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Effect of nursery culture on morphological development of western hemlock seedlings during field establishment. II. Survival, shoot length components, and needle length

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Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings grown in two different container cavities that received four different dormancy induction treatments, short (SD) or long days (LD) in combination with moisture stress (D) or no stress (W) in the greenhouse, and lifted and placed in cold storage (November, January, or March), were planted on two adjacent coastal reforestation sites in British Columbia and monitored for survival and morphological development. Survival was greatest in seedlings grown in the larger cavities in the greenhouse, in seedlings lifted in March, and in seedlings not treated to moisture stress. Seedling shoots had more stem units on the southeast than the northwest site, but the amount varied with nursery treatment. Seedlings from the LD treatments produced more stem units during free growth and lammas growth than those from the SD treatment. Nevertheless, most shoot growth was predetermined in the buds during nursery culture, accounting for a minimum of 67% of the final number of stem units. Stem unit length (SUL) was longer in seedlings on the southeast site than on the northwest site for those treated to LD in the nursery. Seedlings treated to short days showed the reverse pattern (SDW) to this, or were unaffected by site (SDD). Shoots and needles were shortest for seedlings from the SDD treatment and for those lifted in November. Shoot growth was greatest for seedlings lifted in March and for those treated with LD, mainly owing to their longer SUL. Lammas growth was most frequent in seedlings from the smaller cavities, and in those from the November and March lifts.

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Des semis de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) ont été cultivés dans des récipients de deux dimensions différentes, soumis en serre à quatre traitements d'induction de la dormance : jours courts ou longs combinés à un stress hydrique ou non, arrachés en novembre, janvier ou mars et conservés au froid. Les semis ont été plantés dans une zone de reboisement dans la région côtière de la Colombie-Britannique et leur survie et leur développement morphologique ont été suivis. Le taux de survie était le plus élevé chez les semis cultivés dans les récipients les plus grands en serre, chez les semis arrachés en mars et chez les semis qui n'avaient pas été soumis à un stress hydrique. Les semis avaient plus de tiges par semis sur le site exposé au sud-est que sur le site exposé au nord-ouest mais le nombre variait selon le traitement subi en pépinière. Les semis soumis à des jours longs ont produit plus de tiges pendant la première et la deuxième poussées de croissance que les semis soumis à des jours courts. Néanmoins, presque toute la croissance des tiges était prédéterminée dans les bourgeons pendant la culture en pépinière expliquant au moins 67% du nombre final de tiges par semis. La dimension unitaire de la tige était plus grande chez les semis du site exposé au sud-est que chez les semis du site exposé au nord-ouest pour les semis soumis à des jours longs en pépinière. Les semis soumis à des jours courts ont réagi de façon inverse s'ils avaient aussi subi un stress hydrique ou n'ont pas été affectés par le site s'ils n'avaient pas aussi subi un stress hydrique. Les tiges et les aiguilles étaient les plus courtes chez les semis soumis à des jours courts combinés à un stress hydrique et chez les semis arrachés en novembre. La croissance de la tige était la plus forte chez les semis arrachés en mars et chez les semis soumis à des jours longs surtout à cause de la plus grande dimension unitaire de la tige. La production d'une deuxième poussée de croissance est survenue le plus fréquemment chez les semis cultivés dans les plus petits récipients et chez les semis arrachés en novembre et en mars.

[Traduit par la rédaction]

Introduction

An array of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedling types that vary in their morphological, developmental, and physiological attributes can be produced by modifying nursery cultural practices (Arnott et al. 1988; Grossnickle et al. 1991a; O'Reilly et al. 1989*a*, 1989*b*). However, little is known about how these seedlings acclimate to the field environment. Information on these responses might help explain why some seedling types outperform others in the field. Arnott (1975) found that the highest

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mortality of western hemlock seedlings planted on Vancouver Island occurred in the 1st year over a 5-year observation period, and the relative differences in shoot growth among stock types remained similar over this period. For this reason, a detailed examination of the 1st-year growth responses may indicate the reasons for differences in the growth and survival of western hemlock seedlings. Grossnickle et al. (1991*b*) have described the physiological responses of western hemlock seedlings during early establishment for seedlings that received the same dormancy induction treatments as seedlings in this study, but their study was carried out in another year and on a lower elevation Vancouver Island site.

This study describes the influence of nursery treatments such as dormancy induction, dates of lifting and cold storage duration, and Styroblock cavity size, on the survival and shoot growth components and needle length of western hemlock seedlings during the 1st year of establishment on two sites on western Vancouver Island. In particular, we attempted to answer a number of questions including the following: (*i*) Does a large number of stem units[2] (NSU) in the bud at time of planting increase shoot growth potential, or does subsequent free growth and(or) lammas growth compensate for this advantage? (*ii*) Is stem unit length[3] (SUL) more important than NSU in determining final shoot length? (*iii*) Are there morphological or developmental reasons why some seedling types perform better on one site than on another?

Materials and methods

Seedling stock types

Western hemlock seedlings of a midelevation seed lot (British Columbia Ministry of Forests registered seed lot No. 3907; 48°39′ N, 123°39′ W; elevation 760 m) from Vancouver Island were grown in BC/CFS Styroblocks (Beaver Plastics Ltd., Edmonton, Alta.) of small (PSB 313, abbreviated to S3[4]) and large (PSB 415B, abbreviated to S4[4]) cavity diameters in an experimental nursery at the Pacific Forestry Centre (48°28′ N). (See O'Reilly et al. (1989*a*) for a detailed description of the greenhouse environmental conditions.) Seedlings were subjected to treatments that had different effects on dormancy development (all referred to as dormancy induction treatments), which included short-day (8 h) (SD) or long-day length (18 h) (LD) photoperiods in combination with moderate drought (D, dry) or no drought (W, wet) conditions. Dormancy induction treatments began in mid-July 1986 and ended 4 weeks later, after which the seedlings were grown under naturally declining photoperiods. Styroblocks in the D treatment were allowed to dry down three times during the dormancy-induction period. Styroblocks of this treatment were rewatered to saturation when predawn xylem water potentials of the seedlings reached -1.0 MPa. Finally, three lifting dates – cold storage (1°C) duration treatments took place in mid-November, 1986 (lift N), mid-January (lift J), and mid-March (lift M) 1987, for a total of 24 nursery treatment combinations (two cavity sizes × two day lengths × two moisture levels × three lifting – cold storage treatments). Seedlings were extracted from the Styroblocks, wrapped in liner bags in waxed cardboard cartons and stored at 1°C until the time of planting.

[2]A stem unit is "an internode, together with the node and nodal appendages at its distal extremity" (Doak 1935).

[3]Stem unit length is distance between stem units, or shoot length divided by number of stem units.

[4]PSB 313 and PSB 415B Styroblocks have cavity diameters of 27 and 35 mm, ribbed cavity volumes of 57 and 107 cm^3, and spatial densities of 932 and 527 cavities/m^2, respectively.

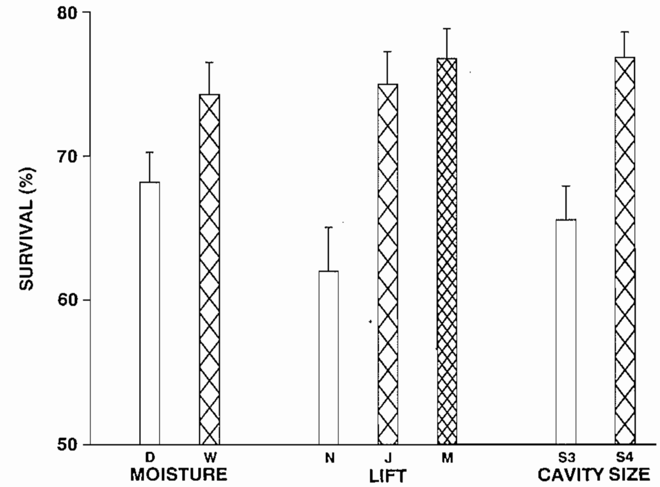

FIG. 1. The influence of nursery treatments and planting site on mean 1st-year field survival of western hemlock seedlings. Means are based on survival percentages per row out of total of 3471 seedlings in 144 rows. Vertical lines indicate one standard error. D and W refer to dry and wet treatments, respectively. N, J, and M refer to November, January, and March lifts, respectively. S3 and S4 refer to small and large Styroblock cavity sizes, respectively.

Study area

The seedlings were planted April 3–4, 1987, on two adjacent sites at Summit Main, Franklin River Division, MacMillan Bloedel Ltd. (48°55′ N, 124°45′ W, elevation 675 m). This area is within the windward submontane maritime wetter coastal western hemlock variant (CWHbl) as described by Green et al. (1984). One site, facing northwest (NW) (280–300°), is classified as wet (hygrotope 5–6, trophotope B–C), while the other is classified as dry (hygrotope 1–2, trophotope B–C) and is of southeast (SE) (140°) aspect. The average slopes on these sites range from 60 to 70% (NW) and 40–55% (SE). The SE site is warmer and receives more photosynthetically active radiation than the NW site.[5]

The soil types on both sites are similar. The soils are derived form granitic parent material, are loamy containing 10–35% coarse fragments (>2 cm), and have 5–10 cm of mor humus form. The soil depth ranges from 0.5 to 1.0 m on the NW site and 0.25–0.5 m on the SE site. The A horizons on the sites are classified as Ae (NW) and Ah (SE).

The sites cover a relatively small proportion of a large clear-cut area and are located immediately adjacent to each other at the top of a small mountain. The clear-cut area was burned in the year previous to planting and the seedlings were largely free of weed competition during the study season.

Experimental design

The seedlings were planted in a randomized block (three) design on each site. Seedlings from each nursery treatment combination (24) were represented in two randomly selected row plots per block, for a total of 48 plots per block. Each row contained 20–25 seedlings, and spacing was at 2 m within rows and 1 m between rows. One of the two replicate rows per block was assigned at random for destructive sampling while the other was retained as a permanent plot.

Data collection

The number of living and dead seedlings in a total of 3471 seedlings was recorded in early October 1987, from all rows retained as permanent plots. Percent survival per row was used in analysis of the data.

[5]Data on file, Forestry Canada, Victoria, B.C.

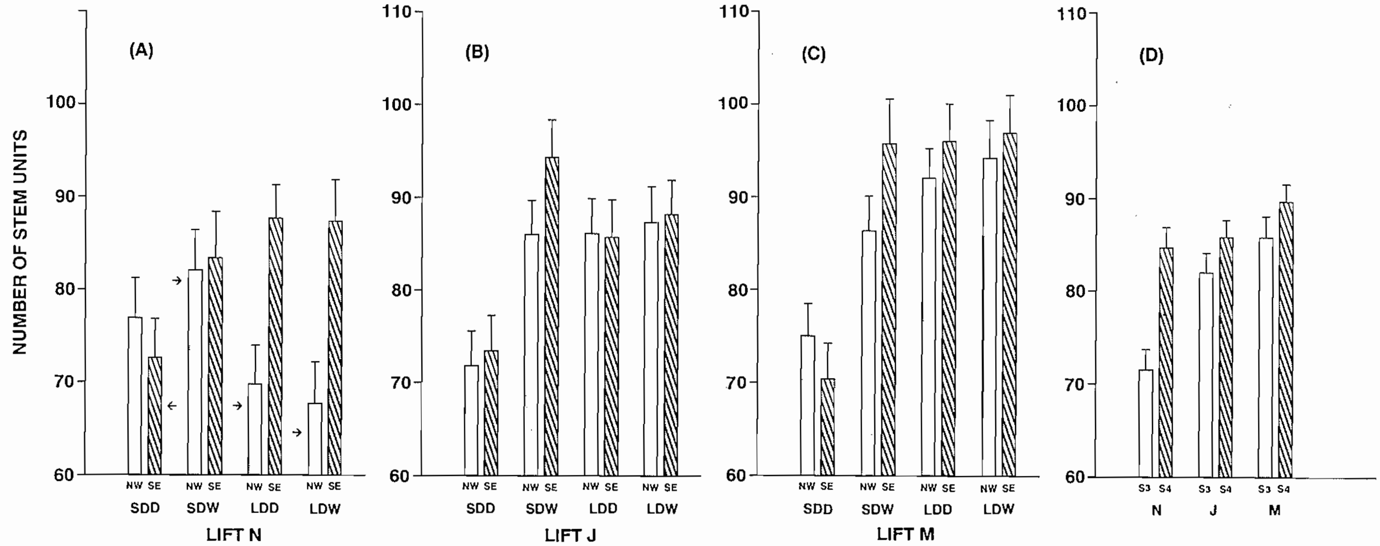

FIG. 2. The influence of dormancy induction treatments and planting site in the nursery within the November- (A), January- (B), and March-lifted (C) stock, and the effects of lift by cavity size pooled across other treatments (D) on the number of stem units at the end of growth in leading shoots of western hemlock seedlings. The stippled area indicates number present before lammas growth took place. The numbers in Fig. 2A, as indicated by arrows, also approximate the number present in the buds at planting in seedlings from all lifts on either site. Means are based on a total of 1104 seedlings from all treatment combinations. Vertical lines indicate one standard error. N, J, and M refer to November, January, and March lifts, respectively. SDD, SDW, LDD, and LDW refer to short-day dry, short-day wet, long-day dry, and long-day wet treatment combinations, respectively. NW and SE refer to northwest and southeast sites, respectively. S3 and S4 refer to small and large Styroblock cavity sizes, respectively.

Morphological data were recorded from seedlings collected in October and November 1987. Eight seedlings per row were sampled, but owing to destructive sampling earlier in season and mortality some rows only contained between four and seven seedlings. A total of 1104 seedlings was examined.

Seedling shoot growth in the field in 1987 consisted of internodal elongation of stem units that originated from the overwintering bud, and from free and lammas growth. The stem units in the bud are predetermined as they were formed during nursery culture. Free growth (Jablanczy 1971) occurred in the first season of field growth from the production of new needle primordia followed by their immediate internodal expansion. Lammas growth occurred from the premature flushing of the new bud that was formed during growth in the field. It was not possible to distinguish needles produced during free growth from those present in the overwintering bud. However, a good estimate could be made of these numbers because needle primordium numbers in the overwintering buds were recorded in another set of seedlings used in the nursery experiment (O'Reilly et al. 1989*b*). The lammas portion of the shoot was identifiable by the presence of bud scales on the new shoot in addition to those of the new overwintering bud. Also, free growth commonly took place as the lammas shoot elongated (O'Reilly et al. 1994). All growth distal to the lammas bud scales was considered as lammas growth despite this fact. The 1987 shoot was divided into two portions for the purpose of this study, the predetermined plus free growth and the lammas growth sections.

The following data were recorded from the 1987 shoot: (*i*) shoot length; (*ii*) length of lammas shoot; numbers of needles or NSU in the (*iii*) predetermined plus free growth and (*iv*) lammas growth portions of the shoot; (*v*) numbers of lammas bud scales; and (*vi*) lengths of five needles at the midpoint of the whole shoot. New variables calculated from the above data included (*vii*) total NSU per seedling, i.e., (*iii*) + (*iv*) + (*v*).[6] SUL was calculated for (*viii*) the whole shoot, the (*ix*) the predetermined plus free, and (*x*) the lammas portions of the shoot by dividing shoot length by NSU for the appropriate portion.

[6]Lammas bud scales were considered as stem units because these were associated stem tissues that underwent intermodal expansion.

Data analysis and presentation

Letting Y denote the variable response a hierarchical (nested) model was fitted:

$$[1] \quad Y_{ijkl} = \mu + S_i + B_{ij} + T_k + (ST)_{ik} + E_{ijk}$$

where i labels the two sites (S), j labels the three blocks (B) within each site, k labels the 24 nursery treatment combinations (T) within blocks, and E is the error term. The factorial nature of the nursery treatments and their interactions with site in [1] are shown in [2] and [3].

$$[2] \quad T_k = \mathrm{D}_l + M_m + L_n + C_p + \ldots (DMLC)_{lmnp}$$

$$[3] \quad (ST)_{ik} = (SD)_{il} + (SM)_{im} + (SL)_{\mathrm{in}} + (SC)_{ip} + \ldots (SDMLC)_{ilmnp}$$

where l labels the two day lengths (D), m labels the two moisture levels (M), n labels the three lifting dates (L), and p labels the two cavity sizes (C).

An analysis of variance according to a split-plot factorial design was used to test for nursery treatment and their interaction effects on variable responses. Each block within site by treatment (or treatment(s) interaction(s)) sum of squares provided the experimental error for testing each treatment (or treatment(s) interaction(s)) effect(s) (see Table 1). The block within site sum of squares was used to test for site differences. The SPSSX MANOVA procedure was used, which also allowed for imbalance in the data (SPSS Inc. 1986). Because few of the higher order interactions were significant, we present only the main effects and first-order interactions in the ANOVA table. Significant ($p \leq 0.05$) higher order interactions are given in the text only. Percent data were analysed after arc-sine transformation.

Results

Only the most important treatment and site effects on the means of these variables are presented in the Figures and in the text.

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TABLE 1. Analysis of variance of treatments and planting site effects on the

Source of variation[a]	df	Survival			Number of stem units: PF			Number of stem units: PF + LAM			Frequency lammas growth		
		MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
S	1	5245	6.2	0.068	4 997	141.3	0.000	6 458	23.5	0.008	21 125	0.5	0.539
Error	4	847			35			274			46 943		
D	1	17	0.2	0.707	8 885	12.0	0.026	10 165	18.8	0.012	40	0	0.981
S×D	1	99	1.0	0.383	1 690	2.3	0.206	1 470	2.7	0.175	1 338	0	0.891
Error	4	103			742			542			63 288		
M	1	931	15.7	0.107	14 219	38.4	0.003	13 745	40.9	0.003	2	0	0.983
S×M	1	4	0.1	0.806	1 739	4.7	0.096	1 049	3.1	0.152	188	0.1	0.814
Error	4	59			371			336			2 957		
L	2	1473	14.1	0.002	7 041	4.2	0.058	9 531	6.0	0.026	124 148	10.7	0.006
S×L	2	24	0.2	0.797	596	0.4	0.714	1 193	0.8	0.505	29 229	2.5	0.142
Error	8	105			1 693			1 601			11 633		
CS	1	2308	54.3	0.002	21 808	19.2	0.012	13 672	9.8	0.035	154 443	4.4	0.105
S×CS	1	0	0	0.987	1 206	1.1	0.361	1 805	1.3	0.319	1 353	0	0.855
Error	4	42			1 134			1 399			35 472		
D×M	1	58	3.2	0.147	14 128	9.0	0.040	12 248	6.6	0.062	75 644	26.3	0.007
Error	4	18			1 576			1 864			2 871		
D×L	2	336	4.3	0.054	3 940	15.0	0.002	4 191	12.3	0.004	14 106	0.7	0.527
Error	8	78			263			341			20 331		
D×CS	1	140	0.7	0.463	178	0.2	0.668	1	0	0.969	43 767	2.4	0.199
Error	4	214			834			447			18 560		
M×L	2	52	1.4	0.306	330	0.5	0.605	673	1.2	0.359	10 413	1.0	0.414
Error	8	38			617			576			10 551		
M×CS	1	3	0	0.846	479	0.3	0.638	499	0.3	0.626	257	0.1	0.787
Error	4	81			1 856			1 801			3 072		
L×CS	2	157	1.6	0.255	1 955	2.9	0.109	2 603	6.8	0.019	21 856	0.8	0.480
Error	8	96			661			383			27 122		

NOTE: To obtain actual MS values for frequency of lammas growth, stem unit lengths, and needle lengths multiply by 10^2.
[a]S, site; D, day length; M, moisture; L, lift; CS, cavity size.
[b]PF, predetermined + free shoots; LAM, lammas shoots, respectively.

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Survival

Moisture availability in the nursery, lifting date, and cavity size significantly influenced field survival (Table 1). Moisture stress in the nursery reduced survival from 74 to 68%. Seedlings from January and March lifts had high survival (75 and 77%, respectively), while those from the November lift had lower survival at only 62% (Fig. 1). Seedlings from the larger cavities had 77% survival compared with 66% for those from the smaller cavities. Survival was higher (p = 0.068) on the NW site (79%) than on the SE site (63%).

Number of stem units and lammas growth

Planting site, day length, moisture, cavity size, day length, and moisture (Table 1), and the interaction between day length, and lift, and planting site ($F_{[2,8]} = 14.5$, $p = 0.002$) affected the number of stem units in the predetermined plus free growth portion of the shoot. However, because most stem units were present in the buds at planting, the analysis of variance results also reflects the effect of treatments other than lifting date – cold storage duration on number of stem units produced in the nursery as well as on those produced during free growth in the field (see below).

The NSU in the predetermined plus free growth portion of the stem, in seedlings on the site having the least NSU within lift N (Fig. 2A) approximated the number of primordia recorded at the end of bud development in the nursery (see also O'Reilly et al. 1989*b*). The SDD, SDW, LDD, and LDW seedlings had approximately 67, 81, 68, and 65 needle primordia, respectively. Therefore, these four (stippled) bars within lift N (Fig. 2A) can be used, (by subtraction), to determine the approximate number of stem units produced during free growth by seedlings on the other site and in other lifts (Figs. 2B and 2C).

Seedlings from the SE site produced significantly more stem units during free growth than those from the NW site, survival and morphological variables in seedlings of western hemlock

		Stem unit length			Shoot length PF			Shoot length PF + LAM			Needle length		
Source of variation[a]	df	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
S	1	29	0.6	0.469	8 097	3.1	0.152	9 638	3.0	0.159	8 045	7.2	0.055
Error	4	46			2 598			3 229			1 117		
D	1	119	10.6	0.031	40 187	51.2	0.002	44 929	165.1	0.000	9 531	16.6	0.015
S×D	1	58	5.2	0.085	8 428	10.7	0.031	7 705	28.3	0.006	143	0.3	0.644
Error	4	11			785			272			574		
M	1	29	5.4	0.082	13 004	10.4	0.032	12 947	10.4	0.032	560	3.0	0.161
S×M	1	22	4.0	0.115	63	0.1	0.834	69	0.1	0.825	358	1.9	0.242
Error	4	5			1 256			1 240			190		
L	2	386	21.7	0.001	43 519	15.2	0.002	50 650	16.9	0.001	16 928	87.5	0.000
S×L	2	12	0.7	0.537	1 615	0.6	0.590	2 138	0.7	0.520	763	4.0	0.064
Error	8	18			2 859			3 005			193		
CS	1	16	1.8	0.252	18 078	16.5	0.015	11 400	8.8	0.041	2 703	13.9	0.020
S×CS	1	12	1.3	0.313	4 111	3.8	0.125	4 758	3.7	0.128	248	1.3	0.322
Error	4	9			1 095			1 298			194		
D×M	1	80	14.0	0.020	20 547	16.3	0.016	19 647	14.0	0.020	10 049	40.1	0.003
Error	4	6			1 259			1 399			251		
D×L	2	10	0.4	0.660	4 190	2.0	0.204	4 481	3.0	0.110	1 977	1.7	0.251
Error	8	23			2 147			1 521			1 198		
D×CS	1	6	0.9	0.398	3 315	8.4	0.045	1 163	2.3	0.208	725	1.7	0.263
Error	4	7			397			517			427		
M×L	2	4	0.3	0.719	337	0.3	0.765	565	0.5	0.631	1 434	3.1	0.101
Error	8	11			1 215			1 160			463		
M×CS	1	4	0.7	0.442	1	0	0.985	15	0	0.925	1	0	0.926
Error	4	5			1 878			1 511			131		
L×CS	2	0	0.1	0.950	419	0.5	0.621	737	1.6	0.254	324	2.6	0.136
Error	8	3			829			451			125		

but the amount varied with nursery preconditioning (Fig. 2). Seedlings from the SDD treatment produced few stem units during free growth across all lifts and on either site. Few stem units were produced during free growth in seedlings treated to SDW of all lifts on the NW site, but those from lifts J and M produced about 10 additional stem units on the warmer SE site (about 12% in addition to those present at planting). Seedlings of both moisture levels treated to LD showed similarity to each other within each lift. Seedlings within lift N treated to LD produced about 20 stem units during free growth on the SE site (about 30% stem units in addition to those present at planting), but produced few stem units on the NW site. Seedlings of the LD treatment within lift J also produced about 20 additional stem units, but on both sites. The pattern was similar for lift M stock, except that numbers were a little larger on the SE site.

The frequency of lammas growth varied with lifting date, day length by moisture (Table 1), moisture by cavity size by site ($F_{[1,4]}$ = 10.9, p = 0.030) and moisture by cavity size by lift ($F_{[2,8]}$ = 5.4, p = 0.032). Lammas growth was most frequent in lift M seedlings (18%) and least frequent in lift J stock (9%) (Fig. 3). Lammas growth was particularly high in LD seedlings of S3 (ranging from 11 to 25%). On average, lammas growth was more frequent on the SE site (15%) than the NW site (12%), but this varied with treatment.

Lammas shoots in seedlings from some treatments contained many stem units, whereas those from other treatments had few stem units (Fig. 2), explaining the inconsistency between the stem unit data and the frequency data (Fig. 3). For example, seedlings from the smaller cavities and those from lift M produced many lammas stem units, whereas seedlings from lift J produced few. Furthermore, most stem units were predetermined, accounting for a minimum of 67% of the final NSU in seedlings from LDW of lift M on the SE site.

Seedlings from S4 had about 10 needle primordia more at planting than those from S3 (see also O'Reilly et al. 1989*b*). Free growth greatly increased this difference in NSU pooled over all treatments in seedlings from S4 over those from S3 within lift N, whereas the differences decreased

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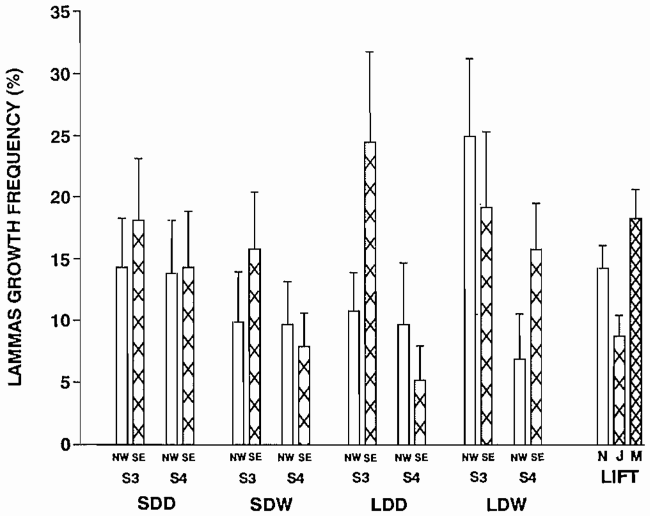

FIG. 3. The influence of nursery treatments and planting site on mean lammas growth frequency in the leading shoots of western hemlock seedlings. Means are based on the percentage of seedlings per row with lammas shoots in a total of 1104 seedlings in all 144 rows. Vertical lines indicate one standard error. SDD, SDW, LDD, and LDW refer to short-day dry, short-day wet, long-day dry, and long-day wet treatment combinations, respectively. S3 and S4 refer to small and large Styroblock cavities, respectively. NW and SE refer to northwest and southeast sites, respectively.

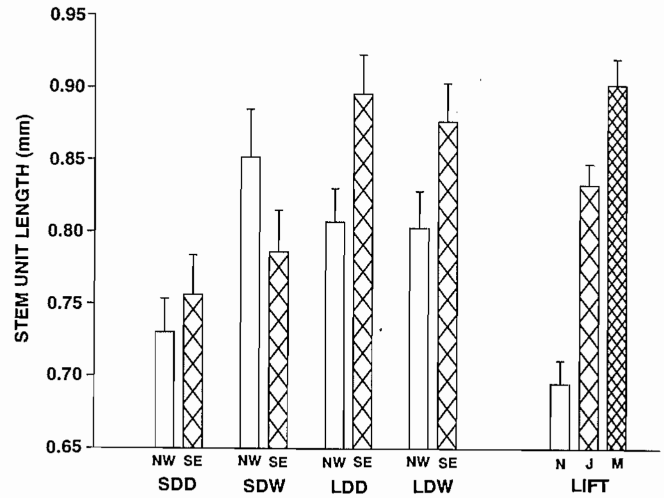

FIG. 4. The influence of nursery treatments and planting site on mean final stem unit length in the leading shoots of western hemlock seedlings. Means are based on a total of 1104 seedlings of all treatment combinations. Vertical lines indicate one standard error. SDD, SDW, LDD, and LDW refer to short-day dry, short-day wet, long-day dry, and long-day wet treatment combinations, respectively. N, J, and M refer to November, January, and March lifts, respectively. NW and SE refer to northwest and southeast sites, respectively.

in those from lifts J and M (Fig. 2D). After lammas growth had occurred, the differences in NSU remained similar for lift N stock, but were reduced for seedlings from lifts J and M.

Stem unit length

Day length and its interaction with moisture, and lifting date treatments, significantly influenced stem unit length (Table 1). Lifting date had the largest effect on SUL. Seedlings from lift N had the shortest SUL (0.70 mm) and those from lift M had the longest SUL (0.90 mm) (Fig. 4). The influence of each dormancy induction treatment varied. Seedlings treated with LD had larger SUL than those treated with SD. Seedlings from both moisture levels in the nursery within LD had similar SUL (0.80 – 0.90 mm), whereas those moisture stressed in the nursery within SD had shorter SUL (0.79 – 0.85 mm) than those not stressed (0.73 – 0.76 mm).

The interactions of planting site, day length, and moisture effects on SUL appeared substantial, although these were not significant (Table 1). Means are presented by site (Fig. 4) because they had an important effect on final shoot length (Fig. 5) when combined with NSU differences. Seedlings treated with long days had larger SUL on the SE site than the NW site, while those treated with short days showed the reverse pattern (SDW) or were relatively unaffected by site (SDD). There were no significant differences in SUL between the predetermined plus free versus lammas portions of the shoot.

Shoot length

Field height growth was significantly affected by day length, and its interactions with both site and moisture, moisture alone, lifting date, and cavity size (Table 1).

Seedlings from the SDD treatment had the shortest shoots (about 55 mm) (Fig. 5), owing to their short SUL (Fig. 4) and low NSU (Fig. 2). Shoot length in SDW seedlings (about 70 mm) on both sites was similar, but was achieved differently. Seedlings on the NW site had greater SUL (Fig. 4), but produced fewer free-growth and lammas-growth stem units (Fig. 2) than seedlings on the SE site. Seedlings from both moisture levels of the LD treatments had similar final shoot lengths. The approximately 10 mm greater growth achieved in the LD-treated seedlings on the SE site was mainly the result of their larger SUL there than on the NW site; NSU produced during free growth and lammas growth contributed less to this difference.

Seedlings from the large S4 Styroblocks had longer shoots than those from the small S3 containers (especially so in predetermined plus free growth portion). These differences in shoot length resulted largely from differences in predetermined NSU, as SUL did not differ between these treatments.

Changes in final shoot length due to lammas growth were proportionately greatest in seedlings from the smaller cavities, in those from the LD treatment, and especially in those from lifts N and M (Fig. 5). These effects were not always reflected in the NSU (Fig. 2) or lammas growth frequency data (Fig. 3), because of the combined influence of NSU and SUL on shoot length.

Needle length

Day length and its interaction with moisture, lifting date, and cavity size had a significant effect on needle length (Table 1). Lifting date had the largest effect on needle length (Fig. 6). Needles were longer on seedlings from the NW site, but the difference varied with dormancy induction treatment. Seedlings from SDW and LDD showed larger between site differences, whereas those from SDD and LDW showed smaller differences. On average, seedlings from LDD had the longest needles (about 9.0 mm), while those from SDD were the shortest (about 7.8 mm).

Treatment NSU and mean needle length values were multiplied to estimate the effect of treatments on total needle length, which is probably a good estimate of the total needle

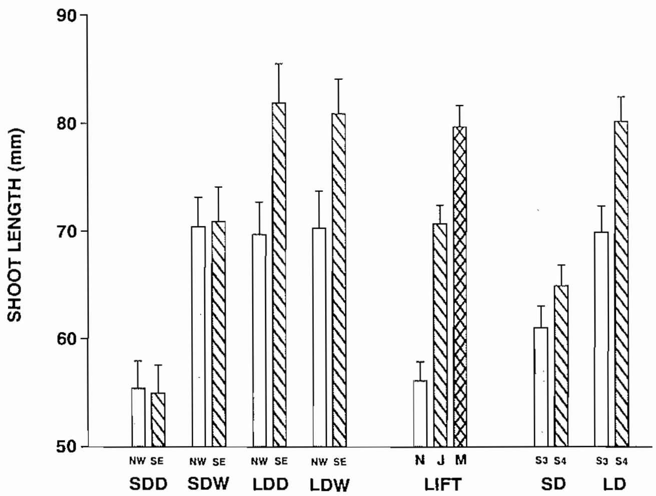

FIG. 5. The influence of nursery treatments and planting site on the mean final length of the leading shoots of western hemlock seedlings. The stippled area indicates length before lammas growth took place. Means are based on a total of 1104 seedlings of all treatment combinations. Vertical lines indicate one standard error. SDD, SDW, LDD, and LDW refer to short-day dry, short-day wet, long-day dry, and long-day wet treatment combinations, respectively. NW and SE refer to northwest and southeast sites, respectively. N, J, and M refer to November, January, and March lifts, respectively. SD and LD refer to short- and long-day length treatments, respectively. S3 and S4 refer to small and large Styroblock cavities, respectively.

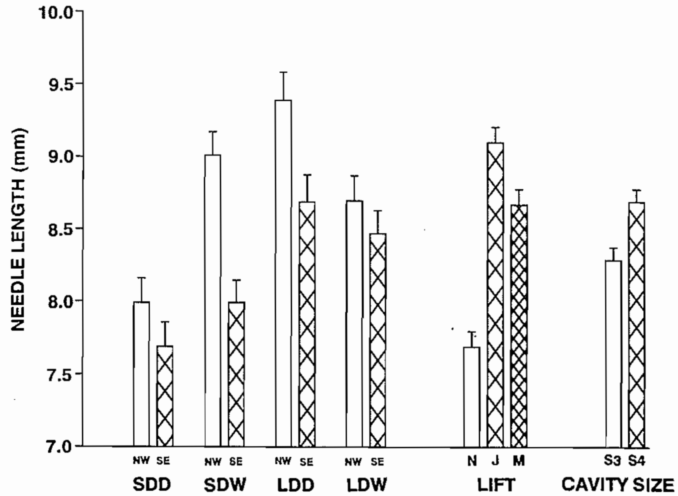

FIG. 6. The influence of nursery treatments on mean final needle length of western hemlock seedlings. Means are based on a total of 1104 seedlings of all treatment combinations. Vertical lines indicate one standard error. SDD, SDW, LDD, and LDW refer to short-day dry, short-day wet, long-day dry, and long-day wet treatment combinations, respectively. NW and SE refer to northwest and southeast sites, respectively. N, J, and M refer to November, January, and March lifts, respectively. S3 and S4 refer to small and large Styroblock cavities, respectively.

surface area of the new shoots. The SDD treatment had the lowest total needle length (57 cm), while differences among SDW (75 cm), LDD (78 cm), and LDW (75 cm) treatments were small or nonexistent. Total average needle length of seedlings lifted in November was 61 cm, compared with 76 and 77 cm for seedlings lifted in January and March, respectively. Seedlings from the small S3 Styroblocks had a total needle length of 66 cm compared with 76 cm for those from the larger S4 containers. Other treatment and site effects were small or negligible.

Discussion

Survival

Moisture stress applied during dormancy development of seedlings in the nursery reduced field survival of western hemlock seedlings planted the following year. Similar results were reported for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings (Jopson and Paul 1985). Furthermore, moisture stress had little impact on root growth potential and dormancy release in western hemlock (Arnott et al. 1988) and was ineffective in inducing dormancy and stimulating bud development (O'Reilly et al. 1989*b*) in the greenhouse.

The November-lifted seedlings had the lowest survival, whereas survival differed little between those lifted in January and March. Survival was much higher (95–97%) for western hemlock seedlings that received similar dormancy induction treatments, that were lifted and cold stored in January, but were planted in another year on a low-elevation site (Grossnickle et al. 1991*b*). The low survival of lift N stock was probably the result of lifting before the seedlings were dormant and had achieved sufficient cold hardiness. Seedlings from lift N, particularly those treated with long days, were not dormant as determined by the presence of apical mitoses at the time of placement in storage (O'Reilly et al. 1989*b*). Furthermore, the low survival of this stock may be attributable to the inability of cold-stored seedlings to acclimate to the field environment (Grossnickle and Blake 1985), damage to the root system during cold storage (Carlson 1985), or the depletion of carbohydrate reserves during cold storage (Ritchie 1982; Duryea and McClain 1984). In addition, these seedlings had low root growth potentials and thus were unlikely to begin vigorous growth in the field shortly after planting. At about the time of shipping for field planting, the root growth potentials were 2.2, 3.1, and 3.5 (after Burdett 1979) for lifts N, J, and M, respectively (Arnott et al. 1988).

Seedlings from the larger containers had greater survival than those from the smaller containers. This response probably reflected differences in seedling morphology because both seedling types received the same nursery preconditioning. The much larger root masses of seedlings from the larger containers (Arnott et al. 1988) probably accounted for this greater survival rate (Lopushinsky and Beebe 1976; Carlson 1986).

Western hemlock seedlings are susceptible to drought stress mortality (Arnott 1975, 1981), possibly because this species lacks both strong stress avoidance and tolerance mechanisms (Livingston and Black 1987, 1988); the warmer regime on the SE site probably accounted for the lower survival there.

Shoot length components and needle length

The results of this study clearly demonstrate the need for examining the components of shoot length if we are to understand the reasons for differences in shoot length owing to nursery treatment. The nursery treatments and planting-site factors that significantly affected shoot length were not necessarily the same as those that affected the components of shoot length (Table 1).

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Seedlings given a long-day treatment in the nursery were more vigorous because they produced many stem units during free growth and lammas growth, compensating for the lower number of stem units in their buds at planting compared with seedlings given short days in the nursery. Nevertheless, most shoot growth was predetermined and stem units produced during free growth and lammas growth never accounted for more than 33% of the final number. The apparent advantage to field shoot growth of the greater NSU at planting in seedlings given short days compared with those given long days, was probably not realized because of differences in the physiological and morphological attributes of the seedlings given different day lengths. For example, seedlings from the SD treatment were shorter and less heavily branched (O'Reilly et al. 1989*a*), had smaller root masses (Arnott et al. 1988), and flushed earlier (O'Reilly et al. 1994) than those from the LD treatment. Variation in predetermined NSU would likely be more important in determining final shoot length if these other attributes did not differ between day length treatments.

Differences in SUL had a much greater impact on final shoot length than variation in NSU. In particular, seedlings from lift N and those from the SDD treatment had very short SUL, and consequently short final shoot lengths. SUL is determined by the number of cells and cell length. If western hemlock is similar to mature *Picea engelmannii* Parry (Owens and Simpson 1988), mitotic activity of the intercalary meristem occurs mostly before the time of flushing, determining the number of cells available for expansion. In contrast, most cell expansion occurs after flushing and continues until about the time of shoot growth cessation (Owens and Simpson 1988). Because some nursery treatments delayed the time of flushing in the field (e.g., as in lift N stock (O'Reilly et al. 1994)), it is possible that they affected the processes of cell division and expansion differently. For example, cell divisions may have begun later in the late-flushing seedlings, perhaps during a period of higher ambient temperatures than experienced by those that flushed earlier. The higher temperatures may have been suboptimal for cell divisions, and consequently may have reduced the number of cells available for expansion. These hypotheses require testing. Furthermore, other physiological differences among stock types may have influenced the growth of the seedlings equally.

Seedlings with a large complement of needles are more susceptible to moisture stress during elongation than those with fewer needles if other morphological and physiological attributes affecting water uptake and transport are equal (Hallgren and Helms 1988). This phenomenon may account for the shorter SUL in seedlings from the SDW treatment on the warmer SE site than on the NW site in this study. Also, the relatively small root masses at planting, and consequently small absorbing surface in the field, of seedlings given short days, compared with those given long days in the nursery (Arnott et al. 1988), may have resulted in moisture stress in the shoots, perhaps restricting stem-unit expansion. Competition for metabolites among elongating stem units may also have resulted in the shorter SUL (Kremer and Larson 1983). In another study of western hemlock seedlings treated with identical dormancy induction treatments as in this study, growing on a single site also on Vancouver Island (Grossnickle et al. 1991*b*), SDW seedlings had longer SUL than other treatments, probably because growing conditions that year were similar to the NW site in this study. Under nursery growing conditions, average SUL was much greater (maximum 2.5 mm) (O'Reilly et al. 1989*a*) than that achieved under field conditions (maximum 0.9 mm).

Seedlings from the SE site produced more stem units during free growth and lammas growth than on the NW site (Table 1), but these differences were not always reflected in shoot length because of differences in SUL. It appears that terminal apical meristematic activity was favoured by the warmer temperatures on the SE site, but this was not necessarily true of intercalary meristematic activity. In particular, the late resumption of shoot elongation of seedlings from the LD treatment of lift N (O'Reilly et al. 1994), especially on the NW site, probably retarded terminal apical activity and subsequent free growth in these seedlings (Figs. 2, 4, and 5).

Lammas growth was frequent in seedlings from lifts N and M and in those from the smaller S3 containers. The among-lift differences were probably the result of different physiological mechanisms. Because of the high physiological quality of lift M stock (Arnott et al. 1988), it is not surprising that they had a high frequency of lammas shoots. In contrast, the seedlings from lift N underwent earlier bud development than those from other lifts (O'Reilly et al. 1994), perhaps making them prone to conditions that induce lammas growth. Lammas growth may also occur as a stress response, because seedlings from lift N, and those from S3, had both higher mortality (Fig. 1) and greater incidence of lammas growth (Fig. 3). Also, seedlings from S3 were smaller but had greater apical dominance than those from S4 (O'Reilly et al. 1989*a*); such seedlings may have been more responsive to environmental changes that induce lammas growth. However, final shoot length was slightly greater in seedlings of S4, largely because of the greater predetermined NSU than in those from S3.

In addition to number of needles, needle length can have a large effect on needle surface area, and consequently on seedling photosynthetic potential in western hemlock, as in other conifers (Brand and Janas 1988). Needle growth of western hemlock seedlings in the field (Fig. 6) was very sensitive to lifting date and cavity size, while the effects of dormancy induction treatments and planting site were variable. Nevertheless, when the influence of needle length and number of needles is combined to estimate total needle surface area, only a few treatments had a substantial effect. In another field experiment, using seedlings from the small S3 Styroblocks that were subjected to identical dormancy induction treatments, lifted, and cold stored in January only, no consistent differences were found among dormancy induction treatments in their physiological responses of the seedlings (net photosynthesis, needle conductance, and shoot water potential) (Grossnickle et al. 1991*b*). Therefore, the photosynthetic capacity of the new shoots probably paralleled the trend outlined for total needle length. That is, new shoots of seedlings treated to short days plus moisture stress, seedlings lifted – cold stored in November, and seedlings grown in the small S3 container cavities had reduced photosynthetic capacities compared with other treatment combinations (which differed little from each other).

Conclusions

Late lifting (January and March) provided better growth and survival than November lifting for western hemlock

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seedlings. Day length treatment did not affect seedling survival; moisture stress reduced survival, and seedlings from the larger cavities survived better than those from the smaller cavities. In response to the questions posed in the introduction, the study showed that a large number of stem units in the buds at planting (the SDW treatment) did not produce more stem units than seedlings from the LD treatment because additional stem units initiated during free growth and lammas growth compensated for this. Nevertheless, most shoot growth was predetermined, accounting for a minimum of 67% of the final NSU. Had other factors been equal, such as seedling size, root system size, and physiological status, differences in predetermined NSU at planting may have been more important. Variation in SUL was a more important factor influencing differences in shoot length among treatments and sites. The effect of site on stem-unit production during free growth and lammas growth and on SUL was highly variable among treatments. Seedlings subjected to long days in the nursery achieved better growth in the field than those given short days, mainly owing to their longer stem unit lengths. Moisture stress in the nursery did not affect growth of seedlings in the field for those treated to long days but greatly reduced growth of those treated to short days. Lammas growth was most frequent in seedlings from the smaller cavities, and in those from the November and March lifts. It is not known if the effects of these treatments persist for more than the first growing season, and Odlum and Columbo (1988) have shown that these effects do not persist for longer than this in *Picea mariana* (Mill.) B.S.P. Further research should be directed at understanding the effects of nursery treatments on dormancy release of seedlings in the field, and how this affects cell division and cell expansion, and ultimately influences shoot growth.

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