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REPRESENTATION OF DOUGLAS-FIR AND WESTERN HEMLOCK FAMILIES IN SEEDLING CROPS AS AFFECTED BY SEED BIOLOGY AND NURSERY CROP MANAGEMENT PRACTICES

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ABSTRACT

The impact of container-nursery management practices on the genetic representation of seedling crops of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were evaluated. Two experiments, one for each species, were conducted to determine the cumulative effects of seed-donor variation on germination parameters (percent and speed) and their interaction with container-nursery practices of thinning and culling on the genetic representation of each seed-donor in the resultant seedling crops. The experimental work was conducted on seedlots that were represented with equal contribution of seeds from 15 seed orchard parents (families). In each experiment, a total of 25,920 seeds were sown in four different arrangements to compare the crop development under single-, two-, and three-seeds per cavity (seeds within cavity were selected randomly among the 15 families) and family blocks (seeds within block belonged to one family). This experimental design allowed determination of inter- and intra-family competition. Within each experiment, a total of 15,015 cavities were used and the identity of every seed within every cavity within each arrangement was maintained throughout the study. Families were compared based on: 1) changes in their rank order from seedling emergence (germination) to post-thinning and post-culling status, and 2) relative performance of each family from seed contribution to seedling production. Changes were observed in both assessments (i.e., rank and relative contribution). Path analysis was used to determine the percent contribution of each factor to seedling production. It was determined that seedling germination, germinant thinning, and seedling culling all affected seedling production, indicating the presence of several consecutive unintentional bottlenecks in the process. Family sowing with culling standards that recognize the growth differences among families in the nursery and single seed sowing after understanding the inter-/intra-family competition are recommended for seedling production to maintain seedling-crop family representation.

Key words: Family representation, container nurseries, germination, thinning, culling, *Pseudotsuga menziesii*, *Tsuga heterophylla*, single-, multiple- and single family sowing.

INTRODUCTION

Container nurseries must strive to balance production and cost, thus maximizing the number of plantable seedlings per unit area is a major goal for reaching maximal economic potential (TINUS & MCDONALD 1979). Biological factors such as seed germination could substantially reduce nursery output due to the presence of empty cavities. This is generally avoided by multiple sowing to ensure, at least, the presence of one germinant per cavity (VYSE & RUDD 1974). However, thinning, the manual removal of excess germinants, is usually necessary following multiple sowing.

EL-KASSABY and THOMSON (1996) evaluated the impact of container-nurseries management practices of germinants thinning and seedling culling and the inherent differences in reproductive output and seed biology among several Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed-donors on family representation of the resultant seedling crop. They maintained the identity of every single seed of 42,000 sown in 14,000 seedling cavities throughout the duration of the trial, so family performance could be monitored. They concluded, after observing substantial over- and under-representations of families in the resultant seedling crop, that when multiple sowing of bulked seedlots was practiced, the commonly observed reproductive output imbalance among seed orchard's seed-donors was further exacerbated by thinning of excess germinants and culling of sub-standard seedlings. Thus, the common assumption that container-nursery seedling crops produced from bulked seed-orchard seedlots would maintain the same genetic representation and gain as the orchard parents was violated. EL-KASSABY and THOMSON (1996) recommended the use of either single-seed sowing of bulked seedlots or multiple sowing on clonal/family basis. Their recommendation, however, did not consider possible changes that might take place due to inter- (when single-seed sowing in multi-family blocks is used) and intra-family (when sowing on clonal/family basis is considered) competition.

The present study was conducted to evaluate the effects of: (1) parental variation in germination parameters (i.e., germinants emergence percent and speed), (2) difference between inter- and intra-family competition, and (3) the interaction of these parameters with container-nursery practices of thinning and culling, and their effect on the genetic representation of parents in the resultant seedling crops. Two studies were conducted using one pioneer (Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and one late-succession (western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) species.

MATERIALS AND METHODS

Seed source

Seed crops were harvested from 15 unrelated Douglas-fir (1995) and western hemlock clones (1996) (hereafter "families"). The Douglas-fir and western hemlock clones are growing in two separate seed orchards at Saanichton, British Columbia. Cones were harvested by individual families, then stored in burlap sacks in an open-sided, freely-ventilated, shed for eight weeks prior to seed extraction. Seeds were extracted and cleaned by family in a commercial facility under operational conditions. In each species trial, families contributed equal numbers of seeds in four experimental designs (see below).

Nursery studies

The two (Douglas-fir and western hemlock) nursery studies were conducted in a commercial container-seedling nursery, using container blocks (Styroblock® container 415C: 91, 130 ml cavities/block), soil mixes, irrigation, heating, and fertilization regimes similar to those operationally applied for growing these species in British Columbia. For each species, the nursery trial was conducted using the following design:

a) 40 blocks sown with 3 seeds/cavity. Seeds from the 15 families were randomly assigned within each cavity and among cavities (10,920 seeds),

b) 40 blocks with 2 seeds/cavity. Seeds from the 15 families followed the same randomization as above (7,280 seeds),

c) 40 blocks with 1 seed/cavity. Seeds from the 15 families were randomly assigned among cavities (3,640 seeds), and

d) 45 blocks, 3 blocks per family, with 1 seed/cavity. Seeds from one family were used within each block (4,095 seeds).

A total of 165 blocks with 91 cavities/block (15,015 cavities in all) were sown for each species. Blocks were randomized and were surround by a single row of buffer blocks to eliminate the edge effect. Douglas-fir seeds were stratified for five weeks following the recommendation of EDWARDS and EL-KASSABY (1995) to reduce dormancy-caused variation in germination and western hemlock was stratified for three weeks following the International Seed Testing Association (1985).

The identity of every seed within every family within each cavity was maintained during the course of the study. Seeds were allocated to the cavities within the 165 blocks for each species using a random-number generator. The Douglas-fir and western hemlock trials were conducted during the 1996/97 and 1997/98 growing seasons, respectively. For the multiple-sowing treatment, seeds within every cavity were kept separate by inserting a 2.5 cm-deep, two- or three-pronged divider that partitioned the cavity into two or three equal compartments for the 2- and 3-seed per cavity treatments, respectively.

Following sowing (Douglas-fir: 6–8 March, 1996 and western hemlock: 25–27 February, 1997), daily seedling emergence and total emergents ("post-emergance") per family were recorded (Tables 1 and 2). Thinning was conducted (April 4, 1996 and May 5, 1997 for Douglas-fir and western hemlock, respectively) following standard operational nursery methods, with a thinning crew that was not informed about the objectives of the study. The common practice of thinning is to leave one germinant per cavity. Most observers indicate that the largest germinant is always left and smaller ones are removed. Following thinning, the number of remaining germinants ("post-thinning") per family was recorded (Tables 1 and 2). At the end of the study (December 18, 1996 and November 17–25, 1997 for Douglas-fir and western hemlock, respectively), survival data on every seedling was recorded (Tables 1 and 2), and seedlings were labeled by their family number before removal from the blocks. Seedlings were then culled according to established standards for each species. The Douglas-fir culling standards were below 18 and over 34 cm for height and below 2.8 mm for caliper, however, seedlings that exceeded 34 cm in height were accepted if their caliper was equal to or higher than 3.3 mm. The western hemlock culling standards were below 15 and over 35

Table 1. Number of seeds, emergents and their emergence %, remaining (post-thinning), survival, and seedlings (crop) for the 15 Douglas-fir families for the four nursery treatments (rank).

Experiment	Family No.	No. of seeds	No. of emergents		Emergence %	Post thinning		Survival		Crop	
1-seed/cavity	1	242	232	(5)	95.9	–[1]		232	(5)	225	(5)
	2	242	235	(2)	97.1	–		233	(2)	231	(1)
	3	242	233	(4)	96.3	–		233	(2)	223	(7)
	4	242	229	(9)	94.6	–		228	(9)	220	(11)
	5	242	231	(7)	95.5	–		231	(6)	223	(7)
	6	242	227	(11)	93.6	–		226	(11)	218	(13)
	7	242	234	(3)	96.7	–		234	(1)	229	(2)
	8	242	224	(14)	95.6	–		222	(14)	214	(14)
	9	242	236	(1)	97.5	–		233	(2)	228	(3)
	10	242	227	(11)	93.6	–		225	(12)	224	(6)
	11	242	227	(11)	93.6	–		224	(13)	220	(11)
	12	242	216	(15)	89.3	–		214	(14)	202	(15)
	13	242	232	(5)	95.9	–		231	(6)	223	(7)
	14	242	229	(9)	94.6	–		228	(9)	222	(10)
	15	242	231	(7)	95.5	–		231	(6)	226	(4)
2-seed/cavity	1	485	467	(2)	96.3	301	(1)	301	(1)	287	(1)
	2	485	460	(8)	94.8	255	(5)	255	(4)	252	4)
	3	485	464	(5)	95.7	231	(11)	231	(11)	221	(11)
	4	485	463	(6)	95.5	246	(8)	246	(8)	235	(8)
	5	485	462	(7)	95.3	252	(6)	252	(6)	243	(5)
	6	485	453	(11)	93.4	252	(6)	252	(6)	240	(7)
	7	485	446	(13)	92.0	282	(2)	282	(2)	268	(2)
	8	485	436	(14)	89.9	216	(13)	216	(13)	201	(13)
	9	485	465	(3)	95.9	237	(10)	237	(10)	225	(10)
	10	485	465	(3)	95.9	222	(12)	221	(12)	214	(12)
	11	485	469	(1)	96.7	256	(4)	253	(5)	243	(5)
	12	485	433	(15)	89.3	174	(15)	174	(15)	172	(15)
	13	485	457	(9)	94.2	244	(9)	244	(9)	231	(9)
	14	485	451	(12)	93.0	184	(14)	184	(14)	175	(14)
	15	485	454	(10)	93.6	272	(3)	272	(3)	267	(3)
3-seed/cavity	1	728	714	(1)	98.1	343	(1)	343	(1)	340	(1)
	2	728	688	(9)	94.5	236	(9)	235	(9)	232	(8)
	3	728	704	(3)	96.7	223	(10)	221	(10)	215	(10)
	4	728	705	(2)	96.8	273	(4)	273	(4)	267	(4)
	5	728	687	(10)	94.4	239	(7)	239	(7)	236	(7)
	6	728	674	(13)	92.6	267	(5)	267	(5)	253	(5)
	7	728	657	(14)	90.2	280	(2)	280	(2)	273	(2)
	8	728	690	(7)	94.8	220	(11)	220	(11)	214	(11)
	9	728	692	(5)	95.1	210	(3)	210	(13)	205	(13)
	10	728	689	(8)	94.6	218	(12)	218	(12)	213	(12)
	11	728	691	(6)	94.9	253	(6)	253	(6)	249	(6)
	12	728	654	(15)	89.8	188	(14)	188	(14)	185	(14)
	13	728	695	(4)	95.5	237	(8)	237	(8)	226	(9)
	14	728	686	(11)	94.2	174	(15)	173	(15)	170	(15)
	15	728	684	(12)	94.0	277	(3)	276	(3)	271	(30)

[1] Thinning was not conducted in these treatments.

cm for height and 2.4 mm for caliper, however seedlings that exceeded 35 cm in height were accepted if their caliper was equal to or higher than 3.3 mm. The culled seedlings were recovered, their family designation was identified and each family's seedling crop ("post-culling") was determined (Tables 1 and 2).

Table 1. (Continued)

Experiment	Family No.	No. of seeds	No. of emergents		Emergence %	Post thinning	Survival		Crop	
Family-block	1	273	270	(11)	98.9	–[1]	268	(10)	262	(4)
	2	273	272	(5)	99.6	–	271	(6)	256	(11)
	3	273	265	(14)	97.1	–	26	(12)	258	(7)
	4	273	273	(1)	100.0	–	272	(2)	262	(4)
	5	273	273	(1)	100.0	–	272	(2)	264	(3)
	6	273	263	(15)	96.3	–	253	(15)	241	(15)
	7	273	270	(11)	98.9	–	267	(11)	257	(10)
	8	273	271	(9)	99.3	–	269	(7)	260	(6)
	9	273	273	(1)	100.0	–	272	(2)	270	(2)
	10	273	272	(5)	99.6	–	269	(7)	258	(7)
	11	273	273	(1)	100.0	–	273	(1)	272	(1)
	12	273	267	(13)	97.8	–	262	(14)	252	(12)
	13	273	272	(5)	99.6	–	272	(2)	250	(13)
	14	273	271	(9)	99.3	–	269	(7)	243	(14)
	15	273	272	95)	99.6	–	263	(13)	258	

[1] Thinning was not conducted in these treatments.

Families within each species were compared based on: 1) changes in their rank order from post-emergence to post-thinning and post-culling (for 2- and 3-seeds per cavity treatments) and from post-emergence to post-culling (for 1-seed per cavity and family-blocks treatment), and 2) relative performance from seed contribution to seedling production. Relative performance was determined as the % deviation from the expected equal representation among families to the resultant seedling crop. Since families contributed equally at the seed stage at the start of the experiment, then it is expected that families' seedling crop should be equal. For example: if a specific family contribution to the seedling crop exceeded the expected under equal contribution, then this family will show positive relative contribution and visa versa.

Seed emergence and emergence speed

Seed emergence, defined as the complete appearance of the seed coat above the artificial soil level, was monitored and recorded for each seed throughout the trial. For Douglas-fir and western hemlock the maximal emergence period was 30 and 44 days, respectively. These periods exceeded the time required for standard germination tests by 9 and 16 days for Douglas-fir and western hemlock, respectively (International Seed Testing Association 1985).

Emergence speed was determined analytically for each species using THOMSON and EL-KASSABY (1993) R_{50}' index (Table 3). This index (R_{50}' = the number of days required for 50 % of the germinating seeds to germinate) is different from the two most commonly used seed germination speed parameters namely: R_{50} (the number of days required for 50 % of the seeds to germinate (CHING 1959)) and PV (a mathematical expression of the break of the sigmoid curve representing a typical course of germination (CZABATOR 1962)) in removing the confounding effect caused by the relationship between germinative speed and the totality of germination.

Data analyses

WRIGHT's (1921) path analysis was used to analyze causal relationships among the different stages of the experimental trials for the 2- and 3-seeds per cavity arrangements (Equation 1). Seedling production (SP) is considered to be the product of seed germination (G), thinning (T), survival (S), and culling (C).

$$SP = G \times T \times S \times C \qquad [1]$$

Equation 1 can be rewritten by transformation in logarithmic values to:

$$\text{Log}\,(SP) = \text{Log}\,(G) + \text{Log}\,(T) + \text{Log}\,(S) + \text{Log}\,(C)[2]$$

The relative contribution (C_i), which measures the effect of the predictors G, T, S, and C on the response SP when other traits are taken into account, can be computed as

$$C_G = P_G \times r_{G.SP},$$
$$C_T = P_T \times r_{T.SP},$$

Table 2. Number of seeds, emergents and their emergence %, remaining (post-thinning), survival, and seedlings (crop) for the 15 western hemlock families for the four nursery treatments (rank).

Experiment	Family No.	No. of seeds	No. of emergents		Emergence %	Post thinning		Survival		Crop	
1-seed/cavity	1	242	232	(9)	95.9	–		229	(5)	211	(1)
	2	242	231	(10)	95.5	–		227	(8)	208	(4)
	3	242	231	(10)	95.5	–		227	(8)	188	(11)
	4	242	216	(14)	89.3	–		210	(14)	182	(12)
	5	242	238	(2)	98.3	–		232	(2)	206	(5)
	6	242	236	(4)	97.5	–		231	(4)	189	(10)
	7	242	234	(6)	96.7	–		225	(11)	176	(14)
	8	242	226	(13)	93.4	–		214	(13)	158	(15)
	9	242	236	(4)	97.5	–		234	(1)	204	(6)
	10	242	234	(6)	96.7	–		228	(7)	211	(1)
	11	242	213	(15)	88.0	–		208	(15)	181	(13)
	12	242	237	(3)	97.9	–		232	(2)	204	(6)
	13	242	234	(6)	96.7	–		222	(12)	192	(9)
	14	242	231	(10)	95.5	–		229	(5)	209	(3)
	15	242	239	(1)	95.5	–		227	(8)	193	(8)
2-seed/cavity	1	485	466	(8)	96.1	299	(4)	298	(4)	252	(2)
	2	485	474	(3)	97.7	224	(9)	223	(9)	176	(8)
	3	485	463	(12)	95.5	287	(5)	284	(5)	195	(6)
	4	485	421	(15)	86.8	193	(12)	193	(12)	149	(11)
	5	485	474	(3)	97.7	188	(13)	185	(14)	158	(10)
	6	485	476	(1)	98.1	306	(3)	306	(3)	194	(7)
	7	485	465	(10)	95.9	187	(14)	187	(13)	137	(13)
	8	485	455	(13)	93.8	252	(7)	250	(7)	169	(9)
	9	485	475	(2)	97.9	259	(6)	258	(6)	207	(4)
	10	485	474	(3)	97.7	316	(2)	315	(2)	272	(1)
	11	485	442	(14)	91.1	141	(15)	139	(15)	112	(5)
	12	485	471	(6)	97.1	200	(11)	200	(10)	149	(11)
	13	485	468	(7)	96.5	236	(8)	235	(8)	199	(5)
	14	485	466	(8)	96.1	324	(1)	322	(1)	247	(3)
	15	485	465	(10)	95.9	201	(10)	197	(11)	135	(14)
3-seed/cavity	1	728	696	(9)	95.6	287	(4)	285	(4)	249	(3)
	2	728	701	(7)	96.3	230	(8)	228	(8)	197	(7)
	3	728	688	(11)	94.5	259	(6)	257	(6)	202	(6)
	4	728	646	(14)	88.7	208	(12)	208	(12)	170	(11)
	5	728	700	(8)	96.2	180	(14)	179	(14)	169	(12)
	6	728	708	(2)	97.3	315	(3)	312	(3)	222	(5)
	7	728	707	(3)	97.1	213	(10)	211	(11)	166	(13)
	8	728	681	(13)	93.5	236	(7)	233	(7)	175	(10)
	9	728	711	(1)	97.7	272	(5)	272	(5)	228	(4)
	10	728	706	(4)	97.0	342	(2)	340	(2)	318	(1)
	11	728	639	(15)	87.8	122	(15)	120	(15)	100	(15)
	12	728	702	(5)	96.4	192	(13)	192	(13)	158	(14)
	13	728	685	(12)	94.1	218	(9)	216	(9)	194	(8)
	14	728	692	(10)	95.1	349	(1)	348	(1)	310	(2)
	15	728	702	(5)	96.4	213	(10)	212	(10)	179	(9)

[1] Thinning was not conducted in these treatments.

$$C_S = P_S \times r_{S.SP}\text{, and}$$
$$C_C = P_C \times r_{C.SP} \qquad [3]$$

where: P_G, P_T, P_s, and P_C are the path coefficients of G, T, S, and C, respectively, which measure the direct effect of the predictors (G, T, S, and C) on the response (SP), and $r_{G.SP}$, $r_{T.SP}$, $r_{S.SP}$, and $r_{C.SP}$ are the correlation coefficients between G, T, S, and C and SP, which

Table 2. (Continued)

Experiment	Family No.	No. of seeds	No. of emergents		Emergence %	Post thinning	Survival		Crop	
Family-block	1	273	273	1	100.0	–[1]	273	1	238	5
	2	273	273	1	100.0	–	273	1	235	8
	3	273	272	5	99.6	–	272	4	241	2
	4	273	266	14	97.4	–	266	12	226	11
	5	273	272	5	99.6	–	272	4	239	4
	6	273	273	1	100.0	–	273	1	205	13
	7	273	270	12	98.9	–	269	10	214	12
	8	273	265	15	97.1	–	265	14	190	15
	9	273	272	5	99.6	–	271	6	229	10
	10	273	271	10	99.3	–	271	6	241	2
	11	273	267	13	97.8	–	264	15	202	14
	12	273	272	5	99.6	–	271	6	251	1
	13	273	272	5	99.6	–	269	10	236	7
	14	273	273	1	100.0	–	266	12	233	9
	15	273	271	10	99.3	–	271	6	237	6

[1] Thinning was not conducted in these treatments.

Table 3. Germination speed[1] (R'_{50})for the 15 Douglas-fir (Df) and western hemlock (Hw) families used in the nursery study.

Family	1	2	3	4	5	6	7	8	9	1o	11	12	13	14	15
Df	8.47	9.92	10.17	9.66	11.19	9.45	10.31	10.81	11.18	11.40	10.01	11.05	11.36	11.09	10.28
Hw	21.53	21.72	22.82	22.07	21.83	19.93	24.73	23.11	23.04	20.91	20.61	21.29	21.33	21.04	21.58

[1] R_{50} = the number of days required for 50 % of the germinating seeds to germinate (THOMSON & EL-KASSABY 1993).

measure the direction and magnitude of the linear relation between the predictors and the response.

Due to the absence of thinning in the 1-seed per cavity and family-block treatments, these equations were further reduced to:

$$SP = G \times S \times C \quad [4]$$

$$\text{Log}(SP) = \text{Log}(G) + \text{Log}(S) + \text{Log}(C) \quad [5]$$

$$C_G = P_G \times r_{G.SP},$$
$$C_S = P_S \times r_{S.SP}, \text{ and}$$
$$C_C = P_C \times r_{C.SP} \quad [6]$$

RESULTS

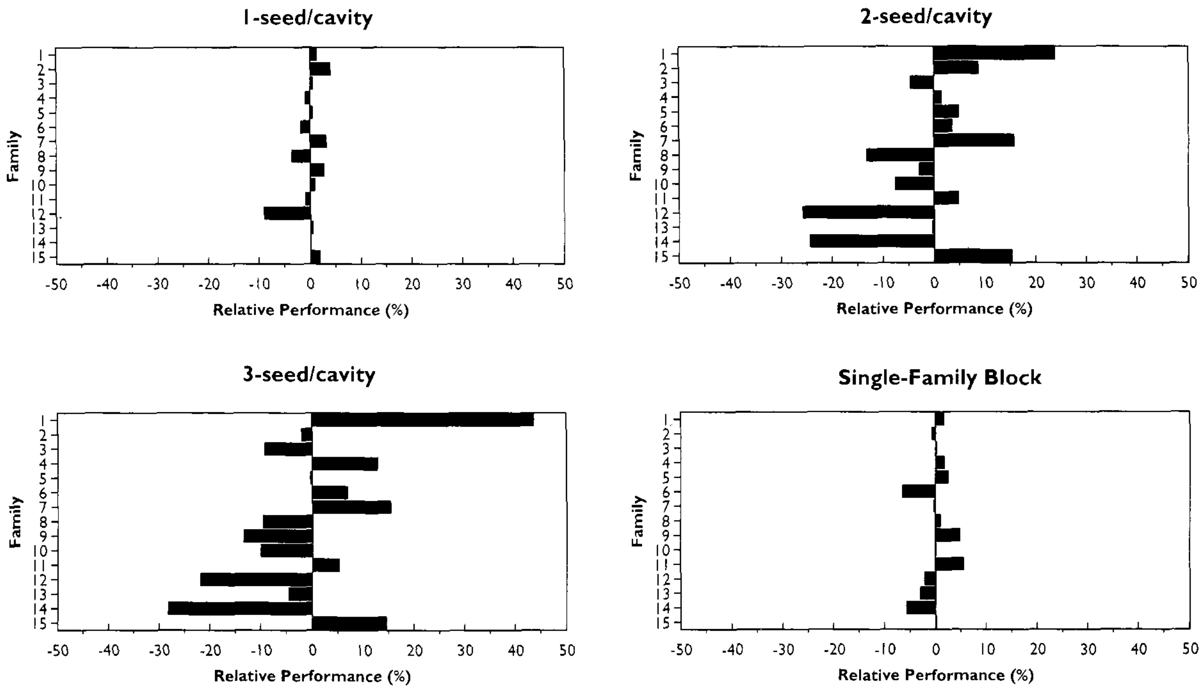
Douglas-fir

The nursery trial produced emergence rates of 94.8, 94.1, 94.4 and 99.1 % for 1-, 2-, 3-seeds/cavity and family block treatments, respectively. As expected, after thinning, 49.8 and 33.3 % of the total seeds used remained in the 2- and 3-seeds/cavity treatments, respectively, thus usually securing the presence of at least one germinant per cavity. The occupancy rate (i.e., cavities containing a single germinant) over the four treatments was very high and ranged between 98.1 (family block) and 99.9 % (3-seeds/cavity). Mortality (i.e., loss of germinants/seedlings) between emergence/thinning and pre-culling was very low and ranged between 4 (0.11 %) and 41 (1.0 %) germinant/seedlings for the 2-seed/cavity and family block treatments, respectively. Culling yielded 3,326 (91.4 %), 3,474 (95.4 %), 3,549 (97.5 %), and 3,863 (94.3 %) plantable seedlings for the 1-, 2-, 3-seeds/cavity, and family block treatments, respectively. The final recovery rate was 94.7 % of the 15,015 cavities sown.

Comparing the family rank, based on the number of germinants/seedlings, between seed emergence and post-thinning for treatments that required thinning (i.e., 2- and 3-seeds/cavity) indicated that only 2 and 3 families out of the 15 studied maintained the same ranking for the 2-and 3-seeds/cavity treatments, respectively (Table 1). In the 2-seeds/cavity treatment, the remaining 13 families experienced 6 negative and 7 positive rank changes indicating that thinning has affected the genetic representation of these families (Table 1). The maximal rank changes (from 3 after seed emergence to 12 post-thinning, for a change of -9 and from 13 after seed emergence to 2 post-thinning, for a change of +11) were observed for families # 10 and # 7 (Table 1). Similarly, in the 3-seeds/cavity treatment, the remaining 12 families experienced 7 negative and 5 positive rank changes, indicating that thinning, once again, has affected the genetic representation of these families (Table 1). The maximal rank change (from 5 after seed emergence to 13 post-thinning, for a change of -8 and from 14 after seed emergence to 2 post-thinning, for a change of +12) were observed for families # 9 and # 7 (Table 1). However, the fastest and slowest families to germinate (#1 and # 10, respectively, see Table 3 for their R_{50}' values) ranked as number 1 and number 12 after thinning for the two treatments.

From the 1-seed/cavity treatment, family relative performance after culling gave 10 and 5 families with higher and lower output, respectively, than expected (Fig. 1). Family number 12 experienced the greatest relative performance reduction (9 %). The level of distortion in family relative performance increased steadily with increase in the number of seeds sown per cavity. For example, the 2-seeds/cavity treatment produced 8 and 7 families with higher and lower output, respectively, than expected (Fig. 1). The level of relative performance reduction was high and reached 26, 24, and 13 % for families number 12, 14, and 8, respectively. This under-representation was associated with appreciable over representation of 24, 16, and 15 % for families 1, 7, and 15, respectively. The 3-seeds/-cavity treatment produced the greatest distortion: the relative performance reduction reached 22 and 28 % for families number 12 and 14, respectively (Fig. 1). Similarly, over-representation was found and in most cases the over-representation was due to the same families (1,7, and 15) (Fig. 1). Family number 1 reached the unprecedented rate of 24 and 44 % over-representation for 2- and 3-seed/cavity treatments, respectively (Fig. 1). Finally, the single-family-block treatment produced the lowest imbalance in relative performance among all treatments, yielding 9 and 6 families with higher and lower output, respectively, than expected (Fig. 1). However, the maximal distortion amounted to 6 % for both over- (family 11) and under- (families 6 and 14) representation.

Path analysis indicated that variation in seedling production was explained mostly by family variation in germination percent and thinning and culling rates (Table 4). Survival did affect final seedling production only in the single-family-block treatment, where intra-family competition contributed to 18 % of the total variation (Table 4). For the remaining three treatments (1-, 2-, and 3-seeds/cavity) with random arrangement of families within blocks, survival had little or no effect on final seedling production and exhibited the smallest



1-seed/cavity

2-seed/cavity

3-seed/cavity

Single-Family Block

Figure 1. Relative performance of the 15 Douglas-fir families from seed to seedlings.

Table 4. Contribution coefficients corresponding to the relations: SP = G x T x S x C for 2-and 3-seeds/cavity and SP= G x S x C for 1-seed/cavity and single-family-block treatments for Douglas-fir and western hemlock (see Materials and Methods).

Douglas-fir	Proportion contribution			
	Germination (g)	Thinning (t)	Survival (s)	Culling (c)
1-seed / cavity	0.65	–[1]	0.04	0.31
2-seeds / cavity	0.09	0.91	0.00	0.00
3-seeds / cavity	0.04	0.95	0.00	0.01
Single family block	0.20	–[1]	0.18	0.62
Western hemlock	**Proportion contribution**			
	Germination (g)	Thinning (t)	Survival (s)	Culling (c)
1-seed / cavity	0.19	–[1]	0.12	0.69
2-seeds / cavity	0.06	0.83	0.01	0.10
3-seeds / cavity	0.07	0.85	0.01	0.07
Single family block	0.08	–[1]	0.00	0.92

[1] Thinning was not conducted in these treatments.

coefficients (range 0.0 to 4 %) (Table 4). The 1-seed/cavity treatment demonstrated that both seed germination (i.e., seed emergence) and culling contributed 65 and 31 %, respectively, to seedling production, indicating the presence of two possible consecutive bottlenecks in the process (Table 4). Thinning was the major factor affecting family balance from multi-seeds treatments, accounting for 91 and 95 % of the total variation for the 2- and 3-seeds/cavity treatments, respectively (Table 4). The second factor was seed germination (i.e., seed emergence) but it did not account for any significant amount of variation, contributing only, 9 and 4 % in family balance. It should be mentioned at this stage that multiple sowing has neutralized variation in percent of filled due to seed emergence. Culling was very negligible, indicating that thinning might have reduced the variation and thus the amount of variation left among seedlings at the end of the growing season was small. The single-family-block treatment produced a different pattern (Table 4). As indicated above, intra-family competition accounted for 18 % of the variation, followed by seed emergence (20 %) (Table 4). The most important factor in this treatment was culling.

Western hemlock

Mean emergence rates of 95.4, 95.6, 94.9 and 99.2 % were recorded for 1-, 2-, 3-seeds/cavity and single-family blocks, respectively. After thinning, as expected, 49.7 and 33.3 % of the total seeds used remained in the 2- and 3-seeds/cavity treatments, respectively, thus, securing the presence of at least one germinant per cavity. The occupancy rate (i.e., cavities containing single germinant) over the four treatments was very high and ranged between 95.5 (1-seed/cavity) and 99.9 % (3-seeds/cavity). Mortality (i.e., loss of germinants/seedlings) between emergence/thinning and pre-culling was very low and ranged between 16 (0.4 %) and 93 (2.7 %) germinant/seedlings for the single-family block and 1-seed/cavity treatments, respectively. Culling yielded 2,912 (80.2 %), 2,752 (75.7 %), 3,037 (83.4 %) and 3,417 (83.4 %) plantable seedlings for the 1-, 2-, 3-seeds/cavity and single-family block treatments, respectively. The final mean recovery rate was 80.7 % of the 15,015 cavities sown.

Comparing family rank between seed emergence and post-thinning for treatments that required thinning (i.e., 2- and 3-seeds/cavity) indicated that only one family out of the 15 studied maintained the same ranking for the 2- or 3-seeds/cavity treatments (Table 2). In the 2-seeds/cavity treatment, the remaining 14 families experienced 9 negative and 5 positive rank changes (Table 2). The maximal rank change (from 3 after seed emergence to 13 post-thinning, for a change of –10, and from 8 and 12 after seed emergence to 1 and 5 post-thinning, for a change of +7) were observed for families number 5, 3 and 14, respectively (Table 2). The fastest (# 6) and slowest (# 7) families (Table 3) ranked as number 3 and 14 after thinning.

Similarly, in the 3-seeds/cavity treatment, the remaining 14 families experienced 7 negative and 7

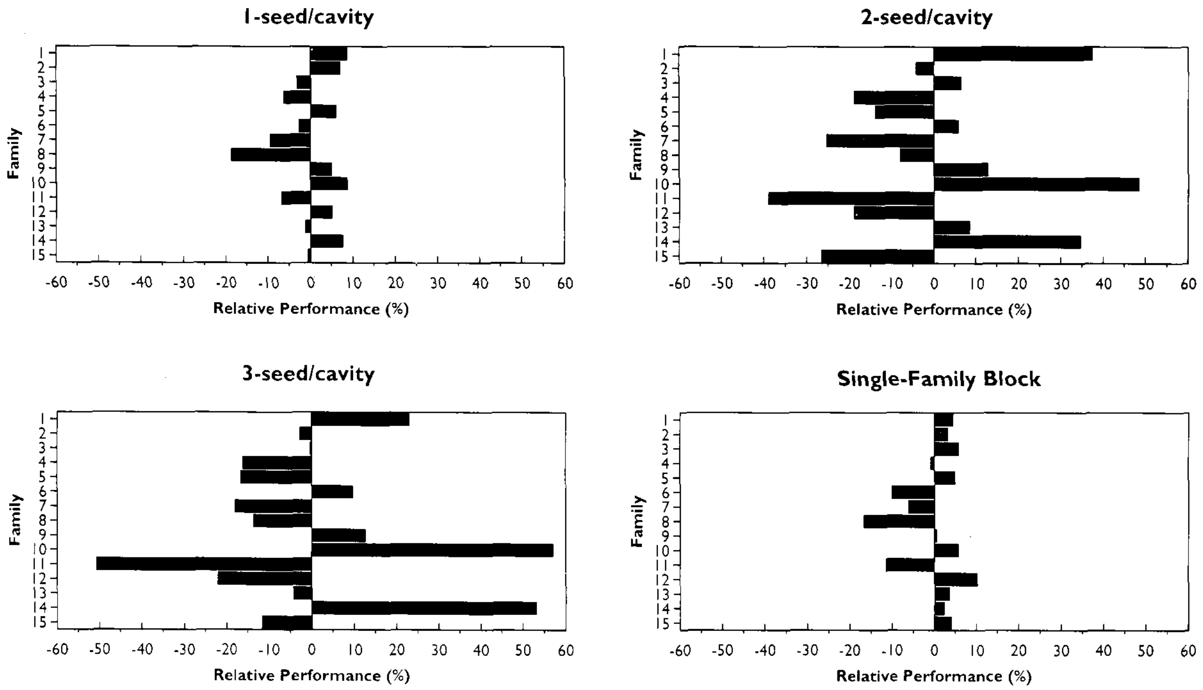


Figure 2. Relative performance of the western hemlock families from seed to seedlings.

positive rank changes, indicating that thinning, once again, has affected the genetic representation of these families (Table 2). The maximal rank changes (from 5 after seed emergence to 13 post-thinning, for a change of –8, and from 10 after seed emergence to 1 post-thinning, for a change of +9) were observed for families number 12 and 14 (Table 3). The fastest (# 6) and slowest (# 7) families ranked as number 3 and 10 after thinning.

In the 1-seed/cavity treatment, family relative performance after culling showed 7 and 8 families with higher and lower output than expected, respectively (Fig. 2). Family number 8 experienced the greatest reduction in relative performance (-19 %). The level of distortion in family relative performance increased steadily with the increase in the number of seeds sown per cavity (Fig. 2). For example, the 2-seeds/cavity treatment produced 7 and 8 families with higher and lower output, respectively, than expected (Fig. 2). The level of relative performance reduction was high and reached 38, 26 and 25 % for families number 11, 15 and 7, respectively. This under representation was associated with appreciable over representation of 48, 37 and 35 % for families 10, 1 and 14, respectively (Fig. 2). The 3-seeds/cavity treatment produced greater distortion than that observed for the 2-seeds/cavity treatment; the maximal relative performance reduction reached 51 % for family 11, while other families showed reduction of 22 % (# 12) and 18 % (# 7) (Fig. 2). Over-representation reached very high rates of 58, 53 and 23 % for families number 10, 14 and 1, respectively (Fig. 2). Most of the families that produced either over- or under-representation in their relative performance were common in the 2- and 3-seed/cavity treatments (Fig. 2).

Finally, the level of distortion among families in relative performance was the lowest in the single-family block and yielded 10 and 5 families with higher and lower output than expected, respectively (Fig. 2). The maximal under- and over-representation distortion amounted to 17 and 10 % for family number 8 and 12, respectively (Fig. 2).

Results of the path analysis indicated that variation in seedling production was explained mostly by family variation in germination and thinning and culling rates (Table 4). With the exception of 1-seed/cavity treatment, survival did not affect final seedling production for the randomized treatments (i.e., 2- and 3-seeds/cavity), indicating that inter-family competition did not contribute much to the total variation (Table 4). The magnitude of the inter-family competition varied between 1 % (2- and 3-seeds/cavity) to 12 % (1-seed/cavity) (Table 4). Survival in the single-family-block treatment did not affect final seedling production, indicating that intra-family competition was not a factor during crop development (Table 4). Seed-germination (i.e., seed emergence) contribution ranged between 6 and 19 %, indicating that germination in this species should be considered as a factor in the process (Table

4). Thinning was the major factor affecting family balance during the nursery production when multiple sowing is employed, amounting to 83 and 85 % of the total variation for the 2- and 3-seeds/cavity treatments, respectively (Table 4). Multiple sowing has neutralized the effect of seed-emergence differences obtained from the multiple sowing treatments (2- and 3-seeds/cavity). Culling contributed between 7 and 10 % of the variation for these two treatments, indicating that thinning might have reduced the variation in seedling size prior to crop harvest. This trend was reversed from that observed for the 1-seed/cavity (69 %) and single-family blocks (92 %) (Table 4).

DISCUSSION

Variation in seed germination attributed such as germination rate, speed, and dormancy of several coniferous species, and, in particular, Douglas-fir (EL-KASSABY *et al.* 1992; THOMSON & EL-KASSABY 1993; EDWARDS & EL-KASSABY 1995) and western hemlock (in preparation), have been reported to be under strong maternal genetic control. Then it is expected that any uniform seed pre-treatment applied to multiple genotypes would produce various results. When seed-orchard cone crops are harvested and processed for seed extraction in bulk, the ability to determine the seed contribution of each clone/family and the expected genetic gain, as well as the level of genetic diversity, is nullified. Similarly, the germination parameters that can be estimated for any particular seedlot are those that represent the weighted average of all parents. Sowing factors, in turn, are determined based on the seedlot germination and the performance of every clone/family, if available, with their unequal contribution rate is not considered.

The variable contribution of seeds to the experimental seedlot of the EL-KASSABY and THOMSON (1996) study was suspected as an additional factor affecting rank change among the various families studied. However, when parental equality among seed donors was imposed, as in the present study, the magnitude of these effects (i.e., seed emergence, thinning, survival, culling, and intra- and inter-family competition) as judged by changing rank and relative performance of individual families remained, indicating that difference in seed contribution is not a major factor. Variation in family contribution to seedling production should be explained mainly by their emergence rate (germination percent), thinning, competition (survival), and culling rates in a complex relationship that is determined partly by the sowing treatment. Survival during the current study was generally high; however, the contrasting relationship between the observed intra- and inter-family competition is of interest. It was expected that the sideways-spreading growth habit of western hemlock seedlings, i.e., neighbouring seedling branches tend to overlap each other, would make inter-family competition a major factor in the randomized treatments. Our results did not confirm that and also indicated that the impact of intra-family competition was virtually non-existent. Douglas-fir, with its upright growing habit, on the other hand, showed the opposite trend and intra-family was more important than inter-family competition. These observations are of interest specifically in the absence of root competition in container nurseries.

The level of over- or under-representation of seedlings among families in the multiple sowing (2- and 3 seeds/cavity) was consistent in both species. Within both species, 12 out of the 15 families maintained their over- or under-representation status, however, the degree of distortion increased with the increase of the number of seeds. The maximal distortion (difference between the % over- and under-representation) observed for the 2-seeds/cavity was 50 and 87 % for Douglas-fir and western hemlock, respectively. This distortion showed marked increase when 3-seeds/cavity was used; distortion of 72 and 104 % was observed for Douglas-fir and western hemlock, respectively. These results are in agreement with the simulation study of EL-KASSABY and THOMSON (1990), confirming that differences in germinative speed among families substantially affect the thinning operation. It is also interesting that the over-/under-representation distortion observed for the single-seed and/or the single-family-block sowing was lower than that observed for multiple sowing (Figures 1 and 2). Additionally, the two species performed differently. Western hemlock showed higher distortion (27 % for both 1-seed/cavity and family-block sowing) than Douglas-fir (13 and 12 % for 1-seed/cavity and family-block sowing, respectively).

Thinning is a major factor in shaping the genetic representation in seedling crops (Douglas-fir: 91–95 %; western hemlock: 83–85 %). Although culling was of greater importance to western hemlock (7–10 %) than Douglas fir (0–1 %), it was concluded that the severity of genetic selection during thinning has reduced the amount of variation among the seedlings. Thus, some uniformity was attained, resulting in a reduction in culling impact. Single-sowing treatments indicated that both germination success and culling were important for both species. The use of a uniform culling standard for rating the crop in the single-family-block treatment represented the greatest source of variation (Douglas-fir: 62 %; western hemlock: 92 %) and multiple culling standards are recommended. The use of multiple culling standards for single-family crops will act as a buffer against the partial and/or complete removal of any family during the nursery stage. PIESCH (1987) observed differences in size among Douglas-fir families after one year in the nursery. These early age differences do not reflect actual performance in the field at later age. PIESCH (1987) ranked several Douglas-fir families based on their nursery performance and compared this early rank to that after eight years in the field. He concluded that some families that ranked the lowest during the nursery phase ended up being the highest rank in the field, thus supporting our recommendation of applying multiple culling standards when sowing is done by family. Based on the results obtained from the present study, we recommend the use of either single-seed or single-family sowing for seedling production for the maintenance of genetic gain/diversity. Knowledge of species biology is required to avoid the pitfalls of differential effects of intra-/inter-family competition.

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