by a "Rota-set" thermoregulator (Lab-Line No. 3200)[2] which is adjusted by means of an external magnetic collar operating an internal revolving contact on a fine pitch thread. This thermoregulator has a sensitivity of ±0.01°C. The thermoregulator was connected to a electronic realy (Lab-Line No. 3230) which is completely transistorized with three convenience outlets on the rear panel for heating, cooling and auxiliary lines. When the power switch is in the "reverse" position the contacts close on a rise in temperature which results in the turning off of the heaters and turns the cooling cycle on via a solenoid valve until the contacts open with a drop in temperature which turns the heaters on again and the cooling water off.

The two 750-watt immersible heaters, 168 cm long, were bent into a "ox-yoke" form to provide uniform heat from the top to bottom of the water bath. Heaters ran lengthwise in the bath and were placed equal distance from the outer edge (Figure 4B).

Sixteen meters of 1.6 cm (o.d.) copper tubing was coiled around the outer edge of the water bath. This tubing was connected by rubber hose to a one-way solenoid valve (Atkomatic pilot-piston model JJ400) and a cold water tap, thus serving as a cooling coil. This arrangement maintained water temperature to within ±0.1°C of the preset test soil temperature. The heaters would heat for about 20 seconds and then shut off and allow the cold water to circulate through the copper coil for

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[2] See Appendix C for complete list of materials and addresses.

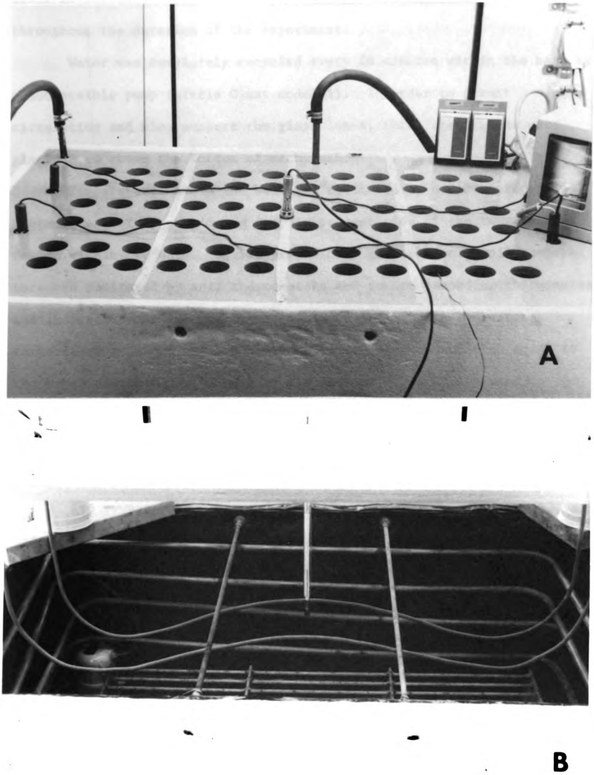

Figure 4. External and internal view of constant-temperature water bath: (A) shows Styrafoam insulation, central thermoregulator and hose attached to cooling coil; (B) internal view showing submerged pump, heaters (ox-yoke shaped), cooling coil around outer edge, and steel support rack at bottom.

about 20 seconds. This was the general cycle encountered and continued throughout the duration of the experiment.

Water was completely recycled every 20 minutes within the bath by a submersible pump (Little Giant model 1). In order to permit circulation and also support the glass tubes, three steel racks were placed 8 cm above the bottom of each bath.

Temperature within the bath was monitored by a remote recording thermometer. This provides a graphic presentation of the temperature regime within the bath. During preliminary calibrations, soil temperature was monitored by soil thermometers and remote recording thermometers, and indicated that the soil came into equilibrium with the water temperature in about one hour. The soil temperature was thus equal to the water temperature. A mercury thermometer (±0.1°C) was used to calibrate each of the temperature treatments.

Environmental Criteria

AIR TEMPERATURE. The growth chambers were programmed to give a 22°C constant day-night temperature at the surface of the tubes. Since the large water baths hampered air circulation, a 25 cm oscillating fan was placed in the chamber to promote good air circulation and maintain constant air temperature. Hygrothermograph records show that there were no significant (±0.5°C) temperature gradients within the chamber at the shoot growth zone.

RELATIVE HUMIDITY. Relative humidity is somewhat more difficult to maintain than other parameters. A high relative humidity is desirable for the growth of the species tested. In this experiment relative humidity ranged between 60 and 70 percent throughout the study.

PHOTOPERIOD. Day length was programmed at 14 hours.

LIGHT INTENSITY. Light intensity varies within most growth chambers. In the large chamber it varied from 4100 foot-candles near the edges to 5000 foot-candles in the center at the level of the plants as measured by a Weston Illumination Meter (Model 756). To adjust for this light gradient the plants were rotated every three days in two directions. Plants were moved one row up and three positions to the right.

SOIL TEMPERATURE. Soil temperature was the only independent variable in this study. This permits the main effects of soil temperature to be determined without confounding interactions. Test temperatures were: 15°, 19°, 23°, 27°, and 31°C. These temperatures were maintained to within ±0.1°C.

SOIL MOISTURE. The amount of water necessary to bring air-day soil up to field capacity (10% by weight) was predetermined for each tube. At weekly intervals the tubes were removed from the water bath, weighed, and brought up to field capacity by additions of distilled water. Larger plants near the end of the growth period required more frequent watering.

SOIL AMENDMENTS. Damping off was a problem with jack pine. In order to avoid seedling mortality the soil surface was sprayed three times a week for two weeks, with a Captan solution (0.3 grams per liter of distilled water).

The fertility status of this soil (page 25) was quite poor in the major nutrients. To correct nutrient deficiencies a complete nutrient solution[3] (3.2 grams per liter of distilled water) was applied

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[3]RX-15 (15-30-15) and RX-30 (30-10-10) plus minor elements, manufactured by Garden Research Laboratories, Ltd., Toronto, Ontario, Canada.

as needed by visual observation to the tubes. During the course of study all temperature treatments received the same volume of nutrient solution as follows:

	ml		ml
Jack pine	60	Tree-of-heaven	130
White spruce	75	Paper birch	40
Douglas-fir	45	Siberian elm	110

Measurements

A short term differential response in the growth characteristics of the seedlings under the various soil temperatures was anticipated. Accordingly, weekly measurements were made for shoot height and diameter.

At the end of the 8-week growing period the soil was carefully washed from the roots, and the shoot and root of each seedling was separated at the root collar. Seedling height was measured to the nearest 1.0 mm. Diameter was measured one centimeter up from the root collar and recorded to the nearest 0.1 mm. Dry weight to the nearest 1.0 mg were recorded after drying 48 hours at 65°C in a forced air oven.

Root lengths were recorded in three categories to the nearest 1.0 mm: tap root length, lateral extension and maximum depth. Root volumes were measured by displacement using a graduated 50 ml cylinder and a buret. Volumes were reported to the nearest 0.1 cc. The presence or absence of the characteristic mantle of ectotrophic mycorrhizae was also noted. Dry weight was measured after 48 hours at 65°C.

Analysis of Data

Data obtained from weekly measurements and final shoot and root measurements for each temperature and species were analyzed for means, standard deviations, standard error of mean and significant differences between means on the CDC 3600 computer, Michigan State University Computer Laboratory. The BASTAT routine was used with a MSD control card and this shortened the run time while giving the desired accuracy.

Since soil temperature was the only criterion for classifying the data, a one-way analysis of variance was used to analyze the data by species. The UNEQ1 routine was used for this analysis and again run on the CDC 3600 computer. This routine has several advantages in that the loss of information due to missing data is small relative to losses with other designs. This was important because in several test runs with extremes in soil temperature there was some seedling mortality. The number of degrees of freedom for estimating experimental error is maximum, which improves the precision of the experiment. The main disadvantage of the system is that the experimental error includes the entire variation among the experimental units except that due to treatments. This routine gave the following analysis of variance table:

Source of Variance	Degrees of Freedom	Mean Squares	F-Statistic
Between Categories	(T-1)	Ms Between	$\frac{\text{Ms Between}}{\text{Ms Within}}$
Within Categories	(N-T)	Ms Within	
Total	(N-1)		

T = number of treatments

N = total number of data observations

This routine will tell whether or not there are significant differences between temperature treatments, but will not tell which treatment is significantly different from another.

To determine which soil temperature treatment(s) was significantly different from another, Duncan's new multiple-range test was utilized. This test was conducted by the Computer Lab, Michigan Technological University. The Duncan test permits decisions as to which differences are significant and which are not at the 0.05 level, and uses a set of significant ranges, each range depending upon the number of means in the comparison.

CHAPTER IV

RESULTS AND DISCUSSION

The objective of this study was to examine the effect of various soil temperatures on the growth and root development of selected conifer and hardwood seedlings grown in independently controlled root and shoot environments. This research presents experimental evidence that soil temperature significantly affects the growth and development of tree seedling. Experimental results are discussed by species.

White Spruce

Root and Shoot Growth

The most constant results for shoot and root development in response to soil temperature are shown by white spruce. The best overall growth characteristics occurred at a soil temperature of 19°C. Means and standard deviations for all measured parameters are shown in Appendix E, Table 1.

Survival of white spruce was 100 percent for all temperature treatments except at the highest temperature (31°C).

Figure 5 shows the effect of soil temperatures on the measured parameters. For shoot characteristics, 19°C is the optimum soil temperature for shoot height, diameter, and dry weight. Note that shoot biomass at the 19°C soil temperature is more than twice that of the other soil temperatures.

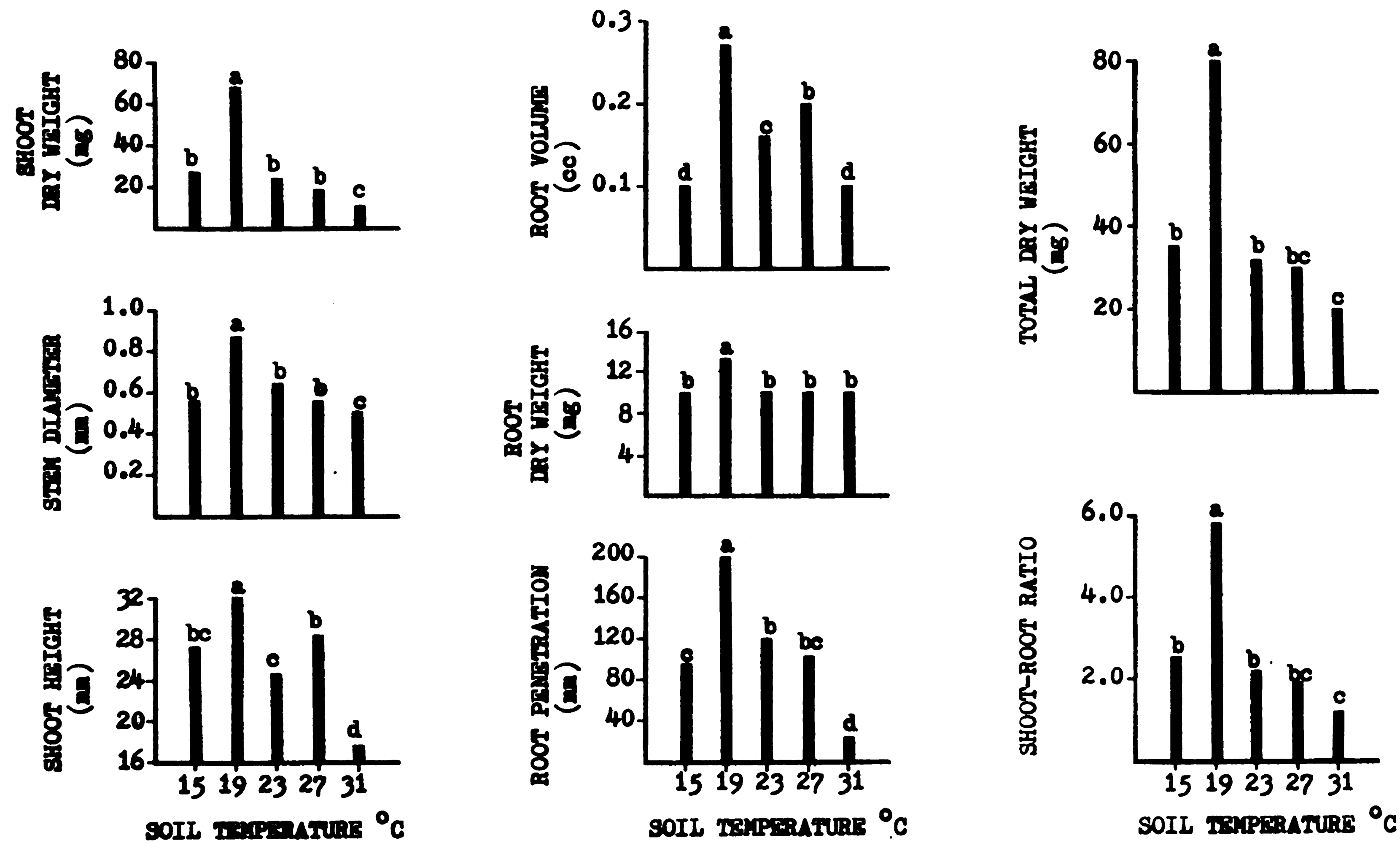


Figure 5. Effect of soil temperature on growth of 8 week old white spruce seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

Root characteristics again show that 19°C is the optimum soil temperature. Root penetration at 19°C is almost doubled that of the other test temperatures. Root dry weight was only slightly higher for the 19°C treatment. Root volumes were again optimum at 19°C soil temperature.

Total seedling biomass at the 19°C soil temperature is more than twice that of seedlings raised at other soil temperatures. The shoot-root ratio of 5.83 for the 19°C soil temperature treatment is very high in comparison to ratios of 2.72 and 2.49 for Engelmann spruce grown at optimum temperatures under controlled environments (Hellmers, et al, 1970). A range of ratios from 1.3 to 2.5 were recorded for one-year-old nursery grown white spruce in Ontario (Armson and Carman, 1961). Seedlings with a high ratio may have poor survival when outplanted because of stress placed on the small root system in assimilating moisture and nutrients.

All variables were significantly affected by soil temperatures, Appendix D. Duncan's multiple range test was utilized to tell which soil temperature treatments are significantly different. In Figure 5, those bars with the same letter are not significantly different at the 0.05 level. It can readily be seen that the 19°C soil temperature treatment is significantly different from all other treatments. Except for the abnormally high shoot-root ratio it appears that under the environmental conditions used in this study, 19°C is the optimum soil temperature for growing white spruce seedlings in containers.

Mycorrhizae

Presence or absence of the characteristics root mantle of ecto-mycorrhizae was noted when the plants were extracted from the containers.

A value of two (2) was used if the mantle was present and the value one (1) was used if there was no mantle present. White spruce seedlings showed some mycorrhizal development at all soil temperatures except for the 15°C treatment where mycorrhizae were completely absent. Mycorrhizal development was most pronounced at the 19°C treatment with an average value of 1.9. It is noteworthy that the optimum soil temperature for white spruce growth was also the best temperature for mycorrnizal development. Palmer (1971) states that the optimum temperature for the culture of mycelial growth of mycorrhizal fungi lie between 18° and 27°C for the majority of species.

Weekly Development

Height growth was measured weekly. However, all plants had an initial two week growing period where soil temperature was uniform. At the end of this initial period, plants of different test cultures were at different heights. Therefore, height was set to zero at the end of the second growing week so that these height measurements have more meaning and growth rates are easier to evaluate. Figure 6 shows the results of this data adjustment. The seedlings grown in soil at 19°C had the fastest rate of shoot growth with a slope of 1.09. The spruce plants grew at a slower rate at all other soil temperatures.

Discussion

Figure 7 shows white spruce seedlings at eight weeks of age grown at various soil temperatures. Seedlings raised at 19°C soil temperature show greatest shoot and root development.

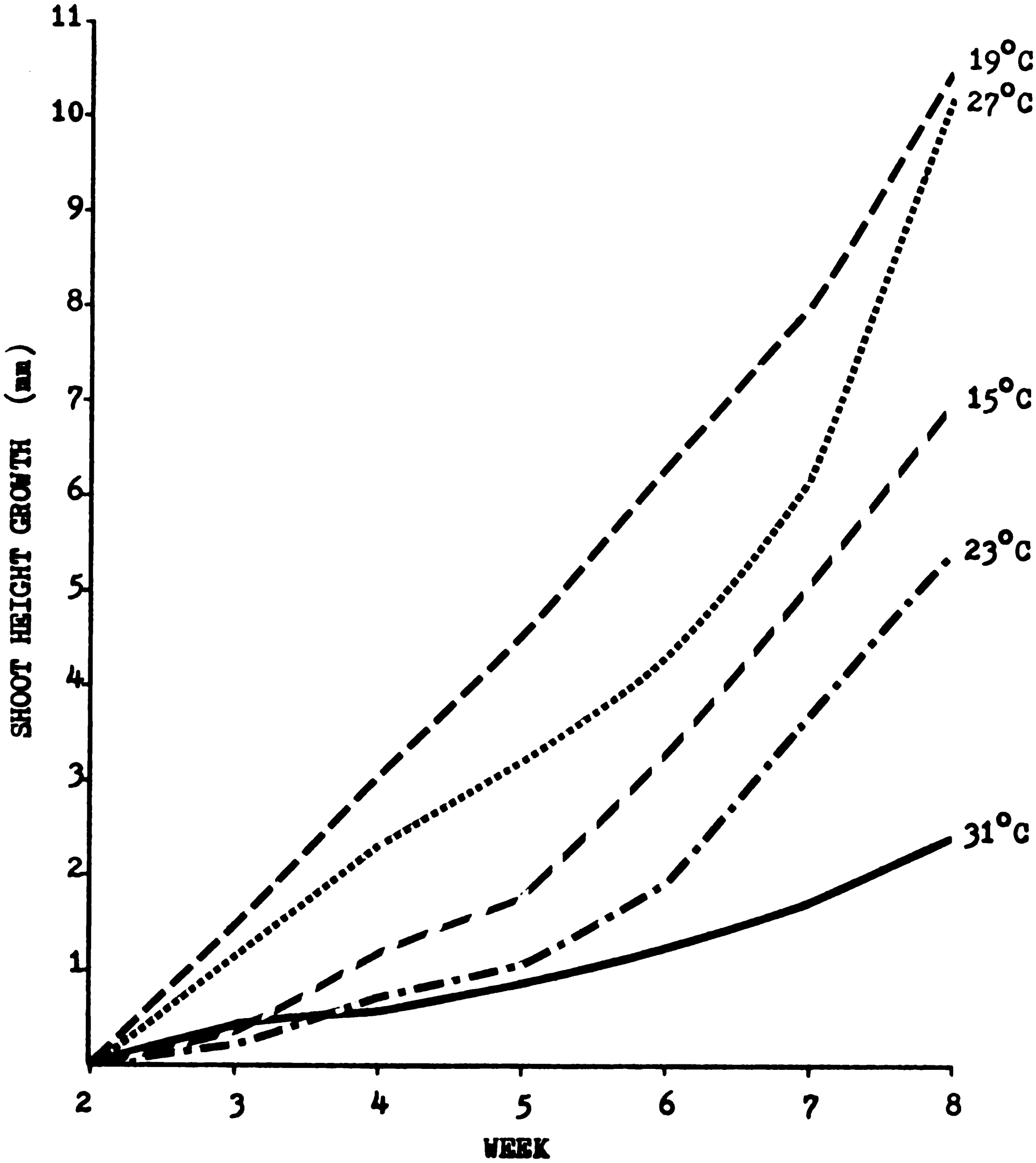
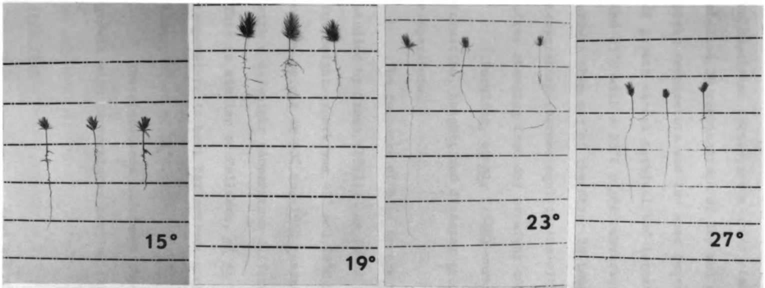


Figure 6. Weekly height growth of white spruce seedlings grown at various soil temperatures.



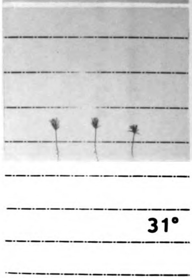


Figure 7. White spruce seedlings at 8 weeks of age grown at various soil temperatures. Seedlings are arranged (l. to r.) largest, average, and smallest to show the range in growth development that occurred at each soil temperature. Lines on photo are 5 cm apart.

As far as spruces are concerned, these results compare well with work done by others on spruces, such as Hellmers, et al (1970) research on Engelmann spruce grown under similar controlled environments. They studied 30 combinations of day and night temperatures and found that night temperature was the most important factor in increasing all aspects of growth except terminal bud formation. Day temperatures of both 19° and 23°C with a 23°C night temperature produced significantly better growth than any of the other 28 temperature combinations. Soil temperature reached equilibrium with air temperatured within one hour after changing from day or night conditions.

Dormling, et al, (1968) working with Norway spruce found that bud formation, height, and diameter growth were best under a constant 20°C temperature.

The response of blue spruce of day and night temperature was studied by Tinus (1971). He found that the optimum day-night temperature for height growth was 23° and 20°C respectively and maximum production of dry weight at 23° and 19°C respectively. Growth was slightly better with a day-night temperature differential than with constant temperatures. This is similar to Hellmers, et al (1970) work indicating a warmer night temperature is best for optimum growth. As in this study, survival was also poorest at 31°C.

Therefore, one concludes that in general spruces have optimum growth with temperatures ranging from 19° to 23°C.

Jack Pine

Root and Shoot Growth

Jack pine survival was 100 percent for soil temperature treatments of 15°, 19° and 27°C, while the 23°C treatment had only 58 percent and the 31°C treatment had 50 percent survival. An unusual bimodal growth relationship with soil temperature development in the case of jack pine (Figure 8). This bimodal growth curve is not what one would generally anticipate in nature, because as temperature increases there should be a corresponding increase in growth until the high temperature produces a detrimental effect on growth and growth rates decrease. The poor survival which occurred at 23°C treatment is most likely a result of the high incidence of damping-off fungi or some other pathogen which affected this set of plants. This may have led to this unusual bimodal relationship. Mean values and standard deviations are listed for all measured parameters in Appendix E, Table 2.

Figure 8 shows jack pine shoot and root parameters as affected by soil temperature. All measured root, shoot and biomass parameters show a maximum value at 27°C soil temperature. However a significant bimodal relationship exists at 19°C for shoot diameter, shoot dry weight, root dry weight and total seedling biomass. This seems to indicate a optimum root temperature for jack pine container stock at 27°C with the possibility that some of the parameters will develop equally well at a somewhat lower temperature. The results of Duncan's multiple range test are also shown in Figure 8, those bars with the same letter are not significantly different at the 0.05 level.

Results of the one-way analysis of variance for soil temperature effects are listed in Appendix D, and shows that there are very highly significant differences between soil temperature treatments.

Shoot-root ratios range from 1.2 to 2.7. Armson and Carman (1961) report that adequate shoot-root ratios range from 1.5 to 2.2 for nursery grown jack pine in Ontario. Miller (1970) reports an average ratio of

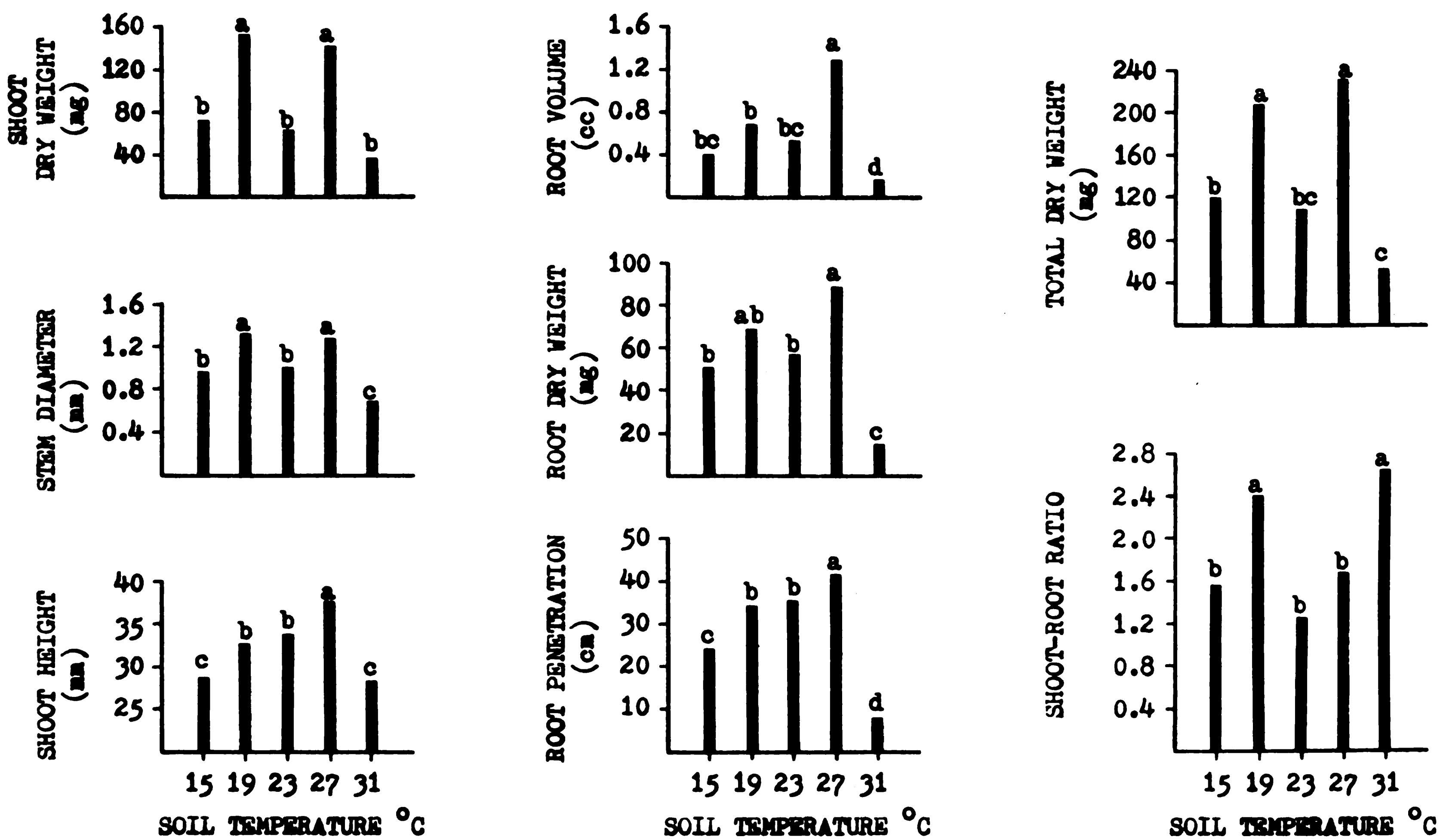


Figure 8. Effect of soil temperature on growth of 8 week old jack pine seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

1.48 for jack pine grown in controlled environmental chambers with soil moisture at field capacity. The 27°C treatment resulted in a shoot-root ratio of 1.7 and is not significantly different from those raised at 15° and 23°C soil temperature.

Mycorrhizae

The characteristic root mantle of ecto-mycorrhizal fungi was noted present with a value of two (2) and absent with the value one (1). Mycorrhizal development was optimum at 19°C soil temperature with an average value of 1.9, and intermediate at soil temperatures of 31° and 27°C with values of 1.6 and 1.4. There was virtually no development of mycorrhizae at the 23°C soil temperature with a value of 1.1 and none at the 15°C soil temperature. As with white spruce, mycorrhizal development on jack pine was optimum at a soil temperature of 19°C.

Weekly Development

Weekly height measurements were made on all jack pine seedlings. There was a uniform initial two week growth period before soil temperature treatments were applied. Seedlings for different runs were not at the same height; therefore, height at the end of the second growing week was set to zero and each succeeding week thusly adjusted. Figure 9 illustrates height growth curves for jack pine seedlings raised at the various test soil temperatures. Jack pine grown at 27°C soil temperature had the fastest rate of growth. Seedlings raised at 19°C soil temperature had a similar growth curve after the fourth week, however; height growth increment for the 27°C treatment almost doubled that of other soil temperature treatments during the first week of soil

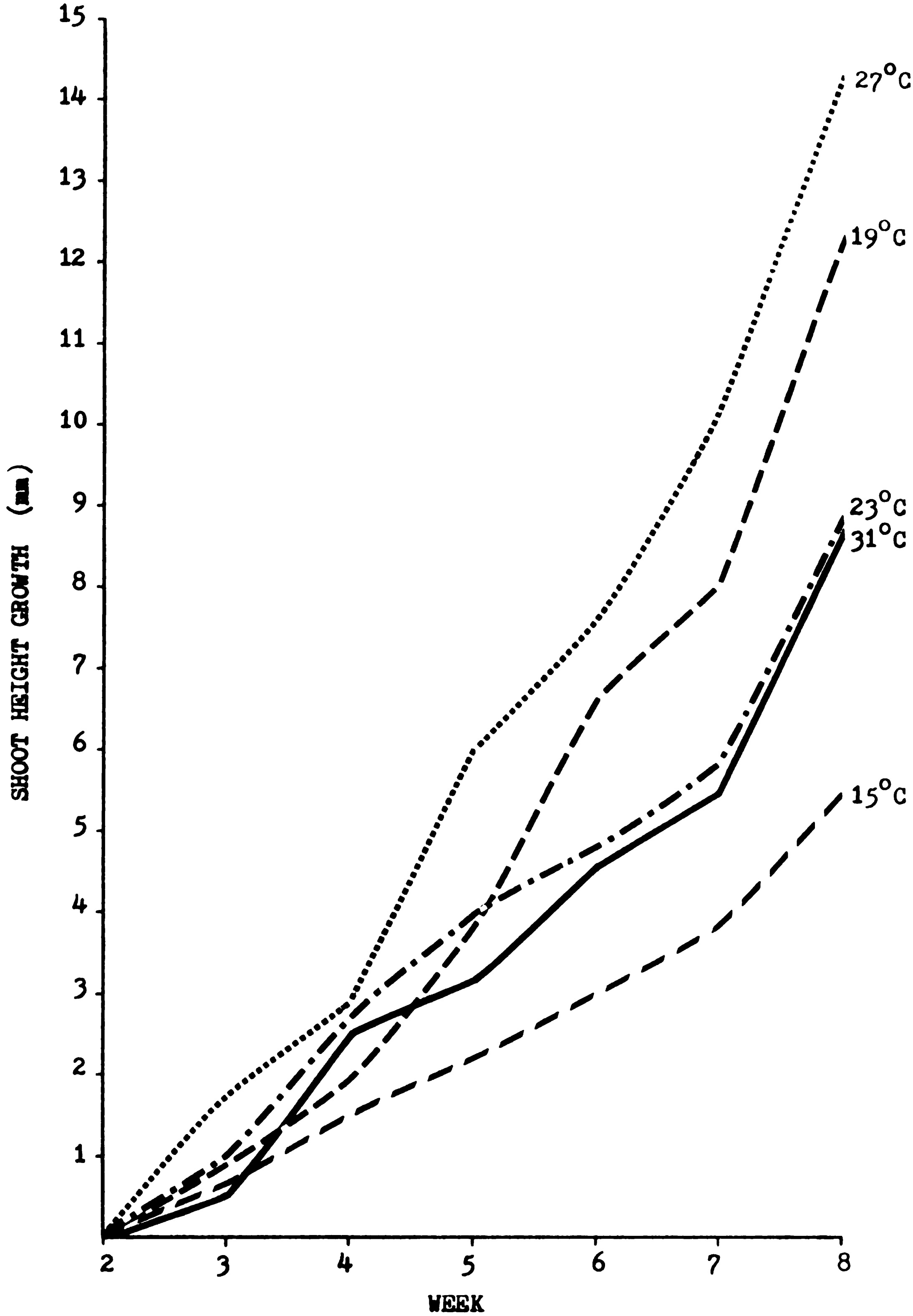


Figure 9. Weekly height growth of jack pine seedlings grown at various soil temperatures.

temperature treatment. The 15°C soil temperature treatment produced the slowest growing seedlings.

Discussion

Figure 10 shows jack pine seedlings shoot and root development by the test soil temperatures at eight weeks of age.

The results reported here compare favorably with those reported for jack pine by Miller (1970). Miller utilized three day-night air temperature regimes (32°/21°C, 24°/13°C, and 16°/5°C) where soil temperature come into equilibrium with the air temperature. The influence of temperature on jack pine growth was most pronounced when soil water was not limiting (at or near field capacity). There were no apparent differences in over-all seedling growth between the moderate and high temperature treatments at the end of 10 weeks, however; a visible decline in seedling vigor was observed at the lower temperature treatment.

Ponderosa pine, another hard pine, was studied for the effects of various environmental factors (Steinbrenner and Rediske, 1964). It was found that root development was significantly affected by soil temperature. High air temperature, 28°C day with 18°C night, in combination with 21°C soil temperature significantly increased seedling dry weights over lower soil temperatures.

Therefore, hard pine root development is favored by soil temperatures ranging from 21° to 32°C.

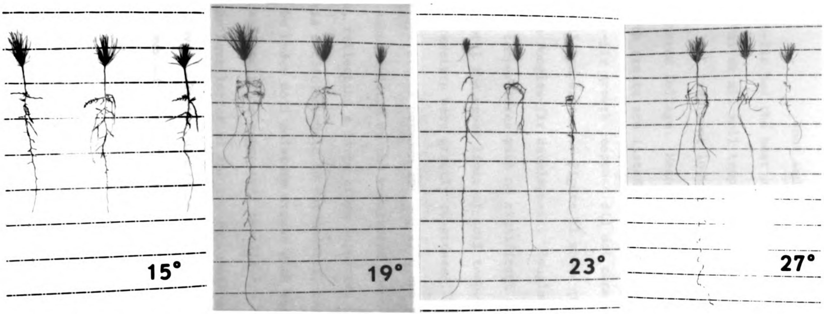


Figure 10. Jack pine seedlings at 8 weeks of age grown at various soil temperatures. Seedlings are arranged (l. to r.) largest, average, and smallest to show the range in growth development that occurred at each soil temperature. Lines on photo are 5 cm apart.

Douglas-Fir

Root and Shoot Growth

Douglas-fir had the best survival of all the test species with 100 percent survival at all soil temperatures. However, the seedlings raised at the 31°C treatment looked almost dead with a pale green color, small and withered foliage. Mean values and standard deviations for all measured growth traits are listed in Table 3, Appendix E.

Douglas-fir growth response did not consistently favor any particular soil temperature. Figure 11 shows the results of soil temperature on Douglas-fir development. Douglas-fir tolerated a wide range in soil temperatures with no significant differences between treatments, until the upper limit of soil temperature was reached where all growth parameters were greatly suppressed. Best growth was obtained with soil temperatures between 15° and 27°C and poorest at 31°C. This is further substantiated by the unbalanced shoot-root ratio at 31°C soil temperature, reflecting a large crown supported by a very small root system. This condition would be detrimental, because outplanted seedlings would be under soil moisture stress with such a small root system.

Duncan's multiple range test results are also shown on Figure 11. Bars with the same letter at the top represent no significant difference at the 0.05 level. These results indicate that shoot and root development were optimum with soil temperatures ranging between 15° and 27°C.

Results of the one-way analysis of variance for soil temperature effects are listed in Appendix D, and show highly significant differences between soil temperature treatments on the growth and development of Douglas-fir.

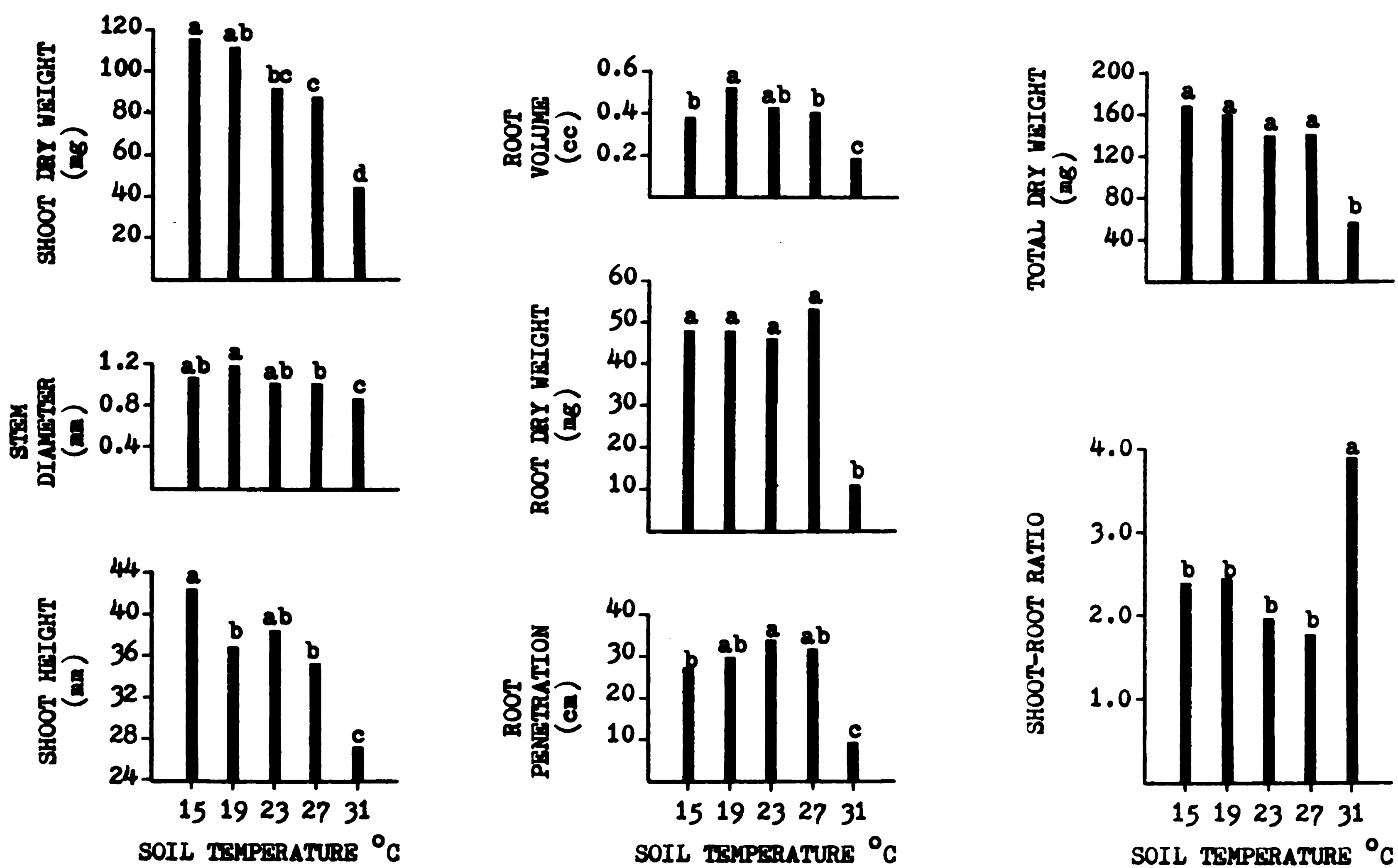


Figure 11. Effect of soil temperature on growth of 8 week old Douglas-fir seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

Mycorrhizae

As with other conifer test species, the characteristic mantle of ecto-mycorrhizal development was noted as present with the value two (2) and absent with the value one (1). Mycorrhizal occurrence was only present on Douglas-fir seedlings grown at soil temperature of 19°C, with an average value of 1.7. All other soil temperature treatments showed no development of mycorrhizal mantle.

Weekly Development

Figure 12 illustrates weekly height growth of Doulgas-fir while the seedlings were under the influence of controlled soil temperatures. Again height of seedlings was set to zero after the initial two week growth period. Growth rates of seedlings does not seem to vary much after seedlings have adjusted to the soil temperature. Seedlings raised at 15°, 19°, and 23°C showed no significant differences in height at the end of the temperature treatment. Growth rate at the 31°C soil temperature was poorest when compared to the lower soil temperatures, and represents a 46 percent decrease in height growth.

Discussion

Figure 13 shows the results of Douglas-fir seedlings at the age of eight weeks after extraction from the containers.

These data and optimum soil temperatures are in general agreement with those reported for Douglas-fir in which soil temperature was positively controlled by immersing pots in water baths. Cleary and Waring (1969) found, under controlled conditions, that 6-month old Douglas-fir performed best with a constant air temperature of 20°C and

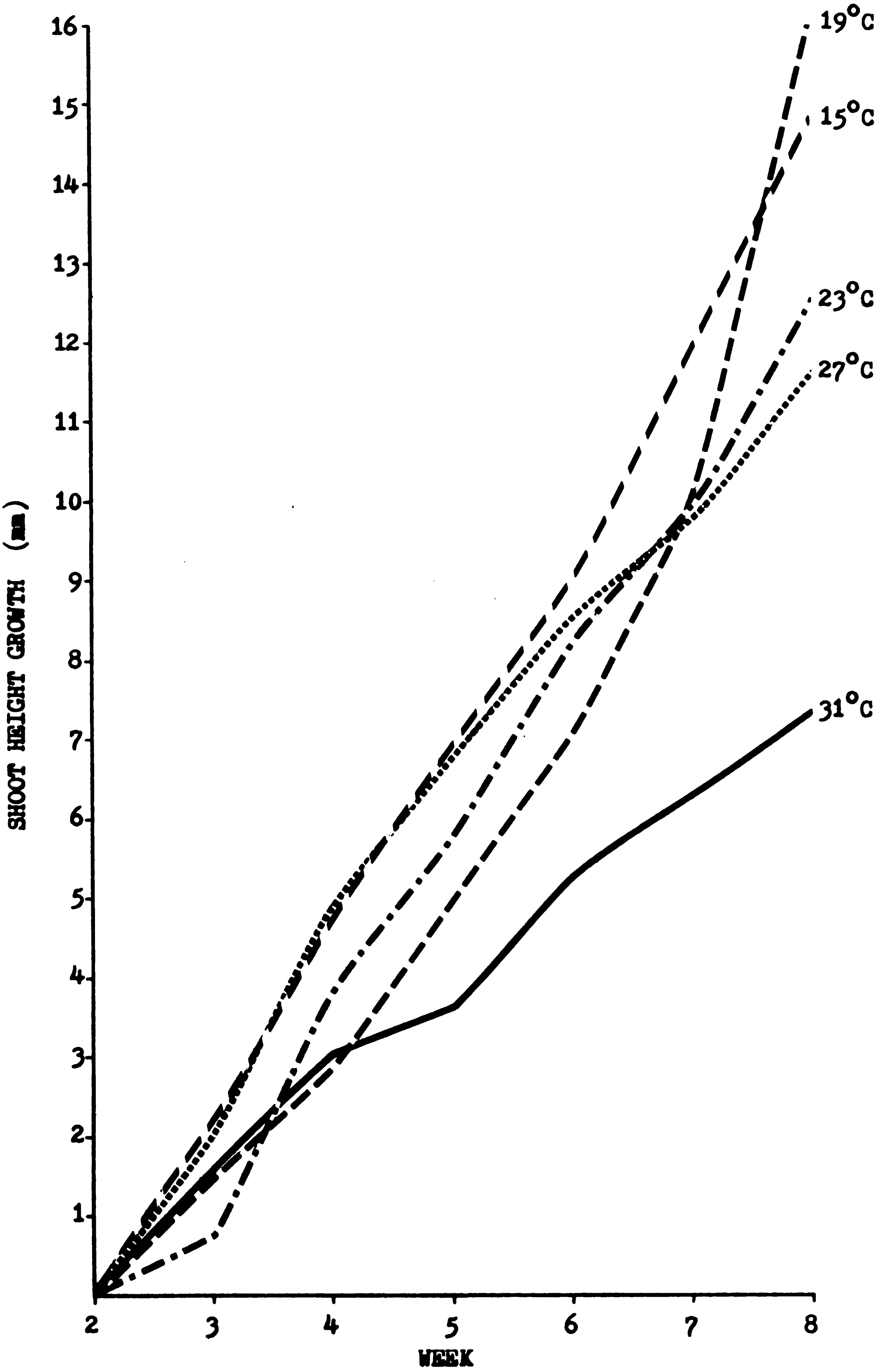


Figure 12. Weekly height growth of Douglas-fir seedlings grown at various soil temperatures.

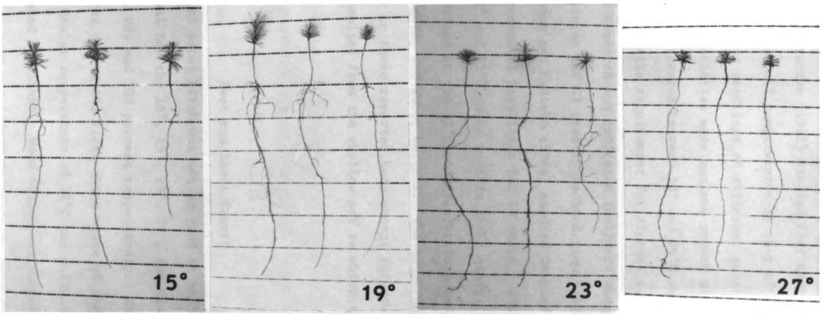


Figure 13. Douglas-fir seedlings at 8 weeks of age grown at various soil temperatures. Seedlings are arranged (l. to r.) largest, average, and smallest to show the range in growth development that occurred at each soil temperature. Lines on photo are 5 cm apart.

soil temperature of either 15° or 20°C.

Lavender and Overton (1972) studied four thermoperiods in combination with three soil temperatures as they affect growth and dormancy of Douglas-fir seedlings of different geographic origin. They concluded that both varieties made maximum growth with soil temperature at 20°C and air temperatures between 18° and 24°C during a 20 week period. There was little requirement for diurnal temperature fluctuations as earlier research had indicated (Hellmers and Sundahl, 1959) and low soil temperatures (10°C) greatly reduced growth and hastened dormancy.

Steinbrenner and Rediske (1964) studied Douglas-fir growth in controlled environmental facilities for 10 weeks. Only two soil temperatures, 10° and 21°C, were used in their study. Results indicated that seedlings raised at the 21°C soil temperature had greater root length, root weights, and shoot heights. The magnitude of their results are very similar to those reported here except for root penetration. This may have resulted from the shallow pot in which they grew their seedlings.

Paper Birch

Root and Shoot Growth

Survival of paper birch was not as good as with the other test species. Survival for the 15°, 19°, 23°, 27°, and the 31°C treatments were 50, 92, 84, 92, and 100 percent respectively. Most seedling mortality occurred during the first three weeks of the soil temperature treatment. The cooler temperature of 15°C was definitely undesirable for the established seedlings. Mean values and standard deviations for all measured parameters are listed in Table 4, Appendix E.

Paper birch grew well over a wide range of soil temperatures. Shoot and root development for birch seedlings are illustrated in Figure 14. Birch shoot development was best at 31°C soil temperature in contrast to Douglas-fir which made the poorest growth at this soil temperature. No significant root growth response differences occurred between soil temperatures of 19° and 31°C. However, with respect to root dry weight and volume there is a slight advantage to the 23°C soil temperature treatment. Total seedling biomass indicates a temperature range of 19° to 31°C is best. All growth traits showed a sharp decrease at 15°C soil temperature.

The results of Duncan's multiple range test are also given in Figure 14. Mean values with the same letter at the top of the bars are not statistically different at the 0.05 level. This suggests that container grown paper birch tolerates a wide range in soil temperatures with shoot development best at 31°C while root development is favored at 23°C soil temperature.

Appendix D presents the results of a one-way analysis of variance between soil temperature treatments and paper birch development. Significant differences occur for each growth trait at various levels of significance, thus showing the importance of soil temperature on the early development of paper birch seedlings.

Weekly Development

Figure 15 illustrates weekly height growth after the initial establishment period of two weeks. Height growth occurs in very small increments during the first two weeks after temperature treatments were applied. After the second week of temperature treatment, the height

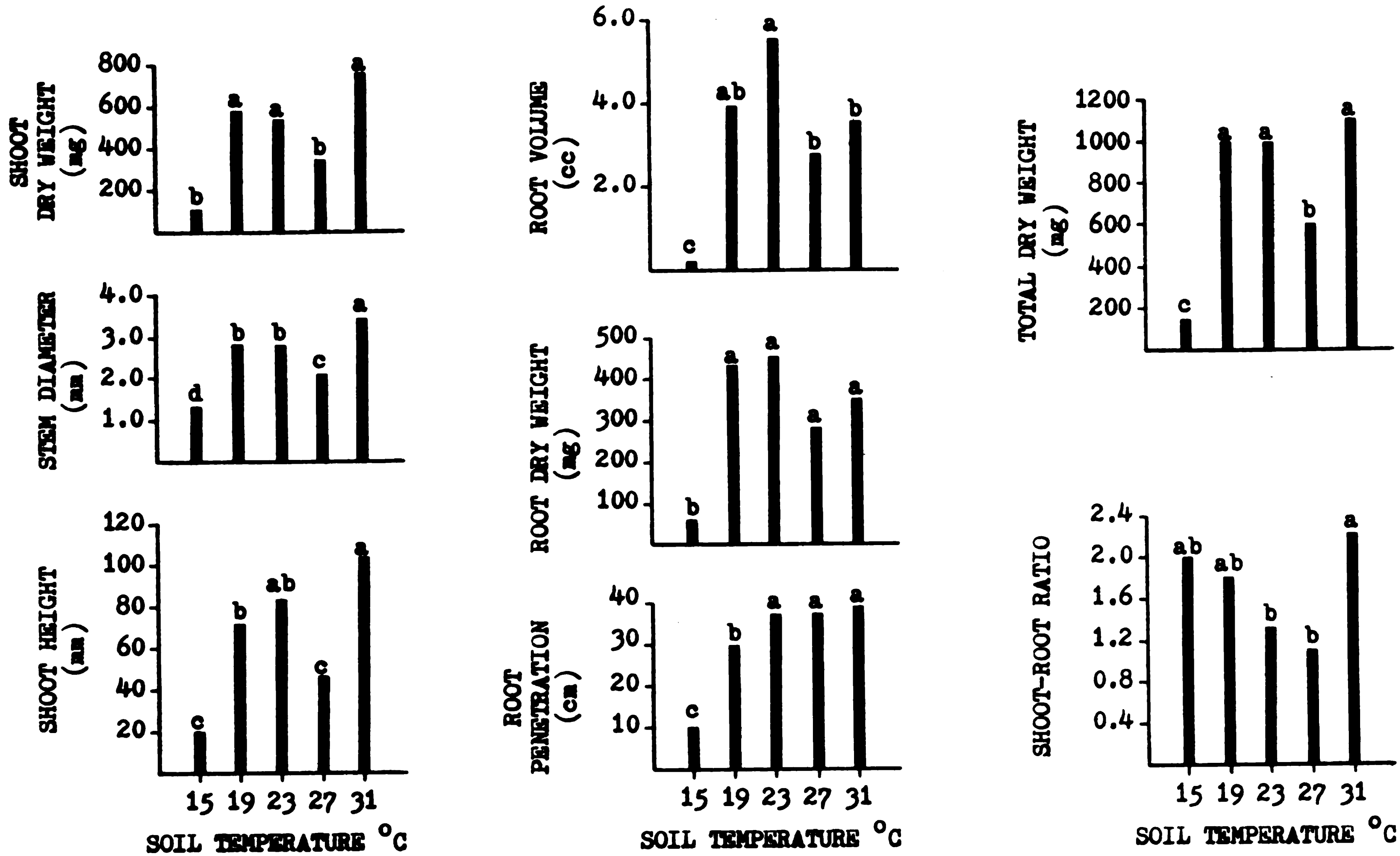


Figure 14. Effect of soil temperature on growth of 8 week old paper birch seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

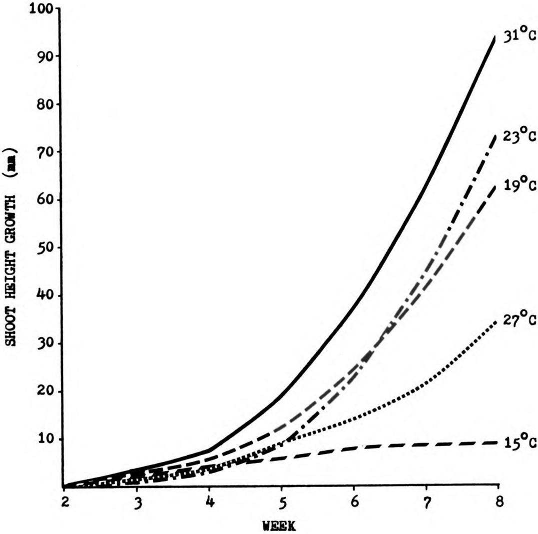


Figure 15. Weekly height growth of paper birch seedlings grown at various soil temperatures.

growth for seedlings raised at 19°, 23°, and 31°C almost doubled each week. The curves for these height growth lines are almost parallel with an average slope of 1.14. Both weekly and total height growth was best at soil temperatures of 31° and 23°C.

Figure 16 pictorially shows the effect of soil temperature on the development of paper birch. Cooler temperatures (15°C) have a detrimental affect on paper birch seedling establishment.

<u>Tree-of-Heaven</u>

Root and Shoot Development

Tree-of-heaven has great potential in revegetating spoil areas because it makes very fast growth, and is exceedingly hardy, especially in its ability to flourish on hard-packed low fertile soils. It is also resistant to smog and smokey atmospheres of industrial cities.

Survival for tree-of-heaven was 100 percent for all soil temperatures except for the 23°C treatment which had a survival of 92 percent. Mean values and standard deviations for all measured parameters are listed in Table 5, Appendix E.

Figure 17 illustrates shoot and root characters as influenced by soil temperatures. All measured shoot, root and biomass parameters show maximum development at 19°C soil temperature. This indicates a clear-cut optimum soil temperature of 19°C for tree-of-heaven container grown stock. Below 19°C there was a sharp decrease in growth. Figure 17 also presents the results of Duncan's multiple range test. Bars with the same letter at the top represent no significant differences at the 0.05 level. The measured growth parameters show that 19°C is the optimum soil temperature for raising tree-of-heaven seedlings in containers under

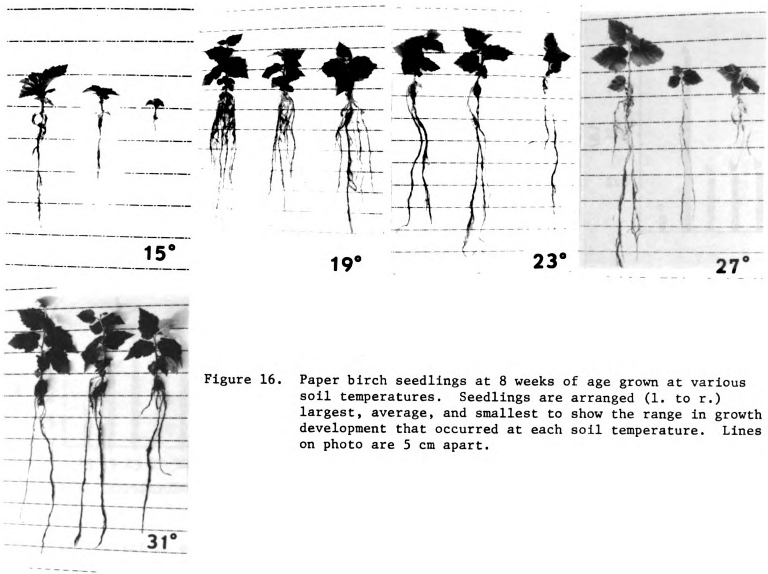


Figure 16. Paper birch seedlings at 8 weeks of age grown at various soil temperatures. Seedlings are arranged (1. to r.) largest, average, and smallest to show the range in growth development that occurred at each soil temperature. Lines on photo are 5 cm apart.

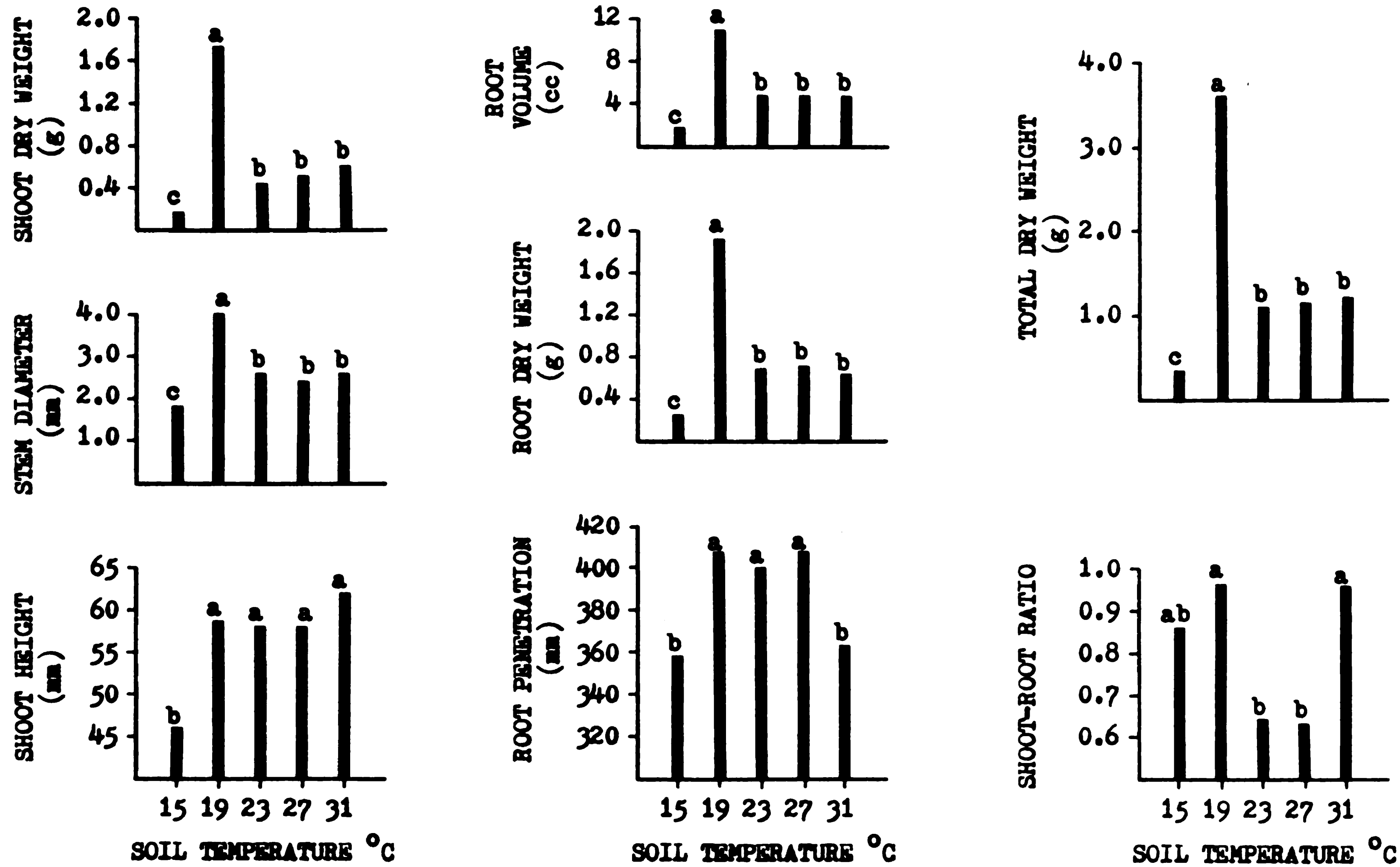


Figure 17. Effect of soil temperature on growth of 8 week old tree-of-heaven seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

controlled environmental conditions.

Results of the one-way analysis of variance are given in Appendix D. All measured parameters show significant differences between soil temperature treatments, thus indicating the importance of soil temperature on tree-of-heaven seedling development.

Shoot-root ratio was near unity at both 19° and 31°C soil temperature. However seedlings raised at 31°C had lower values in shoot diameter, and dry weight, and all root parameters. Therefore, the 19°C treatment, giving larger root values, would be considered the better ratio of the two treatments.

Weekly Development

Weekly height growth was recorded and is illustrated in Figure 18. Seedling height was again set to zero after the initial growth period of two weeks so that height was uniform at the beginning of the soil temperature treatment. Tree-of-heaven raised at 31°C soil temperature had the fastest rate of growth during the first two weeks while under treatment. All soil temperature treatments showed the same linear trend during this first two week period, but the slope of the growth curves is less for those raised at lower soil temperatures. All soil temperatures from the fourth to eighth weeks were similar in shape and slope, indicating the plants have become adjusted to the environment under which they were raised. These results indicate that the first two weeks of soil temperature treatment are the most important because during this time growth was most influenced by the soil temperature.

Figure 19 illustrates the effect of soil temperature on tree-of-heaven seedlings grown under controlled conditions for eight weeks.

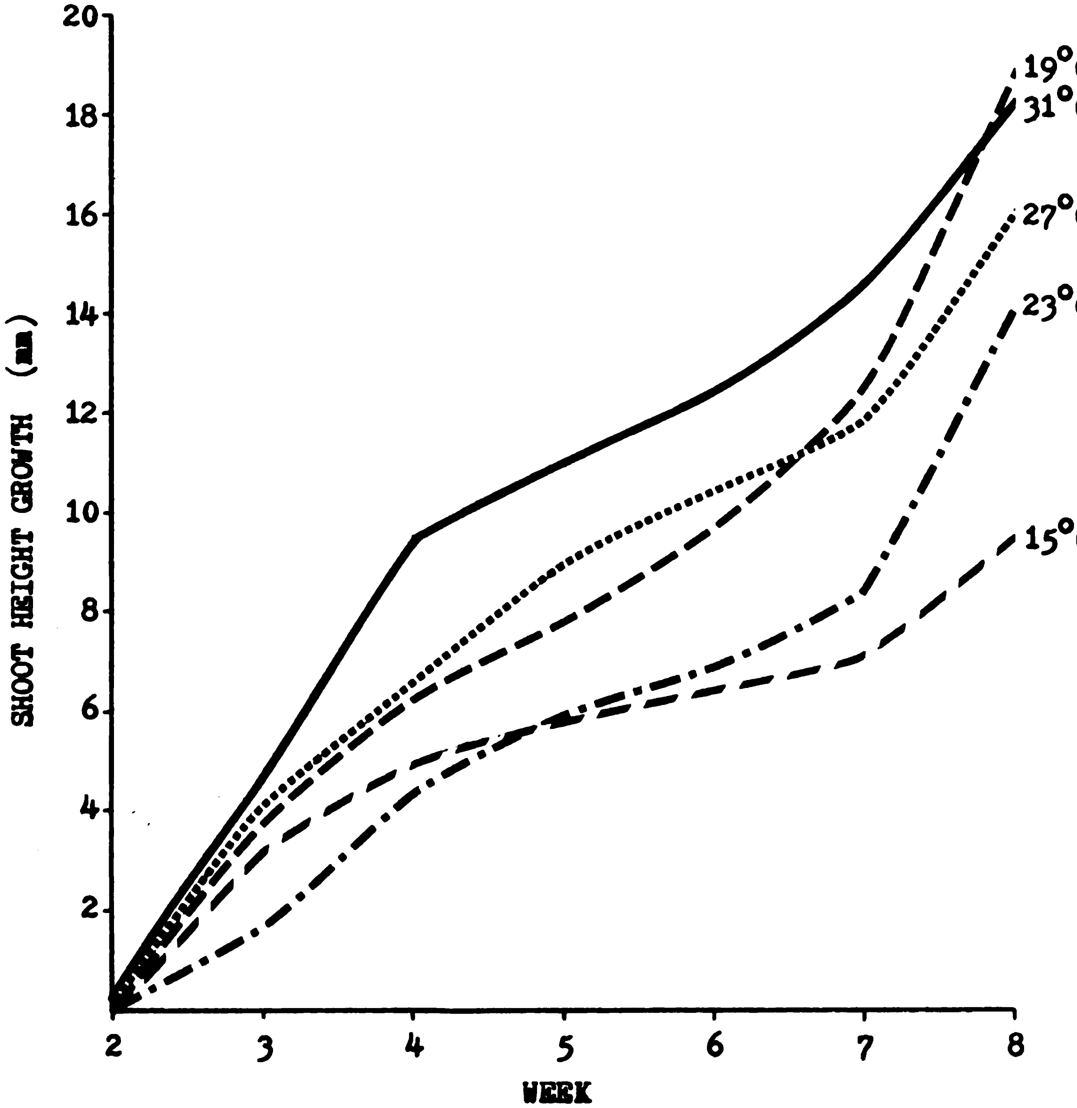


Figure 18. Weekly height growth of tree-of-heaven seedlings grown at various soil temperatures.

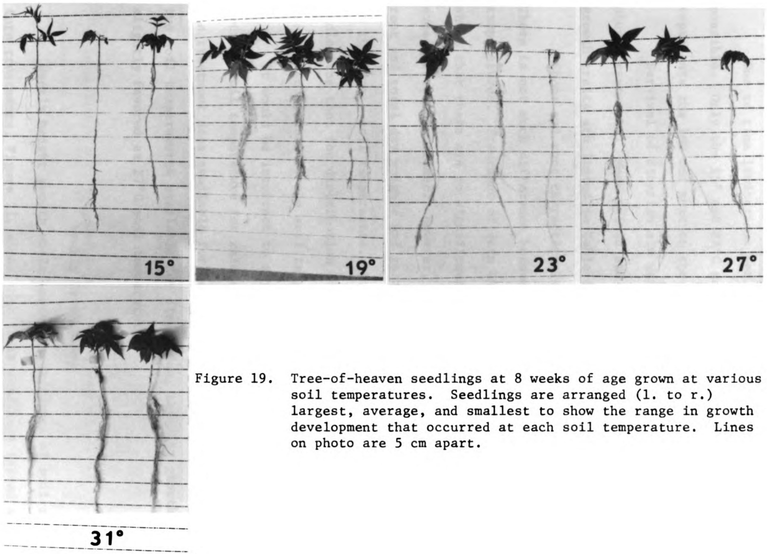


Figure 19. Tree-of-heaven seedlings at 8 weeks of age grown at various soil temperatures. Seedlings are arranged (l. to r.) largest, average, and smallest to show the range in growth development that occurred at each soil temperature. Lines on photo are 5 cm apart.

Siberian Elm

Root and Shoot Growth

Due to time limitations not all Siberian elm treatments were possible. Only the 15° and 27°C soil temperatures were run, which represents the low and next to the highest soil temperature treatments.

Survival of Siberian elm was 100 percent for the two soil temperature treatments. Mean values and standard deviations for all measured growth traits are listed in Table 6, Appendix E.

Shoot and root characters for Siberian elm are show in Figure 20. There is not much difference between seedlings grown at the two soil temperatures. Treatment of data by analysis of variance, Appendix D, shows that there are no significant differences between soil temperatures, except for root volumes. However, with respect to stem diameter, shoot, root and total dry weights and root volume there is a slight advantage to the higher soil temperature. Shoot-root ratios are almost identical, indicating that the distribution of dry weight between shoots and roots was not influenced by the soil temperature treatments.

It would be incorrect to say that the 27°C treatment is the optimum soil temperature for raising Siberian elm without the rest of the treatment data available for comparison. However, with just these two soil temperatures available for discussion, seedling growth was slightly favored at 27°C soil temperature.

Weekly Development

Weekly height growth while under the influence of soil temperature treatments, Figure 21, shows that those seedlings raised at the 27°C treatment had twice the growth rate over those raised at 15°C, with

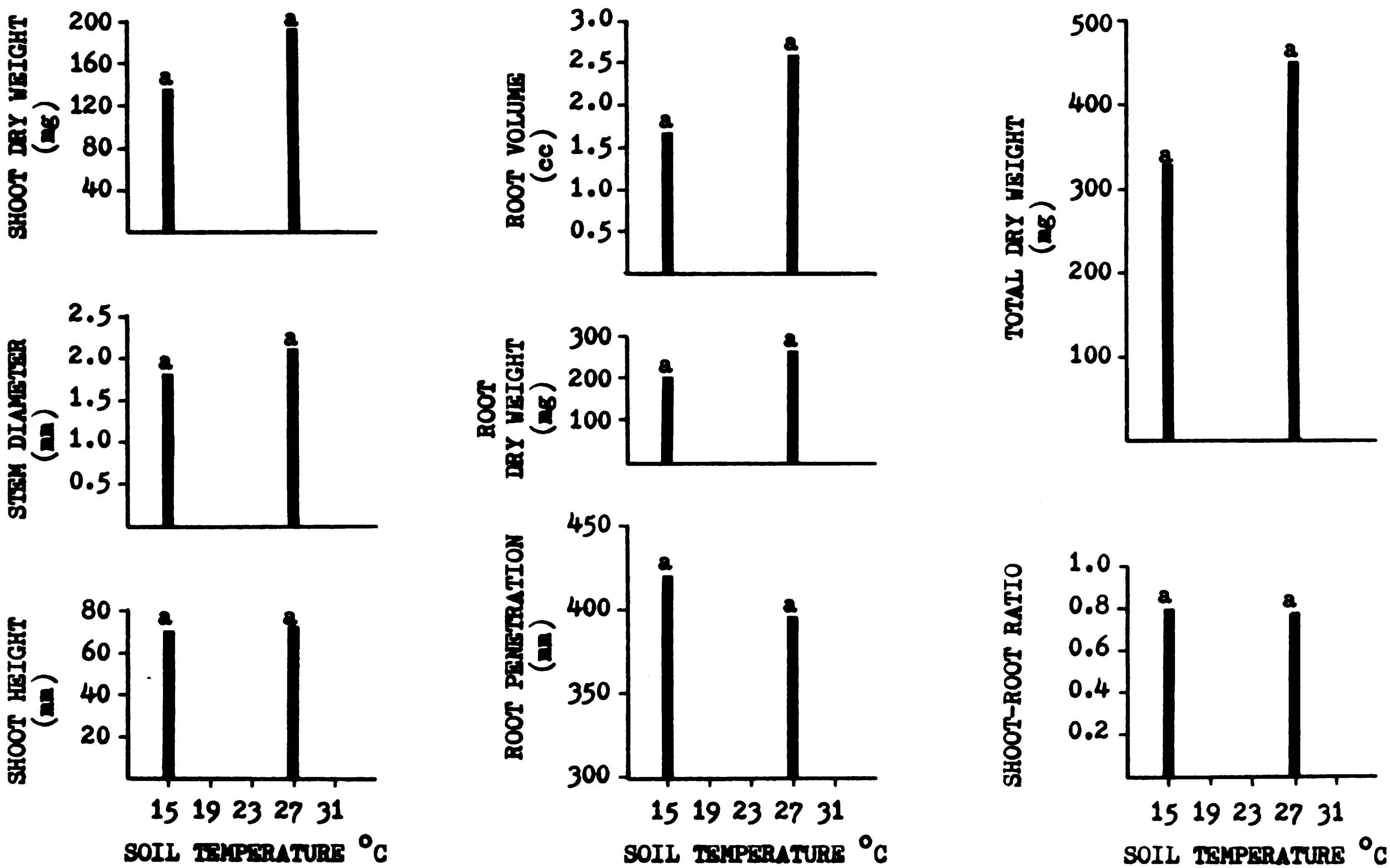


Figure 20. Effect of soil temperature on growth of 8 week old Siberian elm seedlings. Letters atop each bar represent the results of Duncan's multiple range test. Bars with the same letter are not significantly different (0.05 level).

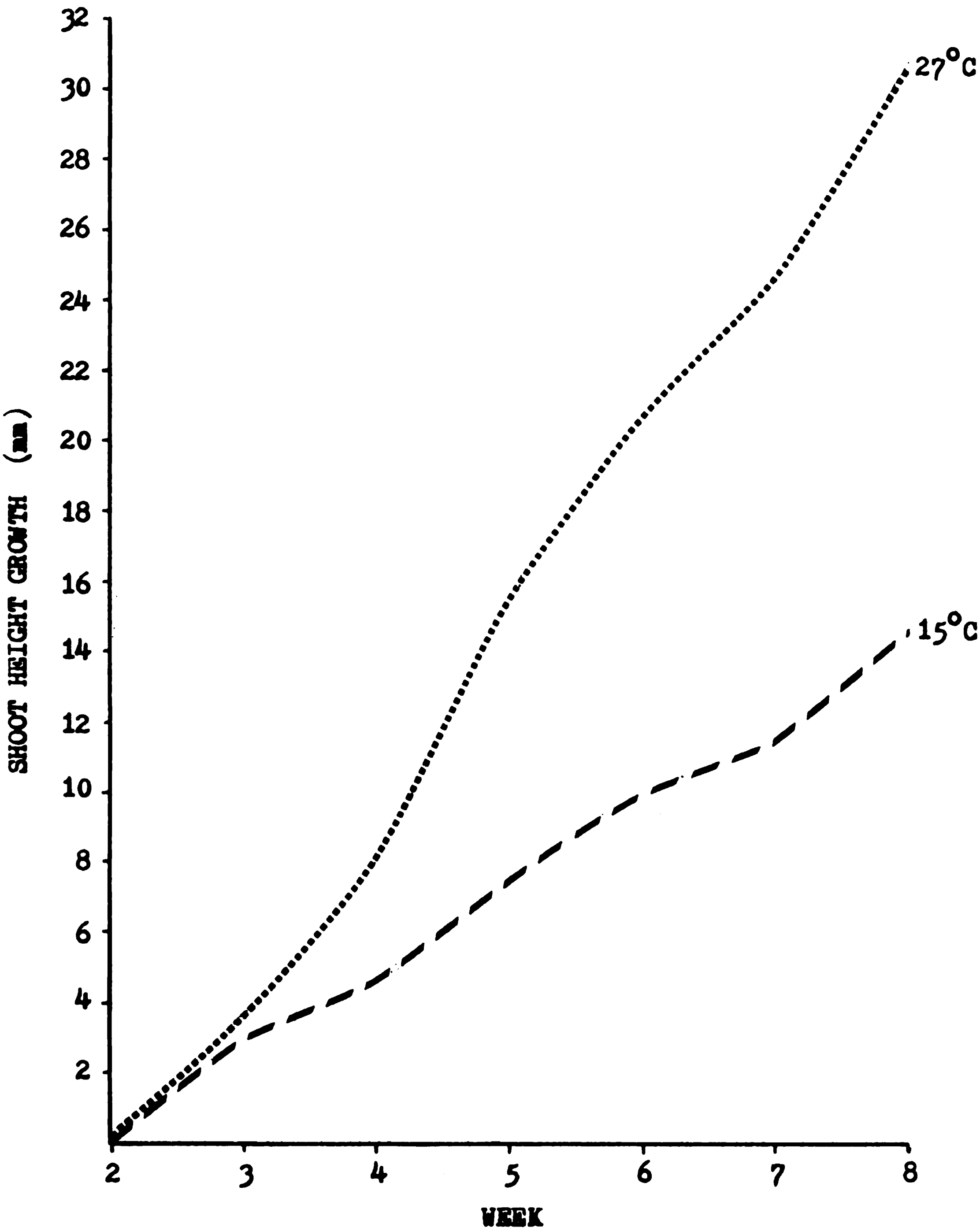


Figure 21. Weekly height growth of Siberian elm seedlings grown at various soil temperatures.

slopes of 1.35 and 0.65 respectively. This represents a highly significant difference at the 0.01 probability level.

CHAPTER V

SUMMARY AND CONCLUSIONS

The objective of this study was to examine the effects of soil temperature on the growth and root development of selected conifer and hardwood seedlings grown in controlled environments.

Seedlings established from seed were raised in large glass tubes for eight weeks in two stages: (1) they were germinated and grown for the first two weeks without control of soil temperature, and (2) transferred into a constant-temperature water bath where soil temperatures were controlled for the remaining six weeks. Soil temperatures were controlled at 15°, 19°, 23°, 27°, and 31°C (±0.1°C). The test soil was a Kalamazoo loamy sand. Soil moisture was maintained at or near field capacity (10 percent moisture by weight) by weighing the containers weekly. Other environmental factors were held constant at levels which simulate natural conditions. The response to soil temperature was determined for shoot, root and total seedling parameters. Weekly height measurements were recorded to establish growth responses.

Soil temperature had a pronounced effect on seedling growth. All species showed a significant effect of soil temperature on shoot and root growth. White spruce, jack pine, and tree-of-heaven showed a single optimum soil temperature for both shoot and root development. White spruce and tree-of-heaven had optimal growth at 19°C soil temperature. Jack pine growth was optimum at 27°C soil temperature. Douglas-fir and paper birch showed good development over a range of soil temperatures. Douglas-fir seedlings responded similarly to soil temperatures between 15° and 27°C. Paper birch grew well between soil temperatures of 19° and 31°C. Best shoot development occurred at the 31°C soil temperature, while root development was favored at 23°C soil temperature. Siberian elm growth was slightly better at the higher soil temperature, 27°C.

Results of the one-way analysis of variance show conclusively that soil temperatures have a significant effect on the development of establishing seedlings grown in containers. Significant results were shown for almost every measured parameter by the test species. The exception was Siberian elm where most results were non-significant. Duncan's multiple range test was utilized to determine which soil temperature treatment(s) was significantly different from the other test temperatures. This procedure allowed the optimum soil temperature and temperature ranges to be selected for the test species.

The characteristic root mantle of ecto-mycorrhizae, the typical type of mycorrhizae associated with coniferous plants, was measured as either present or absent. White spruce, Douglas-fir, and jack pine had the most mycorrhizae development at 19°C soil temperature. Similarly the roots of white spruce, and Douglas-fir also had excellent growth at 19°C soil temperature. Therefore, mycorrhizae may play an important role in the development of these seedlings.

Results from this study may be helpful in designing future semi-controlled greenhouse parameters for raising planting stock in containers. Soil temperatures could be controlled in greenhouse facilities by running heating pipes, steam lines, or electrical heating devices through the soil or benches wherever containers are located. With proper placement of temperature sensors, the soil temperature could be controlled to within the optimum ranges described here.

The data presented suggests that seedlings of these test species had good shoot and root development at 19°C soil temperature. Therefore, in general, 19°C soil temperature would be recommended for growing various forest tree seedlings in controlled environments.

By optimizing root growth and the shoot-root ratio with controlled soil temperatures, it would be possible to increase survival of outplanted seedlings. Theoretically, outplanted seedlings would have a much better chance for survival during the first season. Improved root systems would be more apt to cope with drought stress on harsh sites.

Increasing total seedling biomass by controlled soil temperatures has its advantage. Seedlings raised in this study, eight weeks of age, compare favorably to one-year-old seedlings raised in conventional forest nurseries. Thus, with intensive management, we have grown one year's biomass in eight weeks.

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APPENDIX TABLES

APPENDIX A

Physical Characteristics of Plant Growth Chambers

The small unit controlled environmental chamber used in the first two weeks of study, Sherer-Dual Jet (Marshall, Michigan) model CEL25-7HL, is 26 cu. feet in size and has 7 sq. feet of usable bench space. The chamber is completely self contained with timers, controls, lights, ballasts, fuses, junction boxes, coil, valves, condensing unit, humidifiers, and one access door with observation window. Light bank consists of 10 VHO (very high output) 110-watt cool white fluorescent lamps, 4 feet long, and eight 25-watt incandescent lamps, to provide not less than 200 watts per square foot of plant bed. Light intensities are programmed through two, 24-hour time clocks and a manual switch to provide all fluorescents, two-thirds fluorescents, all incandescents, or any one of five lighting combinations. Temperature is controlled and programmed through an indicating, dual-temperature (day-night) controller and a 24-hour time clock. Temperature range equals 4.4°C to 43°C and is maintained within ±0.5°C. Humidity control consists of a hair element type humidistat (0-100 percent) and a atomizing humidifier which provides a ±5 percent humidity control.

The larger unit, Sherer-Gillett model CEL512-37, used for controlled temperature water baths is 230 cu. feet in size and has 37 sq. feet of usable plant bed space. This chamber is also completely self contained with the items listed above except for these features. Light bank consists of 24 VHO 200-watt fluorescant lamps, 8 feet long, 6 VHO 110-watt cross lamps (three at each end of light bank) and 12, 25-watt incandescent lamps. Light intensities are programmed by three, 24-hour time clocks. This chamber is supplied with four access doors.

APPENDIX B

Seed Source Data

Jack pine seed was obtained from U.S.F.S. Chittenden Nursery, Huron National Forest, Wellston, Michigan, seed lot No. 007, source unknown.

Douglas-fir seed was sent by Arizona Cypress Gardens. Seed source located at Mogollon Rim, Coconino National Forest Arizona, seed lot D-41.

Paper birch and white spruce were obtained from the U.S.F.S. Institute of Forest Genetics at Rhinelander, Wisconsin. Paper birch was collected in Oneida County, Wisconsin, seed lot No. 4710-S-69, while white spruce was collected by Wisconsin State Nursery at Haywood, seed lot No. 5350-S-60.

Tree-of-heaven seed was sent by Forestry Associates, Allentown, Pennsylvania and collected in Lehigh County, seedlot 12820.

Siberian elm seed was obtained from the Tree Nursery, Prairie Farm Rehabilitation Administration, Indian Head, Saskatchewan, Canada, Department of Regional Economic Expansion.

APPENDIX C

List of Materials and Addresses:

1. Lab-Line Instruments, Inc., Lab-Line Plaza, 15th and Bloomingdale Ave., Melrose Park, Illinois 60160.

   a) Direct reading rota-set thermoregulator (temp. range -10° to 110°C), No. 3200.

   b) Lab-Line electronic relay, 15 amperes, No. 3230.

2. Sargent-Welch Scientific Co., 8560 West Chicago Ave., Detroit, Michigan 48204.

   a) 750 watt heater, electric, immersion, flexible, size E, No. S-40825.

   b) Pump, liquid circulating, motor driven, submersible, No. S-71510.

3. Atkomatic Valve Co., Inc., 141 S. Sherman Drive, Indianapolis, Indiana 46201.

   a) Atkomatic "Shorty" series solenoid valve (pilot-piston operated type), size 1/2 No. JJ400, 115V/60 cycle.

APPENDIX D

One-way analysis of variance by test species showing significance of soil temperature upon growth traits.

Growth Trait	White Spruce	Jack Pine	Douglas Fir	Paper Birch	Tree-of-Heaven	Siberian Elm
Shoot Height	***[1]	***	***	***	***	NS
Diameter	***	***	***	***	***	NS
Dry Weight	***	***	***	***	***	NS
Root Tap Depth	***	***	***	***	**	NS
Maximum Depth	***	***	***	***	***	NS
Lateral Extension	*	***	***	**	***	NS
Volume	***	***	***	**	***	*
Dry Weight	*	***	***	**	***	NS
Mycorrhizae	***	***	***	--	--	--
Total Seedling Dry Weight	***	***	***	***	***	NS
Shoot-Root Ratio	***	***	***	*	*	NS
Net Height Growth Under Soil Temperature Treatment (8 - 2 wk.)	***	***	***	***	***	**

[1]Significance Probability: *** = 0.0005, ** = 0.005, * = 0.05, NS = non-significant.

APPENDIX E

Table 1. White spruce growth traits, means and standard deviations.

	Soil Temperature									
	15°C		19°C		23°C		27°C		31°C	
Growth Trait	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	19.08	3.32	19.66	2.80	17.25	2.80	17.16	5.20	14.14	2.48
Week 2	20.08	3.50	21.42	2.61	19.33	3.63	18.08	3.77	15.14	2.79
Week 3	20.42	3.23	22.92	2.27	19.58	3.39	19.25	3.62	15.57	2.63
Week 4	21.25	3.28	24.50	2.23	20.08	3.68	20.41	3.70	16.00	3.21
Week 5	21.83	2.95	26.00	1.91	20.41	3.70	21.25	3.79	16.00	2.58
Week 6	23.33	3.55	27.75	2.14	21.25	3.60	22.33	3.65	16.43	2.23
Week 7	25.16	4.02	29.42	2.57	23.08	3.89	23.08	3.68	16.85	1.86
Week 8	27.08	4.42	31.92	2.39	24.75	5.19	28.50	3.53	17.57	2.07
Stem Diameter	0.56	0.05	0.86	0.12	0.64	0.09	0.55	0.05	0.51	0.07
Shoot Dry Weight	25.00	0.74	67.50	14.22	21.67	5.77	19.16	2.88	11.42	3.78
Root Tap Depth	87.33	19.11	206.75	35.89	123.16	36.12	102.83	12.33	27.43	9.16
Lateral Ext.	10.08	7.43	25.08	13.65	15.50	9.32	20.08	23.45	2.71	2.13
Dry Weight	10.00	0.00	12.50	4.52	10.00	0.00	10.00	0.00	10.00	0.00
Volume	0.10	0.00	0.27	0.06	0.16	0.06	0.20	0.00	0.10	0.00
Mycorrhizae	1.00	0.00	1.92	0.28	1.75	0.45	1.08	0.28	1.71	0.49
Total Dry Weight	35.00	6.74	80.00	15.95	31.67	5.77	29.16	2.88	21.42	3.78
Shoot-Root Ratio	2.50	0.67	5.83	1.85	2.16	0.58	1.91	0.28	1.14	0.37
Net Height Growth	7.00	1.53	10.50	1.88	5.41	2.64	10.42	2.23	2.43	2.76

APPENDIX E

Table 2. Jack pine growth traits, means and standard deviations.

	Soil Temperature									
	15°C		19°C		23°C		27°C		31°C	
Growth Trait	**Mean**	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	21.75	2.14	19.36	2.38	24.29	1.25	22.00	3.13	19.67	2.94
Week 2	22.83	1.90	20.36	2.29	24.71	3.30	23.17	2.72	19.67	2.94
Week 3	23.50	2.15	21.27	2.37	25.71	2.81	24.92	2.84	20.17	2.85
Week 4	24.33	2.10	22.27	2.37	27.43	2.15	26.00	2.26	22.17	3.97
Week 5	25.00	2.30	24.09	1.64	28.71	2.69	29.17	2.44	22.83	3.87
Week 6	25.83	2.59	27.00	2.32	29.57	2.51	30.75	2.26	24.33	4.13
Week 7	26.67	2.57	28.36	1.56	30.57	2.57	33.25	2.17	25.17	4.83
Week 8	28.33	2.23	32.64	2.42	33.57	1.72	37.42	3.26	28.50	3.73
Diameter	0.94	0.07	1.33	0.19	0.98	0.09	1.25	0.16	0.68	0.18
Shoot Dry Weight	70.83	19.75	148.18	62.26	61.43	13.45	139.17	41.88	35.00	15.16
Root Tap Depth	230.58	48.58	337.27	85.33	345.29	62.23	405.16	56.87	78.83	10.15
Lateral Ext.	57.58	24.48	85.64	51.65	112.00	32.78	139.17	70.96	19.00	16.37
Dry Weight	50.00	18.58	67.27	37.44	52.86	17.04	86.67	25.34	13.33	5.16
Volume	0.41	0.10	0.66	0.43	0.48	0.16	0.28	0.43	0.13	0.52
Mycorrhizae	1.00	0.00	1.91	0.30	1.14	0.38	1.42	0.51	1.66	0.52
Total Dry Weight	120.83	37.20	215.45	98.72	114.28	25.72	225.83	66.12	48.33	19.41
Shoot-Root Ratio	1.48	0.26	2.40	0.48	1.23	0.40	1.63	0.19	2.66	0.98
Net Height Growth	5.50	1.38	12.27	3.63	8.85	1.77	14.25	4.88	8.83	2.56

APPENDIX E

Table 3. Douglas-fir growth traits, means and standard deviations.

	Soil Temperature									
	15°C		19°C		23°C		27°C		31°C	
Growth Trait	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	25.00	3.25	19.41	2.90	23.16	4.41	21.00	4.57	21.25	3.95
Week 2	27.25	3.11	20.25	3.41	26.08	2.90	22.92	4.75	21.92	3.92
Week 3	29.42	3.08	21.75	3.91	26.83	3.49	25.00	4.95	23.50	3.83
Week 4	32.00	3.79	23.16	4.65	30.00	3.95	27.75	5.82	24.92	3.78
Week 5	34.17	3.90	25.25	5.51	31.83	4.49	29.75	5.58	25.50	3.85
Week 6	36.33	4.10	27.33	6.34	34.33	4.21	31.50	6.08	27.25	3.84
Week 7	39.16	4.47	30.16	7.52	36.00	5.01	32.75	6.05	28.25	4.56
Week 8	42.08	5.05	36.42	9.03	38.58	5.10	34.58	6.30	26.92	5.10
Stem Diameter	1.06	0.09	1.13	0.22	1.02	0.10	1.00	0.06	0.81	0.14
Shoot Dry Weight	115.00	20.67	109.16	46.01	89.16	16.76	83.33	22.69	42.50	19.12
Root Tap Depth	269.50	32.52	285.83	111.50	338.50	48.36	324.42	100.18	96.42	27.37
Lateral Ext.	25.33	17.54	45.92	31.76	42.08	33.38	16.67	10.97	0.41	1.44
Dry Weight	48.33	7.17	48.33	22.89	46.67	13.03	52.50	18.64	10.83	2.88
Volume	0.38	0.08	0.53	0.19	0.42	0.09	0.41	0.18	0.18	0.05
Mycorrhizae	1.00	0.00	1.66	0.49	1.00	0.00	1.00	0.00	1.00	0.00
Total Dry Weight	163.33	25.34	157.50	68.10	135.83	28.11	135.83	39.41	53.33	21.03
Shoot-Root Ratio	2.40	0.43	2.44	0.61	1.98	0.37	1.79	0.76	3.91	1.50
Net Height Growth	14.83	3.16	16.17	6.21	12.50	3.89	11.67	3.28	5.00	5.18

APPENDIX E

Table 4. Paper birch growth traits, means and standard deviations.

	Soil Temperature									
	15°C		19°C		23°C		27°C		31°C	
Growth Trait	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	10.00	1.90	7.27	1.79	6.70	1.42	8.00	2.75	7.08	1.56
Week 2	12.67	2.34	9.55	2.16	8.70	1.70	10.00	4.12	10.16	2.25
Week 3	14.50	3.83	11.64	2.87	10.10	2.02	11.63	4.27	12.41	2.68
Week 4	16.50	5.65	15.09	4.91	11.80	3.48	13.73	4.08	17.50	5.93
Week 5	18.00	7.24	21.54	8.77	17.00	5.18	18.27	6.18	28.58	9.02
Week 6	20.33	12.04	34.09	15.48	30.80	8.61	24.36	10.18	47.16	11.98
Week 7	20.67	11.80	50.82	24.15	52.40	15.63	31.00	16.64	70.83	18.52
Week 8	21.33	11.99	72.18	34.38	81.00	27.62	44.36	24.97	102.92	24.24
Stem Diameter	1.25	0.62	2.80	0.72	2.78	0.54	2.18	0.50	3.28	0.29
Shoot Dry Weight	96.67	134.71	583.64	300.97	544.00	257.60	321.82	215.26	755.83	225.25
Root Tap Depth	103.67	87.10	300.63	120.63	375.30	68.50	376.00	41.26	382.83	44.84
Maximum Depth	103.67	87.10	300.63	120.63	384.10	65.27	379.64	40.68	386.17	46.48
Lateral Ext.	34.33	26.34	254.27	126.55	242.10	115.70	266.55	100.82	185.67	106.81
Dry Weight	56.67	83.34	436.36	259.47	444.00	262.77	283.64	172.87	352.50	152.92
Volume	0.27	0.32	3.95	2.56	5.48	3.08	2.72	1.59	3.48	1.54
Total Dry Weight	153.33	217.86	1020.00	555.01	988.00	495.37	605.45	364.70	1108.33	367.39
Shoot-Root Ratio	2.06	1.02	1.83	1.42	1.33	0.35	1.19	0.39	2.26	0.42
Net Height Growth	8.67	10.71	62.63	32.78	72.30	27.38	34.36	25.44	92.75	23.87

APPENDIX E

Table 5. Tree-of-heaven growth traits, means and standard deviations.

	Soil Temperature									
	15°C		19°C		23°C		27°C		31°C	
Growth Trait	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	28.00	6.74	30.50	4.76	35.36	5.80	34.17	6.04	39.25	5.63
Week 2	36.58	8.46	39.83	5.56	44.27	5.64	42.33	6.23	43.50	5.58
Week 3	39.83	8.77	43.58	6.46	45.90	5.18	46.42	5.73	48.17	6.16
Week 4	41.67	9.25	46.25	7.77	48.64	6.14	48.91	5.43	53.00	6.54
Week 5	42.33	9.16	47.67	8.38	50.18	6.93	51.42	6.14	54.58	6.48
Week 6	43.08	9.36	49.50	8.93	51.09	6.73	52.75	6.08	55.83	6.55
Week 7	43.67	9.52	52.17	9.31	52.73	6.66	54.08	6.66	58.00	6.13
Week 8	46.03	9.33	58.58	10.48	58.27	7.27	58.33	7.91	61.83	6.69
Stem Diameter	1.78	0.33	4.00	0.59	2.59	0.31	2.49	0.28	2.60	0.31
Shoot Dry Weight	130.00	67.15	1726.67	653.71	428.18	139.77	456.67	261.75	589.16	189.37
Root Tap Depth	357.25	36.65	407.83	47.28	399.27	43.91	407.83	30.16	364.25	34.46
Maximum Depth	362.08	39.60	430.67	34.55	413.27	37.61	425.33	19.34	404.50	22.94
Lateral Ext.	69.33	68.62	200.08	108.08	196.00	58.16	224.75	91.58	244.50	56.36
Dry Weight	210.83	168.33	1899.17	704.04	692.72	27.98	697.50	184.64	635.83	182.53
Volume	1.75	0.97	10.83	3.38	4.65	1.63	4.70	1.52	4.72	1.05
Total Dry Weight	340.83	223.22	3625.83	1266.19	1120.91	410.79	1154.17	436.50	1225.00	322.53
Shoot-Root Ratio	0.85	0.45	0.95	0.29	0.64	0.10	0.62	0.20	0.95	0.33
Net Height Growth	9.50	3.45	18.75	6.39	14.00	3.19	16.00	5.25	18.33	3.08

APPENDIX E

Table 6. Siberian elm growth traits, means and standard deviations.

	Soil Temperature			
	15°C		27°C	
Growth Trait	Mean	Std. Dev.	Mean	Std. Dev.
Height Week 1	38.92	12.00	27.75	4.77
Week 2	55.83	14.97	41.00	8.30
Week 3	58.83	15.72	44.50	9.53
Week 4	60.33	14.96	48.92	8.04
Week 5	63.42	15.76	56.50	10.03
Week 6	65.75	16.30	61.75	11.79
Week 7	67.16	15.93	65.50	12.68
Week 8	70.42	15.69	71.58	15.14
Stem Diameter	1.75	0.46	2.08	0.33
Shoot Dry Weight	134.17	74.89	193.33	75.12
Root Tap Depth	417.25	67.23	394.58	46.84
Maximum Depth	429.33	55.22	421.92	26.12
Lateral Ext.	99.58	66.52	120.92	81.23
Dry Weight	196.67	152.21	258.33	102.23
Volume	1.65	1.32	2.58	0.79
Total Dry Weight	330.83	225.73	451.67	171.19
Shoot-Root Ratio	0.81	0.23	0.77	0.19
Net Height Growth	14.58	6.12	30.58	12.71