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Original article

Early growth performance of salal (*Gaultheria shallon*) from various North American west-coast locations

Charles E. Dorworth[a], Thomas N. Sieber[b,*] and Thomas A. D. Woods[c]

[a] BioCon Technology International, 212 Sunset Drive, Salt Spring Island, B. C., V8K 1L4 Canada
[b] Swiss Federal Institute of Technology, Forest and Wood Sciences, Section of Forest Protection and Dendrology, ETH-Zentrum, 8092 Zurich, Switzerland
[c] Forest Renewal B. C., 727 Fisgard Street, Victoria, B. C., V8V 1X4 Canada

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Abstract – Salal is a native perennial evergreen shrub occurring from the panhandle of Alaska along the entire coast of British Columbia to southern California. In the North American west coast industrial forest it is considered a weed because it is a persistent, serious competitor with coniferous species. Intraspecific genotypic and phenotypic diversity of salal is not well known despite of its ecological and economic significance. A morphometric analyses within and among populations was performed in a statistically appropriate manner. Two-year-old container grown seedlings of 24 collections of salal from throughout the natural area of distribution in western North America were planted in a randomized complete blocks design (6 blocks) on a cleared 0.7 ha plot on Vancouver Island. Each of the 24 seedlots was planted once in each block with 24 plants per seedlot in April 1990. Shoot height and the number of buds prior to planting, the plant spatial volume (product of plant height and plant width on two perpendicular axes) in 1992 and 1993, the relative growth increment (1992–1993) and the number of dead plants in 1992 and 1993 were subjected to analysis of variance. No differences among seedlots were detected for the relative growth increment and the number of dead plants in 1992 and 1993. Conversely, shoot height and the number of buds prior to planting as well as the plant volume in 1992 and 1993 showed statistically significant seedlot effects. Cluster analysis of these effects revealed greatest differences in plant response among the eastern- and southernmost collection and the remainder of the collections; i.e. three geographical races of salal may exist.

***Gaultheria shallon* / geographical origin / experimental design**

Résumé – Potentiel de croissance initiale du Salal (*Gaultheria shallon*) de diverses régions de la côte ouest de l'Amérique du Nord. Le Salal est un arbuste autochtone pérenne à feuilles persistantes réparti depuis la péninsule de l'Alaska tout au long de la côte de la Colombie Britannique jusqu'au sud de la Californie. Dans les forêts industrielles de la côte ouest de l'Amérique du Nord, il est considéré comme une mauvaise herbe parce qu'il est persistant et un compétiteur sérieux des espèces de conifères. La diversité intra spécifique génotypique et phénotypique du Salal n'est pas bien connue malgré son importance écologique et économique. Une analyse morphométrique parmi ses populations a été réalisée selon les règles statistiques. Des semis de 2 ans, ayant poussé en conteneurs, provenant de 24 collections de Salal originaires des diverses régions naturelles de l'ouest de l'Amérique du Nord ont été plantés selon un dispositif complet à blocs randomisés (6 blocs) dans une parcelle nettoyée de 0,7 ha sur l'Ile de Vancouver. Les 24 lots de semis ont été plantés dans chacun des blocs en 1990. La hauteur de la pousse et le nombre de bourgeons avant plantation, le volume spatial (produits de la hauteur du plant par sa largeur sur 2 axes perpendiculaires) en 1992 et 1993, l'accroissement relatif (1992–1993) et le nombre de plants morts en 1992 et 1993 ont fait l'objet d'une analyse de variance. Il n'y a pas de différence significative pour l'accroissement relatif et le

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* Correspondence and reprints
Tel. +41 1 632 5521; Fax. +41 1 632 1380; e-mail: thomas.sieber@fowi.ethz.ch

nombre de plants morts en 1992 et 1993. Par contre, la hauteur de la pousse et le nombre de bourgeons avant plantation, de même que le volume spatial des plants en 1992 et 1993, montrent des différences significatives selon les origines des plants. Une analyse de groupe sur ces effets révèle une plus grande différence de réponse parmi les collections les plus à l'est et au sud par rapport aux autres origines ; c'est-à-dire qu'il pourrait y avoir 3 races géographiques de Salal.

***Gaultheria shallon* / origine géographique / protocole expérimental**

1. INTRODUCTION

Gaultheria shallon Pursh is indigenous in the forests along the Pacific coastline of North America from northern California through British Columbia (BC) to the panhandle of Alaska, extending as much as 200 km eastward, and also occupies a single detached inland site at Kootenay Lake BC (Lat. 49°40' N / Long. 116°52' W). Salal is a particularly persistent, pervasive species with heavily cutinized foliage and tough stems that may reach several cm in diameter and 2.5 m in height [8]. The post-disturbance dominance of salal after logging and burning appears to be due to its ability to reoccupy the site rapidly and completely both above-ground and below-ground from rhizomes present before disturbance, and to resist invasion by other species by pre-emptying resources (nutrients) [11]. Proliferation of salal may render a replanting operation entirely unsuccessful. Thickets of salal may be sufficiently dense as to impede or deter human passage, with a crown sufficiently dense and intertwined in the best sites to support the weight of an average adult. By contrast, the plant is beneficial as a soil stabilizer after site disturbances. It serves as a minor wildlife feed, in commerce it provides green materials for use in floral arrangements and decorations and, increasingly, it is used as a landscape ornamental [8].

Long distance dispersal of salal occurs by seeds which are dispersed by animals, especially birds [22]. The most significant and effective form of short distance dispersal is through vegetative spread by rhizomes [6]. Salal populations are composed of a few to many interdigitated clones. The ramets of one single salal clone may occupy up to 29 m^2 of forest floor with up to 218 m total rhizome length [9]. There is likely considerable genetic and, consequently, phenotypic variation within and especially among populations. Morphometric diversity was studied for many plant species [3, 10, 15–17]. Middleton [12] screened species of *Gaultheria* and *Leucothoe* for a number of flavonoids and simple phenols and discussed the current intrageneric classification of *Gaultheria* and commented on the interspecific variation. Similarly, leaf and stem anatomical traits of 103 species of *Gaultheria* were surveyed [13]. However, intraspecific variation of *G. shallon* is not very well known despite the ecological and economic significance of this plant species. Therefore, we examined phenotypic within- and among-population variation of 3- to 4-year-old seedlings which originated from 24 different seed sources from throughout the area of distribution of *G. shallon*.

2. MATERIALS AND METHODS

2.1. Plant selection

In autumn 1988, salal fruits were randomly collected from several clones within an area of approximately 1 hectare either by the authors or by cooperators at each of 24 sites (*figure 1*) and stored for 4 to 7 months at 5 °C prior to seeding. Seeds were manually removed from the berries, tested for germinability and 24 seedlots were germinated and transplanted in 1:1 peat:vermiculite in 313A styro-blocks at 396 cavities per seedlot in spring 1989. Styro-blocks were misted in the greenhouses three times per day until seedlings emerged, then the blocks were moved to a lath house until used.

2.2. Experimental area and design

A flat area of 0.7 hectares on Vancouver Island (Lat. 48°49' N; Long. 124°30' W) was cleared of logging debris and stumps with heavy machinery. The experimental area was situated on the clearing at about 50 m a.s.l. and 32.5 km east of the Pacific coast. The soil type was sand-gravel intermixed with < 20% forest loam. The seedlings were planted in a randomized complete blocks design with six blocks (a–f) in April 1990. Each of the 24 seedlots was planted once in each block with 24 plants per seedlot and block (144 seedlings planted per seedlot, i.e. 3 456 total seedlings planted). The within-plot interplant distance was 1 m on both the north-south and the east-west axis. The between-plot interplant distance was 3 m on the same axes. The

Figure 1. Map showing the geographic origin of the seedlots.

within-block position of the seedlots was assigned at random.

Throughout the succeeding months, efforts were made to eliminate any natural salal that was detected. The experimental area was weeded at intervals as time permitted. MacMillan Bloedel Ltd. (Franklin Division) interplanted the experimental area with Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in spring 1992 to conform to British Columbian provincial guidelines which require replanting of areas from which the forest has been harvested.

2.3. Measurements and data analysis

Maximum plant height (only aerial plant part) [h_{pp} (pp stands for "prior to planting")] and the number of buds per plant (b) were recorded prior to planting. Thereafter, measurements were made in the spring of 1992 and 1993 of the following dimensions: plant height (h), maximum plant width on both the north-south (x), and the east-west axis (y). Missing values (some plants missing because of animal grazing or snow damage) were estimated using the method proposed by Snedecor and Cochran [18]. The "plant volume" ($v^{(92)}$ and $v^{(93)}$), defined as the product of the three variables h, x and y, was computed for each plant based on the 1992 and 1993 measurements. Additionally, relative growth increments z_{ijk} were calculated by dividing the growth increment of the plant volume between 1992 and 1993 by the plant volume in 1992 (equation 1):

$$z_{ijk} = \frac{v_{ijk}^{(93)} - v_{ijk}^{(92)}}{v_{ijk}^{(92)}} \quad i = 1, \ldots, 24; \; j = 1, \ldots, 6; \; k = 1, \ldots, 24. \qquad (1)$$

with

z_{ijk} relative growth increment of the plant volume from 1992 to 1993 of the k-th plant of the i-th seedlot in the j-th block;

$v_{ijk}^{(92)}$ volume of the k-th plant of the i-th seedlot in the j-th block in 1992;

$v_{ijk}^{(93)}$ volume of the k-th plant of the i-th seedlot in the j-th block in 1993.

The number of dead plants per seedlot in each block was counted in 1992 and 1993 (variables "$d^{(92)}$" and "$d^{(93)}$").

Plotwise mean and standard deviation of the variables h_{pp}, b, $v^{(92)}$, $v^{(93)}$ and z were computed and subjected separately to statistical analyses. With the exception of the relative growth increments, the data were subjected to transformations to obtain normally distributed residuals. Square-root transformation was used for counts, i.e.; the number of dead plants and the number of buds ($d^{(92)}$, $d^{(93)}$ and b), and the log transformation to the base e for the measurement data (h_{pp}, $v^{(92)}$ and $v^{(93)}$). The goodness of fit of general linear models, each of which included the blocks and the seedlots as factors and mean or standard deviation of one of the variables h_{pp}, b, $v^{(92)}$, $v^{(93)}$, z, $d^{(92)}$ and $d^{(93)}$ as dependent variables, was examined by means of analyses of variance (including analyses of residuals) (equation 2):

$$q_{ij} = \mu + \alpha_i + \beta_j + e_{ij}, \quad i = 1, \ldots, 24; \; j = 1, \ldots, 6; \qquad (2)$$
$$q = h_{pp}, b, v^{(92)}, v^{(93)}, z, d^{(92)} \text{ or } d^{(93)}.$$

with

q_{ij} mean or standard deviation of the variable q ($q = h_{pp}$, b, $v^{(92)}$, $v^{(93)}$, z, $d^{(92)}$ or $d^{(93)}$) of the i-th seedlot in the j-th block;

μ population mean;
α_i main effect of the i-th seedlot;
β_j main effect of the j-th block;
e_{ij} random deviation.

Tukey's method was employed for pairwise comparisons of seedlots.

The matrix containing the seedlot effects resulting from the ANOVA for the dependent variables h_{pp}, b, $v^{(92)}$, and $v^{(93)}$ was subjected to average linkage clustering using Euclidean distances [5] to summarize similarities among seedlots. The stopping rule proposed by Mojena [14] with $k = 3.25$ was used to select the appropriate number of clusters.

The analyses were performed using S-plus [20] and Systat 6.0 (Systat, Inc., Evanston, Illinois, USA).

3. RESULTS

3.1. Plant height and number of buds prior to planting

Significant among-seedlot differences existed with respect to both plant height and the number of buds prior to planting to the field (*table I*, *figures 2a and 2b*). In regard to plant height, seedlots 2, 3, 7, 12, 20 and 23 were significantly different from more than half of the seedlots according to Tukey's pairwise comparisons. The more northerly coastal seedlots 2, 3, 7 and 12 were significantly smaller and the more southerly coastal seedlots 20 and 23 significantly taller (*figure 2a*). A completely different situation arose when the seedlots were compared with respect to the number of buds. Tukey's pairwise comparisons showed that seedlots 6, 13, 14, 18 and 24 were significantly different from more than half of the seedlots. Seedlots 13, 14 and 24 had significantly fewer and seedlots 6 and 18 significantly more buds (*figure 2b*). The variables "plant height" and "number of buds" were not correlated. No block effects were observed prior to planting since the plants of each seedlot had been randomly assigned to the blocks (*table II*).

Table I. Summary table of untransformed means and standard deviations (SD) of all characteristics examined (n = 144 for each seedlot).

Seedlot number	Seedlings' height (cm)		Number of buds 1990 (b)		Extension (cm) in the...								Plant height (cm)				Total number of dead plants		Plant volume (cm^3)				Relative growth increment (cm)	
					North-south direction				East-west direction															
	1990 (h_{pp})				1992 ($x^{(92)}$)		1993 ($x^{(93)}$)		1992 ($y^{(92)}$)		1993 ($y^{(93)}$)		1992 ($h^{(92)}$)		1993 ($h^{(93)}$)		1992	1993	1992 ($v^{(92)}$)		1993 ($v^{(93)}$)		1992–1993 (z)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Sum	Sum	Mean	SD	Mean	SD	Mean	SD
1	13.7	2.8	3.4	1.2	23.6	12.2	38.7	18.3	22.2	8.9	40.3	19.0	12.5	3.8	15.6	3.8	4	11	10 495	11 469	36 053	35 049	4.56	4.08
2	11.8	2.5	4.0	1.4	26.5	13.1	48.2	20.0	26.8	13.0	47.4	20.7	10.8	3.4	13.0	3.4	2	6	10 690	12 166	36 756	30 322	4.18	3.93
3	12.3	2.4	3.5	1.4	22.1	9.9	40.0	17.8	22.1	10.5	38.2	14.3	11.4	3.7	16.3	3.7	3	6	8 012	9 543	34 211	37 114	4.41	4.44
4	16.3	2.8	4.6	1.5	26.4	12.4	45.2	19.9	25.9	11.8	45.0	20.6	15.0	4.7	19.8	4.7	3	15	15 586	18 651	57 283	56 872	4.82	5.92
5	15.9	2.4	4.1	1.7	26.6	11.5	46.3	21.5	27.7	12.9	45.5	18.9	13.8	4.9	16.9	4.9	4	6	14 654	17 230	46 813	43 929	3.88	4.51
6	14.9	2.6	5.7	1.9	19.7	9.2	34.1	14.2	19.8	9.0	35.1	15.3	11.9	3.8	17.4	3.8	8	10	6 964	7 571	31 198	30 467	5.05	4.51
7	12.5	2.4	4.6	1.8	24.7	10.0	45.0	19.3	24.6	10.9	42.0	18.7	11.4	3.4	14.1	3.4	0	2	8 774	9 244	33 515	31 263	5.00	7.97
8	14.5	2.5	3.6	1.4	25.6	11.0	42.6	18.6	24.9	10.1	41.9	17.4	13.1	4.4	17.1	4.4	2	9	11 892	11 940	42 453	43 368	4.39	9.52
9	15.0	2.7	3.1	1.3	24.4	9.4	43.9	19.6	25.3	9.7	43.1	17.9	12.4	4.3	17.3	4.3	4	8	10 339	9 391	48 757	47 582	4.12	3.76
10	16.6	3.1	3.0	1.3	26.9	12.0	47.6	21.8	26.3	11.8	46.1	22.6	14.4	4.4	19.0	4.4	4	5	13 841	14 386	56 664	61 808	3.90	2.98
11	14.0	2.5	4.5	1.9	21.7	10.2	39.7	17.6	21.7	8.9	41.4	19.2	11.5	3.2	13.5	3.2	1	12	8 096	9 306	32 745	32 431	4.94	8.39
12	12.8	2.5	3.9	1.7	24.8	11.4	45.9	20.5	25.2	12.3	46.6	21.0	11.5	3.7	16.0	3.7	2	3	10 631	13 291	43 108	38 955	5.93	7.06
13	13.3	2.7	2.9	1.2	23.7	10.0	43.0	16.3	22.5	8.3	41.5	15.2	13.5	4.5	19.8	4.5	7	9	9 646	9 473	42 261	35 939	6.00	6.30
14	16.2	2.7	2.9	1.3	27.4	13.2	44.1	17.7	26.0	9.8	43.9	18.4	12.7	4.3	16.8	4.3	2	11	13 014	14 821	41 292	36 811	4.20	6.14
15	14.8	2.6	3.6	1.6	27.3	11.5	46.0	21.6	26.7	11.6	46.3	21.1	11.2	3.5	14.5	3.5	4	5	10 968	11 534	40 668	39 946	3.87	3.79
16	15.9	2.6	3.7	1.6	29.6	10.9	52.7	20.7	30.0	10.8	51.7	20.2	13.2	4.0	19.8	4.0	1	3	14 700	11 575	67 000	59 530	4.80	4.79
17	16.3	3.1	3.5	1.2	25.2	10.0	45.2	17.3	25.3	10.6	44.2	15.2	13.9	4.5	19.6	4.5	4	9	13 240	13 145	52 247	40 588	5.12	4.63
18	15.4	3.4	5.0	2.0	25.4	12.2	43.6	21.6	25.6	11.7	41.9	21.5	12.6	4.2	16.1	4.2	5	6	12 176	14 994	40 939	44 310	4.19	5.16
19	14.8	3.8	4.6	1.6	28.4	13.2	52.8	22.7	29.8	13.7	50.4	20.9	13.7	4.3	18.9	4.3	1	4	15 868	15 496	60 896	51 519	7.22	25.29
20	18.4	3.0	3.6	1.6	27.9	12.1	50.4	22.2	27.7	11.3	47.8	19.6	15.0	5.1	20.3	5.1	3	8	16 463	18 077	64 853	64 418	4.47	5.04
21	15.7	3.1	3.3	1.1	28.8	12.9	49.1	21.4	27.7	12.7	49.7	21.9	12.4	3.8	17.0	3.8	5	9	13 621	14 447	54 445	55 489	5.00	8.34
22	16.0	2.7	4.4	1.7	22.1	9.5	42.6	19.3	21.5	8.9	40.0	17.0	12.4	3.8	15.5	3.8	4	7	7 919	7 938	36 633	34 685	5.07	4.93
23	18.2	2.9	4.3	1.6	31.8	11.4	51.9	17.7	31.9	11.5	51.3	19.1	17.0	5.1	22.1	5.1	4	4	21 827	17 919	74 716	59 685	3.46	3.42
24	15.2	2.5	2.6	1.8	21.7	10.1	32.1	15.4	21.2	9.3	35.6	19.6	11.7	3.8	15.3	3.8	6	21	7 248	8 299	23 698	24 280	3.91	4.97

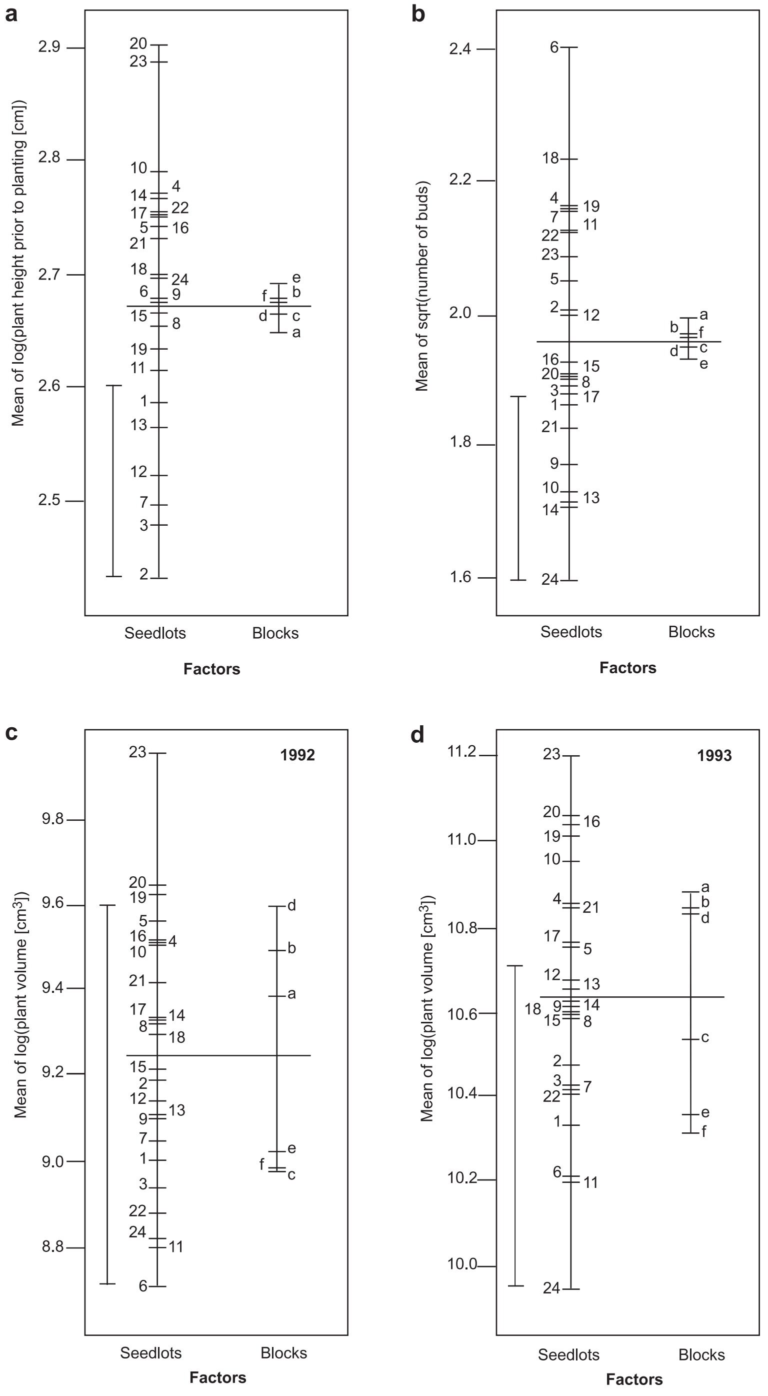

Figure 2. (a) Seedlot (1–24) and block (a–f) effects regarding plant height prior to planting (variable h_{pp}). The big horizontal line in the middle of the plots depicts the overall or population mean. The small horizontal lines on the two vertical lines indicate the block and seedlot means, respectively. The bar indicates the minimum distance between two seedlots to consider them significantly different based on Tukey's pairwise comparisons. The numbers correspond to the seedlot numbers in *figure 1*. (b) Seedlot and block effects regarding the number of buds prior to planting (variable *b*). For explanation of the plot see legend to *figure 2a*. (c) Seedlot and block effects regarding the plant volumes in 1992 (variable $v^{(92)}$). For explanation of the plot see legend to *figure 2a*. (d) Seedlot and block effects regarding the plant volumes in 1993 (variable $v^{(93)}$). For explanation of the plot see legend to *figure 2a*.

Table II. Summary of the p-values of all the performed ANOVAs.

Variables	Source of variability	
	Seedlots	Blocks
Seedlings' height (h_{pp})	< 0.0001	0.599
Number of buds (b)	< 0.0001	0.611
Plant volume 1992 ($v^{(92)}$)	< 0.0001	< 0.0001
Plant volume 1993 ($v^{(93)}$)	< 0.0001	< 0.0001
Relative growth increment (z)	0.375	0.255
Number of dead plants 1992 ($d^{(92)}$)	0.691	0.189
Number of dead plants 1993 ($d^{(93)}$)	0.255	0.012

3.2. Plant volume in 1992 and 1993

Significant among-seedlot and among-block effects were detected for the plant volume in both years as indicated by the results of the analyses of variance (*table II*). However, only the volumes of plants grown from seedlots 6 and 23 were significantly different from more than one of those grown from the other seedlots in 1992 according to Tukey's pairwise comparisons (*figure 2c*) (one significant pairing among 23 pairings, which is the number of pairwise comparisons per seedlot, is considered a random effect). In 1993, eight seedlots (6, 10, 11, 16, 19, 20, 23 and 24) were significantly different from more than one of the other seedlots; seedlots 6, 11 and 24 were smaller and 10, 16, 19, 20 and 23 were larger (*figure 2d*). Plants were larger in blocks a, b and d than in c, e or f in both years (*figures 2c and 2d*). Among-block differences were considerable for some seedlots especially in 1993, e.g. for seedlots 1, 6, 9, 11, 24.

The number of buds prior to planting did not consistently influence plant volume in the following years. Plants of seedlot 24 had fewest buds prior to planting and, subsequently, the smallest plants in 1992 and 1993. By contrast, seedlot 10 also had comparatively few buds but was one of the tallest seedlots in 1992 and 1993. Conversely, seedlot 6 had most buds prior to planting but belonged to the smallest seedlots in 1992 and 1993.

3.3. Cluster analysis of seedlot effects

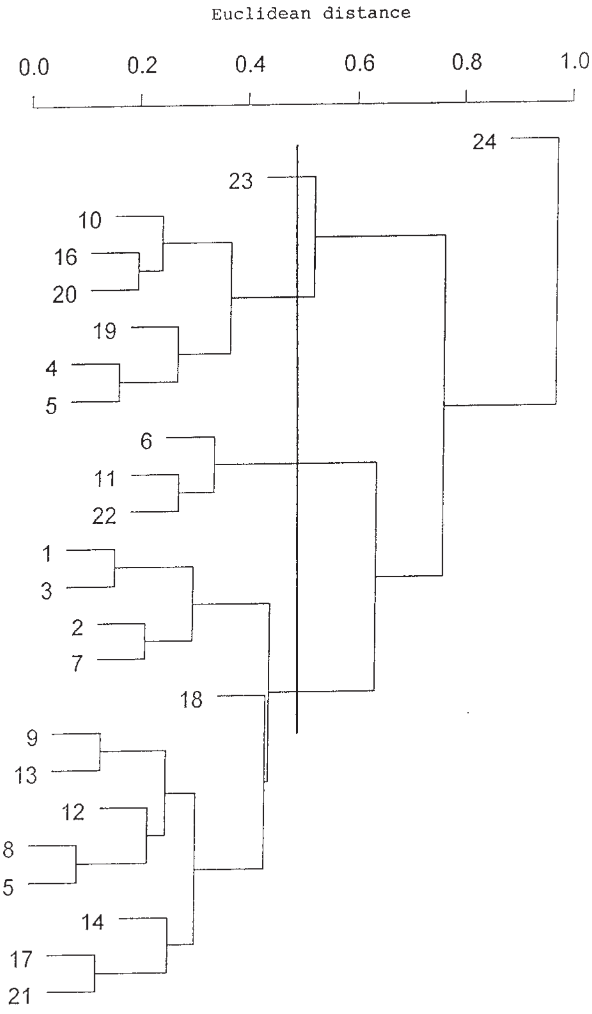

Figure 3. Dendrogram showing the result of the hierarchical cluster analysis (average linkage) of the seedlot effects resulting from the ANOVA on the variables "plant height prior to planting", "number of buds", "plant volumes in 1992 and 1993". The horizontal line cuts the dendrogram into the number of accepted clusters when Mojena's stopping rule with a $k = 3.25$ is applied. See *figure 1* for seedlot numbers.

Cluster analysis revealed five separate groups of seedlots using Mojena's (1977) stopping rule (*figure 3*): {24}, {23}, {4, 5, 10, 16, 19, 20}, {6, 11, 22}, and {1, 2, 3, 7, 8, 9, 12, 13, 14, 15, 17, 18, 21}. Seedlots 23 and 24 form a separate cluster each. Seedlot 24 from Kootenay Lake had fewest buds prior to planting and was the seedlot with the smallest plants in 1993 (*table I*). In contrast, seedlot 23 from Oregon was constantly taller than most of the other seedlots (*table I*). Plants of seedlots 6, 11, 22 were rather small but with many buds, and plants of seedlots 4, 5, 10, 16, 19, and 20 were above average in size. The size and the number of buds of the seedlots in the fifth and biggest cluster (seedlots 1, 2, 3, 7, 8, 9, 12, 13, 14, 15, 17, 18, and 21) were mostly below average.

3.4. Growth increment and number of dead plants

Neither seedlot nor block effects were detected regarding the relative growth increment between 1992 and 1993 (*table II*). Similarly, seedlots didn't differ with respect to the number of dead plants in both years (*table II*). The blocks did, however, in 1993.

The seedlots had no differential effect on the standard deviations of any variable except h_{pp} (plant height prior to planting).

4. DISCUSSION

Intraspecific phenotypic variation and, thus, probably also genotypic variation among seed sources of salal is limited. Consistent differences existed only between each of the two seedlots 23 and 24 and the remainder of the seed sources. Seedlot 24 was characterized by plants of average size prior to planting but had fewest buds and was one of the smallest seedlots in 1992 and 1993. Seedlot 24 originated from a mountainside (at 1 220 m a. s. l.) above Kootenay Lake, which is about 600 km from the coast in the interior of mainland B.C. This contrasts with the other collection sites, which were all within 100 km of the coast and not above 250 m a. s. l. The region of Kootenay Lake is characterized by colder winters and greater accumulations of snow than regions close to the coast. Adaptation to a colder climate may explain the small plant size exhibited by this seedlot. The salal populations in the Kootenay region probably are reproductively well separated from those at the coast; i.e. gene flow between populations in the two regions is low. Thus, the Rocky mountain (Kootenay) and coastal populations perhaps belong to two different geographical and possibly also ecological races. Similarly, coastal and inland populations of wild beet (*Beta vulgaris* L.) from Sicily could be discriminated based on petiole length and period of flowering but differences were small [10].

Plants grown from seeds of seedlot 23 were consistently taller than most of the other seedlots during the whole experiment (*table I*). It was also the seedlot from farthest south (*figure 1*). This seedlot may have adapted to a warmer climate and consequently tends to a greater growth increment per time interval than the seedlots from further north, at least in the early stages of development. Similarly, other seedlots from southern sites (Oregon) also showed a tendency to give rise to taller plants. In contrast, the growth performance of seedlot 15 from farthest north was not reduced compared to seedlots from sites more to the south. It behaved in a similar manner to some seedlots from Vancouver Island. Likewise, there were some seedlots from Vancouver Island which had dimensions similar to those collected in Oregon, e.g. seedlots 4 and 5 from the west coast of Vancouver Island. Seedlots 4 and 5 were expected to cluster with seedlot 6, which originated also from the west coast of Vancouver Island in a distance of about 35 km from the collection site of seedlot 4, but they clustered with seedlots 19, 16 and 20 from Oregon. The differences between the group of the two very similar seedlots 4 and 5 and seedlot 6 were considerable (*figures 2c and 2d*) although the aerial distance between the collection sites of seedlots 4 and 6 was small and of the same magnitude as the one between 4 and 5. At least two possible explanations for the phenotypic differences between these two groups of seed sources can be given. Either the founder plants at these sites originated from pheno- and genotypically different seed sources or fertilization occurred from genotypically different pollen. The seeds of salal are mainly dispersed by animals [22]. Birds may carry the seeds for some dozens of km in a few hours. Thus, it should not be a surprise to find genotypically closely related clones of salal several hundreds of km apart and far distantly related clones in adjacent plots.

A rather rough approximation of biomass was used in this study to characterize the plant individuals whereas extensive measurements and/or counts of various traits of single leaves and/or inflorescences are usually employed for morphometric analyses [2, 4, 15, 16]. Nybom et al. [16] detected high variability of the leaf morphology in *Rosa dumalis* but not in *R. rubiginosa* or *R. villosa*. Nevertheless, differentiation of the three species was possible. Murrell [15] found intermediate forms between two morphological extremes among dwarf dogwood species. Between 91 and 98% (66.8% for a group of hybrids) of the specimens were, however, classified correctly into five groups which correspond to three species and two groups of hybrids thereof using canonical discriminant analysis. Compton and Hedderson [3] detected a number of clear differences in shape and size of plant organs of *Cimicifuga foetida* L. between four geographic areas (Siberia and northern Mongolia, central and western China, Kashmir and western Tibet, middle Europe) and, thus, recognized four geographically delimited species. We can not exclude the possibility that the inclusion of measurements of leaf and inflorescence characters would have led to a different assignment of the salal seed sources to races or morphotypes.

Within-seedlot variation was similar for all seedlots as expressed by the non-significant differences of the standard deviations for most variables. Significant differences were observed only for "height prior to planting" (h_{pp}). Seedlots 18 and 19 showed comparatively high standard deviations (*table I*). This may reflect a higher genetic variability, probably based on a higher degree of recombination, at the sites of origin of these seedlots.

Block effects were significant. The overall performance of the plants was better in blocks a, b and d than in the other three blocks. Differences in microclimatic conditions and water availability may have been responsible for the observed difference in plant performance although site preparation was done very carefully to get soil conditions as homogenous as possible in the whole experimental area. However, variance analysis is the method of choice to separate block effects from other effects, which are the seedlot effects in our study, and, thus, the differences among seedlots presented in this paper are equally valid for all blocks.

Herbarium specimens [1–3, 15], freshly collected specimens [17] or plants grown from seeds in randomized designs in the field [7, 10, 16] are used to study intra- and interspecific variation of morphology. Examination of plants grown from seed sources in the same field has some advantages. For example, direct influences of specific conditions at the site of origin are eliminated and, thus, allow one to make appropriate comparisons based upon plant morphology. González-Andrés et al. [7] successfully used this approach to examine variation within and among Mediterranean populations of woody *Medicago* spp. Similarly, Nybom et al. [16] studied intra- and interspecific variation of the leaf morphology of three dogrose species using plants planted in a randomized design.

In conclusion, this study should be considered a preliminary morphometric analysis of salal. It quantifies both the probability that variation in the species *Gaultheria shallon* does exist and estimates the extent of that variation, establishing the required basis for further research. Extensive measurements and counts of various characteristics of leaves and inflorescences are needed to study within-ramet, within-clone and range-wide variation in naturally grown populations of salal. These measurements can then be compared with equivalent morphometric data of siblings planted in random designs to get a more complete picture of the morphological variability of *G. shallon*. In addition, other methods like those used in molecular genetics (AFLPs, isozyme analysis, microsatellites, RAPDs) might serve to study intraspecific variation and to elucidate the population structure within sites [19, 21].

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