COMPARATIVE DROUGHT RESISTANCE OF FIVE CONIFERS AND FOLIAGE MOISTURE CONTENT AS A VIABILITY INDEX

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Abstract. Whole plant lethal points of foliage moisture content (FMC) for ponderosa pine, sugar pine, Douglas-fir, grand fir, and incense-cedar were established from foliage tissue of various ages. Exact lethal level depended upon the age of the tissue, but there was a general plateau between the ages 6 and 13 months for sugar pine and Douglas-fir and 3 and 13 months for incense-cedar. Whole plant relative turgidity (RT) lethal points were set for the pines and firs using 13-month-old needles. Dry-weight loss upon soaking the needles was found to increase with the severity of the drought, especially for the firs. Soil moisture content (SMC) lethal points were established for all five species on builders' sand (death began at an SMC probably equivalent to tension above 24 atm) and on pumice soil (death points equivalent to tensions from 15 to 19 atm). Foliage moisture content declined with decreasing soil moisture stress in a straight-line relationship; FMC may be used as an index of soil moisture stress within a rather narrow range of SMC and may also be calibrated with leaf tissue diffusion pressure deficits developing under soil moisture stress to give an index of the water balance of the plant.

Based on the SMC at the death point and also upon some species' ability to outlive others under competitive conditions, ponderosa pine, incense-cedar, and Douglas-fir were the most drought resistant, sugar pine the least, and grand fir intermediate. Ways are suggested in which the mixed-conifer forests could become established and retain their mixed composition through maturity. The findings suggest that if planting is used to regenerate clearcuts, ponderosa pine and incense-cedar would be first choice, but that sugar pine would also be a preferred species if seeding is used.

INTRODUCTION

The mixed conifer zone forests in southwestern Oregon are unique in the number of conifer species that successfully compete with one another throughout their lives, growing to maturity in a stand of mixed composition. Major timber species in this zone are: ponderosa pine (*Pinus ponderosa* Laws.), sugar pine (*Pinus lambertiana* Dougl.), incense-cedar (*Libocedrus decurrens* Torr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and grand fir (*Abies grandis* (Dougl.) Lindl.). All of the above species may be found mixed within any one stand at young, intermediate, and mature ages. After harvesting these stands by the clearcut method, however, regeneration, either artificial or natural, of these desirable conifers is often difficult. Summer climatic conditions are hot and dry, and the rapid encroachment of other vegetation results in severe competition for soil moisture, especially on southern exposures. Summer drought is thus thought to be a major factor in the inability to regenerate these areas with conifers.

The present study is concerned with the reaction of seedlings of these conifers under severe soil moisture stress. In the process of studying these reactions a useful index of whole plant life or death, the lethal foliage moisture content (FMC), was established for ponderosa pine, sugar pine, Douglas-fir, grand fir, and incense-cedar. Lethal soil moisture content (SMC) values were established as well for all five species, and lethal relative turgidity (RT) values were set for all species except incense-cedar. The relative drought resistance of these five species and their rooting habits are discussed in relation to their establishment and growth to maturity in a stand of mixed composition in the ecologically complex region of southwestern Oregon.

The author gratefully acknowledges the helpful advice of W. E. Hallin and the technical assistance of Mrs. Mary Wells.

REVIEW OF LITERATURE

When seedlings are subjected to severe soil drought, it is often necessary to establish when the point of death has been reached. Parker (1956) has reviewed many of the methods devised to determine viability of woody plant tissue subjected to severe water stress. With conifers, tests have usually established the lethal point in terms of tissue viability itself, apparently on the assumption that the whole plant was alive until the shoot tissue died.

Several studies have established, however, a lethal point for the foliage in terms of whole plant

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viability after rewatering. Marshall (1931) noted the shoot moisture content at death for numerous conifer species at ages less than a month old, but his data are of limited value because the lethal level changes very rapidly with tissue maturation. Tazaki (1960) determined a lethal shoot moisture content for 3-month-old seedlings of *Pinus thunbergii*, and Brix (1960) established a lethal FMC for seedlings of loblolly pine (*Pinus taeda* L.) in their second growing season. Brix's results stressed the need of a lethal point for the whole plant rather than one based on the viability of foliage tissue alone, since he showed that death of the intact plant occurs while the stem and needle fascicles both are still alive and able to take up water. He concluded that resistance to water transport after drought occurred in the root system rather than the stem and that his index was "merely an indicator of an internal water stress which affects some portion of the roots more significantly than it affects the leaves." Ursic (1961) found a lethal range of FMC for year-old loblolly pines and also concluded that the roots may die before the rest of the plant. Recently Stransky (1963), in comparing FMC with needle color, established a lethal range for whole plants of loblolly pine.

A comparison of the relative drought resistance of western conifers has been made by Marshall (1931), who used the water-supplying potential of the soil at the lethal point of month-old seedlings of various species as his index of drought resistance, and by Stone (1957), who used the soil moisture content (SMC) in the lower root zone as his criterion.

Methods

Seedlings of Douglas-fir, grand fir, ponderosa pine, sugar pine, and incense-cedar were subjected to severe soil droughts in order to establish a lethal point for FMC, RT, and SMC. These lethal points were set by taking samples of the foliage and soil just prior to rewatering and checking the survival at a later date. Just a few of the plants were rewatered at light and moderate stresses. Most plants were rewatered when water stress was severe in an attempt to gather the largest number of samples near the hypothetical lethal point—ideally with an equal number distributed both above and below the critical point. The FMC values obtained on previous days were used as a guide for rewatering after obvious "live" and "die" zones were established. This prevented wasting plants in zones either well above or well below the critical point.

Experiment 1: Spring drought in builders' sand

In early December of the year prior to the test, 2-year-old plants of Douglas-fir, grand fir, sugar pine, and incense-cedar were dug at the Oregon State nursery near Elkton, Oregon, and taken to Roseburg. The seedlings had been grown from seed collected from the following sources: Douglas-fir and sugar pine—Rogue River area; grand fir from the eastern slope of the Oregon Cascade Range; and incense-cedar from the Umpqua National Forest. Ponderosa pine was obtained from the Forest Service nursery in Bend, Oregon, and the source of seed was the eastern slope of the central Oregon Cascades. About 80 seedlings of each species were potted in 5- by 5- by 6-inch plastic pots in builders' sand. In mid-December the pines and the cedar were placed in a florist's greenhouse under actual daylight plus 2 hours of artificial illumination in the middle of the night so that the plants would break shoot dormancy. The firs were not moved into the greenhouse until January 5, so that they would be subjected to at least 2 months of cold, which appears to be necessary for an early and uniform breaking of dormancy. Most plants of all species broke dormancy within 30 days after being placed in the greenhouse. Plants were fertilized biweekly with a modified Hoagland's nutrient solution and kept well watered until the middle of April. All plants were actively growing (both shoot and roots) when watering ceased.

The length of time any one plant was unwatered varied from 9 to over 30 days, depending upon the size of the plant and the degree of water stress to which the plant was to be subjected at the time of rewatering.

The FMC of the 3- to 4- and 13-month-old needles of pines and firs was obtained in the morning immediately prior to rewatering each individual plant. Needles without obvious defects (necrosis, poor color, etc.) were selected from near the middle of the flush. Age of the incense-cedar foliage samples was approximately 13 months. Samples of one or two fascicles from the pines, four to eight needles from the firs, and the outer half inch of several cedar branchlets were taken. Samples were held in clear, moistureproof plastic weighing vials until their fresh weight could be obtained, usually 1 to 3 hours after sampling.

Due to an oxidation of the plastic (contrary to the manufacturer's specifications), the vials could not be tared. Thus, the foliage was weighed separately from the vial which resulted in a fresh weight that was always 1% to 4% low because of a moisture loss to the atmosphere of the vial and air. After obtaining the fresh weight, the needles were ovendried at 105°C to constant weight, reweighed, and the moisture content expressed as a percentage of dry weight. When the weight was measured to the nearest 0.1 mg, possible weighing errors from the balance were about 1% water for the firs, and 0.5% water or less for the cedar and pines.

Just prior to rewatering the seedling, RT of 3- and 13-month-old needles was obtained by a method similar to that described by Weatherley (1950). Results from the 3-month-old needles proved unusable, however, due to extreme variation in the amount of water absorbed during the soaking procedure.

In measuring the RT of older needles (age 13 months) of the pines and firs, the same sampling procedure as for the FMC determinations was used. The RT of incense-cedar was not measured due to the difficulty of blotting the branchlets completely dry after soaking. After fresh weight was obtained, fir needles were sliced crosswise and floated on water in a closed plastic vial for 24 hours (temperature and light conditions were those of a typical office building), after which they were blotted dry, weighed immediately, ovendried, and reweighed. Pine needles, sliced crosswise in halves or thirds, were placed in the vial with one cut end in water and the above procedure followed.

The SMC immediately prior to rewatering each plant was obtained by taking approximately 45 g from the soil in the bottom 2 inches of the pot, since this bottom layer had the greatest concentration of roots. The glass wool plug was removed from a drain hole, soil within an inch of the hole discarded, and the sample taken. The cavity was then filled with glass wool. The soil sample was held in glass screw-top vials and taken to the office for fresh weight measurement. The SMC was expressed as a percentage of ovendry (105°C) weight. These gravimetrically determined SMC values were also expressed in atmospheres of soil moisture tension. The tension values were obtained through the use of pressure membrane and tension table apparatus at the Oregon State University Soil Physics Laboratory.

The survival or death of the rewatered plant was related to the three indices of water stress previously obtained. For plants well above or well below the lethal point, several days were usually sufficient to tell whether the seedling was going to live. However, if the plant had been close to the lethal point, a recovery period of several weeks to over a month was sometimes necessary, and during this period, individual seedlings would seemingly vacillate between life and death.

Experiment 2: Fall drought in pumice soil

The experiment was designed to test each species competitively against the others as well as to obtain foliage and SMC lethal values. Seedlings of the same age and source as described in the first experiment were collected from the nursery at the same time but were heeled-in outside until March. They were then potted in pairs in the center of a no. 10 can in a water-laid pumice soil from Glide, Oregon. A seedling of each species was paired with one of another species, so that there were 10 species combinations possible. At least 12 cans of each combination were prepared, so that there were approximately 120 cans with 240 seedlings. An attempt was made to rewater each can at a time when one species was still alive and the other dead. This purpose was accomplished for about a third of the cans.

Plants broke dormancy in April, were left outside, and kept well watered. They grew well and only one application of nutrient solution was necessary.

Cans were moved into the greenhouse in late June and kept well watered. In early August, light was provided in the middle of every night. Plants were growing vigorously at the start of the drought in early September. The first cans were rewatered in late September. In October the remaining cans with two live plants (105 cans) were moved into the office due to the humid, cool atmosphere maintained in the greenhouse. The office temperature was generally above 60°F. Drought was continued under long-day conditions (added 2 hours of light at night) until the middle of November. After each can was rewatered, it was taken back to the greenhouse.

The FMC of new and old pine and fir needles (6 and 18 months old, respectively) was obtained immediately prior to rewatering by the same technique described in experiment 1. Incense-cedar foliage, approximately 3 and 18 months old, was sampled in a similar manner. Length of time needles remained in vials was shortened to less than an hour, but loss of moisture to vial atmosphere was about the same as described earlier. The RT was not measured in experiment 2.

Sampling of SMC was more complicated in this experiment since there were two plants per can. Preliminary excavation of root systems from sample cans showed that roots of paired plants had become extensively interlaced and had completely permeated the soil during the 6 months they were potted together. However, pockets occurred where roots of one species predominated. Thus, for the first 10 cans SMC of the bottom 2 inches of soil was sampled from four to eight locations

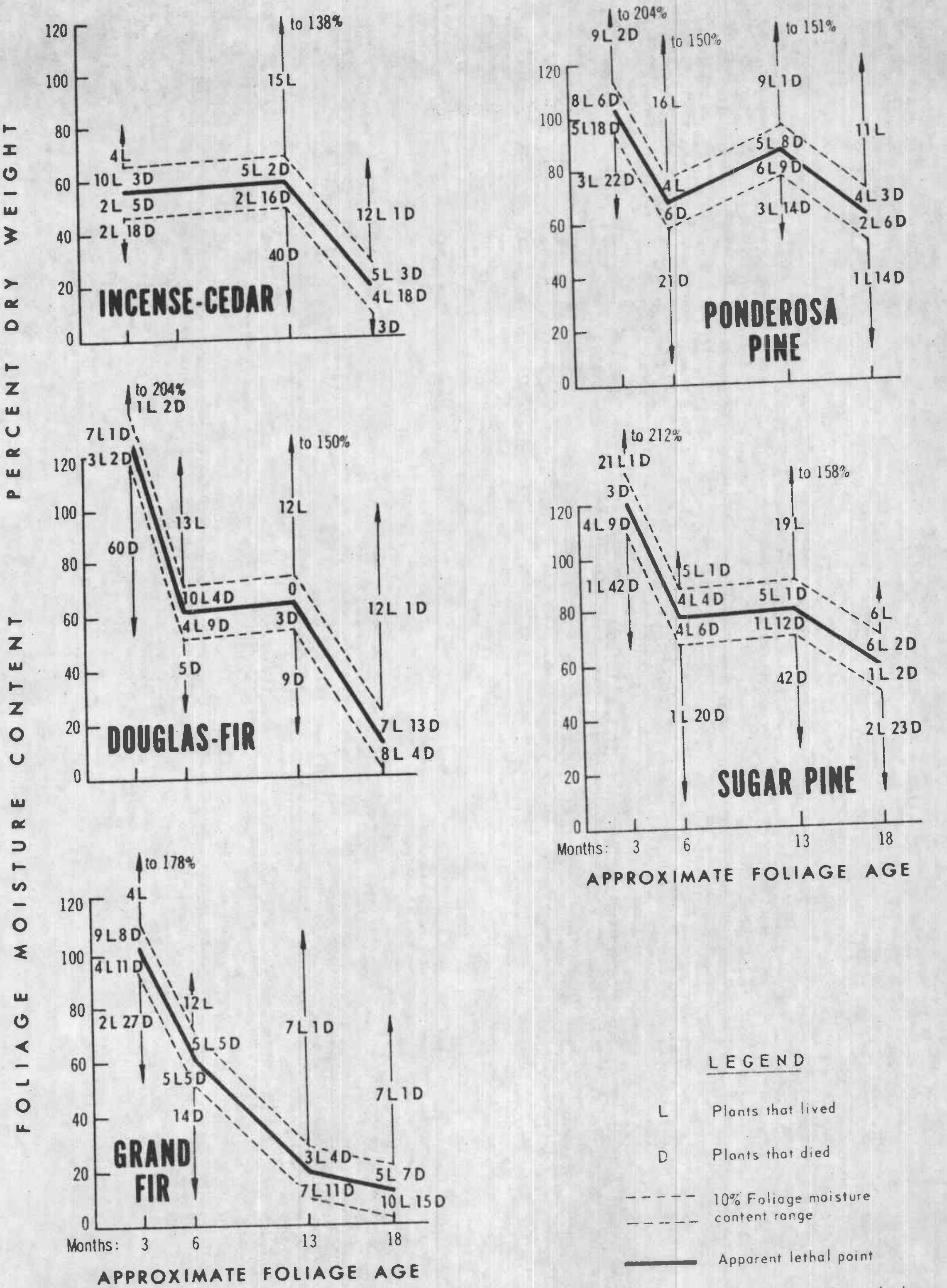

FIG. 1. Entire plant lethal points for moisture content of foliage at various ages. The number of plants that lived and the number that died, when rewatered within a range of (a) 10% above and 10% below the apparent lethal point and (b) > 10% above and > 10% below this lethal point is given.

around the can before rewatering. This preliminary sampling indicated that SMC was usually the same throughout the bottom of the can; but in some cans it varied systematically, with a low point being opposite one species, a high point opposite the other. For this reason, two SMC samples were taken from each of the remaining cans prior to rewatering, each one directly opposite a different seedling. The dry weight of a vial of pumice soil was usually about 13 g. All procedures for rewatering and obtaining soil moisture tension values were similar to experiment 1.

Results and Discussion

Foliage moisture content lethal points

The apparent lethal points shown in Fig. 1 were generally selected by choosing that point having the same number of "wrong" plants (those which lived below or died above the lethal point) below it as above it. Occasionally, however, a large grouping of "correct" plants (those which lived above or died below the lethal point) influenced placement of the lethal point either above or below the mathematically correct level.

In general, foliage lethal points for the death of the entire plant declined with foliage age (Fig. 1). The FMC values of pines and firs for ages 3-4 and 13 months are for seedlings potted in builders' sand and droughted in late spring, while FMC values of pines and firs for ages 6 and 18 months are for seedlings potted in pumice soil and droughted in late fall. The FMC's of incense-cedar at age 13 months are for the spring drought in builders' sand, and at 3 and 18 months for the fall drought in pumice soil.

Incense-cedar.—Recent, but hardened, foliage was estimated to be about 3 months old. The oldest foliage at the base of seedlings was about 13 months old during the first (spring) drought and 18 months old during the second (fall) drought. Apparent lethal points were fairly clear cut at 3 and 13 months and remained constant at about 57% for these ages. Eighteen-month-old foliage turned brown and became almost air-dry while the plant was still obviously alive.

Douglas-fir.—Foliage of 3, 6, and 13 months of age proved to be a good indicator of whole plant viability. A plateau for the lethal point at about 62% appears to exist for needles 6 and 13 months old. However, by 13 months the needles tended to dry up and drop off under even moderately severe water stress; on only about a third of the seedlings were there enough suitable 13-month-old needles left to be sampled. Eighteen-month-old foliage became air-dry.

Grand fir.—Foliage 3 months old proved a fair indicator of whole plant viability (lethal point 100%), and needles 6 months old were least variable and had a lethal point of 62%. Foliage 13 and 18 months old became almost air-dry.

Ponderosa pine.—Foliage 3-4 and 13 months old proved fair indicators of whole plant viability (lethal points of 103% and 86%, respectively), whereas needles 6 and 18 months old (lethal points of 68% and 60%, respectively) were good indicators and had narrow ranges of overlap.

Sugar pine.—Sugar pine proved to be the best species for establishing a whole plant lethal point. Overlapping ranges were narrow, and lethal points of 121%, 78%, 80%, and 58% were readily established for foliage of ages 3-4, 6, 13, and 18 months, respectively. A plateau for lethal points between ages 6 and 13 months is apparent and similar to that found for Douglas-fir and incense-cedar.

The seeming vacillation between apparent life and death for as long as a month after rewatering emphasizes the need for a good index of whole plant viability. Number of "wrongs" (based on preliminary classification of live or die) in the zone of overlap was at a maximum a few days after rewatering, but decreased to the constant level shown in Fig. 1 within about a month and remained this way for almost a year.

Even visual signs of life after rewatering, such as regaining of leaf turgidity overnight, did not always mean the whole plant would live, for death sometimes followed a week later.

Inability to regain turgidity overnight did not always imply death of the seedling, for some individuals took several days before their foliage again looked succulent. One grand fir lived for over a year with needles that remained somewhat flaccid. With ponderosa pine, complete defoliation sometimes occurred except for several juvenile foliage spurs at the base of the seedling which ultimately sprouted. Ponderosa pine and grand fir often lost all but four or five needles, or even all but parts of needles, and later began growth from the terminal. Douglas-fir, sugar pine, and incense-cedar, however, generally died if a major portion of their foliage died.

Age of foliage.—Age of foliage is important in establishing an index of whole plant viability (Fig. 1). Marshall (1931), Tazaki (1960), and Brix (1960) sampled tissue whose age did not vary appreciably between plants. Ursic (1961) sampled needles at random from year-old pines, and Stransky (1963) used needles of the previous year's growth, presumably, however, without regard to flush within that year. Results of Stransky and Ursic were more variable than either Brix or

Tazaki, perhaps due to greater variation in age of needle samples.

Results from the present study indicate that for 2-year-old plants, a relatively stable plateau for lethal FMC probably existed between the ages of 6 and 13 months for Douglas-fir, sugar pine, and ponderosa pine and between 3 and 13 months for incense-cedar. For grand fir, the age limit for any plateau was evidently less than 13 months. Foliage at 3 to 4 months of age was still in a state of flux with regard to the maturative decline of FMC under well-watered conditions for most of these conifer species (Pharis 1963), and it is reasonable to believe that lethal points are also changing rapidly during this period of maturation.

By age 18 months (13 for grand fir) foliage for the firs and cedar became air-dry while the plant was still very much alive, eliminating foliage of this age as a good index for any critical determination of lethal point. For the pines, 18-month-old foliage was still a good indicator, if available. Most pine needles at this age tended to dry very rapidly, while younger foliage remained succulent.

Thus, foliage with a range of age from 6 to 13 months can be used as an indicator of whole plant viability without calibration as to exact age, although a more limited range, e.g., 6 to 10 months, would probably be safer. Foliage much older than 13 months or much younger than 6 months is in general not satisfactory. It should be realized that lethal points obtained in the greenhouse may differ from those obtained on seedlings in the field (natural or planted). For instance, plants that barely managed to survive in the greenhouse will probably die under field conditions. However, the similarity in lethal points of different species of *Pinus* (discussed later) subjected to drought under greenhouse conditions by several other workers implies a rather uniform lethal point for potted seedlings in greenhouses.

Variability.—Variation, or range of overlapping "lives" and "dies," was dependent both upon species and age of tissue. Other factors which could not be definitely accounted for, such as sampling errors, fungus attack, or severe climatic conditions during recovery, may also account for part of this variation.

Overlap between "lives" and "dies" for the 3- to 4-month-old foliage was generally greater than for the 6- and 13-month-old foliage. Since some plants were rewatered over a month after others and the date of flushing varied somewhat from plant to plant, differences in stage of maturation most likely accounted for this variation. However, another reason may have been the tendency of younger shoot extensions, on which 3- to 4-month-old needles are located, to die while the plant remained alive. Death of younger shoots while the plant still lived was also reported by Stransky (1963) for loblolly and shortleaf pines. Physical collapse of the young stem appears responsible for this premature death of the new shoot.

Differences in soil type were eliminated as a possible cause of variability in the spring drought on builders' sand by a later check experiment. Here, half the ponderosa pine seedlings were potted in builders' sand, the rest in pumice, and all were droughted at the same time in late spring. Results of this check drought confirmed the lethal point for 13-month-old needles obtained earlier, and this lethal point was the same for seedlings on both soils.

Differences in climate during drought and recovery, or season of drought, however, may have been responsible. With regard to season, even though plants were kept actively growing prior to both droughts, those droughted in the fall may not have been physiologically equivalent to spring-droughted plants, and thus may have differed in their reaction to drought. Variability, whatever its causes, appeared to be accentuated for ponderosa pine; the other species exhibited remarkably little variation considering diversity of seasons, drought, and recovery conditions.

Using 6- to 13-month-old foliage, future workers with seedlings of these five species should have no problem establishing statistical probability of living or dying if a specific replicated number of plants are rewatered in previously delineated minor zones within the major zone of overlap (Fig. 1). Results of the present study pinpoint the zone of overlap and should eliminate from consideration much of the upper and lower ranges of moisture content. In addition, the common FMC lethal points for several species at different ages imply that these points may be used with a reasonable degree of certainty. For example, a lethal point around 60% occurs for incense-cedar foliage at age 3 months, Douglas-fir and grand fir at age 6 months, and Douglas-fir and incense-cedar at age 13 months. The pines are both higher than the firs with a lethal point near 80% for sugar pine at both 6 and 13 months, and ponderosa pine at 13 months.

Lethal points for ponderosa and sugar pine in this study are about 1% to 4% low (due to moisture loss in vial) but still are virtually the same as for loblolly and shortleaf pine in Stransky's report. They also correspond with the approximate range reported by Ursic for loblolly pine. The higher lethal point of 110% found by Brix

(1960) is probably due to his use of needles younger than 6 months. The similarity of lethal points for the four different species of pine when needles of a similar age were used is intriguing, and further extension of this method to other species of pine might reveal a universal FMC lethal point for *Pinus* spp.

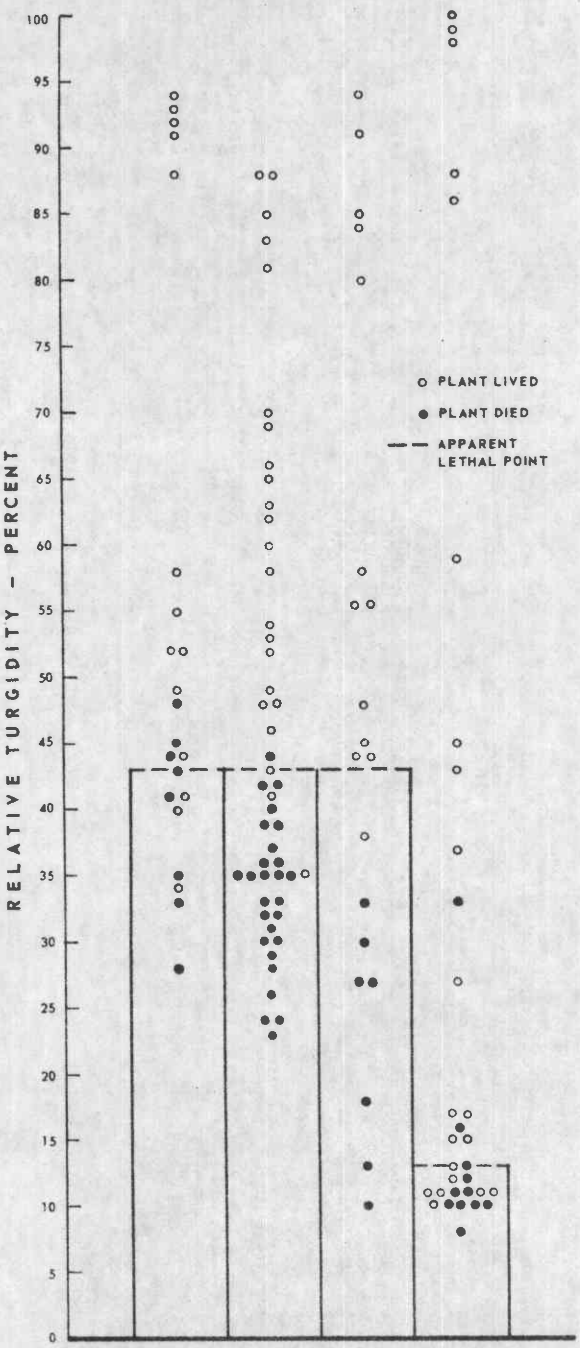

FIG. 2. Whole plant lethal points of relative turgidity for 13-month-old needles.

Relative turgidity lethal points

For ponderosa pine and sugar pine, the RT lethal points fall at 43% (Fig. 2) for 13-month-old needles. This value was assumed to be the lethal level for Douglas-fir as well, although data are too scanty to accurately place a critical lethal point. The near air-dryness of 13-month-old grand fir needles while the younger needles were still succulent makes an RT lethal point meaningless. On the firs the number of samples for RT measurements was limited because of difficulties in finding needles which were not becoming woody.

There are numerous disadvantages to RT as a measure of water stress for conifers. Brix (1960) mentioned several involving time and errors; another major disadvantage found in this study was that an appreciable dry-weight loss (up to 25% for the firs) occurred upon soaking the needles of plants subjected to severe water stress. This loss was readily discernible since duplicate needle samples taken at the same time, weighed, and immediately dried had a fresh/dry-weight ratio much lower than that of needles soaked prior to drying. The loss was slight under well-watered or moderate stress conditions. Leaves are known to convert starch to sugars under water stress (Meyer and Anderson 1952, p. 386); thus, much of the greater loss under stress here is probably due both to diffusion from cut surfaces of sugars and hydrolysis products of other high molecular weight compounds and to an increased respiration rate.

Since Harms and McGregor (1962) found RT's as low as 54% for mature needles of living loblolly pines under water stress, lethal points as low as 43% for sugar pine, ponderosa pine, and Douglas-fir do not seem unreasonable.

Soil moisture content lethal points

Since roots of all species had thoroughly permeated the soil mass, an SMC value above which most plants lived and below which most died is indicative of the maximum water stress to which a plant can be subjected and still remain alive. If this lethal point varies between species, then this variation indicates differences in the ability of one species to survive at a higher soil moisture stress than another. On this basis, then, in builders' sand ponderosa pine with a lethal point of 1.28% was most drought resistant; sugar pine with a value of 1.55% was least resistant; and incense-cedar, Douglas-fir, and grand fir were intermediate with values of 1.39%, 1.45%, and 1.47%, respectively (Fig. 3). Variation and overlapping were greater for pumice soil but the trend was similar, except that incense-ceder was the most drought resistant with a lethal point of

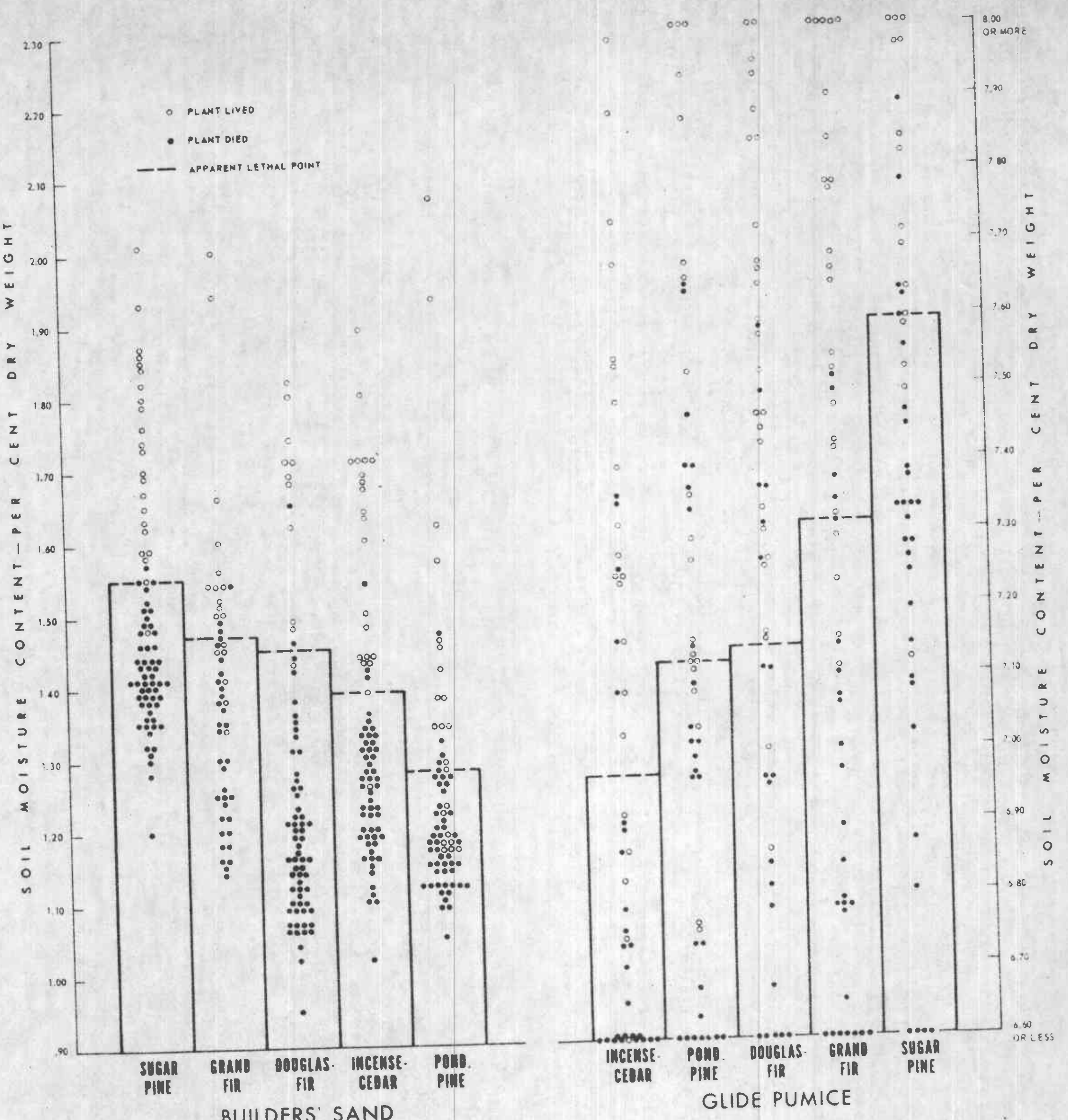

FIG. 3. Soil moisture lethal points. Species are grouped in relation to their relative drought resistance, the plants toward the center being the most drought resistant.

6.97%. Sugar pine was still the least resistant with a lethal point of 7.59%, and grand fir, Douglas-fir, and ponderosa pine were intermediate in their drought resistance with lethal points of 7.31%, 7.14%, and 7.12%, respectively (Fig. 3).

Water remaining in the soil at the approximate death point was used to compare the drought resistance of various western conifer species by Marshall (1931) and Stone (1957). Marshall droughted 24-day-old conifers on a coarse quartz sand and found that ponderosa pine was the most drought resistant, western white pine (*Pinus monticola* Dougl.) the least, and grand fir, Douglas-fir, and western redcedar (*Thuja plicata* Donn) were intermediate. Stone used a clay loam and found the amount of water left at the ultimate wilting point was least for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), most for white fir (*Abies concolor* (Gord. & Glend.) Lindl.), and intermediate for incense-cedar and ponderosa pine.

Results shown in Fig. 3 tie in nicely with both Marshall's and Stone's findings if one substitutes the comparative position of sugar pine for western white pine, and incense-cedar for western redcedar in Marshall's study, and grand fir for white fir in Stone's study.

Facilities were not available for obtaining soil

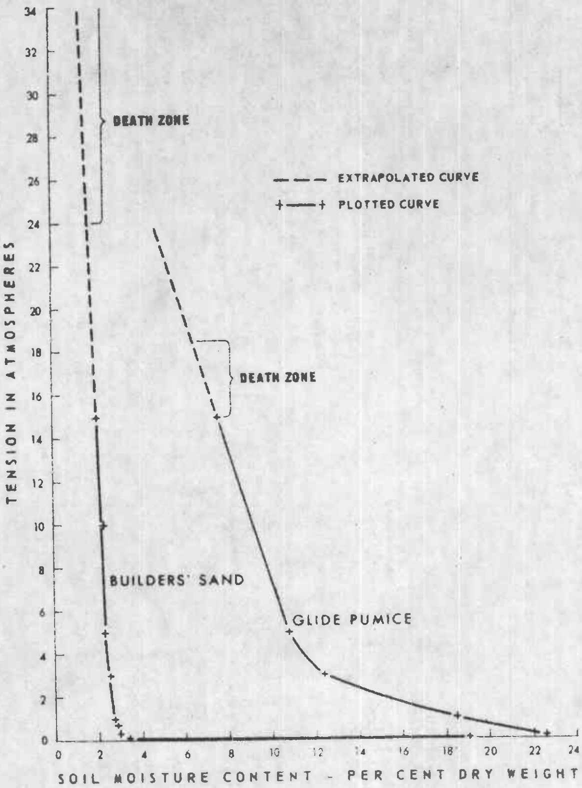

FIG. 4. Soil moisture content-tension curves. Approximate death zones are shown for both soils, the lower boundary delineating the highest moisture content at which any plant died and the upper boundary, the lowest moisture content at which any plant lived.

moisture content-tension values above 15 atm of tension. The curves have been extrapolated above 15 atm, however, and the range of soil moisture contents within which the "lives" and "dies" overlapped for individuals of all five species has been placed on these curves for both soils (Fig. 4). The highest soil moisture content at which a plant died was probably equivalent to a tension as low as 15 atm for pumice and 24 atm for builders' sand. The lowest soil moisture content at which a plant lived was probably equivalent to a tension as high as 19 atm for pumice and 30 or more atmospheres for sand.

Survival of conifers at SMC's equivalent to tensions well above the 15-atm permanent wilting point was reported by Fowells and Kirk (1945) for ponderosa pine and Ursic (1961) who found that loblolly pine died at a moisture content equivalent to tensions between 50 and 100 atm. All of these values are based on samples of relatively large soil volumes; the soil moisture tension within a few millimeters of a rootlet at the death point may be much higher.

The lower tensions of the death zone for pumice soil (Fig. 4) probably occur because the uniformity of moisture removal by the pressure membrane apparatus could not be duplicated by roots for the complicated pore system of pumice. This would not hold true in the builders' sand where all pore space is external and unsaturated movement is relatively rapid.

The rate of water movement under high tensions from the vesicular pumice particles is slower than from sand, presumably because of the tortuous pore arrangement within each particle. For the sand, root ramification was probably complete enough to result in a uniform withdrawal of water from the entire soil mass under high tension. For the pumice soil, however, the large number of vesicular particles may have resulted in numerous untapped reservoirs of soil moisture, their depletion being dependent primarily upon proximity to a rootlet. Incense-cedar was probably the only species which came close to fully occupying the soil mass insofar as uniform withdrawal of moisture at high tensions. Thus, the less extensive ramification of roots of ponderosa pine may have resulted in the reversal of its relative position with incense-cedar in the pumice soil, and may also account for much of the variation shown in Fig. 3. Even so, the relative standing of sugar pine and grand fir as being the least drought resistant and incense-cedar, ponderosa pine, and Douglas-fir the most still holds true for the pumice as well as for the sand.

Exact levels of these lethal SMC points may vary somewhat with different drought or recovery conditions. Also, SMC lethal points are known to vary for different ecotypes of Douglas-fir[2] and probably differ with ecotype for other species, especially those having a wide geographic distribution.

Relationship of decreasing foliage moisture content to soil moisture and to visual damage

Sugar pine FMC's of 13-month-old needles declined in a straight-line relationship (deviation from linear regression is nonsignificant) with a decrease in SMC over a specific range of SMC (Fig. 5). This relationship held true for other species on both soils except for very old and very young needles. Physical collapse of the young upper stem, or the needle itself, often resulted in rapidly drying needles while moisture content of the soil and other needles decreased more slowly. The moisture content of the needles appeared to

[2] A study by the author and William K. Ferrell of Oregon State University, 1963. Unpublished data on file at Silviculture and Brushfield Reclamation Laboratory, Pacific Northwest Forest & Range Experiment Station, Roseburg, Oregon.

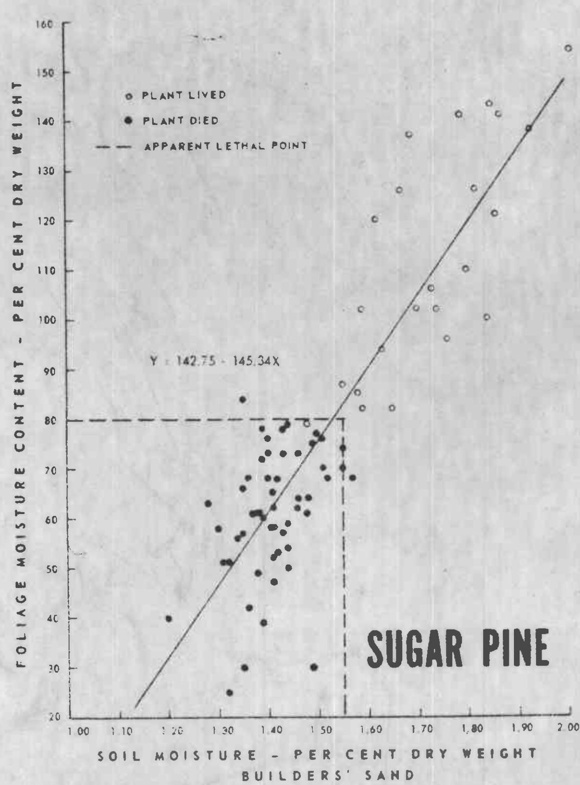

FIG. 5. Trend of moisture content of 13-month-old needles with decreasing soil moisture when potted in builders' sand.

deviate from normal values of well-watered needles at a soil moisture content equivalent to a tension of about 14 atm for builders' sand; while not accurately determined for pumice soil, it was probably well below 14 atm.

There were several degrees of visual damage on a whole plant basis in relation to declining FMC. Moderate damage (up to 20% dead foliage) occurred for all species in a somewhat direct relation to declining FMC, the range being from 100% to 70% where 60% was the lethal point. Severe damage occurred within a 10% zone just above (or around) the lethal point, with no consistent relationship between percentage damage and declining FMC.

Foliage moisture content as an index of soil and plant water stress

The directly proportional decline of FMC with decreasing SMC (Fig. 5) means that FMC can be used as an index of the soil moisture stress to which the plant is being subjected. Calibrating FMC with leaf diffusion pressure deficit (DPD) would probably give the best indicator of actual plant water stress. This calibration would be extremely useful since FMC is more easily obtained than DPD, and measurement of DPD for large numbers of samples is impractical.

Brix (1962) has shown the method described by Monteith and Owen (1958) to be useful for determining the DPD of loblolly pine needles. Weatherley and Slatyer (1957) showed that when leaf tissue DPD of privet and tomato was calibrated with RT, each species had a different curve. Thus, if conifer foliage tissue DPD was calibrated with declining FMC under increasing soil moisture stress for the various conifers, FMC would not only be useful as an index of whole plant viability but also as a very readily obtained index of drought severity.

Comparative drought resistance of the five conifer species

Relative drought resistance of the various species, if measured by ability of one species to outlive the other when grown together in cans and droughted (Table I), is similar to that derived from the amount of soil moisture remaining at the approximate death point (Fig. 3). Ponderosa pine, Douglas-fir, and incense-cedar are the most resistant, sugar pine and grand fir the least. Of 71 cans represented in Table I, there were 38 in which one species lived and the other died after rewatering and 33 in which both species died after

TABLE I. Number of cans in which one tree species outlived a second tree species with which it had been planted

Species combination	Number of cans planted	Number of cans in which first-named species out-lived the second
General combinations:[1]		
Ponderosa pine/other four species	30	21
Douglas-fir/other four species	28	20
Incense-cedar/other four species	31	19
Grand fir/other four species	25	8
Sugar pine/other four species	28	3
Total	71	
Specific combinations:		
Ponderosa pine/Douglas-fir	8	5
Ponderosa pine/incense-cedar	7	5
Ponderosa pine/grand fir	8	6
Ponderosa pine/sugar pine	7	5
Douglas-fir/incense-cedar	8	6
Douglas-fir/grand fir	4	3
Douglas-fir/sugar pine	8	8
Incense-cedar/grand fir	8	8
Incense-cedar/sugar pine	8	7
Grand fir/sugar pine	5	5

[1]A grouping of the species combinations; not a situation in which any one species was potted in the same pot with all four others.

rewatering. For cans that fell into the latter category, it could readily be determined from FMC samples and appearance that one species had outlived the other. Rewatering had been delayed only to reduce FMC of the live plant to a near-critical level, thus better establishing a lethal FMC for that particular species.

The ability of ponderosa pine to survive longer than sugar pine in these pot studies (Table I), as well as to live at an appreciably lower SMC (Fig. 3), may give a partial answer as to why ponderosa pine plantings on south exposures in southwestern Oregon have shown such good survival while sugar pine plantings have generally failed. Coupled with this general drought resistance, however, may be a differential ability of transplanted nursery stock of the two species to produce vigorous root systems during the first year, since seed spotting of sugar pine has been successful. The poor survival of planted Douglas-fir on south exposures may be a combination of lower drought resistance and a less aggressive rooting habit. Studies by Stein (1963) on three typical southwestern Oregon soils have shown that of the five species used in the present study ponderosa pine, incense-cedar, and sugar pine have the deepest root systems, with incense-cedar possessing the most spreading and extensive rooting habit. Thus, insofar as planting on tough south exposures in southwestern Oregon, ponderosa pine and incense-cedar would be the recommended species. If seeding (natural or artificial) was the method of regeneration, then the rapid first-year root growth of sugar pine might place it in a similar category with ponderosa pine and incense-cedar in hypothetical survival ability.

The relative drought resistance of these species noted in the present study (and in studies by Marshall (1931) and Stone (1957)) coupled with what is known about the ecology of rooting (Stein 1963) may be used to draw conclusions as to the way in which they are able to become established and grow to maturity in a stand of mixed composition. With regard to establishment, ponderosa pine and incense-cedar are well equipped as pioneers, being highly drought resistant, as well as having deep root systems and aggressive rooting habits. The poor drought resistance of sugar pine may be more than adequately compensated for by good initial root growth. Douglas-fir and grand fir may have come gradually into the stand during good seed years after the other three species were well established and herbaceous and brushy competing vegetation was at a minimum. The encroachment of both Douglas-fir and grand fir (as well as incense-cedar) into pure ponderosa pine plantations of ages 10 to 20 years is presently occurring in southwestern Oregon. Once all species are established, soil moisture in these relatively deep clay soils is probably no longer important in survival, but instead merely limits growth. It is possible that the resultant mixture of conifer species on southwestern Oregon clay soils may represent a high degree of soil moisture utilization, insuring that all zones of the soil are tapped for moisture.

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