Using Distribution-Modifying Functions to Predict Variation in Frequency Distributions of Tree Heights during Plantation Establishment*

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SUMMARY

The height growth of individual trees was followed during the establishment phase of four progeny tests (three with *Picea sitchensis* and one with *Larix* × *eurolepis*). The relationships between annual height increment and height at the start of the year (distribution-modifying functions; DMFs) were calculated for each year during establishment. These DMFs were used to produce simulated frequency distributions for tree height. Although it has been stated that changes in the frequency distribution of plant sizes can be predicted from DMFs, the reliability of the functions is not good since, with these data sets, the functions accounted for a low percentage of individual tree growth. While the functions do estimate the first moment of the distribution (the mean), they do not accurately predict the second and third moments (standard deviation and skew). The primary reason for the rapid spread in the frequency distribution is variation in growth of seedlings with similar heights. Successful modelling of the changes in frequency distribution can be accomplished only if variation in growth (of seedlings with the same initial height) is included with the DMF. However, calculation of DMFs can be useful in defining the duration of planting check.

INTRODUCTION

This paper deals with the development of frequency distributions in tree heights before canopy closure. Frequency distributions can be important when modelling stand development since, for some species (e.g. *Pinus taeda* L.), the ranking in height at age 5 can strongly influence both survival and volume production during the next 15 years (Switzer and Shelton, 1981). Theoretically, changes in the frequency distribution over time can be modelled by distribution-modifying functions (Westoby, 1982; Cannell, 1989). A distribution-modifying function (DMF) relates the growth of seedlings to their initial size. Cannell (1989) used a single DMF to illustrate how a linear relationship between initial plant height and incremental growth

* Alabama Agricultural Experiment Station Journal Series No. 9–90–2531P

(e.g. DMF 3 in Figure 1) would change the frequency distribution of tree height over a 3-year period. However, in reality, the DMF will vary from year to year. Even though the equations for each DMF will be different, it has been assumed previously that the general shape of the DMF – the relationship of growth to the ranking of the individual's height within the stand – does not change so much as the stand develops (Westoby, 1982).

Although potentially important for those involved in modelling stand development, investigations aimed at identifying DMFs during the establishment phase of forest stands are lacking. In addition, tests of the ability of DMFs to predict changes in the frequency distribution before canopy closure have not been conducted. This paper uses detailed observations on the development of seedlings in four genetic studies established to examine the relationship between nursery height and forest performance. Three of the studies were with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and one was with hybrid larch (*Larix* × *eurolepis*, Henry). These data were used to evaluate changes in shape of the DMFs and to see how these relationships affected observed frequency distributions.

MATERIALS AND METHODS

Details of stock production and stand establishment are provided in Table 1. Additional information about study 3 is reported by Samuel and Johnstone (1979). For the container grown seedlings (studies 1 and 4), seedling heights were measured in the polyhouse (January 1980 and August 1979, respectively) and the identity of each seedling was maintained after outplanting. Extra bare-root seedlings (studies 2 and 3) were grown to ensure there would be a sufficient number of seedlings for each family. Heights of all seedlings were measured in the nursery bed; a total of 25 per cent extra trees were measured in study 2 and 12 per cent extra were measured in study 3. Bare-root seedlings used in the field study were selected at random except for some trees that were culled (they were either too short, had a limited root system, were injured during lifting, were chlorotic, had multiple-leaders, or were diseased). Since the seedlings were not tagged in the nursery, the identity of individual bare-root seedlings was not maintained when outplanted. Bare-root seedlings in study 3 were lifted in the autumn, placed in polybags, and maintained near +1°C in a refrigerated storage chamber. For study 3, the trees that died during the first season after transplanting were replaced ('beaten up') with extra transplants from the same family. In all the other studies seedlings were planted directly after lifting and no beating-up occurred. For each study, annual height measurements were recorded for each seedling for a period ranging from 5 (study 2) to 11 years after planting (study 3).

Distribution modifying functions were derived in a manner following that of Cannell *et al.* (1984). Seedlings were grouped into 10 cm height classes and mean annual growth was plotted against initial height class at the beginning of

TABLE 1: *Details of seedling culture and forest test sites*

	Study 1	Study 2	Study 3	Study 4
Species	*P. sitchensis*	*P. sitchensis*	*P. sitchensis*	*Larix × eurolepis*
Sowing date	Feb./79	April/79	April/70	Jan./79
Pricked out	April	June	June	into Jiffypots
Transplanted into	125 mm sq plastic pots	open beds at Newton	open beds at Newton	125 mm sq plastic pots
Forest	Torridge	Torridge	Wark	Westonbirt
Latitude (°N)	50	50	55	51
Altitude (m)	240	240	200	137
Rainfall (mm/yr)	1270	1270	1220	900
Soil type	brown earth	brown earth	peaty gley	brown earth
Planting date	March/80	Spring/81	June/72	April/80
Spacing	1.5 × 2 m	1.5 × 2 m	1.8 × 1.8 m	2 × 2 m
Blocks	8	5	3	8
Trees/plot	4	8	16	4
Number of families in analysis	57	43	125	18

each year. Height classes with less than five observations were excluded from the analysis. The General Linear Models procedures (GLM) of SAS were used to perform regressions and analysis of variance tests on the data (SAS Institute, 1985). Linear and quadratic equations (fitting height growth to initial height class at the beginning of the year) were developed using a weighted regression procedure (weighted by the number of observations per height class). The sign and significance of the linear and quadratic terms were used as an aid in subjectively classifying the curves (Figure 2) into one of nine general shapes (Figure 1). The changes in frequency distributions were compared with the DMFs to determine how accurately the DMFs were able to predict changes in skew and standard deviations.

Since the nursery heights of bare-root seedlings (studies 2, 3) were not directly comparable on a tree-by-tree basis with field heights, the first year DMFs for these studies were derived by comparing family means in the nursery with family means in the field. For all other years, the growth of individual trees was calculated and the mean value was determined for each height class. However, a change in the sequence of measurement in year 4 precluded the calculation of a DMF for study 3 for that year.

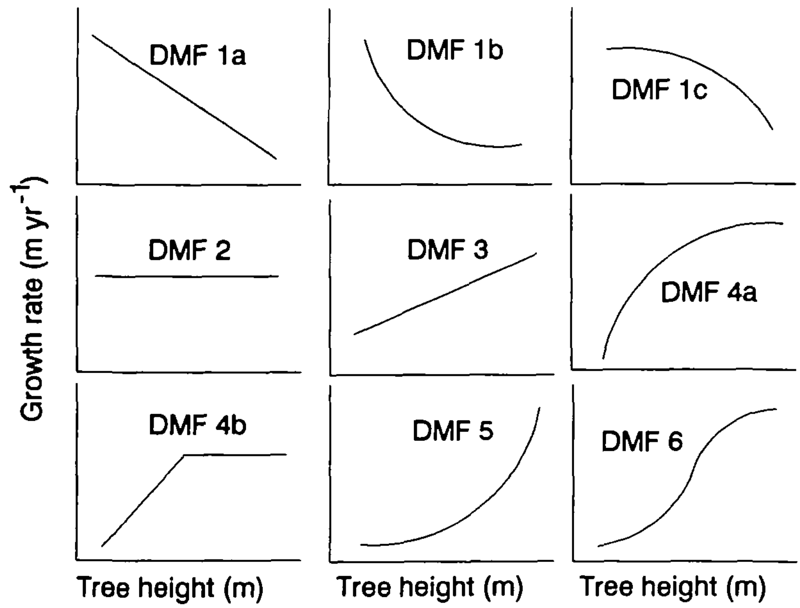

Figure 1. Diagram showing different relationships between tree height and growth rate (distribution modifying functions, DMFs). DMF1a, DMF1b, and DMF1c illustrate different forms of planting check. DMF2 indicates seedlings partially recovered from planting check. DMF3 and DMF4 represent growth of established seedlings. DMF5 and DMF6 are functions that are rarely observed during the first 6 years of plantation development.

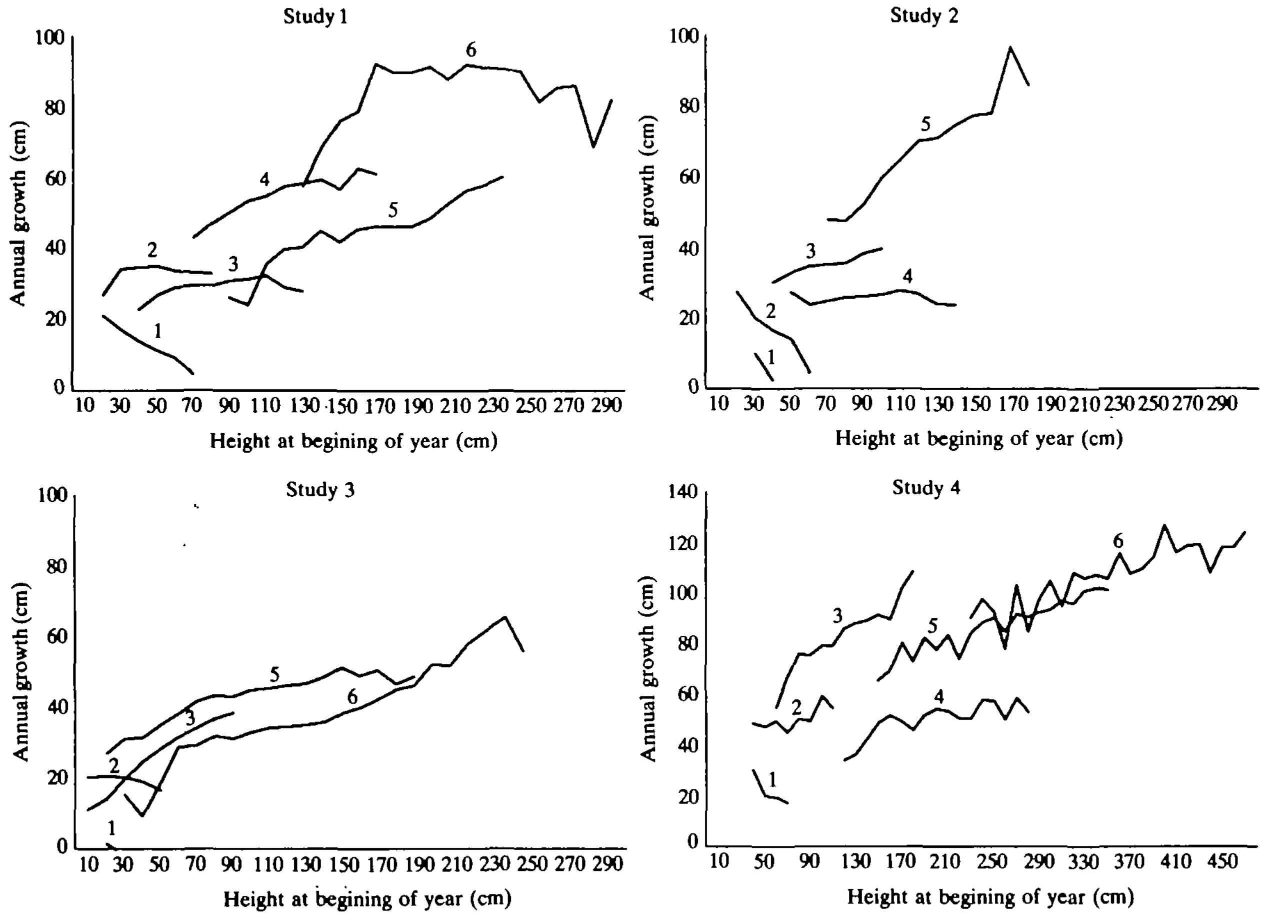

Figure 2. Distribution-modifying functions for Sitka spruce (studies 1, 2, 3) and hybrid larch (study 4) during the initial years after planting. Numbers above curves indicate year of growth in field.

Simulation of frequency distribution

Data from study 1 were used to determine how well the DMFs were able to model changes in frequency distribution. This data was chosen since there was no culling before planting and no beating up after planting. Two sets of simulations were conducted. The first simulation assumed annual growth to be the same for all seedlings of equal height. Heights of individual seedlings in the polyhouse were used in conjunction with the initial DMF to generate a set of predicted first-year heights. Subsequently, this set of predicted heights was used with the second DMF to generate a set of predicted second year heights. This sequence was repeated until six predicted populations were generated. This procedure allowed for no rank changes to occur among individuals (since no DMF had a negative slope less than -1). That is, the height ranking of each individual after six simulations was the same as in the polyhouse. The moments and plots of the derived frequency distributions were compared with the actual data.

The second simulation was conducted using the same DMFs but with the addition of a term to allow seedlings of equal height to exhibit different growth. This additional variation allowed rank changes to occur among individuals. The normal function of SAS was used to generate a normally distributed variation in growth. The amount of variation included was a function of tree height. For the first year, the standard deviation in growth was calculated as 19 per cent of tree height in the polyhouse. The standard deviation for the second year's growth was set at 17 per cent of first-year tree height. The value for the four subsequent simulations was set at 13 per cent of the height at the beginning of each growing season. These values were similar to those observed for study 1.

RESULTS AND DISCUSSION

Initial variation and growth

Initially, the range in heights of outplanted trees was greater for the tests with seedlings grown in the polyhouse than for stock raised outside in a bare-root nursery (Table 2). The large seedlings ranged in height from 20 cm to 83 cm, while the container-grown Sitka spruce ranged from 12 cm to 72 cm. The bare-root seedlings tended to be shorter with smaller standard deviations. In addition, culling of short seedlings before planting reduced the variation of bare-root seedlings, which could explain why the standard deviations were larger in the nursery beds than after one year in the field. The standard deviations of height for container-grown stock increased after planting since culling was not conducted in these studies. As a result, the range of height at planting was about 60 cm for the container-grown stock and 40 cm or less for the bare-root stock.

Growth during the first year after planting varied widely among studies.

TABLE 2: *Statistics for height distributions of Sitka spruce (studies 1, 2, 3) and hybrid larch (study 4)*

Study	Age (year)	*N*	Height (cm) Mean	Min.	Max.	s.d.	c.v. (%)	Skew
1	Polyhouse	1770	38	12	72	9.5	25.1	0.4*
	1	1770	51	13	97	10.6	20.4	0.1
	2	1770	86	23	131	14.2	16.5	−0.1
	3	1770	116	39	195	18.2	15.6	−0.1
	4	1770	171	43	265	25.1	14.6	−0.2*
	5	1770	217	60	340	32.9	15.1	−0.1*
	6	1769	305	60	440	45.6	14.9	−0.4*
2	Nursery	2288	33	13	57	6.4	19.4	0.1
	1	1715	41	21	61	6.1	14.9	0.1
	2	1715	58	11	109	10.9	19.0	0.9*
	3	1715	91	49	165	15.4	16.9	0.7*
	4	1714	117	67	193	18.3	15.6	0.4*
	5	1714	182	70	310	31.6	17.2	0.3*
3	Nursery	8376	26	3	51	6.1	22.9	0.1
	1	5833	26	7	51	5.9	23.0	0.2*
	2	5965	46	2	97	13.6	29.7	0.2*
	3	5955	71	15	153	21.7	30.3	0.1
	4	5958	103	17	215	29.5	28.6	0.0
	5	5957	147	19	275	35.9	24.4	−0.2*
	6	5957	186	20	360	45.1	24.3	0.0
	7	5956	224	20	430	55.2	24.7	0.2*
	8	5957	280	20	520	69.5	24.8	0.1
	9	5958	337	20	600	81.5	24.2	−0.1
	10	5942	404	80	680	88.0	21.7	−0.1
	11	5942	470	110	800	99.7	21.2	−0.1
4	Polyhouse	536	59	20	83	8.4	14.3	−0.5*
	1	463	78	31	119	13.9	17.9	0.2
	2	461	127	53	189	27.7	21.7	−0.4*
	3	459	212	95	311	40.4	19.0	−0.3
	4	458	264	70	400	49.3	18.6	−0.4*
	5	456	353	140	510	59.4	16.8	−0.4*
	6	451	463	160	630	70.6	15.2	−0.5*

* Significantly different from a normal distribution at the 0.01 level of probability using a two-tailed test.

Most growth occurred in the hybrid larch study (average of 29 cm) while the container-grown Sitka spruce averaged 13 cm of growth. The bare-root seedlings lifted and planted in June (study 2) averaged about 8 cm of growth while the seedlings lifted to cold storage in the autumn and planted the following June (study 3) exhibited no mean growth during the first year. As a result, one year after planting, the standard deviations of height for the container-grown stock were almost twice as great as those for the bare-root seedlings.

Planting check

First-year survival was greater than 97 per cent for all three Sitka spruce studies and was 86 per cent for the larch study. Although survival was high for all four studies, the growth of many seedlings was affected by planting check. We define planting check as occurring in years when the DMF has a generally negative slope following outplanting. Distribution-modifying functions indicating transplant check can take one of three basic shapes (DMF 1a, 1b, and 1c in Figure 1). During the first year in all studies, seedlings exhibited a linear relationship similar to DMF 1a (Figure 2). Although the quadratic term was not statistically significant, the DMF for the first year in study 4 appears similar to DMF 1b. The second year of study 3 was similar to DMF 1c. DMFs with negative slopes may be common when stock is transplanted just before the summer months. For example, in all four studies, shorter seedlings grew more during the season after transplanting than did taller seedlings. The regression equations (Table 3) indicate that, on average, seedlings that were 20 cm tall at planting would grow 5–14 cm more during the first year than seedlings that were 40 cm tall. Although not directly comparable, the effect appears to be greater for bare-root stock than for container grown stock. The negative relationship between seedling height and growth can last for up to 2 years.

Pattern of development

Although the studies were planted in different years and on different sites, the change in the shapes of the DMFs tended to follow a similar pattern. Initially, due to planting check, all the first-year DMFs had negative slope (DMF 1a). As the seedlings became established, the slope increased to either a slope near zero (DMF 2) or to a generally positive slope (DMF 3, 4a, or 4b). The time required for current height growth of taller seedlings to exceed that of shorter seedlings varied from 2 years (study 4) to 4 years (study 1).

After recoving from planting check, the shape of the DMFs tended either to be linear (DMF 3) or curvilinear (DMF 4a). After the third year, larch seedlings only exhibited linear functions, while the spruce seedlings tended to be curvilinear (Table 3). This difference may be a result of the difference in growth habit. With determinate growth, tall spruce seedlings (greater than

TABLE 3: *Regression equations and general shapes of distribution-modifying functions for Sitka spruce (studies 1, 2, 3) and hybrid larch (study 4).*
Y = height during year; X = height class at beginning of year. Shape refers to the types listed in Figure 1

Study	Age	Equation for DMF	N	Significance	R^2	Shape
1				$P>r^2$		
	1	$Y = 23.1 - 0.245\ X$	6	0.0001	0.99	DMF 1a
	2	$Y = 35.4 - 0.021\ X$	7	0.4916	0.10	DMF 2
	3	$Y = 24.6 + 0.064\ X$	10	0.0046	0.65	DMF 2
	4	$Y = 0.7 + 0.785\ X - 0.00262\ X^*X$	15	0.0018	0.90	DMF 4a
	5	$Y = 20.5 + 0.148\ X$	22	0.0001	0.72	DMF 3
	6	$Y = - 56.0 + 1.310\ X - 0.00290\ X^*X$	25	0.0001	0.76	DMF 4b
2	1	$Y = 31.8 - 0.731\ X$	43	0.0009	0.24	DMF 1a
	2	$Y = 30.7 - 0.348\ X$	5	0.0126	0.91	DMF 1a
	3	$Y = 25.6 + 0.139\ X$	7	0.0016	0.88	DMF 3
	4	$Y = 11.2 + 0.289\ X - 0.00135\ X^*X$	10	0.0358	0.61	DMF 2
	5	$Y = - 19.3 + 1.063\ X - 0.00277\ X^*X$	12	0.0321	0.96	DMF 3
3	1	$Y = 8.9 - 0.354\ X$	114	0.0001	0.22	DMF 1a
	2	$Y = 18.4 + 0.186\ X - 0.00423\ X^*X$	5	0.0480	0.95	DMF 1c
	3	$Y = 2.3 + 0.681\ X - 0.00326\ X^*X$	9	0.0001	0.99	DMF 4a
	5	$Y = 22.7 + 0.311\ X - 0.00093\ X^*X$	18	0.0001	0.94	DMF 4a
	6	$Y = 26.6 - 0.028\ X + 0.00071\ X^*X$	23	0.0001	0.93	DMF 5
	7	$Y = 25.8 - 0.014\ X + 0.00040\ X^*X$	30	0.0001	0.86	DMF 5
	8	$Y = -10.1 + 0.406\ X - 0.00045\ X^*X$	35	0.0001	0.88	DMF 4a
	9	$Y = 142.1 + 0.587X - 0.00080\ X^*X$	42	0.0001	0.91	DMF 4a
	10	$Y = 56.1 + 0.035\ X$	46	0.0216	0.11	DMF 4b
	11	$Y = 24.5 + 0.099\ X$	51	0.0001	0.86	DMF 4b
4	1	$Y = 33.8 - 0.248\ X$	5	0.0817	0.69	DMF 1a
	2	$Y = 35.5 + 0.177\ X$	8	0.0838	0.42	DMF 3
	3	$Y = 49.5 + 0.283\ X$	13	0.0001	0.87	DMF 3
	4	$Y = 30.4 + 0.100\ X$	18	0.0004	0.56	DMF 3
	5	$Y = 47.3 + 0.156\ X$	19	0.0001	0.85	DMF 3
	6	$Y = 53.7 + 0.153\ X$	24	0.0001	0.64	DMF 3

250 cm) tended to reach a limit of height growth which resulted in reaching either a gradual (DMF 4a) or faster (DMF 4b) change of slope. Equally tall larch seedlings, with indeterminate growth, did not exhibit these types of responses.

Functions similar to DMF 5 were observed for the sixth and seventh growing seasons in study 3 (Table 3). However, although the quadratic terms of these equations were statistically significant, they only accounted for an additional 3 per cent of the variation in class means. Sigmoid curves (DMF 6) were not observed. Although Cannell *et al.* (1984) reported a sigmoid curve for closely spaced Sitka spruce, these curves are not commonly observed before canopy closure.

Changes in frequency distributions

It is apparent from Figure 3 that differentiation within a stand commences during the first years of establishment. Differences in the rates of height growth of individuals within the population results in an increase in the range of heights. In general, the standard deviation of height increases by 3–14 cm for each year during the first six growing seasons. This differentiation occurs before any competition-induced mortality and when the trees are relatively free of inter-tree competition.

Theoretically, the widening of the distribution of height can be explained by DMFs with certain shapes (Figure 1). Thus, functions with negative slopes (DMF 1a, 1b, 1c) should not widen the distribution but result in a decrease in the standard deviation. A linear function with a slope of zero (DMF 2) should not affect the shape of the distribution. Increases in the standard deviation result if the function has a generally positive slope (DMF 3–6). Theoretically, when the function is linear, the magnitude of increase in the standard deviation is directly related to the slope (a slope of +1 doubles the standard deviation while a slope of +0.5 increases the standard deviation by 50 per cent). In addition to increasing the standard deviation, a sigmoid function (DMF 6) is assumed to generate a bimodal frequency distribution (Westoby, 1982).

However, when the DMF functions listed in Table 3 were used to simulate changes in frequency distribution, the simulated distributions (without variation) for study 1 (Figure 4) conformed to theory but bore little resemblance to the real data (Figure 3). Although the DMFs were able to predict the mean of the populations, the standard deviations of the simulated distributions (Table 4; without variation) were much less than those for the actual populations. This finding reduces the usefulness of DMFs for predicting size related changes in the frequency distribution of tree heights. After six growing seasons, the standard deviation was four times greater for observed data than for simulated data. In fact, with the real data, increases in the standard deviation occurred during the first and second year when the slopes of the DMFs were negative although the theory predicts that the standard deviations should decrease.

The extension of the range of height during the initial stages of stand development results from variation in growth among individuals of the same height. None of this variation is accounted for by the use of DMFs. Although the DMFs can account for a relatively large proportion of variation in mean annual growth of seedling classes (Table 3), they may account for less than 12 per cent of the total variation in annual growth among individual trees during the first 6 years of establishment. The underlying assumption necessary for

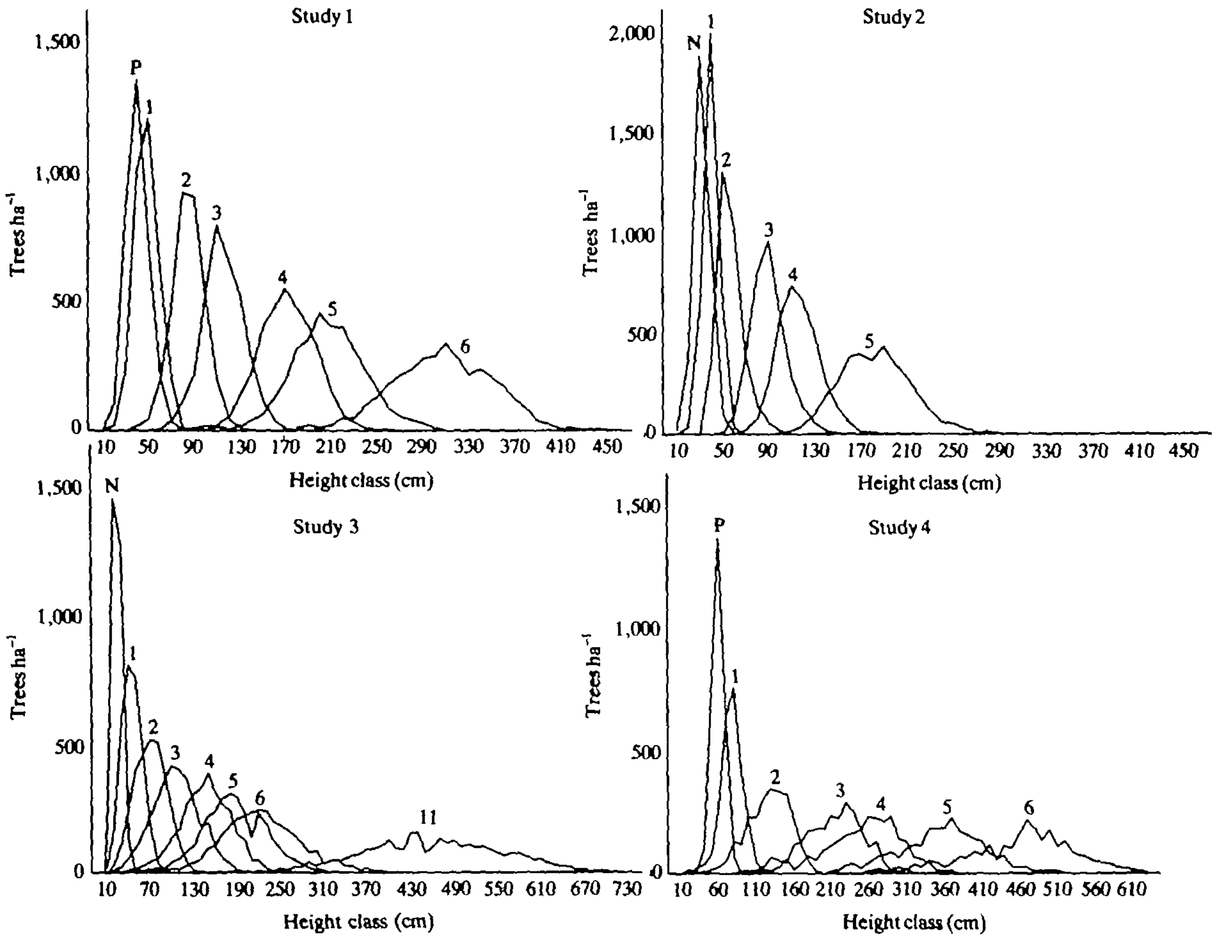

Figure 3. Observed frequency distributions of height classes (10 cm) for Sitka spruce (studies 1, 2, 3) and hybrid larch (study 4) during the initial years after planting. Initial height measurements were made in the polyhouse (P) and nursery (N). Numbers above distribution indicate years after planting.

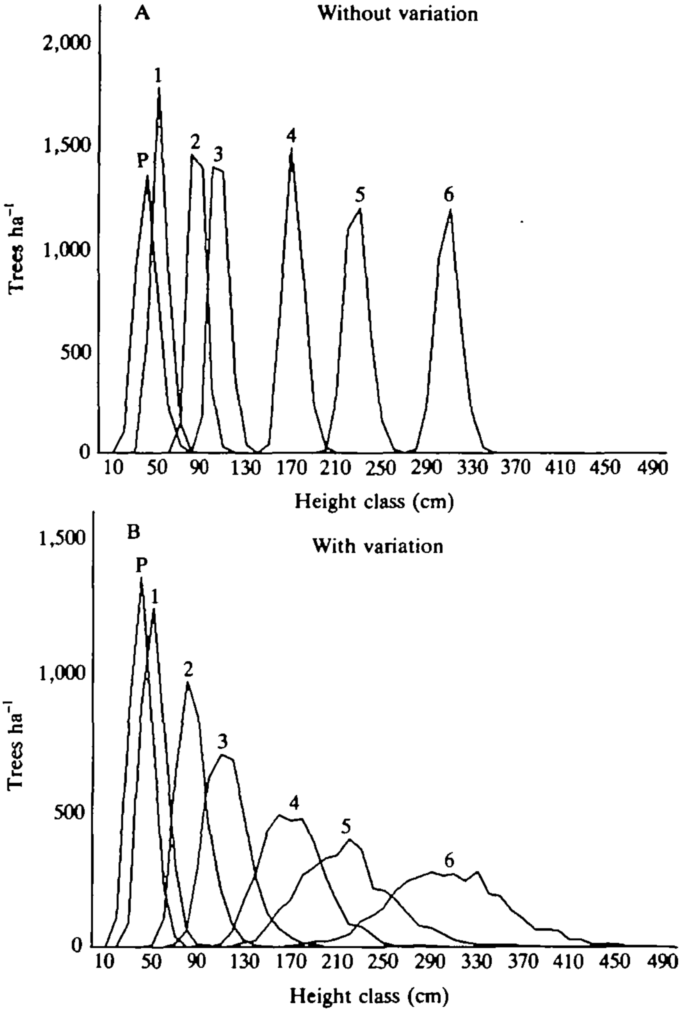

Figure 4. Frequency distributions of height classes (10 cm) in the polyhouse (P), and simulated frequency distributions (numbered) using the distribution-modifying functions listed in table 3 for study 1. (A) Simulated frequency distributions using only the DMFs (no rank changes among individuals). (B) Simulated frequency distributions which include a term to allow for rank changes to occur among individuals. The additional term allows variation to occur in growth of seedlings of the same height.

DMFs to work satisfactorily is that the function accounts for a large percentage of the observed variation in individual tree growth (few rank changes among individuals).

The majority of variation in annual height growth was attributable to differences in seedling morphology, genotype, and site heterogeneity. For example, in study 1, root collar diameters of seedlings with the same original

TABLE 4: *Statistics for simulated and real height distributions of container-grown Sitka spruce using original height measurements in the polyhouse and DMF equations listed in Table 3*

	Age	*N*	Height (cm) Mean	Min.	Max.	s.d.	c.v. (%)	Skew
Simulated without variation	1	1770	52	32	77	7.1	13.9	0.4
	2	1770	86	67	111	7.0	8.1	0.4
	3	1770	116	96	143	7.4	6.4	0.4
	4	1770	172	147	202	8.7	5.0	0.3
	5	1770	218	189	252	10.0	4.6	0.3
	6	1770	309	277	342	10.3	3.3	0.2
Simulated with variation	1	1770	51	25	105	10.2	19.7	0.7
	2	1770	86	51	149	13.3	15.4	0.7
	3	1770	116	66	187	17.9	15.4	0.4
	4	1770	171	92	273	25.9	15.1	0.3
	5	1770	216	126	372	37.4	17.3	0.4
	6	1770	303	186	471	47.4	15.6	0.3
Actual data								
	1	1770	51	13	97	10.6	20.4	0.1
	2	1770	86	23	131	14.2	16.5	−0.1
	3	1770	116	39	195	18.2	15.6	−0.1
	4	1770	171	43	265	25.1	14.6	−0.2
	5	1770	217	60	340	32.9	15.1	−0.1
	6	1769	305	60	440	45.6	14.9	−0.4

height (37 cm) ranged from 5.0 mm to 9.7 mm. This equates to a difference of 275 per cent in stem volume (calculated as a cone). Since study 1 involved 57 different open-pollinated families, seedlings with similar heights but of different genotypes could be expected to grow at different rates. Analysis of variance revealed that family differences accounted for 10 per cent of the variation in first-year growth of individual trees. Although the sites were selected for their uniformity, height growth differences between blocks became significant after just a few years' growth. Even after accounting for variation attributable to height, family, and block, the error mean square often accounted for more than 70 per cent of the total variation in annual growth among individuals.

Adding variation to DMFs

In order to improve the ability of the DMF models to simulate observed height growth patterns, an additional term was added to each of the regression equations. This term added a normally distributed random number, its standard deviation being a function of seedling height. A second set of predicted distributions was generated using this additional variable. The resulting frequency distributions (Figure 4 and Table 4; with variation) proved to be very similar to the observed populations (study 1 in Figure 3 and Table 2). This suggests that the primary reason for the widening of the frequency distributions during the early stages of stand development is not the shape of the DMF but the natural variation in growth of seedlings of the same size.

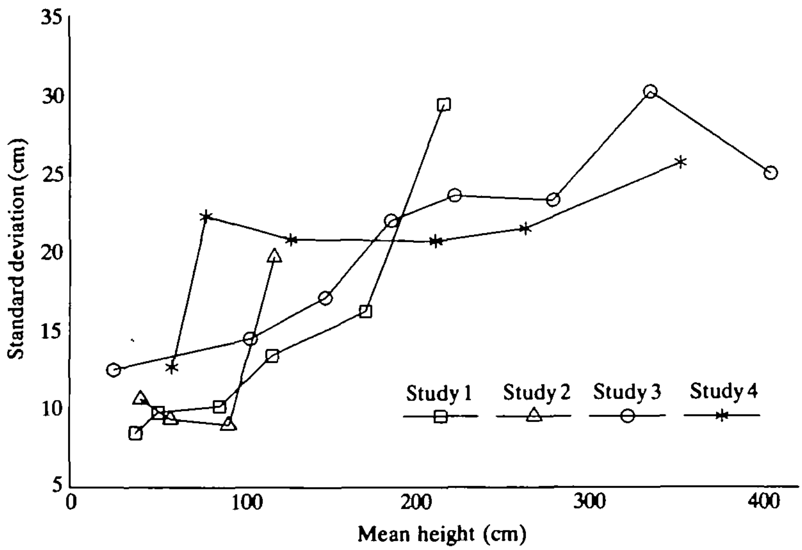

Figure 5. The relationship between variation in annual growth and average tree height for Sitka spruce (studies 1, 2, 3) and hybrid larch (study 4).

In order to predict how the frequency distribution will change with time, it is necessary to know the appropriate DMF (in order to obtain an accurate prediction of the population mean) and also an estimation of the standard deviation in annual growth (which controls how fast the distribution will spread). Figure 3 illustrates that the frequency distribution for the container-grown larch seedlings spreads faster during the first few years than that for the container grown Sitka spruce (study 1). This is attributable to the fact that during the first 3 years, the standard deviation in growth for a given height class of tree was greatest for the larch study (study 4; Figure 5). The rapid spread in frequency distribution is not primarily due to differences in DMFs.

In general, for these studies, the standard deviation in annual growth was about 10 cm for trees 40 cm in height and then increased to 25–30 cm for trees which were 3 m tall. All the data from Figure 5 were pooled to derive the following general equation:

$$\text{s.d.} = 9.8 \text{ cm} + 0.05X$$

Where: s.d. = the standard deviation in annual height growth (cm)
X = tree height (cm) before growth in the year in question.

However, for any given stand, it is obvious that both site and weather will affect the actual values. The standard deviation in growth will be greater for sites with large heterogeneity and for years when lammas growth is prevalent.

Effect of DMFs on skew

Theoretically, the shape of the DMF determines the shift in direct of skew (Westoby, 1982; Cannell, 1989). DMF 5 should result in more positive skew while DMFs 4a and 4b result in more negative skew. Theoretically, the magnitude of the shift in skew should be affected very little by the DMFs. For example, equations for study 1 (Table 3) predict that skew should have changed by only 0.2 units after 6 years (from 0.4 at planting to 0.2 after 6 years; see Table 4). In fact, during this time period the observed skew changed by 0.8 units (Table 2). During the second year in study 2 (Table 2), the skew became positive (changed from 0.1 to 0.9) even though the DMF equation was not shaped like DMF 5. Apparently, for these studies, the DMF equations are not reliable predictors of change in either the magnitude or direction of skew. Again, the reason is due to the natural variation in growth of seedlings of the same size. Ford and Diggle (1981) also found that when the standard deviation of growth of similar sized plants is increased, the ability of DMF 5 to produce a biomodal distribution is lost.

Calculating DMFs

In this paper, DMFs were derived in a manner following that of Cannell *et al.*, (1984). Average growth was determined for each class mean (Figure 6A) and plotted against height class (Figure 6B). However, it is possible that some researchers have calculated DMFs in a manner different than by using class means. A DMF could be derived by plotting the cumultative frequency curves (Figure 6C) and calculating the growth required at various points along the *y* axis (Figure 6D). However, this method can produce a DMF which is very different from that produced using class means. Even though the data set is the same for both examples, an exponential type curve (Figure 6D) is derived using cumulative frequency curves while the true DMF is linear with a negative slope (Figure 6B). The cumulative frequency curve method of calculating DMFs is incorrect since the method only works when there are no rank changes among individuals. This may help to explain why some

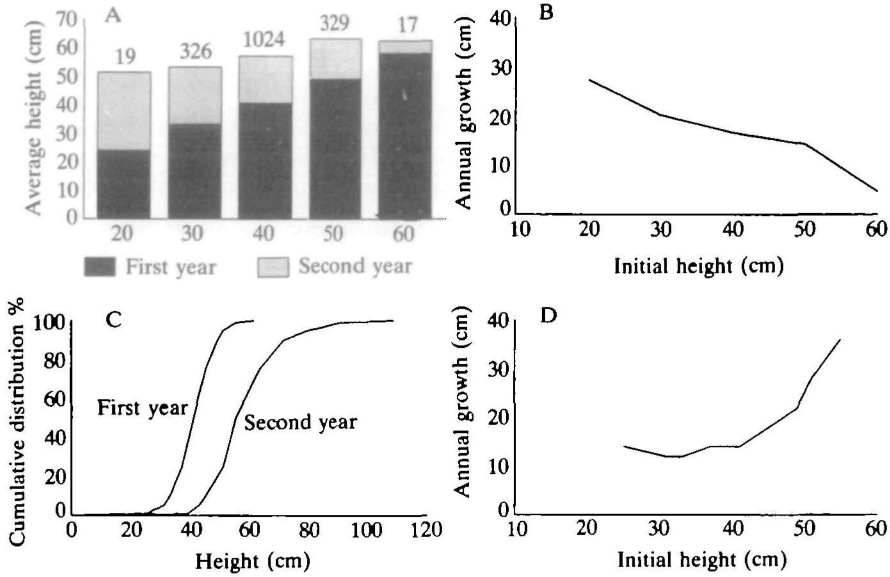

Figure 6. Diagram showing two different methods of calculating distribution-modifying functions (DMFs) from the same data set (study 2). Calculating the average growth of seedlings by height class (A) results in the correct DMF (B). Numbers above bars represent the number of seedlings in each height class. Calculating the difference between cumulative distribution curves at various points on the *y*-axis (C) results in an incorrect DMF (D). This DMF is incorrect because it assumes no rank changes among individuals.

researchers investigating tree competition (before canopy closure) have assumed that trees of various sizes exhibit the same relative growth rate (constant exponential growth). However, trees growing during the early life of the stand do not exhibit constant exponential growth (Cannell, 1989).

CONCLUSIONS

The ability of DMFs accurately to predict changes in the standard deviation and skew of the frequency distribution of heights is limited to those cases where there are few rank changes among individuals. During the establishment phase of plantations, rank changes among individuals reduce the ability of DMFs to account for a large percentage of individual tree growth. In order to simulate stand development with DMFs, variation in growth of similar sized plants needs to be included in the model.

However, DMFs do have utility in describing the duration and degree of planting check. When the general slope of the DMF is negative, the seedlings can be said to be suffering from planting check. Determining the number of years that the slope remains negative can be a simple way of defining the duration of planting shock. The angle of the slope is also useful in determining the severity of the planting check. A comparison of the first year

DMFs would suggest that the container stock in study 1 (with a slope of -0.245 cm cm^{-1}) suffered less planting check than the bare-root stock in study 2 (with a slope of -0.731 cm cm^{-1}).

ACKNOWLEDGEMENTS

We would like to thank C. J. A. Samuel of the Forestry Commission's Tree Improvement Branch for providing data from the four genetic studies. We would also like to acknowledge the various Tree Improvement Branch researchers and foresters who have been responsible for the design and management of these experiments. The comments of A. R. Ludlow, D. B. Paterson, C. J. A. Samuel and I. M. S. White upon an initial draft are gratefully acknowledged.

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Received 10 May 1990