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EXPLANATION OF POLE BLIGHT FROM RESPONSES OF SEEDLINGS GROWN IN MODIFIED ENVIRONMENTS

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Abstract

Seedlings of Douglas fir, grand fir, western larch, western red cedar, and western white pine were grown in modified environments for four growing seasons to see whether characteristic growth responses of roots and shoots might suggest a cause for pole blight of white pine. Environments included three soil profiles (topsoil, hardpan, and rock) and two moisture regimes (adequate and deficient).

Of several variable characteristics of growth, total root weight was the only significant source of variation in diameter and height growth of white pine. Of all five species, white pine also appeared least efficient in competing for moisture on all soil types and was least able to adapt to soils having inadequate available moisture and low potential for recharge. The lack of response to poor environment can result in imbalance of root/shoot ratios. If this imbalance of root/shoot ratios can subsequently cause internal physiological stresses during droughty periods, these stresses, in turn, may cause deterioration of the root system and consequent decline in tree vigor, both of which usually precede appearance of pole blight.

Introduction

The cause of pole blight, a disease of pole-size trees of western white pine (*Pinus monticola* Dougl.), has been only tentatively explained after 20 years of investigation. A previous summary of research on pole blight (Leaphart 1958*b*) suggested a highly complex cause, involving site quality, climate, and possibly fungi; but the fungi were regarded as secondary to the other two factors. All information about the disease subsequently collected supports the belief that the pole blight is a physiological response of white pine to its environment and climate.

Etiological and ecological studies have shown that the disease is most commonly found on sites having shallow soils and soils with low capacity for storing available moisture. Rootlet mortality of white pine trees on such sites is abnormally high (Leaphart 1958*b*; Leaphart and Copeland 1957). Reduction of diameter growth is a consistent symptom of pole blight and precedes other symptoms observable above ground (Leaphart and Gill 1955). Rootlet mortality and overall deterioration of the lateral root system occur in trees that show early symptoms of pole blight (McMinn 1956). Deterioration of

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the root system probably precedes and may be responsible for growth reduction. Furthermore, a high correlation is reported between high rootlet mortality and low summer precipitation (Leaphart 1958*b*).

A dendroclimatological study (Leaphart and Stage, in preparation) of western white pine trees, which revealed that the drought culminating in the 1930's depressed white pine growth, supports the hypothesis (Leaphart 1958*b*) that previous droughts of similar magnitude had not occurred during the life of even the oldest white pine stands. Early observations suggested that all affected trees would eventually die but by mid-1957 it was apparent that some trees had begun to recover (Molnar and McMinn 1958). The authors also have observed that many trees have recovered during the period following the severe climatic conditions of 1917–1940; growing seasons in this later period have been characterized by greater precipitation and cooler temperatures.

The syndrome of the disease and its relation to certain sites provided the impetus for conducting the type of experiment reported here. This paper describes the responses in growth of roots, foliage, and stems of seedlings of western white pine and four associated tree species grown together on three different soil profiles with contrasting soil moisture regimes and discusses the meaning and significance of these responses in relation to pole blight.

Materials and Methods

The experiment, conducted at the Priest River Experimental Forest in northern Idaho, consisted of two replications of six treatments. The treatments were combinations of three soil profiles[2] (topsoil, rock, hardpan) and two moisture levels (adequate and deficient). Five seedlings each of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), western larch (*Larix occidentalis* Nutt.), western red cedar (*Thuja plicata* Donn), and western white pine were included in each treatment. The seedlings were planted June 25–29, 1956, and were allowed to become established during two growing seasons. Then they were exposed to controlled watering for three successive growing seasons, starting in 1958. Detailed data on growth of roots, foliage, and stems of all plants were recorded in August 1960.

Installation

Six adjoining bins, 7 ft square by 3 ft deep (hereafter referred to collectively as a bed), were constructed from $\frac{1}{4}$-in. plywood and 2 × 4-in. lumber in a large excavation in the ground. Two beds (replicates) were constructed parallel and about 3 ft apart. The interior of each bed was covered with asphaltum and the exterior was brush-treated with creosote. The beds did not have artificial bottoms; each rested on a medium- to coarse-textured sand deposit that provided rapid water drainage.

Within each bed, each of the three soil profiles was represented by two bins. Selection of the bins was made at random; the only restriction was that two bins of a soil profile adjoin each other. The rock profile was prepared by filling

[2]"Soil profile," as used here and throughout the text, represents a synthesized soil profile. The three profiles simulated different soils characteristic of the western white pine type on which either healthy or diseased stands of white pine may be found.

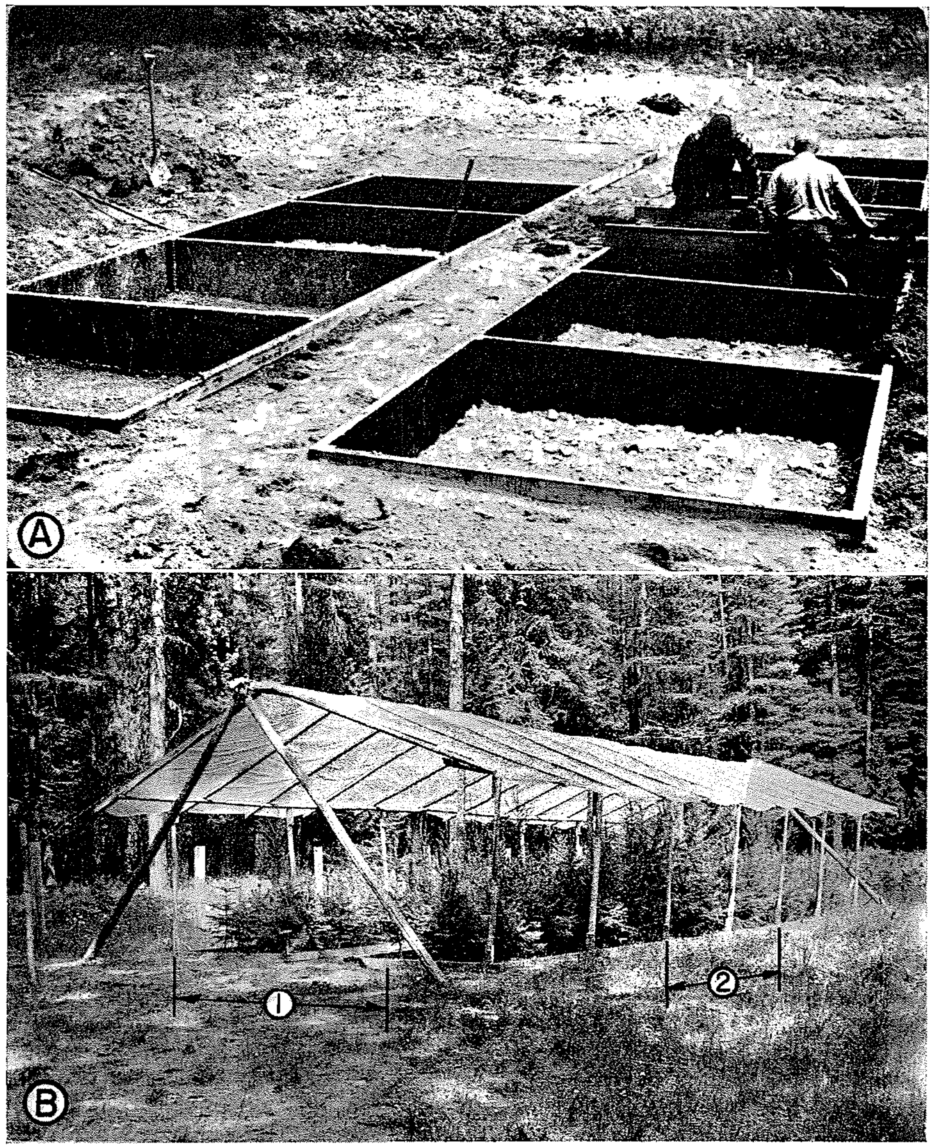

FIG. 1. Installation of experiment to study seedling responses to different moisture and soil environments. (A) Preparation of soil bins. The two adjoining bins in the left foreground and the two in the right foreground had been filled to a depth of 2 ft with rock and hardpan, respectively, before 1 ft of surface soil was added. The two being prepared by the crew were being filled with 3 ft of surface soil, screened of such debris as roots and stones. (B) Plastic shelter used to keep precipitation from the plants during the growing seasons of 1958, 1959, and 1960. The height of seedlings in the hardpan bin (1) is noticeably less than the height of those in the two topsoil bins (2). Vertical shelter supports are installed at each bin separator.

designated bins to a depth of 2 ft with rock material and then adding 1 ft of surface soil (Fig. 1A). Rock material was coarse-textured glacial till ranging from coarse sand to medium-sized cobbles; 46% (by volume) of these particles were greater than 2 mm in diameter. The hardpan profile was prepared by layering silty clay soil from a lacustrine deposit in the proper bins. Each layer was wetted and tamped to simulate the compactness of the original deposit. Depth of the hardpan material was also 2 ft, and 1 ft of surface soil was added to complete the profile structure. The remaining two bins were filled with surface soil to a depth of 3 ft and represented the topsoil profile. Thus, all bins had a total soil depth of 3 ft. All surface soil was a mixture of sandy loam and loam, quite similar to that which occurs to a depth of about 1 ft throughout much of the western white pine type.[3]

After the beds were prepared, five seedlings of each species were transplanted into each bin in a Latin square with a 1-ft by 1-ft spacing; species order in each bin was determined by random numbers. The seedlings were healthy wilding plants, most of which were collected near the study area on the Experimental Forest. All plants were about 18 in. high, but ages varied between 5 and 15 years at time of collection. Lateral and vertical roots were pruned to 3 and 12 in., respectively, on each plant before it was transplanted.

Maintenance

During the summers of 1956 and 1957 the seedling beds were watered and weeded regularly. Some seedlings died in 1956 and in the spring of 1957. These were replaced as soon after death as possible by healthy seedlings of the same type and source as original selections. After 1957, no seedlings were replaced.

A plastic shelter was constructed over both beds early in April 1958 (Fig. 1B). The plastic was a clear polyethylene, 0.006 in. thick. The eaves of the shelter overhung the beds by 30 in. and were 7 ft above the ground; this allowed adequate air movement but excluded precipitation. This shelter was maintained throughout the growing seasons (April to October) of 1958 and 1959, and from April until August in 1960. All plants were exposed to normal precipitation throughout the fall and winter.

One bin in each set of the three soil profiles received the "adequate-moisture" treatment. All bins receiving this treatment were watered weekly during the shelter period, and approximately $1\frac{1}{2}$ to 2 surface inches of water was applied to each bin during the $\frac{1}{2}$-hour watering period. The bins receiving the "deficient-moisture" treatment were all the other bins in each set of soil profiles. They were watered at longer intervals (not more than three times during the 6-month stress period) and received only enough water to keep the plants alive, about 3 to $3\frac{1}{2}$ surface inches of water per bin. All of these bins were watered during the same day.

Data Collection

Seedlings were removed from the bins by hydraulic washing and by hand after termination of the experiment on August 1, 1960. Soil material was washed from the bins into a trench that had been dug alongside the beds

[3]For type classification, refer to Haig (1932).

FIG. 2. Root washing and extraction in a rock bin. Soil was washed from the roots by water under low pressure. Trees were removed from the cross supports as their roots were extracted from the soil and rock mass.

(Fig. 2). The plants were supported by poles strung across the bins during excavation. Removal of plants was completed about 7 weeks after the excavation procedure started.

During removal of the seedlings we observed the following components of all root systems: (1) structure of the tap root (primary root), (2) depth of penetration and distribution of major lateral roots (secondary roots), (3) development and distribution of branch roots (tertiary and lower order roots), and (4) development of absorptive rootlets (fine roots and mycorrhizae).

Immediately after removal, each seedling was photographed against a grid background arranged so that the root system was in approximately the same vertical position it occupied in the bin. Next, the crown was cut off from the root system at the root collar. The following measurements of stem sections were recorded: total height; height growth in 1959 and 1960; diameter growth in 1958, 1959, and 1960 at the root collar; and age at root collar. The foliage was stripped from the twigs and its dry weight ascertained for each plant. Root systems were treated as follows: a 6-in. terminal section of the lateral root oriented closest to a northerly direction at the root collar was detached and placed in water immediately after the crown and root systems were separated. Mortality and density of root tips were determined on this section. All roots were separated into five diameter classes: 1 mm or less (designated elsewhere as fine roots), 1.1 to 5 mm, 5.1 to 10 mm, 10.1 to 20 mm, and 20.1 mm and larger. The dry weight of all roots in each size class was recorded.

TABLE I

Descriptions of development of average root system components of tree species in all treatments

Species	Components of root system: Tap root	Structural and branch roots	Absorptive rootlets
Douglas fir	Well developed, short and sturdy, forced to horizontal growth by either rock or hardpan layers	Prominent and extensive in topsoil bins; restricted to surface soil in rock and hardpan bins	Fibrous in all bins. Ectotrophic mycorrhizae more profuse than on other species
Grand fir	Not well defined in any bin, but best developed in topsoil bins	More widespread and better developed than in other species; minor penetration of rock or hardpan layers	Generally profuse in all bins. Ectotrophic mycorrhizae limited; most sparse in rock bins
Western larch	Better developed than in other species; multiple horizontal branching at rock or hardpan layers	Well developed in both topsoil and hardpan bins, restricted to surface soil in latter; sparsely developed in rock bins, but only in this species did these roots occasionally penetrate the 2-ft rock layer	More fibrous in topsoil and hardpan than in rock bins. Ectotrophic mycorrhizae rare to absent
Western red cedar	Poorly defined or nonexistent	Profuse branching, but widespread only in topsoil bins; confined almost entirely to surface soil in other bins	Very profuse in all bins; confined to surface soil by rock or hardpan layers. Ectotrophic mycorrhizae apparently absent*
Western white pine	Poorly defined and relatively short	Widespread and generally well developed, especially in topsoil bins; negligible penetration of rock or hardpan layers	Fibrous in all bins. Ectotrophic mycorrhizae fairly abundant in all soil conditions†

*Most rootlets were sheathed in a white succulent cover (Leaphart 1958*a*) thought to be the endotrophic type of mycorrhizae.
†As was reported previously (Leaphart 1958*a*), rootlets above rock or hardpan layers were found to be mostly of the mycorrhizal type and devoid of root hairs. Rootlets within these layers were devoid of mycorrhizae and had numerous root hairs.

Results

Root System Characteristics

The average response of root system components to all treatments is described by species in Table I. Since no major differences were noted between development of major structural roots and that of branch roots, their descriptions are combined. Douglas fir and grand fir produced better developed structural systems than cedar, larch, and white pine. Of the latter three species, cedar had the least widespread structural system. However, cedar and grand fir produced a more profusely developed absorptive system than did larch or white pine. The absorptive system of Douglas fir was intermediate.

Responses to Moisture Treatment

When soil moisture was deficient, root systems of all species permeated a greater volume of soil in all soil profiles than when adequate moisture was provided. Roots also penetrated all profiles more deeply in the deficient- than in the adequate-moisture bins. In the deficient-moisture bins, the primary root (when present) was much more distinct than in bins having adequate moisture; likewise, the secondary roots descended at sharper angles from the root collar, and tertiary and lower order roots were more evenly distributed along the secondary roots.

Root density of all species in the upper 6 in. of soil in the adequate-moisture bins was greater than that in the deficient-moisture bins. In bins with adequate moisture, tertiary and lower order roots in the immediate vicinity of the root collar were more dense than they were beyond the root collar region. This contrast was not so well defined in the deficient-moisture bins.

Responses to Soil Treatment

In the topsoil bins, root penetration and distribution were markedly greater than in the rock and hardpan soil profiles regardless of moisture treatment. In the topsoil bins, roots of all species penetrated the entire 3-ft depth; some grew into the sand at the bottom; and others occasionally grew into adjoining bins or the center aisle. Roots were much straighter and more profusely developed throughout their length in the topsoil bins than in bins of the other two profiles.

In the rock and hardpan bins, roots were confined mostly to the upper 1 ft of the soil profile. When major lateral and even tap roots penetrated the rock subsoil, they were flattened, crooked, or enlarged where they grew against, around, or between rocks; but their root tips were much enlarged, flattened, white, and succulent. Tap and major lateral roots abruptly changed direction of growth upon contact with the hardpan layer and grew along its surface. They were attached to the hardpan layer by numerous fine roots. A few fine roots penetrated the hardpan to depths of 6 in. in nonwatered bins, but only 2 in. in watered bins. The root tips on the surface of the hardpan layer were flattened, white, and succulent, but very dark colored and not succulent within the hardpan. Inability of roots to penetrate the simulated hardpan indicated that the natural hardpan layers encountered in certain areas within the white pine type were successfully duplicated.

Analyses of Foliage, Root, and Stem Responses

Those measures of growth, foliage weight, total root weight, fine root weight, 1960 leader growth, 1960 diameter growth, and certain ratios of these variables that were significant in split-plot analyses of variance are shown in Table II. The main effect of species was highly significant and, except for two variables (fine root/foliage ratio and 1960 height growth (Table II)), species was significant in interaction with either soil or moisture treatment. Subsequent discussions of differences both within and among species are based on interpretations of these interactions.

Treatment Effects within Species

Most species had greatest foliage and total root weights on the adequate-moisture combination in topsoil bins; notable exceptions were grand fir and larch (Table III). Foliage weight of both grand fir and larch and total root weight of grand fir were heaviest in the topsoil bins that had deficient moisture. Note especially most of the places in Table III where a shift in ranking of species within each variable is due to a change in the ranking of white pine. This shift is emphasized by underscoring only white pine in Table III, but Douglas fir and larch occasionally cause these shifts in rank.

Moisture Treatment

Consistent and marked differences between moisture treatments are apparent only for white pine (Table III). Foliage and root weights of this species were lowest in the deficient-moisture treatment within all soil profiles. Other species either responded relatively little to moisture or had greater foliage and root weights in deficient than in adequate moisture on certain soils (as did cedar in the hardpan profile), the opposite of the trend for white pine. The component parts of some species responded differently to treatment. For example, in both topsoil and rock the fine root weight of grand fir was greatest in bins that had adequate moisture, but the foliage and total root weights were greatest in deficient-moisture bins.

TABLE II

Sources of variation of selected growth variables

Variate	Sources of variation*		
	Species	Soils	Moisture
Weight			
Fine root†	**	*	
Total root	**	**	*
Foliage	**	*	*
Ratios			
Fine root wt./coarse root wt.‡	**	*	
Fine root wt./foliage wt.	**		
Total root wt./foliage wt.	**	*	
1960 growth			
Height	**		
Diameter	**	**	**

*Significant variation due to either main effects or interaction of main effects at the 1% (**) and 5% (*) confidence levels.
†Fine root weight is weight of roots 1.0 mm or less in diameter.
‡Coarse root weight is total weight of all roots larger than 1 mm in diameter.

TABLE III

Ranking of species by mean responses of growth variables (Table II) to treatment. (Species abbreviations in this table and Tables IV and VI are C, western red cedar; DF, Douglas fir; GF, grand fir; WL, western larch; and WP, western white pine. White pine is set in italic type to emphasize its rank)

Topsoil profile				Rock profile				Hardpan profile			
Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture	
				Foliage wt. (g) *$s_{\bar{x}}$ = 10.74							
GF	134.1	GF	145.9	*WP*	82.9	GF	86.3	*WP*	82.7	GF	73.9
WP	118.0	DF	85.2	GF	81.3	DF	57.2	GF	65.3	DF	65.7
DF	94.2	WL	84.7	DF	71.7	WL	56.8	DF	65.2	*WP*	64.4
WL	79.1	*WP*	69.4	C	42.1	*WP*	56.5	WL	42.2	WL	51.2
C	70.7	C	57.9	WL	39.9	C	14.1	C	21.7	C	33.6
				Total root wt. (g) *$s_{\bar{x}}$ = 7.44							
WL	111.5	WL	101.7	GF	73.4	GF	74.5	*WP*	62.9	GF	73.6
GF	91.5	GF	93.8	*WP*	60.1	WL	66.0	GF	61.7	WL	62.5
WP	71.3	DF	54.8	DF	46.2	*WP*	47.8	WL	53.3	*WP*	43.0
DF	59.0	*WP*	51.5	WL	40.2	DF	36.0	DF	42.5	DF	42.9
C	45.7	C	33.1	C	30.5	C	14.1	C	20.2	C	26.5
				Fine root wt. (g) *$s_{\bar{x}}$ = 2.05							
GF	23.5	GF	22.2	GF	29.6	GF	28.6	*WP*	22.7	GF	26.3
WL	20.8	WL	16.3	*WP*	18.8	WL	16.5	GF	22.5	DF	16.8
WP	20.4	*WP*	15.4	DF	17.2	*WP*	16.1	DF	19.1	WL	15.8
C	16.9	DF	14.5	C	13.6	DF	14.0	WL	16.9	*WP*	15.7
DF	14.2	C	11.6	WL	12.6	C	7.2	C	10.0	C	15.1

*The standard error of the treatment mean ($s_{\bar{x}}$) is based on r = 2 (two block means of five plants per species per treatment).

Moisture was not a significant source of variation for the ratios shown in Table II. However, the increases in the fine root/coarse root ratio for cedar on the deficient-moisture treatment for rock and hardpan soils are notable compared with those for other species (Table IV).

Soil Treatment

Without exception, plant vigor of all species as expressed by total root weight or foliage weight was greater on good soil (topsoil profile) than on the poor soils (rock or hardpan profiles) for both moisture regimes (Table III). Foliage weights of cedar, grand fir, and larch were significantly lower on poor soils than on topsoil; the difference averaged about 56% in cedar. The smallest difference in all species was in white pine.

The effect of soil profile on total root production is most apparent for cedar and larch and least pronounced for white pine (Table III). Although total root weight for all species was less on rock and on hardpan soils than on topsoil, roots did not all respond in the same manner. In fact, fine roots of both Douglas fir and grand fir were more prevalent on rock and on hardpan than on good soil. However, foliage and root weights (both categories of all species) differed very little between rock and hardpan soils.

The response of all species to different soil profiles was to have higher fine root/foliage ratios, and fine root/coarse root ratios on both rock and hardpan soils than on topsoil. Ratios of fine root/coarse root for cedar and grand

TABLE IV

Species ranked by ratios of selected variables within treatments

Topsoil profile				Rock profile				Hardpan profile			
Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture	
Fine root wt./foliage wt. $*s_{\bar{x}} = 0.044$											
WL	0.26	*WP*	0.22	GF	0.36	C	0.51	C	0.45	C	0.45
C	0.24	C	0.20	C	0.32	GF	0.33	WL	0.40	GF	0.36
GF	0.18	WL	0.19	WL	0.32	WL	0.29	GF	0.34	WL	0.31
WP	0.17	DF	0.17	DF	0.24	*WP*	0.28	DF	0.29	DF	0.26
DF	0.15	GF	0.15	*WP*	0.23	DF	0.24	*WP*	0.27	*WP*	0.24
Fine root wt./> 1.0 mm root wt. $*s_{\bar{x}} = 0.085$											
C	0.59	C	0.54	C	0.80	C	1.04	C	0.98	C	1.32
WP	0.40	*WP*	0.43	GF	0.68	DF	0.64	DF	0.82	DF	0.64
GF	0.35	DF	0.36	DF	0.59	GF	0.62	GF	0.57	*WP*	0.58
DF	0.32	GF	0.31	WL	0.46	*WP*	0.51	*WP*	0.56	GF	0.56
WL	0.23	WL	0.19	*WP*	0.46	WL	0.33	WL	0.46	WL	0.34

*The standard error of the treatment mean ($s_{\bar{x}}$) is based on $r = 2$ (two block means of five plants per species per treatment).

fir on rock and hardpan almost double those on topsoil (Table IV), *but* ratios for white pine show little difference among soils. Even though soil was not a significant source of variation for the ratio of fine root/foliage, cedar and grand fir again responded markedly to the rock and hardpan soils compared to topsoil.

Treatment Effects among Species

Significant differences in responses to moisture treatments and soil profiles are apparent among species in the single measurements of growth (Table III). However, most emphasis is placed on comparisons by ratios because ratios reduce the inherent differences in growth rates of species. Ratios and changes in ratios due to treatment seem to be the best means of appraising possible competitive advantages among species.

Moisture was not a significant source of variation for any of the ratios shown in Table II. But marked differences among species did occur within all soil profiles for the fine root/coarse root ratio (Table IV). Of the five species, cedar had the most profusely developed fine root system per unit of structural system, and larch usually had the least profuse system.

Differences among species in response to treatment were most noticeable when increases of the fine root/foliage and the fine root/coarse root ratios were computed for rock and hardpan profiles as a percentage of the ratios on topsoil (Table V). The response in the deficient-moisture treatment was especially noteworthy. The increase in fine root/coarse root ratio for white pine was less than half that for the other species in both profiles.

The significance of species as a source of variation in the fine root/foliage ratio (Table II) was tested; cedar had a significantly higher ratio than all other species except grand fir. No differences existed among the other species. Despite the nonsignificance of moisture and soils as sources of variation for

TABLE V

Increases of root and foliage ratios by species on the rock and hardpan profiles as a percentage of the ratios on topsoil

Soil profile and moisture treatment	Western white pine	Douglas fir	Western larch	Grand fir	Western red cedar
	Fine root wt./foliage wt.				
Rock					
Adequate	35	60	23	100	33
Deficient	27	41	53	120	155
Hardpan					
Adequate	59	93	54	89	92
Deficient	9	53	63	140	125
	Fine root wt./coarse root wt.				
Rock					
Adequate	15	84	100	94	36
Deficient	19	78	74	100	93
Hardpan					
Adequate	40	156	100	63	66
Deficient	35	78	79	81	144

this ratio, the climax species[4] usually ranked highest and white pine lowest on the rock and hardpan profiles (Table IV). Furthermore, in contrast to the seral species, their ratios were markedly higher on these soils than on topsoil. The increases in fine root/foliage ratios (Table V) again clearly demonstrate differences between climax and seral species, especially in the deficient-moisture treatment. In this treatment, the increases of the climax species are more than double the increases of the seral species on both rock and hardpan.

TABLE VI

Ranking of species by mean responses of 1960 diameter and height growth variables (Table II) to treatment

Topsoil profile				Rock profile				Hardpan profile			
Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture		Adequate moisture		Deficient moisture	
1960 height growth (cm) $^{*}s_{\bar{x}} = 3.21$											
WL	55.6	WL	61.9	WL	48.9	WL	43.1	WL	50.3	WL	49.7
GF	47.9	GF	47.9	*WP*	31.9	*WP*	31.1	*WP*	32.7	GF	35.0
DF	39.6	DF	37.1	GF	28.5	GF	31.0	GF	29.4	*WP*	30.1
WP	34.1	*WP*	35.7	DF	27.4	DF	24.0	DF	29.4	DF	27.8
C	26.8	C	24.6	C	20.9	C	17.4	C	21.8	C	18.3
1960 diameter growth (mm) $^{*}s_{\bar{x}} = 0.27$											
WL	6.6	WL	5.1	C	3.2	WL	2.9	*WP*	3.6	WL	3.6
GF	4.5	GF	4.6	DF	2.8	DF	2.5	WL	3.4	GF	3.1
WP	3.9	DF	3.2	GF	2.8	GF	2.5	DF	3.3	*WP*	3.0
DF	3.7	C	3.1	*WP*	2.4	*WP*	2.2	GF	2.7	DF	2.3
C	3.6	*WP*	2.9	WL	2.0	C	1.5	C	2.3	C	2.1

*The standard error of the treatment mean ($s_{\bar{x}}$) is based on $r = 2$ (two block means of five plants per species per treatment).

[4]Grand fir on some sites and western red cedar on most sites are considered to be climax species, while Douglas fir, western larch, and western white pine are always seral species within the western white pine type.

Height and Diameter Relations

White pine responded less than other species to differences in soils as indicated by 1960 height growth (Table VI), but soil was not a significant source of variation (Table II). In nearly all soil–moisture combinations, both diameter and height growth in 1960 were greater in larch and less in cedar than in all other species.

Diameter growth and height growth in 1960 were significantly correlated within all species, but the correlation coefficients[5] were rather uninformative; they ranged from 8% for white pine to 36% for grand fir. Although neither moisture nor soil treatment significantly affected 1960 height growth, both produced significant responses in 1960 diameter growth (Table II).

Since height and diameter growth in 1960 did not respond alike to treatment, foliage weight, total root weight, fine root weight, the ratios of foliage/total root, foliage/fine root, and total root/fine root were tested in multiple correlation analyses as potential sources of variation. Those variables significantly correlated with either diameter or height growth are tabulated below by species with their individual or combined correlation coefficients.

Douglas fir	Diameter: total root weight	$R^2 = 23\%$
	Height: foliage weight, ratio: total root weight/fine root weight	$R^2 = 52\%$
Grand fir	Diameter: foliage weight, total root weight	$R^2 = 67\%$
	Height: foliage weight, ratio: total root weight/fine root weight	$R^2 = 52\%$
Western larch	Diameter: total root weight	$R^2 = 48\%$
	Height: foliage weight, total root weight	$R^2 = 44\%$
Western red cedar	Diameter: foliage weight, total root weight	$R^2 = 58\%$
	Height: foliage weight	$R^2 = 21\%$
Western white pine	Diameter: total root weight	$R^2 = 38\%$
	Height: total root weight	$R^2 = 21\%$

Only foliage weight and total root weight were involved either as linear or ratio combinations, and both are highly correlated (correlation coefficients[6] ranged from 56% in cedar to 84% in Douglas fir).

Root Tip Density and Rootlet Mortality

The data on root tip density and rootlet mortality were too limited to serve as bases for reliable conclusions since they were taken on only a 6-in. section from the distal end of one root per plant. However, several trends were apparent in the average effects of treatment on all species. In both the topsoil and hardpan profiles, mortality was higher under the deficient- than under adequate-moisture treatments; but the differences in mortality between the two moisture treatments were greatest in the topsoil profile. An opposite condition usually occurred in rock soil profile: mortality in most species was highest in bins supplied with adequate moisture. The highest average root tip densities occurred in the hardpan profile for all species except cedar, for which highest densities were in topsoil profiles.

Discussion

Optimum development of a tree can be achieved only if the factors affecting growth provide an optimum environment. If factors affecting growth are held

[5]Basis for R^2 is 60 plants for grand fir and white pine, 59 for larch, 58 for Douglas fir, and 55 for cedar.

[6]R^2 is based on 60 plants for grand fir and white pine, 57 for Douglas fir and larch, and 53 for cedar.

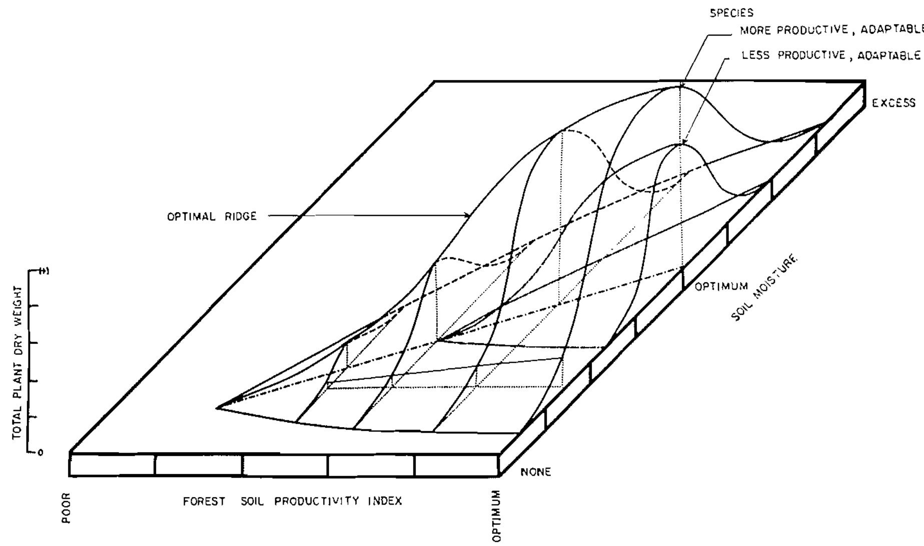

FIG. 3. Schematic relation of total plant dry weight to all levels of moisture and forest soil productivity for both more and less adaptable species having similar optimal trends (forest soil productivity index is an empirical evaluation of combined soil characteristics, such as available moisture storage capacity and root penetrability).

at favorable levels, total plant dry weight should be maximized at optimal soil conditions and moisture levels as shown by the schematic curves in Fig. 3. However, some shifting and alteration of the shapes of these curves would be likely for different species. The advantage of one species over another in adaptability is not likely to be as uniform as pictured, but it should appear roughly as indicated.

Deviation in the results of this study from those expected (Fig. 3) can occur because the final responses to soil profiles and moisture treatments are diluted in sensitivity. If the dry weight values had represented growth during the experimental period (or during the last season under treatment), such values would have reflected treatment responses more accurately than the values that included growth before treatment. Deviations may also be attributed to such factors as initial non-uniformity of seedlings used in treatments, variability of microsoil environment, genetic responses within and among species, or termination of the study before the plants had achieved maximum response to the imposed environmental conditions.

Interpretation of Moisture Treatment

Summer drought is usual in the western white pine type during July and August. Sometimes very little precipitation falls for as many as 3 or 4 months of the summer period. Soil moisture contents within the upper 1 ft of soil profiles, particularly in rocky ones, commonly drop to permanent wilting percentages during the growing period in dry summers (Copeland 1956). Consequently, special interest was centered in this study on responses of the five species to moisture conditions that might prevail on the three soil profiles under extended dry periods in contrast to responses under approximately optimal moisture supply.

Moisture was a significant source of variation in total root and foliage weights (Table II), but the magnitude of the differences in responses within species was most apparent for white pine. Except for height growth on topsoil in 1960, all variables for white pine were of less magnitude in deficient- than in adequate-moisture treatments on all soil profiles (Tables III and VI). Grand fir and larch often reversed this pattern, particularly in the foliage and total root variables. The opposite responses of grand fir and larch and those of cedar and Douglas fir on hardpan were unexpected. Possibly, the adequate-moisture treatment supplied too much water, especially in the hardpan bins; this may have reduced the oxygen level below the optimum for root and plant growth of these species. Most likely, the optimal requirements for growth of grand fir and larch were most effectively provided by the deficient-moisture treatment. The requirements of the other three species, especially white pine, were usually best satisfied in the bins supplied with adequate moisture. Certainly these unexpected responses highlight the need for more critical study to verify moisture needs of the species tested.

Interpretation of Soil Treatment

The three soil profiles used in this study approximated to the most widely occurring classes of soils in the western white pine type and produced the expected responses in plant growth and its component parts (Tables III and VI and Fig. 3). Since growth of most species in the deficient-moisture treatment in topsoil bins was greater than in adequate-moisture treatments in both rock and hardpan bins, the amount of water supplied during the shelter period was not, by itself, the differentiating factor in growth responses. Greater soil depth in topsoil profiles provided both a larger soil volume for root penetration and a greater and more uniformly distributed reservoir of available water. Thus, the influence of moisture on differences in growth in topsoil and in the two other profiles could have been masked. Here, the results suggest that future research should examine the interactions of such factors as mineral nutrition and soil aeration with moisture availability and soil depth to evaluate the separate and combined effects of these factors on the growth of a tree and its component parts.

The complexities inherent in evaluating the direct influence of soil environment on tree growth are further illustrated by the relations between height and diameter growth in 1960. Soil and moisture significantly affected diameter but not height growth (Table II). However, both these growth variables were greatly influenced by the amounts of foliage and roots that individually or in combination account for much variation in height or diameter growth.[7] Terminal and radial growth are controlled by different internal physiological processes (Kozlowski 1963), but the manner in which they are controlled, that is, through the roots or foliage in response to environment, may be a more satisfactory explanation of the low correlation coefficients between these growth variables.

[7]See tabulation.

The correlation coefficients observed between height and diameter within species were low; but growth responses in these two variables on different soils were noteworthy among species. Height growth of white pine in 1960 on the rock and hardpan profiles was slightly (about 10%) less than on the topsoil profile (Table VI). However, this reduction was significantly less than height reductions of the other four species in the same comparison. The same contrast in differences among species occurred for 1960 diameter growth on hardpan; differences in reductions among species on rock were not significant. In height growth, white pine responded very little to moisture treatment; but on soils (rock and hardpan) having low available moisture storage capacity, the energy-procuring and energy-producing systems (roots and foliage) of white pine were markedly reduced. This differential response of white pine to soil environment, further emphasized by the small increases in ratios of its foliage and root on rock and hardpan profiles (Table V), could prove detrimental to it in critically dry seasons or in successively dry years.

Capacity for storing available moisture in the upper 3-ft soil profile and depth of soil limiting root penetration account for less than 15% of the variation in site index (height over age relation)[8] of white pine in the pole-size class.[9] These soil characteristics, incorporated in the soil environment factors of this study, actually influence height growth of white pine only slightly. Relative uniformity of response to soil environment in height growth of trees of different ages is unknown. Nevertheless, the lack of response in height growth of white pine to different soils, when compared to responses of the other species, suggests that white pine might respond poorly to soil environment regardless of age. Thus, the low correlations between soil characteristics and site index observed for white pine are plausible even though high correlations have been recorded for species outside the white pine type.

Implications of this Study for Pole Blight

Investigations of pole blight have heretofore failed to explain why only white pine pole-size trees (usually 40 to 100 years old) are affected by this disease, particularly if the disorder results from site quality complexities. Results of the present study do not completely answer the question "What causes pole blight?" but they do reveal some clues to the answer and support previous concepts (Leaphart 1958*b*; Molnar and McMinn 1958).

Physiological demands of a tree probably reach their peak at the pole stage in stand development. At that time, habitat factors exert maximum influence on growth. Physiological responses of pole-size or larger trees to adverse environment may not be similar to those of seedlings or saplings in identical environments. However, if some response in the seedling stage is demonstrably carried to the pole stage, this would give a clue to the cause of pole blight. If white pine seedlings responded differently from other species, this might explain why white pine trees are affected with pole blight while adjacent trees of other species growing in the same environment are not affected.

[8]For full explanation of "site index", see Haig (1932).

[9]Unpublished data on file at the Forestry Sciences Laboratory, Intermountain Forest and Range Experiment Station, Moscow, Idaho.

Terminal growth of white pine trees affected with pole blight gradually decreases year after year and eventually the trees die from the top down. Terminal growth reduction occurs shortly after radial growth reduction in the lower stem (Leaphart and Gill 1955). The latter apparently follows a decline of the root system. Foliage weight was the most important variable associated with variation in height growth of all species except white pine. Total root weight was the single significant source of variation in white pine. Since decreased growth in height and diameter is correlated with low total root weight, the growth reductions observed in diseased white pine trees very probably are responses to deteriorating root systems. Even though the correlations between foliage and total root weights in all species were high, more study is needed to find how much decline must occur in the root systems of other species to influence foliage production and, in turn, to bring about decline in height growth and tree vigor.

Some apparently healthy white pine stands having high site indices and growing on soils of high moisture storage or recharge characteristics have high rootlet densities. Other apparently healthy stands have high site indices but have low rootlet densities and grow on soils having low potentials for supplying moisture (Leaphart 1958*b*; Leaphart and Copeland 1957). Certain stands having the same characteristics as this latter group have been affected by pole blight. These relations have a distinct similarity to the results obtained in this study. Notably, white pine responded differently from the other species to moisture treatment (Tables II and V). As discussed in the previous section, the tendency of white pine to produce high top to root ratios under soil conditions that reduce available moisture could obviously subject it to severe internal moisture stress when moisture becomes critically limited. Therefore, pole blight logically could be present in stands having excellent site index, as has been observed, even though it is found more frequently in stands having lower site indices.

Definite relations between root decline in pole-size white pine and the pole blight disease had been observed previously (Leaphart 1958*a*, 1958*b*; McMinn 1956); hence the responses of root systems to soil and moisture treatments in this study were of considerable import. Exclusive of the absorptive component of the root systems, the data on rooting characteristics (Table I) suggest that Douglas fir and grand fir produce more profusely developed structural root systems than cedar, larch, or white pine. The profusely developed absorptive component of cedar within the structural system was most apparent.

Comparisons of ratios among species within treatments (Table IV) suggest that white pine is not as efficient in competing for moisture on all soils as other species are. Of the trees tested within species, only the climax species differed significantly among soils for the fine root/coarse root ratio. (They had proportionately more fine roots to coarse roots on both rock and hardpan than on topsoil profiles.) Also, if the topsoil profile might be considered optimum environment for root development of all five species, white pine appears least able to adapt to other soil conditions (Table V). Both rock and hardpan soils in a natural environment have less capacity to store available moisture than deep soils, which are similar to the topsoil profile; therefore they dry out earlier in the growing season. Theoretically then, white pine should be at a disadvantage in competition with seral species on shallow soils because it does not compensate for low available moisture supplies of such soils by increasing its fine root/foliage ratio. For a given weight of foliage, its climax competitors appear to have a double advantage because they have a larger total root system per unit weight of foliage (higher total root/foliage ratios), and the absorbing portion of their root systems is also proportionately greater than that of white pine.

Results of this study support the contentions that white pine may be less adaptable on certain sites than associated species because its lack of response to poor soil environments results in an imbalance of root/shoot ratios. Water supply on sites where pole blight occurs is undoubtedly limited for all species, particularly in dry years. Although all physiological processes of white pine are not yet defined, this species probably does not possess compensating advantages over associated species in obtaining or conserving water. If white pine, or even some trees within this species, cannot produce a root/shoot ratio on all soil types that maintains a favorable moisture regime inside the tree, tree vigor will undoubtedly be reduced. Further, when tree vigor begins to decline, a chain reaction may start that accentuates the unfavorable root/shoot balance observed in diseased white pine trees. Pole blight might then be the terminal stage in such a chain of events.

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