Conclusions

From the assessments in nine-year-old provenance tests of Maritime pine grown on seven sites in Greece the conclusions are

1. Successful planting of the species in areas such as Agios Nikolaos of Karpenisi is practically impossible due to frost hazards (−14° C) and severe snowbreak of trees.
2. Portuguese and Landes provenances, belonging to the same atlantic race grew faster than those from Cevennes and Corsican provenances. The corsican provenance was top in stem straightness and crown form.
3. The provenance by site interactions were insignificant for all characteristics, indicating genetic stability of the provenances tested. Therefore, selecting within the fast grown Portuguese provenance for height and diameter growth and stem straightness is promising for all environments tested.
4. A large variability was found among provenances and among locations in the proportion of fruiting trees. The proportion among provenances varied from 22 (Corsican) to 62 percent (Cevennes) and among location from 24 (Kounoupeli planting) to 76 percent (Varetada planting).

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Frost Resistance and Early Growth of Sequoidendron giganteum seedlings of different origins

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Summary

Frost resistance in 2 year old giant sequoia seedlings was analyzed by an artificial freezing test, in which detached twigs are placed in freezing chambers at different temperatures. The temperature that kills 50% of the twig foliage is called the "frost-killing-point" and is denoted LT50%. The results were compared to damage sustained outdoors by seedlings and support the reliability of the testing methods employed.

The experiment included the open-pollinated offspring of 2 trees growing in Hermeskeil, West Germany, and seedling samples of 22 provenances representing the entire natural range of giant sequoia.

Significant and substantial differences were found in frost resistance, winter damage and in early height. Frost resistance is correlated with outdoor winter damage and elevation, however not with latitude, longitude nor with seedling height. Shoot tip hardness measured by touch is unrelated to frost hardiness .

Key words: giant sequoia, provenances, cold hardiness.

Zusammenfassung

Die Frostresistenz 2jähriger Pflanzen bei 22 Provenienzen von *Sequoiadendron giganteum* wurde mit Hilfe eines Klimakammerfrosttestes ermittelt. Der Test wurde im Herbst während der Abhärtungsphase gemacht, und die Ergebnisse geben daher Auskunft über die Frühfrostresistenz. Die Temperatur, bei der 50% der Zweigbenadelung

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abgestorben ist, wird LT 50% genannt. Die Ergebnisse werden mit den tatsächlichen Schäden nach dem Winter bei den Pflanzen im Freiland verglichen. Zusätzlich wurden die Höhenentwicklung und der Wachstumsabschluß der Pflanzen erfaßt.

Signifikante Unterschiede zwischen den Herkünften werden für die Frosthärte und die Sämlingshöhe ermittelt. Die Sämlingshöhe zeigt eine negative Korrelation zur Höhenlage der Herkünfte.

Eng korreliert sind die Ergebnisse des Klimakammerfrosttestes mit den tatsächlichen Frostschäden im Freiland. Wachstumsabschluß im Herbst und Frostschäden im Winter sind voneinander abhängig. Ebenfalls nicht korreliert sind Höhenwachstum und Frostresistenz.

Introduction

Giant sequoia [*Sequoiadendron giganteum* (Lindley) Buchholz] is indigeneous to the western slopes of the California Sierra Nevada, and occupies a 418 km long zone from 39° 13' to 35° 05' N. latitude. The populations occur most frequently at elevations between 1370 and 2285 m, although some individual trees occur at elevations between 1219 to 2560 m. Eight disjunct northern populations, dispersed 10—90 km apart, occupy over 2/3 of the natural range and 65 southern populations, with distances of 8 km or less between them, comprise the remaining 1/3 of the natural range.

Giant sequoia was first introduced into Europe in 1853 (Krüssmann, 1979) and presently can be found surviving to significant size in 25 European countries (Hartesveldt, 1975). Libby (1981) provides some recent observations of giant sequoia in Europe. In 1980, current increments of an 113 year old giant sequoia stand (1.4 ha), located near Weinheim, West Germany (250 m elevation) was estimated at 20 m^3/ha/year, (Institut für Forstliche Ertragskunde, 1981). This compares favorably to a maximum expected 14 m^3/ha/year for Norway spruce grown under similar site conditions. Other measurements from the Weinheim stand of interest are a mean height of 39 m and a mean diameter at breast height of 85 cm. Such instances of giant sequoia's outstanding performance are motivating interest in introducing giant sequoia into Europe's managed forests. The Lower Saxony Forest Research Institute, Department of Forest Tree Breeding, is conducting a many-phased investigation of giant sequoia's potential in Europe; the data reported below are from this project's provenance trails.

The introduction of an exotic species into European forests requires consideration of many factors, particularly those that influence its survival. Among these, frost resistance performance of different giant sequoia populations is of salient importance, since European experience shows that some sequoias have been severely injured or killed by cold, while others suffered little or no damage during several severe seasons. Because giant sequoia is known to flush relatively late, late frost resistance is not considered crucial, given that this species will not be planted on sites topographically disposed to frost. Early frost (autumn) and severe winter cold (−20 to −30° C) however, are responsible for considerable damage and mortality, even in older stands in Europe.

Two year old seedlings from 22 giant sequoia provenances, covering the entire natural range of the species, were tested for frost hardiness. In addition, the offspring of 2 nonindigeneous giant sequoia trees from West Germany were investigated. Due to limited plant material, one frost test simulating both early and winter frost was conducted in late October. Larsen (1978) reports high correlations between resistance to winter frost in Douglas-fir.

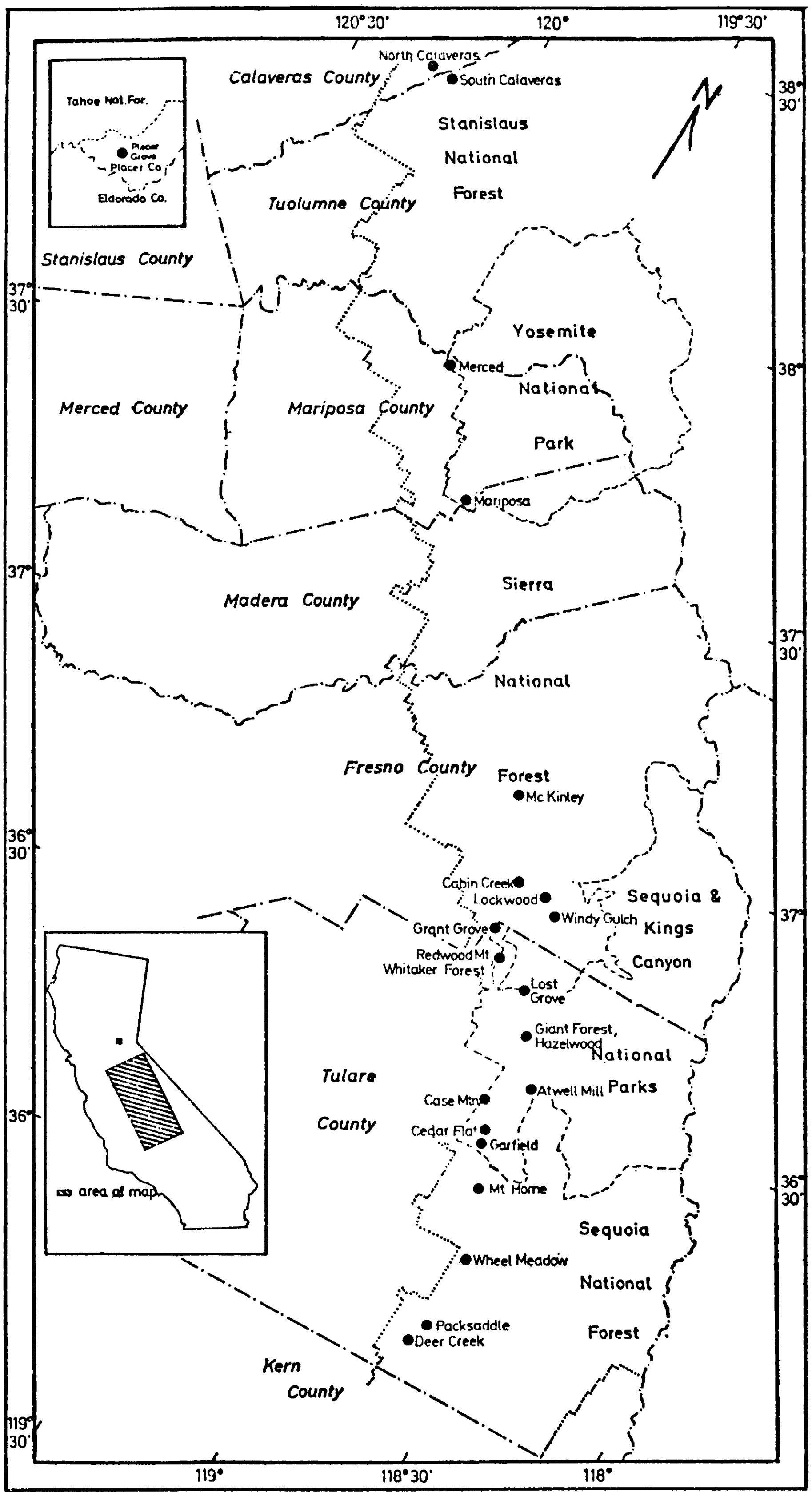
The primary objective of this investigation is to obtain information about variation in frost resistance within and between populations. Because early growth performance also merits consideration, an additional aim is to examine whether frost resistance is related to seedling growth. Knowledge of such variation patterns will aid in selection for frost resistance at the provenance level, and in breeding for this trait.

Table 1. — Geographical data, mean frost resistance, height growth, shoot tip hardness and winter damage of the 24 giant sequoia provenances tested.

					Detached Twig[a]	Seedlings[b]		
Provenance No.	Grove or Tree	Latitude x° y'	Longitude x° y'	Elevation m	Frost Resistance LT 50% in °C	Height cm	Shoot Tip Hardness[c]	Winter Damage Index[d]
	California Groves							
1	Placer	39 04	120 34	1676	-9.9	17.7	2.8	1.0
2	North Calaveras	38 16	120 18	1463	-9.8	21.8	3.2	4.9
3	South Calaveras	38 14	120 14	1494	-9.0	21.6	3.4	2.1
4	Merced	37 45	119 50	1753	-10.1	15.1	3.0	3.6
5	Mariposa	37 31	119 37	1768	-10.7	14.9	2.9	1.1
6	McKinley	37 02	119 07	1920	-8.7	16.3	3.5	7.3
7	Cabin Creek	36 50	118 57	1798	-8.4	16.5	2.7	2.9
8	Lockwood	36 49	118 52	1920	-9.4	21.1	3.4	3.7
9	Windy Gulch	36 46	118 49	2073	-8.6	19.4	3.0	2.6
10	Grant Grove	36 44	118 57	1920	-9.1	17.1	3.0	3.0
11	Redwood Mtn.	36 41	118 55	1768	-10.1	18.2	3.5	1.6
12	Whitaker Forest	36 41	118 55	1524	-9.0	23.9	3.8	2.0
13	Lost	36 39	118 49	1524	-8.3	18.0	3.0	1.9
14	Giant Forest	36 34	118 44	1951	-10.2	20.9	4.0	1.3
15	Hazelwood	36 34	118 44	1951	-10.7	17.8	3.3	1.0
16	Atwell Mill	36 28	118 40	1966	-10.3	21.3	2.3	1.0
17	Case Mountain	36 23	118 47	1859	-7.9	18.8	2.8	9.0
18	Cedar Flat	36 22	118 44	1554	-9.8	17.0	3.9	1.6
19	Garfield	36 20	118 43	1980	-9.5	15.6	3.3	1.1
20	Mountain Home	36 16	118 41	1981	-11.0	19.2	3.7	1.1
21	Wheel Meadow	36 07	118 34	1676	-9.2	18.0	2.4	2.1
22	Packsaddle	35 56	118 34	1067	-9.1	18.3	3.0	3.0
	West Germany Trees							
23	Hermeskeil 1	49 39	06 57	500-1000	-8.3	18.3	3.3	3.9
24	Hermeskeil 2	49 39	06 57	500-1000	-8.4	17.1	3.6	4.1

[a] 5 twigs from each of 7 trees per provenance
[b] 10 to 17 seedlings per provenance
[c] 1 = tender; 5 = hard
[d] 1 = 0—10% damage; 10 = 90—100% damage (foliage)

Map. 1. — Giant sequoia groves



From Meyer, 1952

Materials and Methods

Provenance Material

The investigation's plant material, growing at the Lower Saxony Forest Research Institute in Escherode, West Germany, originated from the recent giant sequoia seed collections by Fins (1979). *Map 1* shows locations of the 22 populations she sampled that were used in this study; these sample the entire natural distribution of the species. In addition, offspring of 2 isolated trees of unknown provenance origin, growing in Hermeskeil West Germany, are included. These 2 trees appear to be unusually cold hardy under the conditions in southwest Germany. *Table 1* presents geographical data for each provenance and is arranged from north to south by provenance.

The giant sequoia seed was sown in an outdoor seedbed in May 1979, and seedlings were transplanted to small pots in July 1979. They were transplanted to 11 cm containers in January 1980 and then to WEHA pap containers in June 1980, and placed in a greenhouse, where active growth resumed. In September 1980, the plants were removed from the greenhouse to an outdoor lathhouse, so that the plants would harden. Each provenance was represented by 7 seedlings randomly taken from a provenance trial's collection of seedlings, except for the provenance McKinley Grove (No. 6) where only 4 seedlings were available. At the time of testing, the plants were 2 years old.

Test Methods

We tested the frost hardiness of the 165 plants included in the study on 26 October 1980, at the Institute of Silviculture, University of Göttingen, West Germany. The artificial-freezing test method is described in detail by Larsen (1978). This procedure requires 5 detached twigs from each plant, thus allowing testing at 5 different temperature levels: we used −5.0° C, −7.0° C, −9.5° C, −12.0° C and −14.0° C. The cooling and thawing rates in our test were −6° C/hour and +6° C/hour respectively, and test temperature duration was 4 hours. After the freezing treatments, the twigs were transfered to a greenhouse, their bases were placed in sandy gravel in a manner similar to cuttings, and they were kept under glass and high humidity at ambient temperatures of 15—20° C. Injury was then evaluated after 4 weeks, based on percent of dead foliage. The temperature that kills 50% of the twig foliage, namely "frost-killing-point" (LT50), was computed for each tree tested.

If plant growth cessation in giant sequoia could be determined, differences among plants should correspond to differences in plant frost resistance. In order to find a method that might estimate the plant's condition with respect to growth cessation, we rated shoot tip hardness, estimated by touch. Shoot tip hardness scores are from 1 to 5, where 1 expresses the most tender shoot tip, and 5 corresponds to the hardest shoot tip. The scoring was conducted by one person, since the estimations include a degree of subjectivity. The shoot tip hardness data herein reported are from 24 October 1980.

In the spring of 1981, after noticing winter damage on the seedlings that overwintered in the lathhouse, we recorded the degree of foliage damage on the provenance collections. Seedlings that had donated twigs for the frost test were included in this evaluation. Percent needle damage indices were ranked such that: 1 = less than 10% damage, 2 = 10—20% damage . . . . 10 = 90—100% damage.

In April 1981, after the second growing season, tree height was measured in cm.

Statistical analyses include linear regressions, analyses of variance and of covariance, and correlation anlyses.

Results

Table 1 presents the provenance mean values for detached-twig frost resistance LT50% in ° C, seedling height in centimeters, shoot tip hardness indices, and seedling winter-damage scores.

Frost Resistance

Analysis of the frost resistance test indicates highly significant differences between provenances ($p < 0.0002$). Provenance samples from Mariposa (No. 5), Hazelwood (No. 15) and Mountain Home (No. 20) exhibit the highest cold resistances, with LT50% values of −10.7° C, −10.7° C and −11.0° C respectively. The Case Mountain provenance sample (No. 17), with an LT50% value of only −7.9° C, is least frost hardy. Offspring from the two German open-pollinated families (No. 23 and No. 24) have LT50% values below the overall provenance average of −9.5° C.

In order to investigate geographical trends in frost resistance, a multiple linear regression analysis was performed, with frost resistance as the dependent variable and elevation, longitude and latitude as regressors (independent variables). The analysis demonstrates no significant effects of longitude ($p = 0.142$) and latitude($p = 0.195$), and the calculated multiple correlation coefficient for these traits is $r = 0.18$. The effect of elevation is statistically significant ($r = 0.40$, $p = 0.036$) such that greater frost resistance generally occurs in population samples from higher elevations.

Although highly significant differences in frost resistance exist between provenances, we found tremendous plant-to-plant variation in frost resistance within population samples. For example, the 26 plants above the 84th percentile (having frost LT50% values lower than −11° C) are members of 13 of the 24 seed sources. *Figure 1* shows the within provenance variation in frost resistance for each provenance tested arranged from north to south.

Shoot Tip Hardness

Highly significant differences between provenances exist for shoot tip hardness indices ($p < 0.0004$), which were used as estimators for plant growth cessation. The Atwell Mill provenance sample (No. 16) had the most tender shoot tips (index average 2.3) whereas the Giant Forest Sample (No. 14) had the hardest shoot tips (index

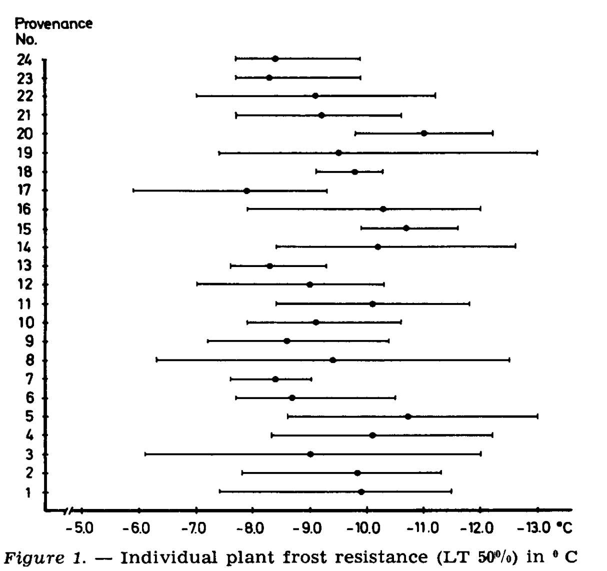


Figure 1. — Individual plant frost resistance (LT 50%) in ° C

average 4.0). We detected no relationship of the geographical parameters to shoot tip hardness by regression analyses.

Winter Damage

The winter damage scores recorded in the spring of 1981 show that seedlings from Case Mountain (No. 17) and McKinley Grove (No. 6) sustained excessive winter damage, with indices of 9.0 and 7.3 respectively (these correspond to about 85% and 68% needle damage). In comparison, seedlings from 6 provenances (Nos: 1, 5, 14, 16, 19 and 20) suffered less than 10% damage. The German-origin seedlings had more damage (3.7 and 4.1) than the overal mean (2.7).

Height

Mean height values of provenance samples range from 14.9 cm (No. 5 Mariposa Grove) to 23.9 cm (No. 12 Whitaker Forest), and the differences among provenances are highly significant ($p < 0.0001$). Longitude and latitude have no significant correlation with height growth, ($r = 0.16$ and $p = 0.117$ and $p = 0.120$ respectively). Elevation however, appears to have a moderate negative correlation with tree height ($r = -0.16$ and $p = 0.059$).

Intercorrelation of Traits

The correlation on the provenance level between frost resistance and height growth is 0.12. On the individual tree level however, no common relationship between these two traits can be demonstrated ($r = 0.19$, $p = 0.470$). Statistically significant negative correlations between height growth and frost resistance occur in two of the 24 provenances, South Calavenas No. 3 and Lockwood No. 8, with $r = -0.71$ and -0.63 and $p = 0.0003$ and 0.004, respectively.

Neither on the individual level nor the provenance level are the two traits frost resistance and shoot tip hardness correlated ($r = -0.12$).

A large negative and statistically highly significant correlation coefficient ($r = -0.70$, $p < 0.001$) again demonstrates the close relationship between frost resistance tested on detached twigs and observed seedling winter damage on the provenance level (winter-damage indices are log-transformed). In comparison, our data suggests little or no relationship between shoot tip hardness and winter damage ($r = -0.02$).

Discussion

Considerable variation is indicated both between and within provenances in frost resistance, height and winter damage. Analyses by FINS (1979) show within-provenance and between-provenance differences in isozyme constitution of giant sequoia, although isozyme variability does not necessarily imply variation for "adaptive loci". However, we observed genetic variability at "adaptive loci", and concluded that selection of better adapted races of giant sequoia for Europe should be possible.

Correlations of elevation and frost resistance are statistically significant, whereas associations of frost resistance with longitude and latitude are weak or absent. Our results are consistent with conclusions of a giant sequoia test at Reinhausen, West Germany for cold susceptibility where one of us found similar elevation and frost resistance relations (LARSEN, unpublished).

A low and statistically non-significant correlation between frost resistance and height indicates that tree breeders need not sacrafice height performance when selecting for frost hardiness. Large and significant negative correlations were found in 2 provenances; however, variation within these provenances may be large enough to find fast growing frost hardy "correlation breakers" if indeed these correlations are generally correct.

Our data suggests that the shoot tip hardness is unrelated to observed winter damage; therefore such assessment of the shoot tip condition appears to be an unreliable method for estimating growth cessation or indicating frost resistance.

The frost LT50% values correlate highly with the winter-damage scores, thus supporting the dependability of the artificial freezing test for evaluating frost resistance in outdoor conditions.

The relatively poor performance of the 2 open pollinated Hermeskeil families is surprising, since these two parent trees have survived several severe cold periods. It is possible that these offspring are largely selfs or other inbreds, and that such inbreds withstand frost poorly. The fact that the 2 parent trees grow side by side without any onther neighbors, and heights of their seedlings were below average, supports this explanation. Within the Hermeskeil families, there is a small group of frost-resistant seedlings which also have greater heights; these plants are likely to be outcrosses. It is likely that giant sequoia planted in West Germany originated from relatively few of the California groves. It is plausible that the general record of cold hardiness of giant sequoia in Europe underestimates the potential of this species, if the original groves were by chance inferior.

Based on this early data the Atwell Mill grove population seems particularly promising, while the populations from McKinley and Cabin Creek groves seem particularly unpromising, and several samples provide a mixed performance in early growth and frost resistance characteristics analyzed. Individual variation patterns within provenances *(Fig. 1)* and between provenances exemplify selection potential for frost resistance. Our data support the conclusion that there is potential for giant sequoia in Europe's managed forests. Selection of clones for immediate use is possible at both the population and individual level, as well as selection of parents in order to established breeding lines. We recommend that a new major provenance study be planned and executed, with particular attention paid to:

1) adequate sampling of most or all 73 extant groves,
2) the use of selected fast-growing frost-resistant clones, both for research and production plantations,
3) further frost resistance studies, especially of late frost, which was not tested in this study.

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Influence de l'état d'activité des racines sur la floraison induite par des gibbérellines 4 et 7 chez Pseudotsuga menziesii (Mirb.) Franco

Par M. Bonnet-Masimbert[1])
avec la collaboration technique de P. Delanzy,
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(Reçu 11 décembre 1981)

Résumé

Deux essais ont été réalisés sur plants greffés sexuellement matures et semis juvéniles de *Pseudotsuga menziesii* élevés en serre selon trois modalités différentes (irrigation normale, sécheresse moyenne, submersion temporaire du système racinaire accompagnée d'hypoxie). Une partie des plants a reçu au moment du débourrement une perfusion par un mélange de gibbérellines 4 et 7 et d'acide naphtalène acétique. Dans l'un des essais, des observations sur l'allongement des racines et des tiges de chaque plant, puis sur leur floraison, montrent clairement que seuls fleurissent des plants ne manifestant aucune croissance racinaire à l'époque de l'initiation florale. Par ailleurs, les croissances très fortes ou très faibles de la tige semblent défavorables à la floraison. Enfin, l'hypoxie racinaire, très efficace pour arrêter l'allongement des racines, stimule la floraison mâle et femelle, y compris en l'absence de traitement hormonal. La discussion porte sur les analogies de comportement du Douglas avec certaines plantes herbacées pour lesquelles une interaction entre croissance racinaire et floraison a été démontrée ainsi que sur l'incidence possible de ce phénomène pour expliquer le rôle de certains traitements culturaux sur la floraison.

Mots clés: Induction de la floraison, Racines, Activité racinaire, Elongation racinaire, Gibbérellines, Hypoxie, Engorgement du sol, Sécheresse, *Pseudotsuga menziesii*.

Summary

In two trials, young grafts of sexually mature scions and juvenile seedlings of *Pseudotsuga menziesii* were grown under a plastic house and cultivated under 3 conditions: Standard irrigation, modest water stress and root flooding with hypoxy. A part of the plants were perfused with a mixture of gibberellins 4 and 7 ($GA_{4/7}$) and of naphtaleneacetic acid (ANA). In one of the trials, observations on root and shoot elongation, and subsequent flowering response of each plant, clearly indicate that only plants with no root growth during the treatment period produce flowers. Also, a shoot growth rate which is to high or too low does not seem favorable to flowering. Root hypoxy, a very efficient way for stopping root growth, stimulates male and female flowering, even without a treatment with growth regulators. We discuss similarity between the reactions of Douglas-fir and of some herbaceous plants for which a clear interaction between root growth and flowering has been demonstrated. Also, this interaction may be causally involved in the control of flowering through cultural treatments.

Key words: Flowering induction, Root activity, Root elongation, Gibberellins, Hypoxy, Flooding, Drought, *Pseudotsuga menziesii*.

Zusammenfassung

In zwei Versuchen wurden im Folienhaus Pfropflinge (blühfähige Reiser auf junge Sämlingsunterlagen) von *Pseudotsuga menziesii* unter drei verschiedenen Bedingungen angezogen, d. h., bei Standardbewässerung, gemäßigtem Wasserstress und zeitweiliger Wurzelüberflutung mit Sauerstoffmangel. Ein Teil der Pflanzen wurde mit einer Mischung aus Gibberellin 4 und 7 (GA 4/7) und Naphtalinessigsäure (ANA) gegossen. In einem der Versuche zeigten Beobachtungen des Wurzel- und Triebwachstums und des späteren Blühens jedes Pfropflings, das nur diejenigen Pfropflinge Blüten hervorbrachten, die während der Behandlungsphase kein Wurzelwachstum gezeigt hatten. Auch ein mehr oder weniger starkes Triebwachstum scheint das Blühen nicht zu begünstigen. Sauerstoffmangel im Wurzelbereich, ein sehr wirksames Mittel, um das Wurzelwachstum zu stoppen, verursachte weibliche und männliche Blütenbildung, sogar ohne eine Behandlung mit Wachstumsregulatoren. Wir haben Ähnlichkeiten der Reaktion bei der Douglasie mit derjenigen bei einigen krautigen Pflanzen diskutiert, bei denen ein klarer Zusammenhang zwischen Wurzelwachstum und Blühen demonstriert worden ist. Es könnte sein, daß diese Interaktion auch durch verschiedene Kulturmaßnahmen hervorgerufen wird.

Introduction

Parmi les problèmes qui se posent aux physiologistes forestiers, la maitrise de la juvénilité et du phénomène d'irrégularité de la floraison, constitue un objectif important pour les améliorateurs d'espèces forestières. Plusieurs techniques culturales (revues par Puritch, 1972) ont été utilisées, parmi lesquelles la sécheresse et le cernage de racines. Souvent traumatisantes pour les plants, elles ont conduit à des résultats très variables d'un essai à l'autre. Mais c'est surtout par l'utilisation de régulateurs de croissance, principalement les gibbérellines 4 et 7 ($GA_{4/7}$) que des floraisons ont pu être induites sur de jeunes plants, ou des copies végétatives d'individus adultes, de plusieurs pinacées (revue par Pharis et Kuo, 1977; Pharis *et al.*, 1980). En fait, il semble que les meilleurs résultats puissent

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