

# Influence of High Light Intensity on Survival of Planted Engelmann Spruce

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**Abstract.** Results of three studies on photosynthesis and needle water deficits are presented. Photosynthesis was higher for Engelmann spruce seedlings grown in the shade than in the open, but it was not significantly different for lodgepole pine seedlings. Spruces reached near-maximum photosynthesis at 4,000 to 5,000 ft-c, but pines did not appear light-saturated even at 12,000 ft-c. Photosynthesis and respiration of potted spruce seedlings were highest at moisture deficits less than 10 percent; with deficits above 20 percent, photosynthesis was zero and respiration minimal. At a deficit of 58 percent seedlings died. Moisture deficits of seedlings during the summer after field planting were below 31 percent and did not differ significantly between sunrise or mid-afternoon measurements, nor between shaded or open-grown treatments. These and other results suggest that solarization occurs in unshaded spruce, has a deleterious effect on photosynthesis, and may be associated with the high mortality in plantations at elevations above 10,000 ft. *Forest Sci.* 16: 331-339.

**Additional key words.** *Picea engelmannii*, *Pinus contorta*, solarization, photosynthesis, respiration, leaf water deficit.

ARTIFICIAL regeneration of Engelmann spruce (*Picea engelmannii* Parry) is difficult in the central Rocky Mountains, where spruce grows at elevations of 9,000 to 11,000 ft in an environment characterized by extremes. Attempts to establish spruce artificially were first made on the White River Plateau of western Colorado where a beetle epidemic, salvage logging, and heavy windthrow had fully exposed the site. Those plantations were not successful, and studies were begun to determine the time and cause of mortality in planted spruce and lodgepole pine (*Pinus contorta* Dougl.)<sup>1</sup> seedlings.

These early investigations indicated that neither drought, frost heaving, nor animal depredations were important causes of spruce mortality (Ronco 1961). Nearly all spruce mortality took place during the first winter sometime after the seedlings were covered by snow. Mortality was significantly reduced when seedlings were partially shaded during the preceding summer. Shade-intolerant pines, on the

other hand, were not benefited by shade, and survived well without treatment. Other responses noted in spruce but not in pine plantations were:

1. Severe chlorosis developed and persisted for many years in spruce seedlings growing in the open at both high and low elevations, whether grown in the field, pots, nursery bed, or hardening beds.<sup>2</sup> In contrast, seedlings grown in the shade remained a normal green.

2. Chlorosis in unshaded seedlings generally appeared first in older needles the first summer after potting or planting, and by the end of the summer even normally green new growth turned yellow. Old chlorotic needles were not shed prematurely, but were retained for several years.

<sup>2</sup> In some instances, seedlings lifted from the low-elevation nursery (about 7,000 ft) were held in hardening beds near the planting site for 1 year prior to field planting.

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<sup>1</sup> Although lodgepole pine is not indigenous to the area, it was included because it has survived when planted at similar elevations elsewhere.

3. Chlorosis, which was previously absent, developed in an unusual manner in field-planted seedlings that were shaded by shingles.<sup>3</sup> Tips of branches that had been shaded for 4 to 5 years after planting became chlorotic as they grew beyond the protective edges of the shingle, while portions of the same or other branches protected by the shingle remained green.

4. Branches on open-grown seedlings tended to die progressively from the top down and from the south-facing to north-facing side. Live branches on those trees were generally on the north side, near the ground, and in many instances were partially covered by litter or twigs.

Behavior of seedlings suggested that solarization—a phenomenon in which photosynthesis is inhibited by high light intensities—was a possible cause of mortality in open-grown seedlings. Light inhibition of photosynthesis has been demonstrated in hardwood and pine seedlings at light intensities of 10,000 ft-c (Kozlowski 1957, Kramer and Decker 1944); light intensities at elevations where Engelmann spruce grows are normally even greater. Spomer (1962), for example, found that light intensities on clear days will remain near 13,000 ft-c from a few hours after sunrise to just before sunset; and when scattered cumulus clouds increase reflection, intensities may reach 16,000 ft-c for several minutes. The physiological mechanism of solarization is still unknown, but Turner and Brittain (1962) have proposed several explanations for inhibition of photosynthesis by excess oxygen, a phenomenon that Rabinowitch (1945) believed was similar to inhibition by excess light.

Emphasis during the investigations reported in this paper was first placed on establishing whether solarization occurred in spruce seedlings. However, since the beneficial effects of shade demonstrated in earlier studies might have been related to a more favorable internal water balance in the seedlings, other investigations were

undertaken to determine whether mortality was related to water stress. This paper summarizes the results of those studies—one related to photosynthesis and two dealing with water relations.

## Methods

*Field Study of Photosynthesis.* Photosynthesis of seedlings grown for three months under three shading treatments was measured at five light intensities. The study was conducted at an elevation of 9,000 ft where the range in light intensity was similar to that on most spruce sites. Three-year-old Engelmann spruce and 2-year-old lodgepole pine seedlings were lifted from a low-elevation nursery (7,000 ft) in mid-March and kept in cold storage until normal planting time. In early June, seedlings were potted and randomly assigned three shading treatments—no shade, partial shade, and full shade. Full shade was provided by a frame covered with cheesecloth and window screen which was supported about 1 ft above the seedlings; the combined overhead and side light intensity was approximately 3,000 to 4,000 ft-c during midday. For the partial-shade treatment, shingles were placed so that seedlings received only indirect light from about 11 AM to 3 PM; light intensity at the seedling level was about 4,000 ft-c. Unshaded seedlings were fully exposed.

During the growing season, seedlings in all treatments were watered at regular intervals to keep soil moisture near field capacity. Photosynthesis was measured in September 30 hr after the seedlings were given a final watering.

The experiment was arranged as a 3 × 5 factorial in a split-plot design. Shade treatments were arranged in five randomized blocks. The five light intensities at which photosynthesis was measured—1,000, 3,000, 5,000, 7,000, and 12,000 ft-c—constituted the split-plot treatments. To reduce experimental errors due to time of day and possible differences due to assimilation chambers, seedlings, one from each shading treatment, were randomly assigned to the three assimilation chambers, and photosynthetic rates measured concurrently. Seedlings were measured once in the

<sup>3</sup> Seedlings were protected against direct solar radiation at midday by wood shingles, 6 to 8 inches wide, positioned on the south side of seedlings at a slight incline from vertical.

morning, returned to their respective treatments, and remeasured in the afternoon.

Photosynthesis was measured outdoors with a Beckman<sup>4</sup> infra-red gas analyzer and a Plexiglas assimilation chamber in an open system (Ronco 1969b). After the chamber was positioned over a seedling, it was shaded with layers of cheesecloth to reduce natural light to the selected intensity. After a ½-hr adjustment period, CO<sub>2</sub> concentrations for each chamber and outside air were recorded, and the shade density adjusted to give the next light intensity. Air temperature inside the chambers was maintained at 21°C. Photosynthetic rates were computed as mg CO<sub>2</sub>/min/cc of foliage. Foliage volumes were determined by water displacement in a volumeter (Ronco 1969a).

*Laboratory Study of Water Deficit, Photosynthesis, and Respiration.* Three-year-old Engelmann spruce nursery stock grown outdoors in pots at an elevation of 5,000 ft for one season were placed in the greenhouse during midwinter to break dormancy. The resulting new growth was allowed to set terminal buds before measurements began.

Photosynthesis and respiration were measured with a Beckman infra-red gas analyzer coupled to a closed-system assimilation chamber (Ronco 1969c). Each seedling was placed in the partially sealed assimilation chamber for a ½-hr equilibration period, during which it was continuously supplied with atmospheric air. Temperature and light intensity during equilibration and experimental runs were 21°C and 12,000 ft-c, the only intensity used in the study. After equilibration, the chamber was sealed and CO<sub>2</sub> concentration raised to 330 ppm. The reduction in CO<sub>2</sub> concentration from 330 to 270 ppm with time was recorded on a strip chart, and expressed as ppm CO<sub>2</sub>/min. Duplicate determinations were made. Respiration was

determined by darkening the chamber and allowing CO<sub>2</sub> concentration to rise from 270 to 330 ppm.

The procedure used to correlate water deficits with photosynthesis and respiration was similar to that reported by Brix (1962). Seedlings were watered 24 hr before measurements began, but not during the succeeding days. Photosynthesis and respiration were measured daily. When photosynthesis of an individual seedling varied by about 10 percent from the rate of the previous day, the water deficit was determined and both respiratory and photosynthetic rates recorded as final for that particular water deficit. Sufficient seedlings were measured so that photosynthesis determinations were obtained at intervals of about 10 percent over the range of 0 to 100 percent of the observed maximum rate. After apparent photosynthesis reached zero, water deficits and respiratory rates were measured at 2-day intervals until it appeared that the lethal deficit might have been exceeded. The seedlings were then placed in the greenhouse and watered regularly to determine their ability to recover.

Water deficits were determined by the procedures of Stocker (1929) and Clausen and Kozlowski (1965). Because spruce needles are small—150 for a 0.3-g sample—it was not feasible to use as large a sample or to place the cut ends of needles in water as recommended by the latter authors. Needles were saturated by floating them in distilled water. Only 1- and 2-year-old needles were used for determinations except when extreme deficits caused those age classes to be shed; it was then necessary to use needles from current growth. Sample weights were obtained (1) immediately after cutting, (2) after floating in water for 24 hr at a temperature of 21°C, and (3) after 24 hr drying at 65°C.

*Field Study of Water Deficit.* This study was conducted on the White River Plateau. Three-year-old Engelmann spruce seedlings were lifted from the nursery in early spring and stored until field planted in randomized blocks during the first week

<sup>4</sup> Trade names and company names are used for the benefit of the reader and do not imply endorsement or preferential treatment by the U.S. Department of Agriculture.

in June. Each randomized block contained one unshaded seedling and one partially shaded with a shingle for 4 to 5 hr during midday. Ten blocks, in which both seedlings were alive, were randomly selected from the remaining blocks at each sampling date—1, 30, 60, and 90 days after planting. Needles were taken from the selected seedlings during midafternoon and again the following morning shortly after sunrise so that water deficits of each of the 80 seedlings were measured twice.

The procedure for determining water deficits was similar to that used in the laboratory study, except that needles were placed in tared, moisture-proof vials which were taken to the laboratory in a portable icebox and weighed 24 hr after sampling. Preliminary measurements showed that water deficits so determined were within  $\pm 2.5$  percent of the deficit obtained immediately after needles were cut from the seedling.

## Results

### Field Study of Photosynthesis

*Engelmann Spruce.* Shaded spruces had higher photosynthetic rates than those grown in the open (Fig. 1), but there were no significant differences between fully shaded and partially shaded seedlings. Differences in photosynthetic rates between the previously shaded and unshaded spruces were significant for the morning, and for the combined morning and afternoon determinations, but not for the afternoon measurements alone. Interactions between light intensities, shading treatments, and time of day were not significant, and it was assumed that the increases in light intensity, whether in the morning or afternoon, had the same effect in all shading treatments.

Regardless of the previous shading treatment or time of measurement, photosynthesis followed a similar pattern with increasing light intensity. Photosynthetic rates increased most rapidly between 1,000 and 3,000 ft-c. At 5,000 ft-c, photosynthesis was about double the rate at 1,000 ft-c, but between 5,000 and 12,000 ft-c there was little change. The near-maximum rates observed at 4,000 ft-c indicated that tolerant spruces (shade plants) became

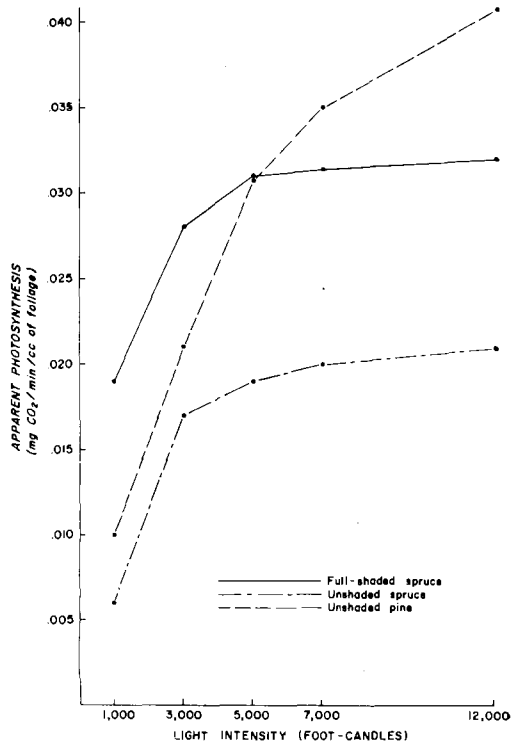


FIGURE 1. Photosynthesis of open- and shade-grown Engelmann spruce seedlings and open-grown lodgepole pine seedlings. Each point represents the mean of 5 seedlings measured in the morning.

light saturated at about one-third full sunlight.

*Lodgepole Pine.* Photosynthesis was higher in shaded than unshaded seedlings when averaged over all light intensities, but the differences were not significant. Again, there were no significant interactions, and the general effect is illustrated by the response of unshaded seedlings measured during the morning (Fig. 1). With all shading treatments, photosynthesis was low at 1,000 ft-c but increased rapidly as light intensity increased to 7,000 ft-c. Photosynthetic rates continued to increase slowly at light intensities greater than 7,000 ft-c, and did not appear to be maximum even at 12,000 ft-c. Light saturation of the intolerant pines (sun plants) was not demonstrated at the highest light intensity used in the experiment.

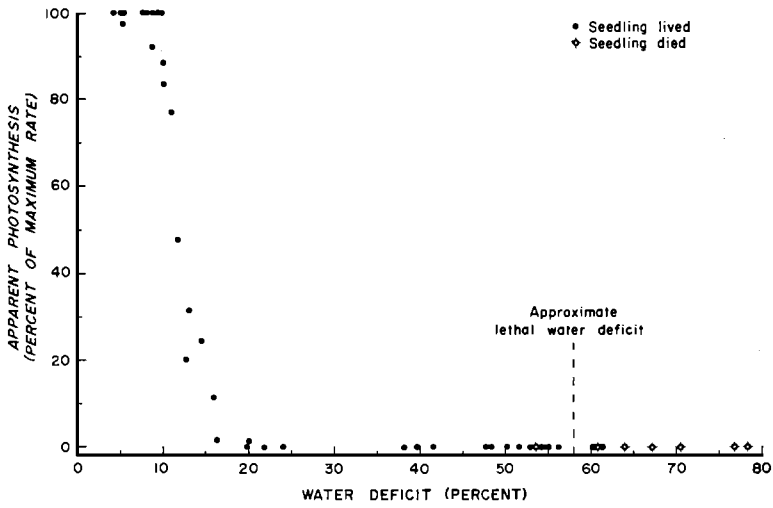


FIGURE 2. Relationship of apparent photosynthesis and viability of droughted Engelmann spruce seedlings to water deficit.

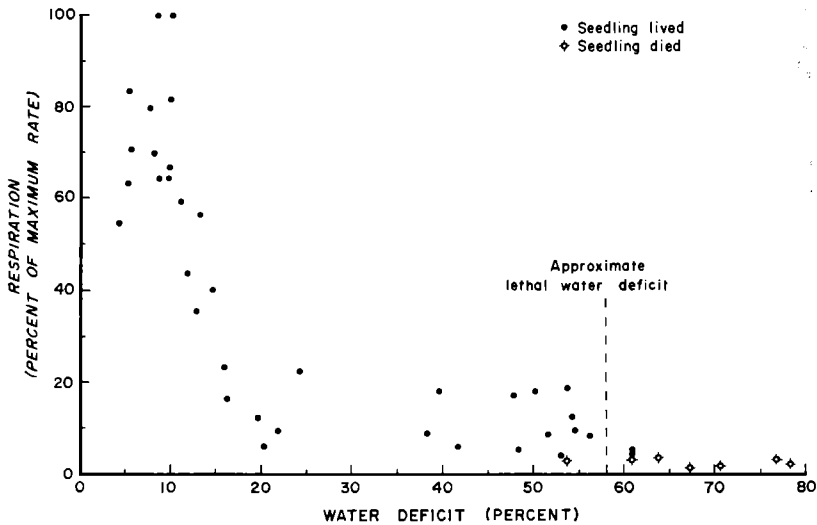


FIGURE 3. Relationship of respiration and viability of droughted Engelmann spruce seedlings to water deficit.

**Laboratory Study of Water Deficit, Photosynthesis, and Respiration**

Apparent photosynthesis of Engelmann spruce seedlings was generally near the maximum observed rate at water deficits less than 10 percent (Fig. 2). On the other hand, at water deficits of 10 percent or less, dark respiration ranged from 55 to 100 percent (Fig. 3). The rates of both processes declined rapidly between water deficits of 10 and 20 percent; minimum rates of both

were reached at a water deficit of 20 percent. At deficits greater than 20 percent, apparent photosynthesis was zero, and respiration, while variable, was less than 20 percent of maximum.

Under the conditions of the experiment, spruce seedlings unwatered for a period of 25 days averaged less than 10 percent water deficit. Deficits increased slowly during this period, but increased rapidly thereafter.

**TABLE 1.** Average percent water deficit of shaded and unshaded Engelmann spruce seedlings at different times of day and sampling dates following planting ( $n = 10$ ).

| Treatment     | Time of day | Days after planting |      |      |      |
|---------------|-------------|---------------------|------|------|------|
|               |             | 1                   | 30   | 60   | 90   |
| Partial shade | Sunrise     | 30.5                | 18.1 | 22.8 | 24.8 |
|               | 3 PM        | 29.1                | 22.8 | 23.0 | 26.0 |
| No shade      | Sunrise     | 28.4                | 20.9 | 21.6 | 25.2 |
|               | 3 PM        | 26.7                | 21.5 | 22.9 | 27.7 |

*Ability of Seedlings to Recover From Drought.* The lethal water deficit of Engelmann spruce seedlings was approximately 58 percent (Figs. 2 and 3). Data were too scanty for a more precise determination, but the approximate value indicated that seedlings could tolerate large water deficits and still recover when rewatered. Furthermore, seedlings lived for prolonged periods as high water deficits developed following cessation of watering; all seedlings that were droughted less than 50 days recovered when rewatered.

Loss of needles was a general indicator of water deficit ranges and the ability of seedlings to recover. Shedding of needles 1 year old and older began at a water deficit of 53 percent, and was complete at 78 percent, the highest measured deficit. At a deficit of 61 percent, young needles less than 1 year of age began to drop and few older needles were retained.

If losses were confined to older needles, most seedlings not only recovered when rewatered, but also put forth new growth. When young needles were shed, however, seedlings did not recover even though some old foliage was still present. Stresses not high enough to cause needle shedding nevertheless produced a reaction. Many buds on seedlings stressed to water deficits of 42 to 52 percent broke dormancy when the seedlings were rewatered.

Needles did not turn yellow as internal water stresses developed, but faded gradually to a light green color, which was retained until they were shed.

### **Field Study of Water Deficit**

The average water deficits of field-planted spruce seedlings grown under no shade

and partial shade were not significantly different at 1, 30, 60, and 90 days after planting (Table 1). Water deficits in both treatments were slightly lower at sunrise than at 3 PM for all measurement periods except the first day after planting, but the differences due to time of day were not significant.

The highest water deficits were measured the first day after planting, and averaged nearly 29 percent over treatments and times of day. Average deficits were lowest at 30 and 60 days after planting, but statistical comparison between sampling dates was not possible with the experimental procedure used.

Neither the treatment  $\times$  time-of-day nor the treatment  $\times$  sample-date interaction was significant, which indicated that treatment effect was the same regardless of the time of day or elapsed time following planting.

The water deficits determined were probably greater than actual because of the presence of dead tissue resulting from injuries sustained from drying winter winds and cold storage after lifting. Dead tissue would absorb more water than live tissue during saturation, leading to an artificially high water deficit for the whole sample. Nevertheless, comparisons between shade treatments and time of day or season are still valid since dead tissue was uniformly distributed throughout the samples.

### **Discussion**

The lower photosynthetic rates of open-grown spruces as compared to shaded seedlings (Fig. 1) was one of several indications from these and other studies that

intense light had a detrimental effect on spruces. Reduced photosynthesis suggested that the photosynthetic mechanism was damaged—presumably by solarization—when seedlings were grown in full light. In addition, the shape of the photosynthetic curve for unshaded seedlings gave no indication that the photosynthetic mechanism of open-grown spruces had adapted to full sunlight. While the magnitude of photosynthesis was higher for shaded than unshaded seedlings, the similar response to increasing light intensity in the two treatments demonstrated that spruces behaved like shade plants—which generally have lower saturating light intensities than sun plants (Böhning and Burnside 1956)—regardless of shading treatment.

Since Kandler and Sironoval (1959) reported that solarization developed within a short time after the photosynthetic mechanism became light saturated, the low intensity at which spruce seedlings were saturated further suggested that open-grown seedlings were injured by intense light. Most needles of open-grown seedlings were fully exposed to light intensities three to four times greater than the indicated saturation intensity because seedlings were small and sparsely branched.

Furthermore, a shortage of organic nutrients (Franck and French 1941) and a lack of CO<sub>2</sub> (Rabinowitch 1945) reportedly increase the susceptibility of plants to injury from intense light by inhibiting or limiting photosynthesis. The low pressure of CO<sub>2</sub> at high elevations may limit photosynthesis (Decker 1959) while, at the same time, food reserves may be depleted by prolonged cold storage before planting, shoot elongation (Kozlowski and Keller 1966), and death of new shoots from frequent summer frosts after planting (Ronco 1967). Such factors exist in many spruce plantings, but their contributory influence to solarization is not known.

The final indication that spruce seedlings were injured by intense light was widespread chlorosis, a consistent indicator of solarization (Kandler and Sironoval 1959). The prevalence of chlorosis in unshaded spruces in these and previous studies

strongly suggested solarization, especially since chlorosis was virtually absent in shade-grown spruces and unshaded lodgepole pines growing adjacent to the chlorotic spruce seedlings.

Although chlorosis may be induced by factors other than solarization (Kramer and Kozlowski 1960), two of the primary causes—nitrogen and water deficiency—were probably not related to the chlorotic condition in spruces. Ronco (1970) found no difference in the nitrogen content of chlorotic open-grown seedlings and those of normal-green color grown in the shade. As the laboratory study of water deficits demonstrated, Engelmann spruce seedlings did not become chlorotic under drought conditions, even when subjected to lethal water stresses.

While it is difficult to correlate laboratory results with events in the field, certain inferences may still be drawn from the droughting study. Potted spruce seedlings, with roots thoroughly occupying the soil, lived for 49 days before the lethal water deficit was exceeded. The probability of lethal deficits developing in field-planted seedlings from such a prolonged drought would be slight because of generally favorable environmental conditions where spruce grows. Weather data were not recorded during the current study, but previous measurements<sup>5</sup> on the study area showed that temperature rarely exceeded 21°C and relative humidity was seldom under 20 percent during the summer. Rain during summers was frequent and generally well distributed, and soil moisture throughout one of the driest summers remained above or near field capacity in the seedling root zone.

Other results indicated more directly that drought was probably not a major cause of the high mortality previously reported for spruces. Water deficits measured during the summer in field-planted seedlings were well below the lethal deficit of 58 percent. Furthermore, it did not seem

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<sup>5</sup> Ronco, F. Unpublished data on file at the Rocky Mountain Forest and Range Exp. Sta., Fort Collins, Colorado.

likely that environmental conditions where spruce grows were conducive to excessive transpiration; water deficits measured at midday were not significantly different from those at sunrise when seedling turgidity would be at maximum. The drought symptoms observed in the laboratory study were rarely seen in the field; further, most seedlings in plantations throughout Colorado lived during the summer following planting, contrary to the immediate loss that would normally follow planting if drought were the causal agent. These studies also showed that spruce seedlings were probably not any more susceptible to drought and irreversible tissue dehydration than other species; the lethal water deficit of 58 percent for spruces was similar to deficits determined by Pharis (1966) for other conifers.

While the investigations strongly indicated that drought-induced water deficits were not the primary cause of spruce mortality, the effect of lower water stresses on seedlings was less clearly defined. The investigations suggested a complex inter-relationship between nonlethal water stress, photosynthesis, and solarization. For example, relatively small changes in water deficits inhibited photosynthesis of spruce seedlings (Fig. 2), and such inhibition may enhance solarization (Rabinowitch 1945). The field study, however, demonstrated that water stresses as measured by water deficits were not altered by shading with shingles (Table 1). Thus, photosynthesis of seedlings may be inhibited by water stress regardless of shading treatment, but perhaps only the combination of water stress and direct exposure to intense sunlight would result in irreversible injury from solarization.

A correlation between water stress and solarization was also implied by the behavior of unshaded planted and potted seedlings in previous studies. The characteristic symptoms of solarization were evident in both cultural treatments, yet mortality of potted seedlings was negligible compared with that of planted seedlings (Ronco 1961). Although planted seedlings were not likely droughted to lethal limits,

water stresses were probably higher than in potted seedlings that were watered regularly. Apparently, potted seedlings received sufficient moisture to lessen the injurious effect of solarization.

Results of the present investigations, together with those of previous studies and observations, indicated that solarization occurred in unshaded Engelmann spruce seedlings, and appeared to be largely responsible for the high mortality of spruce seedlings grown at elevations above 10,000 ft (Ronco 1961).

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## ***Sprouting of Old-Growth Coastal Redwood Stumps on Slopes***

*Note by Robert F. Powers and Harry V. Wiant, Jr.*

**Abstract.** Sprouting of old-growth redwood (*Sequoia sempervirens* (D. Don) Endl.) was studied on slopes clearcut 5 to 10 years previously. Moderate slash burning had no discernible effect on sprouting. Sprout distribution around stumps became less symmetrical as slope gradient increased, tending toward reduced sprouting on the upper face. Sprout production, measured by number of sprouts per meter of stump circumference, was greatest in the 200- to 400-year age range and decreased rapidly thereafter. Excessive logging damage reduced sprout production by one-half. ***Forest Sci.* 16:339-341.**

**Additional key words.** *Sequoia sempervirens.*

OLD-GROWTH redwood (*Sequoia sempervirens* (D. Don) Endl.) can sprout from stumps. And while most stumps sprout soon after cutting, some remain barren indefinitely. Principles controlling sprouting appear complex. While heavy burning and partial debarking depress sprout production, light burning and soil burial may stimulate it (Boe 1965, Neal 1967). Barrette (1966) reported that stumps seldom sprout if their root crowns are covered with soil during logging. And though Barrette (1966) found no sprouting differences among stumps in a wide range of age and size classes,

Wiant and Powers (1967) and Neal (1967) reported that younger, smaller stumps sprout more heavily than older, larger ones.

This paper reports several relationships associated with the sprouting behavior of old-growth redwood on slopes. The aim of the study was to gain a better understanding of the principles that regulate sprout growth.

**Methods.** We selected six sample areas at random from redwood sites clear-cut and tractor-logged 5 to 10 years ago in Humboldt and Del Norte Counties, California. Sample areas extended from 14.5 km northeast of Arcata to 16 km southeast of Crescent City. Mean elevations ranged from 90 to 380 m. Aspects were varied, with slope gradients ranging from

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