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Predicted global warming and Douglas-fir chilling requirements

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Summary – Potted Douglas-fir [*Pseudotsuga menziesii* (Mirb) Franco] seedlings from warm coastal and cool mountainous Oregon seed sources, grown under natural conditions, were chilled at constant temperatures of 5, 7, or 9° C for periods of 9, 11, 13 or 15 wk beginning in mid-October. After a growth period of 9 wk following chilling, the degree of bud break and the weight of new shoot growth were recorded. The longest and coldest chilling treatment produced the greatest growth response for all seed sources. Results are discussed with reference to predicted global warming.

Douglas-fir / chilling / global warming / bud burst / reforestation

Résumé – Réchauffement du Globe et besoin en froid du douglas. *Des semis de 2 ans de sapins de Douglas [*Pseudotsuga menziesii *(Mirb) Franco] ont été transférés en conteneurs, puis placés en conditions naturelles pendant une saison de végétation. Ils provenaient de sites côtiers chauds ou montagneux frais de l'Orégon. A partir de mi-octobre ils ont été soumis à une température constante de 5, 7 ou 9 °C pendant des durées de 9, 11, 13 ou 15 semaines, en vue de lever leur dormance. Ensuite, après une mise en végétation à 15 °C pendant 9 semaines, on a individuellement noté le degré de débourrement des plants et déterminé le poids sec des nouvelles pousses formées. Quelle que soit l'origine des graines, la réponse à la croissance est d'autant meilleure que la phase d'élimination de dormance est plus longue (tableau I) et plus froide (tableau II). Les résultats sont discutés dans la perspective des effets d'un réchauffement du Globe.*

douglas / conditionnement par le froid / réchauffement du globe / débourrement / reboisement

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INTRODUCTION

The role of low temperatures in the breaking of dormancy was first discovered in 1801 (Doorenbos, 1953). Although delayed foliation of peach trees was reported in Georgia in 1890 (Weinberger, 1967), low temperatures were generally not related to the breaking of dormancy of woody plants until 1908 – when it was recognized that peaches differed in their rest period (Chandler, 1957) – and the subsequent decade, when Colville (1920) reported his studies on chilling.

Today, "chilling requirement" refers to the temperature (commonly around 5 °C) and duration of exposure necessary to prepare the apical meristems of temperate perennial plants for resumption of growth when temperatures rise in the spring. This requirement is confined largely to plants that are exposed to freezing winter temperatures, and has evolved to prevent active shoot growth during brief, warm winter spells because such growth could be damaged by subsequent low temperatures.

A number of papers offer evidence that mean global warming of 3-4 °C could occur within the next century, particularly during the winter months (Seidel and Keyes, 1983; Cooper, 1984; McBeath *et al*, 1984; Rind and Lebedeff, 1984; Slocum, 1985; Smith, 1985). This could profoundly affect the amount of chilling that Douglas-fir [*Pseudotsuga menziesii* (Mirb) Franco] receives.

The present study was undertaken to determine:

- the effect of the chilling period upon subsequent growth of Douglas-fir seedlings;
- the efficiency of slightly higher chilling temperatures in preparing seedlings for growth resumption;
- the relative chilling requirements of seedlings grown from seeds collected in areas with different winter climates.

Although previous studies have examined Douglas-fir chilling requirements (Wommack, 1964; Van den Driessche, 1975; Wells, 1979), they have either used seedlings that were not transplanted at least 1 growing season prior to the study, have grown them under artificial conditions, or have exposed seedlings to daily photoperiods longer than 12 h after chilling. Lavender and Stafford (1985) strongly suggest that if data are to be truly relevant for natural populations, the use of undisturbed plants grown under natural conditions is essential; and daily photoperiods greater than 12 h have been shown to compensate for the lack of chilling in Douglas-fir (Lavender *et al*, 1970).

METHODS

Douglas-fir seeds were collected from elevations below 150 m near the central Oregon coast (Western Forest Tree Seed Council seed zones 071-0.5 and 072-0.5) and from the Oregon Cascade Range east of Eugene at elevations of about 1000 m (Western Forest Tree Seed Council seed zones 451-2.5 and 491-4.5). Winters in the coastal area are relatively warm, *ie* the average temperature between 1 December and 1 March is *ca* 7°C, whereas the winters in the mountainous area are cooler with average temperatures for the same period of about 3° C. However, the coastal area experiences about 3 000 h annually of temperatures between 0°C and 7°C, whereas the mountainous area has somewhat fewer, *ca* 2500 h. Seeds were sown in spring, 1982 in the Oregon State Board of Forestry Nursery near Elkton, Oregon. The resultant seedlings were maintained under standard nursery conditions until late February, 1984, at which time they were lifted, stored for 6 wks, and planted in pressed fiber pots (8 seedlings per pot) containing 12 l of forest soil each. Prior to planting, the seedlings were sorted by size within each seed source and the populations for each pot made up from this distribution to assure a relatively uniform seedling size. The seedlings from the coastal seed sources were generally larger than those from the interior at the beginning of the 1984 growing season. The potted seedlings were kept outside with frequent irrigation until mid-summer, and most of them grew vigorously during this period. From mid-summer until early fall, the seedlings were subjected to moderate moisture stress, which induced well-formed buds by mid-August (Duryea, 1984).

Mid-October was chosen for initiation of chilling because it was late enough to satisfy seedling requirements for short, mild days prior to chilling (Lavender and Stafford, 1985) and early enough to avoid natural chilling of seedlings. Previous studies (Lavender *et al*, 1970) have shown that Douglas-fir seedlings cultured under natural conditions are in the mid-rest period of their annual growth cycle at this time and, hence, have a maximum requirement for exposure to temperatures *ca* 5°C to prepare them for resumption of active growth in the following spring. Sixteen pots from each seed source (64 pots in all) were placed in each of 3 growth rooms. These rooms were maintained at constant temperatures of 5, 7, and 9°C with 8 h daily photoperiods (125 µmol of light flux from a 5:1 mixture of fluorescent and incandescent lights). Pots were irrigated fortnightly to maintain soil moisture near field capacity.

After 9 wks of chilling, and every 2 wks thereafter, 4 pots per seed source were moved from each chilling room to a 4th that was maintained at a constant temperature of 15°C and a 12-h daily photoperiod (250 µmol of light flux from fluorescent lighting). The foregoing photoperiod was chosen because, unlike the 16-h photoperiod which has been employed in other studies of dormancy of Douglas-fir, this daily photoperiod does not compensate in part for the chilling requirement and hence does not stimulate bud growth on seedlings which have received little chilling. Moisture in these pots was maintained near field capacity, and seedlings were examined weekly. Buds that had broken (*ie* whose needles had emerged through the bud scales) during the preceding week were marked at the base with a small dot of colored paint (1 color for each examination date). This procedure was followed to permit computation of the date of mean bud break both for the individual chilling temperatures and periods and for the levels within seedling crowns. These data are not presented, however, as they follow the same pattern as that for numbers of active buds, *ie* seedlings maintained at 5°C initiated bud activity more rapidly than, those at 9°C; plants chilled for 15 wk, more rapidly than those chilled for 9. In addition there was no observed effect of position in the seedling crown upon rate of bud break.

Each set of seedlings was harvested after 9 wk in the above environment, and the number of active buds and oven-dry weight of new foliage were recorded. Because care was taken during planting to prepare pots with equivalent seedling populations, it is assumed that these data reflect seedling vigor rather than seedling size and bud number.

The data were analyzed in a factorial 3-way analysis of variance (Snedecor and Cochran, 1967) whose main effects were chilling temperature, chilling period, and seed source. Because only 1 growth room was used for each chilling temperature, there was no true statistical replication of this 1 factor. Therefore, we only considered differences significant at $P \leq 0.01$. We also developed multiple linear regression models with either number of active buds or foliage dry weight as dependent variables and chilling temperature and period as independent variables.

RESULTS

Chilling temperature, chilling period and seed source all had significant effects on the measured growth parameters. For example, the "F" values for the total weight of new foliage shown in table I are 44.249 for chilling temperature, 404.182 for duration of chilling and 15.304 for seed source, respectively. Bud activity and foliage dry weight, for each seed source and averaged over all seed sources, were greatest in the longest and coldest chilling treatments (table I). Although this trend was true for all seed sources, seedlings grown from seed collected in areas with warmer winters generally produced the greatest number of buds and the most foliage (table II). Multiple linear regression models, adjusted for differences in seed source, explained 75% of the variability ($R^2 = 0.75$) in the number of active buds and 86% of the

Table I. Mean oven-dry weight of new foliage and mean number of active buds per seedling for each chilling temperature and period, averaged over all seed sources. Means not followed by the same letter within each growth parameter are significantly different at $P \leq 0.01$ by a Least Significant Difference test (Snedecor and Cochran, 1967).

Chilling period (weeks)	*Chilling temperature* 5 °C	7 °C	9 °C
	Foliage dry weight (g)		
9	0.49 ab	0.20 a	0.20 a
11	1.22 de	0.84 c	0.58 bc
13	1.99 f	1.50 e	1.15 d
15	2.75 h	2.34 g	2.43 g
	Number of active buds		
9	16.30 b	8.40 a	6.20 a
11	31.40 d	25.00 c	15.30 b
13	38.70 e	33.50 d	22.20 c
15	38.80 e	35.60 de	33.30 d

Table II. Mean oven-dry weight of new foliage and mean number of active buds per seedling for each seed source[1] and chilling temperature, averaged over all chilling periods[2]. [1] Seed sources 071-0.5 and 072-0.5 represent coastal areas where winters are warm; seed sources 451-2.5 and 491-4.4 represent mountainous areas where winters are colder. [2] Means not followed by the same letter within each growth parameter are significantly different at $P \leq 0.01$ by a Least Significant Difference test (Snedecor and Cochran, 1967).

Chilling Temperature (°C)	*Seed source* 451-2.5	491-4.4	071-0.5	072-0.5
	Foliage dry weight (g)			
5	1.33 bcd	1.53 ab	1.76 a	1.83 a
7	1.03 cd	1.19 cd	1.32 bcd	1.35 bc
9	0.80 e	1.18 cd	1.14 cd	1.24 bcd
	Number of active buds			
5	36.10 a	25.40 cde	31.30 ab	32.50 ab
7	26.00 cd	21.00 ef	27.10 cd	28.50 bc
9	16.30 f	16.40 f	21.70 e	22.60 de

variability (R^2 = 0.86) in foliage dry weight. The relative importance of the experimental variables is reflected by the "F" value above.

DISCUSSION

Although coastal North American winters are now sufficiently cold and long to satisfy the chilling requirements of indigenous Douglas-fir, a small temperature rise in the warmer portions of its range might have profound effects. Long-term weather records from the Oregon Coast and Cascade Ranges indicate December, January, and February mean temperatures of 5-8 °C for the area that includes seed zones 071-0.5 and 072-0.5 of the present study (Simonson, 1963); if mean winter temperatures of these areas were to increase by the predicted 3-4 °C, the average winter climate would probably be too warm for adequate chilling of Douglas-fir. This hypothesis is supported not only by the differential ability of the tested temperatures to satisfy the chilling requirements, but also by the effect of duration of chilling. The data we have used to characterize the natural climate is based on the average temperature for the coldest 3 months. As the climate warms, the duration of low temperatures will shorten so that Douglas-fir will be affected by both higher minimum temperatures and briefer duration of same. Copes (1983) reported that grafted Douglas-fir coastal clones from Oregon either died or demonstrated very weak shoot growth after being transplanted to the Monterey coast in California, and suggested that the reason was average monthly winter temperatures (9.3-12.2 °C) are too high to satisfy the trees' chilling requirements.

Perhaps of more immediate concern to foresters is the effect of the predicted global warming trend on reforestation success. Most Oregon, Washington, and British Columbia nurseries that now grow Douglas-fir seedlings receive only slightly more natural chilling hours each year than the seedlings require. Because methods of harvest, shipping, and planting definitely affect seedlings' ability to respond to chilling (Lavender and Stafford, 1985), we may expect poorly conditioned nursery stock to be increasingly at risk in the coming years if global temperatures do rise. However, bareroot and container nurseries, whose stock is subjected to cold storage in order to satisfy seedling chilling requirements, might not be directly affected by mean temperature increases.

Cannell and Smith (1984), studying Sitka spruce planted in Great Britain, suggested that another effect of warming climates is increased seedling susceptibility to damage from late frosts. Although a similar situation may be obtained for Douglas-fir, we know of no data which substantiate this hypothesis.

Douglas-fir is a long-lived and therefore slow-evolving species whose budburst is under strong genetic control (White *et al*, 1979), and it is thus unlikely that its chilling requirements would be substantially modified within the 100-year period over which global warming has been predicted. Because our results suggest that chilling requirements of this species are not greatly influenced by the winter climate of the seed source (in a subsequent experiment we observed similar chilling requirements for seedlings raised from seed collected in the State of Washington), it may prove difficult to reduce those requirements through forest-tree breeding techniques. The prospect of global warming thus presents the possibility of a loss in the adaptive synchrony between growth initiation and seasonal temperature. Further, the present climate of the Douglas-fir region is characterized by wet winters and dry summers - over 85% of the annual precipitation commonly falls between October and May. If then, the less efficient chilling of Douglas-fir occasioned by the predicted increased mean temperature results in a delay of growth initiation in the spring, such delay could result in growth severely restricted by late spring and summer drought.

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