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Title: WATER RELATIONS, GROWTH AND SURVIVAL OF ROOT-WRENCHED DOUGLAS-FIR SEEDLINGS

Abstract Approved: ______________________________

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Chapter 1

Growth and Survival of Root-Wrenched Douglas-fir Seedlings

Root wrenching of seedlings (severing the roots 15 cm below the soil surface) was investigated as a nursery practice to improve growth and survival of field-planted Douglas-fir from six local seed sources in the Pacific Northwest. At lifting, shoots of wrenched seedlings were shorter, lighter, and had smaller diameters than those of unwrenched seedlings. Among seedlings from four of the seed sources, wrenching resulted in significantly lighter taproots but did not significantly affect lateral root and total root weights. There were no significant differences between these measurements among wrenched and unwrenched seedlings from the other two sources. Mainly because of lighter shoots, shoot-root ratios were smaller for wrenched than for unwrenched seedlings. In no case did root wrenching improve field height growth or survival after one year, and among four of the sources shoot growth was significantly less than that of unwrenched seedlings.

Chapter 2

Water Relations of Root-wrenched Douglas-fir Seedlings

Root wrenching was investigated as a nursery practice to precondition Douglas-fir seedlings to droughty field conditions. Wrenching shocked the seedlings while in the nursery, lowering plant water potential and transpiration rate. After planting, however, wrenched and unwrenched seedlings transpired at equal rates when exposed to stress with osmotic solutions of Polyethylene Glycol 1000 and under field conditions. Throughout exposure in pots to a drought simulating the Pacific Northwest summer drought, wrenched and unwrenched seedlings did not differ in plant water potential, leaf relative water content, or seedling condition. However, all wrenched seedlings of four seed sources reflushed in the middle of the drought and had significantly fewer active roots than unwrenched seedlings. Among the four seed sources used, differences in ability to withstand drought were apparent.

WATER RELATIONS, GROWTH AND SURVIVAL OF ROOT-WRENCHED DOUGLAS-FIR SEEDLINGS

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Finally, I dedicate this thesis to my supportive, loving family, Mom, Dad, Tim and Dorothy.

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CHAPTER 1. GROWTH AND SURVIVAL OF ROOT-WRENCHED DOUGLAS-FIR SEEDLINGS

INTRODUCTION

The growing season in the Pacific Northwest is often a time of low precipitation, resulting in long periods of low soil moisture and high evaporative demand. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings planted on clearcuts often do not survive this dry period, and regeneration on many dry sites is poor. One possible solution is to manipulate nursery stock so that seedlings are better able to withstand droughty conditions. Wrenching, a nursery practice recently introduced to the Pacific Northwest, has been widely used on both droughty and moist sites in New Zealand for many years.

In New Zealand, root systems of actively growing Monterey pine (*Pinus radiata* D. Don) are wrenched by drawing a large, slightly tilted blade approximately 10 cm deep under the nursery bed, thereby reducing seedling shoot growth and altering root morphology. The long taproot and other deep-penetrating roots are cut off, and a compact mass of fibrous roots develops (Rook 1971). Perhaps because of the improved capacity of their root systems to meet the water demands of the shoots, wrenched pine seedlings have better survival and height increment after one year than do unwrenched ones, especially on droughty sites (van Dorsser and Rook 1972, Rook 1969). In Australia, weekly and biweekly root wrenching of 1-0 *Pinus caribaea* Mor. has improved its field survival, allowing bare root stock to be planted successfully (Bacon and Hawkins 1979).

There have been a limited number of wrenching studies involving pines in the southern United States, with variable results. Wrenching improved survival of longleaf pine (*Pinus palustris* Mill.) but had little effect on slash (*P. elliotii* Engelm.) and loblolly (*P. taeda* L.) pines (Shoulders 1963). In a more recent study, wrenched loblolly pine seedlings survived significantly better than the unwrenched controls (Tanaka and others 1976); this increase in survival was greater on droughty than on moist sites.

A few studies have also indicated that wrenching increases survival of Douglas-fir seedlings. Both the work of Tanaka and others (1976) in the Cascade Mountains of Washington and of Koon and O'Dell (1977) in California indicate that wrenching significantly improves survival of Douglas-fir field-planted in a droughty environment.

The present study was conducted to investigate further the effects of root wrenching on growth and survival of Douglas-fir seedlings. Variables assessed were seed source, frequency of wrenching, lifting date, presence or absence of cold storage, and moisture regime at the field-planting site.

MATERIALS AND METHODS

General Description

The study was divided into two parts: the first involved seedlings from a seed source in southwestern Oregon and another source in southwestern Washington, both of which were grown in local nurseries in 1976-77; the second part involved seedlings from four Oregon seed sources, all of which were grown in a southwestern Oregon nursery in 1977-78. In both studies, seed was sown in a randomized block design--four blocks (seedbeds) in the 1976 sowing and two adjacent seedbeds divided into four blocks in the 1977 sowing. All seedlings were subjected to irrigation regimes characteristic of that particular nursery. At the Oregon nursery, seedlings were watered when they reached certain levels of predawn moisture stress: 3 bars until July 1, 7 bars until July 15, 12 bars until August 1, and 15 bars thereafter, as recommended by Zaerr and others (in press). At the Washington nursery, watering maintained seedlings below 5 bars of predawn moisture stress throughout the summer. During the spring of their second year of nursery growth, all seedlings were undercut at 15 cm with a horizontally mounted blade to sever the taproots and then either wrenched or left as unwrenched controls. Wrenching was done with a fixed blade mounted on a tractor and tilted at 20-30° from horizontal as it was pulled under the seedbed at a depth of approximately 15 cm.

Seedling morphology was measured at the time of lifting. Field survival and growth were evaluated one year after planting in soil boxes and in the field. Data were subjected to an analysis of variance of the calculated means for each treatment within a block.

Study I

One-year-old Douglas-fir seedlings growing at the Lt. Mike Webster State Forest Nursery near Olympia, Washington, and the D. L. Phipps State Forest Nursery near Elkton, Oregon, were root wrenched. Local seed sources were used at each nursery--No. 430, 100 ft (30 m) elevation and No. 252, 500-1,000 ft (152-305 m), respectively. Seedbed density was 65 seedlings/ft^2 (700/m^2) at Webster and 35 seedlings/ft^2 (377/m^2) at Phipps. Seedlings were subjected to one of three treatments--no wrenching (control), a single wrenching (July 15), or multiple wrenching (at biweekly intervals beginning June 15 and ending August 1).

We lifted seedlings twice--November 1 and February 1--by first machine-loosening and then hand-pulling them. All seedlings less than 15 cm in height and 3 mm in shoot diameter were culled. We pruned roots to 25 cm. The following measurements were taken on a subsample of 40 seedlings per treatment (10 seedlings x 4 blocks): shoot height and diameter, needle surface area, shoot and root ovendry weight, total lateral root length, and number of root tips per seedling.

At each of the liftings, one-half of the seedlings from each block were stored at 3°C for 2 months. Stored and unstored seedlings were planted in boxes containing soil from the A-horizon of a forest site near Burnt Woods, Oregon. The experimental design duplicated the one used in the nursery, with a randomized block design for keeping nursery blocks separate. The soil boxes were 60 cm deep and were subjected to either moist or dry regimes. Seedlings in both regimes were watered until June 1, when watering of half the boxes was discontinued to simulate summer drought. Space in the boxes was randomly assigned, with each treatment planted in 10-seedling rows. Hence, the number of seedlings planted in the boxes was 2 (nurseries) x 3 (wrenching treatments) x 4 (blocks) x 2 (moisture regimes) x 2 (lifting dates) x 2 (storage treatments) x 10 (seedlings per row) = 1,920 seedlings. A row of buffer seedlings was planted along all edges of the soil boxes.

Study II

Seedlings from four seed sources--No. 053, coastal, 0-500 ft (0-152 m) elevation; No. 252, Willamette Valley, 500-1,000 ft (152-305 m); No. 491, Cascades, 3,000-3,500 ft (914-1067 m); and No. 501, Cascades, 4,000-4,500 ft (1,219-1,372 m)--were grown at the Phipps nursery near Elkton. Seedlings were thinned to 24/ft^2 (258/m^2) in the winter after one year of growth. Treatments were an unwrenched control and a multiple wrenching (biweekly during the growing season from June 15 through August 1). After lifting in late January, seedlings were planted immediately in soil boxes at the Forest Research Laboratory in Corvallis, Oregon, and in the field at the Peavy Arboretum in Corvallis. As in Study I, the soil boxes were subjected to either moist or dry regimes. The field planting involved a plowed area with no grassy competition (moist site) and a grassy area (dry site). For each location, design of the planting tests again duplicated the one used in the nursery, with 4 (seed sources) x 2 (wrenching treatments) x 4 (blocks) x 2 (moisture regimes) x 18 (seedlings per row) = 1,152 seedlings.

RESULTS

Morphology at Time of Lifting

Seedling height was reduced by wrenching at both Phipps and Webster nurseries in Study I (Table I). At both nurseries, there was a slight reduction in height with single wrenching and a greater reduction with multiple wrenching--Phipps: 30.0, 28.5, and 25.2 cm; Webster: 32.4, 26.4, and 23.3 cm. In Study II, multiple-wrenched seedlings from all four seed sources were shorter than the unwrenched controls (Table II). Seedlings from the high Cascades source were shorter than those from the coastal and valley sources.

Wrenched seedlings were also thinner stemmed than unwrenched ones. Shoot diameters at Webster were reduced from 4.5 mm for unwrenched seedlings to 4.2 and 4.0 mm for single- and multiple-wrenched ones (Table I). At Phipps a similar trend was not statistically significant. In Study II, wrenching reduced average shoot diameters among seedlings from all four seed sources (Table II). Seedlings from the Cascade seed sources had smaller shoot diameters than those from the coast and valley sources.

Needle surface area was not different for wrenched and unwrenched seedlings at either nursery in Study I (Table I). In Study II, however, unwrenched seedlings had more needle surface area than wrenched ones--212 cm^2 versus 179 cm^2 (Table II).

TABLE I. STUDY I: MORPHOLOGY AND FIELD PERFORMANCE OF WRENCHED AND UNWRENCHED DOUGLAS-FIR SEEDLINGS FROM TWO NURSERIES.

	Phipps Nursery					Webster Nursery				
Seedling measurement	Unwrenched control	Single wrenched	Multiple wrenched	Significance[a]	95% LSD	Unwrenched control	Single wrenched	Multiple wrenched	Significance[a]	95% LSD
Morphology										
Shoot										
2-0 height (cm)	30.0	28.5	25.2	**	1.8	32.4	26.4	23.3	**	2.3
Shoot diameter (mm)	4.6	4.4	4.4	NS	--	4.5	4.2	4.0	*	.4
Needle surface area[b] (cm^2)	264	275	289	NS	--	307	261	245	NS	--
Shoot dry weight (g)	3.75	3.41	3.23	NS	--	4.19	3.42	3.17	*	.73
Root										
Lateral root length (cm)	251	301	301	NS	--	220	259	259	NS	--
Lateral dry weight (g)	.80	1.07	1.06	NS	--	.75	.88	1.04	NS	--
Taproot dry weight (g)	1.00	.93	.85	NS	--	.70	.57	.53	NS	--
Total root dry weight (g)	1.81	2.00	1.91	NS	--	1.45	1.45	1.57	NS	--
Total number of root tips	1404	1909	1868	NS	--	841	806	1093	*	236
Shoot-root ratio	2.11	1.79	1.87	**	.10	3.00	2.46	2.13	**	.36
Field performance										
Budburst (Julian day)										
Soil box--Dry & Moist	115.4	114.3	113.7	NS	--	127.5	127.9	127.3	NS	--
Shoot growth (cm)										
Soil box--Dry	13.2	12.3	12.0	NS	--	9.3	8.5	9.7	NS	--
Moist	15.8	15.5	14.5	NS	--	11.0	10.4	11.4	NS	--
Survival (%)										
Soil box--Dry	89	87	82	NS	--	64	73	66	NS	--
Moist	99	99	98	NS	--	99	100	99	NS	--

[a] ** indicates a significant difference at the 0.01 level; * indicates a significant difference at the 0.05 level; NS indicates no significant difference.
[b] Includes both surfaces of the needles.

TABLE II. STUDY II: MORPHOLOGY AND FIELD PERFORMANCE OF WRENCHED AND UNWRENCHED DOUGLAS-FIR SEEDLINGS FROM FOUR SEED SOURCES. (NO INTERACTIONS OCCURRED.)

Seedling measurement	Wrenching treatment (seed sources are combined)			Seed source (wrenched and unwrenched are combined)					
						Cascades			
	Unwrenched control	Multiple wrenched	Significance[a]	No. 053 (Coast)	No. 252 (Valley)	No. 491 (Low)	No. 501 (High)	Significance[a]	95% LSD
Morphology									
Shoot									
2-0 height (cm)	18.8	17.5	*	19.2	19.0	17.9	16.6	**	1.6
Shoot diameter (mm)	4.5	4.0	**	4.4	4.4	3.9	4.3	*	.3
Needle surface area[b] (cm^2)	212	179	**	209	185	187	202	NS	--
Shoot dry weight (g)	3.00	2.44	**	3.00	2.69	2.53	2.67	NS	--
Root									
Lateral root length (cm)	296	298	NS	317	276	263	332	**	43
Lateral dry weight (g)	1.58	1.58	NS	1.78	1.54	1.26	1.72	**	.30
Taproot dry weight (g)	.92	.79	**	.91	.84	.74	.94	**	.12
Total root dry weight (g)	2.49	2.37	NS	2.69	2.38	2.00	2.67	**	.34
Total number of root tips	1334	1347	NS	1685	1349	1083	1244	NS	--
Shoot-root ratio	1.24	1.08	**	1.14	1.18	1.30	1.03	*	.16
Field performance									
Budburst (Julian day)									
Soil box--Dry & Moist	120.1	119.8	NS	123.7	117.5	119.9	118.6	**	2.2
Peavy Arboretum--Grassy	121.0	120.8	NS	122.6	119.7	120.4	120.8	**	1.2
Plowed	123.1	122.0	*	123.9	121.6	122.7	122.0	**	1.2
Shoot growth (cm)									
Soil box--Dry	5.5	5.0	*	5.0	5.8	5.1	5.2	NS	--
Moist	9.2	8.1	NS	10.3	9.6	7.4	7.2	**	1.6
Peavy Arboretum--Grassy	5.0	4.2	**	5.0	4.8	4.3	4.4	*	.5
Plowed	5.3	4.6	**	5.4	5.2	4.7	4.6	**	.4
Survival (%)									
Soil box--Dry	45	49	NS	35	43	45	66	**	16
Moist	98	99	NS	98	99	100	96	NS	--
Peavy Arboretum--Grassy	2	2	NS	1	4	2	1	NS	--
Plowed	96	93	NS	94	97	95	93	NS	--

[a] ** indicates a significant difference at the 0.01 level; * indicates a significant difference at the 0.05 level; NS indicates no significant difference.
[b] Includes both surfaces of the needles.

Shoot dry weights were greater for unwrenched than for wrenched seedlings at Webster in Study I, with single-wrenched seedlings being heavier than multiple-wrenched ones (Table I). A similar trend at Phipps was not statistically significant. In Study II, wrenching reduced shoot weights, but differences among seed sources were not significant (Table II).

Taproots tended to be lighter and lateral roots heavier among wrenched than among unwrenched seedlings at both nurseries in Study I, but the differences were not significant (Table I). In Study II, weight of the taproot was less for wrenched than for unwrenched seedlings, but lateral root weight was the same for both (Table II). Among seed sources, lateral and taproot weights were highest for coastal and high Cascades seedlings.

Total dry weight of seedling roots was not significantly affected by wrenching at either nursery in Study I or in Study II (Tables I and II). There were differences among seed sources, however: coastal and high Cascades seedlings had heavier root systems than did the other sources.

Total length of lateral roots did not differ among treatments in Studies I or II (Tables I and II). In Study II, coastal and high Cascades seedlings had longer lateral roots than did those from the other two sources.

Number of root tips per seedling was increased by multiple wrenching at Webster nursery, but there was no difference among treatments at Phipps nursery or in Study II (Tables I and II). Nor was there a significant difference among seed sources.

Shoot-root ratio was lower for wrenched than for unwrenched seedlings at both nurseries in Study I and in Study II (Tables I and II). At Webster, ratios were reduced from 3.00 to 2.46 and 2.13 for single- and multiple-wrenched; at Phipps, from 2.11 to 1.79 and 1.87. Among seed sources, ratios were lowest among seedlings from the high-elevation Cascades.

Field Measurements

Time of terminal budburst did not differ for wrenched and unwrenched seedlings at either nursery (Table I). At both nurseries, however, budburst for seedlings lifted in February was significantly (0.01) later than for those lifted in November. At Phipps, the average Julian day of budburst was 109 (April 19) for seedlings lifted in November and 120 (April 30) for those lifted in February. At Webster, the average Julian day was 117 (April 27) for seedlings lifted in November and 138 (May 18) for those lifted in February. For both lifting dates, cold storage resulted in a pronounced delay in budburst. At both nurseries, February storage resulted in a significantly (0.01) longer delay than November storage.

In Study II, budburst for wrenched seedlings was earlier (Julian day 122, April 2) than for unwrenched seedlings (Julian day 123) in the plowed area at Peavy Arboretum (Table II). Wrenching had no effect on budburst for seedlings in the grassy area or in the moist and dry soil boxes. In all plantings, budburst was earliest among seedlings from the valley source, intermediate among those from the two Cascades sources, and latest among those from the coastal source.

As already noted, shoot height was less for wrenched than for unwrenched seedlings at the time of planting. One year later, seedlings in dry soil boxes in Study I were shorter than those in moist boxes (Table I). However, in neither the dry nor the moist boxes was shoot growth of wrenched and unwrenched seedlings different. Lifting date had no consistent effect on shoot growth, but cold storage inhibited growth of seedlings from both nurseries, at both lifting dates, and in both dry and moist boxes.

In Study II, shoot growth was consistently greater for unwrenched than for wrenched seedlings of all seed sources. These differences were significant in both the plowed and grassy areas of Peavy Arboretum and in the dry soil boxes (Table II). In the moist soil boxes, unwrenched seedlings were not taller than their wrenched counterparts.

Field survival after one growing season was not different for wrenched and unwrenched seedlings in Study I (Table I). In the dry soil boxes, survival ranged from 64 to 73 percent for Webster seedlings and from 82 to 89 percent for Phipps seedlings. Cold storage did not significantly affect survival except for a decrease from 95 to 78 percent among Phipps seedlings in the dry soil boxes (0.01). Although not significant, the trend was the same for Webster seedlings. Lifting date did not affect survival at either nursery except for a slight decrease from 100 percent (February lifting) to 98 percent (November lifting) at Phipps in the moist soil boxes (0.05).

In Study II as in Study I, there were no differences in survival between wrenched and unwrenched seedlings. In the field, survival of seedlings from the various sources ranged from 1 to 4 percent in the grassy (dry) area and from 93 to 97 percent in the plowed (moist) area (Table II). In the dry soil boxes, survival ranged from 35 to 66 percent among seed sources, and wrenching did not affect survival of any source. In these soil boxes, survival of seedlings from the coastal source was lowest (35 percent), that of seedlings from the valley source was intermediate (43 percent), and that of seedlings from the two Cascades sources was highest (46 and 66 percent). Seedling survival in moist soil boxes ranged from 96 to 100 percent, with no differences among seed sources or wrenching treatments.

DISCUSSION

Morphology

At lifting, shoots of wrenched Douglas-fir seedlings were shorter, lighter, and smaller in diameter than those of unwrenched seedlings, and shoot height decreased as frequency of wrenching increased. Such a decrease in shoot height has also been reported for Monterey pine and has been used to measure severity and effectiveness of wrenching (Benson and Shepherd 1977; van Dorsser and Rook 1972).

Wrenching did not change the total length or dry weight of lateral roots, the total number of root tips, or the total dry weight of the root system, but it did reduce shoot-root ratios in both Studies I and II. The latter result is probably attributable to the lighter shoots of the wrenched seedlings. In Monterey pine, the lower shoot-root ratio for wrenched seedlings is also usually due to a lighter shoot (Benson and Shepherd 1977, van Dorsser and Rook 1972). Monterey pine also undergoes morphological changes in its root system as a result of wrenching. Its well-developed, carrot-like taproot is severed, resulting in a bushy, finer root system. Perhaps the fact that Douglas-fir lacks a dominant taproot but has a naturally bushy root system limits its response to wrenching.

The morphological responses observed here differed from those of a previous study by Tanaka and others (1976) in which wrenching of Douglas-fir seedlings changed the shoot-root ratio from 3.5 to 2.8. Unlike our study, this decrease in shoot-root ratio was attributable to an increase in root dry weight, while shoot dry weights were unchanged. Two factors may account for this disparity in results. First, in the previous study, the shoot-root ratio of unwrenched seedlings (3.5) was much larger than in ours (3.0 at Webster, 2.11 at Phipps, and 1.24 in Study II). Our seedlings were much smaller. Perhaps this difference in seedling size affects the response to wrenching. Second, seedlings in the previous study were wrenched later in the summer (July through October) than ours were (June and July). Seedling height in that study was not affected by late-summer wrenching because most shoot growth was completed by then. In our study, on the other hand, wrenching, especially multiple wrenching, drastically reduced height growth in the nursery. Perhaps with Douglas-fir it is necessary to wrench in late summer or early fall to promote root growth.

Growth

In no case did root wrenching have a beneficial effect on growth in the field. In Study I, shoot growth of wrenched and unwrenched seedlings was not significantly different after the first growing season, and both sets of seedlings were equally inhibited by drought. In Study II, shoot growth of wrenched seedlings from all four seed sources was less than that of unwrenched seedlings, both in the dry soil boxes and in the grassy and plowed areas at Peavy Arboretum. On these planting sites, root wrenching the previous year actually inhibited seedling growth. In the moist soil boxes, shoot growth of wrenched and unwrenched seedlings was not different in either year.

Why was the growth of wrenched seedlings reduced in Study II? The studies reported in Chapter 2 indicate that after wrenching seedlings reach high levels of water stress. Perhaps the repeated stressing of seedlings through multiple wrenchings caused the reduced growth the following year. Water-stressed seedlings have reduced levels of available photosynthate. This reduction could, in turn, reduce the carbohydrate reserves needed for growth (Levitt 1972). Benson and Shepherd (1977) also found that the N and P in shoot tissues of Monterey pine decrease as wrenching severity increases. A deficiency in these nutrients could affect growth. Moisture stress caused by wrenching may also have limited the number of initials or groups of meristematic cells laid down, thus affecting growth the following year. Two recent reports indicate that red pine (*Pinus resinosa* Ait.) and black spruce [*Picea mariana* (Mill.) B.S.P.]

subjected to moisture stress during the growing season form reduced numbers of needle primordia (Garrett and Zahner 1973, Pollard and Logan 1977).

Survival

Wrenching did not improve survival of Douglas-fir seedlings under either favorable or unfavorable field-planting conditions. In contrast, Tanaka and others (1976) reported that wrenched Douglas-fir seedlings on a droughty south-facing slope in Washington survived better than unwrenched ones (88 versus 65 percent), but that on a nearby north slope, there were no survival differences (58 versus 57 percent). Similarly, Koon and O'Dell (1977) reported that wrenching Douglas-fir seedlings at a depth of 20 cm and then planting them on a droughty site in California improved survival from 31 to 56 percent, but that wrenching at 15 cm did not improve survival.

Perhaps the varying responses between our and Koon and O'Dell's study can be attributed to seedbed density. The seedbed density in their study was 5.8 seedlings/ft^2 ($62/m^2$), considerably lower than our densities of 35 and 65 seedlings/ft^2 (377 and $700/m^2$) in Study I and 24 seedlings/ft^2 ($258/m^2$) in Study II. Van Dorsser and Rook (1972) report that at lower seedbed densities, seedlings respond better to wrenching, becoming heavier and stockier and producing more lateral roots. Wrenched seedlings in Koon and O'Dell's study, however, had increased shoot weight but no change in root dry weight. And it should be pointed out that Tanaka and others (1976) obtained superior survival after wrenching with a seedbed density as high as 35 seedlings/ft^2.

Another explanation for these survival differences is that in our study, at Phipps, water stress levels were increased over the summer to harden seedlings, whereas in Tanaka's study, seedlings were watered unrestrictedly throughout the summer (Tanaka, personal communication, 1978). At both the Webster nursery (in our study) and the Humboldt nursery (in Koon and O'Dell's study) there was also continuous watering of seedlings. Several papers report that moisture stress during the growing season promotes early budset in Douglas-fir (Lavender and Cleary, 1974; Griffin and Ching 1977; Emmingham 1978; Blake and others 1979). Seedlings grown at nurseries without restricted watering have later budset in the summer. This, in turn, results in later budburst in the spring; seedlings that demonstrate this delayed budburst have lower field survival potential (Lavender and Cleary 1974). Also, seedlings in the nursery which are still growing in the late summer due to continuous watering are often not adequately hardened or dormant for lifting and field planting. These seedlings have not been allowed to complete their dormancy phases before lifting and their physiology is, therefore, out-of-phase with their environment throughout the winter. After field planting, these seedlings have been shown to have decreased root growth the following spring, in turn, causing lower field survival (Lavender and Cleary 1974).

Because seedlings in Tanaka's and Koon and O'Dell's studies did have continuous watering, wrenching caused earlier budset, inducing hardening, and ultimately improving field survival. Our Phipps seedlings with restricted watering already had earlier budset and dormancy and so were not affected by wrenching. Webster seedlings had lower survival than Phipps seedlings perhaps due to their differences in watering. However, Webster seedlings grown at such high densities (as mentioned above) could not respond morphologically to wrenching and so their survival was not improved. Perhaps, when restricted watering induces adequate hardening of seedlings, wrenching is not necessary to further change seedling physiology. If there is no restricted watering regime at the nursery (or if the nursery is in a more moist geographical area) and seedlings are still growing in late summer, wrenching might be effective in hardening them to improve field survival and growth.

CONCLUSIONS

Based on the results of this study, we are skeptical about the benefits of wrenching Douglas-fir seedlings. It appears that in many situations careful control of water stress may be just as useful in arresting growth and hardening seedlings for lifting. Perhaps in an especially wet summer or moist nursery, wrenching could be used for this purpose. Because of Douglas-fir's varied response to wrenching, the effects of frequency, timing, and depth on the success of this practice should be investigated further, as well as its interactions with seedbed density and such cultural treatments as fertilization and irrigation.

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CHAPTER 2. WATER RELATIONS OF ROOT-WRENCHED DOUGLAS-FIR SEEDLINGS

INTRODUCTION

Water stress often occurs in newly planted Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings subjected to the hot dry summers of the Pacific Northwest. The result is low seedling survival on many clear-cuts. One suggested solution is to precondition nursery stock by root wrenching so that seedlings can better withstand droughty field conditions.

In New Zealand, root wrenching has improved survival of Monterey pine (Pinus radiata D. Don) on both droughty and moist sites. Root systems are wrenched by drawing a large, angled blade approximately 10 cm deep under the nursery bed. The result is reduced seedling shoot growth and a more compact fibrous root system that is better able to meet the water demands of the shoot (Rook 1969, 1971, van Dorsser and Rook 1972). In the few studies with Douglas-fir, wrenching has improved subsequent seedling survival (Koon and O'Dell 1977, Tanaka and others 1976).

The purpose of this study was to investigate possible physiological mechanisms that might enable wrenched Douglas-fir seedlings to withstand drought. We hypothesized that wrenched seedlings, having more highly developed root systems and smaller shoots, could maintain a more favorable internal water balance than unwrenched seedlings. To investigate this, we measured wrenched and unwrenched seedlings under different conditions for leaf conductance of water vapor, plant water potential, relative water content, and phenological response.

MATERIALS AND METHODS

The study was divided into two parts: (1) measurement of seedling transpiration in the nursery bed, after field planting, and under simulated water stress; (2) measurement of seedling response to drought after planting in pots. Both parts of the study compared unwrenched seedlings with those that had been root-wrenched in the nursery.

Two groups of seeds were sown in a randomized block design, four blocks in four adjacent seedbeds in 1976 and four blocks in two adjacent seedbeds in 1977. The 1976 seedlings were grown at the Lt. Mike Webster State Forest Nursery near Olympia, Washington, and the D.L. Phipps State Forest Nursery near Elkton, Oregon. The local seed source was used at each nursery. During their second year of growth, seedlings received one of three treatments: no root wrenching (control), a single wrenching on July 15, or bi-weekly wrenching from June 15 through August 1. The 1977 seedlings were from four seed sources grown at the Phipps nursery: No. 053, coastal, 0-500 ft (0-152 m); No. 252, Willamette Valley, 500-1,000 ft (152-305 m); No. 491, Cascade Mountains, 3,000-3,500 ft (914-1,067 m); and No. 501, Cascade Mountains, 4,000-4,500 ft (1,219-1,372 m). These received one of two treatments: no root wrenching (control) and bi-weekly wrenching during the growing season from June 15 through August 1.

Seedlings were lifted as 2-0 planting stock, and are designated here by their winter lifting dates as the 1978 group and the 1979 group. The 1978 seedlings were lifted on November 1 and February 1, one half from each block stored at 3°C for two months, and the other half planted immediately. The 1979 seedlings were lifted in late January and planted immediately in pots. A detailed description of nursery and planting methods is given in Chapter 1.

Transpiration Study

Leaf conductance (k_ℓ) and plant water potential (Ψ_t) of both groups of seedlings were first measured 4 or 5 days after wrenching in the nursery. After the 1978 field planting, we measured transpiration of seedlings exposed to different levels of osmotic stress and, after the 1979 planting, we measured k_ℓ and Ψ_t in the field.

Leaf conductance was measured on the terminal branch of each seedling with a null-balance diffusion porometer (Beardsell and others 1972). The branch is enclosed in the porometer cuvette where dry air is introduced to balance the transpired water. After balancing at a specific humidity, the flow rate of the air is proportional to the k_ℓ of the enclosed branch. Leaf conductance measurements were taken at 2-hour intervals during the day, beginning when there was light and dew had evaporated and ending at dusk.

Plant water potential was measured before dawn (0500 Pacific Standard Time) with a pressure chamber (Scholander and others 1965, Waring and Cleary 1967). The 1978 seedlings were measured for

Ψ_t again at midday, and the 1979 seedlings were measured at 2-hour intervals during the day.

On the sampling days, air temperature and dewpoint temperature were recorded continuously on a chart as measured with a thermistor and heated lithium chloride sensor located in a vented box 1 m above the ground. Vapor pressure deficit in millibars was calculated from these two measurements.

On each sampling day, leaf conductance was measured repeatedly on 24 of the 1978 seedlings (3 treatments x 4 blocks x 2 seedlings per treatment) and on 32 of the 1979 seedlings (2 treatments x 4 seed sources x 4 blocks). For each sampling day, an analysis of variance was done for each 2-hour measurement period and over all 5 measurement periods with time as a split plot.

To study the effect of osmotic potential of the rooting medium, we measured transpiration of 1978 seedlings while exposing their roots to different osmotic solutions. Seedlings were moved from pots to distilled water for 2 hours, then individually placed in a tightly sealed 1-liter glass jar containing 800 ml of aerated distilled water or one of two concentrations of Polyethylene Glycol 1000 (PEG) for 0 bar, -2.5 bars, and -5 bars osmotic potential. The concentrations of PEG for -2.5 and -5.0 bars osmotic potential were 6 g and 12 g per 100 ml of solvent (Lawlor 1970). Jars were covered with aluminum foil to shield roots from light and placed in a growth chamber with constant light (incandescent and fluorescent), temperature (21°C), and humidity (vapor pressure deficit 5 mb). Transpiration was measured over a 6-hour period by weight loss in grams.

This procedure was repeated in four runs, each time with seedlings of a different combination of nursery and lifting date. The total number of seedlings per run was 4 (blocks) x 2 (treatments) x 3 (osmotic potentials) x 2 (seedlings) = 48. Analysis of variance was done for total water loss (grams) and water loss per cm^2 needle surface and for the 6-hour time period with time as a split plot.

When seedlings were harvested at the end of the experiment, leaf surface area was determined with a LiCor portable surface area meter (Lambda Instrument Corp.).

Drought Study

At the time of lifting from the nursery, seedlings were planted in pots. The 1978 group was planted in 11-liter pots, but because the drought proceeded too quickly, 21-liter pots were used for the 1979 seedlings. The pots were placed outdoors at the Forest Research Laboratory, Corvallis, Oregon, and covered with sawdust to moderate the soil temperature. The 1978 seedlings were planted nine to a pot, three seedlings from each of the three treatments, and the 1979 seedlings eight to a pot, one wrenched and one unwrenched seedling from each of the four seed sources.

Pots were well watered and then allowed to dry. Droughting began June 27 for 1978 seedlings and July 12 for 1979 seedlings. Each week, beginning at week 0 when the pots were well watered, measurements were made of terminal bud condition (set or flushed), number of flushes to date, and condition of seedlings. Condition was rated in six categories by estimating the number of dead needles on each seedling:

category 1, 0 to 5%; 2, 5 to 20%; 3, 20 to 40%; 4, 40 to 60%; 5, 60 to 80%; and 6, 80 to 100%.

Plant water potential and leaf relative water content (RWC) of each seedling were measured weekly before dawn. Approximately 10 cm of the terminal were used to measure Ψ_t. Values below -70 bars (x 10^5 Pascals) were not recorded, being beyond the limit of the pressure chamber. To measure RWC, 30 to 50 needles were removed from the current growth on lateral branches. The needles were quickly weighed to determine fresh weight (F), placed between wet paper towels in plastic boxes, and stored in the dark at 3°C for 36-48 hours. All excess water was then blotted and the needles were reweighed to determine saturated weight (S). Dry weight (D) was obtained by drying at 70°C for 48 hours. Relative water content was calculated as in Slayter (1967): RWC = (F - D)/(S - D) x 100. After these weekly measurements, seedlings were lifted from pots and the number of white (active) root tips over 5 mm was counted.

An analysis of variance using means for each treatment within a pot was done for each week. In the 1978 group, seedlings of each nursery, lifting date, and cold-storage treatment were analyzed separately, since these were in separate pots. Thus, the total number of 1978 seedlings measured was 2 (nurseries) x 3 (wrenching treatments) x 4 (blocks) x 1 (pot per block) x 2 (lifting dates) x 2 (storage treatments) x 3 (seedlings per treatment per pot) = 288. RWC and Ψ_t were also measured on a subsample of unwrenched and multiple-wrenched seedlings, 2 seedlings per treatment per pot (128 seedlings total). The number of 1979 seedlings measured weekly was 4 (seed sources) x 2 (wrenching treatments) x 4 (blocks) x 2 (pots per block) x 1 (seedling per treatment per pot) = 64.

An analysis of variance with time as a split plot was also done over the three measurement dates of 1978 seedlings and the five measurement dates of 1979 seedlings.

RESULTS

Transpiration Study

Wrenching reduced leaf conductance (k_ℓ) and Ψ_t of seedlings in nursery beds at both nurseries (P = 0.01) and among all four seed sources (P = 0.01) (Fig. 1). Maximum k_ℓ occurred in the morning when seedlings had the highest Ψ_t and vapor pressure deficit was near a minimum. Open stomata in the morning permit high transpiration rates as evaporative demand increases; sustained high evaporative demand, however, causes stomata to partially close by midday (Waring and Franklin 1979). By afternoon, leaf conductance leveled off. This diurnal pattern in our study agrees with other measurements of Douglas-fir (Hallgren 1978,[1] Running 1976). In all cases, wrenched (single or multiple) seedlings in the nursery were under more stress and had greater stomatal closure than unwrenched seedlings.

Among seed sources in the nursery, Ψ_t was in the following order: high-elevation Cascades (-11 bars) > coast (-12) > low-elevation Cascades (-13) > the Willamette Valley (-14) (95% LSD = 0.5). While

[1]Hallgren, S. W. 1978. Plant-water relations in Douglas-fir seedlings and screening selected families for drought resistance. M.S. thesis. Oregon State University, Corvallis.

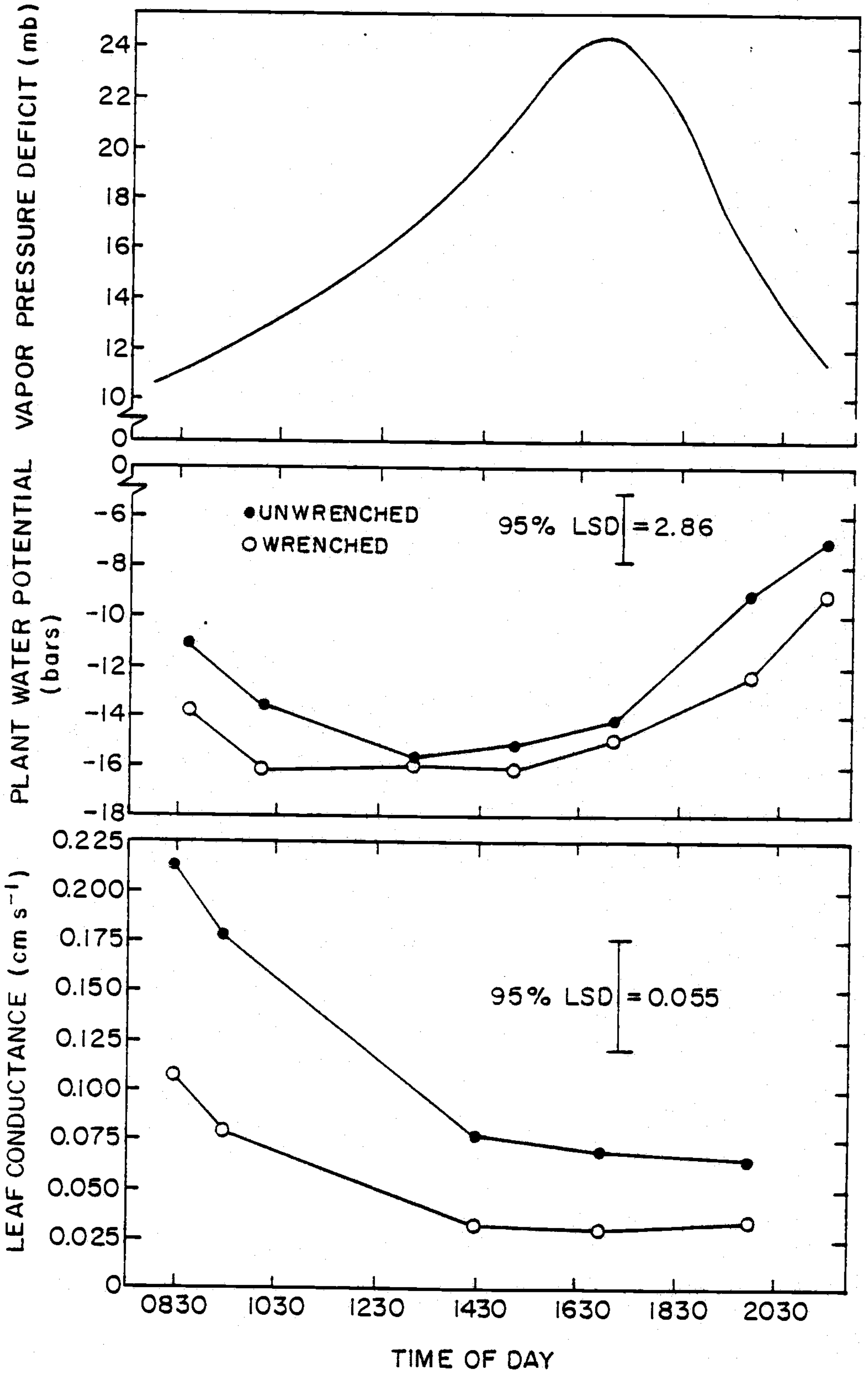

Figure 1. Diurnal measurement of vapor-pressure deficit, plant water potential, and leaf conductance of wrenched and unwrenched seedlings, July 8, 1978. Four seed sources are combined.

the coast, Willamette Valley, and low-elevation Cascade sources averaged diurnal leaf conductances of 0.087, 0.066, and 0.087 cm sec^{-1}, the high-Cascade source averaged 0.114 cm sec^{-1} throughout the day (95% LSD = 0.008). In other words, the high elevation Cascade source had the lowest moisture stress and the most open stomata.

In the PEG tests of 1978 potted seedlings, the two osmotic solutions effectively reduced transpiration of seedlings in all four runs (P = 0.01). For example, the water loss by Webster nursery seedlings lifted in November was 4.9 g for the 0-bar solution, 3.2 g for the 2.5-bar solution, and 3.1 g for the 5-bar solution (95% LSD = 0.9). Wrenched and unwrenched seedlings, however, did not differ in water loss with any of the osmotic solutions. When transpiration was calculated per cm^2 of needle surface, results varied. All seedlings lifted in November were similar, but wrenched seedlings lifted in February from Webster nursery transpired less per cm^2 than unwrenched seedlings (0.79×10^{-2} versus 0.99×10^{-2} g cm^{-2}) (P = 0.05), and the opposite occurred for seedlings from Phipps nursery.

Field-planted seedlings averaged -23 to -25 bars and some as low as -29 bars when measured in mid-August. Leaf conductance was much lower than in the nursery, emphasizing that these seedlings were undergoing the Pacific Northwest summer drought, but no differences appeared among wrenched and unwrenched seedlings in either Ψ_t or k_ℓ. Seed sources did not differ in Ψ_t in mid-August, but the high-elevation Cascade source that had the highest k_ℓ in the nursery had closed stomata and the lowest average k_ℓ (0.037) in the field along with the coast and valley sources (0.041 and 0.039). The other Cascade source had the highest k_{ℓ} (0.057) (95% LSD = 0.013).

Drought Study

At the beginning of the 1978 drought on June 27, from 86 to 100 percent of the seedlings had buds. During drought, buds did not reflush, so by the last week of the study no differences appeared among treatments. As we have mentioned, because small pots were used, the drought progressed too quickly, perhaps limiting results.

In 1979, during week 2, wrenched seedlings reflushed, and 50 percent (versus 78 percent of unwrenched seedlings) had buds (Fig. 2). The wrenching x week interaction was highly significant, indicating a change of rank of wrenched and unwrenched seedlings between the first two weeks and week 3. In the last two weeks of drought, all seedlings began to set buds; at drought end, all seedlings had set a terminal bud.

Budset among seed sources also varied during drought (Fig. 3). The seed source x week interaction was highly significant. In week 1, coast and valley sources had the lowest budset, 56 percent and 44 percent; Cascade sources had 81 percent and 100 percent budset (95% LSD = 25). In week 2, more coast and valley seedlings had reflushed, but by week 3 there was no difference among seed sources, and in week 4, at the end of the drought, all seedlings had set a terminal bud.

The average number of flushes throughout drought in 1979 was higher for wrenched (1.48) than unwrenched (1.30) seedlings (P = 0.01). The flush x week interaction was not significant, indicating

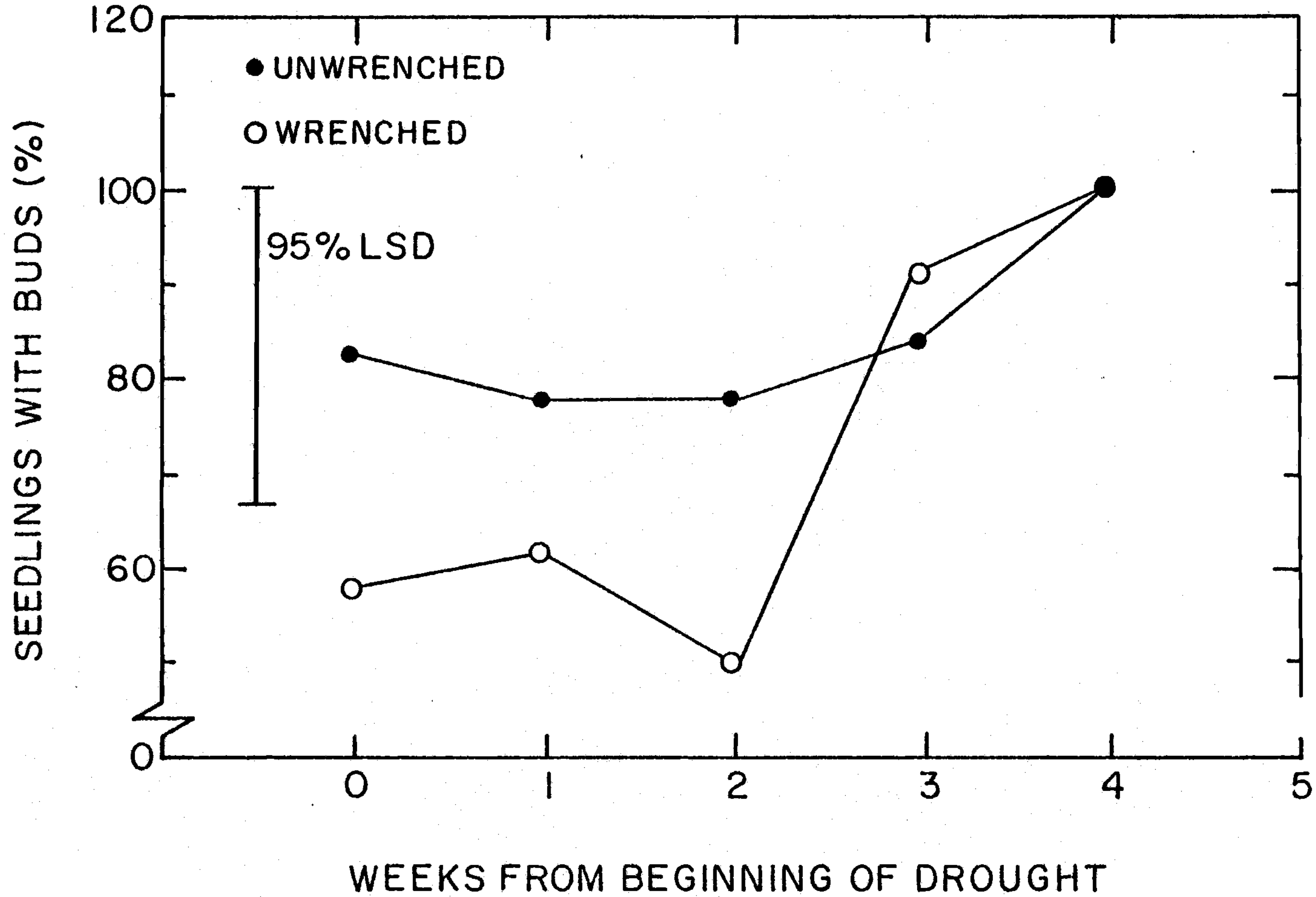

Figure 2. Budset of wrenched and unwrenched seedlings exposed to drought. Four seed sources are combined. Wrenching x week interaction was highly significant.

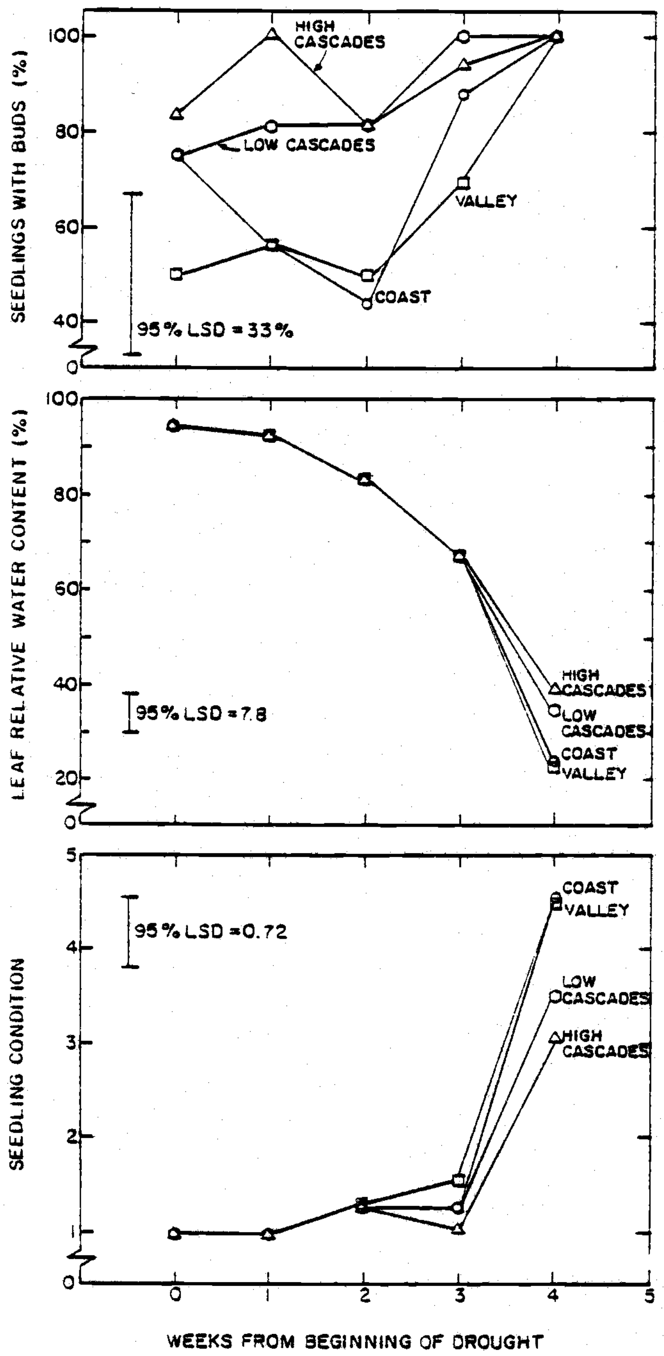

Figure 3. Budset, relative water content, and condition of seedlings from four seed sources during drought. Seed source x week interaction was highly significant.

a consistent relationship. The valley source had the most flushes per seedling (1.65); the valley and low-elevation Cascade sources had middle values (1.44 and 1.35) and the high-elevation Cascade sources had the lowest (1.12) (95% LSD = 0.15).

The number of active roots during drought did not vary among wrenching treatments of 1978 seedlings at either nursery except during week 1. At that count, unwrenched seedlings lifted in November had 34 active roots, single and multiple-wrenched seedlings 17 and 15 (95% LSD = 7). The 1979 wrenched seedlings had consistently fewer active roots (21 versus 25 for unwrenched seedlings) ($P = 0.05$). Wrenching x week interaction was not significant, indicating the relationship was consistent from the beginning of drought through week 4. Among seed sources, the number of active roots did not vary.

Plant water potential was similar among wrenched and unwrenched seedlings throughout drought in both years. Seed sources were also similar in Ψ_t.

Although RWC decreased during the drought (in 1979 from 95 percent in week 0 to 30 percent in week 4), it did not vary for wrenched and unwrenched seedlings. However, it did vary for seed sources, the seed source x week interaction being highly significant (Fig. 3). At the first four measurements, no differences in RWC appeared. In the final week, however, RWC of coast and valley sources decreased to 24 and 23 percent, and low- and high-elevation Cascade sources decreased to 35 and 39 percent (95% LSD = 9).

The condition of 1978 seedlings throughout the drought did not vary with wrenching for either nursery except in one case. Unwrenched

Phipps seedlings lifted in February and planted immediately averaged 10 percent dead needles versus 6 percent for single and multiple-wrenched seedlings. The condition of wrenched and unwrenched 1979 seedlings did not vary--both rating 4.0 at the end of drought, indicating an average of 40 to 60 percent dead needles on all trees.

Seed sources did vary in condition. The seed source x week interaction was highly significant, indicating rank change during drought. No differences appeared in the first two weeks (Fig. 3), but by week 3 there was a slight difference among sources, and by week 4, coast and valley sources each averaged 4.6 while low- and high-elevation Cascade sources averaged 3.6 and 3.1 (95% LSD = 1.1).

DISCUSSION

Seed Sources

Although the high-elevation Cascade source had significantly higher k_ℓ and Ψ_t on the two days of measurement in the nursery, the rank changed on the one day of field measurement. With data from only three days, it is not possible to make conclusion about seed source differences in k_ℓ or Ψ_t in the nursery or field.

In the drought study, however, differences among seed sources were apparent. In the first two weeks of the drought, coastal and valley seedlings reflushed; Cascade sources remained with set buds. At the end of the drought, Cascade sources had fewer flushes per seedling. Similarly, under moderate moisture stress, inner-range California Douglas-fir set final buds earlier than coastal seedlings

(Griffin and Ching 1977). Also, in a drought study of intraspecific genetic variation of southwest Oregon Douglas-fir, seedlings from high-elevation sources set more terminal buds during drought than those from low-elevation sources.[2]

Plant water potential did not differ among seed sources, but RWC did. Coast and valley sources had lower RWC at the end of drought than did Cascade sources. RWC is a measure of dehydration avoidance (Levitt 1972). The ability of Cascade sources to maintain a higher RWC than coast and valley sources while Ψ_t is the same may indicate an ability to adjust osmotically and therefore to maintain more turgor within leaf tissues (Hsaio and others 1976).

The result in our study was that seedlings from coast and valley sources were in poorer condition at the end of the drought than those from Cascade sources. The one field site showing differences among seed sources also showed that Cascade sources had better survival (46 and 66 percent) than coast and valley sources (35 and 43 percent) (see Chapter 1). With no reflushing during drought and the ability to maintain higher RWC, Cascade sources were better able to withstand drought. In southwestern Oregon also, Douglas-fir seedlings from high-elevation families survived drought better than low-elevation seedlings (see footnote 2). Possible reasons for the higher drought resistance may be that Cascade sources have adapted to shorter frost-free periods and greater annual temperature ranges (Griffin and Ching 1977), causing them to have a shorter period of active growth

[2]White, T. L. 1980. Genecology of Douglas-fir from southwestern Oregon. Ph.D. thesis. Oregon State University, Corvallis.

and, therefore, to be more dormant during drought. Also, seedlings from interior ranges, especially in California and southwestern Oregon, have a capacity for a plastic response to moisture stress--seen in this study when Cascade seedlings maintained a favorable turgor with increasing water stress. This capacity has not evolved in coastal populations where summer moisture stress is less severe (Griffin and Ching 1977).

Wrenching

Wrenching shocked the seedlings in the nursery bed, causing lower plant water potential and transpiration rates. After field planting, however, wrenched and unwrenched seedlings transpired at equal rates. Wrenched and unwrenched seedlings showed no difference in transpiration under PEG-induced stress; nor did k_ℓ and Ψ_t of trees planted in the field differ. Rook (1969) has found that, after planting in hot dry conditions, wrenched Monterey pine seedlings have significantly higher transpiration rates than unwrenched seedlings. This he attributes to the higher root-shoot ratio of the wrenched pine seedling and the ability of its more fibrous root system to meet water demands of the shoot. However, wrenched seedlings of Douglas-fir showed no improved ability to avoid water stress in our study. This is in agreement with results of our earlier paper which also found no beneficial effect of wrenching on field survival (see Chapter 1).

In 1978, wrenched and unwrenched seedlings from both nurseries responded the same to droughting in pots. Budset, seedling condition, Ψ_t, RWC, and the number of active roots were consistently the same throughout drought. This again agrees with our earlier study of field growth and survival of wrenched and unwrenched seedlings, which performed the same on dry and moist sites.

In 1979, wrenched and unwrenched seedling condition also did not vary throughout drought. However, wrenched seedlings reflushed in the middle of the drought—an unfavorable response. Drought-resistant seedlings have been shown to set bud earlier and to have fewer flushes when exposed to drought (see footnote 2). That the wrenched seedlings averaged more flushes per seedling during drought than unwrenched seedlings indicates that they were not as dormant.

The ability to grow roots into new areas of soil has also been shown to be important for a drought-resistant plant (Levitt 1972). Unwrenched 1979 seedlings had more active roots than wrenched seedlings. The lessened ability to regenerate roots and to maintain set buds during drought may contribute to lower survival in the field.

We conclude from these and results in Chapter 1 that wrenching of Douglas-fir seedlings does not improve survival in the field and, in some cases, may hinder growth. We therefore do not recommend root wrenching of Douglas-fir in the Pacific Northwest.

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