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The intra-provenance correlation between annual rhythm and growth of single trees of *Pinus silvestris* L.

Sambandet inom proveniens mellan årsrytm och tillväxt hos enskilda träd av Pinus silvestris L.

by

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ABSTRACT

The annual rhythm and height of 21-year-old trees was registered over two consecutive years in three provenance field tests in central Sweden. The rhythm of approx. 200 trees from each of four provenances was characterized by the pattern of needle elongation and the changes in bark colour of terminals.

Correlation, regression and multiple discriminant analyses revealed a strong relationship between origin and annual rhythm but exhibited at the same time a large intra-provenance variation. It was shown that disharmony between the rhythm of the tree and the external climate results in a decrease of growth. The variation within a stand progeny was found to be so large that, irrespective of planting site, there were some trees that were genetically unfit for the climate. Selection in the nursery may decrease this heterogeneity.

It was shown how the regression of height on rhythm among trees within a population may be used in tree breeding to asses plasticity, degree of adaptation to the test site, and potential growth capacity in different environments.

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1. Introduction

In provenance research and tree breeding an essential question is in what degree the tested material is adapted to the environment of the test site. The usual way of determining the degree of adaptation has been to compare the survival and height growth with other material, preferably provenances with an origin which should guarantee a high degree of adaptation. However, this comparison cannot be made until climatic extremes have caused considerable mortality or damage, large enough to make possible a definite ranking of the populations tested. This method is time consuming since the weather extremes of highest significance may not occur for decades after planting (Silen, 1965, describing the importance of mortality in high ages of a provenance test of *Pseudotsuga taxifolia* (Poir.) Britt.). Furthermore, the method is unreliable since the weather extremes on the test site may be of a different type from those occurring in the place where the material is to be economically utilized. Finally, this method cannot be used in short term tests under artificial climatic conditions.

The relative hardiness or climatic adaptation can be described by means of the annual rhythm. This was observed by Linnaeus (1739) and by Örtenblad (1898) and demonstrated for many plant species by Turesson (1930) and for *Pinus silvestris* by Langlet (1936). The usefulness of this procedure in genelogical research has been shown in a large number of investigations since then (reviewed by Levitt, 1956; Dietrichson, 1964; Langlet, 1964; Meryman, 1966; Eiche, 1966; Hagner, 1970). Methods have been developed for the assessment of the annual rhythm for all parts of the growing season, but it is concluded that the development rate during the middle and later part of the season is most significant for hardiness (Langlet, 1936, 1963; Dietrichson, 1964, 1969; Hagner, 1970). The dormancy release is mainly governed by the temperature regime and, though very important for susceptibility to spring frost, is of less significance for survival (Fraser, 1956; Langlet, 1963; Dietrichson, 1964, 1968, 1969; Nienstaedt, 1966; Worral & Mergen, 1967; Dormling *et al.*, 1968). The rate of development during shoot extension in June and July, during maturation in August and September and during "inwintering" in October have all appeared strongly correlated with the long-term hardiness of *Pinus silvestris* (Langlet, 1936, 1959; Dietrichson, 1961, 1964, 1968; Hagner, 1966, 1970).

Even though these investigations have shown that there are good methods available for elucidating the relative adaptation of populations, it has not been demonstrated that it is possible to describe the variation among trees within provenances in this way. Naturally it is of great interest to manifest the means by which the adaptation of the single tree can be expressed and to study in what way the adaptation effects survival and growth. This is why a study was undertaken on 21-year-old specimens of *Pinus silvestris* growing in an experimental field plantation. This material was well known from previous investigations on hardiness (Stefansson & Sinko, 1967; Hagner, 1966, 1970) and by simultaneous measurements of height and rhythm it was possible to demonstrate the relationship between these characteristics.

The results show that many of the morphological characteristics that were earlier found to relate to the adaptation of provenances also describe the fitness of the individual tree. It could not be established whether the rhythm is of importance for the potential survival but it was shown that the growth is influenced by the harmony between the external climate and the inherited annual rhythm, and that the variation in rhythm within a population is so large that a portion of the trees within a stand progeny cannot be considered as adapted to the environment in which they came into existence.

2. Material

The annual growth rhythm was studied during 1968 and 1969 on approximately two hundred 21-year-old trees from each of four provenances in a field test at Björkvattnet in central Sweden (Fig. 1). The provenances originated from many parent trees within one stand. The seed was nursery sown in 1948 and the seedlings were planted in the field in 1950. The growth and survival after ten years in field has been published by Stefansson & Sinko (1967).

For this investigation two provenances were chosen from northern seed sources (316, 115), one (22) from a place close to the test site and one (47) of southern origin (Fig. 1 and Tab. 1). The field test had a randomized block design, with every provenance represented in four plots with 144 trees in each plot. The rhythm was studied on every tree in two different plots for each provenance. While the environment therefore cannot be considered equal for all provenances, the objective impression was that it did not vary to any high degree among the plots.

Mortality had occurred over the past 18 years in the field and in the autumn of 1968 the percentage of survival were 115: 85 per cent, 316: 77 per cent, 22: 61 per cent, 47: 29 per cent.

Tab. 1. Data concerning provenance field tests and environment of seed source.

Name	Latitude	Longitude E	Altitude m	Grow[a] seas	Environment	Age 1969
Field tests						
Bäckstrand	65°04′	16°26′	500	119	forest	21
Brattfors	64°31′	18°24′	310	122	forest	21
Björkvattnet	63°26′	16°02′	460	121	forest	21
					Survival[b] %	Height[c] m
Provenances						
Muodoslompolo no. 115	68°08′	23°15′	275	102	84.7	3.06
Kompelusvaara no. 117	67°03′	22°20′	210	111	87.3	3.35
Moskosel no. 121	65°52′	19°28′	340	112	86.5	3.75
Norrsele no. 316	65°36′	17°30′	360	111	76.7	3.62
Ramsele no. 22	63°32′	16°28′	250	131	60.8	3.64
Ånge no. 47	62°30′	15°38′	170	138	28.5	3.40

Growing season = Number of days per year with a daily mean temperature above +6°C.

[b] Survival 1968 at Björkvattnet as a percentage of planted seedlings.

[c] Average height 1968 of surviving tree at Björkvattnet according to Remröd, 1969 (unpublished).

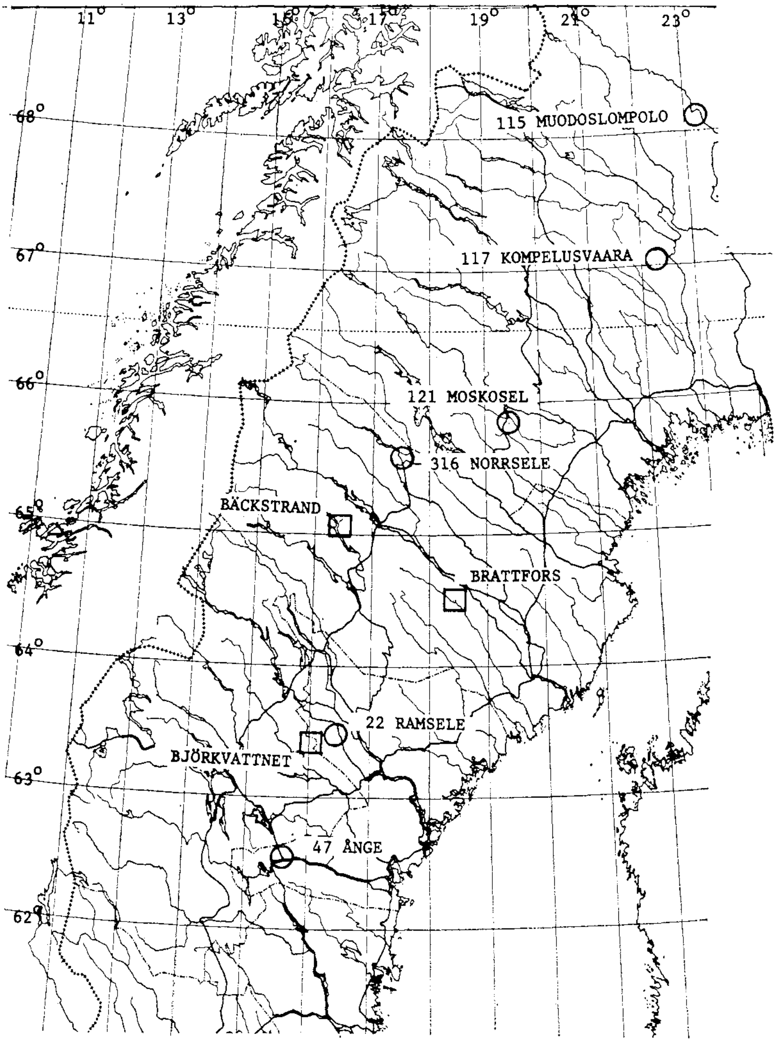

Fig. 1. Seed sources ○, and field tests □ in northern Sweden.

To establish whether the results obtained from the mentioned material held true in different environments, a series of 24 seedlings from each of the seed sources 117 and 316 were studied in two other field tests: Brattfors and Bäckstrand (Fig. 1, Tab. 1). These two field tests are planted with seedlings from the same material as that in Björkvattnet. The test at Brattfors is situated in an ordinary forest climate while the test at Bäckstrand is exposed to high winds and a generally harsh climate.

3. Methods

3.1 Selected variables

The methods measuring the annual rhythm used in this study are the same as those described in a previous paper (Hagner, 1970), but the sampling intensity has been adjusted to give a more precise measure of the individual tree character.

Needle 1968. On 6 July five needle fascicles were sampled from the middle part of one terminal shoot on a large branch on the south side and in the middle portion of the crown. The lengths of these ten needles were measured in the laboratory. On 26 November another five fascicles were sampled from the same shoot. The tree character was expressed as the length of the first sampled needles as a percentage of those sampled in November.

Needle 1969. On 12 July the longest needle in each of two needle fascicles was measured. The needles were situated close to the bud on one terminal shoot on a large branch on the south side and in the middle portion of the crown. The same two needles were measured again on 7 August and the tree character was expressed as the length in July as a percentage of the length in August.

Colour 1968. On 8 August (C68:1) and on 20 August (C68:2) the colour of the bark on five terminal shoots on large branches in the middle portion of the crown was ocularly estimated. An arbitrary scale was used which was based on the colour variation in the whole test plot on the date of measurement. The number 1 was given to the greenest colour and 9 to the brownest colour. To keep the scale stable a set of typical shoots was sampled and used for ocular comparison. The tree character was recorded as the mean without decimals of the five observations.

Colour 1969. The bark colour was registered on 5 August (C69:1) and on 20 August (C69:2). The sampling was the same as in the previous year, but the five values were recorded separately to one decimal.

Shoot 1969. On 24 June the length of the terminal shoot on one large branch on the west side and in the middle part of the crown was measured. A second measurement was taken on 28 August and the tree character was estimated as the length in June as a percentage of the length in August.

Dry matter 1969. On 5 October five grams of needles were collected from the middle part of four terminal shoots from branches in the upper portion of the crown. The needles were placed in paper bags which were moistened and sealed into plastic bags and stored for one month in 5°C. Before analysis the paper bags were exposed to a relative humidity of 95 per cent and 4°C over eight days. The oven-dry weight was recorded after drying at 75 °C for 49 hours. The tree character was expressed by the dryweight as a percentage of the fresh weight.

3.2 Statistical methods

Regression and correlation analyses have been carried out on a computer using a standard programme CORREG at the Data Centre of the University of Umeå. The discriminant analysis was computed at the Data Centre of the University of Uppsala and the programme used, DSCRIM, has been published by Veldman (1967).

4. Results and discussion

4.1 Methods

4.1.1 *Efficiency of the methods*

One measurement per tree

If the variance is divided into the two components: a) variance among trees and b) variance within tree plus error, and measured as a percentage of the total variance within the provenance, it is found that the dry matter method gives the most exact value for the tree where a=85 per cent, b=15 per cent. The needle method gives a=78 per cent, b=22 per cent, and bark colour gives a=39 per cent, b=61 per cent. The least efficient method is the bark colour which shows large variation between repeated measurements on the same tree. The conclusion is that if only one measurement is to be taken on every tree the best estimate is obtained if the rhythm is measured using the dry matter method.

Sample size as used in this investigation

An effective method of describing the annual rhythm of a single tree should result in a small standard error ($s/\sqrt{n}$) of the tree value (e), if compared to the standard deviation (s) of the provenance (d). An estimation of d/e for the different methods gives: bark colour 3.70, needle 3.25, dry matter 2.36. An impression of the effectiveness of the methods is also given by the distributions shown in Fig. 2.

The effectiveness of a method for discriminating between provenances may be indicated by the t-value for the difference between provenance means. If the difference between 115 and 316 is used the following t-values are obtained: bark colour 11.7, needle 14.5 and if the difference between 117 and 316 is used for the dry matter method it gives 1.5.

In this investigation the inefficiency of the bark colour method was compensated for by the large size of the sample (five values/tree) and this method was thus the best for describing the tree character. Values almost as good were obtained from the needle method, but this is qualified by the fact that the two needles measured on every tree were situated on the same shoot. Accordingly the variation among

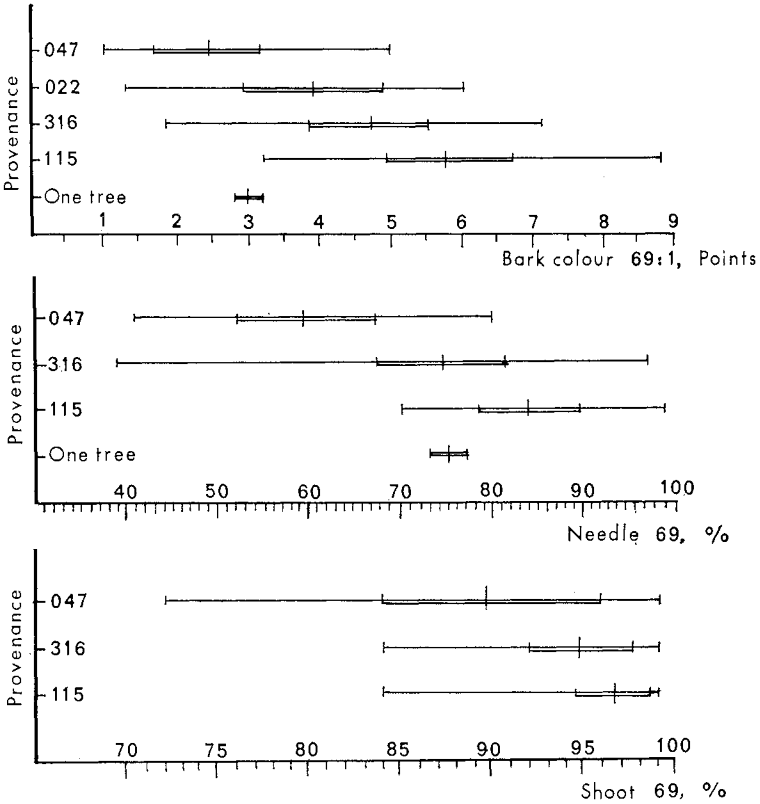

Fig. 2. Variation within provenances and error of a single tree estimate. One line = total range. Two lines for provenances = 2 × standard deviation (s). As a comparison with the variation within provenance, the mean of a randomly chosen tree and the error of the single tree estimate is marked ($\overline{m} \pm 1 \times$ standard error $(s/\sqrt{n})$).

shoots within the tree has now been included in the variation among trees.

Considering the differences between provenance means and the number of seedlings tested in each provenance, the needle method gave the most effective results for comparisons between provenances.

4.1.2 The best method

From the statistical results and from the amount of work in field and laboratory, it may be concluded that bark colour is the best method because of its simplicity and efficiency. Because of the obscurity of the biological background of bark colour and considering the difficulty of obtaining an objective measure of this characteristic, it is, however, best to use the needle or shoot method or some other objective method (Hagner, 1970) on occasions when a correct measure of the annual rhythm of the tree is required.

It must be pointed out that the shoot measurement which did not give any useful values in this study have proved to be a very accurate method for measurement of the annual rhythm in previous investigations (Dietrichson, 1964; Hagner, 1970). The probable reason why the result was not so good here is that the first measurement was made too late, so that 90 per cent of the elongation was complete for provenance 47 and 96 per cent was complete for 115.

4.2 Annual rhythm

4.2.1 Estimation of rhythm during different parts of the growing season

The correlation between values obtained with different methods are positive in all cases where the coefficient significantly differs from zero (Tab. 2—4). Provenance 22 was not included in the correlation analyses since no observations of shoot and needle elongation were made on these trees. The mathematical expression of the rhythm for all methods was chosen so that a high value would indicate a fast rhythm or an early growth termination. Accordingly the positive coefficients show that if a tree had a slow rhythm in June, when the needles were measured, it also showed a slow rhythm in August, when the bark colour was measured.

Inefficiency of the methods, resulting in a large standard error of the single tree value, is one reason for the generally low correlation coefficients. Another source of error has arisen from the difficulty of assessing the accurate date when the biological circumstances were best for each method. This date was difficult to predetermine, especially as several provenances with higly deviant rhythms had to be measured at one time. The biological optimum was passed by the fastest while not yet reached by slower provenances. A third reason for the low correlation coefficients is probably a slight curvilinearity in the relationship. This has not been further investigated.

At Björkvattnet the dry matter was measured on 40 trees in October. The correlation coefficients (Tab. 5) had low significance for all methods since the sample of trees was small. The sum of the coefficients can, in such a case, tell more about the interrelationship between different methods than the single value (Tab. 5). Evidently the

**Tab. 2. Correlation among rhythm variables and height growth.
Population no. 115. Number of observations = 189.**

Height 68							
-0.42***	Colour 68:1						
-0.41***	0.53***	Colour 68:2					
-0.26**	0.57***	0.53***	Colour 69:1				
-0.17*	0.36***	0.36***	0.60***	Colour 69:2			
-0.31***	0.16*	0.18*	0.15*	0.05	Needle 68		
-0.34***	0.26**	0.29***	0.34***	0.13	0.46***	Needle 69	
0.04	-0.07	-0.13	-0.02	-0.02	0.05	0.30**	Shoot 69

**Tab. 3. Correlation among rhythm variables and height growth.
Population no. 316. Number of observations = 180.**

Height 68							
-0.22**	Colour 68:1						
-0.24**	0.55***	Colour 68:2					
0.11	0.42***	0.27**	Colour 69:1				
-0.04	0.29***	0.25**	0.60***	Colour 69:2			
-0.15*	0.22**	0.15*	0.03	-0.06	Needle 68		
-0.00	0.25**	0.26**	0.23**	0.14*	0.41***	Needle 69	
0.01	-0.00	-0.03	0.12	0.09	-0.07	0.06	Shoot 69

**Tab. 4. Correlation among rhythm variables and height growth.
Population no. 47. Number of observations = 37.**

Height 68							
0.00	Colour 68:1						
0.46**	0.12	Colour 68:2					
0.36*	0.16	0.49**	Colour 69:1				
0.27	0.18	0.36*	0.68***	Colour 69:2			
0.02	0.09	0.15	0.13	0.20	Needle 68		
0.20	0.49**	0.42**	0.27	0.24	0.31	Needle 69	
0.10	0.37*	0.05	0.29	0.03	0.15	0.46**	Shoot 69

dry matter was by and large positively correlated with the other methods, that is to say that the trees which show a fast rhythm in August are still fast in October.

In conclusion it may be stated that this material shows that individual trees of *Pinus silvestris* generally exhibit rhythm differences which persist throughout the latter part of the growing season and may thus be measured at any time from June until October. Although this must

Tab. 5. Correlation among rhythm variables.
Population no. 316. Number of observations = 40.

Colour 68:1							
0.47**	Colour 68:2						
0.29	0.35*	Colour 69:1					
0.10	0.40**	0.54**	Colour 69:2				
0.03	-0.36*	-0.01	-0.29	Needle 68			
0.09	0.15	0.42	0.29	0.10	Needle 69		
-0.18	0.16	-0.01	0.07	-0.01	-0.05	Shoot 69	
0.09	0.18	0.20	-0.01	0.13	0.08	0.02	Dry matter 69

Sum of coefficients; C68:1 = 0.90, C68:2 = 1.35, C69:1 = 1.78, C69:2 = 1.00
N68 = -0.41, N69 = 1.08, Sh.69 = 0.00, Drym. = 0.69

be true in general the low coefficients of correlation may partly be caused by a deviation from the general pattern by certain individuals which show a slow rhythm in one part of the season and a fast rhythm in another part. Dietrichson (1967) found in studies on open pollinated progenies of *Picea abies* (L.) Karst. that earliness in June was not always combined with earliness in September. This has not been further analysed in this material.

4.2.2 Comparison of rhythm estimates from two years

The material for elucidation of the constancy between years was chosen from the needle values in 1968 and 1969 of provenances 115 and 47. There were two reasons for this choice: the high degree of objectivity in this method and the more apparent biological background of needle elongation than of bark colour.

Assuming absolute constancy in the two consecutive years a regression of needle 68 on needle 69 would show a completely linear or curvilinear relationship. However, the dispersion about the regression lines is considerable (Fig. 3). The correlation coefficients are: prov. 115, $r=0.46$ ($p<0.001$, $df=188$), prov. 47, $r=0.31$ ($p>0.05$, $df=36$). The question is whether or not this dispersion is greater than can be expected from the error in the assessment of the single tree value caused by inefficiency of the method. A 90 per cent confidence interval, estimated from the standard error ($s/\sqrt{n}$) of the single tree estimate, was drawn in Fig. 3. The result was that only one out of 37 in provenance 47 and only three out of 189 in provenance 115 fell outside this interval. As these trees make up less than 10 per cent of the provenance samples a hypothesis about different rhythm in 1968 and 1969 cannot be accepted.

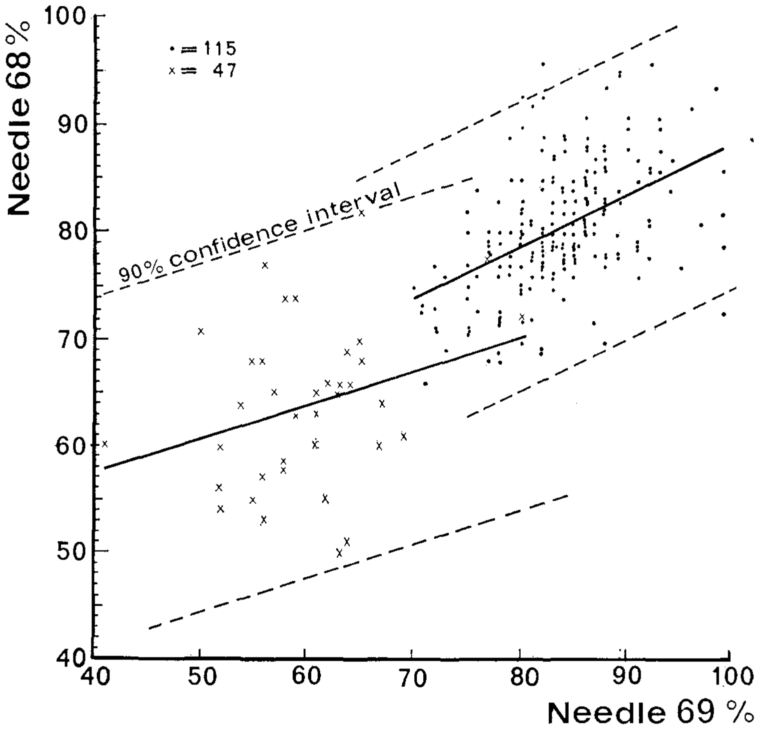

Fig. 3. Distribution of single trees from two provenances (115 and 47) according to the relative development of needles in 1968 and 1969.

4.2.3 Comparisons between trees within provenance and between trees from different provenances

The variation within provenances is large in comparison to the difference between provenance means (Fig. 2) and it is remarkable that in spite of the great geographical difference between seed sources 47 and 115 there are some trees in the two groups which have common values for the three characteristics.

However, a true comparison of the trees should consider not only one characteristic of rhythm at a time, since the trees with one extreme value may show normal values in other measures of rhythm. Thus the dispersions about the means would not appear as high if the distributions were studied in a multivariate way, that is, if all rhythm values were considered simultaneously. This is why a multiple discriminant analysis[1] has been carried out (Veldman, 1967) in which the following six variables were included: Bark colour 68:1, 68:2, 69:1, 69:2, Needle 68, 69.

The results show that the provenances are well discriminated by the dimensions (Tab. 6, Fig. 4). The correlation of the first discriminant and the variables exhibit very high significance ($p<0.0001$) and they show that the most meaningful observation for characterizing the provenances was Needle 69, closely followed by Colour 69:1 (Tab. 6).

However, the dispersion about the centroids is large (Fig. 4) and it may be concluded that even though the rhythm is described by a constellation of six different observations during two successive years the deviation of individual trees from the provenance mean is very large, since for instance 13.8 per cent of the trees in 115 show more similarities to 316 than to the trees from their own seed source. At the same time 0.5 per cent of the trees in 115 show more similarities to

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[1] A discriminant analysis assumes homogeneity of variance and covariance matrices (Cooley & Lohnes, 1962). As the values of rhythm go towards an asymptotic value with time, populations with a fast rhythm have a skewed distribution and a smaller variance. This is most apparent for Shoot 69 (Fig. 2) and therefore this variable has been excluded from the analysis.

The F-ratios of variances of provenances and selected variables were computed and found to have a mean of 1.83 ($p<0.01$, d.f. 37 and 180). Though significantly different from 1.00, the distributions seem to be similar enough for this analysis in view of the following two quotations. Lindquist (1953) discussed the importance of assumptions underlying F-tests and concluded (p. 86); "In general, when the heterogeneity in form or variance is 'marked' but not 'extreme', allowance may be made for this fact by setting a higher 'apparent' level of significance." Boneau (1960) tested violations of assumptions underlying the t-test and the influence from sample size and concluded (p. 63); "By the time the sample sizes reach 25 or 30, the approach should be close enough that one can, in effect, ignore the effects of violations of assumptions except for extremes". As the discriminant analysis "may be conceptualized as an extension of single classification analysis of variance to include simultaneously a group of dependent variables" (Veldman 1967), the conclusions drawn by Lindquist and Boneau should apply to this analysis. Considering the large sample sizes (37, 180) and the relative equality of variances ($F=1.83$) the results are valid and can be used for a study of the distribution of individual multivariate characteristics (Fig. 4).

A note by Mårdberg (1968) that the discriminant analysis assumes linearity between variables may be worth attention. As mentioned in chapter 4.2.1 the coefficients of correlation (Tab. 2, 3, 4) indicate a general linearity, but certain coefficients are low and may be partially caused by a slight curvilinearity. Mårdberg does not suggest any effect from curvilinearity but the plausible result in discriminant analysis is an increased dispersion of the multivariate distribution and a decreased efficiency in the classificaion.

Furthermore, for considerations of the intra- and inter-provenance variation in the multivariate distributions one has to take into account the sampling error. The magnitude of the error of the single tree estimate in the univariate case (se) is illustrated in Fig. 2. A corresponding illustration in Fig. 4 should consist of a circle with a diameter approximately 2/5 of se since the discriminant dimension consists of a function from six variables and the precision increases with additional variables (see Brown (1911); $r_{tt} = s_T^2/s_t^2$; $S_e = S_t \sqrt{r - 1_{tt}}$). Evidently the effect from the sampling error upon the position of individual scores in the multivariate distributions is fairly small.

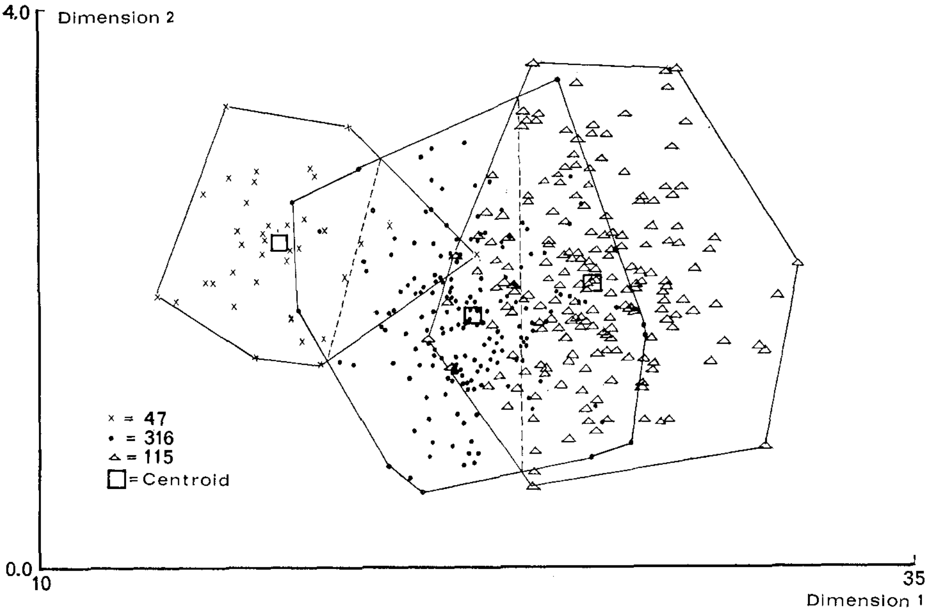

Fig. 4. Scores for single trees from three provenances distributed according to the two dimensions obtained in the discriminant analysis.

47 than to their own provenance. Corresponding values for 47 are: 8.1 per cent are more closely related to 316 and 2.7 per cent are more closely related to 115. Even after allowing for increases in the dispersion due to curvilinearity among variables and due to sampling error, the mentioned figures must be considered as indicating that the intra-provenance variation in adaptation is indeed large.

4.3 Height growth

4.3.1 Interrelationship between rhythm and height

The intra-provenance relationship between rhythm and height was studied by means of regression analyses (Fig. 5—8, Tab. 7, 8). For provenance 115 all methods except the shoot measurement gave significant relationship between height and rhythm. The weakest correlation exists within provenance 47, where only the first colour measurement in 1969 has given a significant regression coefficient. One reason for this is that a smaller number of trees was studied in 47. Another reason is the horizontality of the distribution.

The generally low R^2 values originate from three main sources; the error variance of the rhythm estimate, the variation in height growth

Tab. 6. Discriminant analysis of three groups; Group 1; Provenance 47, number of observations 37; Group 2: Provenance 316, number of observations 183. Group 3: Provenance 115, number of observations 189. Degrees of freedom 12 and 802. F-ratio 57.58 ($p<0.0001$).

	Correlations of discriminant and variables		Univariate analyses of variance	
Variable	Dimension 1[a]	Dimension 2[b]	F-ratio	P
1 Colour 68:1	0.80***	-0.02	157.5	<0.0001
2 Colour 68:2	0.84***	0.21***	195.8	<0.0001
3 Needle 68	0.76***	0.19**	137.1	<0.0001
4 Needle 69	0.90***	-0.01	249.3	<0.0001
5 Colour 69:1	0.88***	-0.26***	231.0	<0.0001
6 Colour 69:2	0.66***	0.36	90.2	<0.0001

[a] Dimension 1: 95.9 % variance, $\chi^2 = 467$, D.F. = 7, $P<0.0001$

[b] Dimension 2: 4.06 % variance, $\chi^2 = 35.6$, D.F. = 5, $P<0.0001$

due to random environmental influence and the incomplete genetic correlation.

The error variance of the rhythm was, for example, very high in such measurements as colour 69:2 and shoot 69, since the measurement was made at a time when the studied parameter had a low correlation with rhythm (too late). The standard error of the rhythm estimate ($s/\sqrt{n}$) is also considerable under favourable conditions (Fig. 2) and could only be decreased by use of better methods or by an enlarged sample size.

An essential cause of the low R^2 is found in the random variation of the height growth. The reasons for this are: competition among trees, pathologic decrease of height, deviation in microenvironment.

As the height growth is only partially governed by the climatic adaptation gene complex it is obvious that the R^2 is also decreased by an incomplete genetical correlation.

The forms of the regression-functions are fairly similar for the various methods (Fig. 5—8). The function of provenance 115 from the northern seed source has a negative slope, which means that the trees with the slowest rhythm or longest growing season grow best. The opposite is true for provenance 47 from the southern seed source. The two intermediate provenances show in all cases, except for colour 68:2, a regression function with a maximum close to the population mean.

These results may be interpreted to show that the two provenances 47 and 115 originate so far from the place where they are now growing that no trees within these provenances have an annual rhythm that

Tab. 7. Regressions of bark colour variables on height 1968.
N = Number of observations; t_{b_1} = "t" value of the first regression coefficient; R^2 = coefficient of determination; F = variance ratio.

	N	t_{b_1}	t_{b_2}	R^2	F
Bark colour 8 Aug 1968 = C68:1					
Prov. 47, Height = 41.39 – 1.797 C681	84	1.43	—	0.024	2.04
Prov. 22, Height = 22.33 + 8.988 C681 – 1.362 $C681^2$	189	3.23**	3.89***	0.10	10.5**
Prov. 316, Height = 46.99 – 2.063 C681	197	3.23**	—	0.051	10.5**
Prov. 115, Height = 41.98 – 0.2918 $C681^2$	201	6.88***	—	0.19	47.4***
Bark colour 20 Aug 1968 = C68:2					
Prov. 47, Height = 30.91 + 1.285 C682	84	1.19	—	0.017	1.43
Prov. 22, Height = 23.09 + 8.170 C682 – 1.197 $C682^2$	189	4.01***	4.59***	0.11	16.1***
Prov. 316, Height = 40.93 – 0.1833 $C682^2$	197	3.57***	—	0.062	12.9***
Prov. 115, Height = 40.15 – 0.2236 $C682^2$	201	6.66***	—	0.18	44.4***
Bark colour 5 Aug 1969 = C69:1					
Prov. 47, Height = 26.85 + 3.344 C691	84	3.32**	—	0.12	11.0**
Prov. 22, Height = 12.84 + 13.00 C691 – 1.704 $C691^2$	188	0.04	3.72***	0.071	13.9***
Prov. 316, Height = 8.469 + 11.43 C691 – 1.139 $C691^2$	193	2.52**	2.35**	0.037	5.56*
Prov. 115, Height = 37.34 — 0.1855 $C691^2$	196	3.89***	—	0.078	15.1***
Bark colour 26 Aug 1969 = C69:2					
Prov. 47, Height = 29.89 + 1.444 C692	84	1.40	—	0.013	1.06
Prov. 22, Height = 39.32 – 0.8208 C692	188	0.97	—	0.005	0.94
Prov. 316, Height = 11.45 + 12.14 C692 – 1.446 $C692^2$	192	0.02	1.65	0.017	2.47
Prov. 115, Height = 37.81 – 1.327 C692	196	2.54**	—	0.032	6.44**
Bark colour. A sum of values from 1968 and 1969 = C89					
Prov. 47, Height = 25.64 + 0.7337 C89	84	1.62	—	0.031	2.63
Prov. 22, Height = 9.133 + 3.901 C89 – 0.1358 $C89^2$	188	2.02*	2.30*	0.057	4.09*
Prov. 316, Height = –3.136 + 4.511 C89 – 0.1260 $C89^2$	193	2.33*	2.54**	0.049	5.41**
Prov. 115, Height = 42.82 – 0.02117 $C89^2$	196	6.35***	—	0.17	40.4***

fits the environment at Björkvattnet, while the two provenances 22 and 316 mainly contain trees that harmonize with the climate. However, the presence of a height optimum in the centre of the distributions of 22 and 316 shows that these provenances contain seedlings which deviate from the population mean positively and negatively to such a high degree that their rhythm makes them unfit for the environment. That is to say that although one can generally state that provenances 47 and 115 are not adapted to the Björkvattnet environment and that 22 and 316 are better adapted, one has to conclude that not one of the

Tab. 8. Regressions of needle, shoot and dry matter on height 1968. For description of characters, see Tab. 7.

	N	t_{b_1}	t_{b_2}	R^2	F
Needle length in per cent 6 July 1968 = N68					
Prov. 47, Height = 34.43 + 0.01074 N68	82	0.12	—	0.001	0.01
Prov. 22, Height = 27.47 + 0.2767 N68 – 0.002183 N68^2	178	0.23	0.26	0.001	0.14
Prov. 316, Height = –50.40 + 2.549 N68 – 0.01845 N68^2	184	2.20*	2.35**	0.049	4.84**
Prov. 115, Height = 61.86 – 0.3805 N68	189	4.37***	—	0.093	19.1***
Needle length in per cent 12 July 1969 = N69					
Prov. 47, Height = 20.35 + 0.2381 N69	39	1.54	—	0.060	2.36
Prov. 316, Height = 16.94 + 0.5020 N69 — 0.003252 N69^2	188	0.66	0.61	0.003	0.37
Prov. 115, Height = 48.84 – 0.002527 N69^2	196	4.85***	—	0.102	23.5***
Shoot length in per cent 24 June 1969 = S69					
Prov. 47, Height = 27.25 + 0.0009003 S69	39	0.81	—	0.018	0.66
Prov. 316, Height = 27.39 + 0.0009694 S69^2	189	0.93	—	0.005	0.87
Prov. 115, Height = 14.73 + 0.1686 S69	196	0.67	—	0.002	0.46
Dry matter 5 Oct 1969 = D69					
Test at Brattfors 117, Height = 146.7 – 1.917 D69	24	1.64	—	0.11	2.68
Test at Bäckstrand 117, Height = –19.83 + 1.090 D69	24	2.12*	—	0.17	4.47*
Test at Brattfors 316, Height = 157.1 — 2.127 D69	32	2.15*	—	0.13	4.63*
Test at Bäckstrand 316, Height = 77.92 — 0.7865 D69	30	1.57	—	0.08	2.45

provenances is fully adapted. As there are trees present in provenance 22 which have too slow a rhythm, and at the same time this provenance contains trees with too fast a rhythm, the conclusion is that the variation in climatic adaptation among trees within an open pollinated stand progeny is so large that the progeny cannot be considered as fully adapted to any environment, only adapted to a certain extent.

The regression functions for the various provenances show a height maximum at different values of rhythm (Fig. 5—8 and Tab. 9). This is true for all measurements of rhythm and most pronounced for bark colour (Fig. 6). This indicates that there is no absolute rhythm which independent of the provenance would make the tree growth maximal, but that there are other genes interacting with the annual rhythm gene complex to form the base for climatic adaptation.

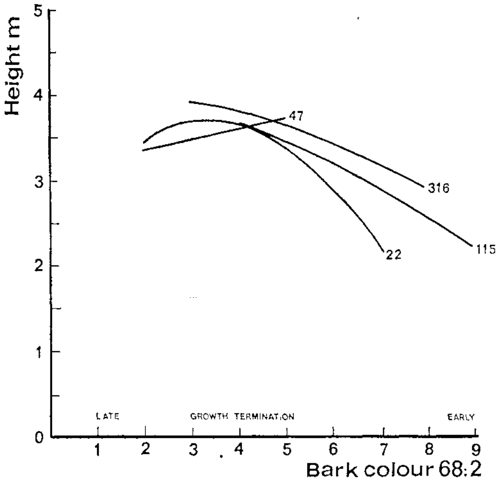

Fig. 5.

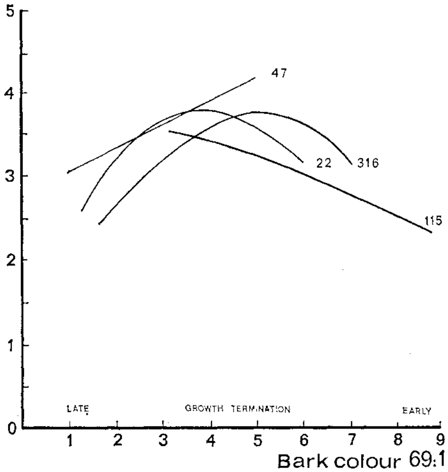

Fig. 6.

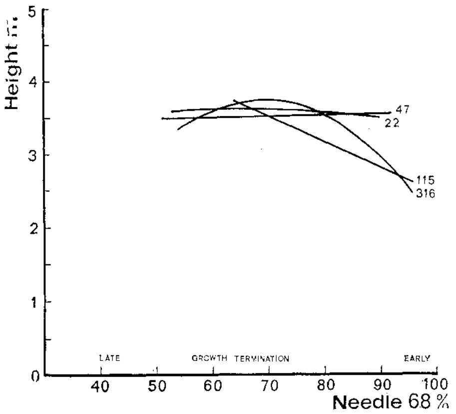

Fig. 7.

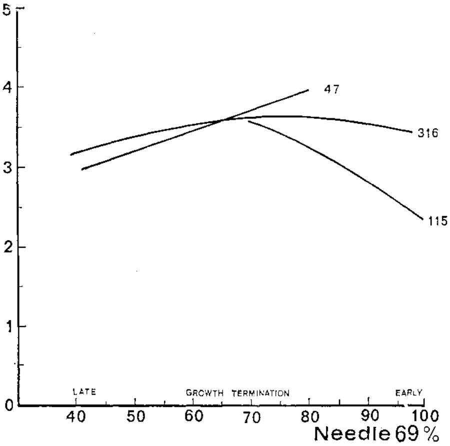

Fig. 8.

Fig. 5—8. Regressions of height on rhythm variables for single trees within four provenances at Björkvattnet. Equations are presented in Tab. 7 and 8.

4.3.2. Are the results at Björkvattnet also valid in a different environment?

To discover whether the relationship between rhythm and height growth would also be found in different environments, the rhythm was measured in October 1969 by the needle dry matter method on

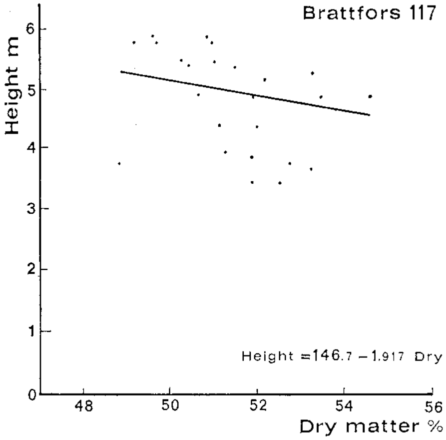

Fig. 9.

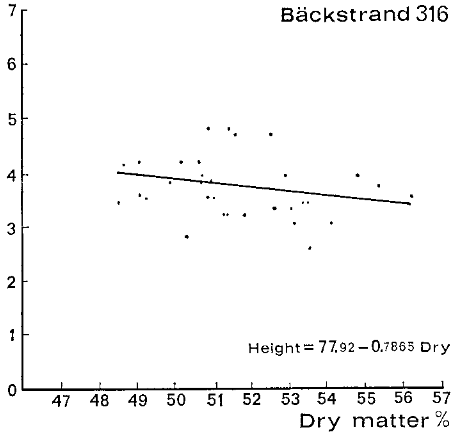

Fig. 10.

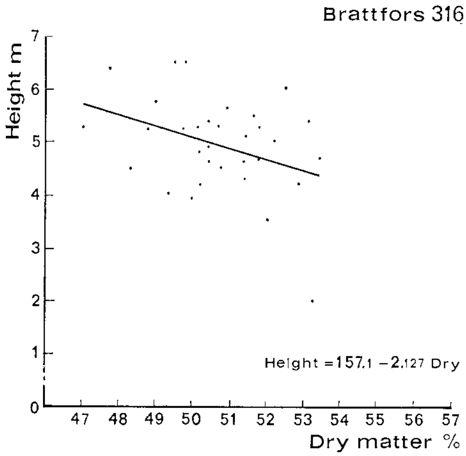

Fig. 11.

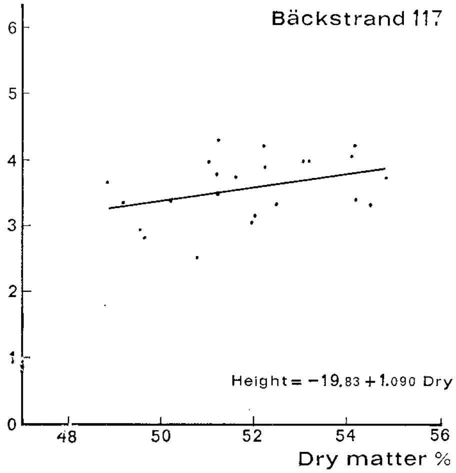

Fig. 12.

Fig. 9—12. Regressions of height on dry matter of needles for trees from two provenances (117 and 316) tested in two different localities, Brattfors and Bäckstrand.

trees from seed sources 117 and 316 grown at Brattfors and Bäckstrand (Fig. 1 and Tab. 1). The significance of the regressions of height on dry matter (Tab. 8, Fig. 9—12) is low, mainly for two reasons; the number of trees studied was low (24) and the regressions are probably curvilinear.

The climate at Brattfors is known from earlier studies (Stefansson & Sinko, 1967) to be fairly good, while that of Bäckstrand is quite severe. The mean height of the studied trees; Brattfors 117: 4.8 m, 316: 4.9 m, Bäckstrand 117: 3.7 m, 316: 3.7 m, also proves that the environments differ between the two places.

If the results are to be in accordance with the results at Björkvattnet, there should be a negative linear regression for both provenances in the favourable climate at Brattfors and a lesser negative or a positive slope in the harsh climate at Bäckstrand. This holds true for both provenances. A comparison of the regression coefficients show that they are significantly different ($p<0.01$) in the two environments for both provenances.

These results do not constitute actual proof, but the tendency is the same as in the material at Björkvattnet, that is, if a provenance is placed in a favourable climate the trees with the slowest rhythm grow best, while the reverse is true if a provenance is placed in a harsh climate. This supports the theory that the results found at Björkvattnet are applicable to different environments.

4.3.3 Is the rhythm influenced by the height growth or is the height growth influenced by the rhythm?

Investigations carried out on shoots of various sizes within a tree crown have shown that long shoots have a slower development rate than short shoots (Dietrichson, 1964, *Pinus silvestris,* and Owston, 1969, *Pinus strobus* L.). If this were true for leaders of different trees, the growth termination would be later for trees with fast height growth, and the statement by Dietrichson (1964) "the provenance problem is a site problem" would be correct.

If the annual rhythm is to a high degree governed by height, and rapid growth should result in slow rhythm, then all regressions of the type: height=f(rhythm), for trees within a provenance, should result in a negative regression coefficient. Furthermore the influence on the slope of the regression from the geographical parameters of the seed source should be small or masked.

As neither the results from Björkvattnet nor those from Brattfors and Bäckstrand show any of these tendencies, the influence of height growth on annual rhythm seems to be fairly small within this material. Furthermore, these results and those that have been shown earlier, i.e. the constancy from one year to the next, indicate that the rhythm is a genetically fixed feature with a relatively low degree of environ-

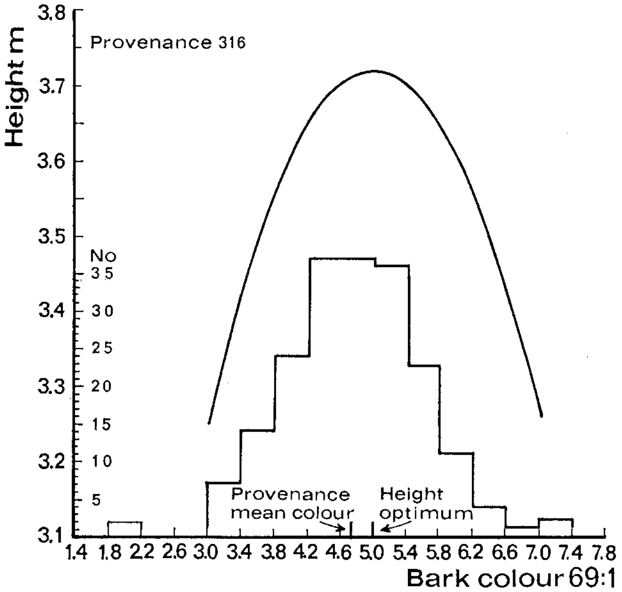

Fig. 13. Regression of height on bark colour for trees in provenance 316, and their distribution over bark colour values at Björkvattnet.

mental modification. This has been demonstrated for *Picea abies* by Dietrichson (1967) who found the broad sense heritability in open pollinated families to be 0.80.

4.3.4 The use of the rhythm character for selection of fast–growing subpopulations

To obtain an example of what the result of a selection within a provenance would be, the bark colour 69:1 of 316 at Björkvattnet was studied in detail (Fig. 13). The tree height has a maximum at 5.03 where it reaches 3.714 m. This is 2.48 per cent better height than the mean of the provenance itself. A selection of that third (37 per cent) of the population that had a bark colour around the maximum (from 4.6 to 5.4), gave a mean height of 3.709 m or 2.35 per cent higher than the mean.

A corresponding selection within provenances 115 and 47, which have regression curves that are steadily decreasing and increasing respectively towards higher bark colour values, resulted in subpopulations with greater difference to the provenance mean than for 316. A choice within 115 of that five per cent of the trees with the greenest colour (lowest values) gave a subpopulation with 12.2 per cent taller trees than that of the provenance itself.

As the regression analysis of data from provenance 47 showed that there is an insignificant curvilinear relationship within this distribution, with a maximum just outside the right-hand end of the distribution (Height$=22.74+6.678 \cdot C691-0.6206 \cdot (C691)^2$; max. at colour 5.38) it is more adequate to refer to this regression when dealing with the outer portion of the distribution. If a selection of that five per cent of the trees with highest bark colour values is made, the selected subpopulation is 14.2 per cent taller than the mean.

Although the percentage gain from the selection seems to be larger in populations from south and north, the smaller mean heights of these populations make the final result less good. By the use of percentages presented above on the mean heights in the whole provenance test at Björkvattnet (Tab. 1), the selected subpopulations will have the following heights; 316: 3.70 m, 115: 3.43 m, 47: 4.00 m.

These figures show that selection in population 47 would be beneficial. The height 4.00 is actually 6.7 per cent better than the height of the best provenance (121) among all of those tested at Björkvattnet. However, the comparison is not quite valid since the competition is much larger within 121 (87 per cent survival) than within 47 (29 per cent survival). Conversely, reduced competition will mostly affect the diameter growth and can hardly be the sole reason for the discussed difference in height.

The above-mentioned results can hardly be obtained in forestry practice by, for instance, selection in the nursery before planting. The reason for this is that the results can be achieved only if one can assume:

a. that there is no variation in bark colour among shoots within the tree that restricts the efficiency of the selection.
b. that the environment of the place where the seedlings are planted and the age of the tree have no influence upon the ranking of seedlings by bark colour that was made e.g. in the nursery.
c. that it is possible to determine, before selection, the bark colour that will give the optimum growth in the forest environment, e.g. at Björkvattnet.

The first assumption is false, and it is most improbable that a method will be developed that totally excludes variation between repeated measurements on the same tree. Accordingly the gain from selection will be less than the above mentioned figures show. Assumptions b. and c. cannot be considered as true until further research has been carried out in this field.

The gain from selection is mainly dependent on the degree of intra-population variation in rhythm. The open pollinated stand progeny has been found to vary considerably and as it is quite possible that the seed orchard progenies, which will become our future stock, exhibit an even larger internal variation in rhythm, it may be concluded that there is reason to continue research on these matters.

4.3.5 The assessment of degree of adaptation of a population

It is logical to expect that the best growing provenances in the field test at Björkvattnet are those best adapted to the test site (Tab. 1, Fig. 1), and accordingly, the main portion of the trees within these provenances should have an annual rhythm that enables them to harmonize with the climate. This could be expressed so that the maximum growth would occur among trees with a rhythm equal to the provenance mean under the assumption of non-skewed distribution. As a logical extension of this reasoning, one could state that the mutual position of the provenance mean rhythm and the rhythm for which the function for the regression of height on rhythm has a maximum, would describe the degree of adaptation of the provenance to the environment.

The colour measurements illustrated in Fig. 6 could be taken as an example. Provenance 22 has a height maximum for colour 69:1 at 3.82 and the provenance mean colour is 3.88, which is almost the same. Accordingly this could be taken as an indication of optimal adaptation to the environment. Provenance 316 has its height maximum at 5.03 while the mean is 4.72. This is a very small difference but could be taken as an indication of an adaptation to a better climate.

These examples can be systematized by the remaining measurements of bark colour and needle length for which there have been found regression curves with a maximum (Tab. 9) (functions with insignificant regression coefficients are not presented).

In Fig. 14 the difference between the value at height maximum (a) and the provenance mean (m), a—m, is illustrated for different provenances and rhythm estimates. A positive difference shows that the provenance is adapted to a more favourable climate than that of Björkvattnet.

Tab. 9. Maximum, minimum and mean values of the distribution, and the rhythm value for which the regression of height on rhythm has a maximum. For regression functions, see Tab. 7 and 8.

Provenance no.	Min. value	Mean value	Max. value	Value at height max.
Bark colour 68:1				
47	2.0	3.52	6.0	—
22	3.0	3.92	7.0	3.30
316	3.0	5.16	8.0	—
115	4.0	6.13	8.0	—
Bark colour 68:2				
47	2.0	3.22	5.0	6.48
22	2.0	3.97	7.0	3.41
316	3.0	4.90	8.0	2.81
115	4.0	6.38	9.0	—
Bark colour 69:1				
47	1.0	2.43	5.0	5.38
22	1.3	3.88	6.0	3.82
316	1.8	4.72	7.1	5.03
115	3.2	5.77	8.8	4.41
Bark colour 69:2				
47	2.2	3.53	4.8	3.90
22	2.4	3.94	6.3	—
316	2.8	4.23	6.4	4.20
115	3.0	5.13	8.0	—
Needle 68				
47	50	66	92	79
22	53	68	90	63
316	54	73	96	69
115	64	81	96	—
Needle 69				
47	41	60	77	77
316	39	74	97	77
115	70	84	99	54

The small and slightly negative values in Fig. 14 shown by 22, could be taken as an indication of a full adaptation to the climate at Björkvattnet. However, the height at age 21 (Tab. 1) shows that optimal growth occurs among those provenances originating north of the seed source 22. The survival percentages (Tab. 1) also indicate that the trees from 22 generally suffer from a lack of hardiness. Obviously, there are reasons to doubt the conclusion about a full adaptation of provenance 22.

The discrepancy between the trend in Fig. 14 and the practical results may be the effect of a rhythm-environment interaction or of mortality.

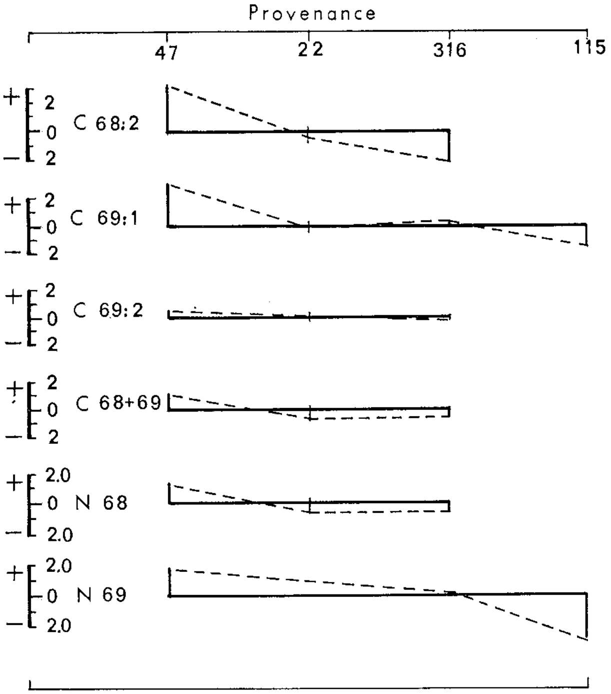

Fig. 14. The difference, a–m, between the rythm value for which the regression of height on rhythm shows a height maximum (a) and the mean rhythm of the provenance (m). For a and m see Tab. 9.

The influence of height growth on the rhythm has been discussed in chapter 4.3.3 and was found to be generally low or non-existent. However, if there is some influence, and a rapid height growth causes late growth termination, this should decrease the difference: regression optimum—provenance mean, and lower the dotted connecting line in Fig. 14.

The climatic adaptation or the annual rhythm of the provenance influences its survival and resistance to frost, pathogens and mechanical injuries (Dietrichson, 1961, 1964, 1968; Eiche, 1966; Stefansson & Sinko, 1967). It is most probable that this is also true among single trees within a provenance. In fact the small height of trees with a too long growing season may be partially caused by an inferior resistance. Any relationship between annual rhythm and resistance influences the mutual position of the height maximum and mean of rhythm, and it is necessary to establish such a correlation and reveal its form before the discussed method for assessment of degree of adaptation to the testing environment may be used.

If mortality were solely restricted to trees with a long growing season, the distributions of rhythm within the two provenances 47 and 22, which have low survival, (29 per cent and 61 per cent respectively) would have been skewed. This is not so (Fig. 2, colour 69:1, needle 69) and this problem therefore requires further research.

4.3.6 The use of the single tree rhythm character in tree breeding

It has been found that the intra-provenance variation in climatic adaptation of *Pinus silvestris* is large, consequently this fact should be considered in tree breeding provided the heritability is high.

As early as in 1918 Raunkiaer showed a similarity in leafing time between parents and progenies of *Fagus silvatica* L. and he concluded that "... the striking correspondence between mother and descendants ... shows that early or late leaftime is genotypically determined". Hagner (1966) established a high parent-progeny correlation in patterns of shoot extension of progenies after controlled crossings of *Pinus silvestris*. Dietrichson (1967) estimated the broad sense heritability in open pollinated families of *Picea abies* and found h^2 for shoot extension to be as high as 0.80. These findings indicate a firm basis for breeding.

The production of a progeny depends upon the potential growth capacity and on the degree of adaptation to the testing environment. A lack of climatic adaptation to the site results in a non-optimal growth and an abnormal survival. The tree breeder faces an intricate problem when he must act on the production figures from a progeny test, because he has to decide where a progeny shall be utilized and what its potential production will be. Unless he can assess to what degree a progeny is adapted to the test site, and how a lack of adaptation influences the production, he will not be able to know the potential growth capacity. As far as this is concerned the tree breeder will benefit in three ways from a recording of the annual rhythm of the single tree in the progeny test: a. Assessment of plasticity, b. Assessment of the degree of adaptation to the testing environment, c. Estimation of potential growth capacity.

a. *Plasticity*

The genetic concept of plasticity is "the extent to which the expression of an individual's genotype can be modified by environmental factors" (Rieger *et al.*, 1968) or in other words the sensitivity for lack of adaptation. In tree breeding we are interested in trees and progenies showing high plasticity since these could be used over a wider geographical and climatical range. The plasticity may be estimated as an "adaptive stability" (Finlay & Wilkinson, 1963; Nienstaedt, 1969) that is the correlation, e.g. of the provenance height and the plantation mean height in a series of geographically distributed field tests. The plasticity could also be described in terms of a relationship between annual rhythm and height. The curve in Fig. 6 could be used as an example. If the plasticity had been higher among the trees in provenance 22 the curve would have been more flat and the trees with a rhythm deviating from the rhythm for which the regression function has a maximum, would have been negatively affected to a lesser extent.

b. *Assessment of the degree of adaption to the testing environment*

As has been shown in chapter 4.3.5, it is possible to assess the degree of adaptation of any progeny on the basis of the relationship between population mean rhythm and rhythm for which the regression function has a maximum. It is essential to note that this method does not rely on a comparison with other populations, and accordingly, it is possible to determine the relative adaptation to the testing environment even when only one population is tested. This will benefit studies in climate chambers, where limitation of space is an acute problem. Assuming that this method is applicable to other species it may be possible to interpret the production data from old plantations and arboretas where often only one provenance is tested.

c. *Estimation of the potential growth capacity*

The regressions in Tab. 7 and 8 demonstrate the decrease in height growth of the single seedling that is caused by an inoptimal annual rhythm. If the rhythm of the individual seedling in progenies are recorded prior to planting, and if assumptions a and b in chapter 4.3.4 are valid, it will be possible to estimate corresponding regressions for each progeny at the time the results of the progeny test are to be considered. The height maximum (hmax) of such a function is a better expression of the potential growth capacity than the average height of the progeny, because it is influenced to a lesser degree by a non-optimal rhythm of the progeny as a whole and by the intra-progeny variance in annual rhythm. Even though it is probable that other genes independent of the rhythm gene complex interact with the environment and influence the hmax, the information obtained in this way will increase the possibility of making a correct judgement about the growth capacity of progenies even when they are tested in an environment to which they are not adapted.

5. Conclusions

It has been established that the methods of describing annual rhythm, which earlier have proved useful for prediction of climatic adaptation and hardiness of populations, can also be used for studies of adaptation of the single tree within populations.

The variation in annual rhythm among trees from a stand collection is so large that a natural population cannot be considered as fully adapted to any site, since it always contains a portion of trees which are not genetically adjusted to the environment. A disharmony between the rhythm of the tree and the testing environment results in a decrease of growth.

In tree breeding one can benefit from recording the rhythm of single trees in connection with progeny testing, since regressions with height growth will enable assessment of the degree of adaptation to the test site. This will improve the prediction of what environment a progeny is adapted to and it will increase the precision in the evaluation of the potential growth capacity of the progeny.

Research has to proceed in this field and establish more efficient methods and elucidate the interaction of the inherited rhythm and external climate on height growth and resistance of the individual tree.

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Sammanfattning

Sambandet inom proveniens mellan årsrytm och tillväxt hos enskilda träd av *Pinus silvestris* L.

Inledning

En väsentlig fråga vid skogsträdsförädling och proveniensforskning är hur man skall fastställa klimatanpassningen hos fältprövat plantmaterial. Den vanligaste metoden har hittills varit att jämföra överlevnaden hos den prövade populationen med överlevnaden hos provenienser, som haft sin ursprungsort nära försökslokalen. Denna metod är tidskrävande eftersom år med extremt klimat oftast inträffar med långa intervaller och dessutom missvisande i de fall där klimattypen på försöksplatsen avviker från den som råder på den plats där den praktiska odlingen skall ske. Inte heller kan metoden användas vid korttidsstudier eller i klimatkammare.

Den relativa härdigheten eller klimatanpassningen kan emellertid fastställas genom kartläggning av den årliga tillväxtcykeln. Detta blev uppenbart för växtforskare redan på ett tidigt stadium (Linnaeus, 1739) och man vet nu att tallens klimatanpassning med framgång kan kartläggas genom mätning av utvecklingshastigheten under skottskjutningen i juni—juli, under avmognaden i augusti—september och under invintringen i oktober. (Langlet, 1936, 1959; Dietrichson, 1961, 1964, 1968; Hagner, 1966, 1970). Även om dessa rön visat att det finns säkra metoder för beskrivning av populationers klimatanpassning har det inte klarlagts att det enskilda trädets anpassning kan beskrivas på samma sätt.

Avsikten med denna undersökning som företogs på 21-årig tall i ett proveniensförsök i Jämtland var att utreda hur klimatanpassningen hos det enskilda trädet skall beskrivas och vilken inverkan anpassningsgraden har på tillväxten. Resultaten visar att klimatanpassningen hos det enskilda trädet liksom hos populationen, speglas av utvecklingshastigheten under högsommaren och avmognadsförloppet under sensommaren och hösten. Vidare framgår av resultatet att graden av anpassning påverkar trädets höjdtillväxt.

Material

Den årliga växtrytmen studerades under 1968 och 1969 i ett proveniensförsök, anlagt 1950 i Björkvattnet, på ca 200 träd inom var och en av fyra provenienser från 62:a, 63:e, 65:e och 68:e breddgraderna (fig. 1, tabell 1). Som jämförelse till de resultat som erhölls i Björkvattnet utfördes 1969 en mindre studie på två provenienser (117, 316) i vart och ett av de två parallellförsöken i Brattfors och Bäckstrand (fig. 1, tabell 1).

Metoder

Årsrytmen skattades med hjälp av fyra metoder, vilka utförligt beskrivits av Hagner (1970). Skottens sträckningscykel kartlades genom mätning dels av skottlängden i juni och dels av de till hälften utvecklade barren i juli. Dessa mått uttrycktes i procent av de fullbildade organen, vilka mättes i augusti. Skottets avmognad bedömdes genom okulärskattning av dess barkfärg i augusti, under vilken månad färgen förändras från klar grön till mörk brun. Barrens mognadsgrad skattades genom mätning av deras torrsubstans i oktober, vilket skedde med hjälp av ugnstorkning (75°C, 49 tim.). Statistiska analyser har främst utförts med två standardprogram, CORREG på Umeå universitets datacentral och DSCRIM på Uppsala universitets datacentral.

Resultat och diskussion

Den bästa metoden

Genom studier av variationen, dels inom och mellan olika provenienser och dels mellan upprepade mätningar på samma individ (fig. 2), framgick att bedömningen av barkfärgen var den bästa metoden men att barrmätningen givit i det närmaste lika korrekta resultat. Torrsubstansbedömningen gav säkra resultat men var betydligt mer arbetskrävande. Skottmätningen, som i andra undersökningar gett synnerligen goda resultat, utfördes i detta fall när skottskjutningen var i det närmaste fullbordad och gav därför oanvändbara värden.

Överensstämmelse mellan skattningar av rytmen under skilda delar av vegetationsperioden

De olika metodernas värden jämfördes genom korrelationsanalys (tabell 2—4). Koefficienterna visar i stort att den bedömning av rytmen som gjorts i juli överensstämmer med den som gjordes i augusti men också med den som på ett begränsat material gjordes i oktober (tabell 5). De tämligen låga koefficienterna antyder emellertid att många träd har en avvikande rytm.

Jämförelse av rytmen under två på varandra följande år

En jämförelse av barrutvecklingen 1968 och 1969 hos träd inom provenienserna 47 och 115 visade en stor spridning och tämligen svag korrelation (figur 3). Genom att ett konfidensband beräknades med ledning av mätfelet kunde man konstatera att spridningen runt regressionen inte var oväntat stor och att en hypotes om att rytmen under 1968 och 1969 var olika därför inte kunde accepteras.

Jämförelse mellan träd från olika provenienser

En studie av fördelningarna av rytm inom provenienserna gav vid handen att en överlappning förelåg t. o. m. hos de båda mycket olikartade provenienserna 47 och 115 (figur 2). Då en rättvisande jämförelse emellertid endast kan ske med samtidig hänsyn tagen till samtliga uppmätta rytmkaraktärer, utfördes en multipel diskriminantanalys, i vilken sex variabler inkluderades (två observationer av barkfärg under 1968 och två under 1969, en barrmätning 1968 och en 1969) (figur 4, tabell 6). Även sedan hänsyn tagits till att spridningen inom provenienserna ökats något, dels p. g. a. att provenienserna inte hade exakt samma varians, dels genom att variablerna företedde något krökta sambandsfunktioner och dels p. g. a. mätfel, kunde man konstatera att spridningen inom provenienserna var anmärkningsvärt stor. Sålunda hade många av tallarna från Muodoslompolo (115; lat. 68°) en rytm motsvarande medeltalet för dem som härstammade från Norrsele (316; lat. 65°).

Samband mellan trädets höjd och dess rytm

Rytmens inverkan på höjdtillväxten studerades genom en serie regressionsanalyser (tabell 7, 8). Krökta samband förelåg inom de flesta provenienserna. Av funktionernas lutning framgick att de träd som växte snabbast hade en årsrytm som ungefär motsvarade medeltalet hos proveniensen 22, d. v. s. »lokalproveniensen» (figur 5—8). Denna tendens var påtaglig hos plantor oberoende av proveniens men var även tydlig hos plantor inom samma proveniens. På grund av att krökta sambandskurvor förelåg även inom de provenienser som växte bäst, d. v. s. 22 och 316, var det tydligt att även dessa innehöll vissa plantor med en årsrytm som omöjliggjorde optimal tillväxt, trots att provenienserna som sådana kunde anses vara i hög grad anpassade till försökslokalen. Detta innebär följaktligen att spridningen inom en beståndsavkomma är så stor att populationen inte kan anses vara fullt anpassad till någon lokal utan endast i viss högre eller lägre grad.

Gällde resultaten som erhållits i Björkvattnet även i annan miljö om rytmen uppskattades med annan metod?

I de två fältförsöken i Brattfors och Bäckstrand mättes höjden hos 24 träd inom vardera provenienserna 117 och 316. Samtidigt (den 5:e okt.) insamlades barrprover på vilka torrsubstanshalten senare mättes. Regressionsanalys visade svaga men i två fall signifikanta samband mellan trädhöjd och torrsubstanshalt. En jämförelse inom samma proveniens mellan regressionskoefficienterna i Brattfors och Bäckstrand visade för båda provenienserna starkt signifikanta skillnader ($p < 0{,}001$). Koefficienterna hade mer utpräglat negativa värden i Brattfors-materialet. Då klimatet är mycket strängare i Bäckstrand än i Brattfors har resultatet en med Björkvattnet-materialet överensstämmande tendens, eftersom träd som har en kortare utvecklingscykel, d. v. s. inleder sin avmognad tidigare på hösten, tillväxtmässigt hävdat sig bättre i det strängare klimatet.

Påverkas rytmen av tillväxten eller tillväxten av rytmen?

Undersökningar, utförda på skott av varierande längd på samma trädkrona, har visat att utvecklingen är senare hos långa skott (Dietrichson, 1964; Owston, 1969). Om detsamma skulle gälla mellan skott hos skilda individer kan näringshalten hos marken genom inflytande på tillväxten modifiera årsrytmen. »*Proveniensproblemet*» blir »*ett bonitetsproblem*» (Dietrichson, 1964).

Om snabb tillväxt medför sen avmognad bör de regressionsfunktioner av typen höjd=f(rytm) som härletts ur det föreliggande materialet alltid ha en negativ regressionskoefficient. Vidare bör härkomsten i så fall inte påverka lutningen hos regressionskurvan. Eftersom detta inte överensstämmer med de resultat som tidigare presenterats, kan markförhållanden knappast påverka årsrytmen i någon hög grad. Den höga heritabilitet för skottskjutningscykeln (broad sense heritability=0,80) som Dietrichson (1967) beräknat på avkommor av gran bekräftar också detta påstående.

Användningen av årsrytmskattning för selektion av snabbväxande subpopulationer

En beräkning av den effekt som en selektion med ledning av barkfärgen skulle få har gjorts på provenienserna 47, 316 och 115. Sambandet mellan höjd och färg framgick av regressionsfunktioner i tabell 7 och i figurerna 6 och 13 samt av en krökt regressionskurva för proveniens 47, vilken inte presenterats i någon tabell. Ett urval av de 5 % av träden som hade barkfärgsvärden närmast regressionskurvans maximum resulterade i subpopulationer med följande medelhöjder 316: 3,7 m, 115: 3,4 m, 47: 4,0 m. Beräkningen har gjorts på grundval av dessa populationers medelhöjd i fältförsöket i Björkvattnet.

Dessa siffror antyder att en selektion i proveniens 47 skulle vara fördelaktigast och resultera i en höjd, som med 6,7 % överstiger medelhöjden hos den mest snabbvuxna proveniensen i försöket (nr 121). Jämförelsen är emellertid felaktig eftersom konkurrensen är betydligt större i 121 (87 % överlevande) än i 47 (29 % överlevande). Emellertid påverkar minskad konkurrens knappast höjdtillväxten i så hög grad att detta kan förklara hela skillnaden.

Det resultat som redovisats kan inte uppnås vid praktisk selektion i plantskolan, eftersom detta förutsätter att följande antaganden är korrekta:

a. att ingen variation som nedsätter effektiviteten i selektionen förekommer i barkfärgen hos skilda skott inom samma träd.
b. att miljö och plantålder inte påverkar årsrytmen.
c. att det är möjligt att redan före planteringen förutsäga vilken barkfärg som ger optimal tillväxt.

Det första antagandet är felaktigt och vi kommer troligen aldrig att förfoga över metoder för en exakt uppskattning av årsrytmen. De övriga antagandena kan endast belysas genom ytterligare forskning.

Selektionsvinsten står i direkt relation till spridningen i årsrytm inom populationen. Eftersom vårt framtida skogsodlingsmaterial kommer att hämtas från fröplantager, där vi har moderträd med större genetisk spridning än i de studerade beståndens, är det möjligt att selektion för årsrytm blir av större betydelse i framtiden än vad som för närvarande är fallet.

Bestämning av klimatanpassningen hos en population

Av regressionsfunktionerna framgick att de mest välväxande populationerna, 22 och 316, hade ett höjdmaximum som låg nära populationsmedeltalet medan de mindre snabbväxande, d. v. s. den proveniens som flyttats från söder och den som flyttats mycket långt norrifrån, hade ett maximum som låg utanför fördelningen. Detta innebär att anpassningsgraden skulle kunna beräknas på det inbördes avståndet mellan höjdmaximum och populationsmedeltal. Vidare följer, att populationen är underhärdig om höjdmaximum ligger på den sida av medeltalet som innebär tidig invintring, medan den däremot är överhärdig om höjdmaximum ligger på andra sidan av medeltalet. Detta förhållande belystes ytterligare genom studier av samtliga andragradsfunktioner (även icke signifikanta; ej presenterade i tabell 7, 8) (tabell 9, figur 14).

Tillämpning av metoder för mätning av årsrytmen hos träd vid skogsträdsförädling

Variationen i årsrytm har visat sig vara stor bland träd inom samma proveniens. Resultaten av denna undersökning tyder på att rytmkaraktären är en starkt genetiskt betingad egenskap, vilket även bekräftas av den höga heritabilitet (broad sense heritability=0,80), vilken Dietrichson (1967) beräknat på skottskjutningen hos avkommor av gran efter fri avblomning. Det finns därför all anledning att ta hänsyn till och utnyttja denna karaktär i skogsträdsförädling.

En kartläggning av årsrytmen hos enskilda träd redan i plantskolestadiet borde gagna avkommeprövningen på i första hand följande sätt: a. bestämning av plasticiteten, b. bestämning av avkommans grad av anpassning till försökslokalen, c. bestämning av potentiell tillväxtkapacitet.

a. *Plasticiteten.* Plasticiteten »the extent to which the expression of an individual's genotype can be modified by environmental factors» (Rieger *et al.*, 1968) är av intresse vid skogsträdsförädling. Detta beror på att en mindre känslighet hos plantmaterialet för avvikelse från det klimat som plantorna fordrar för optimal utveckling, möjliggör användningen av förädlat material över större områden. Plasticiteten kan fastställas genom krökningsgraden hos sambandskurvan för tillväxt och rytm inom en population, eftersom högre plasticitet medför en mindre accentuerad krökning.

b. *Anpassning till försökslokalen.* Som tidigare visats kan relationen mellan populationsmedeltalet och höjdmaximum användas för att beskriva graden av anpassning. Det bör noteras att detta inte bygger på jämförelse med andra populationer och alltså är en metod som kan användas även när endast en population prövas. Detta bör kunna öka värdet av äldre försöksytor i vilka jämförelsematerial saknas. Metoden borde även kunna effektivisera t. ex. klimatkammarförsök, vid vilka utrymmet alltid är minimalt.

c. *Potentiell tillväxtkapacitet.* Den potentiella tillväxtkapaciteten, med vilken här avses de tillväxtresurser en avkomma besitter vid sidan av den tillväxtförmåga som betingas av graden av anpassning till odlingsmiljön, speglas av höjden vid maximumpunkten (hmax) hos sambandskurvan för höjd och rytm. Trots att andra gener än de som ingår i rytm-genkomplexet troligen samspelar med miljön och påverkar hmax, bör denna värderingsgrund möjliggöra en bättre bedömning av moderträdens avelsvärde än när värderingen grundas på avkommans medelhöjd, särskilt i de fall då avkomman ej är anpassad till försökslokalen.

Slutsatser

Ett flertal av de morfologiska metoder som kan användas för att beskriva populationernas klimatanpassning kan också användas för beskrivning av anpassningen hos enskilda träd.

Trädets höjdutveckling påverkas av dess nedärvda årsrytm.

Spridningen i rytm inom en beståndsavkomma är så stor att det, oberoende av odlingsmiljö, alltid förekommer träd som växer inoptimalt p. g. a. dålig anpassning.

Vid skogsträdsförädling kan en beskrivning av varje plantas årsrytm effektivisera avkommeprövningen.

Ytterligare forskning på detta område är angelägen.

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