Geographic variation in winter drought resistance of Douglas-fir (Pseudotsuga menziesii Mirb. Franco)[1]

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Summary

The winter drought resistance of 40 Douglas-fir provenances from the IUFRO collection in 1967—1969 was investigated. The two-year old seedlings were tested in a climate (growth) chamber under the following conditions.

Soil temperature:	-5^0 C
Air temperature:	$+12^0$ C
Relative humidity:	40%
Light intensity:	30000 lux
Photoperiod:	10 hours

A method was developed, which allows the independent testing of the drought avoidance and the drought tolerance. The avoidance component against winter desiccation was measured in the rate of increase (negative) in water potential (bar) per day ($\frac{\triangle WP}{dt}$). The tolerance was computed as the water potential (bar) where 50% plant mortality occurs (WP50).

The tested provenances can be divided into three groups:

1. Provenances from the coastal regions and the Cascades of British Columbia, Washington and Oregon had very low drought avoidance and also a very low drought tolerance.
2. Provenances from the interior of British Columbia and Idaho had good drought avoidance and a good drought tolerance.
3. Provenances from Arizona, Colorado and New Mexico had very high drought avoidance as well as a very high drought tolerance.

Among the relatively drought sensitive provenances from the Cascades there was an increase in winter drought resistance with increasing elevation.

Key words: *Pseudotsuga menziesii*, drought resistance, provenance, genetic variation.

Zusammenfassung

Die Frosttrockenresistenz von 40 verschiedenen Douglasienherkünften aus der IUFRO-Ernte 1967—1969 wurden in der Klimakammer unter folgenden Austrocknungsbedingungen geprüft:

Bodentemperatur:	-5^0 C
Lufttemperatur:	$+12^0$ C
Relative Luftfeuchtigkeit:	40%
Lichtintensität:	30000 Lux
Photoperiode:	10 Stunden

Dabei wurde eine Methode entwickelt, die eine getrennte Prüfung von Austrocknungswiderstand und Austrocknungstoleranz ermöglichte. Der Austrocknungswiderstand wurde als Wasserpotentialanstieg pro Tag in bar ermittelt, die Austrocknungstoleranz konnte als Wasserpotential (in bar) bei 50%iger Abtötung des Pflanzenmaterials berechnet werden.

Die Herkünfte ließen sich in drei Gruppen aufteilen:

1) Herkünfte aus dem Küstengebiet und den Kaskaden von British Columbia, Washington und Oregon. Diese zeigten einen sehr geringen Austrocknungswiderstand und waren wenig austrocknungstolerant.
2) Herkünfte aus dem Inland von British Columbia und aus Idaho waren durch eine gute Austrocknungstoleranz und einen guten Austrocknungswiderstand gekennzeichnet.
3) Herkünfte aus Arizona, Colorado und New Mexiko, zeigten einen sehr hohen Austrocknungswiderstand und eine extrem gute Austrocknungstoleranz.

Innerhalb der sehr frosttrocknisempfindlichen Gruppe von Herkünften aus dem Kaskadenraum wurde eine Zunahme der Resistenz mit zunehmender Höhenlagen festgestellt.

Introduction

On sunny and windy winter days, when the soil is frozen due to low night temperatures in combination with no or little snow cover, trees can suffer drought damage. They are unable to take up and replace the water lost by transpiration. This phenomen is known in the literature as Frosttrocknis (frost-drought) (Larcher 1957, Michael 1966, Sakai 1970).

Resistance to drought damage according to Levitt (1972) may be divided into two components:

Drought avoidance --- avoiding desiccation by lowering water loss or increasing uptake.

Drought tolerance --- tolerating great water losses and surviving after severe desiccation.

Winter drought damage is in many years of decisive importance for the survival of young Douglas-fir (Schönhar 1965, Oeschger 1973). A number of field experiences seem to indicate, that there are differences in frost drought resistance between different provenances. By means of artificial simulation of frost drought a preliminary study of 10 seed lots demonstrate differences in drought avoidance: Coastal provenances from Washington and British Columbia were very sensitive to frost drought, whereas provenances from interior parts of British Columbia and from New Mexico and Colorado showed very high degrees of resistance (Larsen 1978a).

In the above mentioned study only drought avoidance was measured. In the present investigation drought tolerance was also considered, and the number of provenances investigated was increased to 40, covering the whole natural range of the species.

Material and Methods

The material tested consisted of plants from 40 different seed sources of Douglas-fir from the IUFRO-collection of 1967—69. The 40 seedlots cover all parts of the natural range with particular emphasis on the Cascade and coast regions of British Columbia (Canada) and Washington (USA). *Table 1* gives a survey of the provenances used including the geographical data.

The seed sources were sown in containers (volume content 250 cm³) in spring 1974 and grown outside for two growing periods (1974 and 1975). During this period the

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Table 1. — Location and response to winter drought stress of 40 Douglas-fir provenances.

Seed lot no. IUFRO no	State or province of origin	Lat. °N	Long. °W	Elev. m	Drought 1) avoidance Daily change in waterpotential (bars)	Drought 2) tolerance Level of water potential to cause 50% mortality (bars)	Drought 3) resistance Days of drought stress needed to cause 50% mortality
1109	Interior B.C.	53.1	119.8	820	- 9.1	- 83	8.0
1111	Interior B.C.	52.3	121.3	820	- 9.5	- 92	8.0
1112	Interior B.C.	51.1	121.5	1040	- 9.9	-100	8.3
1007	Interior B.C.	51.7	120.0	460	-10.2	-102	8.2
1018	Interior B.C.	50.7	119.2	470	-10.5	- 87	6.9
1020[x]	Interior B.C.	50.6	119.6	910	- 9.1	-102	9.7
1016	Interior B.C.	50.1	119.2	520	-11.1	- 85	6.5
1035	Interior B.C.	49.5	117.3	820	-11.5	- 88	6.5
1175	Idaho	47.3	116.5	700	- 9.5	-102	8.9
1024	Coastal B.C.	50.3	122.7	210	-15.0	- 76	4.7
1030	Coastal B.C.	49.8	123.2	15	-18.1	- 74	3.1
1034	Coastal B.C.	49.5	123.9	180	-17.1	- 70	3.4
1038	Coastal B.C.	49.1	121.7	910	-17.7	- 69	3.7
1036	Vancouver Isl. B.C.	49.3	124.3	140	-17.1	- 72	3.5
1041	Vancouver Isl. B.C.	48.9	124.4	210	-17.9	- 73	3.5
1045	Vancouver Isl. B.C.	48.4	123.7	45	-20.6	- 80	3.0
1046	Western Washington	48.7	121.1	430	-17.1	- 82	3.7
1049	Western Washington	48.6	121.4	500	-20.0	- 73	3.2
1050	Western Washington	48.6	121.4	120	-21.9	- 79	3.3
1051	Western Washington	48.5	122.3	60	-22.9	- 77	2.7
1056[x]	Western Washington	48.1	121.3	660	-17.8	- 81	3.6
1059	Western Washington	48.0	121.5	610	-17.7	- 74	3.3
1067	Western Washington	47.7	121.3	300	-18.1	- 77	3.1
1072	Western Washington	47.4	121.7	610	-22.5	- 75	3.0
1073	Western Washington	47.3	123.9	140	-15.2	- 69	3.4
1074	Western Washington	47.3	123.4	502	-20.1	- 69	2.9
1075	Western Washington	47.3	121.9	240	-20.9	- 70	3.0
1079	Western Washington	47.0	121.6	730	-16.2	- 74	3.5
1084	Western Washington	46.6	121.7	300	-19.9	- 73	3.2
1113	Western Oregon	44.8	122.7	170	-19.7	- 66	2.5
1114	Western Oregon	44.7	122.2	490	-16.6	- 67	3.2
1117	Western Oregon	44.5	122.0	1070	-17.0	- 77	3.7
1128	Northwest Calif.	41.8	124.0	120	-21.3	- 65	2.6
1141	Northwest Calif.	40.8	123.2	1310	-15.7	- 70	3.3
1145	Northwest Calif.	39.8	123.0	1550	-18.3	- 93	4.0
1162	Arizona	36.5	112.2	2410	- 8.2	- 89	9.1
1156	Colorado	39.0	104.0	2290	- 3.5	-107	23.3
1161	Colorado	37.2	106.9	2440	- 3.7	-101	20.5
1168	New Mexico	36.1	106.8	2870	- 5.8	-106	15.6
1169	New Mexico	32.9	105.5	2440	- 4.4	-108	20.5

1) $\frac{\Delta WP}{dt}$: a value close to zero corresponds a high drought avoidance.

2) WP50: a value close to zero corresponds a low drought tolerance.

3) DAY50: a high value corresponds a high drought resistance.

x) The results of these two provenances, one representing the coastal type (1056) and one representing the interior type (1020), are shown in fig. 1 and 2.

material was divided into 8 blocks (7 replications) and the provenances were randomly distributed within a block. Furthermore, the design was rearranged every month to prevent site variation within a block.

In periods of severe frost the plants were moved into a greenhouse kept at 5° C to prevent damage. At the time of investigation in February 1976 the plants were two years old, and they were hardened off under natural outside condition prior to the test. The frost drought test was carried out in a growth chamber using the equipment developed and described by LARSEN (1978a). For the test, 25 plants per provenance were maintained in the growth chamber under the following conditions: Soil temperature −5° C, air temperature 12° C, relative humidity 40%, a 10 hours photoperiod, and 30000 lux light intensity. By keeping the root medium frozen the uptake of water through the roots was completely interrupted and the desiccation process therefore could be established under defined and controlled condition. Since only 330 plants could be tested simultaneously, all 40 seed sources were randomly distributed and tested in time and space: At the beginning of the test 325 plants from 13 different provenances were placed in the test devise. During the following test period a new provenance was included as soon as space for 25 plants occurred. After having tested all 40 seed sources, four of the first provenances tested (no. 1008, 1050, 1132 and 1175) were tested once more with each 25 plants. By analysing the reaction of these four seed sources tested at the beginning an at the end of the testing period it was found, that the time of testing did not influence the test results.

The test was carried out over a period of four weeks in February. The desiccation process of the seed sources was analysed through measurements every 24 hours of the xylem-pressure-potential (water potential = water stress) of 3—6 plants of each provenance being tested by means of the pressure-chamber-method (WARING 1970) immediately prior to the beginning of the light phase (pre dawn). The pressure chamber technique determine the water stress of a plant by measuring the pressure required to force xylem water back to the cut surface of a severed twig. The vitality or extent of damage to each plant was tested as soon as the water potential had been determined by stopping the desiccation process by sprinkling the tops with water. Subsequently the plant's root area was slowly thawed to +2° while the relative humidity was 100%. The plants were moved from the test device and placed in a greenhouse under moist conditions at 15° C. The drought damage was evaluated when the buds burst the following spring. Damage to the individual plants was measured as bud damage of the uppermost 10 buds in intervals of 10% (0% = no damage to 100% = all 10 buds killed). The seedlings average from 24 to 43 cm, and they had all more than 10 buds.

In order to be able to determine drought tolerance, some plants from all seedlots should experience a water potential below −110 bars, which is considered to be lethal. Therefore the data from the first two mornings' test were used to estimate daily change in water potential; and the rate of change was then used to govern the frequency of sampling of each provenance (intervals of 1, 2, 3 and 5 days were used depending upon the desiccation rate of the provenance concerned). Each morning 40—60 determinations of water potential were made, which required from 60 to 90 minutes for two persons (one preparing the sample, the other measuring). A preliminary study failed to show significant changes in water potential within 90 minutes under darkness therefore this relative long testing period was not considered to affect the measurements. In order to eliminate possible effects of time of measurement, the plants furthermore were randomly selected and measured in time.

From the development of the water potential and the mortality rate, it was possible to determine the degree of *drought resistance* of plants from the individual provenances. *Figs. 1* and *2* show measured values and the principle of calculating the resistance of plants from two provenances.

Fig. 1 illustrates the relation between drought stress (in bar) and the corresponding vitality (mortality in %). This relation, has the shape of the Gauss cumulative curve. By transforming the linear percentage scale into a linear probit scale, the efficiency curve is transformed into a straight line. By means of a probit analysis (see WEBER 1972) it was

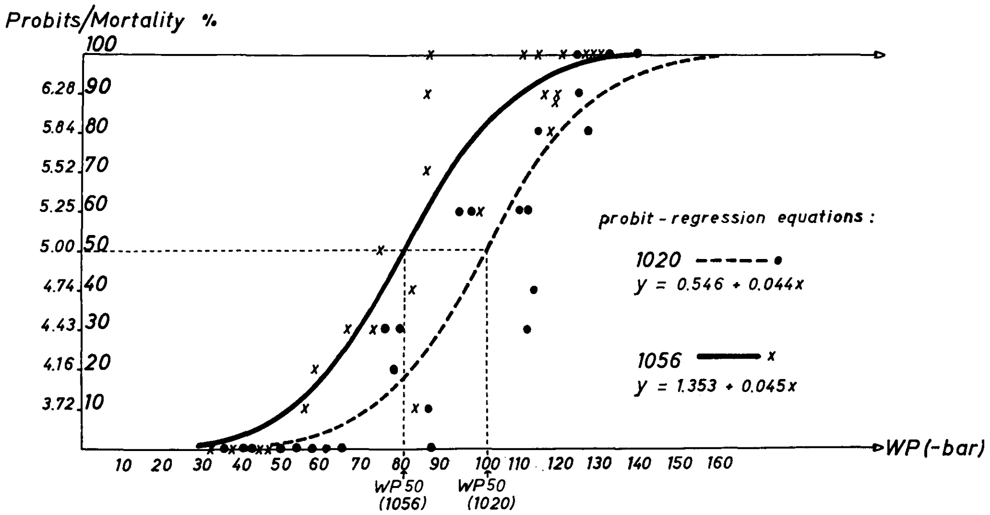

Fig. 1. — Relation between xylem-pressure-potential (WP) and bud mortality (in %) of the individual seedlings.

● apply to individual seedlings of the provenance no. 1020
x apply to individual seedlings of the provenance no. 1056

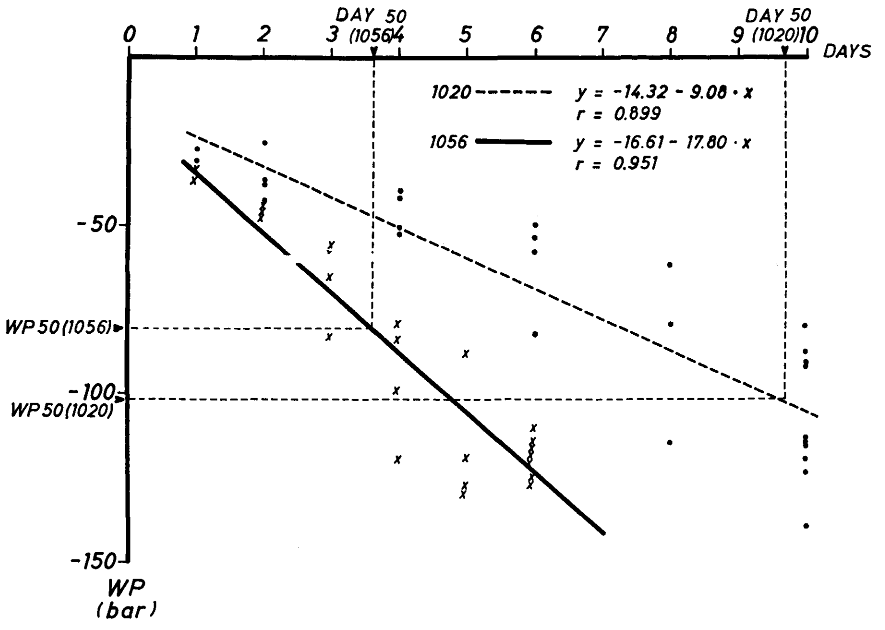

Fig. 2. — The development of the xylem-pressure-potential (WP) during the drought treatment (in days).
● apply to individual seedlings of the provenance no. 1020
x apply to individual seedlings of the provenance no. 1056

possible to compute the drought stress (water potential in bar) which statistically produces a mortality of 50% among plants from the provenance. This value (WP50) would then be an expression of the *drought tolerance.*

Fig. 2 shows the relation between the duration of the drought stress (in days) and the water potential of the plant (in bar). This relation is approximately linear (LARSEN 1978a). The slope (b) of the regression lines ($y = a + bx$) therefore represents a value for that part of the drought resistance which can be attributed to resistance against desiccation *(drought avoidance,* $\frac{\triangle WP}{dt}$).

By means of the two analyses (the probit analysis and the regression analysis), the duration in days of the drought treatment up to a mortality of 50% can be calculated. This value (DAY50) is therefore an expression of the total *drought resistance.*

In *Figs. 1* and *2* the drought resistance conditions of plants from two provenances are shown. Provenance No. 1056 represents a typical Cascade provenance from Washington, and No. 1020 is typical for the provenances from the inner parts of British Columbia. Provenance 1020 displays a higher drought avoidance (—9.08 bar/day) compared with 1056 (−17.80 bar/day), as well as a higher drought tolerance (−102) bar against −81 bar). The total drought resistance of provenance 1020 of 9.7 days is therefore far higher than that of provenance 1056 (3.6 days).

Results

Due to limited test capacity it was not possible to test the same number of seedlings by all provenances every day and to have a uniform interval between sampling dates. Since all the analyzed provenances were randomly distributed and tested both in time and within the growth chamber, possible errors due to the above mentioned sampling inequalities should be randomly distributed between seedlings within a provenance and therefore hardly affect the results on the provenance level.

Drought avoidance

In Table 1 the index of the drought avoidance for plants from 40 provenances is shown. This index ($\frac{\triangle WP}{dt}$) illustrates the daily reduction of the water potential(increase in water stress).

The highest drought avoidance values of the provenances tested were established for the plants originating in Colorado (Nos. 1156 and 1161), Arizona (No. 1162), and New Mexico (Nos. 1168 and 1169). It is common for these provenances, that they all come from the southern, interior parts of the Douglas-fir's area of distribution, and mainly from elevations between 2200 and 2900 m above sea level. Their drought avoidance value was between −3.5 and −8.2 bar/day. The provenances of the northern interior parts of the area of distribution from British Columbia (Nos. 1007, 1016, 1018, 1020, 1035, 1109, 1111, 1112) and from Idaho (No. 1175) displayed a lower, but still good drought avoidance with $\frac{\triangle WP}{dt}$ — values of −9.1 to −11.1 bar/day. In contrast, plants originating from the coastal areas of British Columbia (Nos. 1030, 1034, 1038) and Vancouver Island (1036, 1041, 1045), as well as from Western Washington (1046, 1049, 1050, 1051, 1056, 1059, 1067, 1072, 1073, 1074, 1075, 1079, 1084), Western Oregon (1113, 1114, 1117) and Northwest California (1128, 1141, 1145), with indices between — 16.2 and 22.9 bar/day, formed a group with poor drought avoidance qualities.

Within the group originating from the Cascades of British Columbia, Washington and Oregon, a change in drought avoidance in relation to altitude is obvious: The provenances from altitudes below approx. 300 m above sea level, for instance (Nos. 1050, 1051, 1075, 1084, 1113) exhibited very poor drought avoidance qualities (from −19.7 to −22.9 bar/day). But the provenances from above 300 m (Nos. 1038, 1046, 1049, 1056, 1059, 1079, 1114, 1117) with indices between −16.2 and −20.0 bar/day had a higher degree of resistance. Provenance No. 1072 from an altitude of 610 m −22.5 bar/day does not fit into this trend, however.

Drought tolerance

With regard to drought tolerance (see *Table 1)* almost the same geographical grouping of provenances occurred as for the drought avoidance. The plants originating from the southern, interior part of the area of distribution (Colorado, New Mexico) displayed the highest tolerance of all provenances (from −101 to −108 bar). With tolerance values between −85 and −102 bar the group of provenances from the interior parts of British Columbia was intermediary (provenance no. 1162, Arizona, however was also in this intermediate group), whereas provenances from the coast and Cascade regions of British Columbia, Washington, Oregon, and California were most sensitive to desiccation (drought tolerance for these provenances lay between −66 and −82 bar). In contrast to what applies to drought avoidance, no evidence could be found that the elevation had an influence on drought tolerance of seed sources from the Cascade region.

The total drought resistance

The total drought resistance (DAY50) of the 40 provenances can be seen in *Table 1.* The DAY50-value corresponds to the duration of the drought treatment (in days) until 50 per cent bud mortality has occurred among the plants of the tested provenance.

The analysed drought resistance, the combined effect of drought avoidance and drought tolerance, varied among the tested provenances from 2.5 to 23.3 days. The highest total resistance was found for plants coming from Colorado (1156, 1161) and New Mexico (1168, 1169), i.e. from 15.6 to 23.3 days. With 9.1 days the provenance from Arizona (1162) lay considerably lower, however. With resistance values from 6.5 to 9.7 days, provenances from the interior parts of British Columbia (1007, 1016, 1018, 1020, 1035, 1109, 1111, 1112) and from Idaho (1175) demonstrated intermediary qualities. With resistance values from 2.5 to 4.0 days on the average, the drought resistance of the group of provenances from the coast and Cascade regions of British Columbia (1030, 1036, 1038, 1041, 1045), Washington (1046, 1049, 1050, 1051, 1056, 1059, 1067, 1072, 1073, 1074, 1084), Oregon (1113, 1114, 1117), and California (1128, 1141, 1145) was very poor. Among the Cascade provenances of British Columbia, Washington and Oregon, which are especially important for North-west Europe, a distinct increase in the total resistance with increasing elevation could be observed. This relation is shown in *Fig. 3,* and with r = 0.732, it shows a highly significant correlation.

Relation between drought avoidance and drought tolerance

In accordance with the results of the investigation, the 40 provenances were divided into three groups with respect to drought resistant: 1) The southern inland provenances with very high drought tolerance and also high drought avoidance qualities, 2) the northern inland provenances that displayed intermediary tolerance and avoidance qualities, and 3) the coast and Cascade provenances whose drought avoidance and drought tolerance qualities were very poor. These results point to a close, positive correlation between drought avoidance and drought tolerance.

A correlation analysis comprising all the 40 provenances tested resulted in a highly significant correlation coefficient (r = 0.829). It is interesting to note, however, that within the individual groups there is no correlation between drought tolerance and drought avoidance.

Discussion

In an earlier investigation (Larsen 1978a) it was shown, that even under conditions of fairly moderate drought Douglas-fir reacts with rapidly rising water stress, as soon as the uptake of water through the roots is interrupted by frost in the soil. Big differences in drought avoidance between the different provenances were also demonstrated. Through a continued development of the test method it became possible not only to determine the drought avoidance, but also to calculate the drought tolerance and thereby the total drought resistance. The earlier results of the drought avoidance test demonstrate very close agreement with the results of the above mentioned investigations, inasmuch as the provenance material could be devided into the same three geographical groups.

In relation to this Saetersdal (1963) was able to prove that provenances of Douglas-fir from southern low-lying

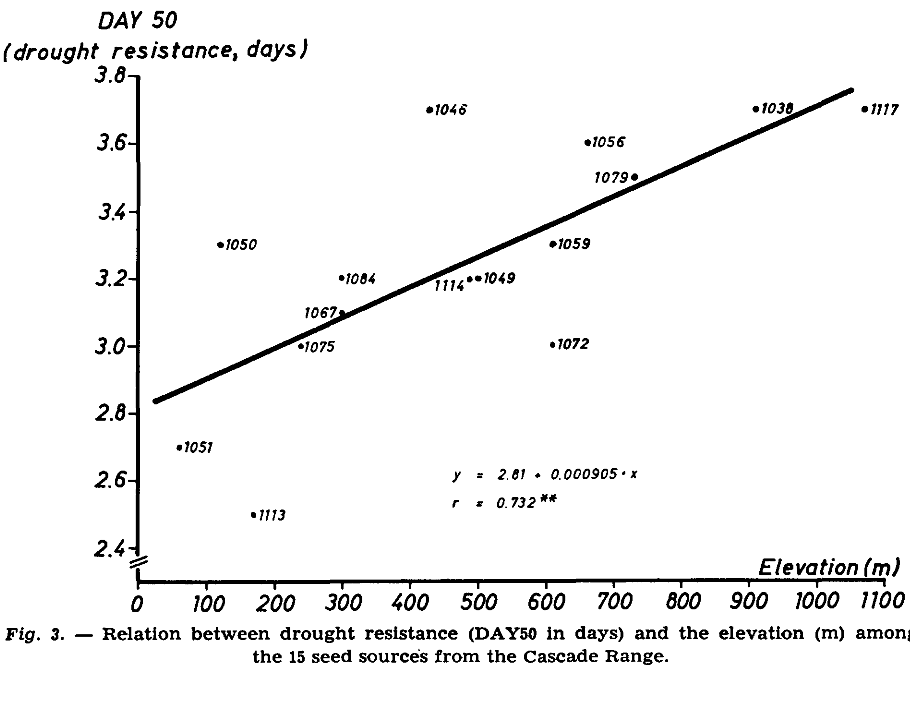

Fig. 3. — Relation between drought resistance (DAY50 in days) and the elevation (m) among the 15 seed sources from the Cascade Range.

altitudes showed higher cuticular desiccation rates than provenances from continental regions and higher elevations. Investigations of the desiccation rate during winter of 35 of the same provenances as in the present investigations (Rossa and Larsen 1980) had a similar three-way grouping of the provenances with regard to their cuticular desiccation rate. It could then be established, that the very resistant provenances from Colorado and New Mexico have a considerably thicker cuticle of the needles than the less resistant coastal provenances from British Columbia, Washington and Oregon, which have significantly thinner cuticle layers. In the same investigations a positive correlation between drought avoidance and stomatal depths could furthermore be demonstrated. Differences in drought avoidance between different Douglas-fir provenances can therefore to a large extent be explained by differences in the anatomical characteristics of the needles. Drought avoidance associated with frost drought, however, concerns only that part of the resistance which can be attributed to the plant's discharge of water. The components of drought avoidance, which depend on the uptake of water by roots, is of no importance as regards frost drought resistance.

Up to now it has been assumed that differences in drought resistance among various provenances have mainly been due to the drought avoidance factor (Larsen 1978a). Drought tolerance was made responsible for the differential desiccation resistance only to a small extent. The present investigations showed a different picture. In fact, very big differences were demonstrated between the provenances in drought tolerance as well, from approx. -70 bar (coast and Cascade provenances) to -105 bar (high-altitude provenances from Colorado, Arizona and New Mexico). Investigations by Pharis and Ferrell (1966) and Ferrell and Woodard (1966) of drought resistance of two Douglas-fir provenances (one from a dry region of north-east Washington, the other from a more mesic region in the Oregon Cascades) also point to differences in both components (drought avoidance and drought tolerance).

The positive correlation between drought avoidance and drought tolerance, (*i.e.* drought avoidant provenances were also very tolerant, and vice versa) leads to marked differentiation in the drought resistance between provenances.

In view of their relatively slow growth rate (Larsen 1978b, Herrmann 1973), their susceptibility to late frosts (Larsen 1978b and 1979) and their susceptibility to *Rhabdocline pseudotsuga* (Stephan 1973), the provenances from the interior of British Columbia as well as from Arizona and Colorado, which demonstrated a high frost drought resistance, will probably not be considered for cultivation in north-west Europe. If we look at the provenances from the coastal areas and the Cascades of British Columbia, Washington and Oregon, they all show relatively poor resistance to frost drought. It is of special importance, therefore, that within this group of provenances which are all sensitive, relatively big differences in the resistance to frost drought have been found (from 2.5 to 3.7 days). The provenances from high elevations of the Cascades were considerably more resistant than those from the lower elevations and from the coastal area. So it appears, that there are possibilities in the choice of provenances with respect to frost drought resistance within the Cascade region of British Columbia, Washington and Oregon.

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