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Variation between and within populations in a provenance trial of *Pinus sylvestris* at Nordanås, Lat 64°19′, Long 18°09′, Alt 400 m

Mellan- och inompopulationsvariation i ett proveniensförsök med tall vid Nordanås, Lat 64°19′, Long 18°09′, 400 m ö h.

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Abstract

ODC 232.12—174.1 Pinus sylvestris (488)

Data on survival, stem height, stem volume and yield per hectare from a provenance trial with Scots pine (Pinus sylvestris) *at Nordanås, lat 64°19′, long 18°09′, alt 400 m, are presented in this report. Regression analyses were carried out to test the influence of transfer on the parameters studied. For the most important characteristics, yield per hectare and survival, it was found that a transfer by 1—2 latitudes southward will imply an improvement.*

Since the progenies from individual trees within the populations were kept apart the variation within populations could be analysed. This variation was found to be considerable both for survival and height in some of the populations.

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Contents

1 Introduction

The value of a provenance trial is considerably increased if the provenances are represented by progenies from individual trees, since such a trial will give information about the genetic variation between as well as within provenances (cf. Stern 1964). To our knowledge only limited data from forest tree provenance trials of such hierarchial design have been published. There are observations from *Abies lasiocarpa* (Dietrichson 1971), *Picea abies* (Langer and Stern 1964, Dietrichson 1967 and 1969 b), *Picea mariana* (Dietrichson 1969 a, Morgenstern 1969), *Pinus contorta* (Dietrichson 1970), *Pinus sylvestris* (Wright 1963), *Pseudotsuga menziesii* (Rehfeldt 1974 a and b) and *Betula alleghaniensis* (Clausen 1972). All these references treat plants studied at a young age.

There are of course many investigations reporting on various characteristics in open pollinated progenies from individual stands. Among Swedish investigations the ones by Nilsson (1968) on the quality of *Pinus sylvestris* and by Johnsson (1967) on height and volume production of *Betula pubescens* and *Betula verrucosa* may be mentioned. In both reports a significant within-stand variation was proven for some of the populations.

The purpose of the present investigation was to supplement older hierarchial provenance trials, thus permitting an analysis of differences between as well as within stands of *Pinus sylvestris*. The data were collected from a field trial at the age of 20 (height and volume) and 23 (survival) years, respectively.

2 Material and methods

Before any data of the material included in the present investigation are given it may be pointed out that the terms provenance, stand, and population are used in the same way as in the scheme worked out by OECD for the control of forest reproductive material moving in international trade.

The experimental series with Scots pine (*Pinus sylvestris*) populations established in 1952—1954 (Eiche 1966) was in 1955 extended by another experimental plantation (EP) at Nordanås (lat 64°19′ long 18°09′ alt 400 m). All populations included originate from indigenous stands. The plants (2+2) were planted at a spacing of 2.5×2.5 metres. The surface area of this EP is flat, which is an unusual case in northern Sweden, with fertile moraine soil sites. The edaphic conditions were thus suitable for an EP.

The details as regards the origin of the 20 populations tested at Nordanås will be found in Table 1 (see also Figure 1). It is worth mentioning that population 112, Funäsdalen contains four populations of the same provenance (bulk collected seeds). Except for this population it was planned that all others should be represented by single

Table 1. The origin of the populations tested at Nordanås.

Number and name of population		North lat	East long	Alt m	Length of the growing season
Norway					
4	Målselv, Moen, Olsberg	69°07′	18°35′	100	114
56	Vinje, Prästgården	59°35′	7°50′	550	144
Sweden					
10—210	Norrbotten, Korpilombolo, Smedberg	66°53′	23°03′	175	116
310	Norrbotten, Korpilombolo	66°50′	23°09′	185	116
20	Norrbotten, Älvsbyn, Asplövberg	65°38′	21°07′	75	125
22	Västerbotten, Krångfors, Backen	64°46′	20°28′	130	131
23—223	Västerbotten, Malå, Strömfors	65°08′	18°53′	305	122
26	Västerbotten, Robertsfors	64°12′	20°48′	50	129
28	Västerbotten, Vindeln, Svartberget	64°14′	19°43′	200	127
30	Västerbotten, Vilhelmina	64°35′	16°50′	350	120
32—232	Västerbotten, Lycksele, Storberget	64°34′	18°15′	525	113
33—233	Västerbotten, Örträsk, Höglunda	64°08′	18°39′	475	120
34	Västernorrland, Örnsköldsvik, Alfredshem	63°15′	18°47′	8	136
35	Jämtland, Bispfors, Stadsforsen	62°59′	16°39′	92	141
42	Jämtland, Sveg, Malmbäcken	62°03′	14°19′	385	130
49	Kopparberg, Orsa, Högståsen	61°05′	14°58′	365	140
51	Kopparberg, Sälen, Hundfjället	61°09′	13°00′	720	115
106	Jämtland, Harrsjön	64°18′	15°23′	360	119
107	Jämtland, Bispfors, Torresjölandet	63°08′	16°39′	455	125
108	Västernorrland, Galtström	62°10′	17°27′	5	140
112	Jämtland, Funäsdalen	62°34′	12°35′	450/800	

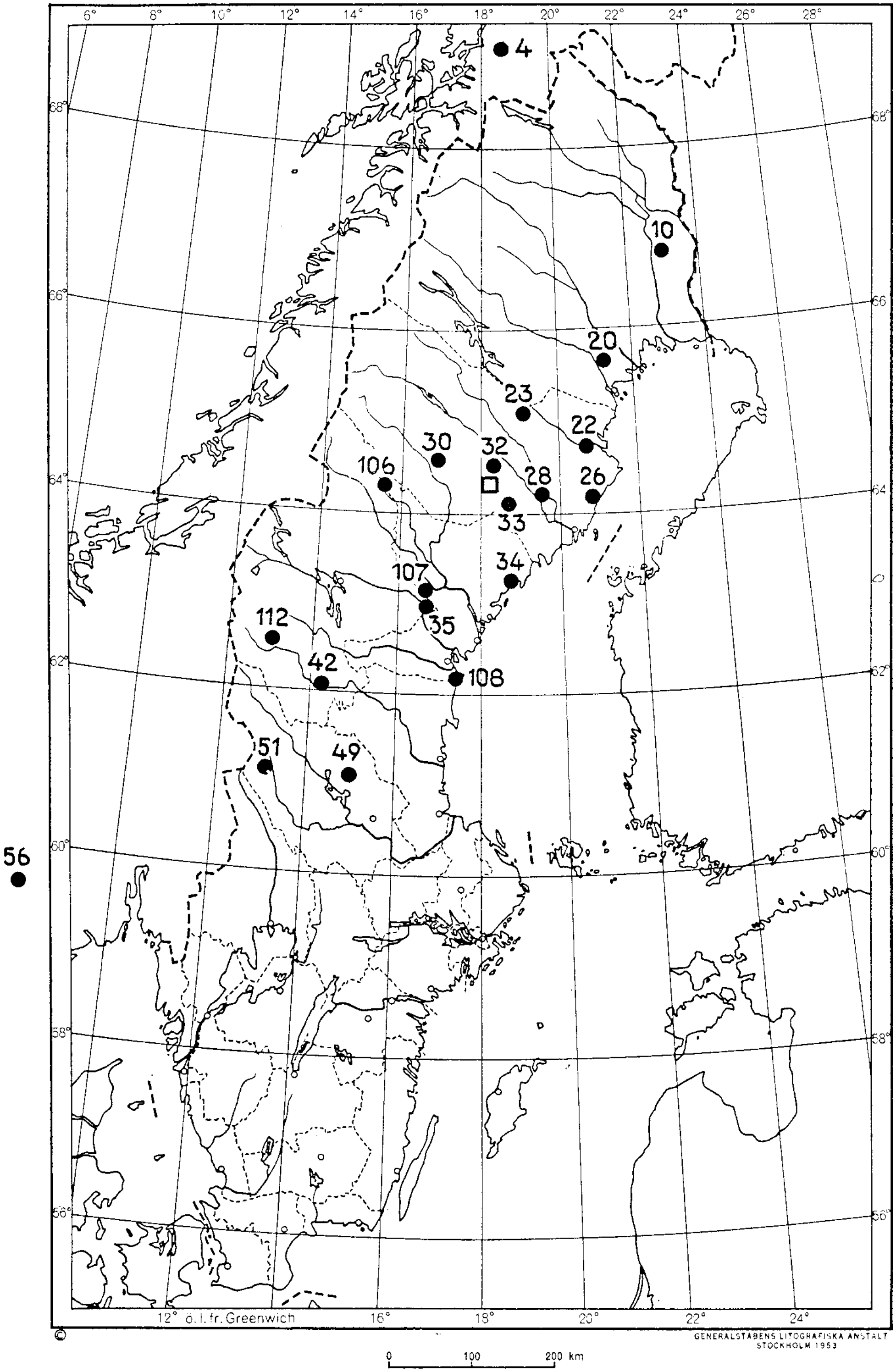

Figure 1. Map showing the origin of the populations tested at Nordanås.

tree offsprings from 20 trees in each population. As will be evident from the presentation of the data from this EP this goal could not be fulfilled entirely. The mother trees were selected at random among those carrying cones in the different stands.

A split-plot design was used. There are randomised replications each originally consisting of 20×15 plants. Each plot should contain 20 sub-plots of 15 plants in a row originating from open pollinated seed of a single mother tree.

A hard broadcast burning was carried out on a felling area two weeks before the planting began. Furthermore, a severe drought started in the summer of 1955, which caused the death of plants on a large scale. Losses of plants were replaced in 1956 by reserve plants grown on the EP site. However, due to the lack of progenies from several individual trees the original design of the experiment with 20 randomised families in each replication could not possibly be fully restored.

Observations and control of the EP were made every year. Contrary to the tending of the other EPs, the plants here were not sprayed with CaS-solution, which is used as a protection against the infection by the snow-blight fungus (*Phacidium infestans*). In spite of this no plants were killed by this fungus. Infection of plants by fungii occurred only sporadically. A very severe invasion of voles (*Microtus agrestis*) might have destroyed the plants during the winter of 1966/67. Due to the immediate treatment of the stems by protective chemicals, the damage was to a great extent avoided and only on two plots (populations 20 and 106) did some of the trees become the victims of the voles. No other biotic factors caused the death of plants. It should be stressed that the weather conditions were the primary cause of the damage and mortality in plants of this EP. The mortality of the plants was registered at intervals of a few years.

3 Results and discussion

3.1 Survival

3.1.1 *Variation between populations*

The death rates of the 20 populations are demonstrated graphically by time-age mortality curves in Figure 2. This figure reveals that there was a high mortality in the first year after establishment of the experimental plantation. This high death-rate was probably to a great extent caused by the protracted drought in the summer of 1955. However, it should be noted that the populations which later on showed the highest mortality rates were also most severely affected in the first years after plantation. The resistance against drought and cold may be related phenomena.

In Figure 3 we have tried to illustrate the effect of transfer on plant mortality. The calculated percentage (cf. equation 1) for the local population is also illustrated in this diagram. As may be seen from this figure populations transferred in a southern direction mostly show a lower plant mortality than the local population even if this change is connected with a transfer to a higher altitude. This seems to be a general observation in the experimental series established by Eiche (*e.g.* cf. Eriksson and Eiche 1975).

Since the populations cover a geographically wide area of Sweden it is easy to prove a genetic influence on the plant survival. However, a genetic influence *per se* is of limited value since it does not reveal the factors which may influence the plant survival. Therefore, besides a conventional analysis of variance we have tried to relate

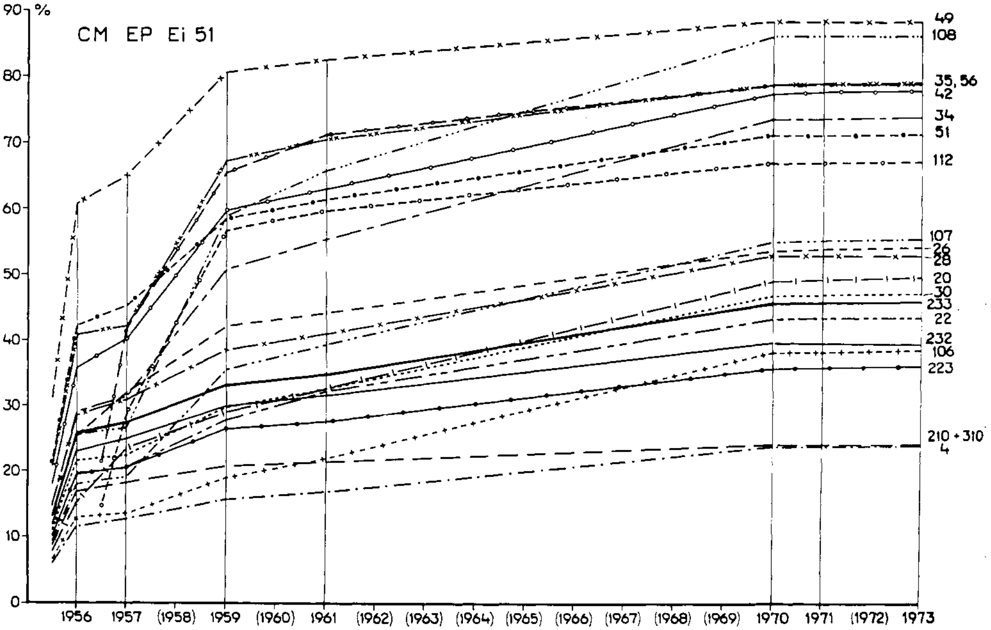

Figure 2. The cumulative mortality of the 20 populations tested at Nordanås.

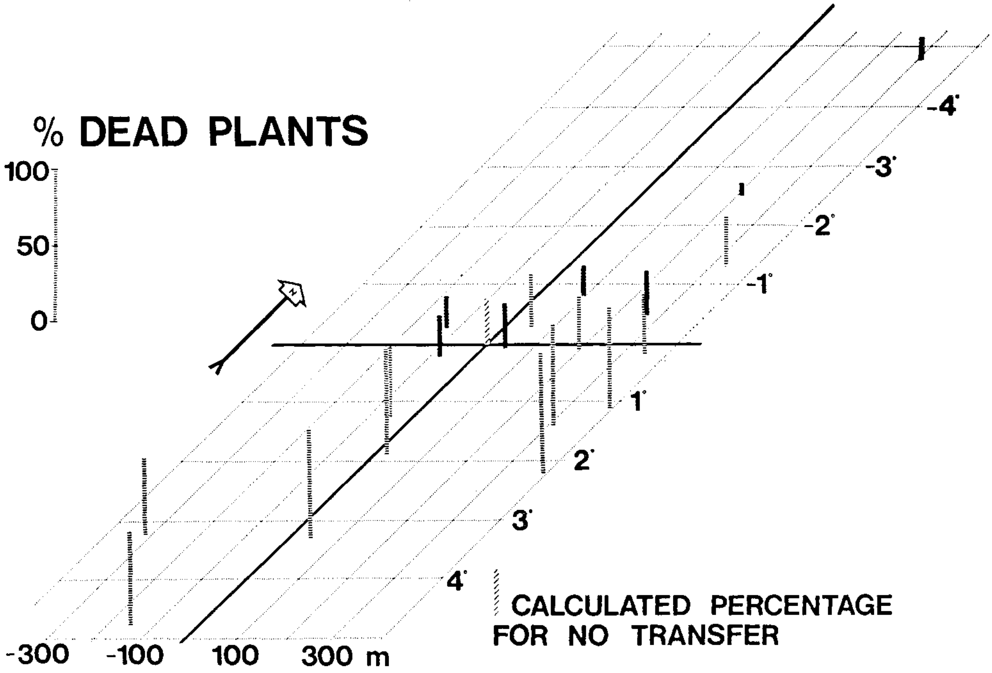

Figure 3. The percentage of plant mortality between the years 1956—1973 of the populations tested at Nordanås. The populations showing a lower percentage of dead plants than the calculated value (cf. text) for the local population are indicated by dark columns. The location of the columns in the grid indicates the transfer made in altitudinal and latitudinal direction. Thus columns below the horizontal line indicate populations which were moved in northern direction. Columns to the right of the diagonal axis show populations which were moved to a higher altitude.

changes in latitude and altitude to the plant survival by regression analysis.

The analysis of variance was carried out on nominal percentages as well as on arcusinus $\sqrt{\text{percentage}/100}$ transformed values. The results are shown in Tables 2 and 3. The repeatability was extremely high, which means that the data as regards differences in plant mortality (1956—73) between populations are highly reliable in the present experimental plantation.

Of greater implications for forest tree breeding are the other approaches which (ΔY) for different populations was obtained will be presented below. The relationship between the changed length of the growing season and the cumulative mortality is illustrated graphically in Figure 4. The length of the growing season (Y) as well as the changed length of the growing season

Table 2. Analysis of variance as regards plant mortality between 1956—1973, nominal values.

Source of variation	Df	M Sq	Expectation values
Between blocks	2	100.69	
Between populations	19	1460.68	$\sigma_e^2 + 3\,\sigma_p^2$
Error	36	26.51	σ_e^2

$$\text{repeatability} = \frac{\sigma_p^2}{\frac{\sigma_e^2}{r} + \sigma_p^2} = 0.982$$

σ_e^2 = variance component for experimental error.

σ_p^2 = variance component for population differences.

r = number of replications.

Table 3. Analysis of variance as regards plant mortality between 1956—1973, arcsin $\sqrt{\text{percentage}}$ transformation.

Source of variation	Df	M Sq	Expectation values
Between blocks	2	53.44	
Between populations	19	708.04	$\sigma_e^2 + 3\,\sigma_p^2$
Error	36	15.61	σ_e^2

$$\text{repeatability} = \frac{\sigma_p^2}{\frac{\sigma_e^2}{r} + \sigma_p^2} = 0.978$$

σ_e^2 = variance component for experimental error.
σ_p^2 = variance component for population differences.
r = number of replications.

by interpolating the data after 30 years of meteorological observations from stations situated closest to the population sites. Y is defined as the number of days when the daily mean temperature is $\geq 6°$C and is given for each population in Table 1. For the experimental plantation at Nordanås, Y is calculated as 118 days.

Since part of the plant mortality could be attributed to drought the first summer after planting, we have preferred to relate the percentage of plant mortality between the years 1956 and 1973 to the changed length of the growing season. As seen from Figure 4 there is a relatively strong relationship between the plant mortality and ΔY.

To test whether or not other relationships would give a still better fit to the obtained data a regression analysis was used. The change of the altitude in metres (Δalt), the transfer in a southward ($-\Delta$lat) or northward ($+\Delta$lat) direction (kilometers) as well as $(\Delta\text{alt})^2$, $(\Delta\text{lat})^2$, and $\Delta\text{alt} \times \Delta\text{lat}$ were used as independent variables. These variables were selected since it is known that there is a climatic gradient by changing latitude and altitude. However, there may be a curvilinear dependence of the climate on Δalt or Δlat. Therefore, $(\Delta\text{alt})^2$, $(\Delta\text{lat})^2$, and $\Delta\text{alt} \times \Delta\text{lat}$ were used as independent variables. The best agreement was obtained for the following equation:

$$f\,(\text{plant mortality } 56\text{—}73) = 30.6 + 0.071\ \Delta\text{lat} + 0.029\ \Delta\text{alt} + 0.00012\ \Delta\text{alt} \times \Delta\text{lat} + 0.00008\ \Delta\text{lat}^2 + 0.00003\ \Delta\text{alt}^2 \quad (\text{equation 1}) \quad R = 0.9358^{***}$$

$$\left.\begin{array}{l}\Delta\text{lat is expressed in km}\\ \Delta\text{alt is expressed in m}\end{array}\right\}\ \text{plus sign means a transfer upwards or in a northern direction}$$

One example may suffice to explain the meaning of equation 1. A transfer to Nordanås of a population from the same elevation (400 m) but 100 km from the south will increase the mortality with 7.9 percentage units. Conversely a transfer over the same distance in a southward direction would reduce the percentage of dead plants from 30.6 to 22.7 per cent. The effect of transfer on the plant survival is visualized in Figure 5.

Although equation 1 constitutes the best agreement between the obtained data and the independent variables tested, it should be stressed that some other equations give almost as good an agreement. The relative importance of the different variables may be obtained from Table 4. It is evident that Δlat is the most important variable, followed by Δalt, whereas the three other variables contribute little to the increase of R.

General rules cannot be worked out when based upon data from just one experimental plantation. However, it can be added that the pattern revealed in this EP agrees well with the data from other EPs belonging to the same series of EPs as EP 51. Moreover, the data presented by Remröd (1972) for five north Swedish provenance trials with *Pinus sylvestris* are also in good agreement with the present data.

3.1.2 *Variations within populations*

Pooled estimates of the cumulative mortality in 1973 as well as for the interval between

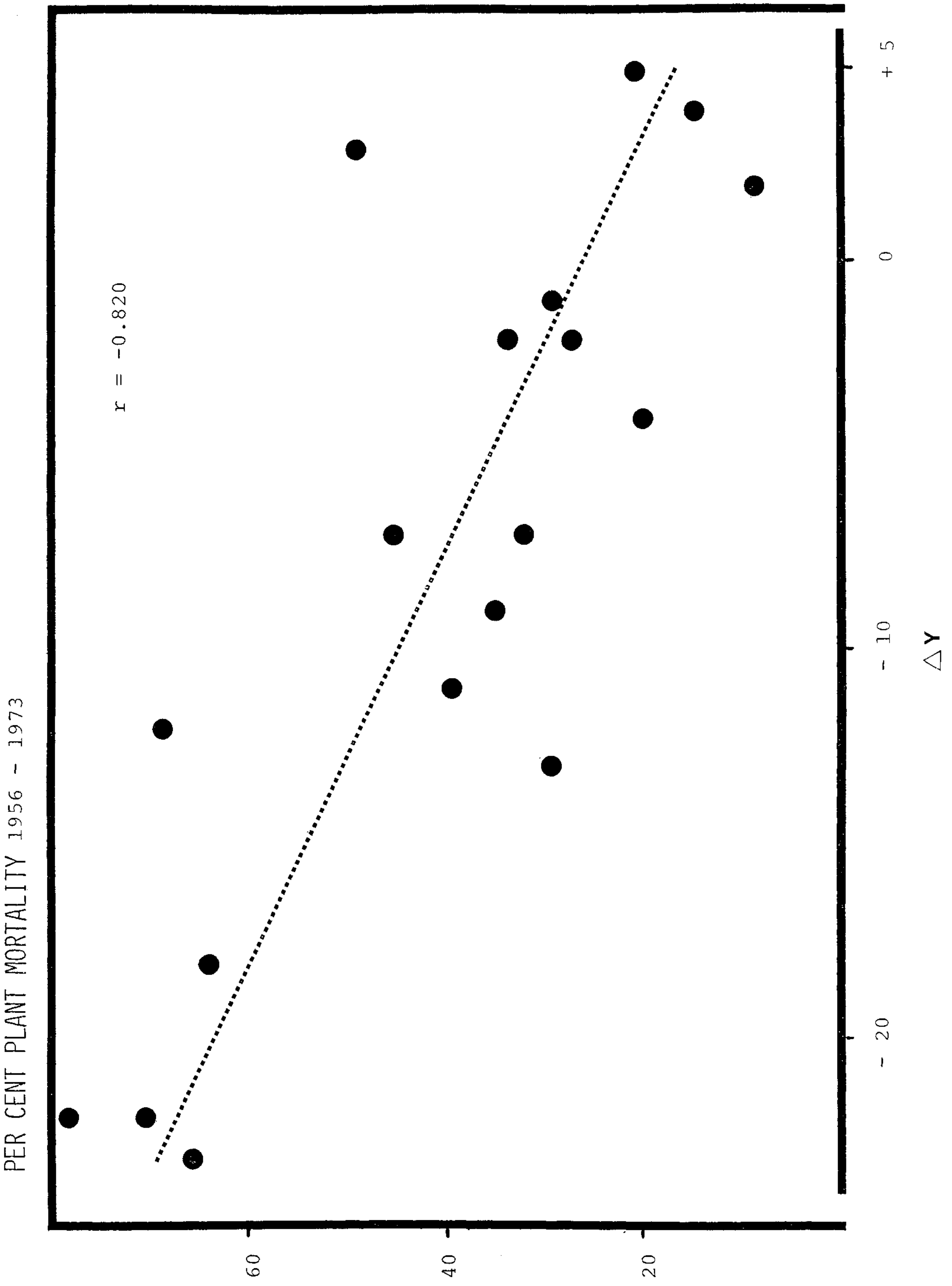

Figure 4. The relationship between the changed length of the growing season, ΔY, and the percentage of dead plants between the years 1956—1973.

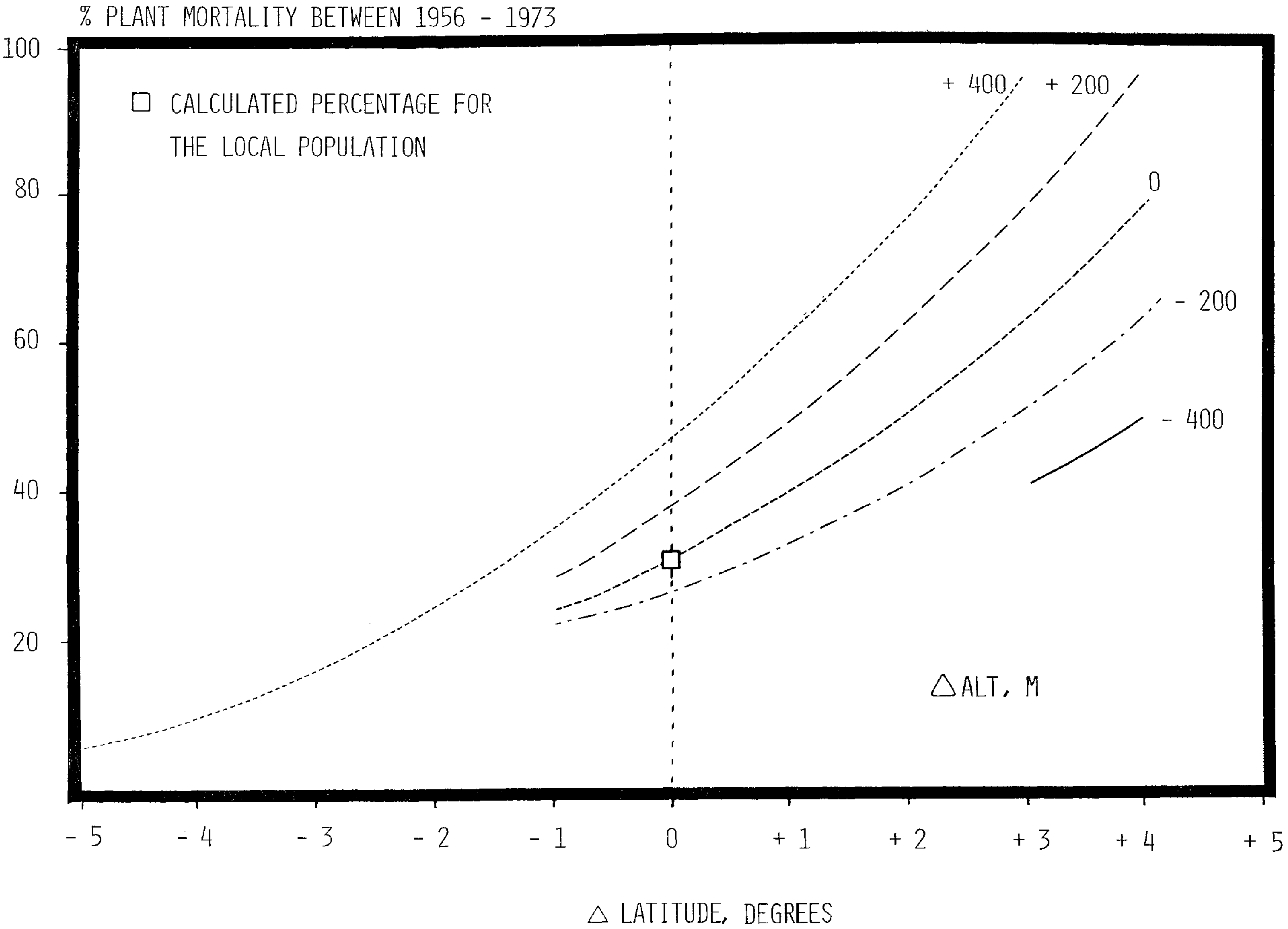

Figure 5. The effect of latitudinal transfers at constant altitudinal transfers on the percentage of dead plants between the years 1956—1973. Plus signs mean a transfer upwards or in a northward direction, respectively.

Table 4. The multiple correlation coefficients obtained from the stepwise regression analysis of the relationship between plant mortality 1956—1973 and geographic variables.

Step	Variables tested					R	F-ratio
	Δalt	Δalt^2	Δlat	Δlat^2	Δalt $\times$ Δlat		
1			×			0.8072	31.784
2	×		×			0.9190	43.460
3	×		×	×		0.9261	30.131
4	×		×	×	×	0.9345	24.119
5	×	×	×	×	×	0.9358	18.335

Table 5. The pooled values for cumulative mortality (CM) in 1973 and plant mortality between 1956—1973 (PM 56—73) as well as variance ratio obtained after two-way analysis of variance based on nominal values and arcsin $\sqrt{\text{percentage}}$ transformation.

Population	n	CM	Variance ratio		n	PM 56—73	Variance ratio	
			Nominal values	Arcsin $\sqrt{\text{percentage}}$			Nominal values	Arcsin $\sqrt{\text{percentage}/100}$
4	20	24.1	4.5023***	4.5086***	20	14.33	3.0064**	2.3963*
210	10	24.4	2.5912*	2.0115	10	8.3	0.9805	1.1437
310	10	23.1	4.0863**	3.6945**	10	8.2	1.0061	1.2104
20[1]	16	40.3	0.6123	0.7128	16	31.6	0.5170	0.5116
22	20	43.7	2.2621*	2.2019*	17	29.4	2.1879*	1.8334
223	12	36.0	1.8486	1.8359	12	20.1	1.3813	1.2983
26	20	54.2	3.0094**	3.2680***	18	39.4	2.4625*	2.4254*
28	20	53.2	2.7361**	2.5860**	18	34.9	2.7490**	3.4582***
30	19	47.7	0.9571	0.9693	19	33.7	1.1028	1.0985
232	12	39.1	1.3500	1.2665	12	20.6	1.1045	1.1791
233	18	46.2	1.8170	1.7733	17	27.1	0.5227	0.5890
34	20	74.2	2.5237**	2.5726**	20	64.3	1.2458	1.2125
35	20	79.1	1.8784*	1.6573	12	66.0	1.5421	1.5109
42	18	78.8	1.4511	1.6561	14	69.2	1.1698	1.2881
49	19	89.1	1.9508*	2.0494*	10	70.6	0.5003	0.4796
51	18	72.1	2.2102*	2.7799**	13	49.1	0.6569	0.5807
56	12	80.4	5.8376***	6.2068***	10	63.5[2]	1.8335	1.5827
106[1]	17	38.6	0.8799	0.8859	17	29.2	1.2964	1.0997
107	17	56.1	1.3962	1.4394	16	45.3	1.2703	1.2601
108	20	86.6	2.8942**	2.8068**	15	79.1	1.8355	1.7390

n = number of single tree progenies tested.

[1] Represented in two blocks only, in population 20 missing values had to be used for two of the single tree progenies since they were represented in one block only.

[2] Percentage of dead plants based on the number of surviving plants in 1957.

the years 1956—1973 are presented in Table 5. To test whether or not there were significant differences between single tree progenies within the different populations two way analyses of variance were performed separately for each population. Both nominal values and arcsin $\sqrt{\text{percentage}/100}$ transformed values were included in the analyses. The analysis was carried out by the regression technique suggested by

Snedecor (1950). The variance ratios and the significances obtained are indicated in Table 5.

As may be seen from Table 5 there are at least three populations in which the difference between the single-tree progenies was proven to be significant. It should be added that the possibility to prove differences between the single-tree progenies is highest when the percentages are close to 50. Therefore, it is not expected to obtain significant differences for all populations tested. Furthermore, it may be added that the variation within the populations is, with a high probability, underestimated, by making use of the plant mortality between 1956—1973, since part of the plant death during the winter 1955—1956, especially in the southern populations, could probably be attributed to cold damage and not to drought during the summer in 1955.

The differences really observed between the single-tree progenies within populations are best seen in diagrammes. Therefore, Figures 6—14 were drawn.

All populations which showed a significant difference as regards the plant mortality between 1956—1973 are illustrated. Also their extreme counterparts, populations 20 and 233, in which differences were small, are illustrated.

3.2 Height growth

3.2.1 *Variation between populations*

The mean height at age 20 years ($\bar{h}$) and mean length of the leader at age 20 ($\bar{l}$) as well as the number of trees per replication ($\bar{n}$) are listed in Table 5. Replaced plants were excluded from the calculations. Missing values for populations 20 and 106 in block II were calculated according to Yates' formula (Cochran and Cox 1950).

The curvilinear relationships between the tree height ($\bar{h}$) in the years 1961, 1967 and 1970 (ages 11, 17, and 20 years, respectively) and the changed length of the growing season (ΔY) for different populations are visualized in Figure 15. Populations 56 and 112 were not included in the calculation since population 56 was planted one year later than the other populations and 112 was not uniform but originated from different elevations (cf. Table 6). The regressions of these years show a pronounced variation. The $\bar{h}$ values for populations Nos 4 and 107 need a special comment since they deviate from the regression curves of the years 1967 and 1970. The low $\bar{h}$ values for population 4 are probably caused by an abnormally heavy yield of cones during the past years. For population No 107 a probable explanation for the low $\bar{h}$ values might be inbreeding depression in the progeny of several mother trees. More or less pronounced dwarfs segregated in these families. The $\bar{h}$ value for population 210 has in fact been obtained from two populations Nos 10—210 and 10—310.

Table 6. Mean values of the number of trees per replication ($\bar{n}$) length (cm) of the leader at age 20 ($\bar{t}$) and tree height at age 20 ($\bar{h}$) for 18 populations in 1970.

Population	$\bar{n}$	$\bar{t}$	$\bar{h}$
4	221.7	29	309
10[1]	225.3	33	332
20	143.0	36	370
22	168.0	35	353
223	189.6	36	370
26	136.0	34	343
28	140.3	36	366
30	157.3	33	351
232	170.3	34	350
233	158.3	35	354
34	76.7	32	317
35	61.7	32	311
42	63.0	35	344
49	33.0	32	308
51	82.3	36	344
106	154.3	34	349
107	111.7	33	333
108	40.3	31	311
Standard error ±	7.8	0.7	9

[1] Mean value for populations 210 and 310.

The regression equations for the total material for different years are as follows:

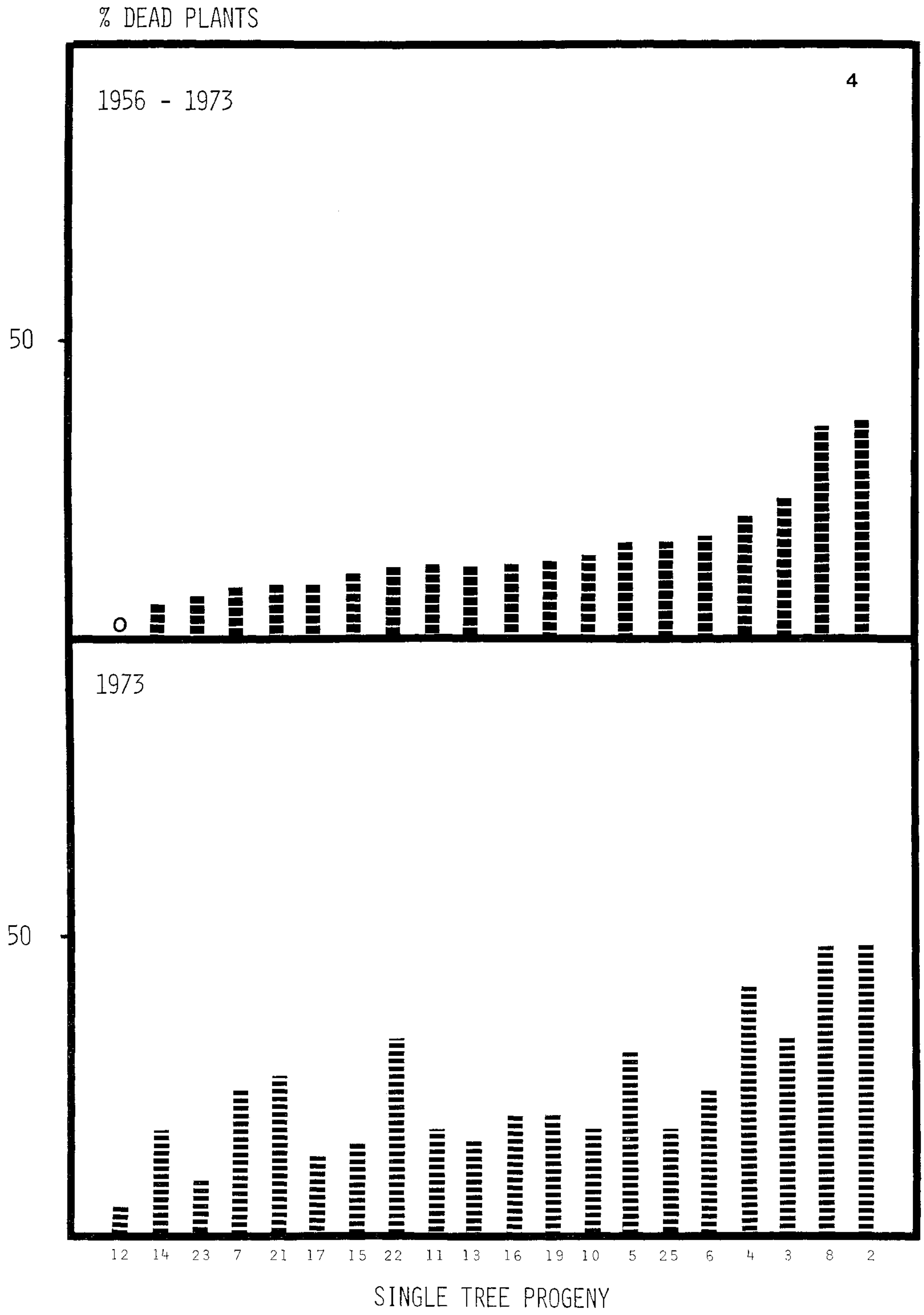

Figure 6. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 4.

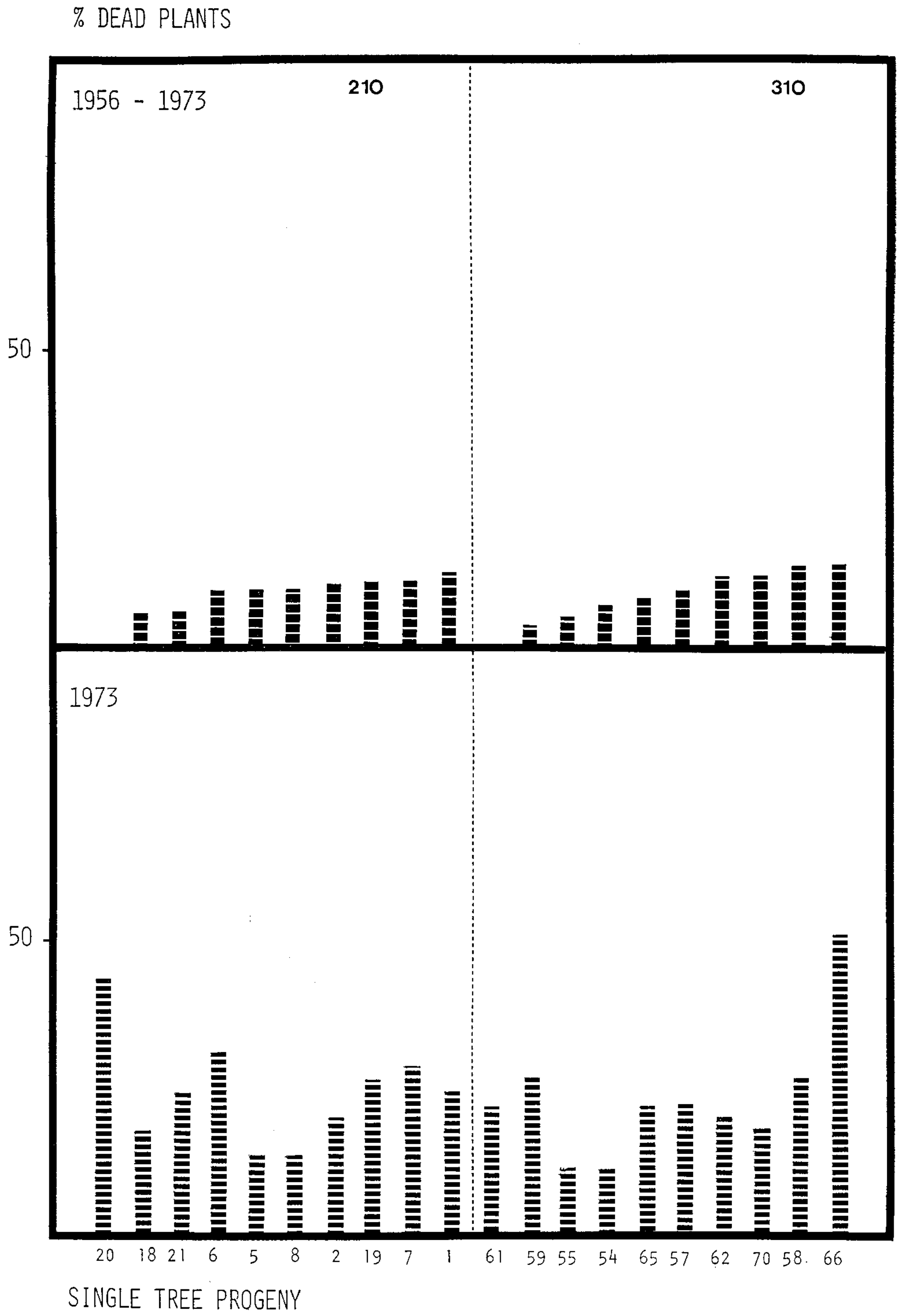

Figure 7. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within populations 210 and 310.

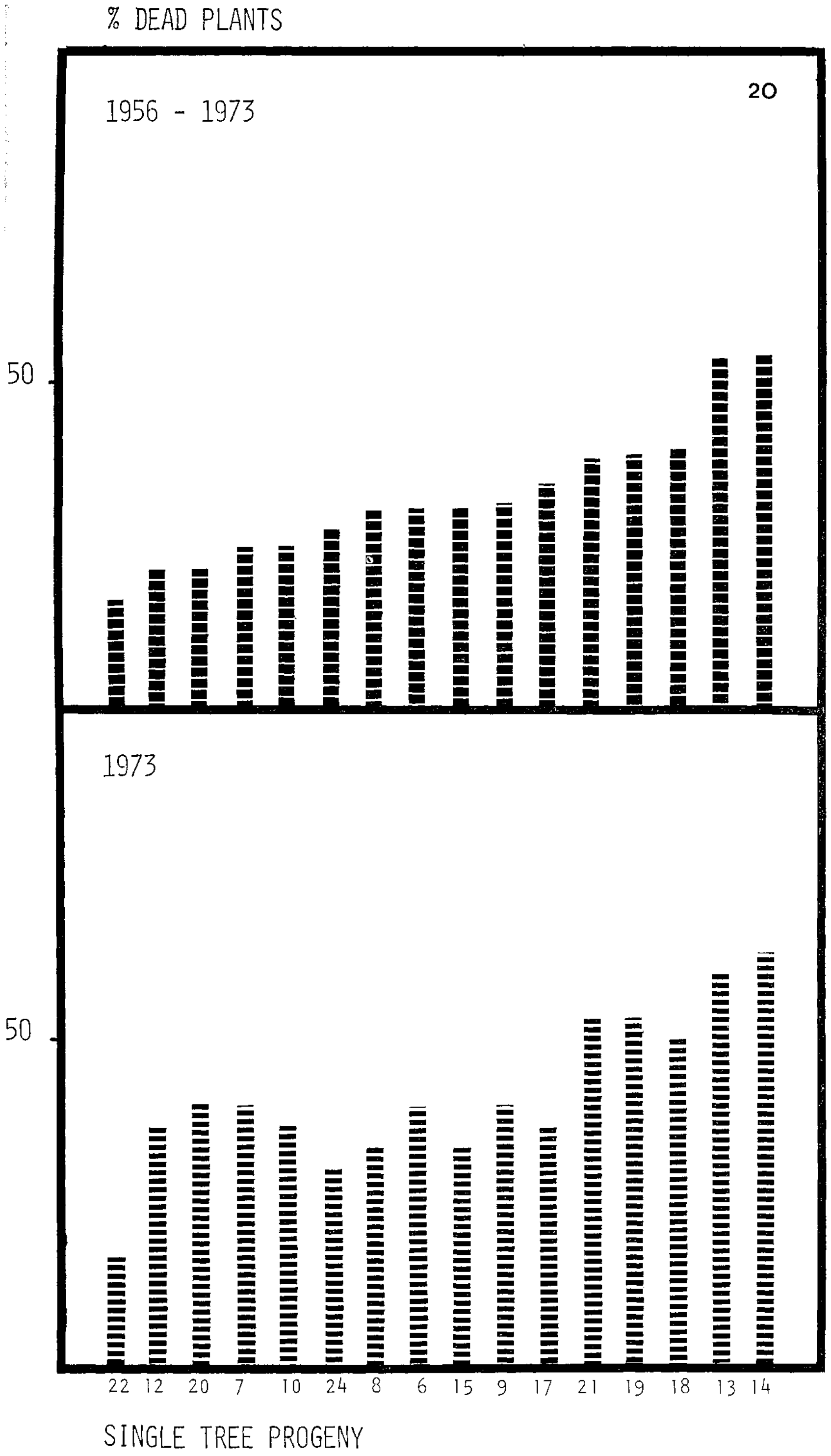

Figure 8. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 20.

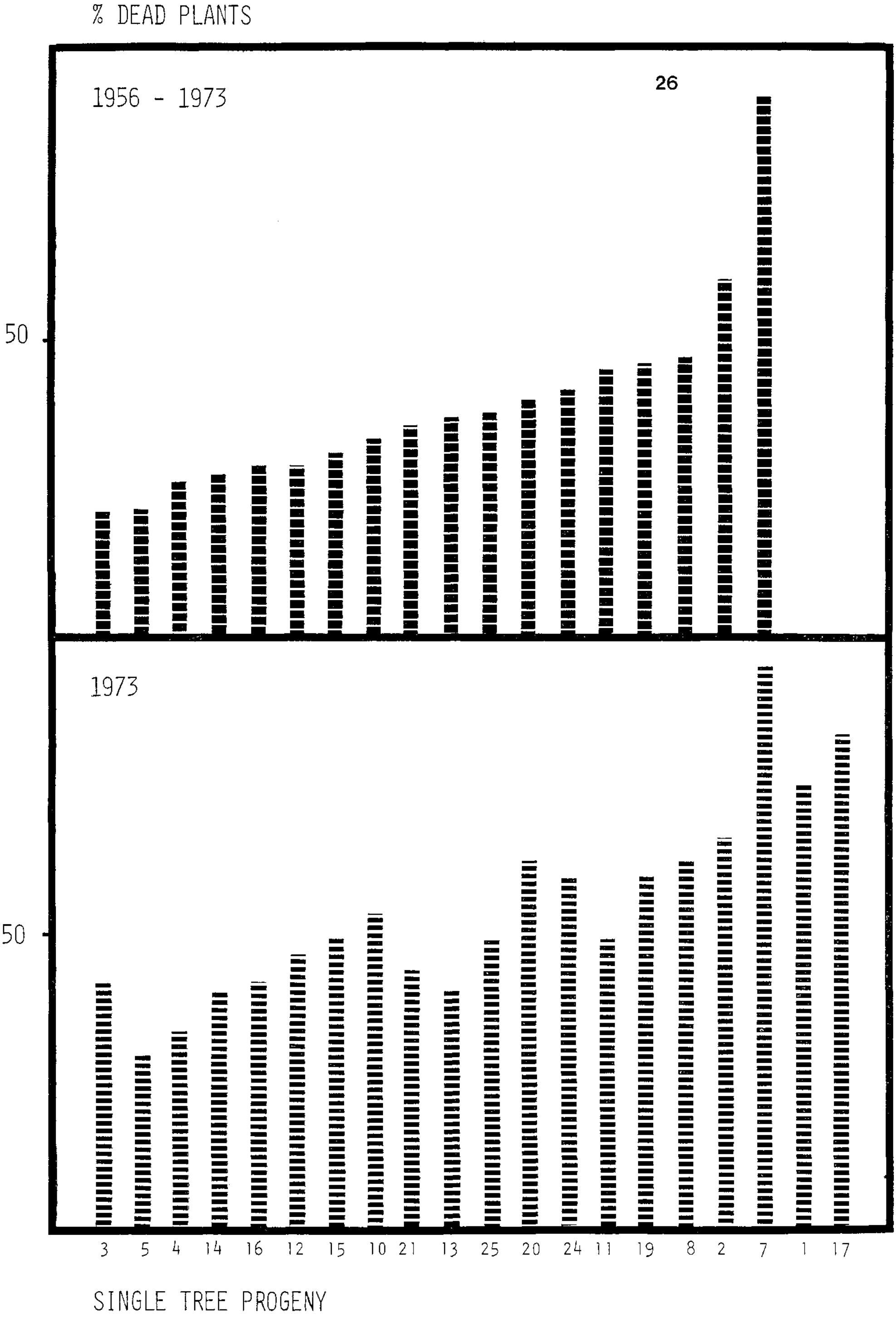

Figure 9. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 26. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

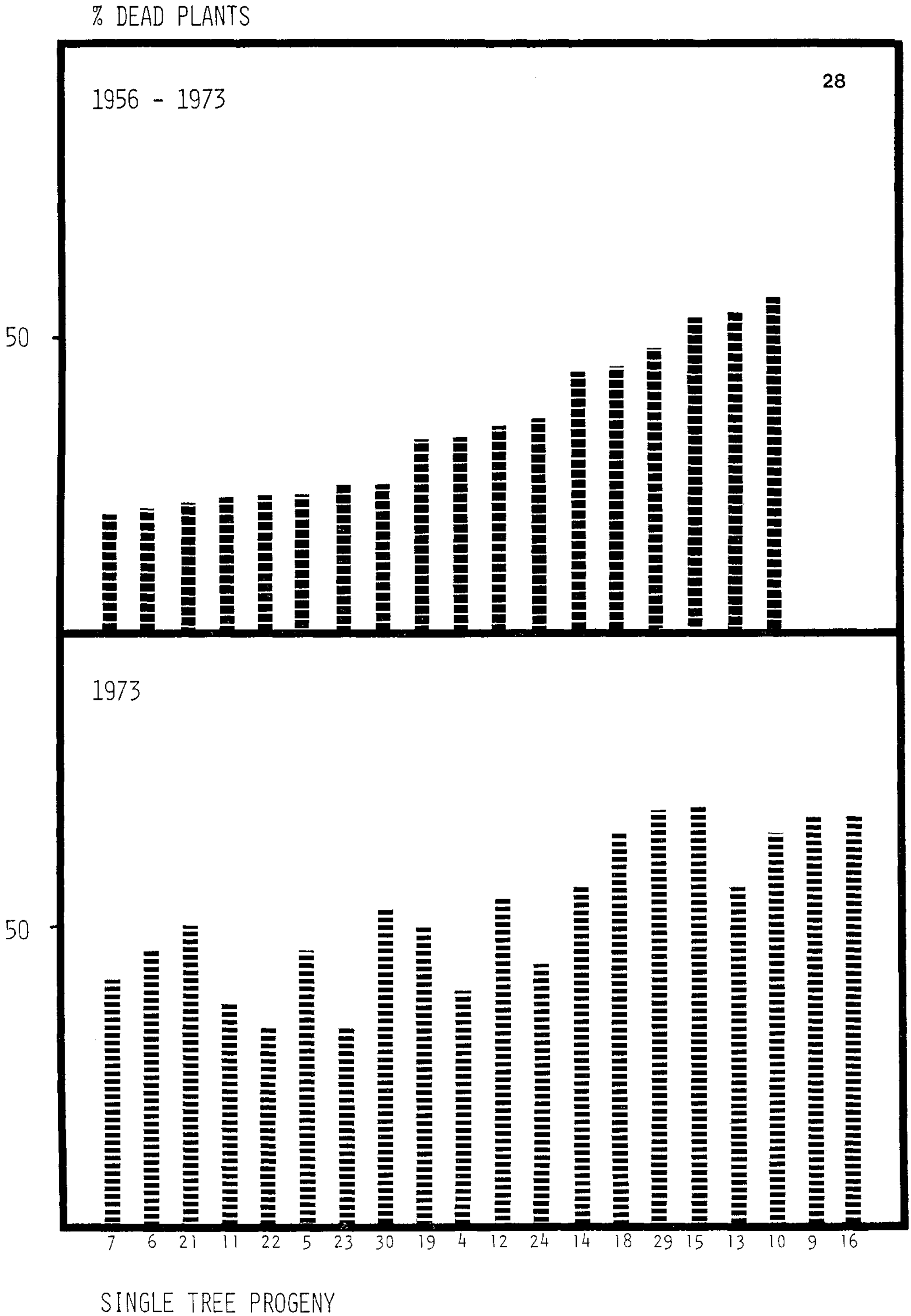

Figure 10. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 28. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

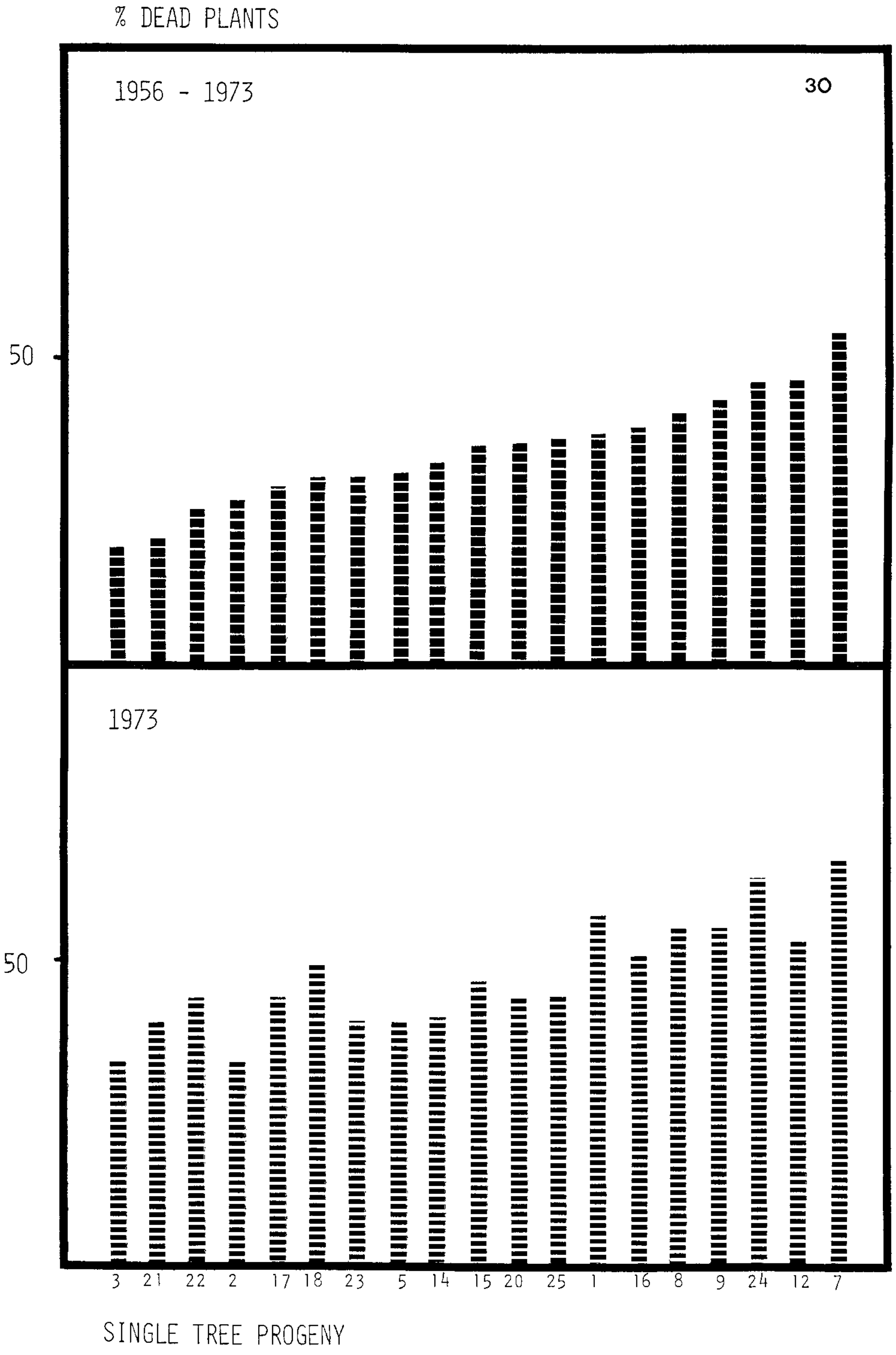

Figure 11. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 30.

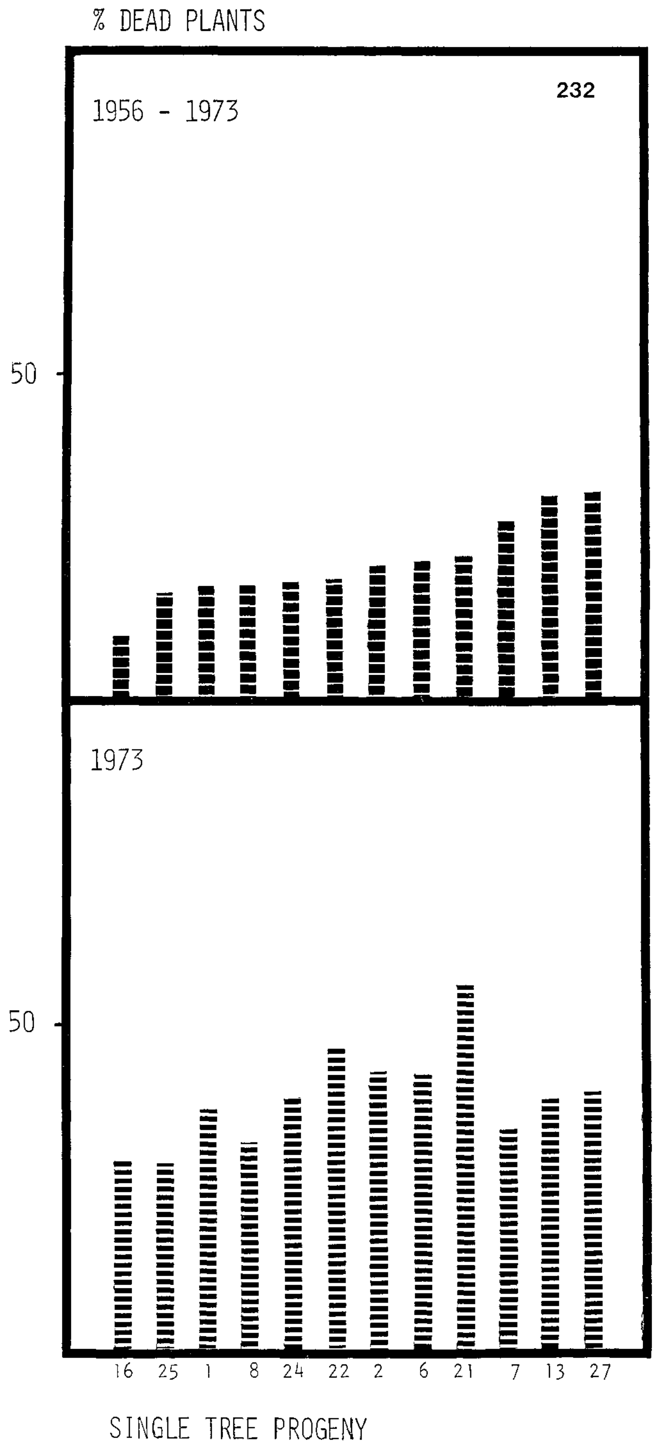

Figure 12. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 232.

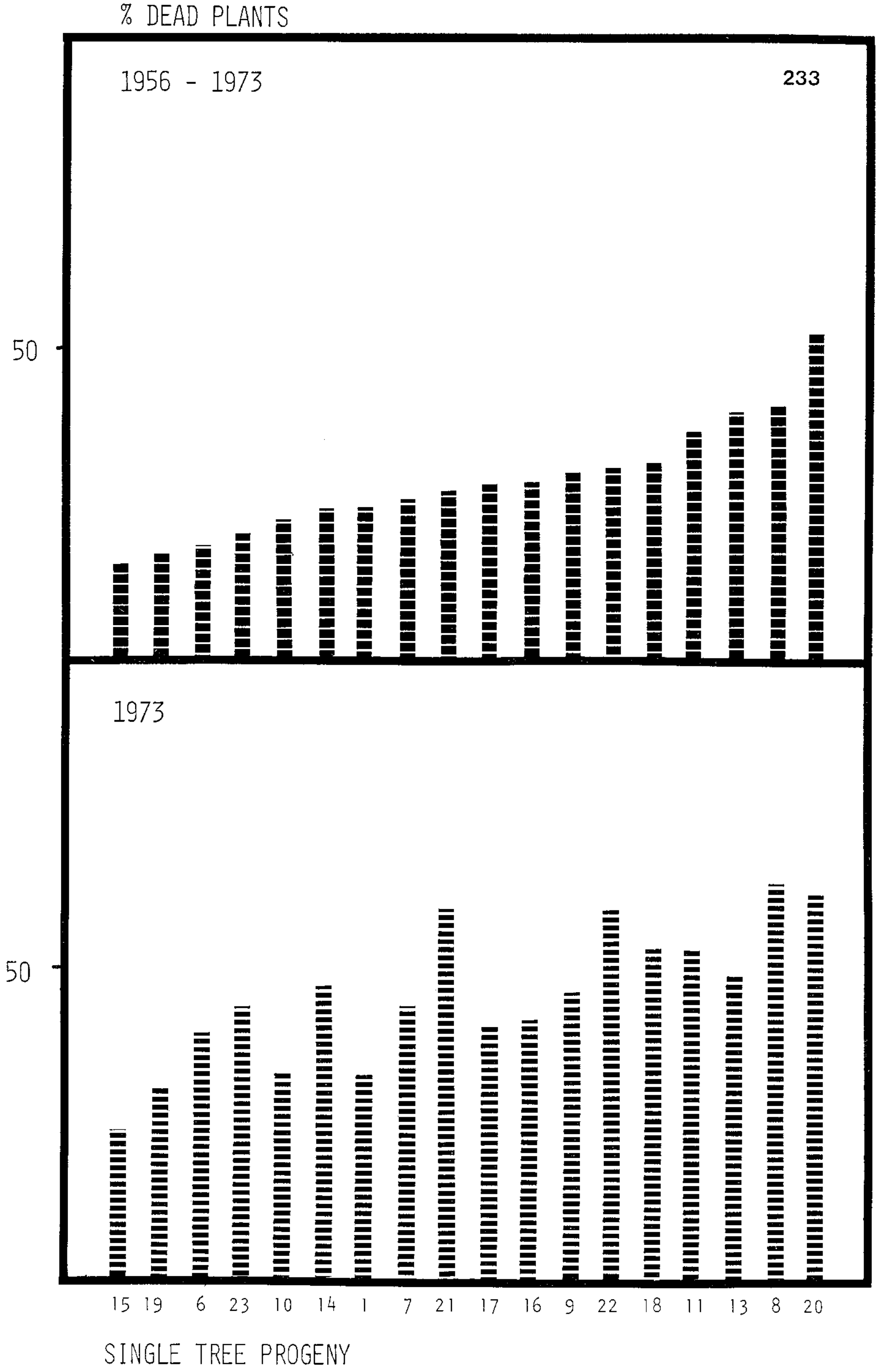

Figure 13. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 233. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

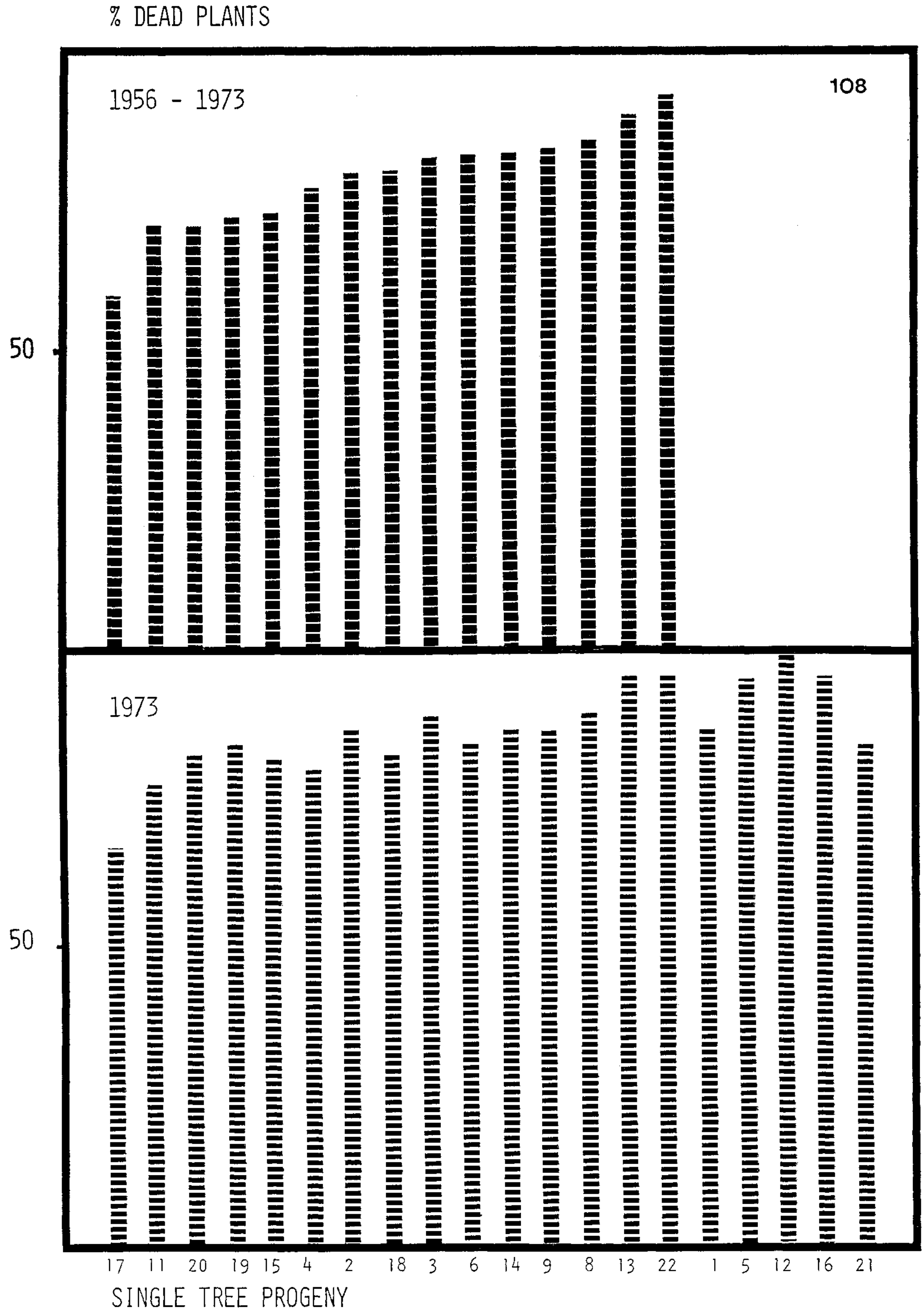

Figure 14. The plant mortality between the years 1956 and 1973 and the percentage of the cumulative mortality up to 1973 of single tree progenies within population 108. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

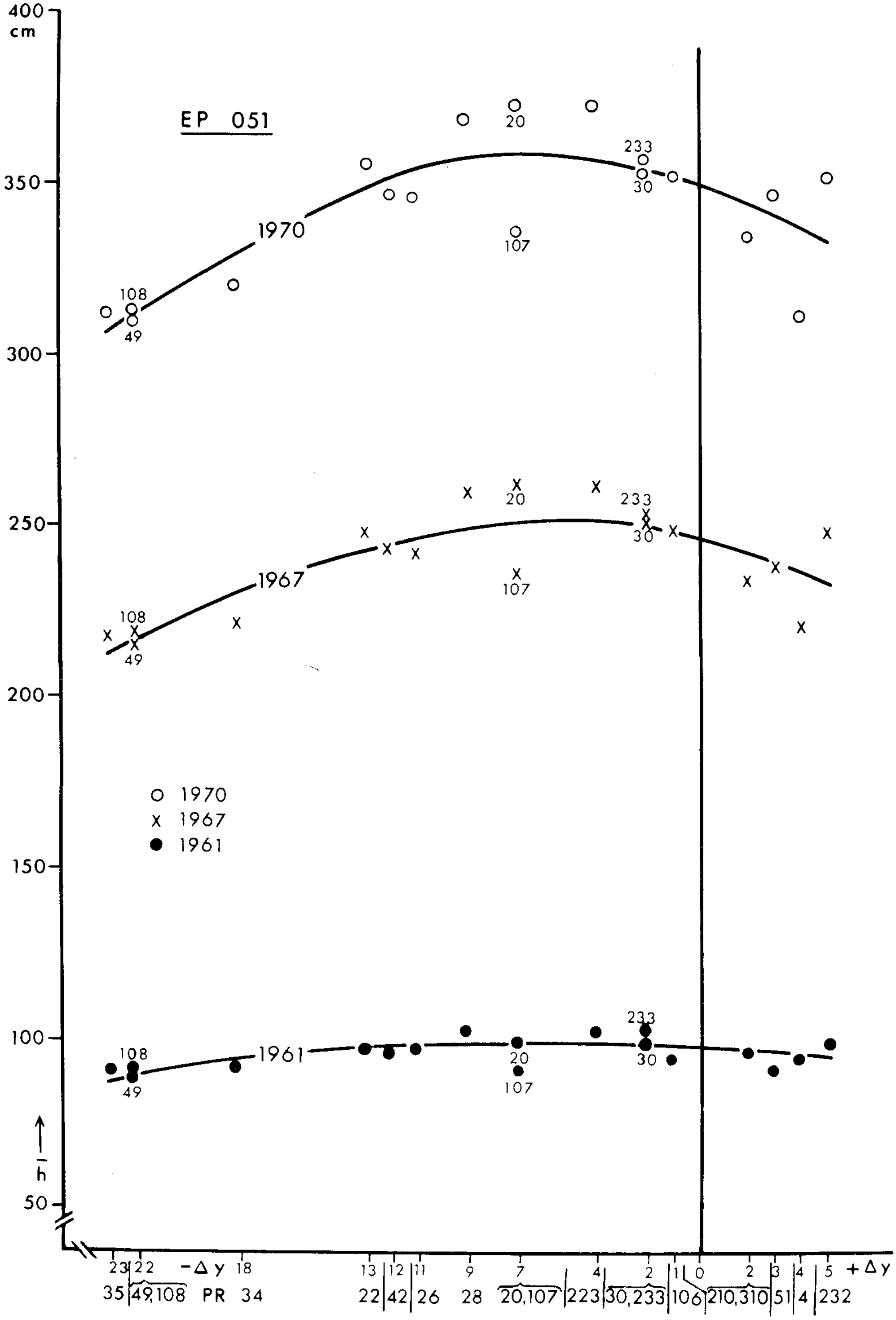

Figure 15. The relationship between the tree height in 1970 and the changed length of the growing season (ΔY) of 18 transferred populations.

	Equation	R	F
1970	$\bar{h}(\Delta Y) = -0.19(\Delta Y)^2 - 2.42(\Delta Y) + 347.28$	0.7486	9.56** equation 2
1967	$\bar{h}(\Delta Y) = -0.13(\Delta Y)^2 - 1.54(\Delta Y) + 244.76$	0.7308	8.60** equation 3
1961	$\bar{h}(\Delta Y) = -0.03(\Delta Y)^2 - 0.29(\Delta Y) + 96.73$	0.5843	3.89* equation 4

Table 7. The multiple correlation coefficients obtained from the stepwise regression analysis of the relationship between height and geographic variables.

Step	Variables tested					R	F-ratio
	Δalt	Δalt^2	Δlat	Δlat^2	Δalt × Δlat		
1				×		0.5595	7.291
2				×	×	0.8715	23.686
3		×		×	×	0.8774	15.613
4	×	×		×	×	0.8784	10.976

A test of the relationship between height and the changed length of the growing season calculated according to Langlet's (1936) formula was also tested. The same type of curvilinear regressions as demonstrated in Figure 15 was obtained also in this case.

A regression analysis evaluating the effect of transfer of population on plant height was carried out in the same way as for the plant mortality.

The equation below showed the best agreement:

$$f\,(\text{stem height}) = 352.88 + 0.00575\,\Delta\text{alt} - 0.00033\,\Delta\text{lat}^2 - 0.00005\,\Delta\text{alt}^2 - 0.00033\,\Delta\text{alt} \cdot \Delta\text{lat}\ (\text{equation 5})\ R = 0.8784^{***}$$

The relative importance of the five independent variables tested may be read from Table 7. In contrast to the plant mortality $(\Delta\text{lat})^2$ was found to be the most important factor for height growth followed by $\Delta\text{alt} \times \Delta\text{lat}$. The other variables were of limited importance.

The effect of transfer on tree height is illustrated in Figure 16. This figure reveals that a simultaneous transfer to the north ($>1°$ latitude) and to a higher altitude (200—400 m) causes a pronounced reduction of the height growth of individual trees. The good growth displayed following a transfer of two degrees of latitude in a southward direction with an elevation transfer of 400 m upwards is worth mentioning. This type of effect seems to be common in many of the experimental plantations belonging to the same series as EP 51.

3.2.2 *Variation within populations*

Analyses of variance were carried out separately for 13 of the populations to test whether or not any significant differences between single tree progenies as regards the tree height existed. These analyses were performed in the same way as for the plant mortality between the years 1956—1973, thus excluding progenies represented by few trees. Whole populations having too few trees per single tree progeny were also excluded from this analysis. Except for population 108, the same populations as illustrating the variation in plant mortality are shown also in this case.

For the above-mentioned 13 populations, the pooled, unweighted mean values ± the standard errors for plant height at the ages 11, 12, 13, 17 and 20 years are listed in Table 8 (see also Figures 17—25). Significant differences within a population at a certain age are indicated in this table.

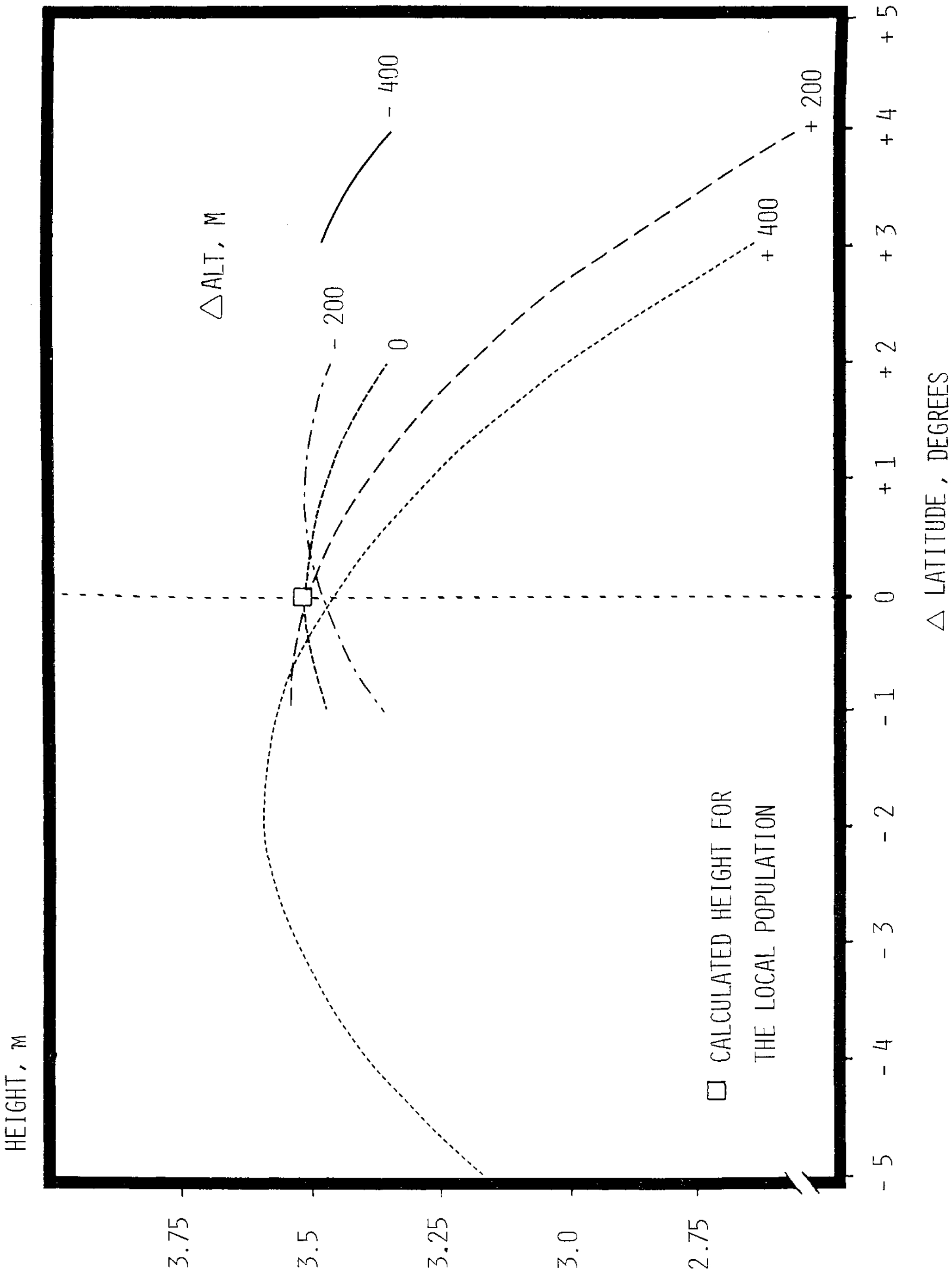

Figure 16. The influence of latitudinal transfers at constant altitudinal transfers on the tree height at an age of 20 years. Plus signs mean a transfer upwards or in a northward direction, respectively.

Table 8. Pooled unweighted mean values ± standard error for height at different ages and for breast height diameter at age 20.

Population	n	Age					
		11	12	13	17	20	20 Diametre at breast height
4	20	95 ± 1	117 ± 2*	133 ± 2	220 ± 2	307 ± 3	47 ± 1
210	10	100 ± 2	124 ± 2	142 ± 2	246 ± 5	348 ± 6	56 ± 1
310	10	89 ± 2*	111 ± 2*	127 ± 2*	219 ± 4**	313 ± 5**	51 ± 1
20	16	98 ± 3*	124 ± 4*	142 ± 4*	247 ± 6*	352 ± 7**	58 ± 2*
22	19	98 ± 2	123 ± 2	141 ± 2	247 ± 4	352 ± 4	57 ± 1
223	11	102 ± 2	128 ± 2	147 ± 3	257 ± 4	366 ± 5	61 ± 1
26	18	96 ± 2	121 ± 3	138 ± 3	241 ± 5	343 ± 6	57 ± 1
28	20	101 ± 2	128 ± 2	146 ± 2	257 ± 3	365 ± 4	61 ± 1
30	19	100 ± 2	126 ± 2	144 ± 3	246 ± 4*	347 ± 4**	56 ± 1*
232	12	97 ± 2	123 ± 2*	141 ± 3*	247 ± 4	349 ± 5*	56 ± 1
233	18	97 ± 2*	123 ± 2*	141 ± 2	249 ± 4*	353 ± 5**	59 ± 1*
106	17	92 ± 2	117 ± 3	134 ± 3	237 ± 5	335 ± 7	55 ± 1
107	15	90 ± 2	115 ± 2	132 ± 3	232 ± 5	330 ± 6	54 ± 2

Single tree progenies which in at least two replications contained less than half the number of surviving trees of the populations average were omitted from the analysis of variance.

3.3 **Volume**

The volume of every single tree has been calculated according to Näslund (1941), function No 4, if the diameter over bark at breast height is at least 5.0 cm. If the trees are smaller their volume was calculated according to Andersson (1954), function No 1. The symbols below are common for both of these functions:

v = volume of stem over stump including bark, dm^3
d = tree diameter at breast height (1.3 m above ground), cm
h = tree height above ground, m

The functions are as follows:

DBH ≥ 5 cm $v = 0.09314\, d^2 + 0.03069\, d^2h + 0.002818\, dh^2$
DBH < 5 cm $v = 0.22 + 0.08786\, d^2 + 0.03045\, d^2h + 0.002809\, dh^2$

By using the volumes calculated with these functions, the arithmetical mean volume per tree and the total stem volume per hectare have been calculated for every population. The values are shown in Table 9.

Table 9. Volume of populations growing at Nordanås at age 20.

Population		Mean volume per tree, dm^3	Total volume per ha m^3 over bark
4	Målselv	5.4	6.4
210	Korpilombolo	6.9	8.4
20	Älvsbyn	8.1	5.8
22	Krångfors, Backen	7.8	7.0
223	Malå	9.2	9.4
26	Robertsfors	8.0	5.8
28	Vindeln	8.8	6.6
30	Vilhelmina	7.8	6.6
232	Storberget, Lycksele	7.7	7.0
233	Örträsk	8.5	7.2
34	Alfredshem	6.2	2.5
35	Bispfors, Stadsforsen	6.0	2.0
42	Sveg	7.4	2.5
49	Orsa	5.8	1.0
51	Sälen	7.9	3.5
106	Harrsjön	7.5	5.0
107	Bispfors, Torresjölandet	7.1	4.2
108	Galtström	5.7	1.2

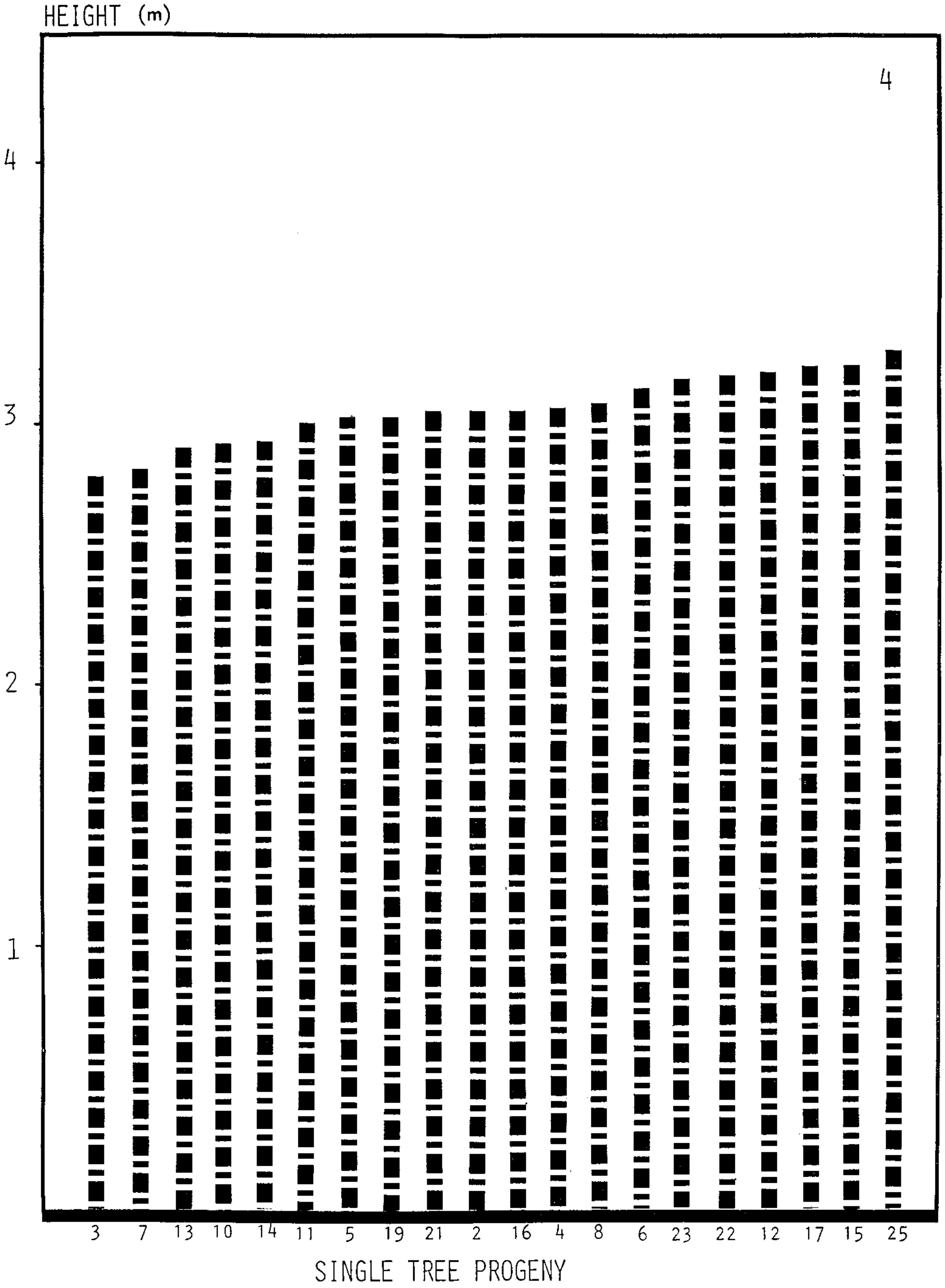

Figure 17. The mean tree heights at an age of 20 years of single tree progenies from population 4.

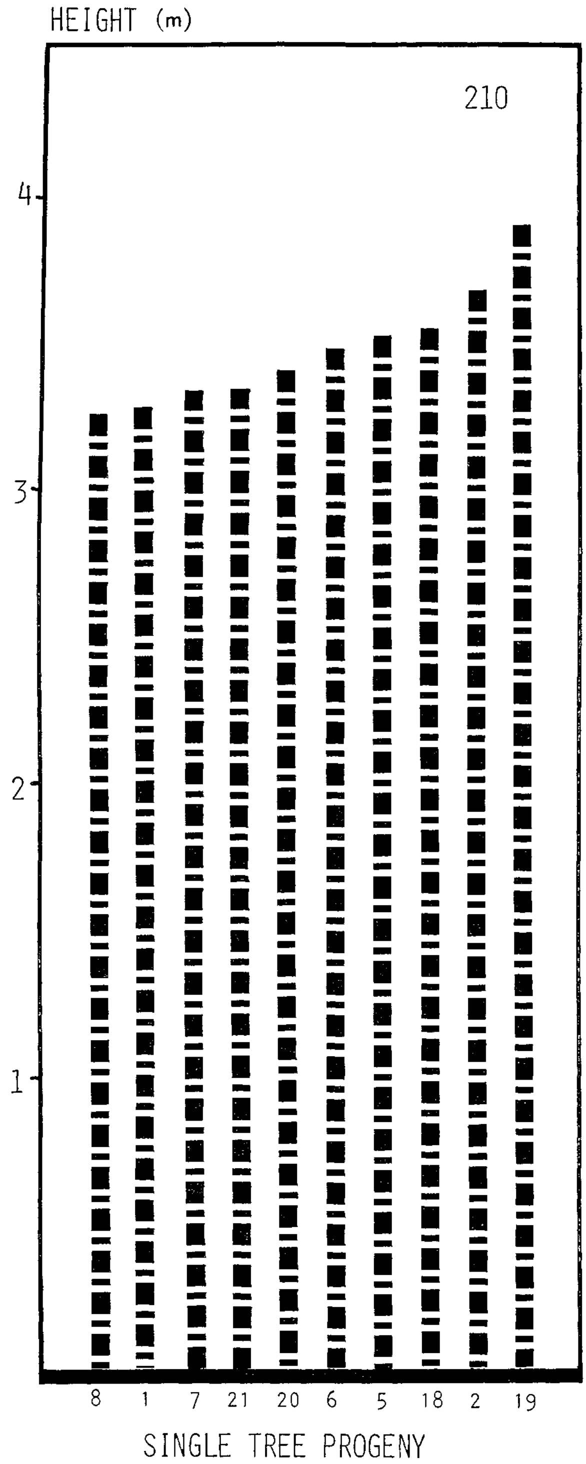

Figure 18. The mean tree heights at an age of 20 years of single tree progenies from population 210.

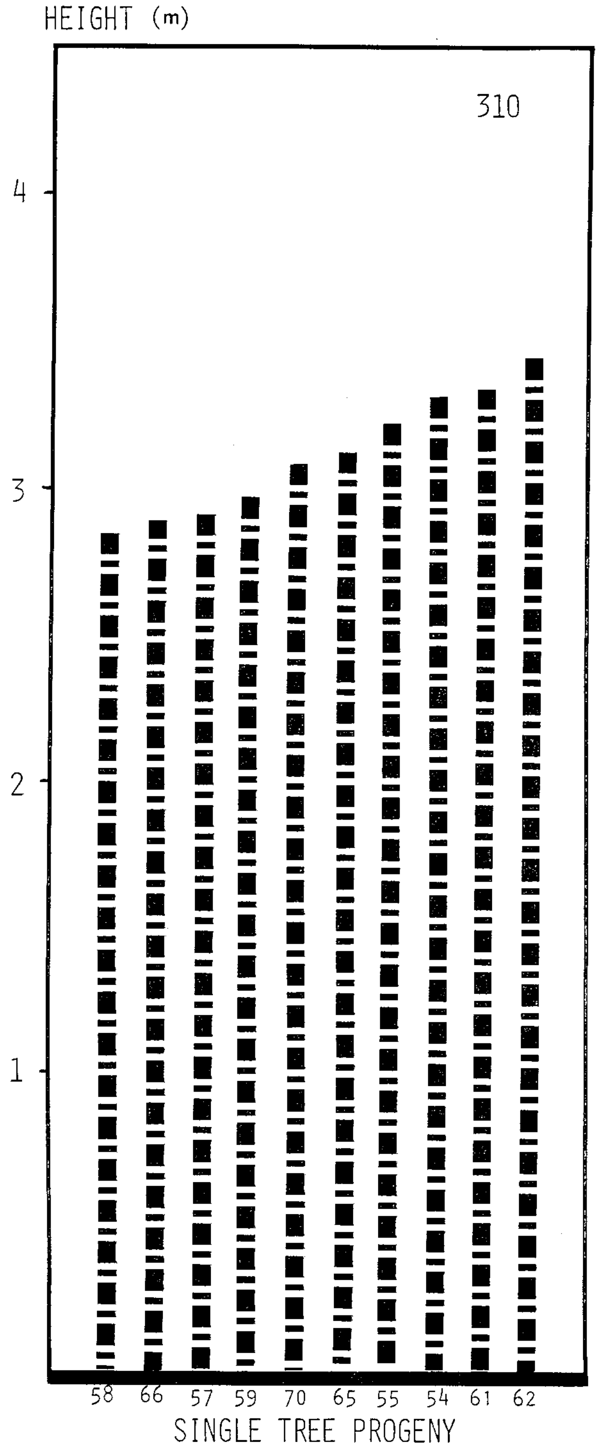

Figure 19. The mean tree heights at an age of 20 years of single tree progenies from population 310.

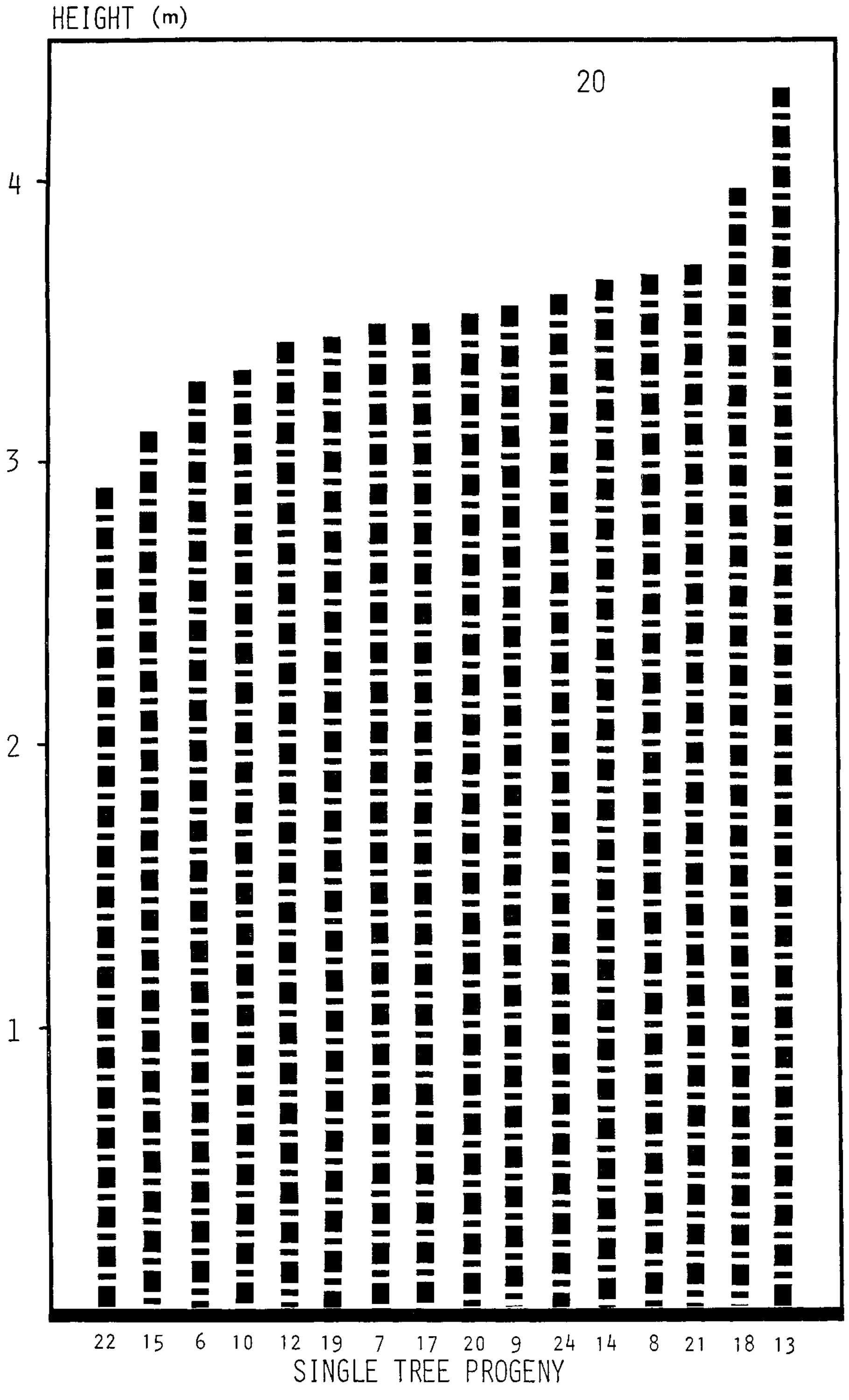

Figure 20. The mean tree heights at an age of 20 years of single tree progenies from population 20.

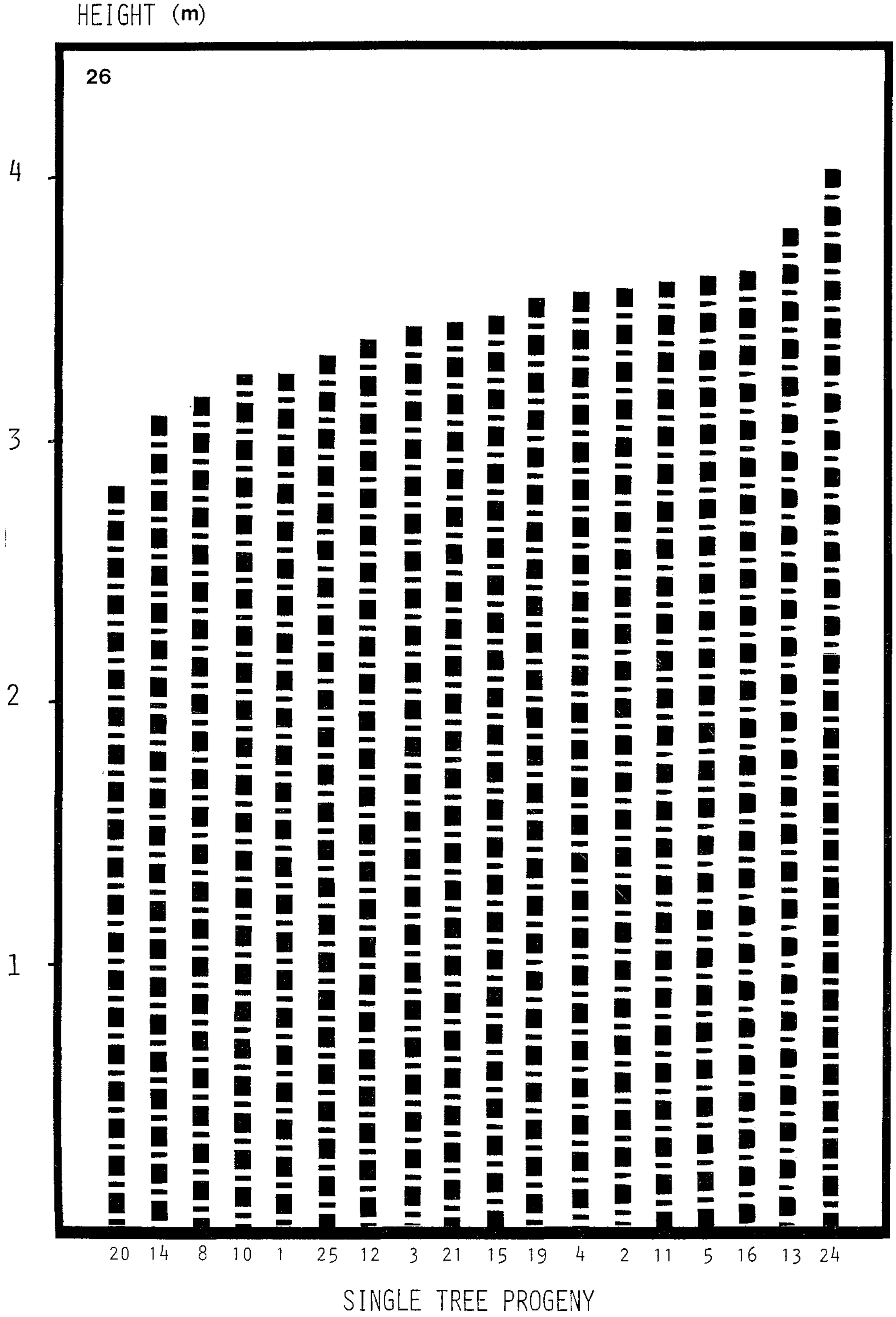

Figure 21. The mean tree heights at an age of 20 years of single tree progenies from population 26. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

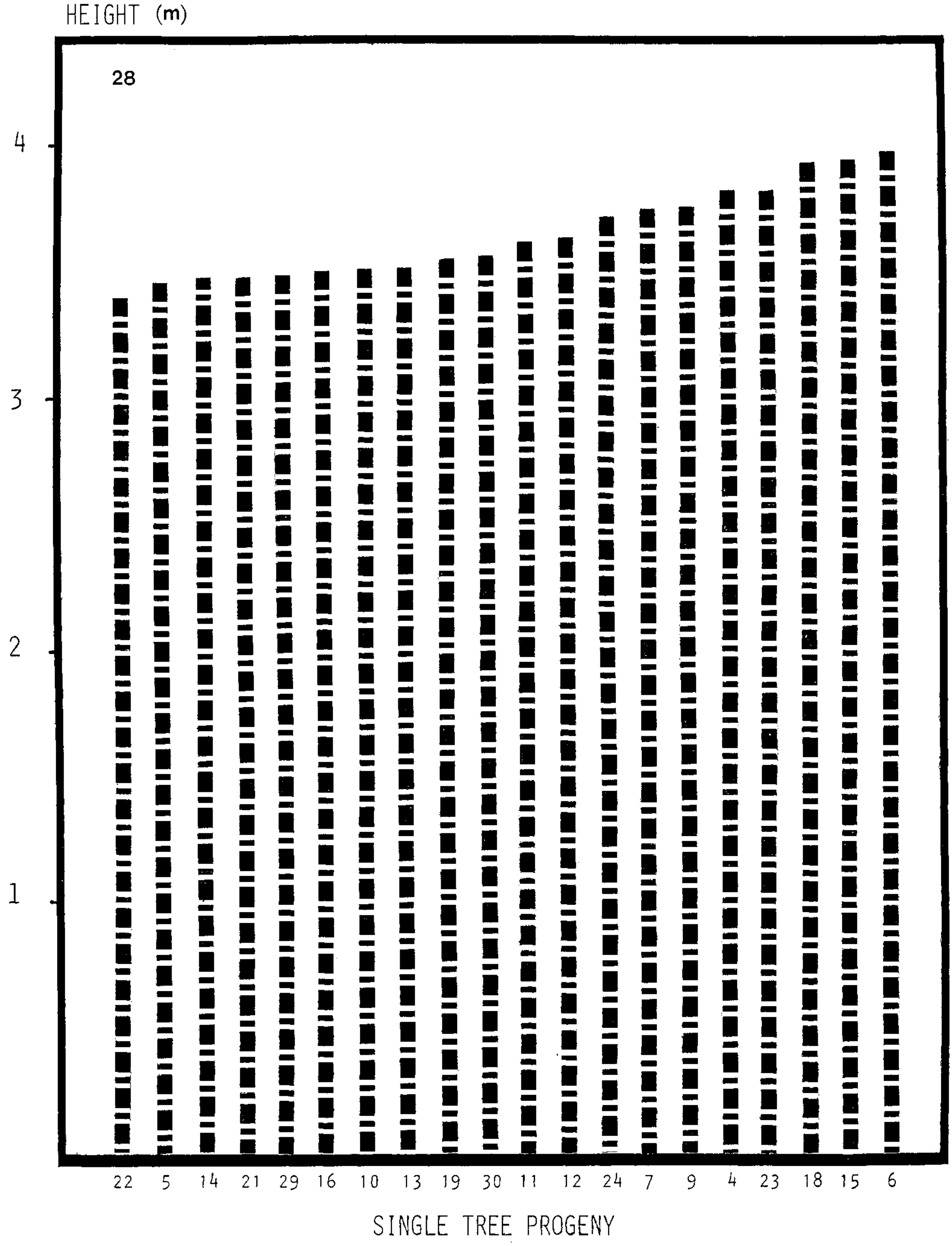

Figure 22. The mean tree heights at an age of 20 years of single tree progenies from population 28. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

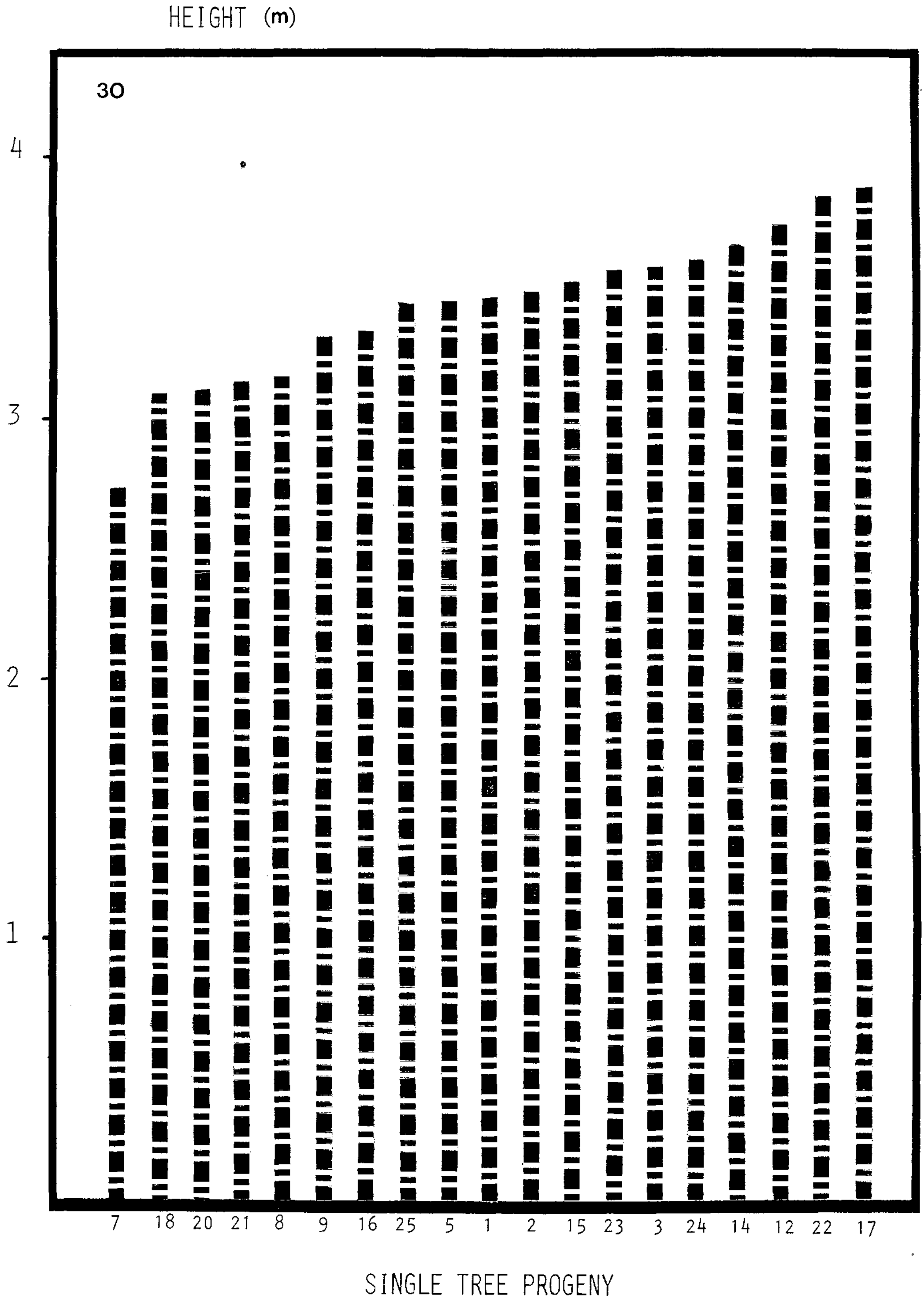

Figure 23. The mean tree heights at an age of 20 years of single tree progenies from population 30.

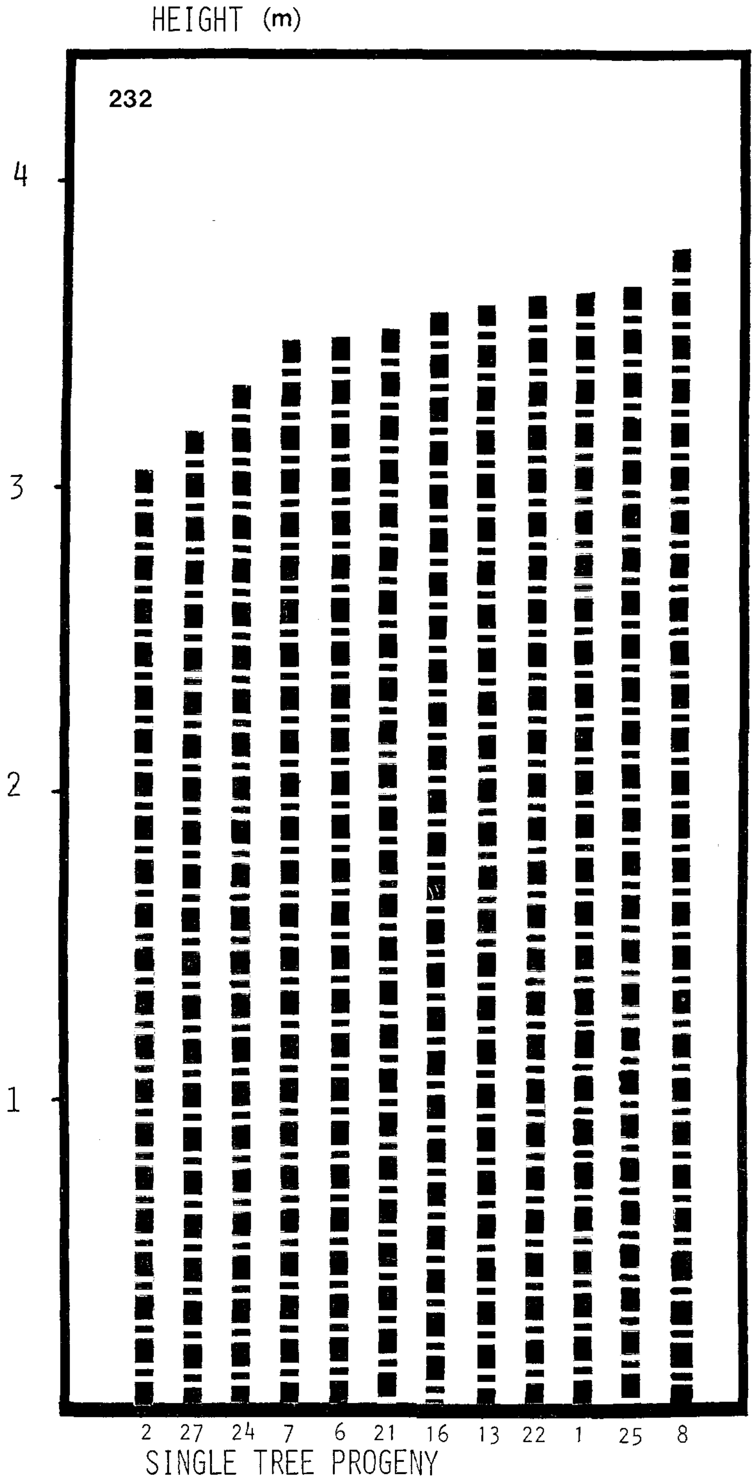

Figure 24. The mean tree heights at an age of 20 years of single tree progenies from population 232.

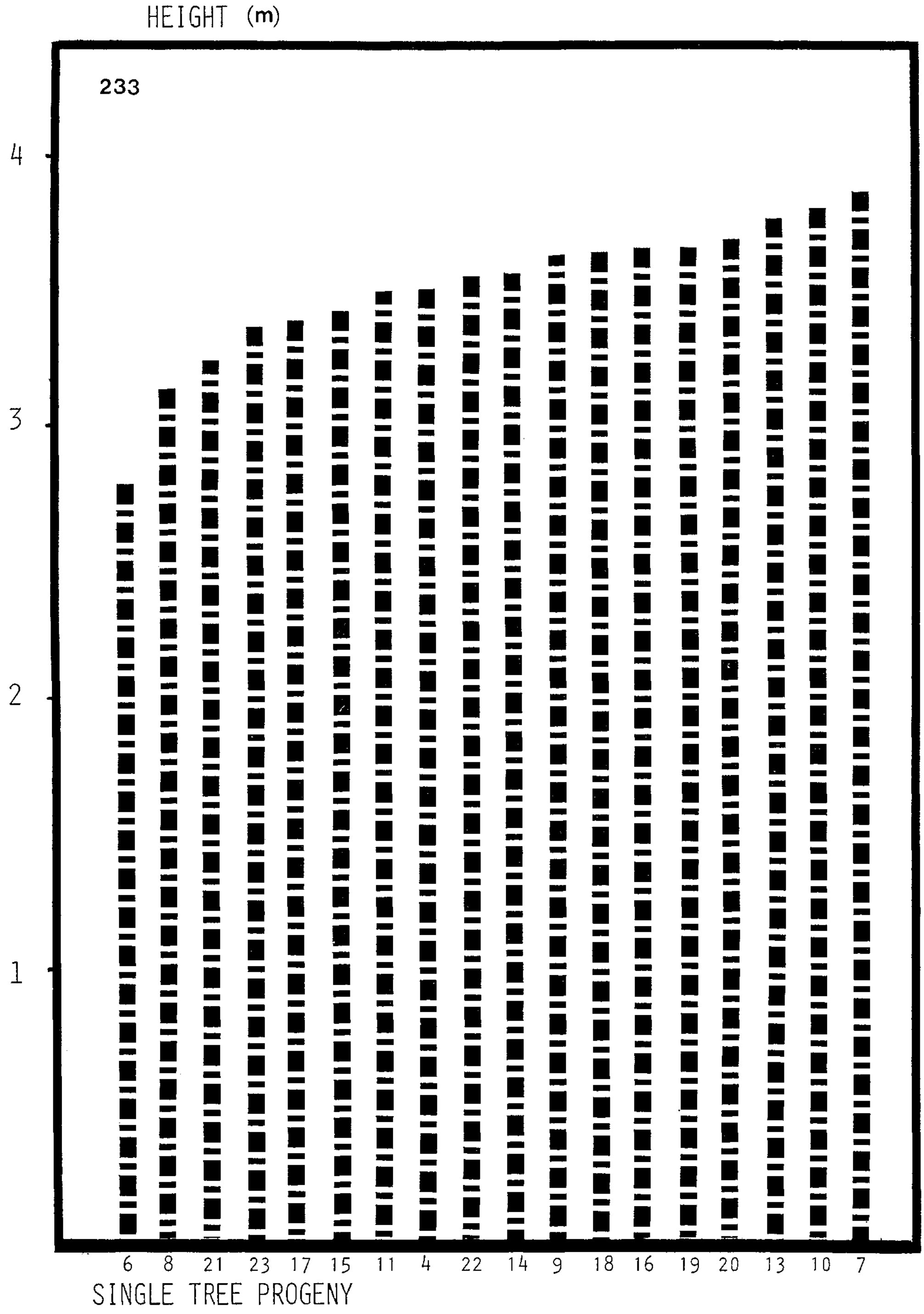

Figure 25. The mean tree heights at an age of 20 years of single tree progenies from population 233. Single tree progenies which in at least one block did not contain half the value of the mean value were omitted from the analysis of variance.

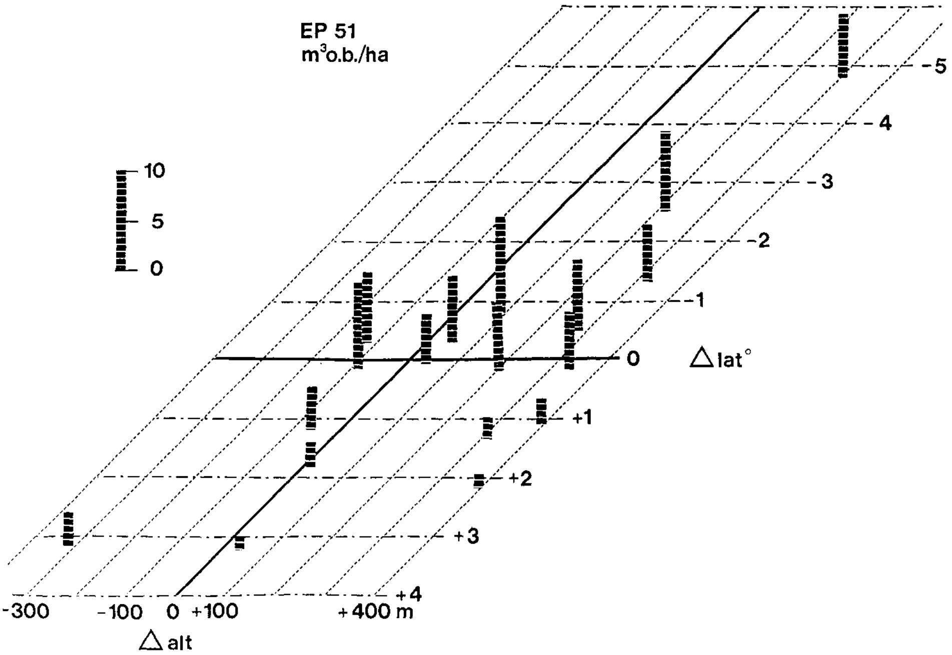

Figure 26. Volume per hectare over bark at an age of 20 years for populations transferred as shown (cf. the text for figure 3). A plus sign means transfer in a northward direction or to a higher altitude, respectively.

In Figure 26 the volume yield per hectare of the various populations is shown in a three-dimensional graph. It shows clearly that a moderate transfer in a southward direction has had a favourable effect on the yield. It is also obvious that long transfers from lower altitudes south of the experimental plantation has had a nearly catastrophic effect on the yield.

A regression analysis evaluating the effect of transfers of populations on volume over bark per hectare at age 20 years (V) was carried out in the same way as for the plant mortality.

The selection of independent variables was based on earlier knowledge of how transfer of seed affects the growth of the trees. The analysis resulted in the following function:

$$V = 6.6568 - 0.01021\,\Delta lat - 0.00395\,\Delta alt - 0.00002\,\Delta lat^2 - 0.00001\,\Delta lat \times \Delta alt.$$
$$R = 0.916^{***}$$

$$\left.\begin{array}{l}\Delta lat \text{ is expressed in km}\\ \Delta alt \text{ is expressed in m}\end{array}\right\}\ \begin{array}{l}\text{plus sign means a transfer upwards}\\ \text{or in a northern direction}\end{array}$$

The relative importance of the independent variables included is shown in Table 10.

Table 10. The multiple correlation coefficients obtained from the stepwise regression analysis of the relationship between volume over bark/hectare and geographic variables.

Step	Variables tested					R	F-ratio
	Δalt	Δalt^2	Δlat	Δlat^2	$\Delta alt \times \Delta lat$		
1			×			0.7211	17.331
2			×	×		0.8207	7.060
3	×		×	×		0.9107	12.771
4	×		×	×	×	0.9162	0.812

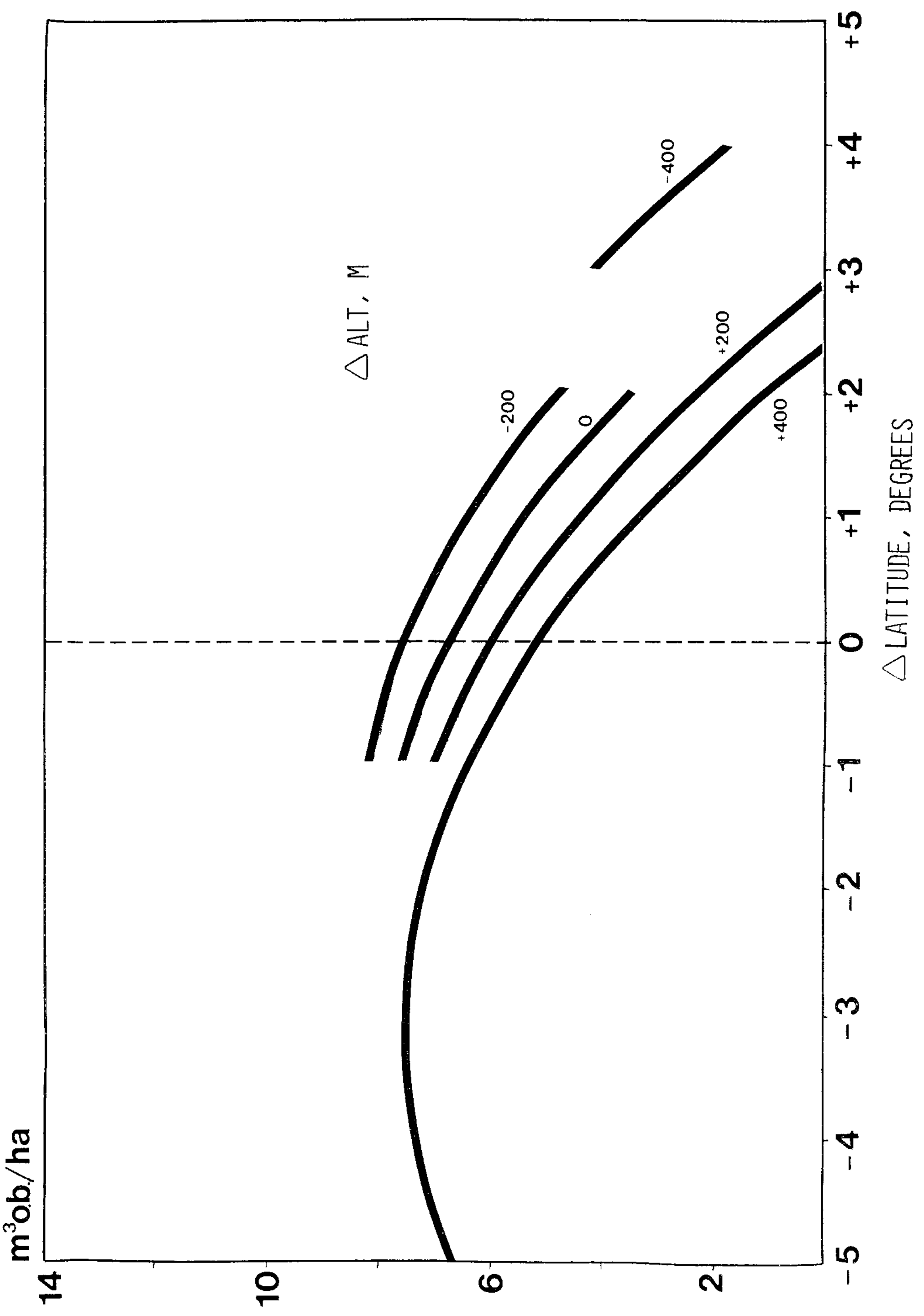

Figure 27. The effect of transfer on the volume at an age of 20 years with varying latitude of origin at fixed levels of transfer in altitude. A plus sign means transfer in a northward direction or to a higher altitude, respectively.

As for plant mortality, Δlat was the independent variable which had the strongest influence on the volume yield. Δalt^2 did not have any effect.

In Figure 27 the effect on a transfer in latitude at some fixed levels of transfer in altitude is shown. The curves are drawn only within the limits of the material studied. This figure indicates that the maximum gain in comparison with the local population would be obtained by using material from one latitude north of the planting area and from 200 m higher in altitude. In that case the gain in volume yield would be 22 per cent. This is a gain in level with maximum gains indicated by Remröd (1972) when transferring seed in the same direction. Only further studies at older age can show whether this superiority tends to increase or decrease with time.

No analysis of differences between volume yield of single tree progenies has been carried out. Such analyses are planned after clarifying the role of competition when comparing volume yield in progenies planted in rows.

4 Concluding remarks

For north Sweden it has once more been proven that a transfer in a southward direction of Scots pine increases the plant survival (cf. Eiche 1966, Stefansson and Sinko 1967, Eriksson 1972, Remröd 1972, 1974, Eiche and Andersson 1974). Both latitudinal and altitudinal transfers influence the plant survival markedly as revealed from the regression analysis, the change in latitude being of greatest importance. The curves in Figure 5 indicate that a transfer of 3—4 degrees to the south combined with a transfer upwards would be advantageous to obtain a higher survival.

The variation in plant mortality within the populations in many cases was considerable (cf. Figures 6—14). This observation is in no way unique for Scots pine. Thus, in most of the papers referred to in the introduction the variation within stands was found to be large. It may be added that in most cases young plants were studied.

The question "Is the variation between populations larger than the variation within populations?" which is sometimes raised is, according to our opinion, pointless since the answer to this question is dependent on the geographic diversity of the material studied. With the great difference in geographic origin of the present material, the difference between populations must always be the dominating one. However, the existence of a great variation between single tree progenies from the same population must be regarded as very promising for the forest tree breeder. Especially on harsh sites a sufficient survival can never be obtained by using bulked seed from a population. For such sites seed orchards including progeny-tested trees might be the solution to the problem of getting a hardy progeny. Since the mother trees of the populations tested are in many cases included in clone archives it will be no problem to get scions for grafting.

A selection of trees of superior growth and quality within this EP as well as in other EPs of the same series is also worthwhile.

Although the age of the plantation is low an estimation of the volume yield per hectare was made. According to the regression analysis the maximum gain in volume yield compared to the local population will be obtained by using material from one latitude north of the planting site and an altitude 200 metres higher. Thus, considerable gains could be obtained by selecting an appropriate material. The value of the parameter volume yield at an age of 20 may be debated. It has obviously no economical value as such at this early stage. The real value may be as a prognosis of future volume yield. It can be mentioned that preliminary studies of some old provenance trials with Scots pine have revealed that no considerable changes in ranking actually occurred when comparing the reforestation result at age 13 with the volume yield at age 60 (Persson 1975). As a parameter for the reforestation result at age 13 the product (survival, per cent) × (mean height) was used, that is, a parameter having certain similarities with volume/hectare. In another case, at Holminge near Stockholm (EP 008) a promising start has turned into failure for a provenance which had been transferred from Central Europe.

Finally it may be mentioned that the relationship between plant mortality and the mean plant height of single tree progenies within the populations was studied. Only in one case, population No 20, there was a significant correlation ($r = 0.509^*$) between plant height and plant mortality.

5 Acknowledgements

We wish to express our sincere thanks to professor Bertil Matérn for statistical guidance and to Mrs Lucyna Smolowicz for carrying out the computer programming. We would also like to thank Mr Kjell Lännerholm for drawing all the diagrammes. Financial support was obtained from the Swedish Council for Forestry and Agricultural Research.

6 Sammanfattning

Ett proveniensförsöks värde ökas väsentligt om de ingående provenienserna representeras av enkelträdsavkommor. Få äldre proveniensförsök är upplagda efter denna hierarkiska modell, vilken tillåter en bestämning av variationen såväl mellan som inom provenienserna. I den föreliggande uppsatsen lämnas resultat beträffande överlevnad, höjdtillväxt och volymproduktion från ett dylikt försök med tall. Försöket planterades 1955 vid Nordanås (lat 64°19′, long 18°09′ h.ö.h. 400 m) med fyraåriga plantor (2/2) i tre upprepningar och 2,5× 2,5 m förband. Eftersom varje proveniens är representerad av ett bestånd kommer vi fortsättningsvis att använda termen population istället för proveniens. Varje population bestod vanligtvis av 20 enkelträdsavkommor. De ingående populationernas ursprung framgår av figur 1.

Överlevnad

Plantavgången fram t.o.m. 1973 är återgiven i figur 2. Som framgår av denna figur var avgången stor redan under första sommaren, vilket får tillskrivas den svåra torkan 1955. För att eliminera effekten av torkskador från övriga väderbetingade skador har vi funnit det ändamålsenligt att beräkna den procentuella avgången under perioden 1956—1973 i stället för den totala avgången 1973. Resultaten på populationsnivå har sammanfattats i figur 3. Denna figur visar att en förflyttning mot söder vanligtvis leder till en lägre plantavgång. En stegvis regressionsanalys har använts för att beskriva förflyttningseffekten. Denna analys avslöjade att breddgradsförflyttningen hade det största inflytandet på plantavgången (tabell 4). I figur 5 har innebörden av regressionsekvationen åskådliggjorts. Sambandet mellan förändring av vegetationsperiodens längd efter förflyttning av populationerna till Nordanås å ena sidan och plantavgången å den andra sidan har likaså analyserats. Även vid denna analys har ett gott samband erhållits som framgår av figur 4.

Variationen inom olika populationer har illustrerats i figurerna 6—14. I vissa fall visade sig skillnaderna mellan enkelträdsavkommorna vara signifikanta (tabell 5).

Höjdtillväxt

I överensstämmelse med bearbetningen av data för plantavgången har även beträffande höjdtillväxten en stegvis regressionsanalys utförts för att erhålla en beskrivning av förflyttningseffekten.

Resultaten finns sammanfattade i tabell 7 och figur 16. I analogi med analysen av avgången har förändringen av tillväxtperiodens längd studerats (jfr figur 15). Även beträffande höjdtillväxten har signifikanta skillnader mellan enkelträdsavkommorna förekommit inom vissa populationer (tabell 8).

Volym på bark per hektar

De olika populationernas produktion finns redovisade i tabell 9 och figur 26. Förflyttningseffekten på denna karaktär har likaså studerats med regressionsanalys. Resultaten redovisas i figur 27 och tabell 10. Även i detta fall är det breddgradsförflyttningen som väger tyngst i regressionsekvationen. Jämfört med lokalpopulationens volymproduktion beräknades en maximal avkastningsstegring av 22 % efter en samtidig förflyttning en breddgrad söderut och 200 meter nedåt.

Slutord

De i denna uppsats redovisade resultaten står i god överensstämmelse med tidigare publicerade resultat från tallproveniensförsök i inre Norrland. Under förutsättning att man även i fortsättningen avser att plantera i 2×2 meters förband eller ännu glesare måste skogsodlingsmaterialet hämtas 1—2 breddgrader norrifrån för att erhålla en någotsånär tillfredsställande slutenhet i det nyanlagda beståndet. Undersökningen har även visat att det ibland råder en stor ärftligt betingad *inom*-beståndsvariation. Detta visar att ett rätt utfört individurval i de bästa bestånden bör ge goda resultat i framtiden.

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