THE INFLUENCE OF LIGHT ON TREE GROWTH

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INTRODUCTION

This paper does not attempt to take into consideration all factors which affect tree growth, but rather to take measurements of a single factor and to see how these measurements may be correlated with the vegetation present. It has been shown that air temperature, soil temperature, soil moisture, and evaporation have a direct influence on a tree's behavior. All of these factors, as well as light intensity, are more or less directly correlated with solar radiation. If, therefore, within any climatic and edaphic unit area a single factor is chosen for influence on forest growth, light would seem to merit first consideration.

It should be remembered, however, that root competition for both moisture and nutrients is an important concurrent factor to be taken into account in determining the significance of the light data obtained in this study.

FACTORS INFLUENCING LIGHT CONDITIONS

The quantity and quality of light is subject to modification by a multiple of factors. The more important ones could be included under the headings latitude, altitude, atmosphere, and local obstructions.

The primary influence of latitude is the affect it has on length of day. Near the equator the length of day varies only slightly from season to season. However, as the distance north or south of the equator increases, the change in the length of day and total amount of daylight for a given season becomes very noticeable and is influential in plant distribution.

This change in amount of daylight, which varies with the season, is controlled by the position of the earth in its orbit with relation to the sun. In England it has been shown that 74 per cent of the year's light was received between May and October, the leafy months.[1] Latitude will also have an indirect influence on the intensity and quality of light reaching the earth's surface because the distance of the sun from the earth varies with latitudes and seasons of the year.

The highest value of solar radiation ever measured was 12,000 foot-candles per minute; this measurement was made on a mountain top. The highest value measured at sea level was 10,000 foot-candles per minute. It has been found that intensity and quality of light received at any point on the earth's surface depends on the solar constant, distance of the sun from the earth, and diffusion of the light by the atmosphere.[2] No reason was given for this difference in intensity at the different elevations; but one conclusion might be that atmospheric diffusion and absorption were responsible. It has been shown that

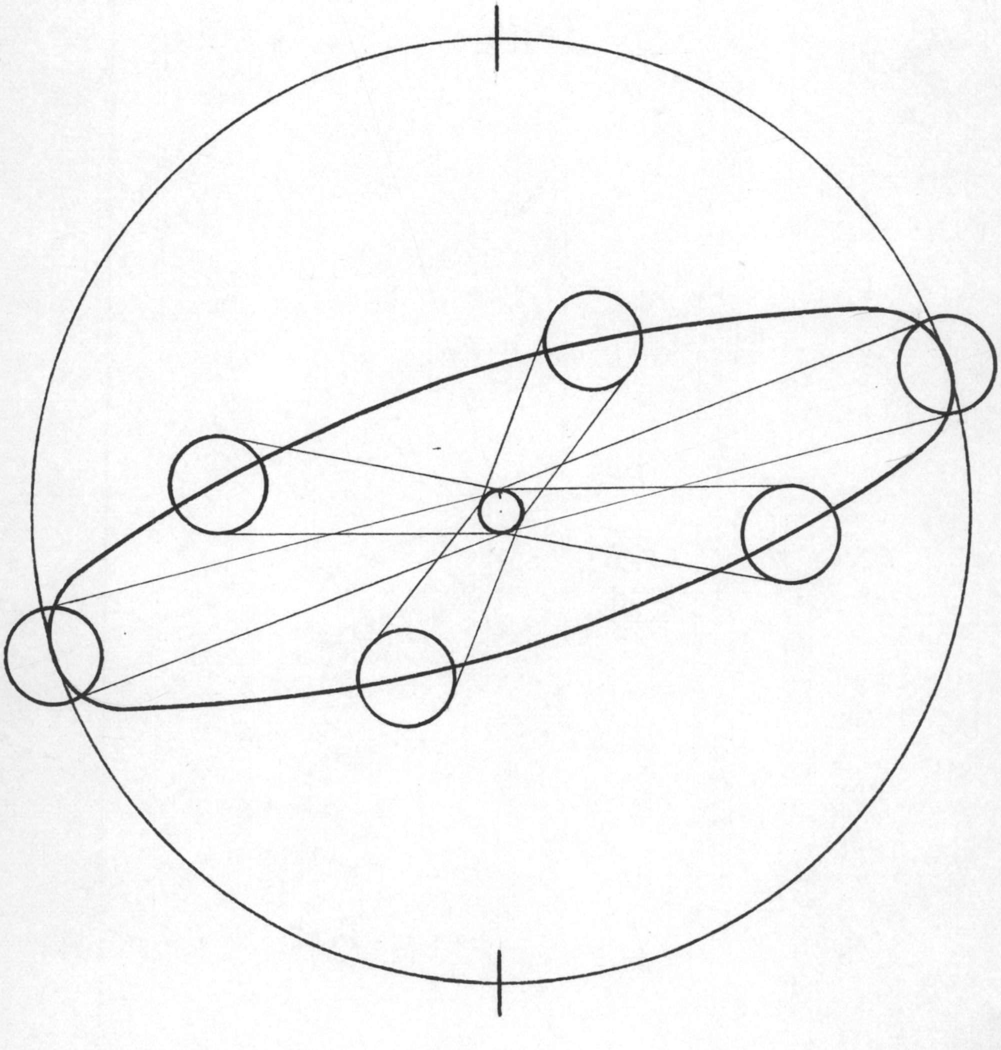

Figure 1.

Diagram showing how the quantity of light varies with latitude and season of the year.

absorption by the atmosphere is one of the most important agents in reducing light intensity, while diffusion is one of the most important factors in changing energy distribution.[2] Solar radiation is also greatly influenced by atmospheric variations.[3] Measurements made on days when there was a complete overcast show that the intensity of sunlight is well under 50 per cent of normal or full sunlight.

Certain wave lengths of light have also been filtered out, but the nature of the influence of this filtration has not been demonstrated. It is believed, however, that full sunlight is more beneficial for plant growth than any portion thereof.[2] Atkins believes that total quantity of light regardless of other light factors is the most important influence for plant growth.[1]

The forest canopy is the most influential factor classified under "local obstructions". While the herbaceous cover is influential with regards to seeds and seedlings the greatest over-all influence on quality and quantity of light is by the crown canopy.[4] Light under an ordinary continuous canopy is usually reduced below 10 per cent of full sunlight;[5] measurements as low as 0.1 per cent of full daylight have been made.[5] According to Shirley the distribution of spectral energy is influenced by the crown canopy; hardwoods have more influence on this factor than the conifers do.[4] However, light intensity rather than quality is usually a limiting factor in growth under a forest canopy.[4]

PHYSIOGRAPHIC INFLUENCES

Maximum illumination governs plant distribution.[1] The physiographic influence of light is subject to temperance by several factors of varying degrees of importance. In this paper temperature and moisture are considered to merit discussion.

Garner has found that the response to day-length factor is dependent upon temperature conditions.[6] Pearson also states that soil temperature is an index of the amount of solar radiation reaching the ground and leaves.[7] Temperature is further influenced by the type of vegetation; vegetation will influence air temperature through transpiration, and will influence surface temperature by interception. Air movement will also influence air and soil temperatures.

Temperature is discussed in order to point out the influence it has, in conjunction with light, on the distribution of species of plants. If the soil temperature is too high, seedlings will not survive. It has been found in the Douglas-fir region that soil temperatures of 125° Fahrenheit are often fatal to young seedlings. This temperature, however, is very seldom found under a canopy where direct solar radiation is intercepted. This would seem to indicate that in many cases something less than full sunlight might be required for optimum growing conditions. This could also be looked upon as one indirect method by which light might limit the range of a species of plant.

Often when lack of light is held responsible for the lack of growth, competition for moisture is the real reason.[8] This factor often makes field records open to doubt. The intensity of solar radiation has a direct bearing on the amount of soil moisture at a given time, and the two working together often determine the range limits of a particular plant. Observations have shown that light requirements among different species appears to vary with the amount of moisture in a species natural range.[9] Either of these two factors could be responsible for the lack of occurrence of a species on an otherwise good site or for poor growth on the part of a species that is present.

Variation in the length of day, to some extent, controls the growing season of certain tree species.[10] This would limit the geographical distribution of plants because of the great variation of growing seasons throughout the world. Another hypothesis that can be considered along this same line of reasoning is the possibility that an insufficient amount of light could be the cause for a lack of seed production on the part of an exotic plant. There seems to be a critical length of day required during the growing season in order to carry on sexual reproduction. If the day length is less or beyond this point, the plant tends to become purely vegetative.[6] Obviously, natural plant distribution would be limited by a plant's ability to sustain and reproduce itself.

The degree of sensitivity to light is not the same among all plants; this is evidenced by the fact that many plants are tolerant of a great deal of shade, some are only slightly tolerant, and some plants are found in all kinds of environments.

PHYSIOLOGICAL INFLUENCES

The amount of influence that solar radiation exerts on the growth processes of a tree is still subject to a great deal of study. Many partial influences are known, and many hypothesis have been formed, which as yet, are not proven theories. Other interrelated factors often play an equally influential role, and data which have been collected should be considered very thoroughly.

The influence of light on reproduction merits a great deal of consideration. Very often the quantity of light will determine what plant is going to dominate an area. The dominant plant will determine the value of the area to the owner and to the country.

To insure reproduction under an old stand, light intensity on the seedlings during the day should seldom fall below 5 per cent and for two hours or more should be as high as 30 per cent.[5] This insures establishment of any species indigent to the area; however, to obtain a desired species, light conditions must very often be controlled. In many cases nature does the controlling through overstory, amount of moisture, and competition between seedlings. Man can control competition from overstory and growing stock by proper silvicultural practices.

The tolerance of a tree is measured directly through observations of trees under a natural forest canopy, observations of light changes and interruption in the crown canopy, and by instrumental measurements of light and heat intensities.

A climax type of vegetation has adapted itself to the existing set of environmental conditions so adequately that it is completely stabilized. This group of plants will dominate a site until the conditions influencing establishment and growth are changed.

A climax species returns in definite stages under natural regeneration. Intolerant species return first because of their more exacting sunlight requirements and rapid growth. These species, when growing in competition with other species, tend to grow straight and to produce comparatively clean boles over a great portion of their total height. Tolerant species under similar conditions tend to have a bushier crown and to retain their limbs over the entire bole. After a stand of intolerant trees has become established, a tolerant species will often come in as an understory, and eventually shade out the less tolerant species.

In many cases, the various parts of the tree often have exactly opposite reactions to the influence of solar radiation. Low light intensities stimulate height growth at the expense of diameter growth, top growth at the expense of root growth, leaf area at the expense of leaf thickness, and succulence at the expense of strength and sturdiness.[5] Exposure to full sunlight gives a slight decrease in height and leaf area but gives an increased percentage of dry weight. As the light intensity increases and becomes progressively less favorable for stem growth, there is a tendency toward more branching.[11]

It appears, however, that there is a peak of intensity beyond which the plant begins to lose its efficiency; this peak apparently varies to some extent with the time of day. It has been found that under conditions of high light intensity plants exposed to full sunlight in the morning and shaded in the afternoon produce better growth than those exposed all day or those receiving full light in the afternoon only.[2] The relative demand is based on the cambium surface and the surface of the crown in stands at different ages and on different quality sites.[12]

One indication of light need is the capacity of a species to endure crowding of its crown at a designated age. The minimum intensity required to insure survival for most species is about 1.0 per cent; below this point root development is poor, tissues fail to harden, and the tree is unable to produce a food reserve.[5]

Diffusion of light will often cause plants to become somewhat etiolated. Certain portions of the spectrum such as infra-red seem to cause etiolation also. However, the light quality changes under a forest canopy are not likely to have an unfavorable influence on growth.[5]

As was stated, the intensity of the incident light influences the different parts of the tree differently. Too great an intensity of light tends to decrease the rate of photosynthesis due to an accumulation of carbohydrates in the leaves; this is termed "Solarization of the Leaves".[2] The influence of light is not restricted to photosynthesis; respiration rate is also dependent to a considerable extent on the intensity of light and the resulting influence of solar radiation on temperature.[7] The formation of pigments, and the resulting functions of these pigments, is directly dependent upon solar energy. The intensity of radiation is also important in controlling the rate of transpiration and the water content of the tissues of the entire tree.[11] While the affect is not immediately apparent, roots appear to receive the most damage from a lack of light. Unlike other parts of the plant, if the low intensity persists, the damaging influence tends to leave a permanent impression; the root lengths and branchings are markedly reduced, suggesting that the seedling would die under any added unfavorable condition.[9]

INSTRUMENTS

Methods of designating light quantity vary with the accuracy of the experiment performed or observation made. On some occasions only a weather description is required. The term "cloudy" infers that there is not as much light present at a site as there would be if no clouds were present. The exposure of sensitized papers is another slightly more precise indication of the relative amount of light present for a given amount of time. These methods are satisfactory when only a rough approximation of the quantity of light present is required. The expense incurred in obtaining scientific instruments is not merited for this type of work; however, for experiments requiring accurate observations precision equipment is required. Nearly all of these instruments measure solar radiation; some do it by measuring heat in caloric units, and others by measuring in units of light. There are three main types of instruments, with variations, now being used in most controlled experiments. They are the Photo-electric cell, the Thermopile, and the Radiometer.

The photo-electric cell measures electric current in foot-candle units. A foot-candle is defined as "the direct illumination on a surface everywhere one foot from a uniform point source of one international candle".[13]

The sensitive element of the cell is a thin sheet of metal, usually lithium, sodium, or selenium. The instrument used by the author in the experiment presented here contained a selenium plate. These plates are given a negative charge and then mounted in bulbs. When the cell is connected and exposed to light the readings obtained are a measure of the electric current generated by the energy falling on the sensitive surface of the cell. Measurements up to 12,000 foot-candles per minute have been recorded on mountains; 10,000 foot-candles per minute is the highest recording at sea level.

The thermopile measures the heating affects of solar radiation. These instruments are accurate from 0.1 gram-calorie per square centimeter per minute to full sunlight.

Basically, a thermopile is a short length of bismuth wire to which a length of silver wire is soldered; this forms a thermocouple. When one bismuth-silver junction is heated above the temperature of the other, an electromotive force is produced and may be detected by connecting the silver wire to a galvanometer. The magnitude of the electric potential is almost directly proportional to the temperature difference between the junctions. Two or more thermocouples connected in a series form a thermopile.[14]

There are several variations of the thermopile. (One of the better ones for use in forest work is the modified constantan-silver instrument. This instrument is comparatively rugged and not as likely to be broken or to go out of adjustment as the other types are.

In reality a radiometer is a modified constantan-silver thermopile with a portable microammeter* and a small resistance box. The radiometer is sensitive from 0.1 gram-calorie per square centimeter per minute to full sunlight at noon and is uniformly sensitive to all wave lengths.

WIND RIVER STUDY

Figure 2.

Shade Frame
At Wind River
Experiment Station

This study was set up to measure the overhead light requirements of Douglas-fir regeneration under controlled conditions. Three frames were constructed of slats. These slats were so arranged that each frame

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* A microammeter is an ammeter registering millionths of a volt.

received a different amount of light, based on a percentage of full sunlight. These amounts were designated as light shade, medium shade, and heavy shade. The overhead slats were run north and south so that the bands of sunlight would not stay in one place long enough to super-heat the surface.

Photometer readings were made every hour from 8:00 A.M. to 4:00 P.M. at various intervals during the summer months. The instrument was exposed to a reflecting surface of grey cardboard. Records of exposures in the frames were compared with natural shade.

Daily maximum temperatures were read during July and August. The temperature did not vary appreciably between the three frames, but it was lower for the frames than it was on open plots. Isaacs believes that this consistent difference in temperature, due to shade, is an important factor in seedling survival and growth.

Under the "light" shade frame, survival was better than for seedlings grown in open plots; however, the seedlings in the frames were slightly etiolated, their stems were slender and their foliage had an unhealthy color. In the event that the shade and protection should be removed their chances of survival were considered slight.

Under the "medium" shade frame, both survival and growth was below that of open grown seedlings. The remaining seedlings were on a definite decline.

Only a few of the seedlings remained alive under the "heavy" shade frame, and they were dying rapidly.

While these records covered only three consecutive seasons, and many other factors were not considered, some facts that were found established a basis for further study.

It has been shown that successful establishment of Douglas-fir requires 20 per cent of full overhead light at noon, even with a complete lack of overstory competition. It is further shown that a rapid and proportional decline in seedling survival occurs with the reduction of overhead light in the controlled shade frames.

LIGHT CONTROL EXPERIMENT BY HARRIS AND WIESE

This study was set up to observe the general reaction of Douglas-fir (Pseudotsuga taxifolia) seedlings and Port Orford cedar (Chamaecyparis lawsoniana) seedlings to controlled light conditions. A second observation was to be made on the seedlings after release, the idea being that the removal of the shade frames would correspond somewhat to the removal of an overstory. Root competition, with the exception of grass roots, was nonexistant.

In this study 3-0 fir stock and 2-0 cedar stock were used. These seedlings were obtained at the Oregon Forest Nursery at Corvallis. Because of weather conditions they were heeled in for two weeks before planting.

The plot was prepared by spading six individual sample plots in the main plot. The rest of the plot was left in its natural condition. Each sample plot contained five fir and five cedar seedlings. The seedlings were planted on January 12, 1947, and were allowed time to become established. The light control started April 8, 1947; at that time there was no mortality among the seedlings and all appeared to be in good condition. The six sample plots were exposed as follows:

Plot 1 Control group--not covered; received full sunlight.

Plot 2 Control group--covered throughout experiment; received no sunlight.

Plot 3 Received lowest amount of light.

Plot 4 Received twice the amount of light allowed Plot 3.

Plot 5 Received twice the amount of light allowed Plot 4.

Plot 6 Received twice the amount of light allowed Plot 5.

The light measurement was based on photo-electric meter readings. Because the meter is too delicate to read full sunlight, the soil of the plots was used as a reflecting surface. The meter was placed three feet above the main plot and pointed straight down. In this manner, all controllable influences were unchanged throughout the entire period of light measurement, and the same angle of light incidence was measured.

In order to be sure that all plots received a constant amount of light, a unit of light measurement was set up. This unit was designated as a foot-candle-minute, which is the number of foot-candles read on the meter multiplied by a number of minutes to give a constant. Constants were set up as follows:

Plot 1 Full light.

Plot 2 No light.

Plot 3 800 foot-candle-minutes per day.

Plot 4 1600 foot-candle-minutes per day.

Plot 5 3200 foot-candle-minutes per day.

Plot 6 6400 foot-candle-minutes per day.

The following is an illustration of the procedure used in measuring the light on the plot. The meter reading at the time of exposure was 200 foot-candles per minute. Therefore, plot 3 would receive 4 minutes of exposure, plot 4 would receive 8 minutes of exposure, plot 5 would receive 16 minutes, and plot 6 would receive 32 minutes. These exposures were made daily throughout the period of light control. The time of

EXPOSURE TABLE FOR PLOTS

Foot Candles of Light

Group Number	8	12	16	25	32	50	64	100	125	200	250	400	500	800	1000
1				N O T C O V E R E D											
2				C O V E R E D											
3	100	67	50	32	25	16	12.5	8	6.4	4.0	3.2	2	1.6	1	0.8
4	200	134	100	64	50	32	25	16	12.8	8.0	6.4	4	3.2	2	1.6
5	400	268	200	128	100	64	50	32	25.6	16.0	12.8	8	6.4	4	3.2
6	800	536	400	256	200	128	100	64	51.2	32.0	25.6	16	12.8	8	6.4

Figures Are Time In Minutes

day for starting the exposures was varied from day to day. If the meter readings were low, more time, controlled by the constant, was allowed for each sample plot. In this way the daily amount of light was as constant as instruments permitted.

An average of the amount of light per day, for this season of the year at this latitude, was computed to set up a percentage ratio for each plot. This average was based on the official time of sunrise and sunset and on the highest and lowest meter readings taken during the control period. The following percentages were obtained with conversion of the constants to per cent of full sunlight.

Plot	Foot-Candle-Minutes per Day	Per Cent of Total Light
1	53,380	100
2	0	0
3	800	1.5
4	1,000	3
5	3,200	6
6	6,400	12

The study was carried on under controlled conditions until June 3, 1947. At this time all shade was removed and observations were made on each plant in each sample plot.

Plot 1 - Full Sunlight

There was full survival for both fir and cedar seedlings at the time of these observations. Three of the fir had lost their leaders, and the length of new growth was greatest on the lateral buds, several of which attained a length of two inches. The average length of new growth of the lateral buds was about one and one-half inches. Some of the new needles had rather large brown spots, and many of the old needles had turned entirely brown. All buds had opened, and the tips of the branches were brushy and healthy in appearance.

At the time of planting, all of the cedar had a muddy brown appearance. These trees maintained this color, and evidenced no sign of change throughout the control period.

Plot 2 - No Sunlight.

This plot also had 100 per cent survival. Growth among the fir was retarded. Several of the lateral buds had not started to swell and one leader showed no signs of growth. Many of the lateral buds were still partially encased in the scales.

All of the new growth was spindly and lacked color, denoting a probable lack of chlorophyll development. The needles were slender and hugged the stems closely; all of the new growth on the stems showed a tendency to droop. Growth was longest on the lateral stems, some of the growth reached four inches. All of the needles appeared to be alive and retained their original coloring.

The cedars changed color when they were without light. The old growth changed to a light green color, and the new growth was a cream color. In some cases, a quarter of an inch of new growth was distinguishable; this new growth was inclined to curl in a manner similar to the fingers of a clenched fist. In comparison with the fir in the same frame, the new growth on the cedar appeared much sturdier.

Plot 3 - 800 Foot-Candle-Minutes per Day.

On this plot the terminal growth was far behind the lateral growth. Several of the terminal buds on the side branches had not yet opened; whereas, nearly all of the lateral buds had opened, and growth was being made at the time of the examination. These plants appeared to have fewer needles per stem on the new growth and a consequently greater spacing between needles. The new needles appeared to be slightly burned and slightly curled, and the new growth had a tendency to droop. The old growth retained the original color, and very few of the needles turned brown. The new growth was slightly darker than the new growth of Plot 2. In this case, as before, the muddy brown color had changed to a clearer green. In all cases the growth appeared to be comparable to the growth made by the samples in Plot 2.

Plot 4 - 1600 Foot-Candle-Minutes per Day.

All buds opened on this plot; however, one leader was missing. The needles were thin and rather far apart, and some of them appeared to be badly burned. Indications are that the tendency to hug the stem varies inversely with the amount of light the plant receives. The new needle growth had a greater tendency to spread away from the stem than did that on the preceding shaded plots. The length of the new stems varied from one-fourth of an inch to two and one-half inches. The old needles retained their characteristic color, and none of them turned brown.

The external appearance of the cedar on this plot varied very little from that on plots 2 and 3.

Plot 5 - 3200 Foot-Candle-Minutes per Day.

The second greatest amount of growth was made by the fir on this plot. It varied from one-fourth inch to three inches. The new needles showed no indication of being burned, and the new growth appeared to be stronger and darker than that on plants receiving less light. The seedlings in general were bushier than those on plots receiving less light. On this plot all buds except one lateral bud on the under side were open, and no leaders were missing.

The cedar on this plot made the greatest apparent growth of all the cedar. In general the shade of green was somewhat deeper.

Plot 6 - 6400 Foot-Candle-Minutes per Day.

All leaders were making healthy growth and none were missing. The new stems were bushy and up to one and one-half inches long. The new growth was considerably darker in color than that on other plots, indicating that there was probably enough light to carry on the chlorophyll manufacturing process and to carry on some photosynthesis. The new growth of fir was considerably stronger than on other shaded plots; however, the new growth still was not as strong as the growth made by plants in full sunlight. There was some loss among the old needles. The cause, however, could not be traced to the lack of sufficient sunlight.

The cedar on this plot was darker than that on other shaded plots. The seedlings on this plot were the only ones covered by shade frames to show traces of the yellow-brown coloring which was characteristic of the seedlings at the time of planting and which was retained by the full sunlight control plot. New growth was just barely discernible.

On April 8, 1948, the final observations were made on the plots. The seedlings had had no shade, nor any special care after the shade frames were removed. They received a great deal of competition from grass throughout the entire period.

Plot 1 - Full Sunlight.

There were no dead fir seedlings on this plot. All of the seedlings appeared to be healthy. The plants were bushy, and there were no bare spots on either the old or new growth.

All of the cedar appeared to be healthy, and there was no mortality. They were very yellow-brown in appearance with the exception of one. This plant was rather small and somewhat greener than the others. It appeared to receive a considerable amount of shade from the grass.

Plot 2 - No Sunlight.

One fir seedling had died; the remaining seedlings were weak and malformed. The new growth was very spindly and had large bare spots along the stems. The needles were slightly yellow.

Two of the cedar seedlings had died; the remaining plants appeared to be strong. They had turned somewhat yellow. One plant had some dead foliage in the top.

Plot 3 - 800 Foot-Candle-Minutes per Day.

On this plot one of the firs had died and one was very sickly. The needles were sparse and somewhat narrower than the normal appearing fir needle. In many cases there were large bare spots on the new growth. The new foliage was arranged in tufts around the tips of the branches.

Two of the cedar seedlings were dead and one of them had a great deal of dead material in the top. The rest of these plants received afternoon shade and were considerable greener than the other plants on the plot.

Plot 4 - 1600 Foot-Candle-Minutes per Day.

There was no mortality on this plot. The new growth was weak and spindly. Most of the new growth was bare along large areas of the stem, and most of the new needles were in tufts at the tips of the branches. In many cases the tips of the new needles appeared to have been burned off.

One of the cedars was dead. The rest of the plants appeared to be sturdy; they were nearly as yellow as those on Plot 1.

Plot 5 - 3200 Foot-Candle-Minutes per Day.

There was no mortality among the fir on this plot. The new growth was spindly. Many of the plants were bare of needles along the stem. What needles there were were clustered around the tips of the branches.

One of the cedars was dead. The remaining plants appeared to be strong. Although there was no shade close enough to have any influence, these plants were turning from yellow to green.

Plot 6 - 6400 Foot-Candle-Minutes per Day.

There was no mortality among the fir on this plot. Only one stem was bare of foliage. On most of the new growth, the growth of needles was rather sparse. The leaders on most of the plants had a tendency toward bushiness.

Three of the cedars were dead. Those that were still alive were greener than those on Plot 1. There was a possibility of some shade on this plot during the day.

SUMMARY AND CONCLUSIONS

This study was based on six different exposures of sunlight on six different plots containing five Douglas-fir seedlings and five Port Orford cedar seedlings each. Each plot received a designated amount of light based on a computed number of foot-candle-minutes. Each plot received a given number of foot-candle-minutes every day. When the shade control period was terminated the plants were released and a survival check was made.

This study was not carried on long enough, nor was the scope great enough, to form any definite conclusions. The data presented here indicates that full sunlight is not optimum for either fir or cedar. More overall growth was made by the fir on the plot receiving full sunlight than the fir on the other plots; however, there were too many branches, and the form was poor. In most cases the lateral growth exceeded the terminal growth when the plants received full sunlight.

The cedar, on the other hand, appeared to be sturdier on the plots receiving some shade. There was no noticeable growth made by the cedar in full sunlight. Growth made by the cedar on the other plots appeared to be uniform over the entire plant.

The reaction of the fir to extreme shade conditions indicates that fir is very unlikely to appear under heavy shade conditions; since growth appears to be carried on by stored energy rather than created energy. While the amount of new growth was much greater on the part of the fir it is the opinion of the author that this was the response to darkness stimulus described by Dr. Atwood of the Botany Department of Oregon State College. The cedar, however, was green in all cases except that on the plot receiving no light. This fact indicates that cedar is capable of producing a sufficient amount of chlorophyll to maintain at least some growth under all but very extreme conditions.

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