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Tolerance of Lodgepole and Ponderosa Pine Seeds and Seedlings to High Water Tables

Introduction

Reasons for the distinct type lines which often occur between lodgepole and ponderosa pine stands in south-central Oregon are not clearly understood. Stands of almost pure lodgepole pine on depressions and flat areas with ponderosa pine or a mixture of ponderosa and lodgepole pine on adjacent higher sloping topography may be due to greater low-temperature tolerance of lodgepole seedlings during the emergence period (Berntsen, 1967). However, some of these lodgepole stands exist on areas with seasonal or permanent high water tables and, as summarized by Tarrant (1953), a number of investigations have suggested that lodgepole pine is more tolerant of high soil water levels than is ponderosa pine. The purpose of this study was to determine effects of high soil water levels on seed germination, seedling survival, and early growth of lodgepole and ponderosa pine.

Methods and Materials

Apparatus

To control soil water contents in the suction range between 0 and −50 cm of water, the apparatus shown in Figure 1 was constructed. An Alundum filter disk was cemented with PVC cement 5 cm from the bottom of a Lucite cylinder 17 cm in length and 10 cm in diameter. A Lucite plate was then fastened to the bottom of the cylinder, and two Lucite tubes 3 cm long were fastened in holes drilled through the cylinder wall 1 and 4.5 cm from the Lucite plate. The lower tube was used as a water inlet, and the upper tube was used to remove air bubbles from beneath the filter disk.

The small pores in the filter disk allow the disk to support a hanging water column. Height of the hanging water column above free water level in the jug controls soil pore sizes which will take up water through the wet porous disk. At equilibrium, there is a water gradient in the soil corresponding to a suction gradient of 1 cm of water per cm depth of soil.

Soils

Soil materials used in this study were taken from the A1 horizon of a Lapine soil, the AC horizon of a Wickiup soil, and from the upper foot of a small peat bog. The Lapine soil is a well-drained benchmark series developed on Mazama pumice. Reservoir construction in recent years has subjected small acreages of this soil which support both lodgepole and ponderosa pine to periodic flooding. The Wickiup soil is the most common poorly drained soil developed on Mazama pumice in south-central Oregon. Wickiup soils support stands of lodgepole pine with very little, if any, ponderosa

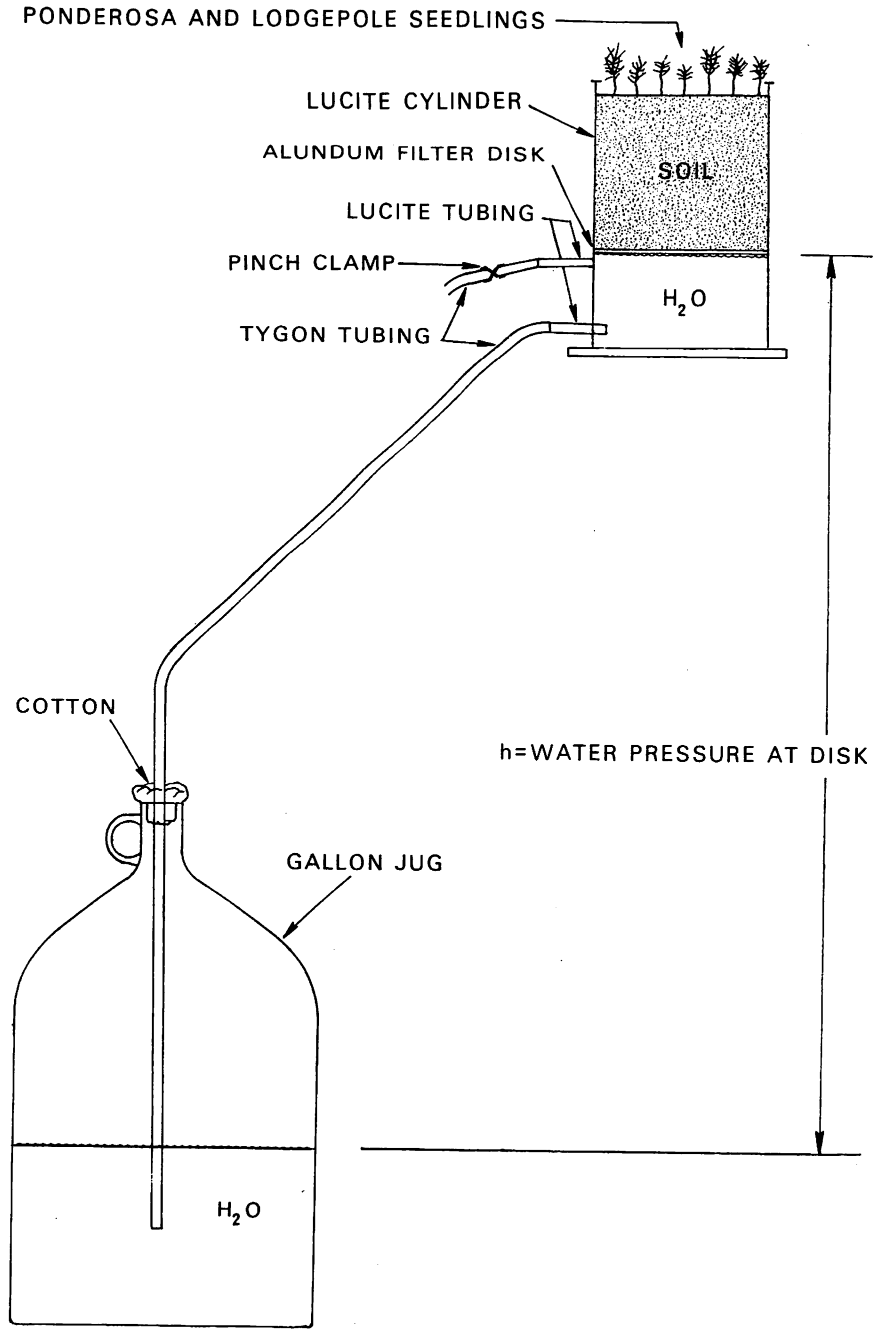

Figure 1. Apparatus for controlling soil water suction.

The peat bog occupies a topographic depression and has a water table within 10 cm of the soil surface. Although the bog is surrounded by Lapine soil supporting a mixed stand of lodgepole and ponderosa pine, only a few small lodgepole saplings are present on the peat soil.

Seeds

Seeds used in all experiments were collected at an elevation of 4500 ft approximately seven miles west of Lapine, Oregon. Germination of the lodgepole seed lot was 84 percent, compared with 72 percent for the ponderosa seed lot.

Experimental Design

Five different experiments were run using the cylinders. All experiments were completely randomized split-plot designs. In experiments 1-4, soil water level was the whole plot treatment and species was the sub-plot treatment. In experiment 5, length of time that the water level was maintained at the surface was the whole plot treatment.

Germination

Methods

The first experiment tested the hypothesis that high soil water level did not affect germination of either species. Soil material from the Wickiup AC horizon was put through a 2 mm sieve. This material was packed in the cylinders at a density of 0.72 g/cm^3. Soil depth was 5 cm. Ten seeds of lodgepole and 10 seeds of ponderosa pine were planted in each cylinder so that their tops were level with the soil surface. The free water levels were then adjusted so that water pressures at the upper soil surface equivalent to 0, –5, –10, –15, and –20 cm of water were obtained in the different cylinders. Each treatment was replicated four times. Percent germination values were angularly transformed (Li, 1957) before subjection to analysis of variance.

Results

Greater total numbers of lodgepole seed germinated because of the higher percent germination of the lodgepole pine seed lot. As free water rose from 15 to 5 cm of the soil surface, ponderosa seed germination was limited more than lodgepole (Fig. 2 and Table 1). Some germination for both species occurred on saturated soil, but the number of germinants was very small.

TABLE 1. F values for split plot analysis of the measured variables for experiments 1 through 4.

Variable	Soil	Soil water pressure	Species	Species x soil water pressure
Germination	Wickiup AC	18.13*	24.93*	3.27*
Seedling dry weights	Lapine A1	2.69	649.92*	2.61
	Peat	2.73	184.54*	4.35*
	Wickiup AC	12.03*	538.79*	2.22
Top-root ratios	Lapine A1	0.20	1.85	0.09
	Peat	1.40	.81	2.01
	Wickiup AC	9.25*	1.21	7.96*

* Significant at the 5 percent probability level.

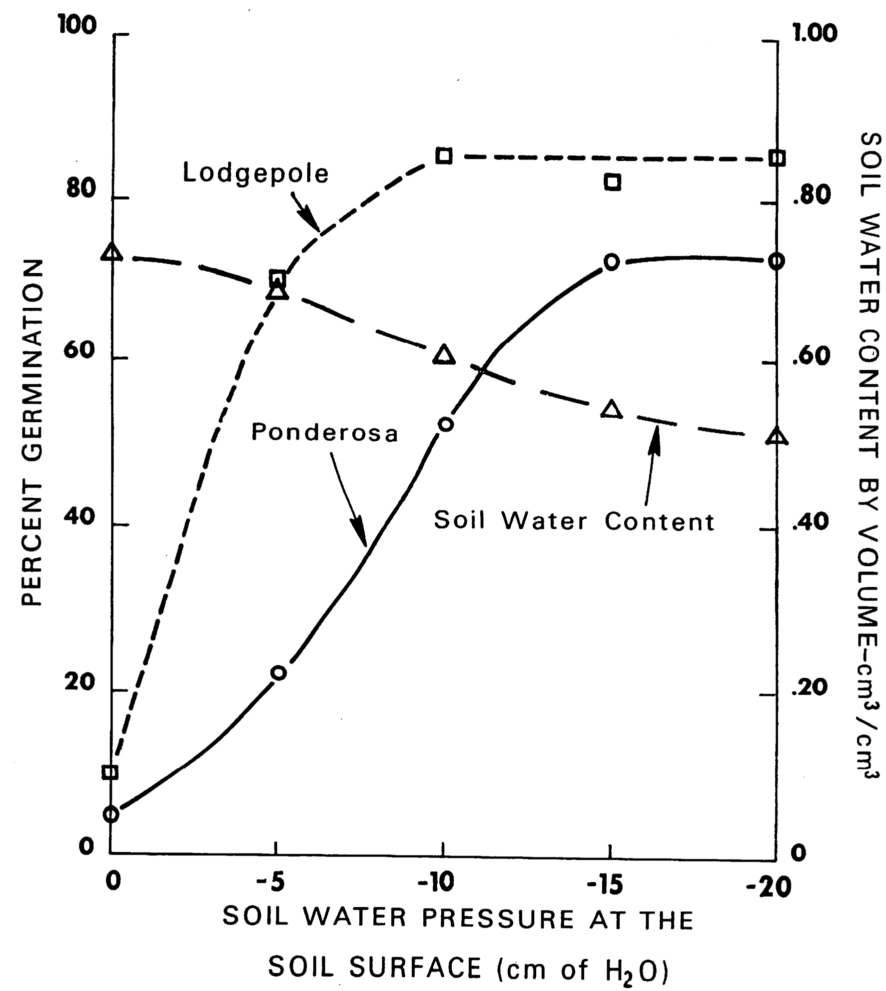

Figure 2. Percent germination of lodgepole and ponderosa pine seeds and soil water content by volume as a function of water pressure at the soil surface. Each point represents an average of four replications.

Survival and Growth—Soil Water Level

The second, third, and fourth experiments tested the hypothesis that high soil water level has no detrimental influence on survival or growth of either species.

Methods

In the second experiment, seedlings were germinated in perlite; and when one week old, four seedlings of each species were transplanted to soil in each individual Lucite cylinder. The soil was Lapine A1 horizon material packed at a density of 0.70 g/cm^3. Soil depth was 10 cm. Before transplanting of seedlings, water levels were adjusted so that water pressure was equivalent to –40 cm of water at each disk. One week after transplanting of seedlings, free water levels were changed so that pressures at various disks were equivalent to +10, +5, 0, –5, –10, –20, –30, and –40 cm of water. Each water pressure was replicated twice.

In the third experiment, the procedure of the second experiment was followed except a peat soil was used. The peat was put through a 2 mm sieve and packed into cylinders at a bulk density of 0.30 g/cm^3.

The fourth experiment was similar to the second and third experiments, except only four different pressures were applied at the disk surfaces (+10, 0, –10, and –20 cm of water equivalents) and each pressure was replicated four times. The soil used was Wickiup AC horizon put through a 2 mm sieve and packed to a bulk density of 0.72 g/cm^3.

For all three experiments, seedlings were allowed to grow in a greenhouse for 130 days, the length of time necessary for the majority of trees of both species to set buds. The greenhouse photoperiod was 15 hours, and average day and night temperatures were approximately 78° and 65° F. Oxygen diffusion rate was then measured as described by Letey and Stolzy (1964). Five platinum microelectrodes were placed with tips at 1.5-, 5-, and 9.5-cm depth within the soil in each cylinder for a total of 15 measurements within each cylinder. After determination of soil oxygen diffusion rates (ODR's), the plants were removed and soil water content, ovendry weights of tops and roots, and top-root ratios for the plants were determined.

Results

In experiment 2, where seedlings were transplanted into Lapine A1 horizon material, no mortality occurred even under saturated conditions. Although dry seedling weights tended to be lower for plants grown under saturated conditions, the lower weight was not significant (Tables 1 and 3). Weights of ponderosa seedlings were significantly greater than weights of lodgepole seedlings, but this is to be expected since dry weight of a week-old ponderosa pine seedling is approximately four times that of lodgepole. Species differences in weight were not influenced by soil water levels. The ODR's for this experiment ranged from 0.061 x 10^{-6} g O_2/cm^2–min for saturated soils up to 0.191 x 10^{-6} g O_2/cm^2–min for the driest A1 soils (Fig. 3). These values represent averages of 15 measurements and they indicate that even the driest soil was poorly aerated. There was only a 13 percent difference in volumetric water content between the wettest and driest treatments (Table 5).

Top-root ratios averaged 1.7 for ponderosa pine and 1.5 for lodgepole pine (Table

TABLE 2. F values for split plot analysis of seedling dry weights and top-root ratios for experiment 5.

Variable	Soil	Weeks of soil saturation	Species	Species x weeks of soil saturation
Seedling dry weights	Wickiup	2.13	42.51*	0.17
Top-root ratios	—	2.02	11.87*	4.59*

* Significant at the 5 percent probability level.

3). This difference was not significant, and top-root ratios were not influenced by soil water pressures (Table 1).

For experiment 3 where peat soil was used, survival of both species was again excellent. A total of four lodgepole pine and two ponderosa pine were lost, none

TABLE 3. Average dry weights of individual seedlings as a function of soil water pressure.

Species	Water pressure	Dry weights: Lapine A1	Dry weights: Peat	Dry weights: Wickiup AC	Top-root ratios: Lapine A1	Top-root ratios: Peat	Top-root ratios: Wickiup AC
	cm of H_2O	g					
Ponderosa pine	+10	0.11	0.12	0.08	1.2	1.7	1.6
	+ 5	.18	.38	--	1.5	1.4	--
	0	.17	.33	.09	1.8	2.4	1.2
	– 5	.16	.41	--	1.7	1.8	--
	– 10	.19	.56	.10	1.9	1.9	1.0
	– 20	.17	.44	.11	1.8	2.0	.9
	– 30	.17	.45	--	1.5	2.0	--
	– 40	.15	.43	--	2.0	1.8	--
Average		0.16	0.39	0.10	1.7	1.9	1.2
Lodgepole pine	+10	0.04	0.06	0.02	1.0	1.5	1.2
	+ 5	.05	.12	--	1.2	1.7	--
	0	.05	.12	.05	1.2	1.8	1.2
	– 5	.05	.22	--	1.1	1.7	--
	– 10	.04	.12	.04	2.4	2.2	1.0
	– 20	.06	.13	.03	1.8	2.2	1.0
	– 30	.06	.09	--	1.5	2.2	--
	– 40	.05	.13	--	1.8	1.8	--
Average		0.05	0.12	0.04	1.5	1.9	1.1

TABLE 4. Oxygen diffusion rates (ODR) and average dry weight and top-root ratios of individual lodgepole and ponderosa pine seedlings as a function of length of soil saturation.

Length of soil saturation	ODR x 10^{-6}	Dry weight: Ponderosa pine	Dry weight: Lodgepole pine	Top-root ratio: Ponderosa pine	Top-root ratio: Lodgepole pine
weeks	g O_2/cm^2-min	g			
52	0.05	0.38	0.18	0.57	0.58
21	.42	.32	.14	.62	.80
12	.40	.42	.20	.67	.87

TABLE 5. Average soil water content by volume as a function of water pressure at the disk for experiments 2, 3, and 4.

Water pressure at disk	Soil water content: Lapine A1	Soil water content: Peat	Soil water content: Wickiup AC
cm of H_2O		cm^3/cm^3	
+10	0.62	0.95	0.73
+ 5	.57	.90	--
0	.59	.85	.64
– 5	.55	.86	--
– 10	.53	.86	.52
– 20	.51	.72	.48
– 30	.51	.68	--
– 40	.49	.70	--

in saturated soil. Again, seedlings produced under saturated conditions tended to be smaller, but this tendency was not significant. Ponderosa pine seedlings were again significantly larger than lodgepole, and this difference was influenced by soil water level

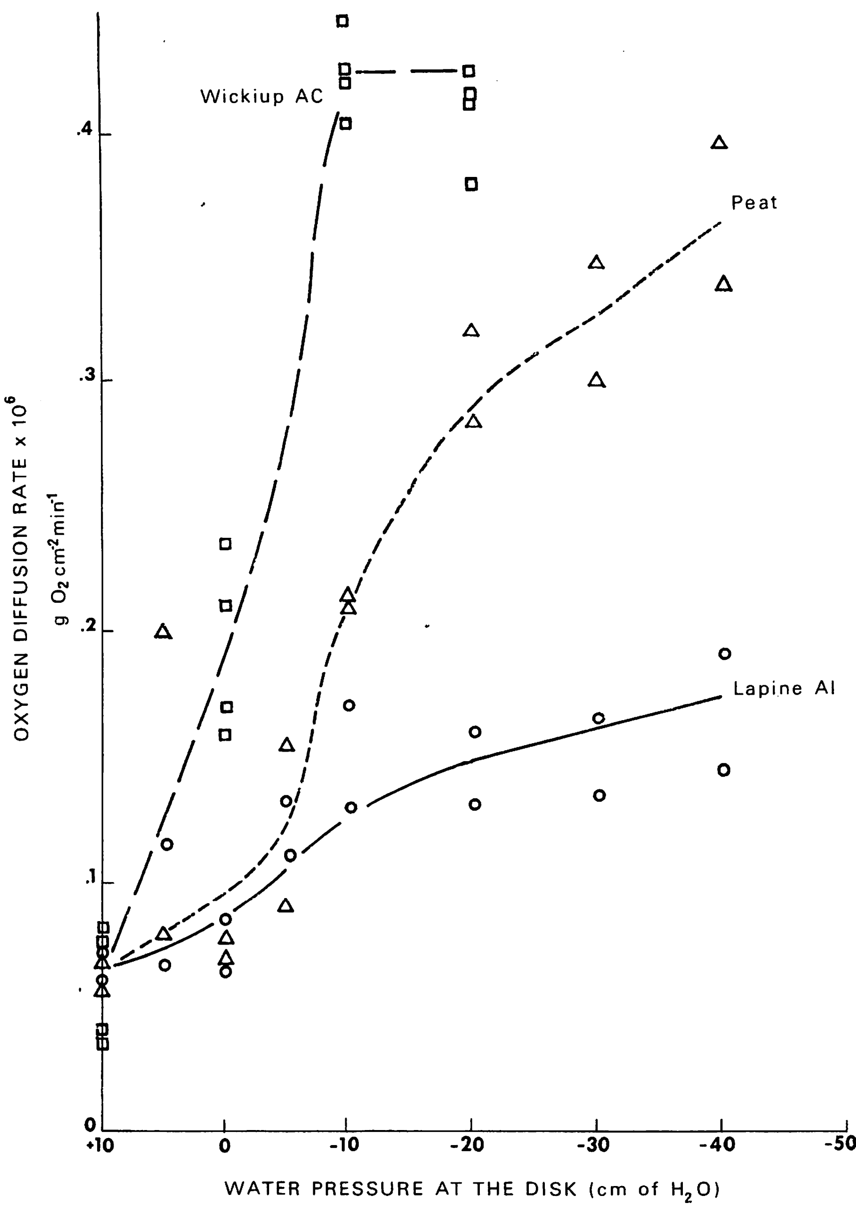

Figure 3. Oxygen diffusion rates as a function of water pressure at the disk. Each point represents an average of the 15 measurements taken in each cylinder.

(Tables 1 and 3). Oxygen diffusion rates ranged from 0.061 x 10^{-6} g O_2/cm^2–min to 0.399 x 10^{-6} g O_2/cm^2–min, indicating greater soil aeration than in the Lapine A1 horizon (Fig. 3). This soil also exhibited a greater range of soil water content than the Lapine (Table 5). Under these conditions, decreasing soil water pressure coupled with decreasing soil water content and increasing soil aeration seems to favor growth of ponderosa pine over that of lodgepole pine. Top-root ratios did not change significantly for either species as soil water levels changed (Table 1). Average top-root ratios were 1.9 for both species (Table 3).

In experiment 4, with poorly drained Wickiup soil, survival of both species was again excellent. Only one seedling of each species was lost, and these losses took place in the driest soil. Oxygen diffusion rates were more widely spread—.038 x 10^{-6} g O_2/cm^2–min to 0.448 x 10^{-6} g O_2/cm^2–min—than in the Lapine A1 and peat soils (Fig. 3). Again, ponderosa pine seedlings were bigger than lodgepole pine (Tables 1 and 3). Both species increased in size where water contents were lowered before saturation. Increasing depth to free water and the accompanying increase in aeration did not favor growth of ponderosa pine over lodgepole pine as was the case with peat soil.

Top-root ratios decreased more for ponderosa pine with decreasing soil water levels than for lodgepole pine (Tables 1 and 3).

Methods

The fifth experiment tested the hypothesis that the length of time soil is saturated affects growth and survival of both species identically. Four one-week-old ponderosa and four one-week-old lodgepole seedlings were transplanted into cylinders containing soil from the Wickiup AC horizon. The soil was put through a 2 mm sieve and packed to a density of 0.72 g/cm^3. Soil depth was 5 cm.

For two weeks after transplanting, a pressure equivalent to –30 cm of water was applied to the disk surfaces. Then the free water level was adjusted so that pressure was equivalent to +5 cm at the disk surfaces. This saturated condition was then maintained for 12 weeks in four cylinders, 21 weeks in four other cylinders, and 52 weeks in four additional cylinders. In the 12- and 21-week treatments, pressure was lowered to the original –30 cm of water at the disk surface after the saturated period was over. The plants in the 12- and 21-week treatments were then allowed to grow at original soil water pressure for the remainder of the year, when the entire experiment was terminated. Oxygen diffusion rates were measured at depths of 1.5 and 4.5 cm. Five determinations were made at each depth for a total of 10 measurements per cell. Plants were then removed, and the ovendry weights and top-root ratios were determined.

Results

Survival of both species was good. In all but two cylinders, at least three plants of each species survived. In one of the cylinders where soil was saturated for 52 weeks, only two lodgepole pine survived; and in one other cylinder where soil was flooded for 12 weeks, only one lodgepole pine survived. Treatment did not significantly influence survival, and there was no significant difference in survival between species.

Total dry weights were not influenced by length of time that the soils were saturated (Tables 2 and 4). Ponderosa pine was heavier than lodgepole pine, but this is to be expected because of its initially larger size.

Top-root ratios of lodgepole pine were larger than top-root ratios of ponderosa for treatments flooded 12 and 21 weeks (Tables 2 and 4).

The majority of plants of both species set buds during the twelfth week of flooding. Reducing water pressure at the plate surface provided a more favorable ODR (Table 4). Still, neither species responded by significantly increasing total dry weights.

Root Morphology

In all of the experiments where plants were grown until bud-set, a modification of root development was noted for both species in saturated and near-saturated treatments (water pressures equivalent to +10, +5, and 0 cm of water at the disk surface). Root depth and the number of lateral roots were restricted, and the roots exhibited a radial swelling. Root cross sections revealed a normal center protostele. However, the pericycle was enlarged somewhat more than normal, and both cells and intercellular spaces were large. Greatest deviation from normal was in the cork cambium which did not produce regular periderm cells. Instead, the cork cambium intermittently formed ridges of suberized parenchyma with very large cells and intercellular spaces. Such root development is usual in flood plant tissue.

Discussion and Conclusions

Seeds and seedlings of both species exhibited a surprisingly high tolerance to very wet soils and low oxygen diffusion rates.

The differences in germination of the two species with soil water level coupled with more frequent lodgepole pine seed crops may be a factor governing the presence of lodgepole pine on some sites. Areas do exist where water tables are within 15 cm of the surface during the germination period, and the extent of these areas varies from year to year. However, it is safe to say that the total extent of these areas is not great compared with the total lodgepole acreage even in the wettest springs. Extensive areas of lodgepole on soils where water tables are deeper than 15 cm or absent suggest other environmental factors influence stand distribution patterns.

High soil water levels, including saturation, did not cause significant mortality of either species even when the saturation period was 52 weeks. This result is particularly interesting for ponderosa pine which normally but not always grows on well-drained sites throughout its range. This high tolerance of saturated conditions may change with age for one or both species. However, exclusive presence of lodgepole pine on soils with high water tables is not a result of differential species tolerance to high soil water content alone during the early seedling stage.

Growth of both species combined tended to be lower on the saturated treatment for both Lapine A1 horizon and peat soils. Perhaps these differences would have been significant if more replications had been employed. Growth of both species combined was significantly decreased by raising water levels for the Wickiup soil where more replications were used. Growth of the two species was influenced differently by changing soil water levels only for peat soil. For peat, decreasing soil water levels produced greater increases in ponderosa than in lodgepole pine growth. Perhaps exclusive presence of lodgepole in the peat bog is because lodgepole seedlings are able to grow better than ponderosa seedlings under the very wet conditions. Lodgepole may be able eventually to grow above the 18 inches of grass and forb competition, but ponderosa pine may never grow well enough to do so. Since no differences in species dry weights occurred with changes in soil water level for the mineral soils, differences in growth rates in the early seedling stage cannot explain the exclusive presence of lodgepole on mineral soils with high water tables.

Significant differences in top-root ratios were obtained only in experiments where Wickiup AC horizon soil material was used. Top-root ratios of ponderosa pine decreased more with decreasing water levels than those of lodgepole. This is contrary to what would be expected if lodgepole root growth is more tolerant to high water levels and low soil aeration. The larger top-root ratios for lodgepole in experiment 5 for plants flooded for 12 and 21 weeks indicate that lodgepole had no more and perhaps even less ability to increase its root system after initial flooding than did ponderosa. The lack of change in dry weights with treatment in experiment 5 indicates that initial flooding prevents both species from immediately responding to lowered water levels.

Stolzy and Letey (1964) report that root growth of snapdragons was reduced or stopped when soil ODR's were in the range of 0.18 to 0.23 x 10^{-6} g O_2/cm^2–min. Newport bluegrass required an ODR of 0.20 x 10^{-6} g O_2/cm^2–min for root growth, and barley can grow roots at an ODR as low as 0.15. The present study indicates that both lodgepole and ponderosa pine seedlings can tolerate much lower oxygen diffusion rates than these plants.

This study shows that for the seed source used the influence of high soil water content alone on initial survival and growth of both species is not a factor governing "wet-site" occupancy by lodgepole pine on mineral soils.

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