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THE INFLUENCE OF LIGHT INTENSITY AND SOIL MOISTURE ON THE GROWTH AND MORPHOLOGY OF RED PINE SEEDLINGS

by
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INTRODUCTION

Red pine (*Pinus resinosa* Ait.) is one of the most valuable conifers in the Lake States, and its successful regeneration and establishment are matters of prime concern throughout the region. Much is already known about its germination and growth requirements, but much more still remains to be learned.

The species is generally regarded as relatively intolerant (Baker, 1949), although perhaps somewhat more tolerant in the seedling stage than later in life (Rudolf, 1957). This reaction to competition of a species has much to do with its rate of growth, general development, and survival under various environmental conditions.

The influence of environmental factors is, however, indirect, for, as Kramer (1962, p. 171) points out, the only way in which an environmental factor can affect plant growth is by affecting the internal physiological and biochemical processes and conditions which control growth.

Furthermore, since a change in any single environmental factor brings about a change in the physiological and biochemical processes of a plant, a change in one factor indirectly moderates the influence upon the plant of other factors. For example, a soil moisture shortage which causes an internal moisture deficit in a plant will reduce vegetative growth in several ways. Photosynthesis will be reduced directly by reducing the moisture content of the photosynthetically active mesophyll cells of the leaves, and indirectly by closure of

stomates, which reduces the supply of carbon dioxide for photosynthesis (Kozlowski, 1958). Therefore, even though the light intensity may remain unchanged and favorable for photosynthesis, the rate of photosynthesis may be reduced by internal moisture stress caused by drought. As Cain (1944, p. 17) points out, it is impossible to speak of a single condition of a factor as being the cause of an observed effect in an organism.

Such interacting effects of the various environmental factors, together with the fact that any one, if sufficiently limiting, can cause the death of a plant, makes it of little value to try to determine which factor in an absolute sense is most important. It is, however, appropriate and useful to study how the growth patterns of seedlings may differ when they are subjected to different levels of such factors as light and soil moisture, and thus to evaluate the relative influence of these two factors upon various facets of seedling growth.

Specifically, the objectives of this study were to determine how various degrees of competition for light and/or moisture influenced the following aspects of red pine seedling development:

1. The start, rate, and duration of height growth.
2. The amount of height growth.
3. The start, rate, and duration of needle elongation.
4. The amount of needle elongation.
5. The number of needles produced.
6. The length and diameter of the winter terminal bud.
7. The diameter of the stem at groundline.

8. The amount of root extension.

9. The amount and distribution of dry-matter production.

The foregoing emphasis on environmental factors is not intended to imply that they are the only factors which determine the growth pattern of a plant. As Spurr (1962, p.9) points out, the ultimate growth pattern of any living organism (the phenotype) results from the interaction of both environmental and genetic factors. Thus, the growth responses of two seedlings of a given species will invariably differ to some extent, even though they are growing in identical environments. Fortunately for the purposes of this study, red pine is genetically more homogeneous than most tree species common to the Lake States. That some genetic variability exists, however, is recognized, but the evaluation of it falls outside the scope of this study.

It was decided for several reasons to study the competitive influences of light and moisture in the field rather than in the greenhouse. For one thing, it was thought desirable that these aspects of competition follow the normal pattern encountered in nature, starting with the breaking of dormancy in the spring and continuing through the gradual leafing out of the brush and herbaceous vegetation, the early summer peak of development, the late summer curing and shriveling of the deciduous leaves, and the ultimate loss of leaves and return to dormancy in the fall. It would be extremely difficult, if not impossible, to simulate all of these natural conditions in the greenhouse.

Furthermore, it was desired that the competition for light

and moisture be provided by the actual species which normally provide this competition in the field. Since the most serious of these competitors on Minnesota's upland pine sites is hazel brush, it would have been unfeasible to conduct the study in the greenhouse available, due to the sheer magnitude of the space requirements.

Having decided to install the study in the field, it would have been possible to include the competition from an overstory of large trees, as well as that from the brush and herbaceous vegetation. The reason for not doing so was partly because of the added environmental variability which would have been introduced, but chiefly because past experience in stand conversion work in Minnesota and elsewhere has indicated that conifer seedlings encounter their severest competition, not from the overstory, but from the understory vegetation on sites where both layers are present (Shirley, 1941, 1945a).

In a field study, of course, the precise control over environmental factors, such as is possible in the greenhouse or in a growth chamber, is lacking. This posed some problems in the present study, particularly with regard to soil moisture. This is discussed in more detail in a later section of this paper.

REVIEW OF LITERATURE

Man's interest in tree growth and the factors which influence it can be traced back many centuries. An excellent summary of some of these historical chapters is presented by Studhalter (1955) who has delved back into the writings of early Greek authors of about 400 B. C. The present review, however, begins at a much more recent point in history.

THE LIGHT VERSUS MOISTURE CONTROVERSY AND RELATED EXPERIMENTS

According to Gatherum, McComb, and Loomis (1963), modern interest in evaluating the relative importance of light and soil moisture on forest reproduction can be traced back to the first writings of Heyer (1852). Many investigators in the latter half of the 19th century, following the lead of Heyer, ranked light as the most important factor accounting for the presence or absence of reproduction in the forest. This was the viewpoint that generally prevailed among foresters until the early 1900's.

About the turn of the century, however, this viewpoint was seriously challenged. The trenching experiments of Fricke (1904) raised doubt as to whether light was, indeed, the all-important factor in governing the establishment of reproduction in the forest. Fricke dug trenches around plots of unthrifty Scotch pine seedlings under stands of older trees and found that, when freed of root competition, they responded by vigorous growth. He also seeded both trenched and untrenched plots

and found that seedlings became established on the trenched plots but failed to do so on the untrenched plots. The inference was that soil moisture was the dominating factor, and that light might well be of secondary importance.

Fricke's experiments in Europe were followed by similar studies in America. Among the more notable of these were the trenching studies of Toumey, begun on the Yale Demonstration and Research Forest near Keene, New Hampshire, in 1922. One experiment was installed under a canopy of grey birch where light intensity ranged from one-eighth to one-ninth of that in the open (Toumey, 1929). Toumey found that growth of underplanted red and white pine seedlings was better on the trenched than on the untrenched plots, and that soil moisture also was consistently higher on the trenched plots. He felt that the reduction in light intensity was entirely inadequate to explain the poor growth of the underplanted pine, and attributed the poor growth to moisture deficiencies on the untrenched plots.

Grasovsky (1929), also working in the Northeast, studied the minimum light requirements of red pine, white pine, hemlock, black oak, and chestnut oak over a 10-month period. He found that all species were able to survive for the entire period under light intensities which never exceeded 300 foot-candles (although red pine seedlings died when light intensity dropped below 65 foot-candles). He found that light intensity under canopies of white pine on the Yale Forest in all cases exceeded the minimum light requirements of the seedlings in his experiments, and concluded that in these stands light intensity was not a determining factor in accounting for the presence or

absence of reproduction.

Korstian and Coile (1938), working with trenched and untrenched plots in the Piedmont region in the Southeast, reached a similar conclusion. They felt that light intensity was usually subordinate in importance, and that only on sites where available soil moisture or factors other than light intensity were not critical did the shading influence of the forest canopy become the most significant factor.

With the passing of time, however, some of Toumey's original trenched plots on the Yale Forest no longer demonstrated so clearly that light was of relatively minor importance (Toumey and Keinholz, 1931). On plots installed under a 41- to 60-year-old white pine stand, conifer seedlings grew much better on the trenched than on the untrenched plot, but the authors also noted that in spite of being freed of root competition, white pine seedlings on the trenched plot made less than one-fifth as much growth as seedlings of the same species in a nearby open area. Hemlock seedlings, on the other hand, grew very well on the trenched plots. The authors acknowledged that for white pine the light intensity was simply too low to achieve good growth even though root competition was minimal.

Lutz (1945) re-examined one of Toumey's original trenched plots under the white pine stand 21 years after its establishment and found the hemlocks still present and thriving. All of the white pine reproduction which had been there at the time of Toumey's earlier examination, however, had subsequently died. While it was true that root competition within the plot had increased over the years, Lutz felt it was unlikely that the

moisture supply could be too low for the pine, yet ample for hemlock. He concluded that inadequate light was the factor mainly responsible for the disappearance of the white pine, and summarized by stating that while the plot strikingly illustrates the importance of root competition, it illustrates with equal force the importance of solar radiation.

At the time that Toumey was arguing the case for soil moisture, several other investigators were again focusing attention upon the importance of light. Among these was Shirley who delved into the many facets of light, or more properly, solar radiation. One series of studies involved the growing of several species of woody and herbaceous plants under four sets of light conditions to determine the influence of light intensity and light quality upon growth (Shirley, 1929a). He found that at low light intensities the dry weight of the plants was almost directly proportional to the light intensity received up to about 20% of full sunlight; also, that as light intensity increased, there were increases in the proportion of dry weight in the roots, the density of growth, the strength of the stem, and the thickness of the leaves.

In another study he investigated light intensity in relation to plant growth in a virgin red pine forest in northern Minnesota (Shirley, 1932). He found that none of the three native pines (jack, red, or white) became established by natural means where light intensity was less than 5% of full sunlight. Establishment was fair at 17% of full light, and the old-growth overstory alone never reduced the intensity

below this level. A dense understory of species such as hazel and alder, however, reduced light intensity to values ranging from 0.7% to 15.8%, averaging 4.4% of full sunlight. These findings indicated that the density of the underbrush is of major importance in determining whether conifers can become established and survive in virgin pine stands. A similar conclusion was reached by Logan (1962) concerning the adverse effects of the underbrush on pine reproduction under aspen stands in Ontario.

Though convinced of the importance of light in the establishment and survival of young seedlings under forest canopies, Shirley did not overlook the limiting effects of moisture. In a series of drought studies involving jack, red, and white pine in the laboratory, greenhouse, and nursery, he investigated numerous relationships between drought and various aspects of seedling growth (Shirley and Meuli, 1939). Findings were that plants subjected to moderate drought tended to develop relatively more extensive root systems and smaller tops than those grown in continuously moist soil, and that, in general, plants with well-developed root systems were more resistant to drought than those with less extensive root systems. The latter observation was not always true, however, indicating that drought resistance in young conifers does not depend solely upon size of the root system or relative root development.

In Shirley's most extensive treatise on the subject of competition for light and soil moisture, he reported that in

nursery experiments maximum height growth of the three pines was achieved at light intensities of 43% to 46% (Shirley, 1945a). Maximum dry weight of red pine, however, was attained in 98% light. He also reported on the results of trenching experiments under aspen and pine canopies, and concluded that either shade or root competition may be limiting factors in the growth of young conifers. Shade is likely to be the more important under the secondary canopies in aspen stands, and root competition the more important among low shrubs, grass, and other herbs beneath red pine and jack pine stands.

Another investigator who concluded that solar radiation was frequently more important than soil moisture was Pearson (1930). He installed some trenching experiments in Arizona in which small seedlings of ponderosa pine were grown in the vicinity of large trees of the same species. Seedlings growing in the shade of the older trees, both on trenched plots and untrenched plots, were generally unthrifty and made comparatively little height growth. Those growing in the open were much more thrifty and made much better height growth. He found that even in untrenched areas, moisture conditions for seedlings are actually more favorable under a group of older trees than in open areas occupied by herbaceous vegetation. Yet pine seedlings do become established in these open areas, whereas they do not become permanently established under groups of trees. Pearson concluded that in the Southwest, soil moisture cannot be considered the dominant factor in seedling growth and survival, even though it is more critical in this region than in

many others.

In another study Pearson (1936) grew ponderosa pine seedlings in a nursery for five years under uniformly favorable moisture conditions, but under varying degrees of sunlight. Four levels of light; namely, full light, 50%, 20%, and 10% were compared. All plants in the lowest light intensity died during the first winter, and all but two of those in 20% light died during the 5-year study period. Atkins (1957) also found that development of white pine was generally poor when light intensity was 20% or less of full sunlight.

Studies in northern Wisconsin (Stoeckeler and Limstrom, 1942) indicated that a light overstory of aspen which intercepted about 25% of the sunlight was beneficial to the survival of underplanted pine. First-year survival of planted 2-0 and 2-1 red pine was about four times as high under the aspen as in the open, even though soil moisture under the aspen was slightly lower. The difference in survival was attributed primarily to a marked reduction in evaporation stress under the aspen. Over a 4-year period, however, height growth of the surviving red pine was 49% greater in the open than under the aspen canopy, indicating that while partial cover had a favorable influence on initial survival, it also definitely reduced subsequent height growth.

Moore (1926) conducted a series of experiments on Mt. Desert Island, Maine, using six northeastern conifers growing under different light intensities and on different types of seedbeds. He noted a marked difference between shaded and

unshaded plots, not only in survival, but more particularly in rate of growth and general seedling vigor. In the shade the stems were so thin that many seedlings were flattened or bent over during the winter. He concluded that light is of great importance, even for a tolerant species such as red spruce, and that favorable moisture can modify, but not overcome, the deleterious effects of shade.

Bilan (1960), studying root development of loblolly pine under a variety of ground cover and light conditions, found that shaded plots averaged more moisture throughout the soil profile than did bare, exposed plots, yet produced less dry weight. He concluded that available soil moisture was not a critical factor in seedling development during the course of the study, and that it was the direct reduction of photosynthesis by shading which reduced dry weight.

Mann (1950, 1952) reported on studies aimed at resolving the light vs. moisture controversy at Crossett, Arkansas. Forty-eight small plots were established, each having a one-year-old loblolly pine seedling surrounded and overtopped by hardwoods from 1 to 3 inches in diameter. Various combinations of trenching and tying back of the brush were employed to eliminate competition for moisture or for light. First-year observations indicated that competition for soil moisture was more detrimental to growth of the pine seedlings than was competition for light, but second- and third-year results indicated the reverse. Mann felt that the first-year results might have been due to a too sudden release of previously suppressed year-old seedlings.

Other studies dealing with the light and moisture requirements of the southern pines have shown that both needle length and needle dry weight of shortleaf and loblolly pines increased significantly with increasing light (Jackson, 1962); that shade increased heights, but reduced stem diameter and seedling dry weight of loblolly pine (Koshi and Stephenson, 1962); that loblolly pine seedlings survived and removed significant amounts of soil moisture from a sandy loam soil after the wilting point of sunflowers had been reached (Ursic, 1961); that survival of both shortleaf and loblolly pines is poor at light intensities of 20% or less (Jackson, 1959); and that low light intensity is a more important factor than lack of water in the failure of shortleaf pine seedlings to survive under forest stands (Oosting and Kramer, 1946; Kramer, Oosting, and Korstian, 1952).

An interesting attempt to completely isolate the influence of light intensity on conifer seedling growth is described by Baker (1945). He germinated seeds of eight conifers in sand flats and then transferred the young seedlings to nutrient solutions under various light intensities ranging from full light to as little as 2% of full light. All species increased in dry weight more rapidly at high light levels than at low, but the rate of increase varied greatly between species. Some species showed a nearly uniform increase in dry weight up to full light, whereas others tended to level off at high intensities. The top/root ratios of all species were greater under 10% light than under full light which implies that reduction in light intensity reduces root growth to a greater

extent than top growth. Some mortality occurred during the course of the study, but no direct correlation between the mortality and dry-weight increment was noted, suggesting that the death of intolerant trees in shade is not wholly a matter of starvation.

Another novel experiment designed to determine the relative light requirements of some coniferous seedlings was carried out by Bates (1925). He constructed a table, five feet square, on which he grew from seed, seedlings of eight species on two media, sand and loam, for eleven months. A 200-watt G.E. Mazda "Daylo" lamp was suspended above the center of the table at a height of six inches above the soil surface. After six months the light intensity was reduced by substituting a 75-watt Columbia Mazda blue-glass lamp. The experimental layout automatically provided for circular zones of varying light intensity, but any individual seedling was growing constantly under a fixed light intensity (except for the change in light bulbs), depending on its distance from the light source. Abundant soil moisture was maintained throughout the study.

Bates found that for any given species there was only a comparatively narrow zone of overlapping for the surviving and dead seedlings, showing clearly that survival was very definitely limited by the light intensity. The minimum light requirement for red pine was found to be 2.3% of full sunlight. For all species tested, root development suffered more than top development under weak light. Bates recognized that this, in turn, made seedlings growing in weak light much more vulnerable to

conditions of drought or lack of nutrients because of their inferior root systems. In a subsequent study (Bates and Roeser, 1928) the authors confirmed the earlier findings, and reiterated the observation that the poor root growth under weak light leaves the seedling unprepared to cope with late-season drying of the surface soil which is a common occurrence in many areas.

In their work on plant competition, Clements, Weaver, and Hanson (1929, pp. 277-289) reported on a series of experiments aimed at determining the direct response of several herbaceous species to varying amounts of the three primary factors--light, moisture, and nutrients. They felt that responses could best be evaluated on the basis of the two integrating criteria, leaf area and dry weight, and found that with practically no exception these values were highest when both water and nutrients were adequate, and lowest when both were deficient. A deficiency in water was usually much more decisive than one in nutrients. Light was relatively less important until a much greater reduction had taken place than with the other two factors.

The tentative conclusion reached was that, of the three factors examined, water was most important, light second, and nutrients third. They noted that, although light is indispensable, a reduction of intensity in this factor can proceed very much further than can reduction of the other factors before untoward effects are manifested.

The influence of drought on tree morphology and growth patterns has been the subject of many investigations. Larson (1963), working with 5-year-old red pine trees under greenhouse

conditions, found that, as soil moisture depletion occurred, there was a marked decrease in needle elongation, and that needle growth remained low as long as the drought continued. Following rewatering, however, needle elongation recovered rapidly.

The influence of drought on oak and several fruit tree seedlings as concerns the time of bud-bursting was studied by Guzhev (1958). He noted that the earliest bud-burst occurred in seedlings grown under conditions of relative soil drought (25-30% of field capacity). With an increase in soil moisture up to 60% of field capacity, an increasing delay in the beginning of bud-burst was observed, but moisture increases beyond this point did not lead to further delay in bud-bursting.

Numerous studies have been conducted on the influence of drought on older trees, but only two will be mentioned here. Copeland (1955) induced drought artificially for six healthy 35-year-old shortleaf pine trees by constructing a large shelter over the soil to keep rainfall from recharging the soil water content. He found that a lack of moisture curtailed diameter growth, shoot growth, and needle length.

Lotan and Zahner (1963) grew six 20-year-old red pine trees under two extremes of moisture--simulated drought, and irrigation--for one growing season. They found that bud set and time of cessation of shoot elongation were not influenced by soil moisture treatment, but that the magnitude of shoot elongation was increased 40% in the main stem terminals by irrigation. Irrigation also increased the average needle

elongation by 40% over the amount taking place on trees growing in dry soil, and it extended the period of needle elongation into September, whereas the needles on trees in the dry soil ceased elongation in mid-August.

THE COMPETITIVE SUCCESS OF CONIFERS AND HARDWOODS, AND FACTORS INFLUENCING PHOTOSYNTHESIS

A number of investigators have studied the relative competitive abilities of pine and hardwoods in an attempt to find out why the former so often loses out to the latter. Most of these studies have shown that the photosynthetic efficiency of pine is lower than that of its common hardwood competitors, or, expressed in another way, the hardwoods usually attain maximum rates of photosynthesis at much lower light intensities than does pine (Kozlowski, 1949). Ferrell (1953) found, in studying the light and moisture requirements of 1-year-old seedlings of loblolly pine, shortleaf pine, white oak, southern red oak, red gum, and flowering dogwood, that the pines were the only species to show survival response to light, although light intensity had a strong influence in determining the dry weight increment of all species.

Korstian and Bilan (1957), working with loblolly pine, called attention to the complex interrelationships which exist between the factors involved in plant competition. They found that in abundant light, pines can grow where moisture conditions are equal to or less than those required for hardwoods. However, under shade, the light intensity is often insufficient

for them to produce enough food for the development of a good root system, and consequently they are unable to absorb the water needed to sustain them. Kozlowski and Scholtes (1948) also concluded that the poor root system of loblolly pine as compared to such hardwoods as black locust, flowering dogwood, and white oak was largely responsible for its inability to survive and grow under hardwood competition.

Not only does pine make a poor competitive showing at low light intensities, but as Kozlowski (1949) found, oak seedlings had higher absolute rates of photosynthesis than did pine seedlings even at the higher light intensities. He also found that in either sun or shade, height growth, dry weight of stems, dry weight of roots, and total dry weight were greater in oak than in pine. With decreasing soil moisture, the effect of decreased light intensity on photosynthesis was much greater in pine than in oak.

Gatherum, McComb, and Loomis (1963) conducted experiments both in the field and in the greenhouse to determine the effect of light and soil moisture on the establishment and growth of underplanted conifers in Iowa. They found that the rates of photosynthesis were considerably higher for hazel and dogwood than for white pine and Norway spruce. They concluded that the growth and photosynthetic rates of the two brush species were sufficiently high to cause serious competition for coniferous species.

Kramer and Decker (1944) studied the relationship between light intensity and the photosynthetic rates of loblolly pine

and certain hardwood associates. They found, as have others, that the maximum rate of photosynthesis for hardwoods was reached at about one-third of full light, whereas the maximum photosynthetic rate of the pine was not reached until the intensity exceeded 90% of full light. This led them to speculate that mutual shading of the pine leaves may be an important factor in the difference in rates of photosynthesis between pines and hardwoods.

In a follow-up study (Kramer and Clark, 1947) this hypothesis was investigated. Working again with loblolly pine, they devised an apparatus which would permit a few leaves to be inserted in a chamber in such a way that no mutual shading would take place while measurements of apparent photosynthesis were being made. Their tests showed that the photosynthetic rate of an entire seedling (where normal mutual shading occurs) increased with increasing light intensity up to the brightest light used (9,200 foot-candles). However, the rate for individual, fully exposed, needles increased only up to about one-third of this intensity and then remained unchanged with further increases in light intensity. They concluded that mutual shading of needles may well account for much of the difference between pines and hardwoods with respect to light intensity needed for maximum photosynthesis.

Bormann (1956), investigating still another aspect of photosynthetic efficiency of loblolly pine seedlings, found that very young seedlings with juvenile needles alone, or with some juvenile and some secondary needles, reached maximum rates

of photosynthesis at relatively low light intensities. Older seedlings with only secondary foliage were less responsive to low light intensities. This helps to explain why pine seedlings can frequently become established under fairly dense forest canopies, but then after a few years tend to die out.

Some further ramifications of the light factor were studied by Hacskaylo and Snow (1959). They studied the development of mycorrhizae on the roots of pine seedlings growing under different conditions of light and soil nutrients. They found that the heaviest formation of mycorrhizae occurred on plants growing in a natural sandy loam soil under full sunlight. On this same soil with only 10% full sunlight, no mycorrhizae developed on the roots of either Virginia pine or eastern white pine, and only a very few developed on loblolly pine.

The interrelationship of photosynthesis and soil moisture has received considerable study. Burns (1926) worked with seedlings of white pine, Norway spruce, Scotch pine, and ponderosa pine. He noted little decrease in net photosynthesis with decreasing soil moisture until the seedlings reached the point where they also showed symptoms of drought. He concluded that decreasing the soil moisture content does not decrease photosynthesis until death from drought is imminent. However, most other investigators have found, contrary to the findings of Burns, that the rate of photosynthesis does decline well before the permanent wilting point is reached (Loustalot, 1945; Negisi and Satoo, 1954; Shimshi, 1963).

Brix (1962) studied the mechanism through which photo-

synthesis is reduced when soil moisture is decreased. Working with seedlings of tomato and loblolly pine, he concluded that the reduction in transpiration and photosynthesis with increasing water stress was caused mainly by increase in the diffusion resistance of the stomates and possibly of the mesophyll cells. He also studied the rates of recovery of leaf turgidity and photosynthesis following rewatering after a drought. By comparing these rates for seedlings with severed root systems and seedlings with intact root systems he found that recovery of the former is much more rapid. He inferred from this that during wilting, changes occur in the root system which reduce the water-absorbing or water-conducting capacity of the roots.

THE PATTERN AND PERIODICITY OF HEIGHT GROWTH AND ITS CONTROLS

A great many studies have been conducted which deal primarily with the seasonal height growth pattern of trees, both coniferous and broadleaf, and either with or without concurrent measurements of environmental factors. Height growth, like any other aspect of growth, is influenced by genetic or internal factors which usually establish a certain basic pattern. This pattern, in turn, is modified to varying degrees by the external or environmental factors.

Considering first the internal factors, a series of excellent, penetrating studies dealing with the controls of cambial and apical activity, and with the time scale of morphogenesis at the stem apex, was conducted by Duff and Nolan (1953, 1958).

In essence, they found that the terminal internode of red pine is formed in two stages. The first stage occurs in one year and comprises the formation of a bud in which the primordia of all parts of the next year's terminal growth are laid down. This stage of growth is largely differentiative. In the following year after the bud has overwintered, the second stage occurs. In this stage the bud undergoes its extension growth, and the primordia of all the parts laid down the previous year undergo their full development to form the new terminal shoot.

The annual shoot elongation of species which develop in this manner goes through what Büsgen and Münch (1931) described as a "great period of growth," Red pine fits this pattern well, its terminal elongation being characterized by an early start, rapid increase in growth, a relatively short season, and an abrupt ending (Cook, 1941). Cook's observations were made in eastern New York, and he also noted that in nearly all of the five growing seasons, height growth was completed by July 1.

Friesner (1942), studying height growth of red pine in Indiana, found a pattern similar to that reported by Cook. Also, he noted that the amount of elongation was related to the initial height of the tree, the most height growth occurring on the trees which were tallest at the start of the measurement period.

Kramer (1943) was impressed by the strong influence of genetic controls over the shoot growth pattern of a species. He studied the amount and duration of growth of eleven different

tree species (including red pine) at Durham, North Carolina. In comparing the height growth patterns in North Carolina with those in New Hampshire, he found that even so large an environmental difference as this merely influenced the absolute length of the growth period, but did not change the basic shape of the growth curve. He felt that, aside from severe droughts or excessively low temperatures which may check growth, the usual variations in environmental factors have little effect on the course of shoot growth.

Kozlowski and Ward (1961), studying shoot elongation of five species of conifers and nine species of hardwoods in central Massachusetts, reached similar conclusions. They felt that the relative independence of the shoot growth pattern from environmental influences is due to the comparatively short period during which shoot growth occurs. In addition, they found that shoot growth of individual trees is fundamentally a variable and intermittent process, with growth taking place in spurts rather than continuously.

Walters and Soos (1963), studying the shoot growth patterns of some British Columbia conifers, also found that the rate of growth, and the dates of annual commencement and termination of growth of individual trees were highly variable phenomena. However, the general form of the growth curves was similar from year to year, again indicating the influence of strong hereditary control. Another finding was that there seemed to be no correlation between the total amount of leader growth and the length of the growing period, an observation

also made by Hanover (1963), working with ponderosa pine. Trees which begin shoot elongation late may still make as much total shoot growth for the season as those starting earlier.

Kozlowski and Ward (1957) studied the seasonal distribution of height growth of five coniferous species in central Massachusetts. They found that the growth curve for red pine in this locality was similar to those reported for this species in North Carolina and New Hampshire. Comparing the periods of maximum growth, however, they noted that in North Carolina the peak occurred in April, in Massachusetts in May, and in New Hampshire in June.

Several investigators have studied the redistribution of stored food reserves and the contribution of various plant parts to seedling height growth. Rutter (1957) studied the annual growth cycle of young Scotch pine trees by following weight changes in various parts through periodic sampling. He found that immediately following bud-break there was a period of about one month in which, although meristematic and extension growth were rapid in both root and shoot, there was no gain in weight by the plant. The fact that, concurrent with this rapid extension growth, there was a significant loss in weight of the old needles suggested that this new growth was mainly at the expense of materials stored in the old needles during the winter.

Allen (1964), using a somewhat different approach, studied similar interrelationships for longleaf pine. He used various combinations of girdling and needle removal to isolate the

individual contributions of the stem, the old needles, the new needles, and the roots to the elongation of the terminal bud. He found that the young trees made 31% of their elongation from food reserves in the woody stem. The roots supplied materials for an additional 15% when the old needles were present, or 29% in their absence. The old needles apparently furnished enough materials for 40% of normal elongation, but this was increased to 54% when the roots were partially isolated from the top by girdling. The removal of new needles from the elongating shoot reduced its growth more than 40%, and the placement of a girdle just below the elongating bud stopped growth completely and almost at once.

While the hereditary controls are strong, environmental factors nevertheless do exert a modifying influence on the shoot growth of trees. The light factor has received much attention, with both the intensity and duration aspects being widely studied. Logan (1959) studied the effects of light on the growth of 4-year-old white pine seedlings. He used five different light intensities; namely, full sunlight, 55% light, 22% light, 19% light, and 14% light. He found no significant differences in seedling heights between those grown in full light and those grown in 55% light; also none between those grown in 22% light and those in 19% light. There was, however, a very decided difference in height growth between the levels of 55% and 22% light, and also between 22% and 14% light.

Fraser (1959) studied the germination and early growth

of jack and red pine as related to the number of hours of exposure to direct sunlight. He found that the newly-germinated red pine seedlings made the best height growth with a 6-hour exposure, and that height growth was less for periods that were either shorter or longer. Fraser speculated that the decreased height growth with exposure periods of greater than six hours may have been due to an adverse effect on root development because of excessive heating and drying of the soil under the long exposure periods.

Baldwin (1931) measured weekly terminal shoot elongation of eight conifers in the Northeast. He found that the growing period was somewhat longer in the open than in the forest and also reported that shade had the general effect of delaying the start of growth.

Soil moisture is frequently regarded as not being too important in influencing the current year's shoot elongation of many species, especially those which make very rapid early season growth and complete their elongation before the midsummer drought periods occur (Kozlowski and Ward, 1961). However, for some species and under some conditions, it can be significant. Pearson (1918) found that height growth of ponderosa pine saplings was strongly influenced by the April and May precipitation of the current growing season on sites where moisture is frequently limiting. During years in which the moisture stored during the winter months was supplemented by frequent rains in April and May, height growth was much greater than when the April and May precipitation was low. White (1958)

found that on coarse soils in Michigan following an unusually dry spring, both terminal growth and needle length of pines were considerably less than during previous, more normal, growing seasons.

Williston (1951), studying the annual height growth of loblolly and shortleaf pine seedlings at Crossett, Arkansas, concluded that the amount of rainfall does not appear to affect the length of the growing period as much as it affects the amount of height growth. However, Husch (1959), studying the height growth of white pine in New Hampshire, found that the cessation of growth in late summer was controlled by an interaction of photoperiod and soil moisture. Leader elongation continued longer in years of ample soil moisture than in drier years.

Leyton (1954) studied the growth of Sitka spruce, Scotch pine, and Corsican pine on heathlands in Great Britain. He found that shoot growth responded noticeably to improved moisture conditions during the early months of the current growing season, but felt that, in general, height growth was influenced more by conditions of the previous than of the current year. Motley (1949) also noted this correlation between previous year's rainfall and current year's shoot growth for white and red pine in Indiana.

Zahner (1962) studied the terminal growth and wood formation of young loblolly pine trees under two soil moisture regimes. Under the wet regime the soil moisture content was kept between 80% and 100% of field capacity all year. Under

the dry regime the soil was maintained near field capacity only during the winter and early spring and was allowed to approach the wilting point during the summer. During the last pre-treatment season all trees in the study added three internodes of height, which is normal multiple flushing for loblolly pine after it passes the seedling stage. However, during each of the two treatment years, the trees under the wet regime added four internodal flushes of terminal growth, and those under the dry regime added only two. Also total height growth of the former was twice that of the latter for each year of treatment.

The temperature factor also seems to be of considerable importance in modifying the shoot growth pattern of trees. Baldwin (1931) measured weekly shoot elongation of eight species of conifers in the Northeast. He concluded that temperature was the most important factor in determining both the beginning and the rapidity of height growth. Also, he found that little growth took place until mean weekly soil and air temperature reached 50°F.

Farnsworth (1955) found that shoot elongation of red pine was very responsive to increases in temperature until it reached its seasonal growth peak. Thereafter it was much less responsive to temperature variations. Corsican pine is also strongly responsive to temperature, the rate of shoot growth doubling with an increase of 7°F. in mean shade temperature (Hiley and Cunliffe, 1922).

Hertz (1929) reports that an increase in temperature

accelerates, and a drop in temperature delays shoot elongation. Reed (1939) found that temperature appeared to control the seasonal course of shoot growth for both shortleaf and loblolly pine. Kramer (1957) studied the effects of various combinations of day and night temperatures on the height growth of loblolly pine seedlings. He found that the best growth occurred when there was a large difference between day and night temperatures, and very poor growth resulted when the seedlings were kept at a constant temperature. The highest temperature resulted in the most rapid resumption of growth in the spring, and the most spring growth, but also resulted in less growth after mid-summer, and earlier cessation of growth.

Kienholz (1934), observing various growth aspects of five coniferous species near Keene, New Hampshire, found that daily needle elongation showed a positive correlation with daily mean temperature. This correlation was most evident when growth was either very slow or very rapid.

Numerous additional studies could be cited which have dealt with the influence of environmental factors on seedling growth, but the foregoing review is representative of the principal findings which are of special relevance to the present study.

By way of summary it may be stated that most ecologists today recognize that the growth responses of a plant represent the interaction of the plant's genetic make-up and the entire array of environmental factors impinging upon it. They are aware that Liebig's Law of the Minimum which states, in essence,

that the rate of growth of an organism is controlled by that factor which is available in the smallest amount can no longer be taken at face value. The law still retains much usefulness but, as Spurr (1962, p. 16) points out, in its modern form it is usually restated to take into account the interactions existing between the various single factors. Thus, it is generally recognized today that the individual factors of the environment do not act as separate forces with simple and direct effects on a plant, but rather that their influences are interrelated and that a change in one may well bring about changes in the requirements of the plant for the others.

DESCRIPTION OF THE STUDY AREA

LOCATION AND CLIMATE

The study was located on the Cutfoot Experimental Forest, a part of the Chippewa National Forest, in north central Minnesota. It is near latitude 47°30' N, and longitude 94°W.

The climate is typically continental with maximum precipitation occurring during the growing season. Long-term weather records for Winnibigoshish Dam (about 9 miles south of the study area) show the average precipitation during the growing season to be distributed as follows: May, 2.83 inches; June, 3.66 inches; July, 3.75 inches; August, 3.22 inches; and September 2.38 inches. This 5-month period normally receives 67 percent of the total annual precipitation of 23.67 inches (U.S. Dep't. Comm., Weather Bureau, 1962). Summers are typically warm and relatively humid, with the average annual maximum temperature being about 95°F. (U.S. Dep't. Agric., 1941).

Winters are long and characterized by periods of severe cold intermingled with periods of more moderate temperatures. The average annual minimum temperature is about -40°F. (U.S. Dep't. Agric., 1941). Winter is also the season of least precipitation, the 3-month total for December, January, and February averaging only 2.08 inches, almost all of which occurs as snow.

Even though maximum precipitation occurs during the growing season, there are periods during which evapotranspiration exceeds precipitation. When this continues for a long enough

time, a drought condition develops. The probabilities of soil moisture stress occurring during each month of the growing season in Minnesota have been computed (Blake et al., 1960), based on average daily precipitation, available water-holding capacity of the root zone, and the calculated daily rate of water loss by evapotranspiration (by Penman's method).

These calculations show that in the north central part of the state where the present study was located, and on soils with similar water-holding capacities, the probability is 50% that there would be at least 12 drought days (days with no available soil moisture) during May, 11 during June, 14 during July, 12 during August, and 10 during September. In other words, in one year out of every two it is probable that there will be no available soil moisture on one-third or more of the days during the growing season. This is on the assumption that the rooting zone is limited to the upper foot of soil, which is the case with young seedlings. Older trees, of course, have much deeper root systems and can utilize water stored at much lower levels. Consequently the number of drought days which they would experience per season would be far fewer.

Expressed in terms of inches of water deficiency per month, the deficiency in May will probably be at least 1.44 inches one year in every two, the June deficiency will be 1.65 inches, the July deficiency 2.24 inches, the August deficiency 1.56 inches, and the September deficiency 0.90 inches. This means a growing season deficiency of about 7 or 8 inches of water in the upper foot of soil in one year out of every two on sandy soils such as

those on the Cutfoot Experimental Forest.

VEGETATION

The study was installed on a site recently occupied by a mixed stand of red and jack pine. The pine on this area was clear-cut in 1956 due to severe porcupine damage to this portion of the stand. The hazel brush and other understory vegetation which had been present prior to cutting responded vigorously to the reduced overstory competition, and within about two years it formed a nearly solid and uniform brush canopy in the clear-cut area. This made it an ideal site for a study of the influence of brush competition on young red pine seedlings.

By far the major component of this brush community was hazel brush (chiefly beaked hazel, but also some American hazel). It comprised about 70 percent of the sheer bulk of vegetation on the area, and ranged in height from two feet to about six feet, with an average height of about four feet.

A listing of the most common plants present on the area is given in Table 1. The list is undoubtedly incomplete, but whatever species may be omitted would comprise less than five percent of the plant community in terms of space occupied.

TOPOGRAPHY AND SOIL

The topography of the area is gently to moderately rolling, with the landforms being the result of glacial activity. Specific details of the glacial history are still in doubt, but recent studies (Wright, 1962; Arneman and Wright, 1959) indicate

Table 1. List of the most common shrubs and herbaceous plants growing on the study area.[1]

Common Name	Scientific Name
Beaked hazel	Corylus cornuta Marsh.
American hazel	Corylus americana Walt.
Prairie willow	Salix humilis Marsh.
Raspberry	Rubus sp.
Round-leaved dogwood	Cornus rugosa Lam.
Green alder	Alnus crispa (Ait.) Pursh
Juneberry	Amelanchier spp.
Pin-cherry	Prunus pensylvanica L.
Brake	Pteridium aquilinum (L.) Kuhn
Blueberry	Vaccinium spp.
Rose	Rosa spp.
Blackberry	Rubus sp.
Wild sarsaparilla	Aralia nudicaulis L.
Large-leaved aster	Aster macrophyllus L.
Wild pea	Lathyrus venosus Muhl.
Wild strawberry	Fragaria virginiana Duchesne
Mountain-rice	Oryzopsis asperifolia Michx.
Sweet-scented bedstraw	Galium triflorum Michx.
Bluebead lilly	Clintonia borealis (Ait.) Raf.
Ragwort	Senecio sp.
Early meadow-rue	Thalictrum dioicum L.

Also some grasses and sedges.

1/ Nomenclature follows Gray's Manual of Botany, Eighth ed., by M. L. Fernald.

that the latest glacial activity in the area was either the Mankato or Valders advance of the Wisconsin period. Radiocarbon dating places the former as occurring about 12,000 years ago, and the latter about 11,000 years ago (Wright and Rubin, 1956).

The soils have subsequently developed from a gray-drift outwash derived primarily from the limestones and shales of Manitoba. Specific soil types on the Cutfoot Experimental Forest have never been described, since this area to date has not been included in any soil survey or mapping project.

However, recent reconnaissance which has been conducted by the University of Minnesota Soils Department[1/] indicates that the soil sola on parts of the experimental forest consist of brown podzolics developed on medium to coarse outwash sands. The "A" horizon textures are typically loamy sands to medium and coarse sands. Relatively narrow (1- to 3-inch) textural layers are found in some areas between depths of 6 and 9 feet, and elsewhere as near to the surface as 2 to 4 feet.

As part of the present experiment the soil on the study area was examined in some detail. A soil pit was dug to 54 inches, and a soil auger used in the bottom of the pit to probe to a depth of 8 feet. The main purpose of the deep probing was to determine whether or not a water table existed within capillary reach of the surface. None was found.

Soil samples were taken from the various strata exposed in this pit, and their characteristics are shown in Table 2. The chief features of interest are the high percentage of total sands present in all strata throughout the profile; the rather pronounced pH change from moderately acid to strongly basic as sampling proceeded from the surface to about the 3-foot depth; and the large percentage of coarse material (larger than 2 mm. in diameter) occurring at depths below 15 inches. Some scattered clay lenses were also noted, however, at depths of about 3 feet, which give the subsoil better moisture-holding characteristics than would otherwise be expected.

1/ Under the direction of H. F. Arneman and D. Pluth.

Table 2. Characteristics of soil strata to depth of 54 inches on the experimental area. Samples were obtained from a soil pit, and each entry is the average of two separate runs. All percentages are on a weight basis.

Item	Sampling zone					
	0-1" (A_1)	1"-6"	6"-15"	15"-30"	30"-39"	39"-54"
Percent clay		2.35	1.70	3.50	3.55	0.80
Percent silt		14.00	6.85	5.55	4.00	0.30
Percent total sands		83.65	91.45	90.95	92.45	98.90
		100.00	100.00	100.00	100.00	100.00
Percent very coarse sand		7.80	8.95	16.35	18.85	11.70
Percent coarse sand		16.30	16.25	28.55	36.25	35.45
Percent medium sand		27.15	30.90	26.55	27.25	45.55
Percent fine sand		25.75	30.80	17.05	8.60	5.95
Percent very fine sand		6.65	4.55	2.45	1.50	0.25
Percent total sands		83.65	91.45	90.95	92.45	98.90
Percent of total sample which is larger than 2 mm.		9.9	9.4	25.6	25.7	5.9
pH 1/	5.7	5.4	5.6	6.0	8.0	7.4
Bulk density (grams/cc) 2/		1.30	1.40			
Percent organic matter 3/	6.83	1.65	0.81			

1/ As determined by Hellige-Truog soil reaction tester.
2/ Each value represents the average of three samples.
3/ Determined by loss-on-ignition method.

In addition to the samples taken from the soil pit, composite samples of the upper 15 inches of soil were taken from nine other spots on the study area. These were subjected to mechanical analyses, the main purpose being to obtain some measure of the variability in surface soil texture on the experimental area. Only the upper 15-inch zone was sampled because this was the zone in which virtually all of the seedling roots developed during the course of the study. These nine samples were taken at the end of the experiment after the seedlings had been lifted.

A systematic pattern was used in taking these samples to insure that all portions of the area would be represented. Sampling was begun on plot 5, which was the most easterly one, and then samples were taken from every tenth plot thereafter; i.e. 15, 25, 35, etc. to plot 85. Table 3 shows how these samples compare in the particle-size analyses.

It is apparent from this table that the texture of the surface soil is quite uniform throughout the area. The range in percent of clay between the plots having the greatest and the least amounts is only 1.30, the range for silt is only 7.95, and for total sands only 8.75. Variations within a given sand particle size class are greater, but on all plots except 75 and 85 the big majority of sand particles fall into either the medium or fine sand categories. On these two plots the medium size still predominates, but the coarse category slightly exceeds the fine category.

Table 3. Mechanical analysis[1/] of soil samples from nine plots on the study area taken from the upper 15 inches of soil. Values are percent (by weight) of the total sample passing through a 2 mm. sieve. Each entry is the average of two separate runs.

Particle class	Plot 5	Plot 15	Plot 25	Plot 35	Plot 45	Plot 55	Plot 65	Plot 75	Plot 85	Ave.
Clay	3.05	3.30	2.90	2.95	3.55	2.25	3.00	2.35	2.75	2.90
Silt	12.30	12.25	11.20	12.55	16.20	10.95	11.35	10.65	8.25	11.74
Total sands	84.65	84.45	85.90	84.50	80.25	86.80	85.65	87.00	89.00	85.36
Total sample	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Sand classes:										
Very coarse sand	4.75	5.65	2.85	2.30	3.15	4.80	3.80	8.05	7.95	4.81
Coarse sand	12.30	13.55	10.70	8.70	9.90	12.75	11.10	23.95	23.20	14.02
Medium sand	29.95	29.90	29.70	25.30	24.95	22.70	20.20	33.15	36.35	28.02
Fine sand	30.60	28.45	34.65	37.35	33.50	35.65	35.05	18.40	18.60	30.25
Very fine sand	7.05	6.90	8.00	10.85	8.75	10.90	15.50	3.45	2.90	8.26
Total sands	84.65	84.45	85.90	84.50	80.25	86.80	85.65	87.00	89.00	85.36

1/ Using the hydrometer method.

EXPERIMENTAL DESIGN, TREATMENTS, AND INSTALLATION

The study involved two levels of light and three levels of soil moisture, or a total of six treatments. Each treatment was represented by 15 single-tree plots (15 replications), thus providing a total of 90 seedlings for detailed observations during the two growing seasons. Since the area appeared to be quite uniform, there was no reason to subdivide it into blocks. Therefore a completely randomized design was chosen in which any of the 90 pre-selected spots could be assigned any one of the six treatments.

The six treatments were as follows (also see Fig. 1):

1. Full competition for light; full competition for moisture; natural rainfall only.
2. Full competition for light; no competition for moisture; natural rainfall only.
3. Full competition for light; no competition for moisture; natural rainfall plus supplemental water during dry periods.
4. No competition for light; full competition for moisture; natural rainfall only.
5. No competition for light; no competition for moisture; natural rainfall only.
6. No competition for light; no competition for moisture; natural rainfall plus supplemental water during dry periods.

The seedlings used for this study were 1-year-old red pine seedlings obtained from the U.S. Forest Service nursery at Eveleth, Minnesota. They were grown from seed collected on the Chippewa National Forest in 1957. The seedlings were not root-pruned, either at the nursery or in the field, prior to planting.

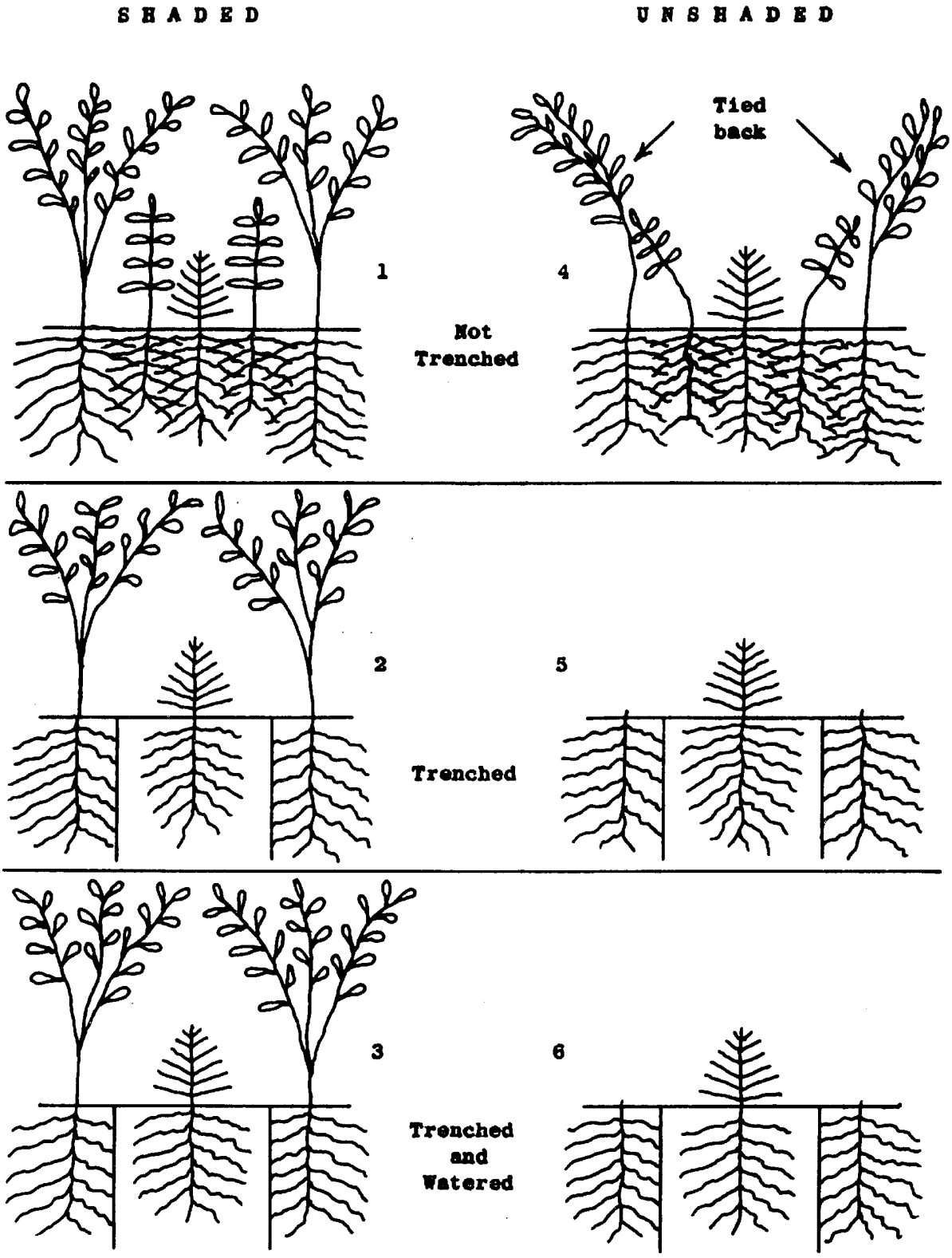


Figure 1. Treatments employed in the study.

This type of stock was selected in preference to older stock because it could be more easily planted in the dense brush with a minimum of disturbance to the environment, and because the shock of transplanting was likely to be less than with larger stock.

The center-hole method of planting was used in which a hole was dug with a soil auger, and the seedling roots then spread out as much as possible in the hole while soil was sifted in around them.

On treatment 1, where full brush competition was desired, the brush was disturbed as little as possible when the seedling was planted. Rapid development of competitive conditions between the brush and the seedling was thus encouraged.

Treatments 2, 3, 5, and 6 all involved the elimination of root competition, this being accomplished by means of trenching. On all four of these treatments a one-foot-deep trench was made by inserting a tiling spade around the perimeter of a circle whose area was exactly one square foot. A sheet-metal cylinder (Fig. 2) was then inserted in the trench to provide a permanent root barrier. Next, all vegetation growing inside the cylinder was pulled out, removing as many of the roots as possible without too seriously disrupting the natural soil profile. All of these operations--the trenching, the insertion of the cylinder, and the removal of the vegetation inside the trench--were done before the pine seedling was planted.

Treatment 4 involved the elimination of competition for light, but the retention of competition for soil moisture.



Figure 2. Sheet-metal cylinder used for eliminating root competition. (Cylinders are 12 inches high and 1 square foot in cross-sectional area).

This was accomplished by tying the stems of the brush and herbaceous plants to one side or another, thus permitting full (or nearly full) sunlight to reach the planted seedling, while still leaving the roots of the competing vegetation undisturbed to withdraw moisture from the same soil in which the seedling would be growing (Fig. 3).

On treatments 5 and 6 where both above-ground and below-ground competition were to be eliminated, the stems of all brush and herbaceous species which would cast shade on the plot were clipped at the ground-line. Occasionally a slight compromise was made, and a stem which was needed to provide shade on an adjacent plot was left standing if it only shaded the cleared plot early in the morning or late in the afternoon.

Treatments 3 and 6 involved the addition of supplemental water during dry periods, but otherwise they were the same as treatments 2 and 5, respectively. They were included to insure that on at least one treatment under each light condition soil moisture would never be limiting. It was possible to assure that light would not be limiting on certain treatments by simply manipulating or removing aerial parts of the vegetation. However, optimum moisture conditions could be assured only by supplying additional water artificially when rainfall was inadequate.

The amount of water needed each week was determined by computing the potential weekly evapotranspiration by Thornthwaite's method, using the graphic technique described by Palmer and Havens (1958). Weekly precipitation was measured



Figure 3. Brush tied back to eliminate shading but still permitting root competition. (Note protective conical screen over seedling at center of picture).

with a recording rain gauge located at the study site. To the extent that the precipitation fell short of equalling the potential evapotranspiration in any given week, water was artificially added to the plots on treatments 3 and 6.

In practice the water thus added was somewhat in excess of the actual evapotranspiration on the plots for several reasons. For one thing, Thornthwaite's method assumes full occupancy of the site by vegetation. In the present study the small pine seedlings which were planted inside the trenched plots fell considerably short of meeting this requirement, at least during their first year in the field. Hence, less water was removed from the soil through transpiration than would be the case if the ground were fully occupied.

Secondly, any excess of precipitation over potential evapotranspiration in a given week was ignored in computing the water requirements of subsequent weeks. This was done because of the sandy nature and rapid internal drainage of the soil profile, which might lead to the development of soil moisture stresses in the surface 6 or 8 inches even though the lower parts of the profile were amply recharged. The objective here was not the precise application of Thornthwaite's water-balance technique, but rather the assurance that the moisture in the upper foot of soil was always maintained at or near field capacity. Thornthwaite's method served primarily as a convenient guide to indicate the expected water loss under ideal conditions for any given week.

It was unfortunate that steps were not taken to assure

that the other soil moisture extreme (a serious drought condition) would also be represented. The year immediately preceding the study installation had been unusually dry, and it was hoped that the drought effects would at least partially carry over into the following year. This proved to be a vain hope, however, since the growing season precipitation in 1962 was considerably above normal. In retrospect, it would have been better to exclude moisture from one pair of treatments with artificial rain shields of polyethylene or some other transparent material, even though these have some undesirable side effects on factors such as temperature and air movement.

For various reasons planting of the red pine seedlings was unavoidably delayed until late in May of 1962. By this time the seedlings had already broken dormancy and had begun to candle out. Planting conditions were good, however, with cool temperatures, cloudy skies, and occasional drizzle. Nevertheless, within about two weeks 10 seedlings showed dieback of the new shoot growth. These 10 were then replaced by healthy seedlings which had been "heeled in" nearby for just such an emergency.

There was no reason to believe that the tip-dying was in any way related to treatment, since the injured seedlings were found throughout the area and on all treatments except number 2. And, at the time that the injuries occurred, treatments 2 and 3 were identical, since no supplemental water had yet been added on the latter.

In addition to the 10 seedlings on which the new shoot

growth had died back, one seedling was damaged by rabbit nibbling. This tree was also replaced with an undamaged one, and all seedlings were subsequently protected from this type of damage by covering them with conical (and later cylindrical) screens made of 1-inch-mesh poultry netting.

MEASUREMENT OF ENVIRONMENTAL FACTORS

The five environmental factors which were measured in this study included light, soil moisture, air temperature, precipitation, and relative humidity. Interest was centered primarily on the first two, but the others are useful in describing the general climatic conditions under which the seedlings developed.

LIGHT

Light, as a factor in this study, encompassed the full range of effects associated with the broader term "solar radiation," including the invisible as well as the visible rays of the spectrum, and all forms of energy found in ordinary sunlight. However, for practical reasons, only the visible components were measured in this study, although some related temperature data (as described in a later section) were also obtained.

Measurements of light or solar radiation are usually made in one of two ways. Either a number of instantaneous readings are taken under a variety of conditions and then averaged; or some instrument is used which integrates light energy for whatever measurement period is desired, and these cumulative readings under different conditions are then compared. Both techniques are useful, and each has its place in ecological research.

The purposes of the present study seemed to be best served by measuring the light intensity over a period of time, that is,

by obtaining cumulative light measurements. However, most commercially available instruments for recording such measurements are quite expensive, and since it was desired to take simultaneous readings at all 90 seedling locations, the use of such elaborate and costly instruments was precluded.

Fortunately, several much less expensive (though admittedly less accurate) means of making cumulative light measurements have been developed. Among these are chemical light meters using anthracine (Dore, 1958; Marquis and Yelenosky, 1962); those using potassium iodide (Pearsall and Hewitt, 1933); and those using uranyl oxalate (Atkins and Poole, 1930). Photographic methods have also been in use for some time and, as Friend (1961) points out, they are easier to use than most chemical methods because the latter usually require titrations or spectrophotometer estimations. For these reasons the Ozalid paper method described by Friend (1961) was adopted with minor modifications. Details of the method, including the assembling, developing, and calibrating of the packets, are given in Appendix A.

In applying the method in the field, a wire holder with a horizontal loop at the top was inserted into the ground next to each seedling (Fig. 4). These were installed early in the first growing season and left in place for the remainder of the experiment so as not to damage the seedling root systems by repeated insertion and removal. The holders were designed to hold the light packets in a horizontal position just above the terminal shoots of the seedlings, and the loop could be



Figure 4. Making a cumulative light measurement in the field with the Ozalid paper light meter. (Number in foreground is the plot number).

swung aside when light measurements were not being taken. The holders were of sufficient length so that they could be gradually pulled up as the seedlings grew taller.

On days when a light measurement was to be made, the prepared packets were brought to the study area in a closed briefcase. At the proper time they were set out as rapidly as possible on the holders, and in the afternoon picked up again in the same sequence, numbered with a grease pencil, and returned to the briefcase. They were then brought into the laboratory for dismantling, developing, and counting the exposed sheets as described in Appendix A.

During the course of the study seven such light measurements were made, three in 1962 and four in 1963. They were taken at approximately monthly intervals, the 1962 ones being in July, August, and September, and the 1963 ones in May, June, July, and August. Except for the September measurement, which was made after most aspects of growth were essentially completed, these measurements give a good portrayal of the comparative light conditions under which the 90 seedlings grew during their two years in the field.

Most of the days on which light measurements were taken were clear and bright, although some were partly cloudy or hazy. Some bias thus exists in favor of bright days, but it is felt that the average light values obtained are nevertheless a good index of the relative light intensities which prevailed at the various seedling locations during the two seasons of observation.

The usual exposure period was 6½ hours, although on one occasion the packets were left out for a full 24 hours, primarily to test the durability of the wrapping materials. The relative light values between treatments were, however, the same regardless of exposure duration.

Light measurements were always made under the protective screens which covered the seedlings. Since these screens were intended primarily to afford protection against rabbits, their open mesh intercepted very little sunlight. During each light-measuring period, test packets were placed outside some of the screens, and rarely did they record more light than their counterparts underneath the screens. Thus for all practical purposes, the amount of light which each seedling received was determined solely by the presence or absence of competing vegetation.

It should be mentioned that the manner in which these packets were assembled and held in position limited their detection of light to that which comes mainly from above. While this is the direction from which by far the greatest amount of solar radiation is received, it is true that the reflected radiation from below and from the side is also of some consequence in plant growth. These could not be measured by the technique used here, but Friend (1961) suggests that the method can be adapted to measure light falling on a spherical surface rather than on a flat surface by the simple expedient of cementing half a celluloid table tennis ball on top of the lid of a plastic dish in which the packet can be exposed.

SOIL MOISTURE

The four major methods currently in use for determining soil moisture are (1) gravimetric, (2) resistance blocks, (3) tensiometers, and (4) neutron scattering. Each has its advantages and disadvantages. Of these four the last two were quickly eliminated as possibilities for this study, the tensiometers because they are not satisfactory when moisture content drops much below field capacity, and the neutron method because of the high cost of equipment. The choice between the first two was made in favor of the gravimetric method, primarily because the use of resistance blocks involves certain calibration and other problems.

The gravimetric method does have one serious disadvantage in that it involves the removal of a soil sample from the site each time a determination of moisture content is to be made. This causes soil disturbance which could pose a problem when repeated samples are taken from a small area. Several steps were taken to minimize the magnitude of such disturbances.

One step was to use a small-diameter sampling tube as shown in Figure 5. This sampler was made from a piece of brass tubing 12 inches long and 7/16 inch in diameter. The leading edge of the tube was serrated so that, when twisted into the soil, it could effectively cut through small roots and other obstructions. A small supplemental study in which this sampler was compared with the conventional King tube sampler is described in Appendix B.

Soil moisture sampling was done at weekly intervals except



Figure 5. Small-diameter sampling tube used in obtaining soil samples for moisture content determinations. Serrated edge aided in severing small roots as sampler was twisted into the soil to the desired depth.

during rainy periods, with care being taken never to sample the same spot more than once during the course of the study. To avoid excessive site disturbance, and also because it was not feasible to sample all 90 plots each week, the plots were randomly grouped into 5 sampling series. Each series contained 3 plots from each treatment, and only one series was sampled each week.

Soil moisture samples during 1962 were taken from the 2- to 8-inch depth. This was considered sufficiently deep to sample the zone in which the seedling roots would be growing during their first field season, since they averaged only about 5 inches long at time of planting. The surface 2 inches were deliberately omitted because of the considerable variability in the thickness of the A_1 horizon, and consequently of the organic matter content at the surface. Also, planted seedlings, in contrast to those starting in the field from seed, have relatively few roots near the surface, at least for the first year or two. This is because the roots at the time of planting are wet when removed from the planting box or pail, and even the laterals hang downward into the planting hole. This condition was further fostered in the present study by sifting soil around the roots from above to refill the planting hole, and then adding water from above to force out the air pockets.

During 1963 the soil moisture samples were taken from the 2- to 10-inch depth. The deeper sampling was intended to keep pace somewhat with the downward extension of the root systems during the second field season, and yet not reach below the

bottom of the sheet-metal cylinders which extended to about 11 inches below the soil surface.

Soil moisture percentages, by themselves, are of little value as indices of moisture stress since they fail to tell how readily available the moisture is to plants. Consequently, two soil moisture release curves were developed (Fig. 6) to show the amount of moisture present in the soil at various tensions for both the 0-6 and 6-15-inch depths. For each depth, four samples were run at each of six tensions. The laboratory data are given in Appendix B.

As can be seen from the curves in Figure 6, the soil water in this sandy soil is very readily available (held at tensions of 2½ atmospheres or less) until the water content, by weight, drops to less than 5% in the upper 6 inches, and to less than 3% in the 6- to 15-inch zone. The permanent wilting point (15 atmospheres tension) was not reached until the moisture content had dropped to about 3½% in the surface soil, and 2% in the zone below it. At the other extreme the curves do not extend far enough to show true field capacity since the lowest tension used in the laboratory (0.1 atmosphere) was not low enough to establish this constant for such sandy soils. However, based on field samples taken 24 to 48 hours after heavy rains, the field capacity is probably in the range of 12 to 15 percent moisture by weight in the upper foot of the soil.

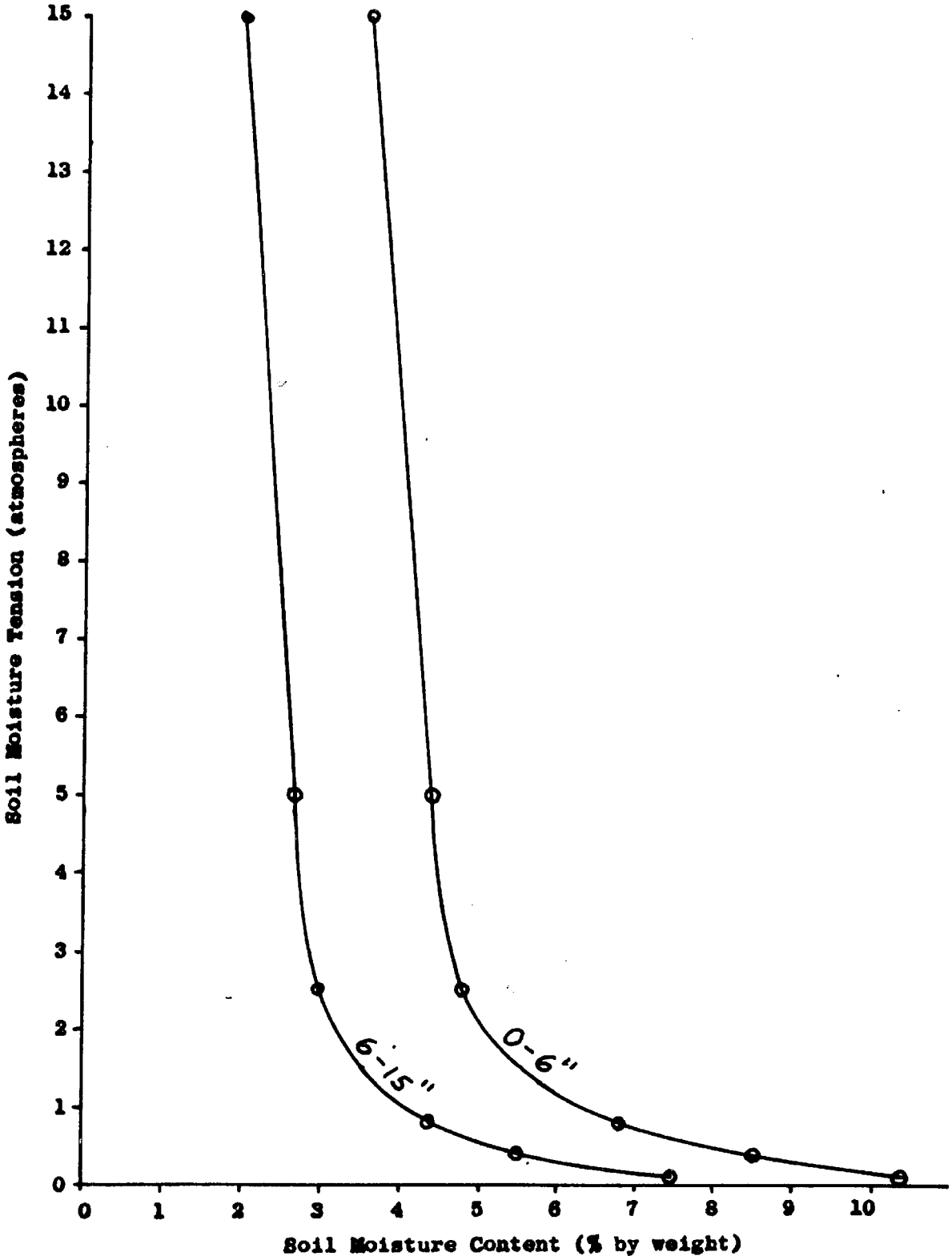


Figure 6. Soil moisture release curves for two soil depths. Each plotted point is a mean of four samples.

TEMPERATURE

During the two growing seasons of 1962 and 1963, temperature data were obtained for the experimental area by means of a recording-type hygrothermograph installed in a standard instrument shelter (Fig. 7). The floor of the shelter, however, was only about 18 inches above the ground because temperature information near seedling level rather than at the conventional 4½-foot height was desired. The accuracy of the temperature data recorded by the hygrothermograph was checked weekly by comparison with Weather Bureau type maximum and minimum thermometers housed in the same shelter. No temperature data were obtained during the winter months.

In addition, during the 1963 growing season, weekly maximum and minimum air temperatures were obtained near a representative seedling on each of the six treatments. This was done by means of the U-shaped Taylor maximum-minimum registering thermometers (no. 5458) mounted on the north side of a stake and shielded from above against sun and rain (Fig. 8). These thermometers are less accurate than the Weather Bureau type, but are very convenient to use and sufficiently accurate to provide useful information for comparisons between basically different micro-environments.

The primary consideration in choosing the six plots to represent the six different treatments was that they be as close as possible to one another. This was to minimize possible differences in elevation, slope, air drainage, and factors other than treatment which might have some influence

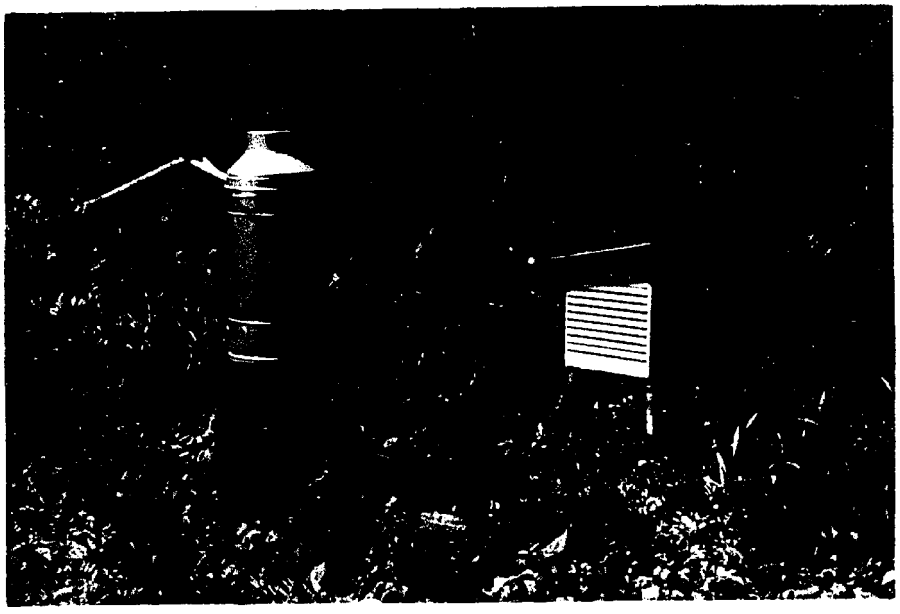


Figure 7. Instrument shelter and recording rain gauge installed on study area.

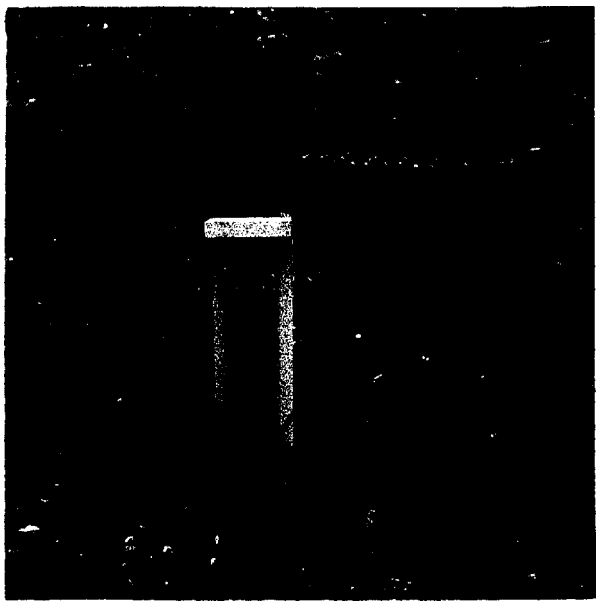


Figure 8. Measurement of maximum and minimum temperatures near seedling, using a Taylor Model 5458 recording thermometer. (Thermometer is mounted on the north side of the supporting holder).

on air temperatures on the plots.

It is regrettable that soil temperature measurements were not taken, since differences may well have been large enough to influence seedling development differently on the various treatments. With the benefit of hindsight, temperature just below the soil surface, and perhaps at a depth of about 6 inches might have been significantly related to root development and general seedling growth. The investigation of such possible correlations will have to await a future experiment.

PRECIPITATION

Precipitation was measured on the study area by means of a Belfort recording rain gauge (Fig. 7). This information was needed, along with temperature, to work out the weekly water requirements for the plots on treatments 3 and 6. It was also needed to characterize the relative wetness or dryness of the two growing seasons as they compare with the long-term means for the area.

RELATIVE HUMIDITY

The relative humidity was obtained simply as incidental information in getting the temperature data with the recording hygrothermograph. It is of interest only as another means of characterizing the general atmospheric conditions which prevailed during the course of the study. No attempt was made to correlate relative humidity with any of the seedling growth responses.

MEASUREMENTS AND OBSERVATIONS ON SEEDLINGS

During the first field season, height growth was the only seedling characteristic which was measured on a weekly basis, and because of the late planting date, some height growth had already been made before measurements were begun. The reference point for height measurements was the soil surface on the north side of the seedling stem. The soil was leveled and firmed before the seasonal measurements were begun. This admittedly is not as unchangeable a reference point as is a pin or other object inserted into the seedling stem, but because the seedlings were only one year old when the experiment was started, it was felt that serious injury might be caused by such a marking technique. The method used seemed to be satisfactory, particularly since the protective screens kept most rodents and other burrowing creatures from disturbing the soil around the seedling. Height was measured to the tip of the terminal bud with a rule graduated in millimeters.

Additional measurements were made on each seedling at the end of the first growing season. These included calipering, to the nearest 0.1 mm., the length and diameter of the terminal bud, and the stem diameter at ground-line. Also, five needle pairs, selected at random on the new terminal shoot, were measured to the nearest 1 mm. In the majority of cases the two needles in each fascicle were virtually identical in length, but when one occasionally was longer than the other, the longer of the two was measured. Also, the number of lateral buds

surrounding the newly formed terminal bud was counted.

During the second field season, weekly measurements of height growth were made as before. In addition, as height growth was approaching culmination on the main stem, and after the new winter terminal and lateral buds began to set, some of these lateral buds broke dormancy and put on a second surge of growth. These lammas shoots in many cases grew taller than the main terminal or apical shoot and, when this occurred, height measurements were also made weekly on the tallest lateral shoot.

Also during the second field season, three of the newly elongating needle pairs on the terminal shoot of each seedling were measured weekly. Selection of the sample needles was done mechanically by dividing the new shoot into quarters and selecting the needles which originated nearest to the one-quarter, one-half, and three-quarter points on this shoot. The needles were marked for subsequent identification by means of tiny loops of colored thread which were slipped over the ends of the needles and worked down to the base of the fascicle sheath.

Weekly measurements of the newly developing winter buds were also contemplated, but because of the extreme delicacy of these structures during their period of formation, it was decided not to subject them to weekly handling, especially under the sometimes less than ideal field conditions. Measurements were therefore taken only at the end of the growing season.

In addition to the terminal bud measurements, numerous other field measurements and observations were made at the end of the second growing season. These included calipering the

stem diameter at ground-line, counting the total number of buds on the seedling, and counting the number of lammas shoots. Also, when the seedlings were lifted for obtaining additional data in the laboratory, measurements were made of the longest root present on each seedling.

The laboratory measurements and observations for each seedling included a count of all 1963 needles produced on the main stem, the lateral shoots, and the lammas shoots; also, the green weight and the oven-dry weight of the entire seedling; and the oven-dry weight, separately, of the roots, the stem (including branches and buds), and the needles.

RESULTS

TREATMENT INFLUENCES ON ENVIRONMENT

Before considering the results of the study in terms of seedling response, it is of interest to note how the various treatments modified the physical environment in which the seedlings were growing. These modifications will be discussed separately for each of the three factors of light, temperature, and soil moisture.

LIGHT

As mentioned earlier, seven light measurements using the Ozalid paper packets were made during the course of the study. However, the one taken in late September of 1962 was made after nearly all growth for the season had been completed, and it was therefore excluded from the averages. The results of the remaining six measurements are averaged and summarized in Table 4.

It is evident from this table that at the time of the May 23 measurement, the brush species were just beginning to leaf out. At this time the shaded treatments (1, 2, and 3) averaged only about 20% less light than the unshaded treatments (4, 5, and 6). This May measurement is of interest, however, because active shoot elongation of the red pine seedlings was already underway by this date.

The remaining five measurements were made when the brush foliage was fully developed, although some drying and shriveling had begun by late August. A more detailed description of the

phenological development of the vegetation on the study area is given in Appendix D.

Table 4. Average percent of full light received by seedlings in each treatment during the two growing seasons. Each value for a specific date is the average of 15 determinations using the Ozalid paper light meter.

Date 1/	Shaded			Unshaded		
	Trmt 1	Trmt 2	Trmt 3	Trmt 4	Trmt 5	Trmt 6
	(average percent of full light received)					
5-23-63	62	69	63	81	90	88
6-21-63	5	9	6	80	88	85
7-12-62	6	7	6	80	90	83
7-18-63	6	8	7	73	87	80
8-20-63	9	10	7	84	74	83
8-22-62	13	12	12	77	87	85
Ave. (excluding 5-23-63)	8	9	8	79	85	83
Ave. (all dates)	17	19	17	79	86	84

1/ Dates of the two years are intermingled so that the monthly changes in light intensity as the growing season progresses are more readily apparent.

Whether or not the May measurement is included in the overall averages, it is readily apparent that a major difference in light intensity existed between the shaded and unshaded treatments. With the May measurement included, the average light intensity on the shaded plots was about 18% as compared to 83% on the unshaded. Excluding the May measurement, and basing the comparison on the light conditions which prevailed

during most of June, July, and August, the shaded plots averaged only 8% of full light as compared to 82% on the unshaded plots.

The reason that the light intensity on the unshaded plots was somewhat less than 100% is that some early-morning and late-afternoon shading from the nearby brush was unavoidable. On treatment 4 in particular, the surrounding brush could be bent back only so far without breaking the stems or causing serious injury which would have reduced its effectiveness in competing for soil moisture. And since light conditions on treatments 5 and 6 were intended to be similar to those on treatment 4, brush removal was generally restricted to a zone of about the same size as was achieved by the tie-back technique on treatment 4.

The light intensity on treatment 4 was nevertheless somewhat lower than on treatments 5 and 6, averaging 79% as compared to about 86% on treatment 5, and 84% on treatment 6. These differences between the mean light intensities on the three unshaded treatments are statistically significant,[2/] as are the smaller differences between the means on the shaded treatments. The possible influence which these differences in light intensity may have had on seedling growth will be discussed later.

2/ In evaluating the results of the study the 5% level of probability was selected as being adequate to establish that significant differences existed between treatment means. Therefore all differences which are subsequently reported as being significant are significant at this level or higher. A summary of the analyses of variance showing sources of variation, degrees of freedom, and mean squares is given in Appendix C.

The lowest light intensity measured during the course of the study was 2% of full light. This very low level was found on three plots, but only on one measurement date in each case. At the other extreme, a number of plots on the unshaded treatments gave readings of 100% on various measurement dates. However, because of changes in brush position and sun angle, no particular plot consistently registered the maximum light intensity.

Using a Weston Model 756 illumination meter, light intensities as low as 100 foot-candles were recorded on several of the shaded plots in June of 1963. Slight movements of the light-sensitive target, however, caused considerably higher readings as it was moved into or out of the scattered sun flecks which resulted from slight openings in the brush canopy. Brush movement due to wind also caused wide fluctuations in meter readings as small patches of light moved quickly onto and away from the light-sensitive target. In this respect the Ozalid paper meter was superior to the expensive Weston meter in that it integrated the hundreds of daily fluctuations in light intensity at a given spot into a single value representing the light received over a 6½-hour period.

TEMPERATURE

Measurements obtained with the hygrothermograph in the standard instrument shelter showed that a maximum air temperature of 88°F. was reached on the area in 1962, and a maximum of 91°F. in 1963. Of greater interest, however, are the air

temperature measurements recorded with the six Taylor maximum-minimum thermometers located on the plots themselves. These thermometers were in place from early May until mid-October of 1963, and the temperatures which they recorded are shown in Figure 9.

As would be expected, the maximum temperatures were higher in the open than under the brush canopy. The greatest temperature differences between the shaded and unshaded plots was attained in late July and amounted to 15°F. (88° vs. 103°). This difference is considerable, particularly when it is remembered that these are air temperatures recorded by shaded thermometers, and not surface temperatures of objects exposed to direct sunlight. Differences are much less in May when the brush is just beginning to leaf out, and again in October when most of the leaves have dried up and fallen.

Differences in minimum temperatures were not great, averaging about 2°F. colder at night on the unshaded plots than on the shaded plots. These lower temperatures on the unshaded plots were undoubtedly due to the greater night-time radiation losses in the open as compared to under the brush canopy. It is also interesting to note that minimum temperatures well below freezing were still recorded late in May when shoot elongation of the red pine seedlings was already several weeks underway.

MOISTURE

The differences in soil moisture regimes between the various treatments were not as large as was hoped for, and

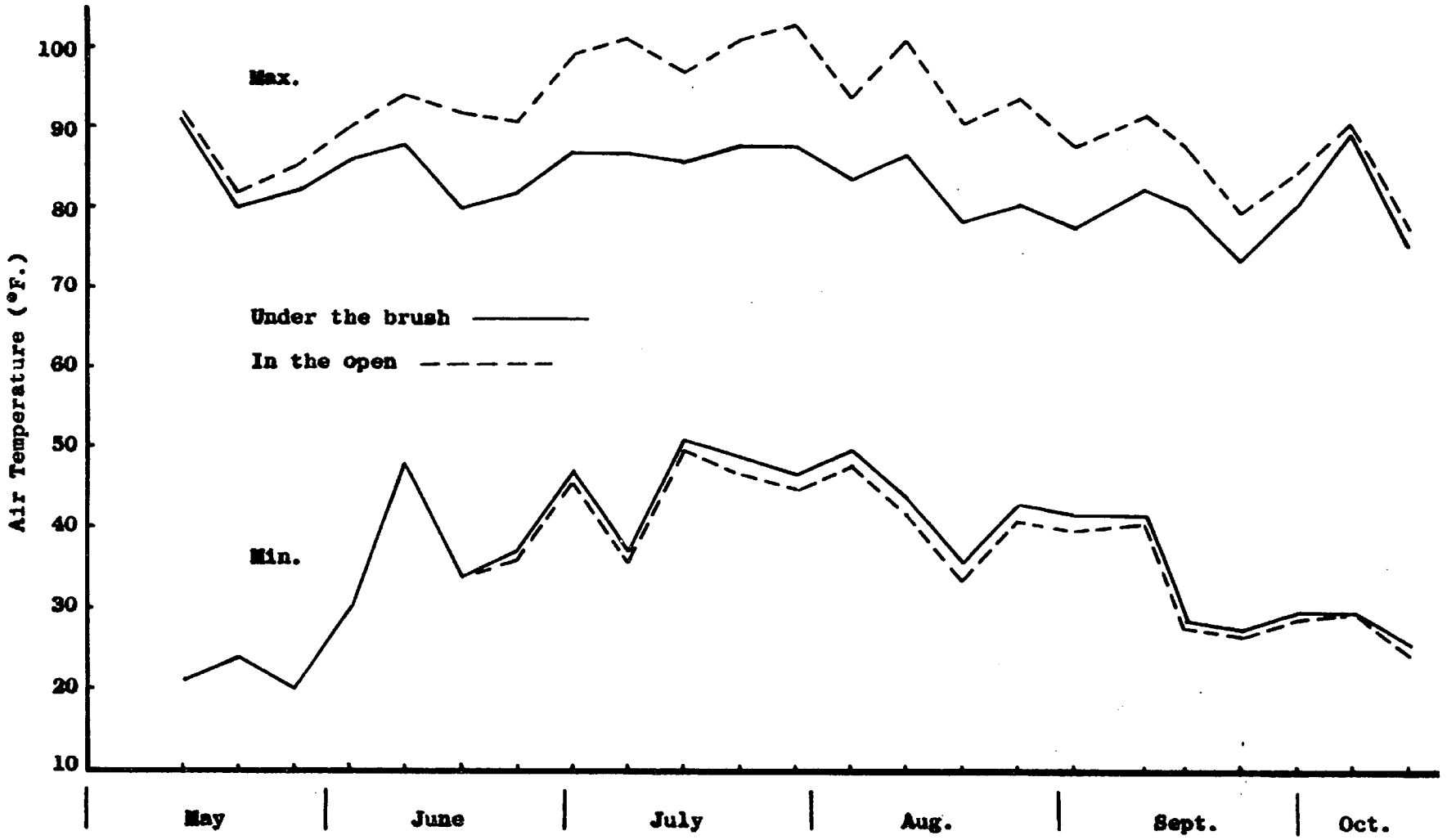


Figure 9. Average weekly maximum and minimum air temperatures under the brush and in the open during 1963. Each plotted point is the average reading of three thermometers.

a really dry regime was not represented in the study. As noted earlier, the precipitation during the 1962 growing season was substantially above normal. The 1963 growing-season precipitation, however, was about 7% below normal. A comparison between the monthly distribution of precipitation during these two seasons and the long-term average is given in Table 5.

Table 5. Comparison between growing-season precipitation in 1962 and 1963 and the long-term average.

Period	Inches of precipitation		
	Long-term average	1962	1963
May	2.83	8.26	4.17
June	3.65	6.60	2.51
July	3.75	5.63	3.57
August	3.22	4.37	3.34
September	2.38	2.82	1.18
Season total	15.83	27.68	14.77
% above or below normal	--	+ 75%	- 7%

The abnormally high precipitation in May of 1962 did not directly affect the study in that virtually all of it fell before the seedlings were planted. Each succeeding month during this year, however, was also wetter than normal and this prevented any semblance of a dry condition from developing until early September.

In 1963 only the May precipitation was substantially above normal, although August was also slightly wetter than normal. The remaining months were all drier than normal. As a consequence, three distinct dry periods developed during this second

field season.

The influence of the three basic soil moisture treatments (untrenched; trenched; and trenched and watered) on the soil moisture regime during the two years is shown in Figure 10. For easier perception of trends both the shaded and unshaded plots in each moisture treatment have been combined. The higher moisture levels on the plots which were both trenched and watered are quite apparent, the average on these remaining above 10% on all measurement dates except one when it dropped to about 9.8%. The supplemental watering, when needed, was always done on Mondays and the soil moisture sampling was almost always done on Fridays so as to obtain the moisture percentage near its low point for the week on these plots. Rain, of course, altered the sampling schedule somewhat.

It is also evident from Figure 10 that the untrenched treatments were consistently drier than the others during the four major moisture depletion periods. The trenched but unwatered plots showed a similar moisture pattern, but depletion did not proceed as far during the dry periods.

The high recharge peak for the untrenched plots in September of 1962 (Fig. 10) was undoubtedly due to the phenomenon of stem flow. This particular moisture determination was made about four days after heavy rains totaling more than 2 inches fell on the area. The untrenched treatments were the only ones on which the brush stems emanated from the same soil area as did the pine seedlings. On all trenched treatments the flow of raindrops down the brush stems was conducted to

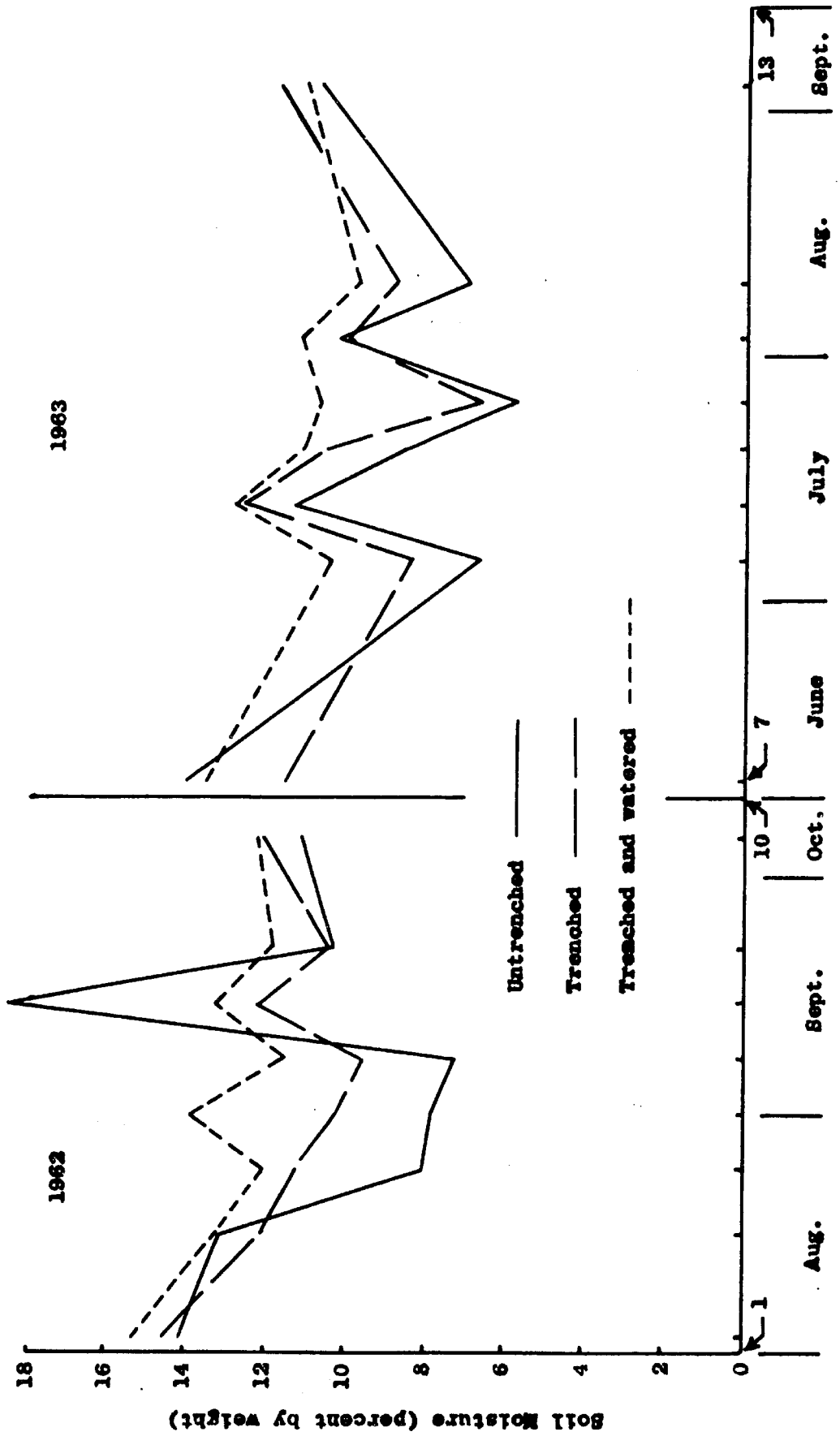


Figure 10. Soil moisture regimes during the two growing seasons under the three basic moisture treatments. The shaded and unshaded plots for each soil treatment have been combined. Each plotted point represents the average of six samples.

the soil outside of the sheet-metal cylinders, and consequently outside the zone from which the soil moisture samples were taken.

Figure 11 shows how the moisture patterns compare when the plots are sorted into just two groups on the basis of whether they were shaded or unshaded. The differences are much smaller when the treatments are grouped in this manner, but the unshaded treatments are consistently drier than the shaded ones during the four major periods of moisture depletion. During the first year this difference is undoubtedly due mainly to the greater evaporation losses on the unshaded plots. During the second year, however, the drier conditions on the unshaded plots can be attributed primarily to the greater transpiration capabilities of the large seedlings which developed on these plots, although evaporation losses would still remain a minor factor.

The average soil moisture percentages on the six treatments for these four depletion periods are presented in Table 6. When the moisture values on all sampling dates are averaged, it is noted that the driest treatment is treatment 4 and the wettest, treatment 3. This is as one would expect, since treatment 4 being untrenched and unshaded would have maximum losses from both transpiration and evaporation; and treatment 3 being both trenched and shaded as well as receiving supplemental water would show minimum moisture depletion.

An analysis of variance to test the moisture level differences among the six treatments during the four dry periods

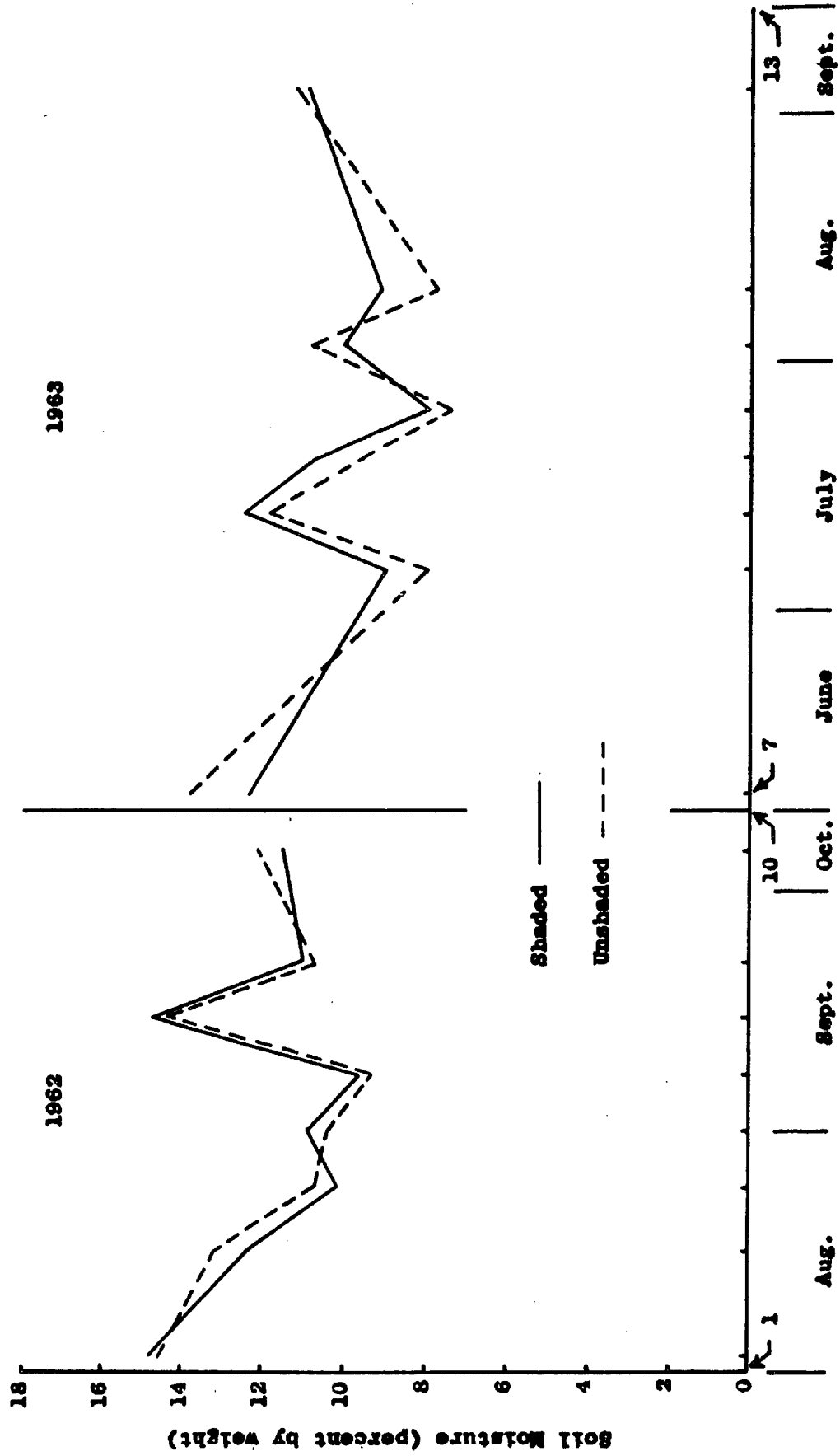


Figure 11. Comparison of soil moisture regimes between the shaded and unshaded plots during the two growing seasons. All soil treatments have been combined within each group. Each plotted point represents the average of nine samples.

Table 6. Average soil moisture content on the plots during the four moisture depletion periods. Each entry for a given date is the average of three samples.

Treatment number	Ave. soil moisture (% by weight) on dates listed				
	8-31-62	7-5-63	7-25-63	8-9-63	All dates
1	8.8	7.8	6.3	7.6	7.61
2	10.5	8.7	6.2	9.5	8.73
3	13.3	10.3	11.4	10.5	11.39
4	6.8	5.4	5.1	6.3	5.89
5	10.0	8.1	7.2	8.1	8.34
6	14.4	10.4	10.0	9.0	10.97

is summarized in Table 7. With five degrees of freedom available, five orthogonal tests between treatments or treatment groups were possible. While numerous other breakdowns could have been chosen, the one shown in Table 7 seemed to be the most logical.

Table 7. Analysis of variance of the soil moisture data to determine whether the soil moisture levels of the six treatments were significantly different during the four depletion periods.

Source of Variation	DF	SS	MS	F 1/
Dates	3	87.8878	29.2959	5.345
Treatments	5	258.3000	51.6600	9.425
1 vs. 4	1	17.6817		3.226 NS
2 vs. 5	1	.9204		.168 NS
3 vs. 6	1	1.0838		.198 NS
2, 5 vs. 3, 6	1	83.7408		15.278
1, 4 vs. 2, 3, 5, 6	1	154.8733		28.256
Interaction (D x T)	15	39.1755	2.6117	.477 NS
Sampling error	48	263.0867	5.4810	
Total	71	648.4500		

1/ F values marked NS are not significant at the 5% level of probability; all others are significant at this level.

Table 7 shows that there were no significant differences between the shaded and unshaded treatments within each basic soil moisture treatment. However, moisture differences between the trenched-only treatments (2 and 5) and the trenched-and-watered treatments (3 and 6) are significant. So are the differences between the untrenched treatments (1 and 4) when tested against all of the trenched treatments (2, 3, 5, and 6). It would thus appear that while the differences between the basic moisture treatments are not large, these differences are nonetheless real.

SEEDLING SURVIVAL AND VIGOR

Turning now to the responses of the seedlings themselves, under the conditions of this study there was a marked difference in seedling survival on the basis of light, but not of moisture. Not a single seedling growing on the three unshaded treatments died during the two field seasons, whereas 17 of the 45 seedlings growing on the three shaded treatments died.3/

3/ With reference to the analyses, certain problems arose as a result of the death of some of the seedlings (or parts of seedlings) before the termination of the study. The development of some structures was pretty well completed at the time of death, but other structures would have required considerable additional time to reach full development. The general rule for deciding whether dead seedlings (or structures) should be included or excluded from a particular analysis was that if, for the variable in question, development was essentially completed, the dead seedlings were included. If, on the other hand, development was considerably short of completion at the time of death, the dead seedlings (or structures) were excluded.

Virtually all of the mortality occurred during the second field season, with only one seedling dying during 1962.

The mortality by treatments was as follows: treatment 1, 6 seedlings; treatment 2, 5 seedlings; treatment 3, 6 seedlings. This nearly identical mortality on the three shaded treatments, each with a different soil moisture regime, would seem to indicate that even very favorable soil moisture conditions have little effect in reducing seedling mortality if the light intensity is too low.

Figure 12 shows the contrast in seedling development among the six treatments when the seedlings were still growing in the field shortly before the close of the study. The comparative development of the roots as well as the tops is shown in Figure 13, for which the most vigorous seedling from each treatment was chosen at the time of excavation. From these two figures it is apparent that the seedlings in treatments 5 and 6 (the treatments with no competition for either light or moisture) are decidedly larger and more vigorous than the others. The seedling representing treatment 4 (unshaded but with root competition) is considerably less vigorous than the aforementioned two, but still decidedly superior to those in the three shaded treatments.

Detailed comparisons of specific morphological features will be made in the sections which follow. However, one final observation on general vigor which is not apparent in Figures 12 and 13 is that the foliage of the seedlings in treatment 6 (trenched and watered) was a darker green than

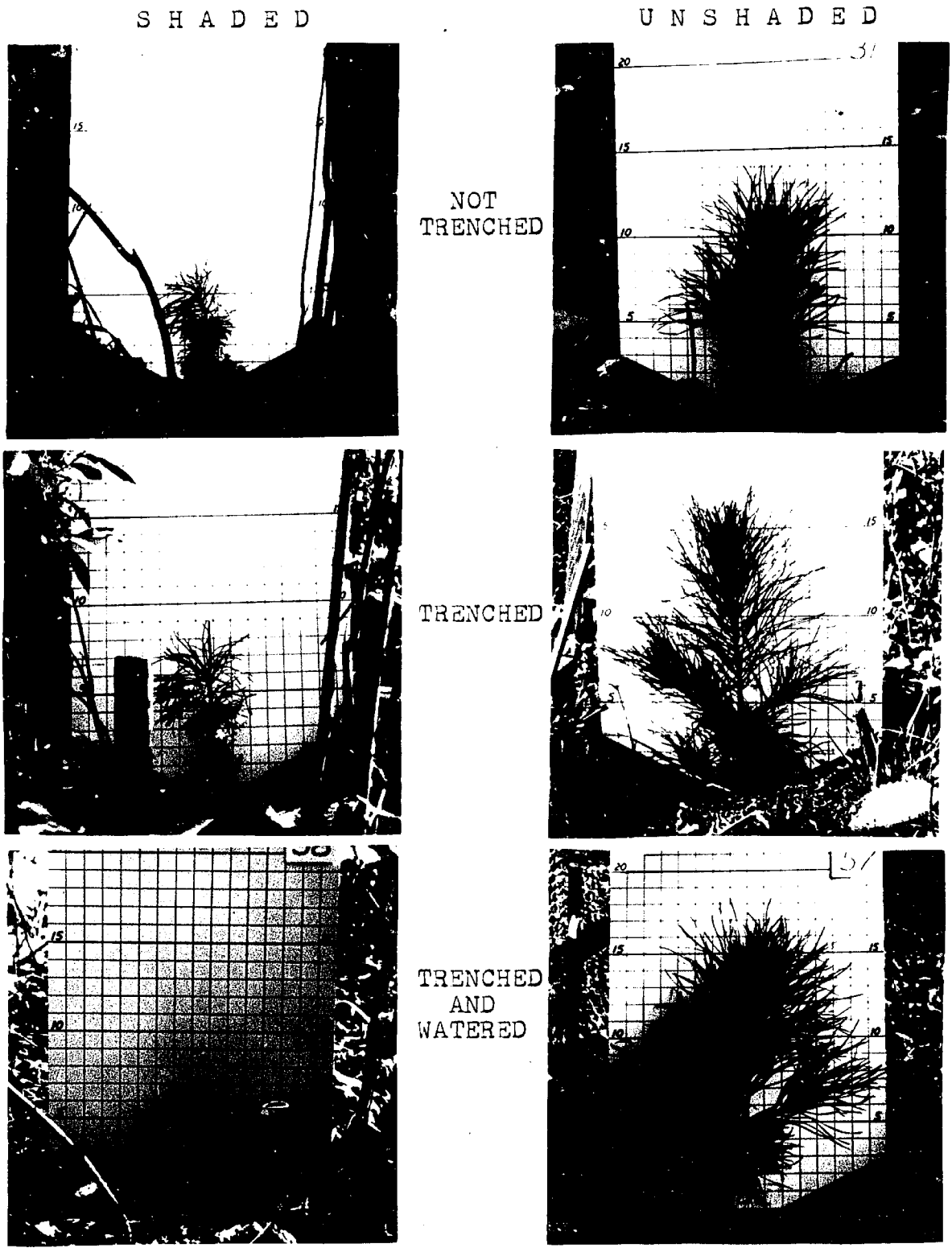


Figure 12. Representative seedlings on the six treatments as they appeared in the field after two growing seasons. (Background grid is in inches).

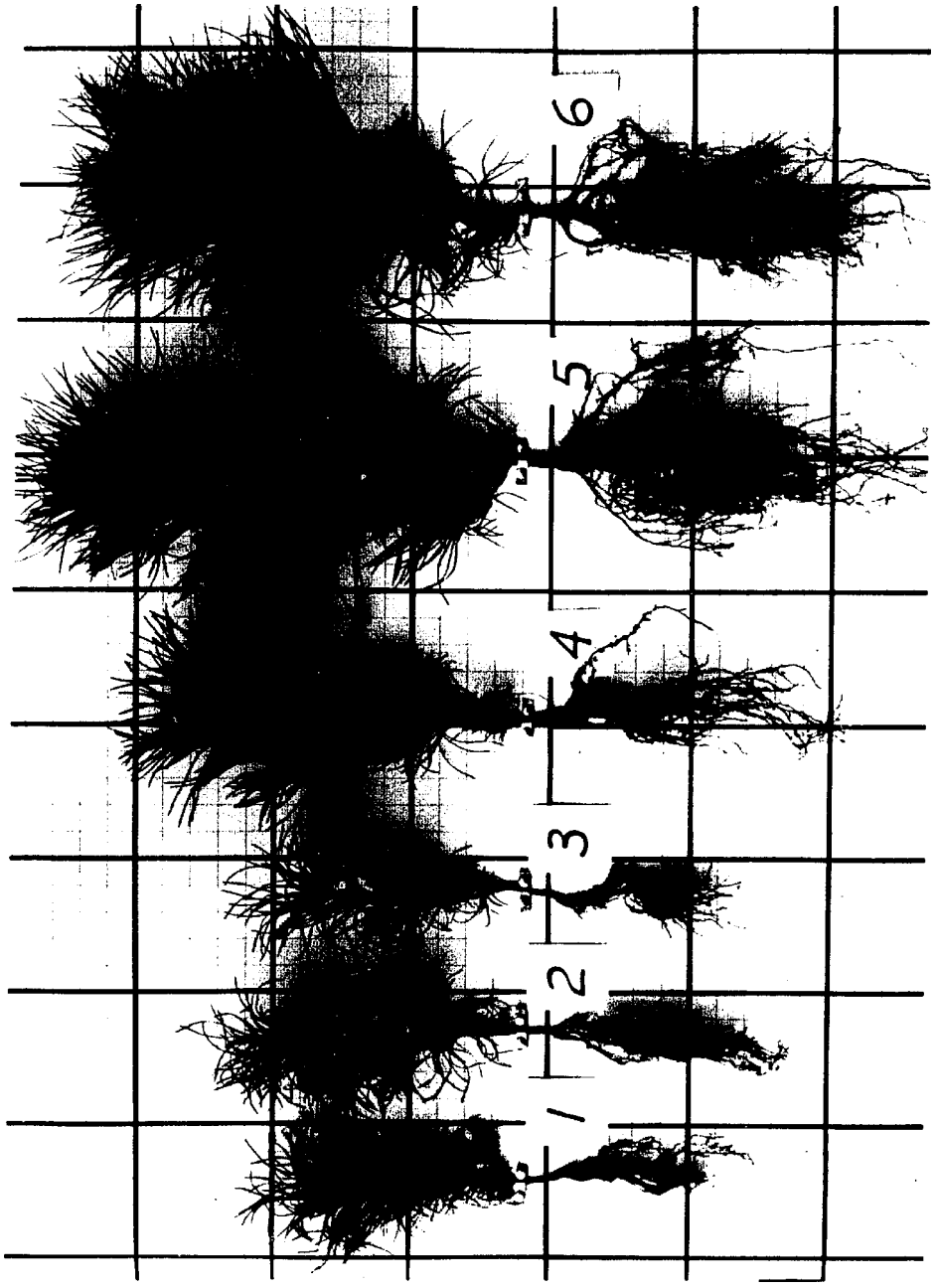


Figure 13. Top and root development of the most vigorous seedling on each treatment. Numbers near seedlings are treatment numbers (1, 2, and 3 were shaded; 4, 5, and 6 were unshaded; 1 and 4 were untrenched). Heavy lines are at 5-inch intervals.

it was on the seedlings in treatment 5 (trenched only). Also, the individual needles were thicker, giving the crowns a denser appearance. The other watered treatment (treatment 3), which was installed under heavy shade, did not show this foliage superiority over its unwatered counterpart (treatment 2).

HEIGHT GROWTH

The average initial height of the seedlings on each treatment, and various aspects of height growth during the course of the study are given in Table 8. For ease of comparison, the average initial seedling height, and the height at the end of the first and second field seasons are also shown graphically in Figure 14. From the table and figure it can be seen that, while there were some differences in average height at the start of the experiment, these differences were not large. Treatment 6 started out with the shortest average seedling height (4.86 cm.), and treatment 2 with the tallest average height (5.51 cm.).

Height growth differences between treatments increased somewhat during 1962, but were still not large during this first year in the field. Each of the three treatments without shade outgrew the three treatments with shade. These differences, though relatively small, were significant. Differences on the basis of soil moisture treatments, however, showed no definite pattern and were not significant.

Table 8. Average initial height of the seedlings, and subsequent height growth under treatment conditions.

Item	Light level	Moisture level		
		Untrenched	Trenched	Trenched & Watered
Initial height in spring of '62 (cm.)	Shaded	5.26	5.51	5.21
	Unshaded	5.33	5.40	4.86
Height in fall '62 (cm.)	Shaded	11.37	12.24	11.28
	Unshaded	12.53	12.21	11.69
Height in fall '63 (cm.)	Shaded	14.57	17.18	15.27
	Unshaded	23.93	30.82	27.49
Height growth in '62 (cm.)	Shaded	6.11	6.73	6.07
	Unshaded	7.20	6.81	6.83
Height growth in '63 (cm.)	Shaded	3.20	4.94	3.99
	Unshaded	11.40	18.61	15.80
Total height growth during study (cm.)	Shaded	9.31	11.67	10.06
	Unshaded	18.60	25.42	22.63
Total height growth as % of initial ht.	Shaded	177	212	193
	Unshaded	349	471	466

During the 1963 field season the effects of treatment on height growth began to be strongly manifested. This is quite evident in both Table 8 and Figure 14. The superiority in height growth of the unshaded over the shaded treatments is readily apparent, averaging over 15 cm. on the former, and only about 4 cm. on the latter.

Differences attributable to the soil moisture regimes are considerably smaller than those attributable to the influence of light, but are also significant. Contrary to expectations, the trenched-and-watered treatments, theoretically the most favorable, did not grow as well as the

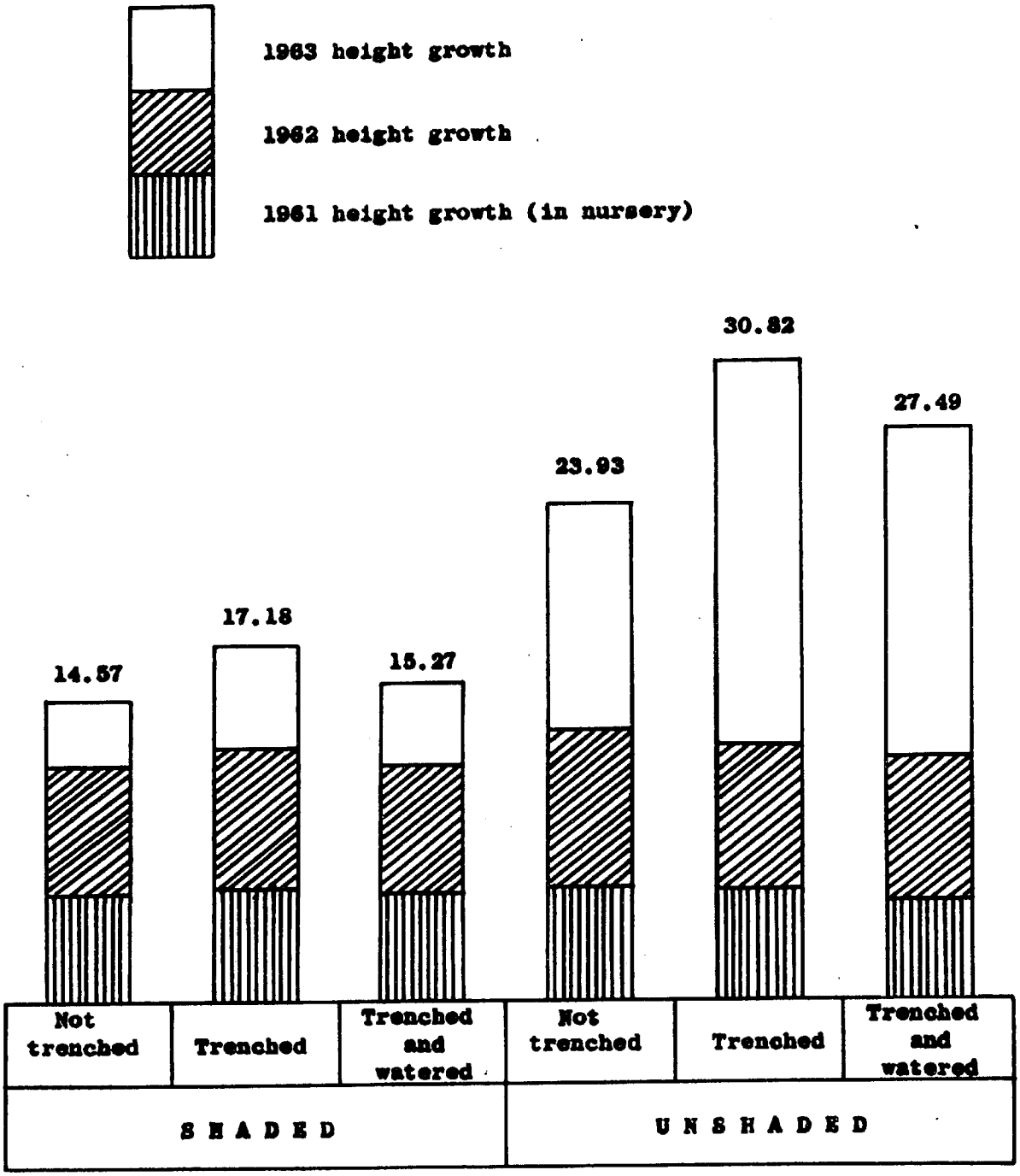


Figure 14. Average seedling height on each treatment at the start of the experiment, and at the end of the first and second field seasons. (Figures above columns are total height in cm. at the conclusion of the study.)

trenched-only treatments under either light condition. Possible explanations for this will be reserved for the Discussion and Conclusions section.

The analysis of variance also revealed that there was a significant interaction between light and moisture with respect to the 1963 height growth. This, too, will be elaborated upon in the Discussion and Conclusions section.

It is interesting to note in Table 8 that all three of the treatments growing in the shade averaged less height growth in 1963 than in 1962. The unshaded treatments, on the other hand, all made substantial increases in height growth in 1963 as compared with the previous year, with growth more than doubling on treatments 5 and 6.

The last item in Table 8 shows, by treatment, the total height growth for the two-year period expressed as a percentage of the initial height. This technique tends to compensate for differences in initial height, adjusting for the greater absolute growth which the larger seedlings would be expected to make. On this basis it can be seen that the treatment 5 height growth is not much greater than that on treatment 6 (471% versus 466%), whereas, on an unadjusted basis it appears to be appreciably greater (25.42 cm. versus 22.63 cm.).

The weekly height growth patterns on the 6 treatments have also been charted and are shown in Figure 15. Only the 1963 measurements have been plotted because measurements were not begun soon enough in 1962, and furthermore the seedlings were still adjusting to their new surroundings during this

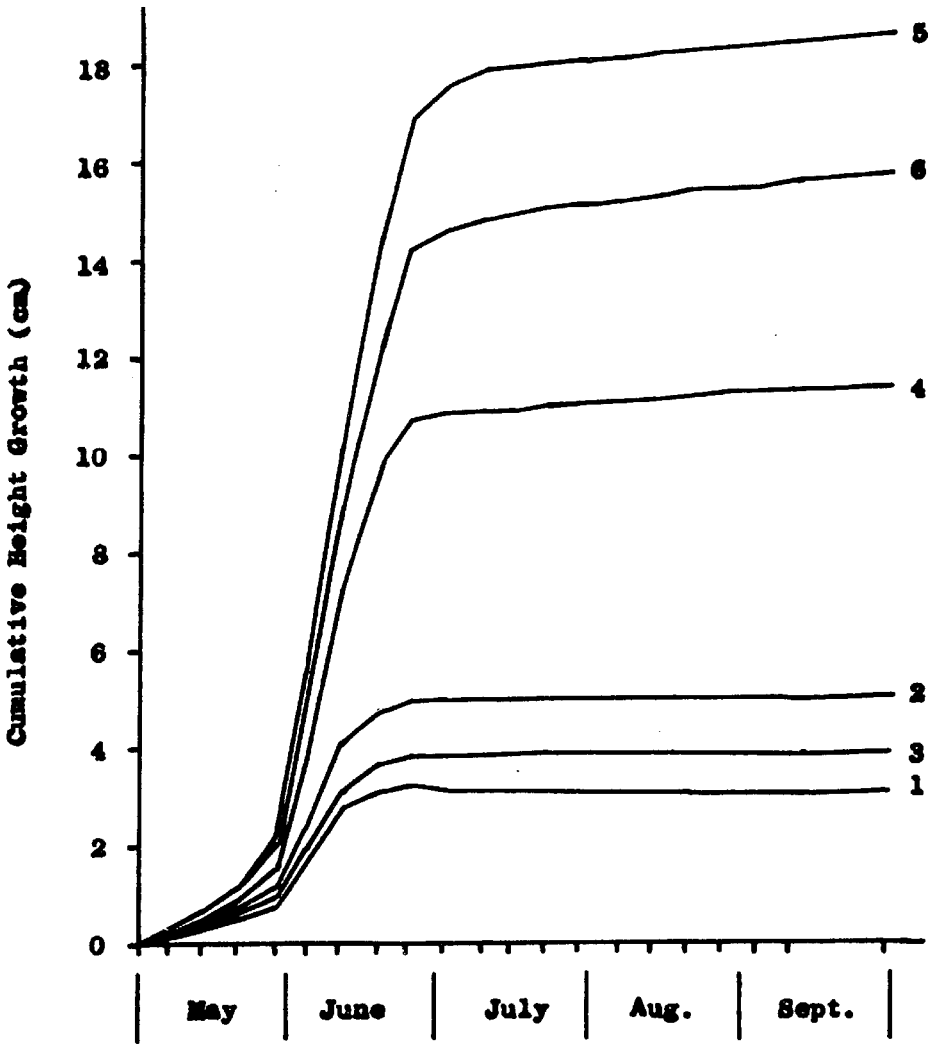


Figure 15. Terminal shoot elongation patterns by treatment during the 1963 growing season. Numbers on curves refer to treatments (1, 2, and 3 are shaded; 4, 5, and 6 are unshaded). Each curve represents 15 trees excepting no. 2 which represents only 14. Markings along the time scale indicate measurement intervals.

first year.

It is impossible to say on precisely what day height growth actually began when observations were made only once per week, but it can be said with reasonable assurance that none had yet taken place on May 1. By May 7, however, bud elongation was definitely in progress. May 1 was therefore arbitrarily established as the zero reference point for Figure 15.

This figure clearly shows again the marked difference in height growth between the shaded and the unshaded treatments. Not only did the shaded seedlings make far less total height growth, but they started more slowly (though not necessarily on a later date), they never grew as rapidly, and their growth rates declined at an earlier date than did the unshaded seedlings. Seedlings on all treatments, however, attained their maximum growth rates during the same week--the week of June 4 to June 11.

The slight drop in the growth curve for treatment 1 during the last week in June was caused by the die-back and loss of the new shoot on one of the seedlings, which resulted in a net loss in height growth on this treatment.

The percentages of the total seasonal height growth which had been completed by various dates during the 1963 growing season are shown in Table 9. While Figure 15 shows that actual growth up to any given date was always less on the shaded than on the unshaded treatments, Table 9 shows that the percentage of total growth completed on any date was greater on the

Table 9. Percent of the total seasonal height growth completed by various dates during the 1963 growing season.

Date	Shaded			Unshaded		
	Not trenched (Trmt 1)	Trenched (Trmt 2)	Trenched + water (Trmt 3)	Not trenched (Trmt 4)	Trenched (Trmt 5)	Trenched + water (Trmt 6)
	(Percent of total growth completed)					
May 1	0	0	0	0	0	0
May 7	3.7	4.1	4.0	2.0	1.6	1.9
May 14	8.7	8.6	8.8	4.3	3.5	4.2
May 21	14.6	14.1	15.1	7.2	6.0	7.0
May 29	22.7	22.1	23.1	12.7	11.6	12.6
June 4	51.2	46.2	47.0	32.3	29.8	31.2
June 11	86.3	80.8	77.9	63.4	54.6	56.0
June 19	97.2	93.0	92.7	85.9	77.1	77.6
June 25	100.0 1/	97.1	95.5	93.7	90.6	90.2
July 2	97.2	97.7	96.2	94.9	94.4	92.5
July 10	97.2	98.0	97.0	95.5	95.9	93.9
July 16	97.5	98.2	97.2	96.0	96.6	94.6
July 23	97.5	98.4	98.0	96.9	97.0	95.4
July 30	97.8	98.4	98.0	97.3	97.4	96.1
Aug. 7	97.8	98.4	98.2	97.7	97.6	96.4
Aug. 14	97.8	98.4	98.2	97.8	98.1	97.1
Aug. 21	97.8	98.6	98.5	98.5	98.4	97.7
Aug. 28	98.1	98.8	98.7	98.9	98.7	97.9
Sept. 4	98.8	98.8	99.0	99.3	99.0	98.4
Sept.11	99.1	99.0	99.2	99.5	99.3	98.9
Oct. 1	100.0	100.0	100.0	100.0	100.0	100.0

1/ Average height on treatment 1 dropped after June 25 due to tip die-back of one of the seedlings. However, by October 1 the average height had again increased to this same level.

shaded treatments. By May 14, for example, nearly 9% of the total growth for the season had already been made on treatments 1, 2, and 3, whereas only about 4% of the total growth had been made on treatments 4, 5, and 6. By May 29 more than 22% of the total height growth had been made on the shaded treatments, but only about 12% on the unshaded treatments.

During the week of June 4 to June 11 (the week of most

rapid height growth on all treatments), the seedlings on treatments 1 and 2 made about 35% of their total height growth, those on treatments 3 and 4 about 31%, and those on treatments 5 and 6 about 25%. The big majority of the season's height growth was made within about a 3-week period running from May 29 to June 19. During this period 65% or more of the total height growth for the season was made on all treatments. Over a 7-week period starting on May 1, height growth was more than 90% completed on the shaded treatments; and, after an additional week, it was also over 90% completed on the unshaded treatments.

One other point of interest concerning height growth relates to the growth pattern of individual trees. Work done by other investigators (Kozlowski and Ward, 1961) has shown that the shoot growth of individual trees is fundamentally a variable and intermittent process, with growth taking place in spurts rather than continuously. This was also noted in the present study, although this pattern is masked when the weekly growth increments of all 15 trees in each treatment are combined and averaged as was done for Figure 15.

LAMMAS SHOOT DEVELOPMENT

While no late-season (or lammas) shoots were produced during 1962, such shoots were numerous in 1963. They invariably developed on the more vigorous trees, and were rare or absent on the weaker trees. Thus, lammas shoots were produced by every seedling on treatments 5 and 6; by over half

of the seedlings on treatment 4; by two seedlings on treatment 2; and by none of the seedlings on treatments 1 or 3.

In all cases except one these lammas shoots arose either from the upper whorl of newly formed lateral buds, or from the newly formed terminal buds of lower lateral branches. On only one seedling did the newly formed terminal bud on the main stem (the apical bud) also exhibit premature elongation and produce a lammas shoot. Thus, on most seedlings where lammas growth appeared, one of these lateral lammas shoots rather than the main stem was actually the highest woody part of the seedling at the end of 1963. The height measurements of the previous section, however, refer to the height of the main stem and not to the height of a sometimes taller lammas shoot.

The lengths of the lammas shoots were not measured, but measurements were made of their height above the terminal bud of the main stem. On treatments 5 and 6 they exceeded the height of the main stem by an average of about 2.5 cm.; on treatment 4 by about 1.1 cm.; and on treatment 2 by only about 0.2 cm.

NEEDLE DEVELOPMENT

Comparisons of needle development will be made for two characteristics--needle length, and number of needles produced. These will be presented separately.

NEEDLE LENGTH

The length of the current year's needles was measured at

the end of the 1962 growing season, and at weekly intervals during the 1963 growing season. The average final length, by treatment, during each of these two years is shown in Figure 16. From this figure it is apparent that there is a general progression in needle length from the left side of the chart to the right side, or in other words, from a condition of heavy competition for light and moisture to a condition of little or no competition. On all treatments the 1963 needles were longer than those formed in 1962, due probably to the seedlings being more fully adjusted to their surroundings by this time.

The differences in needle length between the various treatments in each of the two years are significant. These differences are attributable to differences in both light and moisture levels as well as to the interaction of the two factors.

As was true for height growth, the two treatments having no competition for either light or moisture had decidedly better needle development than did the four treatments with one or both forms of competition. Unlike height growth, however, the best needle development (at least during the second field season) took place on treatment 6 which was both trenched and watered.

Again, as with height growth, it was of greater interest to study the needle development patterns as they evolved, rather than to simply compare the end-of-the-season results. These weekly needle elongation patterns for the 1963 growing

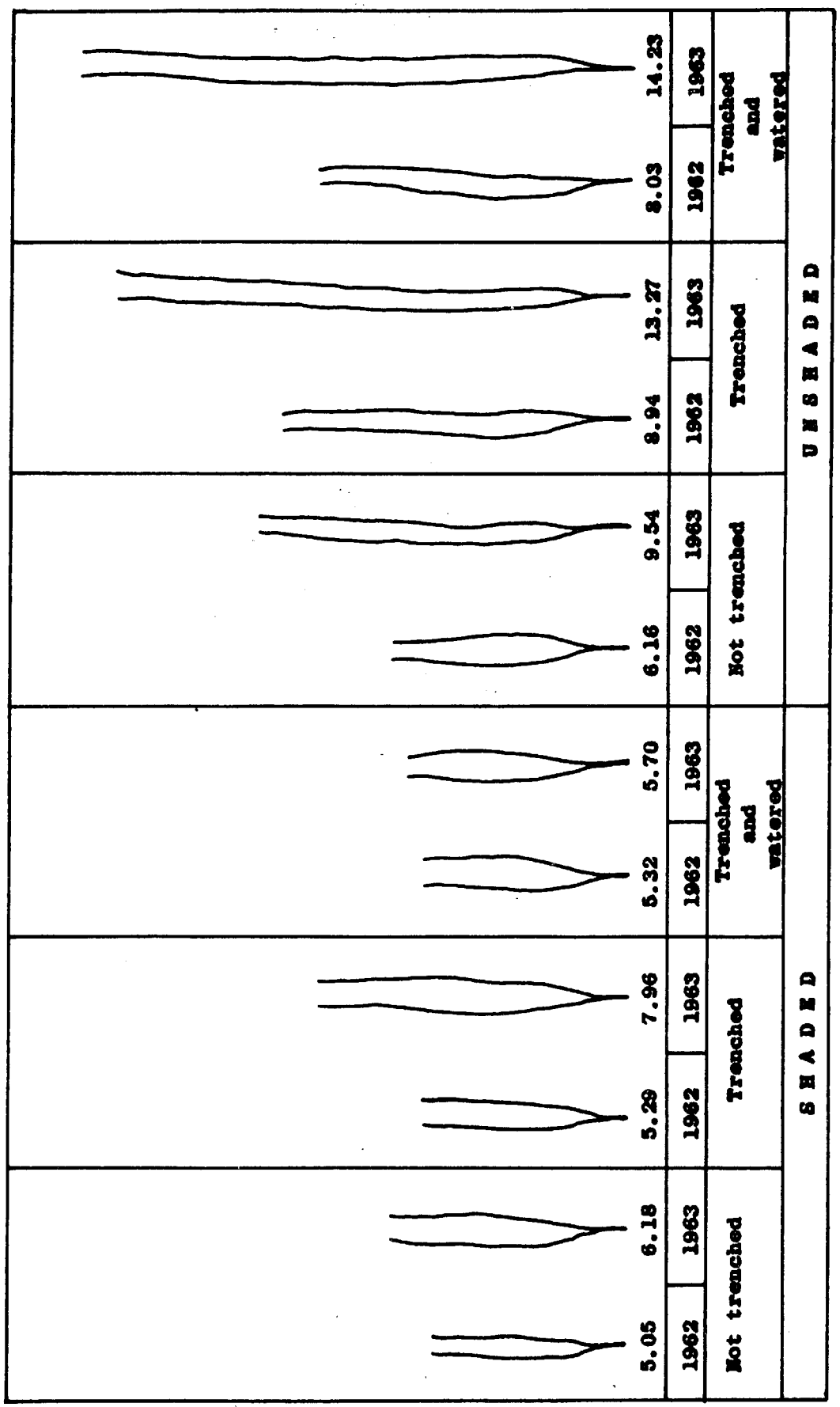


Figure 16. Average needle length at the end of the 1962 and 1963 growing seasons. (Numbers directly below needles are length in centimeters).

season are shown in Figure 17.

Although perceptible needle growth started about June 10, and the initial stages probably a week earlier, the weekly measurements were not begun until June 25. There were several reasons for delaying the start of these measurements, one being that until rapid height growth was pretty well over, it would have been impossible to select sample needles which were at the one-quarter, one-half, and three-quarter points along the new shoot. Another reason was that some assurance was desired that the selected needles would show at least normal vigor, and not abort or fail to develop.

The early stages of growth were thus missed (see Figure 17), and this unfortunately represents more than 50% of the total needle elongation on treatments 1 and 3. Nevertheless, the growth patterns for the season as a whole are pretty well shown.

As was true of height growth, needle elongation also seemed to get underway at almost the same time on all treatments, although with observations made only once per week, it is possible that growth on some treatments actually started a few days earlier than on others. Once started, however, needle elongation on the unshaded plots proceeded more rapidly, and this rapid growth rate was maintained for a longer time than on the shaded plots. This was particularly true of the needles on treatments 5 and 6 which distinctly outgrew all the others. Even the needles on treatment 4, however, though lagging slightly behind those on

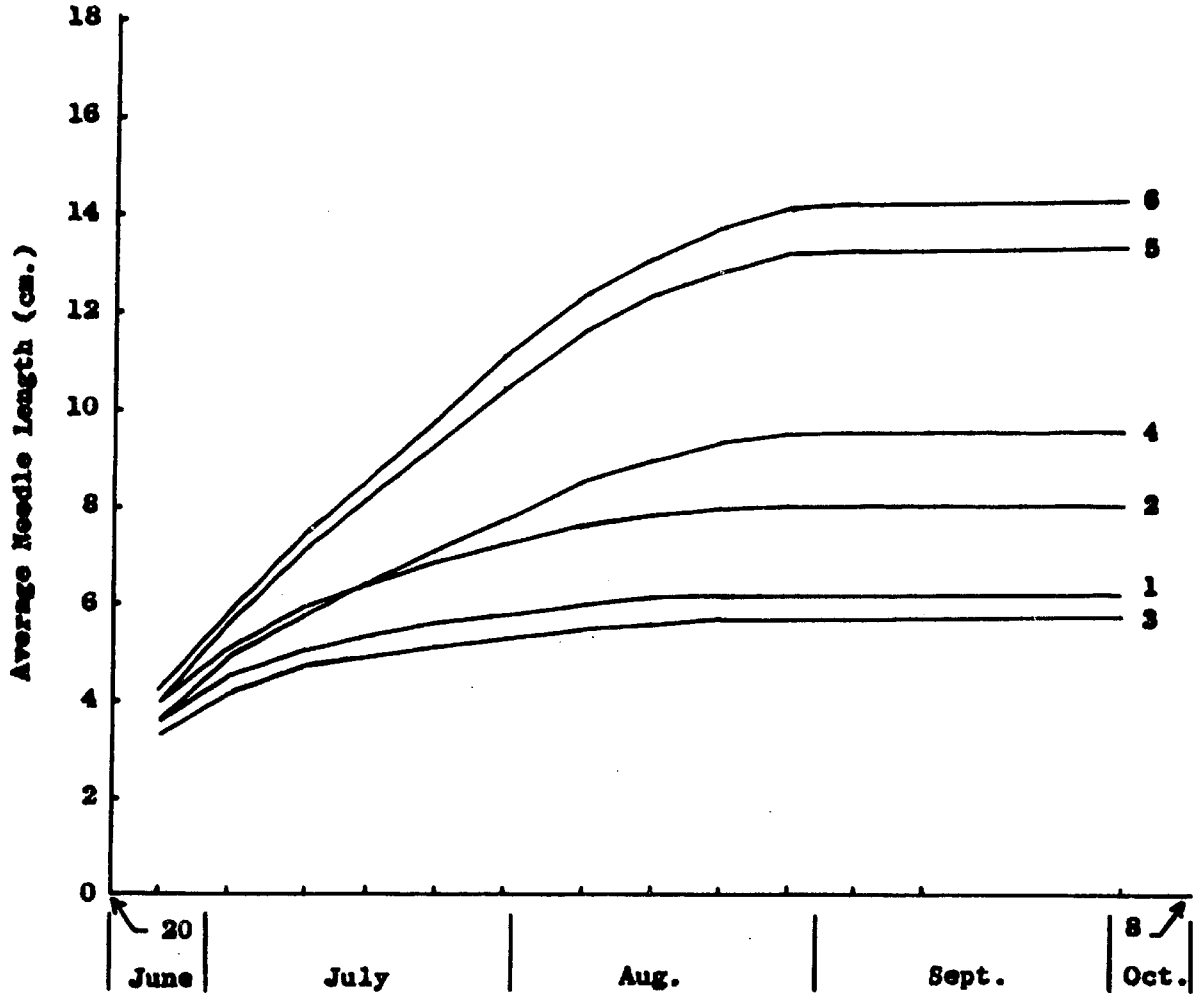


Figure 17. Needle elongation patterns by treatment during the 1963 growing season. Numbers on curves refer to treatments. Each point on curves 4, 5, and 6 is the average of 45 needles. Curves 1, 2, and 3 are based on slightly fewer needles because some needles were lost on these treatments during the course of the season. Only needles which remained throughout the season are represented in the above curves.

treatment 2 at the outset, overtook the latter by mid-July. Treatment 3, shaded but well watered, showed the poorest needle growth of all, though it was only slightly inferior to treatment 1.

It is of interest to note that needle elongation seems to be a more gradual, less abrupt process than shoot elongation, although the difference is not as great as a casual comparison of Figures 15 and 17 would suggest because the time scales along the horizontal axes are quite different. Allowing for this, however, needle elongation still proceeds more slowly than does shoot elongation. Whereas the most rapid 65% of the shoot elongation on all treatments took place within just a three-week period, six weeks were required before the most rapid 65% of the needle elongation was completed on all treatments.

The progress of needle elongation in percent of the season's total completed by various dates is shown in Table 10. The date used as the zero reference point for needle growth is June 10, although a small amount of growth had already taken place during the preceding week, particularly along the lower part of the new shoots. On this date, however, the upper needles were still only rudimentary structures which were yet to appear on the still elongating stem.

The percentage of needle elongation which is completed by any given date (Table 10) is much higher on the shaded treatments (1, 2, and 3) than on the unshaded treatments (4, 5, and 6). On June 25 when needle measurements were first

Table 10. Percent of the total seasonal needle elongation completed by various dates during the 1963 growing season.

Date	Percent of total elongation completed					
	Tr. 1	Tr. 2	Tr. 3	Tr. 4	Tr. 5	Tr. 6
June 10	0	0	0	0	0	0
June 25	58.3	49.1	58.4	36.9	29.8	29.6
July 2	72.7	63.0	72.5	50.6	41.9	40.6
July 10	81.4	74.4	82.3	60.2	53.7	52.6
July 16	86.2	79.8	85.3	67.1	61.1	60.2
July 23	90.5	85.0	89.1	74.5	69.8	68.7
July 30	93.2	89.8	92.3	81.3	78.4	78.0
Aug. 7	96.8	94.8	95.6	89.4	87.4	86.9
Aug. 14	99.0	97.5	97.5	94.0	92.5	92.3
Aug. 21	99.4	99.1	98.8	97.6	96.6	96.6
Aug. 28	99.5	99.9	99.3	99.5	99.3	98.9
Sept. 4	99.5	100.0	99.6	99.7	99.8	99.6
Sept. 11	99.8	100.0	99.8	99.9	99.9	99.9
Oct. 1	100.0	100.0	100.0	100.0	100.0	100.0

begun, the needles on treatments 1 and 3 had, on the average, already completed over 58% of their total elongation, and those on treatment 2 over 49%. In contrast, the needles on treatment 4 were only about 37% fully elongated and those on treatments 5 and 6 less than 30% elongated. Three weeks later, on July 16, needle elongation was more than 85% completed on treatments 1 and 3, but only slightly over 60% completed on treatments 5 and 6.

It should be mentioned that both Table 10 and Figure 17 are based on only those sample needles which were present throughout the entire season. This includes all of the original sample needles on treatments 4, 5, and 6 where growth was vigorous and no losses were sustained. It includes only 80% of the original sample needles on treatments

1 and 2, and about 93% of those on treatment 3.

Considering now the pattern of needle growth at different heights on the newly formed shoot, Figure 18 illustrates the different elongation trends exhibited by needles growing in the lower, the middle, and the upper third of the shoot. This figure shows the growth patterns for treatment 6 which, in this respect, is representative of all treatments.

It will be noted that on June 25 when the first needle measurements were made, the lower needles were longest, the middle ones intermediate, and the upper ones the shortest. Viewed in another way, the dates on which the lower, the middle, and the upper needles reached a length of 5 cm. were, respectively, June 26, June 28, and July 1. This illustrates the fact that a wave of growth moved upward along the new shoot from its base to its tip. Even while the actively growing shoot tip was still elongating, and the rudimentary upper needles were mere closely-crowded stubs of green, the lower needles were already beginning to elongate slightly.

As the season progressed, however, the growth gap between the lower needles and those higher on the stem gradually narrowed. By mid-July the middle needles had reached the same average length as the lower needles, and thereafter they exceeded them in length. By early August the upper needles had also overtaken and surpassed the lower needles in average length. Ultimately the upper and middle needles attained almost the same average length, which was approximately

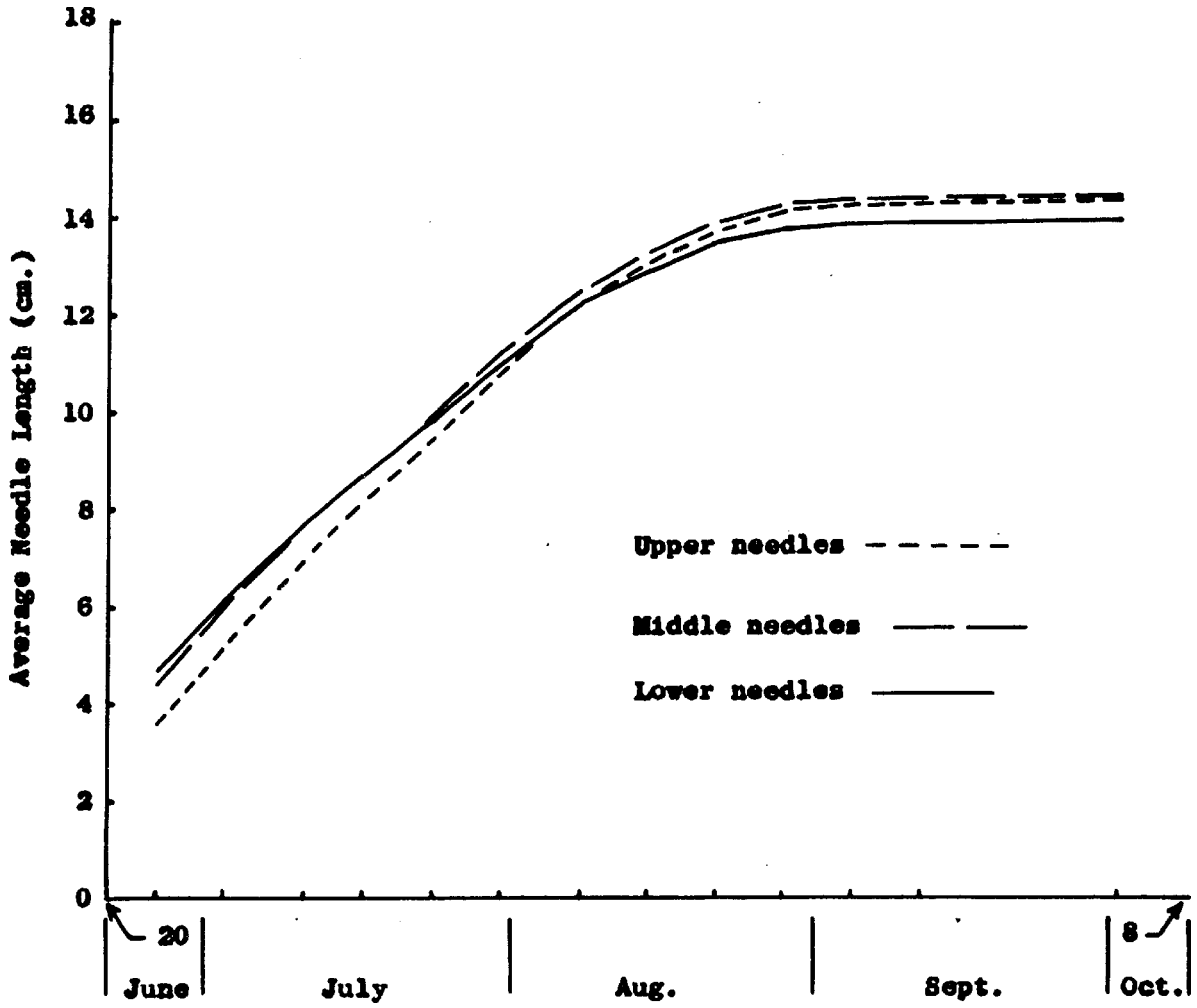


Figure 18. Needle elongation patterns by needle position on the seedling during the 1963 growing season. Curves are for treatment 6 which is typical. Each curve represents the average weekly elongation of 15 needles.

0.5 cm. greater than that reached by the lower needles.

At the time of sample needle selection on June 25, the needles met the predetermined requirements of being at the one-quarter, one-half, and three-quarter points on the new shoot. However, since some shoot elongation still occurred in the upper portion of the stem after this date, the final spacing was slightly different. There was little, if any, further shoot elongation between the middle and lower needles, but there was elongation between the middle and the upper needles. The net result was that the middle and lower sample needles ended up closer together than did the middle and upper sample needles. Also, all sample needles were somewhat below the positions intended for them on the new shoot; i.e., the lower needles were below the one-quarter point, the middle needles below the midpoint, and the upper needles below the three-quarter point when shoot elongation finally culminated.

NUMBER OF NEEDLES

At the close of the second field season, after the seedlings were lifted and brought into the laboratory, a complete count was made of all the needles which developed in 1963 on each seedling. Separate counts were kept of needles growing on the main stem, on the lateral shoots, and on the lammas shoots. These needle counts were made on the dead as well as on the live seedlings, since most needles still remained on the stem, and it was possible to determine with reasonable accuracy how many may have fallen by noting the scars where

they had been attached.

Actually the number of needle fascicles rather than the number of individual needles was counted, since the normally developed needles almost always numbered two per fascicle. In the case of the needles produced on the lammas shoots, however, about half of the fascicles contained three needles instead of two, and on the most vigorous seedlings an estimated two-thirds of the fascicles on the lammas shoots had three needles.

All seedlings also bore the 1962 needles, and a few still had some of the dead 1961 needles at the time they were brought into the laboratory. Needles from these earlier years were not counted but were also stripped from the stem at the time the 1963 needles were removed and counted. The several stages of needle removal are shown in Figure 19.

The seedling shown in these photos is typical of the vigorous trees which developed on treatments 5 and 6. It is quite apparent that the normal 1963 needles on the main stem and branches constitute by far the major bulk of the needles on these seedlings. The much shorter length of the needles on the lammas shoots (referred to in the figure as "late 1963 needles") is also readily seen. The 1962 needles are confined to a relatively short portion of the stem, illustrating again the much greater height growth made during the 1963 field season. The stem on this seedling was cut at the ground-line.

The short lammas shoots, with needles removed, can be



Figure 19. The three age classes of needles commonly found on the vigorous seedlings at the end of 1963. Photos show various stages of their removal from the seedling stem.

seen in the photo on the right in Figure 19. The three visible buds at the upper end of the stem are all lammas shoot terminal buds. The main stem terminal (apical) bud is not visible, being hidden behind the middle lammas shoot.

The average number of needle fascicles which developed on the seedlings in each treatment during 1963 is given in Table 11. The table shows that more than twice as many fascicles of needles were produced on the main stems of the unshaded seedlings as on the main stems of the shaded seedlings. The difference is even more striking when the comparison is based on the number of needle fascicles on the lateral shoots. Comparing treatments having the same moisture regimes, the unshaded seedlings produced from 9 to 10 times as many needle fascicles on the lateral shoots as did the shaded seedlings. This is largely due to the fact that the unshaded seedlings produced more lateral shoots on which needles could develop. The greatest difference comes when the comparison is made on the basis of number of needles produced on lammas shoots because two of the shaded treatments did not produce lammas shoots.

When comparisons are made between seedlings on the basis of the three soil moisture regimes, appreciable differences are also noted. As with height growth, the treatments which made the best showing in terms of needle production were those which were trenched but not watered. The untrenched treatments were again the poorest. Differences in needle production were greater between the moisture regimes on the unshaded

Table 11. Average number of needle fascicles which developed on the seedlings in each treatment during the 1963 growing season.

Needle location	Light level	Moisture level		
		Untrenched	Trenched	Trenched and watered
		(Ave. no. of fascicles per seedling)[1/]		
Main stem	Shaded	30	38	34
	Unshaded	59	98	76
Lateral shoots	Shaded	2	10	7
	Unshaded	20	92	63
Lammas shoots	Shaded	0	2	0
	Unshaded	9	109	95

1/ Each fascicle on the main stem and on the lateral shoots usually had two needles. Fascicles on the lammas shoots had either two or three needles with about equal frequency.

plots than between those on the shaded plots, at least on the main stem, suggesting that adequate light must be available before differences in moisture levels become important. That there was a light-moisture interaction was revealed by the analysis of variance which showed that differences in needle production due to light, to moisture, and to their interaction all were significant.

BUD DEVELOPMENT

At the end of each of the two growing seasons, both the length and the diameter of the main stem terminal bud were measured with calipers. The results of these measurements, as well as the measurements of stem diameter (which will be

discussed in the next section) are illustrated in Figure 20. Only the buds of living seedlings are included in these averages because bud development was prematurely halted on the seedlings that died.

Figure 20 shows the striking contrast in terminal bud size between the shaded and the unshaded treatments, particularly when the latter were trenched. At the end of the 1963 growing season the terminal buds on treatments 5 and 6 were about three times as long as those on the shaded treatments. Treatment 4, unshaded but with competition for moisture, produced buds which were about twice as long as those on the shaded treatments. Bud diameters were also greater on the unshaded treatments than on the shaded, but the differences were less pronounced. However, differences in both the length and diameter of the terminal bud attributable to differences in the amount of light received were significant.

Differences in bud size due to the moisture treatments were also appreciable. At the end of the second growing season the terminal buds were about 40% longer on the trenched than on the untrenched treatments. As with height growth, the treatments which were watered as well as trenched had somewhat smaller terminal buds than did the trenched-only treatments. However, this difference seemed to be decreasing on the unshaded plots. In 1962 the difference in bud length between treatments 5 and 6 was 1.42 mm., and the difference in bud diameter was 0.30 mm. In 1963 these differences were reduced to 0.80 mm. and 0.10 mm., respectively. Thus, on a

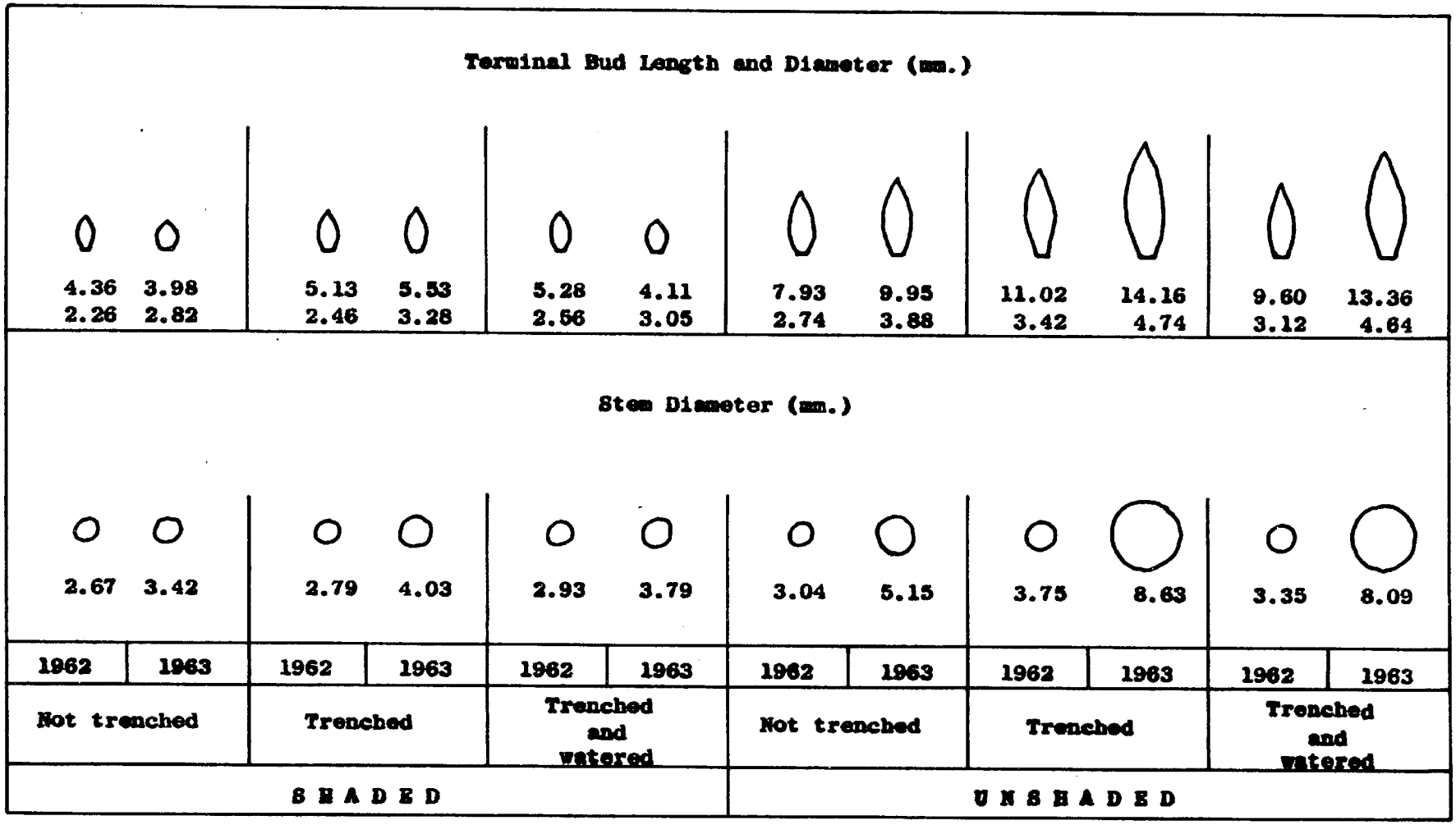


Figure 20. Average length and diameter of terminal bud, and diameter of stem at ground at the end of the 1962 and 1963 growing seasons.

percentage basis, there was a greater increase in bud size on treatment 6 than on treatment 5.

The reverse occurred on the shaded treatments. Here the trenched-and-watered treatments had terminal buds which were both slightly longer and thicker in 1962 than the buds on the trenched-only treatments. At the end of the 1963 growing season, however, the trenched-only treatment had buds which averaged 1.42 mm. longer and 0.23 mm. larger in diameter than those on treatment 3 which received supplemental water.

Another observation of interest is that the seedlings on all of the unshaded treatments produced substantially larger terminal buds in 1963 than they did in 1962. The seedlings on treatment 2 (shaded and trenched) also produced somewhat larger buds during the second field season than during the first, but the difference was much smaller than on the three unshaded treatments. Seedlings on the other two shaded treatments, however, produced shorter terminal buds during the second season than during the first, although bud diameters did increase the second year. These 1963 terminal buds on treatments 1 and 3 were therefore short and stubby instead of having the more normal slender appearance (see Fig. 20).

To obtain a general index of terminal meristematic activity, a count was made of the total number of buds on all live seedlings at the end of the 1963 growing season. The results of this count are given in Table 12.

The familiar pattern again emerges, with seedlings on

the unshaded treatments producing more than twice as many buds as those on the shaded treatments under comparable moisture conditions. And, under a given level of light, the seedlings on the trenched plots produced about twice as many buds as those on the untrenched plots.

Table 12. Average number of buds which were produced per seedling during 1963 by seedlings which were alive throughout the year.

Light level	Moisture level		
	Untrenched	Trenched	Trenched and watered
	(Ave. no. of buds per seedling)		
Shaded	1.9	3.8	3.2
Unshaded	4.4	8.3	7.5

The time of bud set was also noted in both 1962 and 1963, but only the latter year gives a true picture of response to treatment because the seedlings had hardly become established before the time of bud set in 1962. The first evidence of terminal bud set in 1963 was noticed on June 19, at which time all seedlings on the unshaded treatments, and all but 16 seedlings on the shaded treatments, appeared to be initiating buds. Of these 16 shade-grown seedlings, 9 were on treatment 1 (untrenched), 2 were on treatment 2 (trenched), and 5 were on treatment 3 (trenched and watered). All 16, however, had initiated buds by the time of the next observation on June 25.

STEM DIAMETER GROWTH

The average stem diameter for each treatment at the end of each of the two field seasons is shown graphically in Figure 20. For convenience the numerical data are also presented in Table 13.

Table 13. Average diameter of the seedling stems in each treatment at the end of the 1962 and 1963 growing seasons. Measurements were made about one-eighth inch above ground-line.

Time of measurement	Light level	Moisture level		
		Untrenched	Trenched	Trenched and watered
		Stem diameter (mm.)		
Fall 1962	Shaded	2.67	2.79	2.93
	Unshaded	3.04	3.75	3.35
Fall 1963	Shaded	3.42	4.03	3.79
	Unshaded	5.15	8.63	8.09

Stem diameter measurements at the start of the first field season would have been desirable, but were not made due to the press of such urgent tasks as the frequent manipulation of the brush during the first few weeks to assure the maintenance of proper treatment conditions. Thus, comparisons between treatments as to initial stem diameters are not possible, but the differences were not great and were probably in about the same proportion between treatments as were the initial seedling heights.

Marked differences in stem diameter growth developed, however, as the study progressed (Fig. 20 and Table 13).

While first-year differences were large enough to be significant, the contrast increased dramatically during the second field season. At the close of this second season, the seedlings on treatments 5 and 6 had stem diameters more than twice as large as those on the shaded treatments with the same moisture regimes.

The diameters on treatment 4 (ample light but limited moisture) were considerably smaller than those on treatments 5 or 6 and, in fact, were closer in general magnitude to those of treatments 1, 2, and 3. This suggests that moisture played an important role in influencing stem diameter growth. Without ample light, however, the differences in diameter growth under different moisture regimes were comparatively small. At the end of two field seasons, the average diameter on treatment 2 (best of the shaded treatments) was only about 18% greater than that on treatment 1 (poorest of the shaded treatments).

ROOT GROWTH

The general pattern of root development was illustrated earlier in Figure 13. From this figure it appears that root development was hampered to about the same extent as was top development by restricted light or restricted moisture. Root development in terms of dry-matter production and top-root ratios will be presented in the next section. Comparisons for the present will be confined chiefly to root extension growth.

When the seedlings were excavated at the end of the second field season, considerable care was taken to remove the root systems intact and to follow each root to its terminus. A few of the very fine rootlets were undoubtedly lost, but the vast majority remained attached. After excavation and the removal of most of the soil, the distance between the root collar and the furthest extremity of the free-hanging root system was measured.

A comparison of the average length of the longest roots which developed on the seedlings in each treatment is given in Table 14. When moisture was not limiting (as on the plots which were trenched), the longest roots of the seedlings growing in the open averaged more than twice as long as those on the shade-grown seedlings. Where competition for moisture was present, however, the longest roots on the unshaded seedlings averaged only about 50% longer than those on the shaded plots.

Table 14. Average length of the longest roots which developed under each treatment during the two-year study period.

Light level	Moisture level		
	Untrenched	Trenched	Trenched and watered
	Ave. length of longest root (cm.)		
Shaded	21.9	26.5	21.9
Unshaded	34.3	55.4	48.8

By the same token, differences due to moisture levels

were not large unless light was not limiting. On the plots in the open, the longest roots on the trenched seedlings averaged 61% longer than those on the untrenched plots. On the shaded plots, however, the average maximum root length was only 21% longer on the trenched than on the untrenched plots; and on the shaded plots which were both trenched and watered the average length of the longest root was identical to that on the untrenched shaded plots (21.9 cm.).

It was also found that the seedlings which died on the three shaded treatments had considerably shorter maximum rooting lengths than the seedlings which remained alive. On treatment 1 the seedlings which died had a maximum root length averaging only 17.9 cm. as compared to 24.6 cm. for the seedlings which survived. On treatment 2 the longest roots of the dead seedlings averaged 21.3 cm. as compared to 28.6 cm. for those which survived; and on treatment 3 these values were respectively, 19.1 cm. and 23.8 cm.

At the time of excavation in October of 1963, all live seedlings showed active root growth as evidenced by numerous white root tips. These growing tips varied considerably in length, however, ranging from as little as 1 mm. on the weakest seedlings in treatments 1 and 3 to as much as 30 mm. on the most vigorous trees in treatments 5 and 6. Also, it was observed that mycorrhizae were present on the root systems of all live seedlings, their abundance being generally proportional to the size and vigor of the seedling as a whole.

One other interesting feature observed during the excavation process was that some of the primary roots frequently narrowed to almost thread-like diameters as they were progressively uncovered. Yet they almost invariably thickened again as excavation proceeded, and often the terminal inch or two was appreciably thicker than portions nearer to the point of origin. This phenomenon is illustrated in Figure 21.

DRY-MATTER PRODUCTION

Perhaps the single most useful measure for evaluating the influence of environmental conditions on seedling growth is dry-matter production, since this expresses growth in terms of the actual amount of plant material produced. Also, the distribution of this dry-matter within the plant as a whole is of interest. These findings are presented in Table 15 and graphically in Figure 22.

From both the figure and the table, the overwhelming superiority of the seedlings which grew essentially without competition for either light or moisture is readily apparent. Dry-matter production on the most favorable treatment was 15 times as great as it was on the treatment where heavy competition for both light and moisture prevailed. Where moisture was not limiting (as on the four trenched treatments), the seedlings in full light produced about ten times as much dry-matter as did those in the shade.

Freedom from shade, however, was not of itself sufficient to assure a high rate of dry-matter production. This

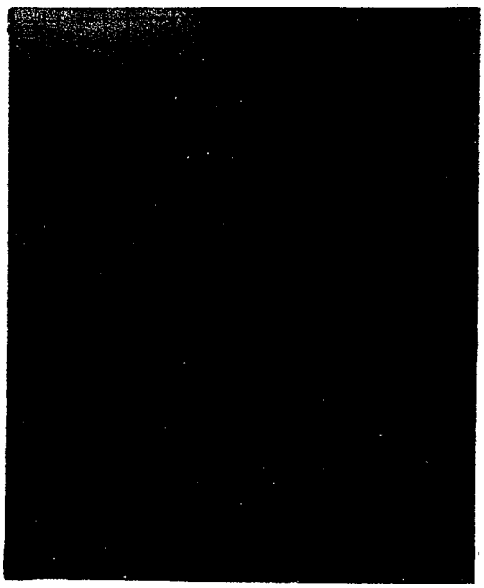


Figure 21. Root development of a vigorous seedling showing the thickened root ends. Heavy lines are at 5-inch intervals.

is evident from the mediocre showing made by the seedlings on treatment 4 which received abundant light but were forced to compete with the brush for moisture. These seedlings produced only about one-quarter as much dry-matter as did the treatment 5 seedlings which were free from the root competition of the brush as well as from its shading effects.

Table 15. Various aspects of dry-matter production on a per-seedling basis as determined at the end of the second field season. Dry weight was obtained by oven-drying to constant weight at 70°C.

Item	Light level	Moisture level		
		Untrenched	Trenched	Trenched and watered
Oven-dry wt. of:			(grams)	
Needles	Shaded	0.86	1.37	0.90
	Unshaded	3.70	14.85	12.75
Stem, branches, and buds	Shaded	0.47	0.70	0.54
	Unshaded	1.48	5.27	4.17
Entire top	Shaded	1.33	2.07	1.44
	Unshaded	5.18	20.12	16.91
Roots	Shaded	0.56	0.88	0.57
	Unshaded	1.86	8.34	6.99
Entire seedling	Shaded	1.88	2.94	2.01
	Unshaded	7.03	28.45	23.90
Percent total wt. in:			(percent)	
Needles	Shaded	44.4	46.1	44.4
	Unshaded	52.1	52.0	52.9
Stem, branches, and buds	Shaded	25.4	24.8	27.9
	Unshaded	21.0	18.4	17.3
Roots	Shaded	30.2	29.1	27.7
	Unshaded	26.9	29.6	29.8
Top/root ratio	Shaded	2.39	2.50	2.68
	Unshaded	2.79	2.41	2.43

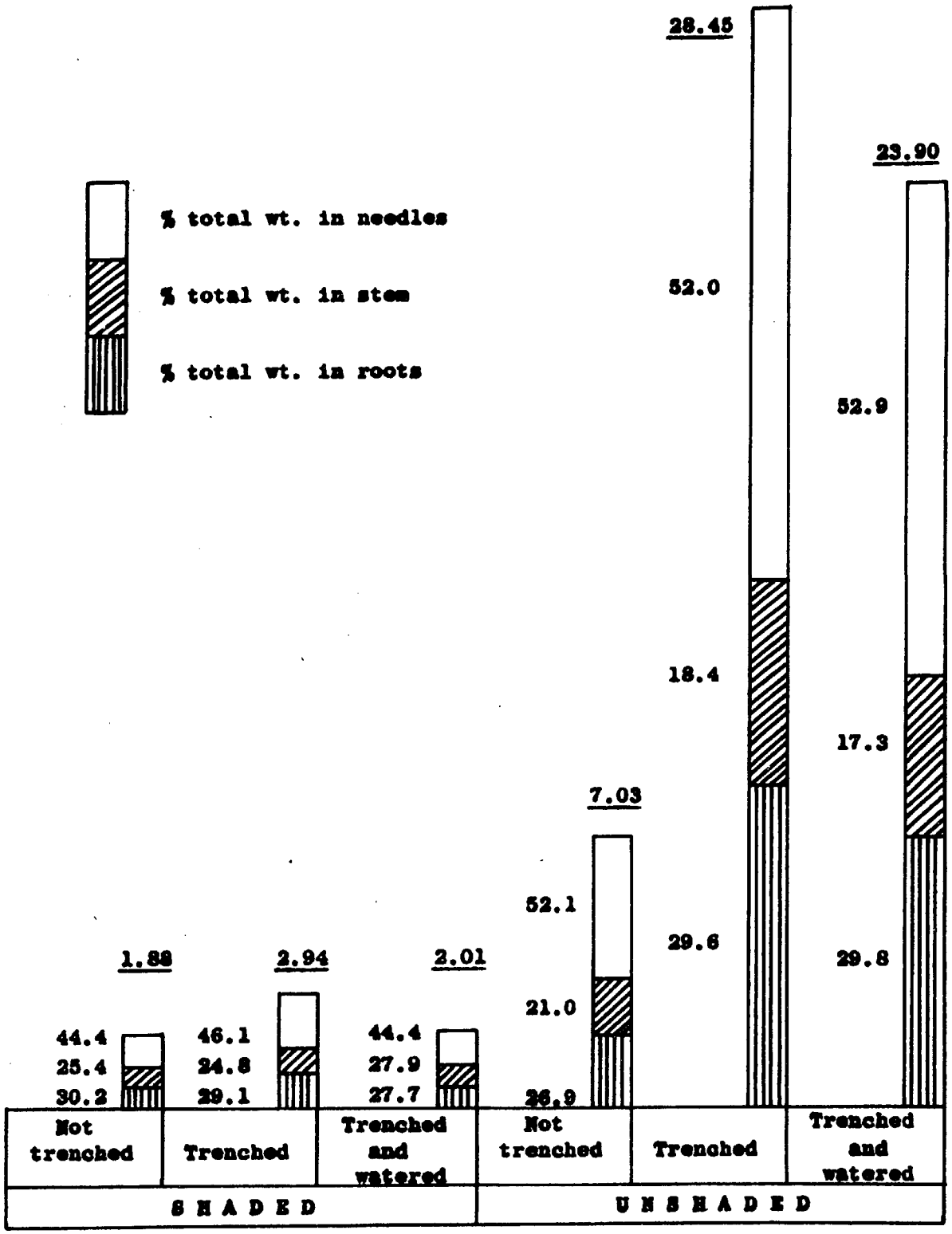


Figure 22. Average seedling dry weight and proportion of weight in needles, stem, and roots after two field seasons. (Figures above columns indicate total oven-dry weight in grams; figures next to columns indicate percent of dry weight in various parts of the seedling.)

Similarly, when light intensities were low, the elimination of competition for moisture stimulated dry-matter production only moderately. The average dry weight of the seedlings on the shaded plots which were trenched but not watered (treatment 2) was about 56% greater than the average dry weight of those which were subjected to root competition (treatment 1). And treatment 3 (trenched and watered) produced seedlings which were only about 7% heavier than those on treatment 1.

Thus, while the two factors of light and moisture made their individual contributions to seedling dry-matter production, they contributed far more when both were at favorable levels than when either one was deficient. This apparently strong interaction of the two factors was corroborated by the analysis of variance which showed that differences between treatments due to light, to moisture, and to their interaction all were significant.

Of special interest is the way in which the dry weight was distributed within the seedlings under the different combinations of light and moisture. This is also shown in Figure 22 and Table 15. For this purpose each seedling was partitioned into three components or component groups, and each portion was oven-dried and weighed separately. The three groups were as follows: (1) the needles; (2) the stem, branches, and buds; and (3) the roots.

Of these three groupings, the proportion of total seedling weight which was contained in the roots fluctuated the

least among the 6 treatments. This percentage in roots varied from an average of 26.9 for the seedlings in treatment 4 (untrenched and unshaded) to 30.2 for the seedlings in treatment 1 (untrenched and shaded), representing a total range of only 3.3%. Thus, most of the differences in weight distribution between the treatments were due to the way in which the dry weight of the tops was subdivided between the needles on the one hand, and the stem, branches, and buds on the other.

The differences in weight distribution within the tops appear to be a response to light more than to moisture. On the three unshaded treatments the percentage of total seedling dry weight represented by the needles averaged between 52.0 and 52.9; on the three shaded treatments it averaged between 44.4 and 46.1. Apparently, high light intensity favors needle development to a greater extent than the development of other parts of the seedling.

As a corollary to the high proportion of the total weight of the unshaded seedlings which is in the needles, a smaller percentage of their total weight is in the stem, branches, and buds. On seedlings on the three shaded treatments, these other structures comprise about 25% to 28% of the total dry weight, whereas on the unshaded treatments they comprise only 17% to 21%.

It was unexpected to find that the average top/root ratios for the various treatments did not differ greatly from one another (Table 15). This, of course, follows from the obser-

vation already noted that there was not a great deal of difference between treatments as to the proportion of seedling dry weight which occurred in the roots. The average top/root ratios ranged from 2.39 to 2.79, with the ratios on the treatments which had essentially no competition averaging about 2.42.

Surprisingly, the seedlings on treatment 1, which grew under heavy competition and which were in most respects the poorest, had top/root ratios very similar to those with no competition, averaging 2.39. Even more surprising was the finding that the seedlings which died on treatment 1 had smaller top/root ratios on the average than those which survived (2.26 vs. 2.47). On the other two shaded treatments, however, the seedlings which died had decidedly larger ratios than those which survived. On treatment 2 the average ratios for the dead and living seedlings were, respectively, 2.90 and 2.33; and on treatment 3 they were 3.14 and 2.37.

Because of some overlap in top/root ratios of seedlings which died and of those which survived, and also because of the relatively small number of those which died, no attempt was made to establish whether differences in average top/root ratios between surviving and non-surviving seedlings were statistically significant. However, an analysis of variance was made based on all seedlings (except the one that died the first year) to ascertain whether there were significant differences in top/root ratios between the six basic treatments.

This analysis revealed that differences attributable to the individual influences of light and moisture were not significant, but that differences due to their interaction were significant. The same results were obtained for differences in the percent of total weight occurring in the roots. On the other hand, differences in the distribution of the dry weight within the tops (i.e., the percent in needles, and the percent in stem, branches, and buds) were significant on the basis of the light treatments, but not of the moisture treatments.

SPECIAL GROWTH CORRELATIONS

It has been reported in the literature that for certain species the amount of height growth in a given year is closely correlated with the size of the previous year's terminal bud (Duff and Nolan, 1953; Wenger, 1955). It was, therefore, of interest to see just how strong this correlation might be under the conditions which existed in the present study. Another relationship of interest was the possible correlation between the number of needle fascicles produced on the main stem in a given year and the size of the previous year's terminal bud.

These two relationships were tested by regression analysis using the data from all seedlings regardless of treatment. The only seedlings excluded were those which did not have a live terminal bud at the end of the 1962 growing season. Three seedlings were excluded on this basis, one having

died during the 1962 growing season, and the other two having the terminal shoot die back before the end of the season.

There is, of course, the confounding influence of treatment in these regressions. That is to say, not only did the formation of the buds take place under different environmental conditions during 1962, but the subsequent development of the shoots and needles also took place under different environmental conditions during 1963. Thus, while high correlations were obtained for both regressions, it is not known whether these were high because of, or in spite of, the added influence of the 1963 environmental conditions superimposed upon 1962 bud length.

The equation for the regression of 1963 height growth on 1962 terminal bud length is:

Height growth (in cm.) = 2.124 x bud length (in mm.) - 5.614

The standard error of estimate is $\pm$ 2.45 cm. and the correlation coefficient is 0.928.

The equation for the regression of number of needle fascicles on the main stem in 1963 on 1962 terminal bud length is:

No. of needle fascicles = 9.59 x bud length (in mm.) - 13.39

The standard error of estimate is $\pm$ 8.9 needle fascicles and the correlation coefficient is 0.952.

In the first regression more than 86% of the variation

in height growth in a given year can be accounted for by differences in length of the previous year's terminal bud if height growth takes place under the same general environmental conditions as did bud formation. In the second regression more than 90% of the variation in number of needle fascicles produced in a given year can be accounted for by differences in length of the previous year's terminal bud if the development of the needles takes place under the same general environmental conditions as did bud formation.

It would have been possible to run separate regressions for the seedlings within each treatment, but this would have reduced the sample size considerably. Furthermore, since there was some variation in light and moisture even within each treatment, the factor of environment would still have to be regarded as a variable. It was, therefore, not considered worthwhile to compute these additional regressions.

DISCUSSION AND CONCLUSIONS

In evaluating the results of this study, one important consideration must be kept in mind; namely, that the influences of the two major environmental factors--light and moisture--were not studied over the same proportion of their total normal ranges. The two levels of light used probably came close to representing the two extremes of this factor which would normally be encountered under field conditions, but the three moisture levels did not completely bracket the full normal range of this factor. The wet end of the spectrum was well represented, but only the fringes of the dry end were reached. Thus, while the limiting effects of inadequate light were strongly brought to bear upon some of the seedlings, the limiting effects of inadequate moisture were brought into play to a somewhat lesser degree.

The lowest moisture content encountered corresponds to a moisture tension of about 5 atmospheres. This tension is considerably below the wilting point, but yet the amount of available water remaining at tensions above this value is less than 1% of the dry soil weight, indicating that there would have been little additional water to draw upon had the drying continued. And in all probability the seedlings were experiencing some moisture stress even at 5 atmospheres tension.

A second point which must be kept in mind in interpreting the results of this study is that under field conditions changes in either light or moisture levels produce associated

changes in other factors. A change in light intensity, for example, is almost invariably accompanied by changes in temperature, humidity, evaporation rate, and probably air movement. Thus, the differences in seedling response which are noted between two treatments with different degrees of shading cannot be attributed solely to differences in light intensity, but are the result of differences between two environmental complexes. For the sake of simplicity in the discussion, these differences will be spoken of as differences due to light, or differences due to moisture, but all of the associated differences are also implied.

One pattern which emerged rather consistently as the results were tabulated was that for many of the variables studied the response was only mediocre unless both of the environmental factors were at favorable levels. In other words, a near-optimum level of one factor could not compensate for a serious deficiency in the other, nor could either factor make its full contribution to growth if the other one was seriously limiting.

Whether or not a precise quantitative interrelationship may exist between the various factors which influence plant growth can only be conjectured. It may be hypothesized, for example, that if light, moisture, temperature, and nutrients were the only four factors which influenced plant growth, (which they are not), and if each were present at exactly 50% of its optimum level, the organism might develop at the rate of 50% x 50% x 50% x 50% or 6.25% of its maximum possible rate. In the present study, control over the environmental

factors was far too crude to permit any inferences of this type to be drawn. Indeed, we do not yet know just what the optimum levels of each of these factors might be as they relate to the growth of red pine seedlings. Future studies in controlled environment chambers will be needed before there is any hope of learning whether such a quantitative interrelationship between factors may exist.

In any event, as Kozlowski (1955) has pointed out, failure of trees to grow and survive is basically the result of some disruption of the balance and coordination in rates of physiological processes. He suggests that growth may be viewed as a manifestation of the rates by which certain anabolic processes exceed catabolic ones. Also, since carbohydrates compose over three-quarters of the dry weight of woody plants, tree growth is closely related to the production of photosynthate. Therefore, any environmental factor that alone or in combination with others influences carbohydrate production will influence growth.

Both light and moisture strongly influence carbohydrate production. Water, for example, as Kozlowski further points out, is important as a constituent of living protoplasm, a reagent in chemical reactions, a medium in which reactions occur, and a solvent. It is also very important in the maintenance of leaf turgidity which affects photosynthesis, since wilted or partially wilted leaves are ineffective photosynthetic mechanisms. Furthermore, it has been observed that plants growing in soil which was drying, but still above the

wilting point, may undergo marked depletion in carbohydrate reserves stored in the roots, stems, and leaves (Kozlowski, 1955).

Light intensity also exerts a major influence on photosynthesis, but as Shirley (1945b) has emphasized, the ultimate rate of photosynthesis depends on whether other essential factors are at favorable or unfavorable levels. If one or more factors are below optimum, photosynthesis reaches a certain plateau value and remains more or less constant regardless of further increases in light intensity. If, on the other hand, all factors are favorable, photosynthesis continues to increase with light intensity until secondary effects set in, such as high respiration caused by high light intensity and high temperature, solarization (the overaccumulation of photosynthate in the leaves), internal water deficits which cause the stomata to close, or some other internal limitation.

Thus, as Kramer and Kozlowski (1960, p. 513) point out, under conditions of competition, a complex of environmental factors exists with light and water as major components. Under natural conditions these factors are interacting and interdependent. When both light intensity and soil moisture operate as limiting factors, a sudden marked improvement in one of the factors alters the limiting effect of the interaction. The relative importance of each factor at any time depends on the physiological tolerances of the species involved and on fluctuations in physical factors of the environment.

With reference to the specific behavior of the seedlings in the present study, the mortality which occurred seemed to be primarily related to low light intensity. Whether this was the direct result of the inability of the seedlings to produce sufficient photosynthate to sustain their metabolic processes, or whether the effects were indirect was not determined. Some of the studies cited earlier, and that of Shaw (1963), have shown that when photosynthetic activity is low, root development is more adversely affected than is top development, thereby reducing the seedling's ability to satisfy its water and nutrient requirements.

This pattern of inferior root growth of the seedlings which died (all of which were growing under moderate to heavy shade) was noted in the present study. This was particularly true of root length, but was also true of the proportion of the dry weight which occurred in the roots, at least on the trenched plots.

A possible explanation for this poorer root development at low light intensities is given by Shiroya, et al.(1962), who found that seedlings of red and white pine which had been grown in the open translocated more photosynthate to the roots than did seedlings which were grown in only 6% of full sunlight. They also found that translocation of photosynthate to the roots was correlated with the respiratory activity of the roots, and that the roots of pine seedlings grown under weak light had a lower rate of respiration than did those grown under strong light.

It is not clear why the dry weight of the roots of the

shaded seedlings which were not trenched should constitute a larger proportion of total seedling weight than was the case for the shaded seedlings which were trenched. A possible explanation is that since the untrenched seedlings made the least growth of all, their top/root ratios were the least changed from the more favorable balance which had been developed in the nursery.

The fact was mentioned that only one seedling died during the first year, the remaining mortality not occurring until late in the second field season. This indicates that the adverse effects of low light intensity are not always manifested immediately, a conclusion also reached by Shirley (1929b). He cites experiments in which numerous woody as well as herbaceous species were able to survive for from three to six months under as little as 1% of full summer daylight.

This delayed mortality under low light intensities probably accounts in part for the apparent discrepancies in the findings of early investigators concerning the importance of light. Some of these early studies, both in the field and in the greenhouse, were run for periods of six months or less, with the lowest light intensity often being well above 1% of full sunlight. Since little or no mortality occurred within this period, some of these investigators concluded that light was of relatively minor importance. Had they continued their studies for two or three years, they might have reached a different conclusion.

With reference to seedling response to the three levels of moisture used in this study, an apparent anomaly exists. Theoretically it would seem that the seedlings on the plots which were both trenched and watered would show better growth in all respects than the seedlings which were trenched but not watered. This was true for only one characteristic; namely, the average length of the 1963 needles, and then only on the unshaded treatments. There was, however, some indication that for several other variables the gap between the watered and unwatered seedlings in full light was gradually narrowing. This was particularly true of the length and diameter of the terminal bud, and possibly also of stem diameter.

There are several explanations which could account for the superior growth of the trenched but unwatered seedlings over the trenched and watered ones. Among these are (1) larger initial seedling size, (2) higher average light intensity, (3) possible adverse effect on soil aeration due to the extra watering, and (4) possible reduction in soil temperature due to watering. The growth differences could be due to any one or to all of these things.

The first of these probable causes is almost certainly involved. While differences in the average initial size of the seedlings on the various treatments could have been minimized by stratifying the seedlings according to size at the time of planting, the fact that the terminal buds had already broken dormancy made it imperative that planting be

done as quickly as possible and with a minimum of extra handling. It was assumed that the random distribution of treatments over the entire area, and the random way in which the sizes were mixed in the planting box would pretty well assure equal size-class representation on all treatments. However, as chance would have it, the two treatments which were both trenched and watered had the shortest average seedling height, and the two treatments which were trenched but not watered had the tallest average seedling height at the start of the experiment.

Since the height growth of red pine in a given year has been found to be correlated with its height at the start of that year (Friesner, 1942), these differences in initial height are undoubtedly responsible for much of the poorer subsequent height growth on the trenched and watered plots. It is also quite likely that these initial size differences had an influence on the development of characteristics other than height growth.

The second possible explanation---higher average light intensity on the trenched but unwatered plots--could also account for some of the growth differences. While the difference in average light intensity between these treatments was not large (only about 2% both in the open and in the shade), it could be enough to produce at least small differences in growth responses, particularly on the shaded treatments. Shirley (1929b) reports on experiments which have shown that at light intensities below 20% of full light the

increase in dry-matter production is almost directly proportional to the light intensity.

Explanation number 3--the possible adverse effect of the additional watering upon soil aeration--could also be a minor factor, although it would likely be quite small in such a sandy soil. Nevertheless, since the weekly water deficit was supplied in a single application of water, frequently amounting to an inch or more, these plots regularly had part of their large-pore as well as small-pore volume filled with water, although probably for only short periods of time. As Loustalot (1945) found in working with pecan seedlings, excessive moisture can cause subnormal rates of photosynthesis on sandy soils as well as on fine-textured soils. This is due to the fact that excess soil moisture actually produces a water deficit in the plant by interfering with water absorption (Kramer, 1958).

Explanation number 4--the possible reduction in soil temperature due to watering--may or may not be important. Since soil temperatures were not measured in this study, there is no way of assessing their possible influence on seedling growth. That watering does reduce soil temperatures, particularly at the surface, has been shown by Maguire (1955) who studied this factor in relation to ponderosa pine survival in California. He found that one day after an artificial watering equivalent to one inch of rain, the soil surface temperature of the watered soil was 41°F. lower than was the temperature of the dry soil.

Two days later the surface temperature of the watered soil was 26°F. lower, three days later it was 17°F. lower, and one week later it was still 6°F. lower. Temperature differences below the surface would, of course, be far smaller.

Maguire was concerned with excessive temperatures at the soil surface and with a situation where the cooling effect of watering was beneficial to seedling establishment and survival. In cooler climates, however, and at greater soil depths, lowered soil temperatures often have a retarding effect on growth. Adams (1934), working with white pine seedlings, found that there was a steady improvement in both top and root growth as soil temperatures at the 8-inch depth increased from 45°F. to 87°F.

The first two hypotheses are probably of greatest importance. If the seedlings on these treatments had been the same size at the outset, and if they had grown under identical light regimes, the seedlings which had received the additional water would probably have shown superior growth for most of the measured characteristics.

With regard to time of bud-burst and the start of shoot elongation, it was found that there was not much difference between treatments. This is not surprising since the breaking of dormancy in the spring is generally recognized as being largely temperature-induced. Since in the present study all competition for light and moisture was provided by deciduous brush and herbs, and since these were leafless and essentially dormant until well into the month of May, there

were no appreciable temperature or other environmental differences between the treatments at the time the pine seedlings broke dormancy during the first week in May.

The time of bud setting, however, was apparently influenced somewhat by treatment, with high light intensity tending to promote earlier bud setting than low light intensity. The word "apparently" is stressed because the identification of the initial stages of bud formation was by macroscopic inspection with the unaided eye. It is thus possible that tiny incipient buds were also present on all of the suppressed seedlings at the time they were first recognizable on the much larger open-grown seedlings, but that they were overlooked on some of the former. On the large open-grown seedlings the upper needles surrounding the buds were clearly spread away from the stem tip, making the new buds easy to see. On the suppressed seedlings, however, the upper needles were often interlocked above the stem tip, making the inspection for bud initiation much more difficult.

Assuming that a real difference in time of bud setting existed, a response to moisture as well as to light was also indicated. Of the 16 seedlings which formed their buds about one week later than the rest (all 16 being on the shaded treatments), 9 were on the untrenched treatment where full moisture competition was present.

The reasons for the delayed bud setting on these 16 seedlings which were growing under some degree of competition are not known. Duff and Nolan (1958) indicate that the

start of primordium production in the terminal meristematic regions of red pine is coincident with a decline in the local auxin supply, but they do not claim that a causal relationship necessarily exists. It might also be speculated that bud formation is initiated by the build-up of some special substance, and that this material is produced more slowly when the general growth conditions are unfavorable than when they are favorable.

The cessation of height growth was also influenced by treatment but, in contrast to the formation of the buds, growth terminated sooner on the shaded than on the unshaded seedlings. This is in agreement with the findings of Collins (1961) who noted that young red maple seedlings growing beneath an oak overstory ceased height growth sooner than did seedlings growing in the open. This earlier cessation under the oak overstory coincided with the leafing out of the oak, leading Collins to postulate that light intensity might be the controlling factor.

In the present study the major brush species had attained full leaf development by about June 18 (Appendix D). Height growth on the shaded seedlings essentially ceased one week later, but on the unshaded seedlings it continued for several additional weeks. Thus, there is a definite difference in time of cessation on the basis of treatment. However, this may not be a direct response to decreasing light intensity, but may instead be due to the earlier depletion of the much smaller food reserves stored by the shaded seedlings.

That light intensity alone is not directly responsible is indicated by the fact that even the unshaded seedlings ceased height growth (except for new bud enlargement) by about mid-July, even though light and moisture were at near-optimum levels at that time, particularly on the trenched plots. The termination of height growth under such favorable levels of moisture and light intensity suggests that the cessation may be controlled by other factors such as photoperiod, the build-up of a growth inhibitor, or the exhaustion of food reserves.

The high correlation which was found to exist between the length of the 1962 terminal bud and the amount of the following year's height growth was not unexpected. Wenger (1955) found a similar relationship for loblolly pine seedlings, obtaining a correlation coefficient of 0.91 as compared with 0.93 found here for red pine. This further substantiation of the close correlation of these two characteristics increases confidence in the predicting value of terminal bud size as an indicator of the following year's height growth.

The absence of major height growth differences between seedlings during their first year in the field can be explained on the same basis. During the previous year they had all grown under almost identical conditions in the nursery and, therefore, the buds formed at that time were all very similar in size. Consequently, when the seedlings were field planted in 1962, even though in radically different environments, their ultimate height growth for that year had already

been largely predetermined by the previous year's environmental conditions in the nursery.

The high correlation which was found to exist between the length of the 1962 terminal bud and the number of needle fascicles which developed on the main stem the following year was also not surprising, but is worthy of documentation. As reported by Duff and Nolan (1958), the winter buds contain all the primordia for the structures which will undergo extension growth the following spring and summer (i.e., primordia for male flowers, female flowers, needle fascicles, and lateral shoots). Normally, however, the lateral budlets which develop will differentiate only budlet scales during the year of their formation, and the specific differentiation of leaf fascicle primordia does not take place until the following spring. Nevertheless, the generative centers for these structures are present in the winter bud, and their number is apparently highly correlated with the length of this bud.

The amount of elongation of the needles, however, is a direct reflection of the environmental conditions prevailing during the year of their extension growth (Duff and Nolan, 1953). Since the needles are important structures for food storage (Allen, 1964; Rutter, 1957), their length and thickness as well as their number would presumably exert considerable influence on the amount of growth which the seedling could make the following year. Although this possible correlation was not tested in the present study, Wenger (1955)

found a high correlation between needle length and the following year's height growth of loblolly pine. A similar correlation quite likely exists for red pine.

This is not contradictory to what has already been said concerning the strong relationship between height growth and the size of the previous year's terminal bud. Many of these seedling attributes go hand-in-hand, and red pine seedlings which have large terminal buds in a given year are also likely to produce long needles during that same year.

The lammas (or late-summer) shoot growth which was noted on the more vigorous seedlings in the present study has also been reported on red pine by other observers (Carvel, 1956; McCabe and Labiski, 1959). Carvel noted that these shoots originated exclusively from the newly formed lateral buds surrounding the terminal bud of the main stem. In the present study this likewise seemed to be the main point of origin of these shoots, although some also originated from the terminal buds of lower lateral branches.

Carvel attributed the formation of these shoots to a weather pattern involving a severe drought in June and July which was then followed by a later summer rainy period. He postulated that the early summer drought had shortened the normal growing period, and then the increase in precipitation in late July apparently stimulated a renewed growth of the lateral buds.

In the present study, however, no summer drought condition was involved since these lammas shoots were most abun-

dant and vigorous on the seedlings growing under the most favorable conditions of light and moisture. These shoots seemed to develop in response to conditions which were continually favorable to growth rather than to a sequence of unfavorable followed by favorable growing conditions.

It is possible that on some seedlings one or more of these upper lammas shoots could have eventually taken over apical dominance from the main stem if the study had been continued. The extent to which this might have happened can only be conjectured, but it seems unlikely for several reasons that all or even most of these seedlings would have been deformed in this manner. For one thing the terminal buds which finally formed at the end of these lammas shoots late in the season were, without exception, smaller than the main stem terminal bud. Secondly, the needles on these shoots were thin and only about one-half the length of the normal needles; and furthermore, they were more chlorotic in appearance than the normal needles. Thus, for the most part, these lammas shoots did not exhibit the vigor which characterized the main stem.

Of particular interest was the obviously strong interaction of the factors of light and moisture in dry-matter production. For most other seedling characteristics, the improvement in light conditions alone resulted in an appreciable increase in growth over that exhibited by the seedlings experiencing both types of competition. This was far from true, however, for dry-matter production. The increase

in this variable was decidedly mediocre unless both light and moisture were at favorable levels.

This would suggest that the dimensional growth (particularly in length) of certain structures takes place quite readily in response to an improvement in light intensity, but that such size increase is not necessarily accompanied by a proportionate increase in dry weight. Ordinarily, such elongated spindly growth is associated with shade-grown plants. The shade-grown seedlings in this study did, in fact, develop weak and spindly stems and needles, but this was not conspicuous because these structures were also shorter than those which developed on the seedlings without shade. Judging by the findings of the present study, it appears that red pine seedlings will tend to develop thin stems and slender needles even under about 80% full sunlight if moisture is a limiting factor.

It is true that these untrenched plots in the open received somewhat less sunlight than did the trenched plots (79% vs. about 85%). While this difference in light intensity undoubtedly played some part in the resulting growth differences between the trenched and untrenched seedlings, it is inconceivable that any major response differences would have resulted on the basis of this factor alone. Numerous investigators have found that small variations in light are of minor importance at the higher light intensities (Clements, Weaver, and Hanson, 1929; Blackman and Wilson, 1951).

Thus it would seem that even a moderate moisture stress has a seriously depressing effect on carbohydrate production. By considering only height growth, little evidence of the extent of this reduction is obtained. Stem diameter growth must also be taken into account before the magnitude of the reduction in dry weight is appreciated.

Drawing together the general findings, and keeping in mind that they may not fully apply in a real drouth year, the following conclusions concerning the growth of planted red pine seedlings on brushy areas in northern Minnesota can be drawn:

1. If only one of the two forms of competition is removed, the removal of competition for light will, without exception, produce a larger growth response than will the removal of the competition for moisture. This was most apparent with respect to shoot elongation, terminal bud size, number of needles produced, needle elongation, and root elongation, but was also true for every other variable observed. (Note the point made that it is the competition for light that is regarded as being of more importance than the competition for moisture under conditions which are commonly encountered; not that light per se is more important than moisture per se for the growth of red pine seedlings).

2. While competition for moisture certainly cannot be regarded as of minor importance, the responses to the elimination of moisture competition are very small unless the competition for light is also eliminated. On the other hand, responses to the elimination of competition for light are

quite substantial for most variables, even though nothing is done to eliminate or reduce the moisture competition.

3. For all observed characteristics maximum growth occurs when both types of competition are eliminated. The growth resulting when both factors are at favorable levels is almost always greater than that which would be expected if the separate contributions of the two factors were merely additive. This demonstrates a decided interaction between these factors.

4. The interaction is most apparent in what is probably the best single measure of growth; namely, dry-matter production. The increase in this variable is relatively small if either light or moisture is seriously limiting, regardless of how favorable the other factor may be. Thus, for improvement in the really important facets of growth--carbohydrate production and the actual increase in plant material--both light and moisture must be at favorable levels.

While the primary aim of the study was to learn more about the basic growth responses of red pine seedlings when grown under given levels of competition for light and moisture, the findings also have practical implications. Simply stated, the study strongly reinforces the case for prompt release of planted red pine seedlings. This will come as no surprise to most practicing foresters, but the magnitude of the loss in growth which results from delaying release may not be fully appreciated.

Within two years after planting, lack of release resulted in a reduction in survival of 38%, a reduction in height

attained of about 50%, and a reduction in total dry weight attained of about 93%. Rudolf (1950), reporting on earlier experiments on the Chippewa National Forest, states that after five years these losses on unreleased areas are likely to be as high as 70% in survival, 90% in height growth, and 99% in total dry weight.

SUMMARY

In the spring of 1962 a study was installed on the Chippewa National Forest in north central Minnesota for the purpose of evaluating the relative importance of competition for light and competition for moisture on the growth and morphology of red pine seedlings. Interest was centered on the competition furnished by a heavy shrub layer since previous investigators had found that in brushy areas the understory vegetation rather than the overstory was mainly responsible for the poor growth and survival of newly planted red pine seedlings.

The study area was occupied by a dense and relatively uniform stand of hazel brush, with small percentages of several other species intermixed. The brush ranged in height from two to six feet, averaging about four feet tall. No overstory trees were present. The soil was a deep, well-drained loamy sand, the upper 15 inches of which averaged about 85% sand, 12% silt, and 3% clay.

A factorial design was used involving two light levels and three moisture levels. The light levels were (1) no release from shading, and (2) essentially full release from shading; the moisture levels were (1) no release from root competition, (2) root competition eliminated by trenching, and (3) root competition eliminated by trenching, plus the adding of supplemental water during dry periods. These six basic treatments were replicated 15 times using single-seedling plots as replications; thus, 90 seedlings in all were

planted. The various growth responses of the seedlings were followed for two growing seasons, the first of which was considerably wetter than normal, and the second slightly drier than normal.

Midsummer light intensities averaged about 83% of full light on the released plots and about 8% of full light on the unreleased plots. Moisture levels during dry periods averaged 6.75% water (by weight) on the untrenched plots, 8.54% on the trenched plots, and 11.18% on the trenched and watered plots. Some of the heavily shaded plots had light levels as low as 2% of full light at certain times during the study. And some of the untrenched plots had moisture levels as low as 3.5% during dry periods, which corresponds to a moisture tension of about 5 atmospheres.

Temperature, precipitation, and relative humidity were measured on the study area by means of continuously recording instruments. In addition, weekly maximum and minimum temperatures were obtained near representative seedlings on each treatment during the 1963 growing season. Light measurements were made seven different times during the course of the study, obtaining simultaneous readings on all plots by means of light-sensitive Ozalid paper packets which were left in place for periods of about 6 hours. Soil moisture samples were taken at intervals during the two growing seasons by means of a small-diameter sampling tube which permitted gravimetric sampling close to the seedlings without causing serious problems of disturbance.

Findings were that under the range of conditions tested, seedling mortality was definitely more closely related to competition for light than to competition for moisture. No mortality occurred on any of the unshaded plots, whereas 38% of the seedlings on the shaded plots died before the end of the second growing season. There was little difference in the percent of mortality under the different moisture regimes, indicating that even near-optimum moisture conditions have little effect in reducing mortality if the light intensity is too low.

All aspects of seedling growth showed greater response to the elimination of competition for light than to the elimination of competition for moisture. This was true for height growth, needle elongation, terminal bud size, root elongation, number of needles produced, stem diameter growth, and dry-matter production.

Responses to the elimination of moisture competition were invariably small unless the competition for light was also eliminated. On the other hand, responses to the elimination of competition for light were appreciable for most variables even when nothing was done to eliminate moisture competition. However, the best responses were obtained when both types of competition were eliminated.

The improvement in growth when both forms of competition were eliminated was more than the increase which would be expected if the separate effects of an improvement in light and an improvement in moisture were simply additive. This

demonstrates the existence of interaction between the factors of light and moisture as they affect seedling growth.

This interaction was particularly apparent with respect to increases in total dry-matter production which is one of the best single measures of plant growth. In contrast to many other variables which showed fair response when only the competition for light was eliminated, dry-matter production was decidedly mediocre unless both forms of competition were eliminated. In other words, carbohydrate production was seriously hampered unless both light and moisture were at favorable levels.

The distribution of the dry weight within the seedlings on each treatment was also studied with reference to the percent of total weight in the needles; in the stem, branches, and buds; and in the roots. The proportion of dry weight in the roots was surprisingly similar for all treatments; top/root ratios were, therefore, also quite similar. The largest differences were in the way that the weight of the tops was subdivided between needles on the one hand, and stem, branches, and buds on the other. This was primarily a response to differences in light intensity rather than to differences in moisture levels.

The unshaded seedlings averaged between 52.0% and 52.9% of their total dry weight in needles, whereas the shaded seedlings averaged between 44.4% and 46.1% of their total weight in needles. The percentage of total dry weight in stem, branches, and buds was, therefore, smaller on the unshaded

seedlings than on the shaded ones, averaging from 17% to 21% on the former, and from 25% to 28% on the latter.

Weekly height growth measurements were made on each seedling during both growing seasons, and weekly needle elongation measurements were made on three needles on each seedling during the second season only. It was found that height growth started about the same time on all treatments, but the rate of growth was much more rapid, and growth continued for a longer time on the unshaded than on the shaded seedlings.

Needle elongation followed a somewhat similar pattern but the entire process was less abrupt than was height growth. Needles near the tip of the new shoot began growth later than those near the base, but they grew more rapidly and before the end of the season had caught up with those that had started growth sooner.

The practical implications of the study are that prompt release of young red pine seedlings growing under heavy brush is very important if serious losses are to be avoided. The study showed that within two years after planting, seedlings which have not been released may have experienced reductions in survival of about 38%, reductions in total height of about 50%, and reductions in total dry weight of about 93% as compared with seedlings which were fully released.

APPENDIXES

APPENDIX A: THE CONSTRUCTION AND USE OF THE OZALID LIGHT METER

The Ozalid paper method for measuring light intensity is based on the principle that light-sensitive diazo compounds form deeply colored addition compounds on short exposure to ammonia vapor. This principle has been used to manufacture a variety of photographic copying materials brought out by the Ozalid Company and other firms. In the present study the paper used was Ozalid #402 IT.

The treated side of this paper, as long as it is kept away from light, remains a pale greenish-yellow color. Light, upon striking the paper, has a bleaching action rather than a darkening action, and thus a series of density filters is provided as the light passes progressively through a stack of these sheets. On a bright, sunny day the uppermost sheet will be completely bleached in less than two minutes, but as the light penetrates downward through the stack, it must pass through an ever-increasing number of the bleached sheets, and the bleaching action becomes progressively slower. It was found that a stack of 15 sheets was ample to assure at least 2 or 3 unbleached sheets at the bottom of the stack after 8 hours of exposure on a bright, clear day.

For field use the Ozalid paper was cut into small one-inch squares, 15 of these being stapled together along one edge to form a small booklet, with all treated sides facing

the same way. This was done in a dark-room using a weak red light. Such extreme caution is probably not necessary and the booklets could be made up in a room with weak white light, particularly if the top sheet is discarded just before placement in the field. However, this was not practical with the arrangement used in the present study.

After the booklets themselves are completed, they must be packaged in such a way that, when placed in the field, light can penetrate to the lower sheets only by passing through the bleached upper sheets. Light must not be permitted to enter the booklet from the side or an erroneous reading will result. To assure that light could pass downward only through the center portion of the stack of papers, each booklet was sandwiched between two pieces of black cardboard, each about two inches square. The upper piece of cardboard had a half-inch hole cut out of the center, and all light striking the booklet had to pass through this small opening.

The packet was prepared for field use by placing the cardboard sandwich (with the hole side up) on a piece of $\frac{1}{2}$-inch-thick foam rubber, cut to the same size as the cardboard. Finally, the entire assembly was wrapped in Saran Wrap and fastened with Scotch tape on the underside.

After the packets have been exposed to light for the desired length of time, they can be easily and quickly developed by a "dry" process. This consists of placing the small booklets in a wire hopper inside a large jar containing a small amount of ammonia in the bottom. With the lid tightly

closed, the booklets are developed in the ammonia vapor. The vapor reacts with the unbleached portions of the booklets, turning these parts a dark brown. When the developing is completed, each booklet has a series of sheets the centers of which are bleached white, and the edges of which, on the bleached sheets, are dark brown. The sheets which were beyond the bleaching action of the light will be completely brown. Thus, by counting the number of sheets with bleached centers, the depth of penetration of the light can be determined, and hence its intensity can be estimated.

In practice, the last sheet to be affected by the light will usually be only partially bleached since the bleaching, particularly of the lower sheets, takes place rather slowly. Hence, for greater precision, it is desirable to estimate the degree to which this last sheet has been bleached. This can be made at least somewhat objective by examining a large number of exposed booklets and selecting from them an array of partly exposed sheets which represent as nearly as possible one-tenth exposure, two-tenths exposure, three-tenths exposure, etc., up to full exposure. These sheets can then be used as a set of standards against which all subsequent partly exposed sheets can be compared.

The method is suitable for estimating either absolute light intensity expressed in terms such as foot-candle hours, or relative light intensity expressed as a percentage of full sunlight. The latter basis was chosen for use in this study. In either case a calibration run must be made so that a curve

can be plotted which relates the number of sheets of Ozalid paper bleached to known quantities of light. Figure 23 shows the calibration run in progress.

The test packets were set out in the open on a cloudless midsummer day for 5 carefully-timed exposure periods. The periods ranged from 15 to 360 minutes with 3 packets being exposed during each period. The run was made between 9:00 A.M. and 3:00 P.M., the 3 packets receiving the 360-minute exposure being left in place for the full time. Packets exposed for 15, 45, 90, and 180 minutes were set out and picked up at various times between 9:00 A.M. and 3:00 P.M. to assure that the early, middle, and late portions of the test run would be sampled during each exposure period. In this way any major fluctuations in light intensity during the 6-hour test period would have been evident in comparing the 3 packets within any one exposure period. No great variations in light intensity were apparent during the 6-hour run, although a slight mid-day peak was noticeable, especially in the short 15-minute exposure series.

As pointed out by Friend (1961) the penetration of light through these packets closely follows Lambert's law of absorption, and consequently the number of layers bleached is proportional to the logarithm of the light energy received. This relationship is apparent in Figure 24 in which a straight line results when the number of sheets exposed is plotted over the logarithm of the exposure time. The equation for this regression is as follows:



Figure 23. Making the calibration run of the Ozalid light meter.

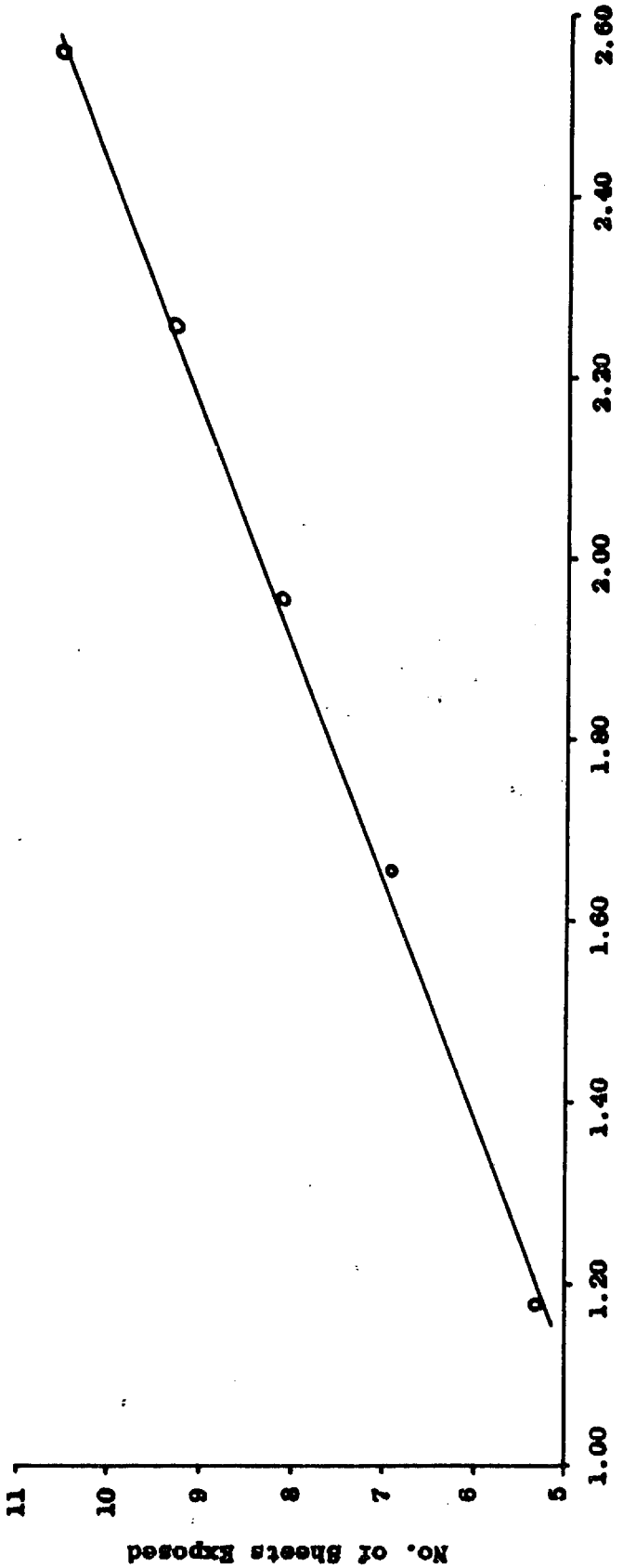


Figure 24. Calibration of the Ozalid light meter. Each plotted point is a mean of three values except the middle one which represents only two. The equation for the relationship is: No. sheets exposed = 3.85 log minutes of exposure +0.68.

No. of sheets exposed = 3.85 ($\log_{10}$ minutes of exposure) + 0.68. The coefficient of correlation is 0.9936, significant at the 1% level. The standard deviation from the regression is $\pm$ .232 sheets exposed.

While this calibration was made by using a relatively constant light source (the sun) and varying the length of exposure time, it could also be accomplished by using a constant exposure time and varying the light intensity received by the different packets. Either method establishes the relationship between the number of sheets bleached and the light energy received.

APPENDIX B: DATA PERTAINING TO THE DETERMINATION OF SOIL MOISTURE

In order to assess the suitability of the small-diameter sampler for providing a reliable means of obtaining soil moisture data, a series of "dummy" sampling plots was installed in 1962. These 12 plots (6 treatments and 2 replications) represented the same environmental conditions as were found on the treatments in the main study, differing only in that no pine seedlings were planted on them. At weekly intervals for 3 weeks a soil moisture sample was taken from each of these plots with a conventional King tube sampler, and two companion samples were taken with the small brass sampler.

The two methods were in excellent agreement as is indicated in Table 16. The moisture difference between a King tube sample and the companion samples from the small tube was never greater than 2.4 percent, by weight, except in one instance where the small sampler encountered a large amount of rotted wood.

The other table included here (Table 17) gives the basic laboratory data upon which the soil moisture release curves shown in Figure 6 are based.

Table 16. Comparison of soil moisture content as determined by King tube and by the small brass sampler. Values are percent moisture by weight based on oven-dry soil.

8-1-62			8-10-62			8-17-62		
King tube	Small sample 1	Small sample 2	King tube	Small sample 1	Small sample 2	King tube	Small sample 1	Small sample 2
15.5	15.6	16.3	13.0	12.6	12.4	13.6	14.0	13.3
15.0	16.5	15.4	14.3	14.1	15.5	14.4	14.7	14.0
15.5	15.5	13.4	11.6	11.4	11.7	12.1	11.2	13.3
14.4	14.5	13.9	15.1	14.1	13.2	14.2	14.2	15.0
11.3	11.1	11.3	11.4	11.2	13.5	14.1	16.0	14.3
11.5	12.8	11.7	12.0	11.7	12.0	12.8	13.2	12.1
12.8	12.7	14.0	12.9	12.3	12.5	12.9	13.2	13.6
13.2	13.9	15.4	12.7	12.3	13.0	14.6	15.3	14.0
14.1	13.4	13.9	14.0	13.6	14.0	16.0 [1]	21.5 [1]	23.6 [1]
11.5	11.8	11.4	11.7	13.4	11.9	11.6	12.5	12.7
11.7	14.1	12.7	11.1	11.6	12.2	10.5	10.5	10.1
7.5	7.4	7.0	11.4	10.8	11.4	11.6	11.3	11.3

59% of small samples are within 0.5% of King tube value

80% of small samples are within 1.0% of King tube value

90% of small samples are within 1.5% of King tube value

94% of small samples are within 2.0% of King tube value

100% [2] of small samples are within 2.4% of King tube value

1/ Group excluded because samples included large (but not equal) amounts of wood.

2/ Does not include the group referred to in footnote 1.

Table 17. Laboratory data upon which soil moisture release curves shown in Figure 6 are based.

Stratum sampled 1/	Weight of oven dry soil (gr.)	Water lost (gr.)	Percent water lost	Ave. moisture percent	Weight of oven dry soil (gr.)	Water lost (gr.)	Percent water lost	Ave. moisture percent	Weight of oven dry soil (gr.)	Water lost (gr.)	Percent water lost	Ave. moisture percent
	Tension = 0.1 atmos.				Tension = 0.4 atmos.				Tension = 0.8 atmos.			
0 - 6"	21.53	2.26	10.49		26.33	2.20	8.36		22.06	1.47	6.66	
0 - 6"	21.79	2.26	10.37		27.96	2.40	8.58		22.35	1.53	6.85	
0 - 6"	21.47	2.20	10.25	10.33	37.07	3.20	8.63	8.49	22.16	1.50	6.77	6.80
0 - 6"	20.42	2.09	10.23		29.80	2.50	8.39		18.30	1.27	6.94	
6 -15"	24.59	1.86	7.57		26.51	1.44	5.44		25.57	1.12	4.39	
6 -15"	27.09	2.05	7.57		34.76	1.91	5.50		30.82	1.33	4.32	
6 -15"	23.15	1.68	7.26	7.45	29.65	1.63	5.50	5.47	30.88	1.33	4.31	4.33
6 -15"	21.10	1.56	7.39		28.01	1.52	5.43		28.36	1.22	4.30	
	Tension = 2.5 atmos.				Tension = 5.0 atmos.				Tension = 15 atmos.			
0 - 6"	22.56	1.06	4.70		16.98	0.73	4.30		19.24	0.65	3.38	
0 - 6"	22.05	1.07	4.85		19.38	0.81	4.18		21.27	0.74	3.48	
0 - 6"	25.27	1.18	4.67	4.78	18.52	0.79	4.26	4.37	22.05	0.81	3.67	3.55
0 - 6"	27.59	1.35	4.89		24.44	1.16	4.74		19.01	0.70	3.68	
6 -15"	22.63	0.70	3.09		20.61	0.54	2.62		24.12	0.48	1.99	
6 -15"	30.27	0.90	2.97		27.25	0.71	2.60		22.85	0.46	2.01	
6 -15"	21.78	0.63	2.89	2.96	27.19	0.70	2.58	2.63	21.22	0.41	1.93	1.97
6 -15"	14.88	0.43	2.89		29.96	0.79	2.74		20.63	0.40	1.94	

1/ Samples were run in quadruplicate for each tension from each stratum.

APPENDIX C: SUMMARY OF THE ANALYSES OF VARIANCE

The analyses of variance were run at the Numerical Analysis Center of the University of Minnesota on a CDC 1604 computer, using an UMSTAT 50 multiple linear regression program and subsequent examination of residuals. The sums of squares were not additive in all cases because of non-orthogonality for some variables. Where conclusions concerning significance were in doubt an exact test was made by desk calculator. In no case did the exact test change the conclusion regarding significance at the 1% or 5% levels.

Variable: Height growth in 1962

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	4.745	1.79	2.33	3.25
Light	1	21.218	7.99	3.96	6.96
Moisture	2	1.014	0.38	3.11	4.88
Interaction	2	0.241	0.09	3.11	4.88
Residual	84	2.656			

Variable: Height growth in 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	642.15	76.77	2.33	3.25
Light	1	2788.78	333.39	3.96	6.96
Moisture	2	169.26	20.23	3.11	4.88
Interaction	2	54.48	6.51	3.11	4.88
Residual	83	8.365			

Variable: Total 2-year height growth

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	707.10	67.18	2.33	3.25
Light	1	3138.16	298.13	3.96	6.96
Moisture	2	174.68	16.60	3.11	4.88
Interaction	2	38.24	3.63	3.11	4.88
Residual	83	10.526			

Variable: 2-year height growth as percent of initial height

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	310726	30.29	2.33	3.25
Light	1	1348860	131.50	3.96	6.96
Moisture	2	73497	7.17	3.11	4.88
Interaction	2	32315	3.15	3.11	4.88
Residual	83	10257			

Variable: Terminal bud length at end of 1962

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	108.294	45.39	2.33	3.25
Light	1	462.784	193.96	3.96	6.96
Moisture	2	26.929	11.29	3.11	4.88
Interaction	2	10.451	4.38	3.11	4.88
Residual	82	2.386			

Variable: Terminal bud diameter at end of 1962

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	2.798	20.13	2.33	3.25
Light	1	9.8730	71.03	3.96	6.96
Moisture	2	1.5177	10.92	3.11	4.88
Interaction	2	0.4781	3.44	3.11	4.88
Residual	82	0.139			

Variable: Terminal bud length at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	240.01	65.83	2.36	3.31
Light	1	1037.17	284.47	3.99	7.04
Moisture	2	67.21	18.43	3.14	4.95
Interaction	2	16.63	4.56	3.14	4.95
Residual	65	3.646			

Variable: Terminal bud diameter at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	7.700	48.73	2.36	3.31
Light	1	30.9292	195.75	3.99	7.04
Moisture	2	3.4942	22.12	3.14	4.95
Interaction	2	0.4241	2.68	3.14	4.95
Residual	65	0.158			

Variable: Stem diameter at end of 1962

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	2.369	11.56	2.33	3.25
Light	1	7.569	36.92	3.96	6.96
Moisture	2	1.322	6.45	3.11	4.88
Interaction	2	0.817	3.99	3.11	4.88
Residual	84	0.205			

Variable: Stem diameter at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	77.589	90.54	2.33	3.25
Light	1	280.410	327.20	3.96	6.96
Moisture	2	36.818	42.96	3.11	4.88
Interaction	2	18.459	21.54	3.11	4.88
Residual	83	0.857			

Variable: Number of live buds at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	130.275	35.18	2.33	3.25
Light	1	508.055	137.20	3.96	6.96
Moisture	2	59.735	16.13	3.11	4.88
Interaction	2	14.837	4.01	3.11	4.88
Residual	83	3.703			

Variable: Maximum root extension at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	3044.72	68.22	2.33	3.25
Light	1	11542.90	258.64	3.96	6.96
Moisture	2	1313.55	29.43	3.11	4.88
Interaction	2	599.70	13.44	3.11	4.88
Residual	83	44.63			

Variable: Average needle length at end of 1962

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	40.094	35.83	2.33	3.25
Light	1	139.627	124.78	3.96	6.96
Moisture	2	18.098	16.17	3.11	4.88
Interaction	2	12.324	11.01	3.11	4.88
Residual	84	1.119			

Variable: Average needle length at end of 1963 (all needles)

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	181.030	65.38	2.33	3.25
Light	1	683.002	246.66	3.96	6.96
Moisture	2	60.168	21.73	3.11	4.88
Interaction	2	47.869	17.29	3.11	4.88
Residual	77	2.769			

Variable: Average length of lower needles at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	164.209	56.98	2.33	3.25
Light	1	628.868	218.21	3.96	6.96
Moisture	2	55.402	19.22	3.11	4.88
Interaction	2	38.094	13.22	3.11	4.88
Residual	77	2.882			

Variable: Average length of middle needles at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	186.871	65.48	2.33	3.25
Light	1	703.192	246.39	3.96	6.96
Moisture	2	58.820	20.61	3.11	4.88
Interaction	2	53.764	18.84	3.11	4.88
Residual	77	2.854			

Variable: Average length of upper needles at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	193.170	66.63	2.33	3.25
Light	1	718.663	247.90	3.96	6.96
Moisture	2	66.622	22.98	3.11	4.88
Interaction	2	53.425	18.43	3.11	4.88
Residual	77	2.899			

Variable: Number of 1963 needles on the main stem

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	43960	39.97	2.33	3.25
Light	1	172904	157.21	3.96	6.96
Moisture	2	17608	16.01	3.11	4.88
Interaction	2	6963	6.33	3.11	4.88
Residual	83	1099.9			

Variable: Number of 1963 needles on side branches

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	80106.8	33.12	2.33	3.25
Light	1	238955	98.81	3.96	6.96
Moisture	2	51842	21.44	3.11	4.88
Interaction	2	30977.5	12.81	3.11	4.88
Residual	83	2418.325			

Variable: Total no. '63 needles on main stem and side branches

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	239392	51.14	2.33	3.25
Light	1	818387	174.82	3.96	6.96
Moisture	2	128715	27.50	3.11	4.88
Interaction	2	66775	14.26	3.11	4.88
Residual	83	4681.41			

Variable: Number of late 1963 needles (on lammas shoots)

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	158191	50.95	2.33	3.25
Light	1	436700	140.65	3.96	6.96
Moisture	2	94435.5	30.41	3.11	4.88
Interaction	2	85584.5	27.56	3.11	4.88
Residual	83	3104.96			

Variable: Oven-dry weight of all needles

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	603.64	76.80	2.33	3.25
Light	1	1964.13	256.41	3.96	6.96
Moisture	2	294.91	38.50	3.11	4.88
Interaction	2	243.83	31.83	3.11	4.88
Residual	83	7.66			

Variable: Oven-dry wt. of stem, branches, and buds

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	64.940	67.65	2.33	3.25
Light	1	194.330	202.43	3.96	6.96
Moisture	2	33.497	34.89	3.11	4.88
Interaction	2	25.258	26.31	3.11	4.88
Residual	83	.960			

Variable: Oven-dry wt. of entire top

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	1063.73	77.35	2.33	3.25
Light	1	3458.71	251.49	3.96	6.96
Moisture	2	526.24	38.26	3.11	4.88
Interaction	2	425.02	30.90	3.11	4.88
Residual	83	13.753			

Variable: Oven-dry wt. of roots

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	184.459	107.49	2.33	3.25
Light	1	570.651	332.55	3.96	6.96
Moisture	2	98.790	57.57	3.11	4.88
Interaction	2	80.775	47.07	3.11	4.88
Residual	83	1.716			

Variable: Oven-dry wt. of entire seedling

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	2133.62	90.27	2.33	3.25
Light	1	6839.15	289.35	3.96	6.96
Moisture	2	1081.04	45.74	3.11	4.88
Interaction	2	876.33	37.08	3.11	4.88
Residual	83	23.636			

Variable: Top/root ratio at end of 1963

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	0.398	1.67	2.33	3.25
Light	1	0.009	0.04	3.96	6.96
Moisture	2	0.148	0.62	3.11	4.88
Interaction	2	0.842	3.54	3.11	4.88
Residual	83	0.238			

Variable: Percent of total dry wt. in needles

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	251.428	15.00	2.33	3.25
Light	1	1221.87	72.89	3.96	6.96
Moisture	2	5.77	0.34	3.11	4.88
Interaction	2	13.41	0.80	3.11	4.88
Residual	83	16.763			

Variable: Percent of total dry wt. in stem, branches, and buds

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	267.812	22.63	2.33	3.25
Light	1	1148.95	97.10	3.96	6.96
Moisture	2	21.43	1.81	3.11	4.88
Interaction	2	76.82	6.49	3.11	4.88
Residual	83	11.833			

Variable: Percent of total dry wt. in roots

Source of variance	DF	MS	F	F required for: 5% level	1% level
Treatments	5	25.923	1.50	2.33	3.25
Light	1	1.122	0.06	3.96	6.96
Moisture	2	5.093	0.29	3.11	4.88
Interaction	2	59.099	3.41	3.11	4.88
Residual	83	17.332			

APPENDIX D: SOME GENERAL PHENOLOGICAL OBSERVATIONS DURING 1963

April 15 - - Willow and hazel staminate flowers in evidence.

April 22 - - Buds beginning to swell on brush species.

April 29 - - Buds starting to burst on alder and hazel. No noticeable swelling of red pine buds.

May 6 - - - Some leafing out on alder, and leaf emergence just starting on hazel. Red pine buds showing first signs of elongating.

May 8 - - - Decided advance in all vegetation following a high of 85° F. on May 7 and 0.2 inches of rain. Alder leaf development ahead of that on the hazel, with largest alder leaves about 2 cm. long, and the most advanced hazel leaves only about 1 cm. long. Red pine buds definitely elongating.

May 13 - - - Most alder leaves now about 20% of full size and the more advanced hazel leaves about 10% of full size, but many just now beginning to unfurl. Elongation of red pine continuing but rapid candling-out has not yet started.

May 20 - - - Leafing-out still slow because of cool rainy weather. Alder and raspberry leaves about 30% of full size with a few approaching 50% full size. Hazel leaves only about 15% of full size, with the most retarded just breaking out of the

buds. Red pine shoot elongation now conspicuous.

May 29 - - - Tempo of growth increasing with alder and raspberry leaves about 65% of full size and hazel leaves averaging about 40% full size. Willow leaves just bursting from buds with a few about 10% of full size.

June 3 - - - Continuation of rapid phenological development due to warm weather and considerable rain. Leaves on alder, raspberry, and serviceberry all about 80% fully grown and hazel leaves about 70% full size. Willow leaves now about 50% fully expanded. Bracken fern about 1 to 2 feet tall with most fronds just beginning to uncurl. Red pine shoots elongating very rapidly.

June 10 - - Most brush species have completed over 90% of their leaf expansion, with willow perhaps 80% fully expanded. Bracken ferns have unfurled their fronds, although the tips are still slightly curled. Red pine seedlings elongating at peak rate.

June 18 - - Major brush species now fully developed, and the unfurled bracken fern fronds are now expanding. Shoot elongation of red pine seedlings still very rapid, but decreased slightly from previous week.

June 25 - - - Bracken fern now about fully developed. Some of the foliage on the brush species, particularly hazel, is already showing signs of deterioration such as brown spots and holes and some curling of margins.

August 12 - - Definite yellowing of some of the brush foliage accompanied by curling and even loss of some of the leaves.

August 26 - - Brush deterioration now quite noticeable. Many leaves on the hazel have curled and are dry and turning brownish with about 10% having already fallen. Bracken fern also deteriorating with many fronds curled, brown, and dry.

September 13 - Brush deterioration well advanced. (Early morning temperature was 25°). Hazel leaves in particular are turning brown and curling, and about 30% have already fallen. Leaves on the upland alder, dogwood, willow, and raspberry, however, are still quite green and intact. Bracken fern has deteriorated considerably, with about 50% of the plants brown and curled, an additional 20% partially cured, and the remainder still generally green.

September 24 - Brush leaf-fall steadily progressing. On the average, about 70% of the hazel leaves have fallen, with individual plants having lost nearly 100%. Leaves on alder starting to turn

brown and curl, but not many have yet fallen. Willow and raspberry leaves still mostly green and intact. All bracken fern now brown and shriveled.

October 1 - - Hazel now virtually bare with about 95% of the leaves gone (on many stems 100% of the leaves are gone). Alder still has about 75% of its leaves, though a few are yellowish and curled. Willow and raspberry still retain almost all of their leaves although some of these are yellowing on the willow. Leaves on oak and aspen sprouts are colored, but still present on the stems.

October 11 - - Hazel now completely bare except for an occasional dry leaf. Willow leaves about 30% gone and those still hanging on are rapidly turning yellow. Alder has lost about 50% of its leaves, but the remaining ones are still surprisingly green. Raspberry leaves are falling (about 60% remain) and those remaining are turning reddish brown. Dogwood also has about 60% of its leaves remaining and these are turning red. Leaves on aspen and oak sprouts turning yellow and brown, respectively, but not many have yet fallen.

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