STUDIA FORESTALIA SUECICA

Nr 80 1970

A genecological investigation of the annual rhythm of *Pinus silvestris* L.

En genekologisk undersökning av årsrytmen hos Pinus silvestris L.

by

MATS HAGNER

Department of Forestry, University of Umeå, Sweden

SKOGSHÖGSKOLAN
ROYAL COLLEGE OF FORESTRY
STOCKHOLM

ABSTRACT

The objective of this study was to find easily measured morphological parameters that illustrate climatic adaptation, and to study the variation within and between provenances as well as to find the main climatic reason for adaptation.

Various methods were tried on two- and three-year-old nursery stock which consisted of provenances from all over Sweden (lat. 55°—68°N). To obtain a true correlation with long term survival under field conditions the methods were also applied to older trees in a provenance field test.

Up to 96 per cent of the variation in survival after ten years in the field could be accounted for by the regression of the data obtained with the following methods: Bark colour of terminal shoot (Aug.), Needle development (July), Shoot development (June), Dry matter percentage of needles (Oct.), Lignification of xylem (Sept.). Budsetting showed a significant but different pattern of variation from the above-mentioned traits.

Growth rhythm was related to latitude and altitude of seed source but not in the same way as suggested by previous studies. Variation in annual rhythm among seedlings within a provenance was considerable, and the height growth of the single seedling was correlated with the rhythm.

Ms. Received 10 February 1970

ESSELTE TRYCK, STHLM 70
010244

CONTENTS

Page
1. Introduction 5
2. Material 6
3. Methods 8
    3.1 Field methods 8
    3.2 Statistical methods 11
4. Results 12
    4.1 Eighteen-year-old *Pinus silvestris* grown at Björkvattnet and Bäckstrand . 12
    4.2 Two-year-old seedlings observed in the nursery 15
    4.3 Three-year-old seedlings in the nursery 18
    4.4 Annual rhythm and climate of seed source 18
    4.5 Bark colour and height of tree 19
    4.6 The influence on annual rhythm of altitude and latitude of seed source 23
    4.7 The use of annual rhythm in progeny testing 27
    4.8 Future studies of annual rhythm 28
5. Conclusions 30
Acknowledgements 31
Literature 32
Sammanfattning 34
Tables 38

1. Introduction

Provenance research carried out on Scots pine in Scandinavia and Finland has shown that the hardiness of the stock is of major importance for the success of artificial regeneration. For future research in this field and for the application of scientific results to practical forestry, there has arisen a need for methods that would enable us to measure the relative hardiness of seedlings and predict to what kind of environment a seedling or a population is adapted.

The objective of this study was to find easily measured morphological parameters that illustrate climatic adaptation, and to study the variation within and between provenances as well as to find the main climatic reason for adaptation.

Hardiness has been studied extensively and world literature in this field is abundant. Good summaries have been presented by Levitt (1956) and by Meryman (1966). It has been shown that adaptation to winter conditions means comprehensive changes that enable the plant to sustain great temperatur fluctuations and drought without suffering damage. Adjustment to winter affects the composition of the protoplasm and brings about a reduction of moisture, an increase in sugar, a reduction of starch, an increase in the contents of fat and hemicellulose, an increase in the amount of swelling colloids, increased nitrogen, changes in the proteins, and increases in the amounts of tannic substances and organic phosphorus. There is still controversy about what changes are most important for frost hardiness. However, it is generally agreed that the changes combine to promote the ability of the cells when freezing to transfer the free water to the intercellular spaces, or to a place between the protoplasm and the cell wall, where it can crystallise without causing damage. The processes of winter adjustment are not needed to facilitate this water transport, because nonhardy plant parts can sustain very low temperature levels (—253°C) without damage by special treatment (Tumanov, Krasavcev & Hvalin, 1959) but the processes serve to improve the water transport. The degree of hardiness usually increases continuously during the fall but temporary weather reversals largely affect the rate of hardening-off. There is no winter dormancy in the strict sense since de-hardening always follows a temperature rise even in winter.

Since hardiness is a continuously changing condition, an effect of interactions between a large number of factors that are partly genetic in nature, partly physiologically conditioned and partly environmental it must be stated that it appears impossible to describe hardiness completely by any one method alone.

When considering what method should be used in this work to achieve the clearest illustration of long-term climatic hardiness in pine, it was assumed from work by Langlet (1936), Ladefoged (1952) and Dietrichson (1961) that measurements of parameters elucidating the annual growth rhythm during the later part of the summer and in the fall would give the best results. When choosing parameters it was assumed that morphological changes would be better and more reliable to observe than chemical properties, because the latter must fluctuate more rapidly with climatic changes than the former.

In the present work emphasis has therefore been laid upon non-chemical methods that can easily be used on a large material while facilitating studies of differences between individual seedlings.

2. Material

To obtain an immediate verification of the usefulness of various methods and to determine the degree to which they illustrate climatic hardiness, an investigation was carried out in a test plot with 18-year-old *Pinus silvestris*. This plot was one in a series of five provenance tests from which could be obtained survival data showing the real hardiness of the provenances which were studied for annual rhythm. The silvicultural results from the series of provenance tests have been published by Stefansson & Sinko (1967). Each provenance can be considered as originating from more than ten trees within one stand (Fig. 1, Tab. I, II).

To determine the usefulness of the methods when applied to young seedlings, studies were extended to the nursery where 64 provenances of three-year-old and 48 provenances of two-year-old Scots pine were grown. The three-year-old provenances originate from several stands at a given latitude and altitude from which the seed was mixed. At the end of the second growing season, the seedlings were transplanted to 1″ spacing and they were measured at the end of their third growing season (Tab. IV).

The two-year-old provenances originated from stands all over Sweden and the seed was a mixture from ten mother trees. The seedlings

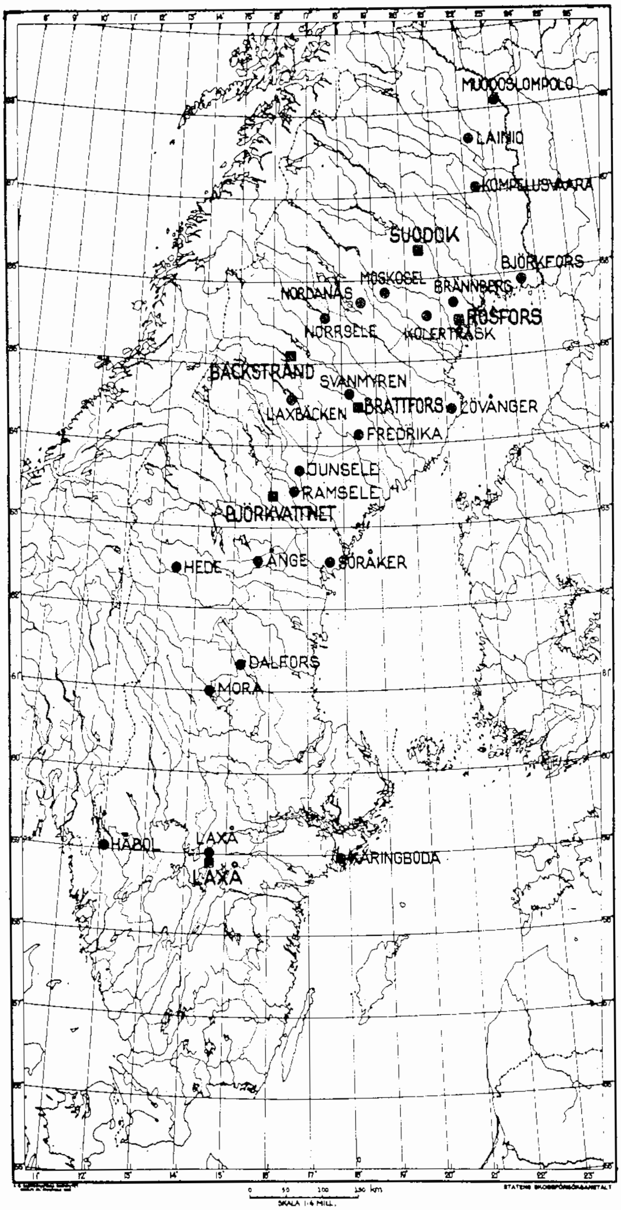

Fig. 1. Map of Sweden showing provenance test sites (■) and seed sources (●). After Stefansson & Sinko (1967).

were kept in the sowing bed during the time of observation (second growing season) and thus were never transplanted (Tab. III).

3. Methods

3.1. Field methods

In the field and the nursery the following methods were used for elucidation of the annual rhythm. The dates on which the measurements were taken and the samples collected are stated in the tables.

Xylem measurements

Previous investigations by Ladefoged (1952), Wardrop (1957) and Dietrichson (1961, 1964a, 1964b, 1968) have shown that the evaluation of lignification in the outer xylem can provide a good idea of degree of winter adjustment. As long as the cambium is forming new wood cells, the outermost cells have poorly lignified walls and lignification is not complete until late in autumn. Since the latest possible date was chosen for the observations in the present investigation, the frequency of peripheral cells in the outermost wood mantle with fully lignified outer walls was estimated (Fig. 2). The tissue was stained with phloroglucin+HCl.

Measurements of shoot elongation

The relative rate of shoot elongation is strongly influenced by the adaptation to a given length of growing season. A northern provenance has a more rapid rate of development than a southern one (Dietrichson, 1964a). The greatest differences occur between the provenances during a mid-stage of the shoot elongation when the thermal elements of climate seem to have a major influence (Mork, 1941; Dietrichson, 1964a). The measurements were made four times during the growing season. The first measurement was taken from a “zero” point (a needle pierced through the shoot below the terminal bud on trees, or from a white spot painted on the stem of two-year-old seedlings) to the bud point. The second and third measurements were taken during the shoot elongation and the fourth measurement after growth was completed.

Measurements of needle length

In a way similar to that used for measurement of shoot elongation, the degree of development at a given time can be expressed in terms

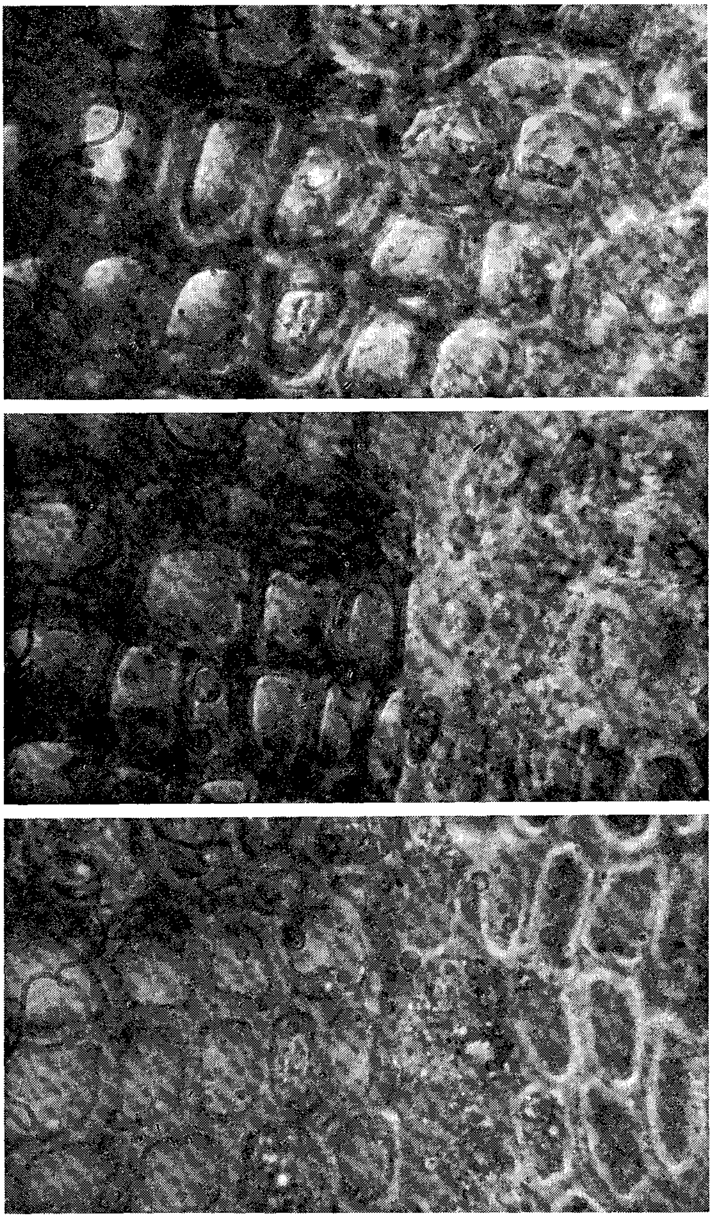

Fig. 2. Photos showing different degrees of lignification of xylem in *Pinus silvestris*. The top picture shows a continuously increasing cell wall thickness from the cambium, on the right, to fully lignified tracheids, on the left. Centre photo shows an almost fully lignified xylem where only the outer walls of the last formed tracheids remain partly lignified. In this work one of the four peripheral cells would have been considered as fully lignified. The bottom photo shows a completely lignified xylem where four of the peripheral cells would have been considered as fully lignified.

of the relative length of needles growing on the terminal shoot compared to those developed one year before. Langlet (1959) and Dietrichson (1964a) have shown that differences among provenances from differing seed sources of *Pinus silvestris* are easily ascertained by this method.

Needles from the preceding shoot were collected simultaneously with the half-developed needles from the terminal shoot and the relative needle length was thus estimated in relation to the length of the old needles. This method is an approximation since the needles vary considerably from one year to another. Nevertheless, the method was chosen because all sampling can be done simultaneously and no tagging of individual seedlings is necessary.

Observations of budding

It is well known that the frequency of seedlings with buds developed at a given time can be used on conifers to express earliness in maturation.

Determinations of bark colour

This method has been used successfully on pine provenances (Hagner, 1966; Stefansson & Sinko, 1967). The bark colour of the terminal shoot is chlorophyll green during elongation, but changes to brown during August and September. In this study the colour was determined ocularly and registered in a scale ranging from 1 to 5. The scale was calibrated after a study of the whole material, 1 being assigned to the greenest colour. Typical shoots representing the colours 1, 3 and 5 were cut and used for comparison throughout the observation.

Determinations of dry matter

The value of this method for differentiation of provenances has already been demonstrated by Langlet (1936). In his investigations he used the oven-dry weight as a per cent of fresh weight of needles. The provenances in the present investigation were represented by a bulk sample consisting of a few needles from each of at least 60 seedlings. The samples were stored in open vials at approximately 100 per cent humidity for 14 days prior to analysis. Drying was conducted at a temperature of 105°C for four hours.

Measurement of electric resistance

The moisture content can be measured directly on the basis of the electric resistance observed when two electrodes are inserted in the tissue (Wilner *et al.*, 1960; Wilner, 1961; Brach, 1964). An apparatus designed for the purpose consisted of a battery, resistance bridge, potentiometer, switch for calibration and electrodes that were placed immediately underneath the cotyledons of the two-year-old seedlings in positions leading the electric current parallel to the vascular tissue of the stem.

3.2. Statistical methods

Most of the analyses were made in a computer where a set of standard programs for stepwise regression analysis were used. As it could be expected in most of this material that curvilinear relationship existed between the variables studied, the independent variables were included in simple and in squared form. In the regressions of annual rhythm on latitude and altitude of seed source it was logical to expect a complicated interaction between the two geographical parameters. These were therefore included in the calculations as simple, and in the following transformations: Latitude×Latitude (LL), Altitude×Altitude (AA), AL, A/L, L/A, 1/L, 1/A.

4. Results

4.1 Eighteen-year-old *Pinus silvestris* grown at Björkvattnet and Bäckstrand

All methods except the electric were applied to the material in the field test at Björkvattnet, and in a series of regressions of survival on the rhythm variables (Tab. II) a strong relationship was found between the annual rhythm at Björkvattnet and the real hardiness, as illustrated by the survival in the severe climate at the exposed site at Bäckstrand (Tab. 1 and Fig. 3). In a series of regressions of rhythm on latitude of seed source a very strong relationship was found between these parameters (Tab. 2 and Fig. 4—7).

The purpose was to search for easily obtained expressions of annual rhythm which would describe the hardiness of seedlings and populations. To evaluate the various methods, we must take into consideration the percentage of the variation that has been explained by the functions in Tab. 1, as well as the number of values supporting the functions. It is also necessary to judge whether the type of function used is suitable, and finally to consider the amount of work conducted in the field and the laboratory.

The bark colour was ocularly evaluated on one shoot of 144 seedlings in each provenance, while the needle length was measured on one pair of needles from each of seven seedlings, and the dry matter was determined on one needle from 60 seedlings in each provenance. The bark colour was recorded in the field, while the needle length and the dry matter content were recorded in the laboratory. Both the measurements of shoot elongation on two shoots from each one of 14 seedlings

Tab. 1. Regressions of survival after ten years in the field test at Bäckstrand on annual rhythm measured in the field test at Björkvattnet.

Regression	N^a	tb_1	tb_2	R^2	F
Surv=166.8—258.7/Bark	14	17.9***		0.96	321***
Surv=3.448 Needl—94.27	15	07.18***		0.80	052***
Surv=21.89 Drym—805.7	15	05.36***		0.69	029***
Surv=38.02 Shoot—0.3798 (Shoot)^2—851.4	08	06.89***	06.13***	0.97	038***

N^a=Number of observations. tb_1="t" value of the first regression coefficient. R^2= Coefficient of determination. F="F" value of the regression. ***=Significant on the 0.1 % level.

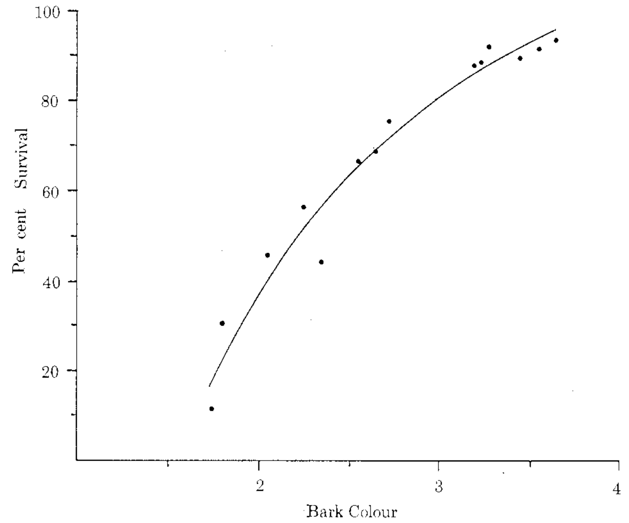

Fig. 3. Regression of per cent survival after ten years in field at the very exposed site "Bäckstrand" on mean bark colour of terminal shoot in August, ocularly estimated on 140 eighteen-year-old trees at the test site "Björkvattnet". Regression equation: Surv = =166.8—258.7/Bark; R^2 =0.96.

and the xylem measurements on one wood sample from 20 seedlings in each provenance were very time-consuming.

Considering the amount of work carried out and the results obtained, it can be concluded that the observations of bark colour produced an outstanding result. The measurements of needle length and the determinations of the dry matter produced good results, but the measurements of needle length were preferred since they produced individual evaluations without additional work. The measurements of shoot elongation may be considered quite informative though time-consuming, while the xylem measurements did not produce convincing results.

Tab. 2. Regressions of annual rhythm on latitude and altitude of seed source for eighteen-year-old trees.

Regression	N^a	tb_1	tb_2	R^2	F
Bark=0.426 Lat—24.80	18	18.90***		0.96	359***
Needl=1281—42.72 Lat+0.3653 Lat^2	21	04.44***	4.80***	0.94	144***
Drym=36.77+0.4978 (Lat—58.5)	19	08.90***		0.82	079***
Shoot=34.09—2.673(Lat—58.5)+0.6199(Lat— —58.5)^2	12	02.05*	5.27***	0.95	080***

a See Tab. 1 for description of characters

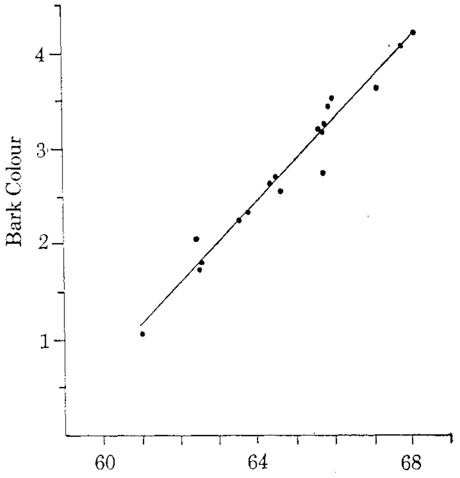

Fig. 4. Regression equation: Bark colour = $= 0.426$ Lat— 24.80; $R^2 = 0.96$.

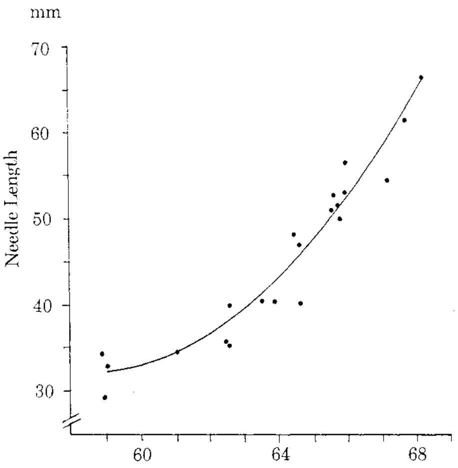

Fig. 5. Regression equation: Needle length = $= 1281 - 42.72$ Lat $+ 0.3653$ Lat^2; $R^2 = 0.94$.

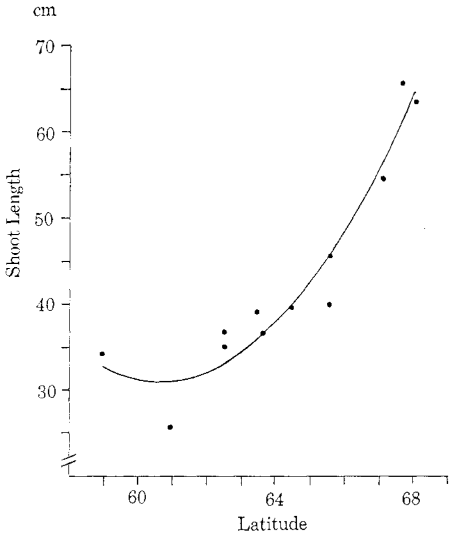

Fig. 6. Regression equation: Shoot length = $= 34.09 - 2.673 \ (\text{Lat} - 58.5) + 0.6199(\text{Lat} - 58.5)^2$; $R^2 = 0.95$.

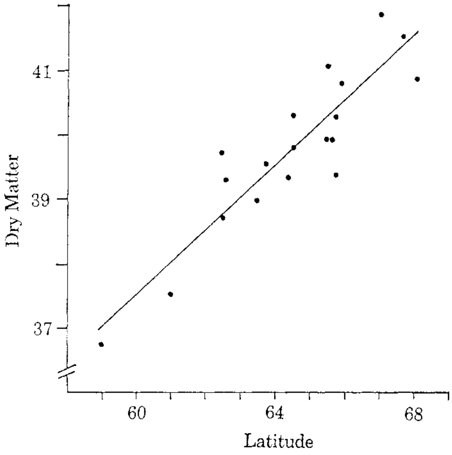

Fig. 7. Regression equation: Dry matter = $= 36.77 + 0.4978 \ (\text{Lat} - 58.5)$; $R^2 = 0.82$.

Fig. 4—7. Regressions of rhythm, measured on 18-year-old trees at Björkvattnet, on latitude of seed source.

Tab. 3. Regressions of annual rhythm on latitude and altitude of seed source for two-year-old seedlings.

Regression	N^a	$tb_{1,3}$	tb_2	R^2	F
$\text{Bark} = 2.718 - 0.5307\,(\text{Lat} - 50.0) + 0.03073\,(\text{Lat} - 50.0)^2$	48	06.30***	9.12***	0.91	219***
$\text{Drym} = 26.63 + 0.02791\,(\text{Lat} - 50.0)^2 + 4.400 \cdot 10^{-6} \cdot \text{Alt}^2$	32	13.40***	2.64*	0.88	102***
$\text{Shoot} = 13.86 + 0.1333\,(\text{Lat} - 50.0)^2$	30	09.95***		0.78	100***
$\text{Xylm} = 76.11 - 8.794\,(\text{Lat} - 50.0) + 0.2819\,(\text{Lat} - 50.0)^2$	30	09.05***	7.20***	0.91	129***
$\text{Buds} = 23.01\,(\text{Lat} - 50.0) + 0.4637\,\text{Alt} - 0.04877\,\text{Alt}\,(\text{Lat} - 50.0) - 162.6$	48	05.91*** 02.80**	2.02*	0.52	15.6***

a See Tab. 1 for description of characters.

Concerning the xylem measurements it must be stressed that the poor result can probably be explained by the samling technique. To avoid damage to the seedlings, no stem sample was taken but a two-year-old terminal shoot was taken from one of the major branches.

4.2 Two-year-old seedlings observed in the nursery

The results clearly show the relative difference in growth rhythm. All methods, except electrical resistance and budsetting, gave values that were strongly correlated mutually and with latitude (Tab. 3 and III and Fig. 8—12).

Bark colour was the best measure because it gave reliable values very easily collected. Dry matter was the second best in spite of the disadvantage of within-strain variation ascertainable only after tedious laboratory work. The third most useful measurement was degree of lignification (xylem) in view of individual judgement. The method employing measurements of shoot elongation came fourth. This method produced very unreliable results for the individual seedling of this age because buds were not developed until the end of the second growing season, and measurements had to extend to the top meristem hidden behind needles.

The shoot measurements were taken at four times during the growing season, since Dietrichson (1964a) has shown that the largest differentiation between northern and southern provenances is found during a mid-stage of elongation. This material, however, showed that the relative elongation up to 15 June, i.e. approximately the first half of the elongation, displayed the greatest correlation with latitude.

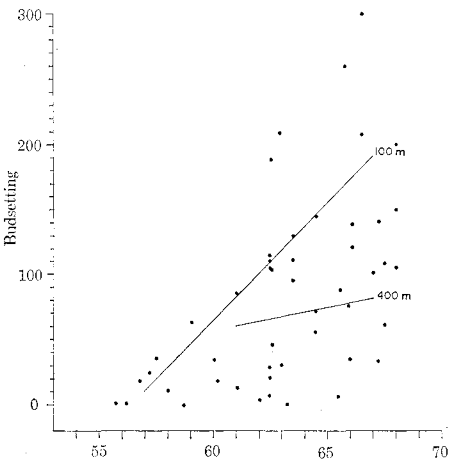

Fig. 8. Regression equation: $\text{Budsetting} = 23.01\,(\text{Lat} - 50) + 0.4637\,\text{Alt} - 0.04877\,\text{Alt}\,(\text{Lat} - 50) - 162.6$; $R^2 = 0.52$

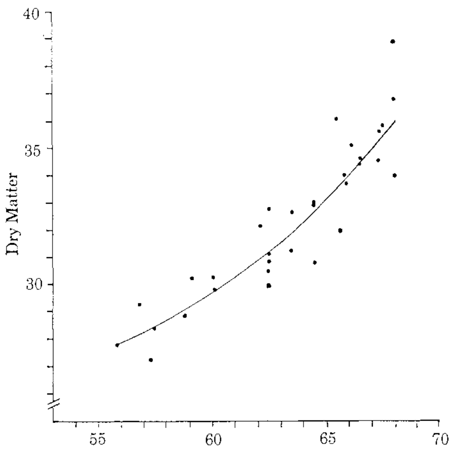

Fig. 9. Regression equation: $\text{Dry matter} = 26.63 + 0.02791\,(\text{Lat} - 50)^2 + 4.400 \cdot 10^{-6} \cdot \text{Alt}^2$; $R^2 = 0.88$.

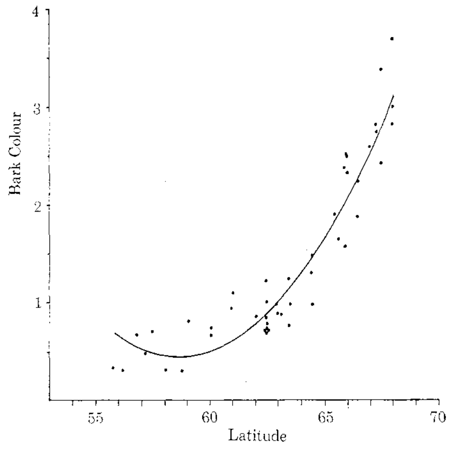

Fig. 10. Regression equation: $\text{Bark colour} = 2.718 - 0.5307\,(\text{Lat} - 50) + 0.03073\,(\text{Lat} - 50)^2$; $R^2 = 0.91$.

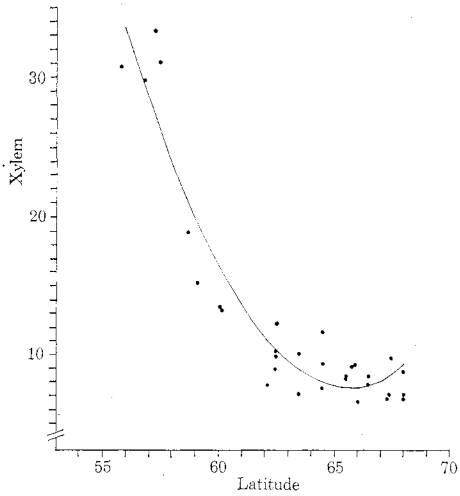

Fig. 11. Regression equation: $\text{Xylem} = 76.11 - 8.794\,(\text{Lat} - 50) + 0.2819\,(\text{Lat} - 50)^2$; $R^2 = 0.91$.

Fig. 8—12. Regressions of rhythm, measured on two-year-old nursery stock, on the latitude and altitude of seed source.

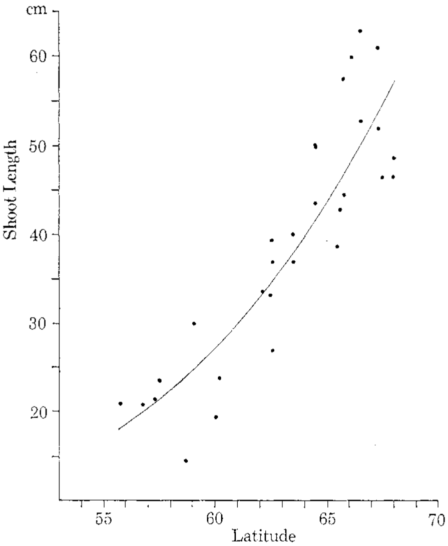

Fig. 12. Regression equation: Shoot length= [illegible] $= 13.86 + 0.1333 \quad (\text{Lat} - 50)^2$; $R^2 = 0.78$.

The two-year-old seedlings were also used for testing the method with electric resistance on several occasions from July to November. It was only at the end of October and in November that the values obtained were slightly correlated with latitude.

A budsetting survey indicated that the correlation with latitude was significant and showed that southern provenances had a positive correlation with latitude but hardly any with altitude, while the northern provenances showed positive correlation with latitude but negative with altitude (Fig. 17). These relationships were constant and very similar in the three separate surveys conducted on 12 Aug., 20 Aug. and 29 Aug. The negative correlation with altitude among provenances from high latitudes is surprising indeed and may be due to a budbreak and renewed shoot growth taking place soon after budset. A survey designed to register the first occurring buds would in such a case have shown a very different result.

The very same seedlings that according to bark colour or dry matter (Fig. 18) are rated as late in development at the same time (August) can be early in budsetting and *vice versa*. Budsetting can obviously vary independently from other features of annual rhythm. The rhythm of any population must therefore be studied in conjunction with budsetting and one or more of the other traits used here. The correlation among the latter traits (Tab. 4) seemed to be so strong that measurement of one also gave a relatively good picture of the others.

Tab. 4. **Correlation coefficients of rhythm among 30 provenances of two-year-old seedlings.**

Bark			
0.80***	Shoot		
0.92***	0.80***	Dry matter	
—0.55**	—0.70***	—0.75***	Xylem

***,** = Significant on the 0.1%, 1% level respectively.

4.3 Three-year-old seedlings in the nursery

Two methods were used for measurement of annual rhythm (Tab. IV). In view of the fact that the bark colour was measured only once (18 August) and on 30 seedlings, the result was very good (Tab. 5, Fig. 13). Xylem measurements also gave good results (Fig. 14) but the volume of work was immense compared to that of the bark colour method.

4.4 Annual rhytm and climate of seed source

The number of days per year with a mean temperature above +6°C and "continentality", which is the difference between July and January mean daily temperatures, were obtained for seed sources from maps published by Langlet (1936). The relationship between these two climatic variables and the rhythm, as expressed by the bark colour, was examined in the data obtained from measurement of the trees at Björkvattnet and of the two-year-old nursery stock. From plotting diagrams it was found that the only curvilinear relationship existed between bark colour and latitude and that it could be best expressed by an arcustangens function.

The bark colour was most closely related to latitude in the two separate materials (Tab. 6) and it may be concluded that the latitude gave the best description of the selective force that causes adaptation in annual rhythm.

Tab. 5. **Regressions of annual rhythm on latitude and altitude of seed source for three-year-old seedlings.**

Regression	N^a	tb_1	R^2	F
Bark = $2.355 \cdot 10^{-3} \cdot Lat^2 - 7.543$	63	19.80***	0.86	388***
Xylm = $312.6 - 0.06733\ Lat^2$	45	14.20***	0.83	202***

a See Tab. 1 for description of characters

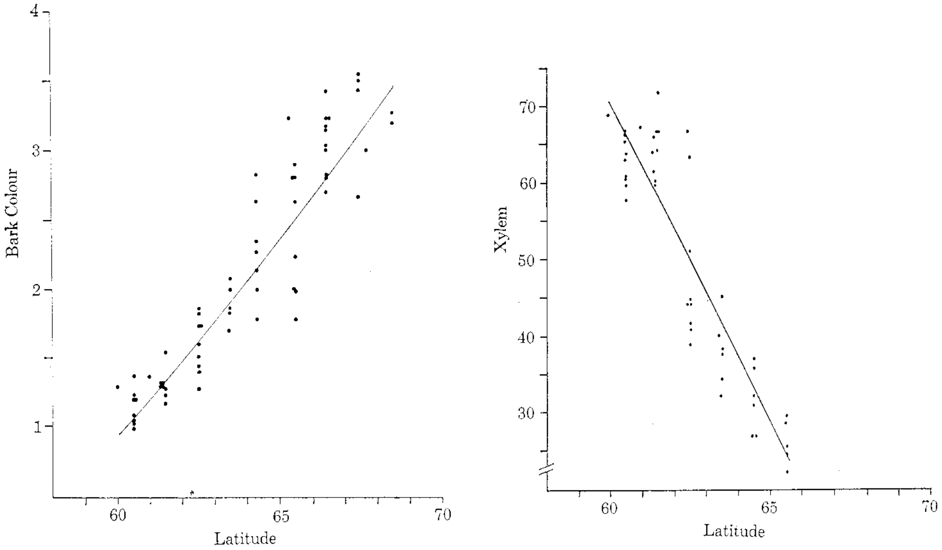

Fig. 13. Regression equation: Bark colour = $= 2.355 \cdot 10^{-3} \cdot \mathrm{Lat}^2 - 7.543$; $R^2 = 0.86$.

Fig. 14. Regression equation: Xylem = $= 312.6 - 0.06733\ \mathrm{Lat}^2$; $R^2 = 0.83$.

Fig. 13—14. Regressions of annual rhythm measured on three-year-old nursery stock, on the latitude of seed source.

4.5 Bark colour and height of tree

Observations of bark colour and measurements of height were made on 8 August on randomly chosen trees in three provenances of 18-year-old *Pinus silvestris* in the field test at Björkvattnet. Bark colour was judged ocularly on the basis of one shoot on one leading branch, and height measurements were obtained with a measuring rod. The

Tab. 6. Correlation coefficients between bark colour and climatic and geographic variables.

Rhythm	Latitude[a]	Altitude	Grow.seas.	Continent.
	Eighteen-year-old trees. N=18			
Bark	0.97***	0.20 N.S.	—0.88***	0.73***
	Two-year-old seedlings. N=49.			
Bark	0.96***	0.22 N.S.	—0.76***	0.81***

[a] Latitude transformed into arctg ((Lat—64.5)/3.50) for eighteen-year-old trees and into arctg ((Lat—66.8)/2.65) for the two-year-old seedlings. See Tab. 1 for description of characters.

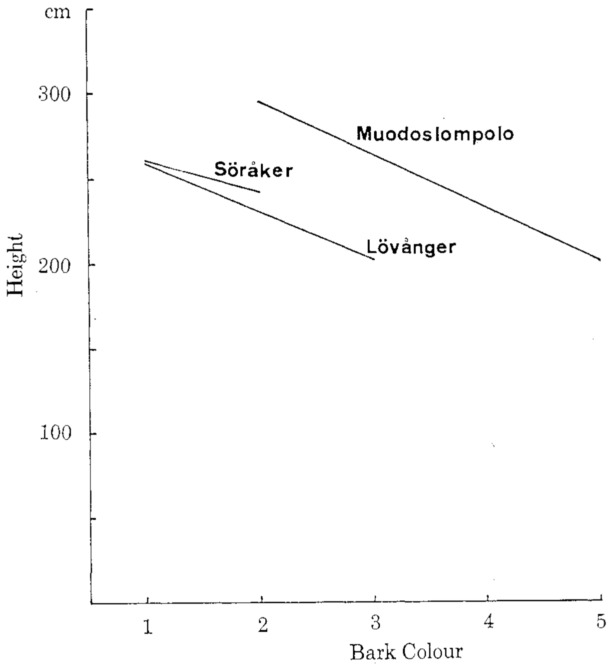

Fig. 15. Regressions of height on bark colour among 18-year-old trees within three provenances grown at Björkvattnet. Equations and correlation coefficients; Muodoslompolo: Height = 360 – 31.9 · Colour; $r = -0.39$ ($p < 0.001$). Lövånger: Height = 287 – 28.1 · Colour; $r = -0.38$ ($p < 0.01$). Söråker: Height = 279 – 18.9 · Colour; $r = -0.15$ ($p < 0.05$).

provenances were chosen so that one of them would be similar to the local strain, Lövånger, while the two others had been moved southward, Muodoslompolo, and northward, Söråker (Tab. II). The number of trees measured was: Muod. 247, Lövånger 51, Söråker 182. These trees were representative of the provenance mean in height, judged by estimates of growth made four years earlier.

All correlation coefficients are significantly different from zero (Muod. $p<0.001$, Lövånger $p<0.01$, Söråker $p<0.05$) (Fig. 15). However, the dispersion about the lines is great and for the Muodoslompolo data the regression accounts for 15 per cent of the variation ($R^2=0.15$). Fig. 16 illustrates four subpopulations of Muodoslompolo characterized by different bark colour. The great dispersion about the lines is not unexpected since random influence from the environment is large and the sampling error was great.

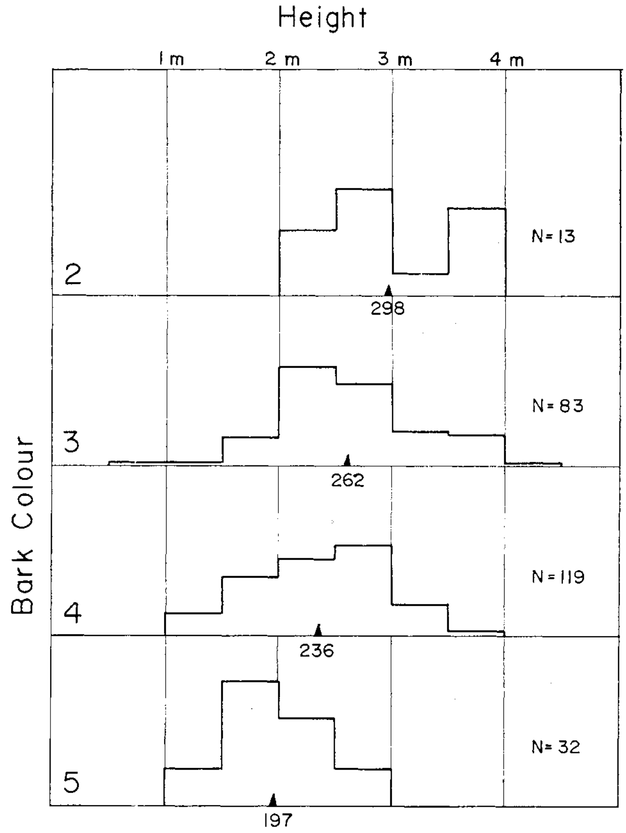

Fig. 16. Height distribution within four subpopulations of the provenance Muodoslompolo characterized by different bark colours of the terminal shoot in August. The populations have significantly different mean heights ($p < 0.001$).

The correlation between height and bark colour is clear in the three provenances (Fig. 15), but the relationship is not the same among individuals within the provenance as that between the provenances within the whole group of provenances. In the latter group the most well adapted, i.e. the local strain, grew tallest (shown by Stefansson & Sinko, 1967). The regression coefficient was negative for Muodoslompolo as expected, since a large number of the individuals terminated growth too early in the fall and therefore grew poorly. In the Söråker strain, however, which was moved northward, the regression coefficient is also negative, which would not be the case if the individuals with the earliest growth termination were the best adapted. The investigation

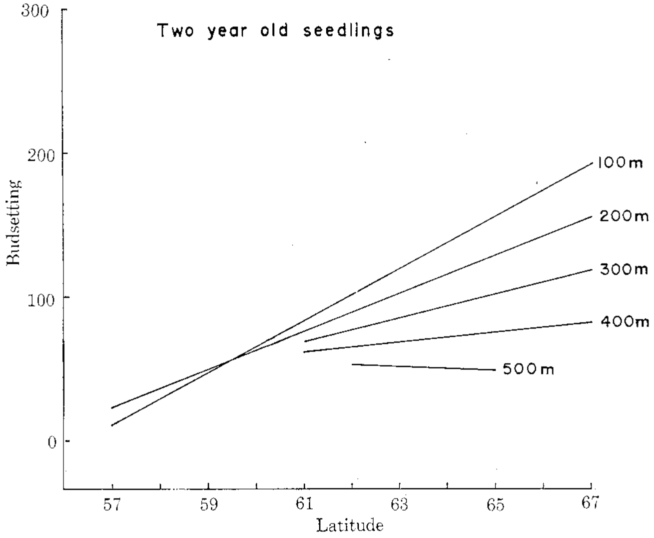

Fig. 17. Regression equation: Budsetting $=23.01(\text{Lat}-50)+$ $+0.4637\,\text{Alt}-0.04877\,\text{Alt}(\text{Lat}-50)-162.6$.

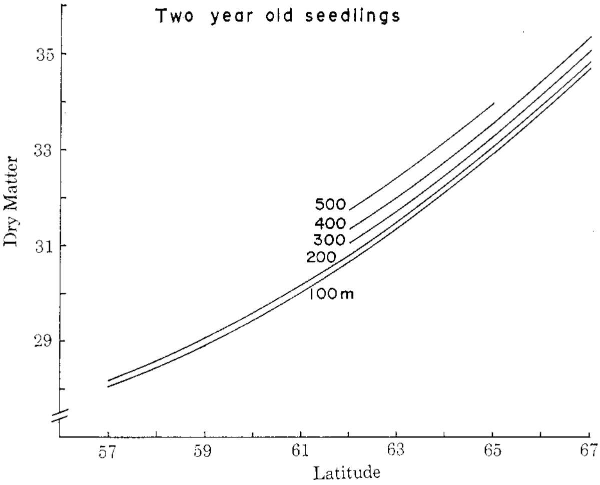

Fig. 18. Regression equation: Dry matter $= 26.63 +$ $+0.02791(\text{Lat}-50)^2+4.400\cdot10^{-6}\cdot\text{Alt}^2$.

Fig. 17—18. Regressions of annual rhythm on the latitude and altitude of seed source. Altitudinal lines are drawn only where they are represented by the material.

may have been carried out so early in the fall that even the seedlings with bark colour "2", in the Söråker strain, belonged to the group "too early".

Oksbjerg (1954) found a correlation between rate of shoot extension and size of shoot among seedlings from *Picea abies* (L.) Karst. and Dietrichson (1964a) found the same relationship among shoots within trees from *Pinus silvestris*. None of them could determine to what degree this was environmentally based or founded on genetical properties.

If the relationship found in this material were a sole effect from the microenvironment, the slopes of the regressions (Fig. 15) should be the same for the three provenances. This is not so, since the coefficients of regression differ ($p<.001$) between Muodoslompolo and Söråker but the negative slope of the under-hardy provenance Söråker indicates that the environmental influence could be considerable.

The group of seedlings with the greenest colour ("2") in the provenance from Muodoslompolo is of special interest. They amount to 5 per cent of the population and they have an actual mean height of 298 cm, which makes them not too different from the best provenances in the whole provenance trial.

If there is a genetical base for the relationship between rhythm and height, it may be possible to create strains with good growth and great hardiness by selection. This has been proposed by Shütt (1962) who found that by selection of individuals with a long annual growth cycle from a provenance from Scandinavia, a population with good growth in Germany could be obtained.

4.6 The influence on annual rhythm of altitude and latitude of seed source

A series of stepwise regressions was made with all material from the nursery and from the provenance test at Björkvattnet. Annual rhythm was used as dependent variable, and latitude and altitude as independent variables. As it was logical to expect interactions between latitude (L) and altitude (A) these variables were also inserted in the analyses in the following transformations: LL, AA, AL, L/A, A/L, 1/L, 1/A. Tables 2, 3, 5 and Fig. 17 and 18 present the final steps of the regressions in which all regression coefficients were significantly different from zero.

From these regressions it was apparent that latitude was of much higher significance for the variation in rhythm than altitude. As the

Tab. 7. Multiple regressions of survival and height on latitude and altitude of seed source. Survival and height after ten years in field. (Data from Stefansson & Sinko, 1967.)

Test site	Regression	N[a]	$tb_{1,3}$	$tb_{2,4}$	R^2	F
Suodok	$\text{Surv}=17.69\,(\text{Lat}-58.5)+0.1350\,\text{Alt}-0.01885\,\text{Alt}\,(\text{Lat}-58.5)+24.02/(\text{Lat}-58.5)-71.36$	21	8.92*** 3.28**	4.25*** 4.34***	0.95	069***
Bäckstrand	$\text{Surv}=12.89\,(\text{Lat}-58.5)+6.53\cdot 10^{-5}\cdot \text{Alt}^2-15.19$	17	19.8***	3.17***	0.87	049***
Brattfors	$\text{Surv}=9.158\,(\text{Lat}-58.5)+6.03\cdot 10^{-5}\cdot \text{Alt}^2+5.585$	21	9.95***	4.18***	0.85	052***
Björkvattnet	$\text{Surv}=19.47\,(\text{Lat}-58.5)-1.073(\text{Lat}-58.5)^2+7.900\cdot 10^{-5}\cdot \text{Alt}^2+0.3681$	21	9.19*** 2.57***	5.13***	0.95	116***
Laxå	$\text{Surv}=93.87-3.290/(\text{Lat}-58.5)$	21	2.47*		0.24	6.1*
Suodok	$\text{Height}=108.5+3.597\,(\text{Lat}-58.5)$	21	4.31***		0.50	019***
Bäckstrand	$\text{Height}=142.9-26.47/(\text{Lat}-58.5)$	17	6.32***		0.73	040***
Brattfors	$\text{Height}=86.88+20.30\,(\text{Lat}-58.5)-1.781\,(\text{Lat}-58.5)^2-170.2/\text{Alt}$	21	8.58*** 2.54***	7.99***	0.82	026***
Björkvattnet	$\text{Height}=152.3-18.86/(\text{Lat}-58.5)$	21	5.58***		0.62	031***
Laxå	$\text{Height}=142.0+14.37\,(\text{Lat}-58.5)-1.880\,(\text{Lat}-58.5)^2$	21	4.47***	6.42***	0.79	035***

[a] See Tab. 1 for description of characters.

inter-relationship between latitude and altitude in some aspects was unanticipated (discussed below) the investigation was expanded into the data for survival and height growth in the provenance test series presented by Stefansson & Sinko (1967). The survival and height were used as dependent variables in a series of regressions where latitude and altitude were the independent variables. The two latter were transformed in the same manner as described above and the results are presented in Tab. 7 and Fig. 19—23.

The regressions of rhythm and of survival generally show very high significance with R^2 up to 0.96. An exception is budsetting which shows an overall pattern very different from other rhythm variables and from survival. Budsetting is generally less related to latitude and more related to altitude than the other variables (Fig. 17).

Most of the variation in height could also be accounted for by the regressions on latitude and altitude (Tab. 7) and it is evident that latitude is the dominating cause of variation in height as well as in survival and rhythm.

Timberline in this area of Sweden is situated approximately at 900 m on 60° of latitude, descending at higher latitudes to about 500 m on 67°. The material presented in this paper has low representation above 450 m.

In most of the regressions the altitude is included in squared form, which is logical since the influence from an additional 100 m should grow as the distance to the timberline decreases. This makes it impossible to make any general statement about how much one degree of latitude equals in meters of altitude. Furthermore the latitude is in many regressions included in curvilinear form and there are also interactions present. One can only conclude that a transfer of seed one degree of latitude to the south is equal to a corresponding transfer into higher elevation by some amount that is unique for every combination of latitude and altitude. However, when numerical examples are studied in relation to the derived regressions, it is striking that the rule used hitherto, that one degree of latitude should equal 100 m of altitude (Schotte, 1923; Eneroth, 1926; Langlet, 1936; Ruden, 1960; Wiersma, 1963), does not apply to any part of this material. On the contrary the results show that 200—500 m to each degree of latitude is a more accurate figure. Langlet (1968) has also recently discussed the matter and suggested that the rule of 100 m is inappropriate.

As an example one could consider survival at Bratten (test site at lat. 64°30'N and alt. 310 m) is illustrated in Fig. 22, where a difference in seed source of one degree of latitude, in the elevation range 300—400 m, corresponds to 213 m. In the elevation range of 200—300 m the figure is 299 m and in the range 100—200 m it is 533 m. Because of limitations of the material no interpretations should be made outside these elevation ranges. This example is chosen because it is also representative for most of the other regressions with survival.

It is of great interest that the variation in dry matter of needles illustrated in Fig. 18 shows the same result. Furthermore, a study of non-significant steps of the regression with bark colour in the two-year-old material, where altitude is included (not presented), also

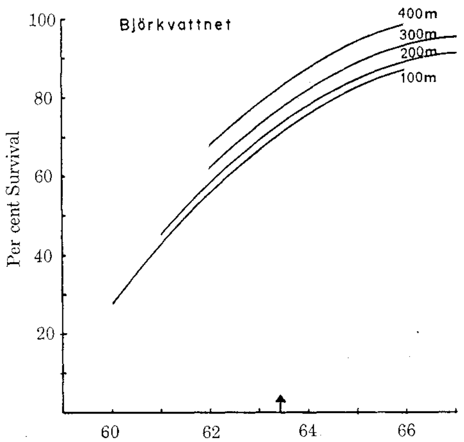

Fig. 19. Björkvattnet. Regression equation: $\text{Survival} = 19.47\,(\text{Lat} - 58.5) - 1.073\,(\text{Lat} - 58.5)^2 + 7.900 \cdot 10^{-5} \cdot \text{Alt}^2 + 0.3681$; $R^2 = 0.95$.

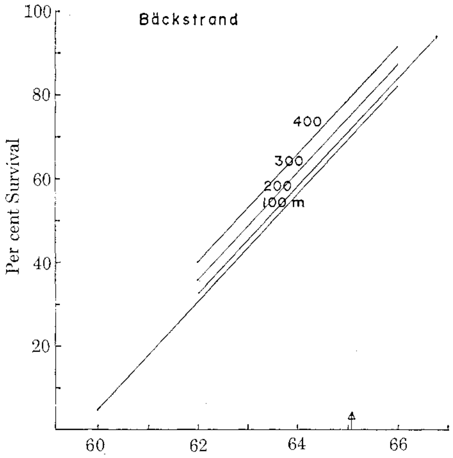

Fig. 20. Bäckstrand. Regression equation: $\text{Survival} = 12.89\,(\text{Lat} - 58.5) + 6.53 \cdot 10^{-5} \cdot \text{Alt}^2 - 15.19$; $R^2 = 0.87$.

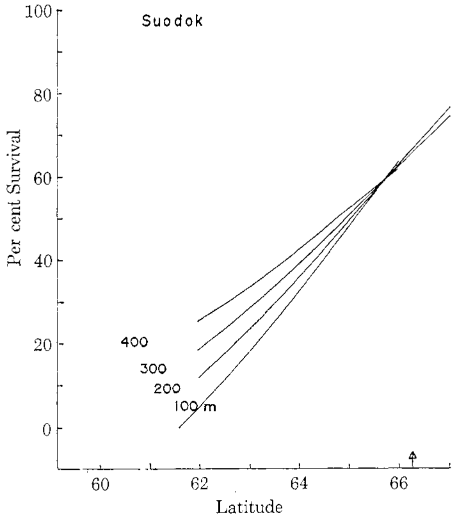

Fig. 21. Suodok. Regression equation: $\text{Survival} = 17.69\,(\text{Lat} - 58.5) + 0.1350\,\text{Alt} - 0.01885\,\text{Alt}\,(\text{Lat} - 58.5) + 24.02/(\text{Lat} - 58.5) - 71.36$; $R^2 = 0.95$.

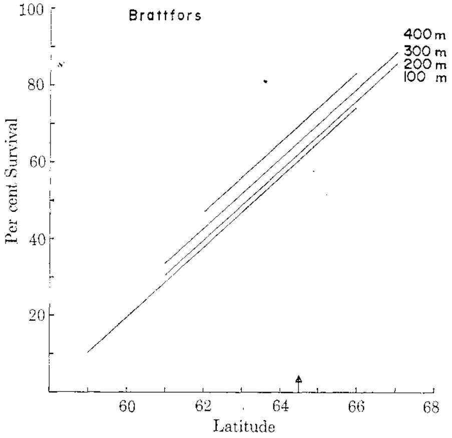

Fig. 22. Brattfors. Regression equation: $\text{Survival} = 9.158\,(\text{Lat} - 58.5) + 6.03 \cdot 10^{-5} \cdot \text{Alt}^2 + 5.585$; $R^2 = 0.85$.

Fig. 19—22. Regressions of per cent survival after ten years in the field on the latitude and altitude of seed source at four localities. The latitudes of the test sites are indicated by arrows.

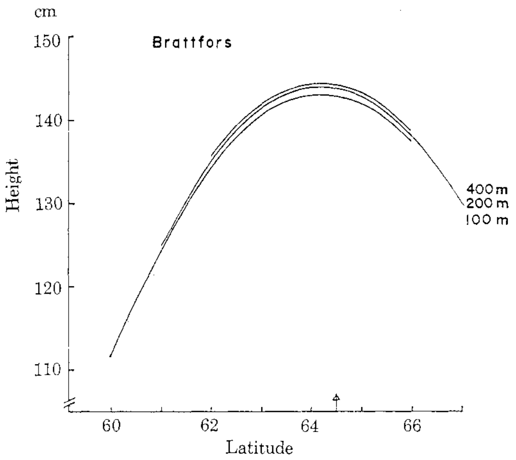

Fig. 23. Regression of height after ten years in field on the latitude and altitude of seed source. The latitude of the test site Brattfors is indicated by an arrow. Regression equation: Height = 86.88 + 20.30 (Lat - 58.5) - - 1.781 (Lat - 58.5)^2 - 170.2/Alt.

shows approximately the same relationship between latitude and altitude.

The regression with height in Brattfors (Fig. 23) shows that the altitude of seed source had a low influence on the variation in height growth. Among the best growing provenances a choice of a provenance from an altitude of 200 m instead of 100 m corresponds to an increase in height of only 0.56 per cent.

4.7 The use of annual rhythm in progeny testing

In the testing of artificially produced populations, economic considerations will always limit the number of test sites. This means that many of the progenies cannot be tested in the environment they require for optimum growth and survival. Rhythm studies are of great value in overcoming these difficulties of testing.

A possible procedure would be to enclose in every progeny test a series of standard provenances. The rhythm studies should include at least one of the methods which are most dependent on latitude, but should also include budsetting which is to a high degree related to altitude. With these results available it is possible by multivariate comparison to pinpoint to what latitude and altitude a certain progeny would be best adapted.

In addition, the internal variation between individuals within the population must be measured and taken into account when the average performance of the population is considered.

With this information it should then be possible to use the production and survival figures for the enclosed standard provenances plus the sort of information from practical provenance tests, that is presented in Fig. 22 and 23 (survival and height at Brattfors), and combine them to obtain an estimate of potential loss of production due to the fact that a certain population is not adapted to the latitude and altitude of the test site.

It should be stressed that the series of provenances of known origin must be enclosed and that these series must represent the geographic district of interest very well. The measurement of annual rhythm will always give only relative values that are totally dependent on the time of measurement. Furthermore, one must expect interactions with the testing environment to influence the result so that expected relative differences between population means may be reversed. An example of this is the budsetting results in the two-year-old nursery stock.

These circumstances also make it necessary to measure the rhythm by many different methods and to analyse the data by multivariate statistical methods to enable comparisons of many variables at once, and to find similarities as well as significant differences in complete profiles of annual rhythm.

4.8 Future studies of annual rhythm

As has been proved both in work by Langlet (1936) and Dietrichson (1961, 1964 a, b, 1968) and by the comparisons in this study between rhythm and survival in the provenance tests, it is possible to design powerful tools for the description of relative hardiness of seedlings and populations. The crude way in which the methods have been used here was chosen because the objective was to obtain a general idea of the potentials of different kinds of rhythm studies. Activity in this field is large and some equipment and techniques described in existing literature should be mentioned here.

For measurement of electrical impedance a special apparatus has been designed for use in the field (Brach & Mason, 1965). Successful measurements of differences in vitality during different parts of the summer season were obtained with another apparatus described by Sinyukhin & Rutkovskii (1965) that measures the biological potentials.

They recommend it for diagnosis of the physiological state of woody plants in phytopathological and plant breeding investigations. Fensom (1963) reported on the bioelectrical potentials of plants and their functional significance.

The vitality or degree of activity can probably also be measured by the radiation balance of the needles. The author studied the heat emittance from potted spruce seedlings with the AGA Thermovision System (Hagner, 1969) and found that the temperature varies considerably with the physiological status of the plant, and that activity and vigour may be measured this way.

Shoot and needle development could possibly be measured very effectively with photographic documentation. Bark colour measurement could be made objectively by a photographic technique or by a spectro photometric analysis, such as has been used by Tralau (1958) for colour test of spruce needles.

The rhythm of diameter growth can be studied with some recently proposed methods. Neilson (1966) and Wolter (1968) have described techniques for mechanical marking of the xylem by injuring the cambium. A more sophisticated method that should cause no injury to the plant would be to tag the wood with C^{14}. Waisel & Fahn (1965) have described the use of this isotope for determination of cambial activity and Balatinecz, Forward & Bidwell (1966) have described the translocation of assimilated $C^{14}O_2$ into xylem on one-year-old *Pinus banksiana*. The author has conducted an experiment on one-year-old *Pinus contorta* with parallel C^{14} and mechanical marking of the xylem. The results show that both methods tag approximately the same cells and that the ring of incorporated C^{14} is narrow enough to enable measurement of the peak intensity to within a few tracheids.

Such studies on the rhythm of diameter growth would enable us to do the tagging many times a year during many years, after which only one wood sample would need to be examined. It could give us information not only about the pattern of seasonal development but also about important wood properties such as per cent latewood and tracheid characters.

5. Conclusions

Methods

It has been confirmed that the following methods for registration of annual rhythm of provenances are efficient: 1. Measurement of the shoot extension (Mork, 1941; Dietrichson, 1964a). 2. Measurement of needle extension (Langlet, 1959). 3. Measurement of lignification of outer woodmantle (Ladefoged, 1952; Wardrop, 1957; Dietrichson, 1964a). 4. Observation of budding. 5. Determination of dry matter of needles (Langlet, 1936). 6. Observation of bark colour (Hagner, 1966; Stefansson & Sinko, 1967). Measurement of the water content of the cambial zone by electric resistance gave logical differences among provenances but proved to be a very unreliable method.

Methods 1, 2, 5 and 6 gave very good results when applied to 18-year-old trees while methods 1, 3, 4, 5 and 6 were useful with two- and three-year-old nursery stock.

From a practical point of view the observation of bark colour produced an outstanding result since this method gave easily obtained values for the single seedling and tree without interference with its metabolism. The usefulness of the method on young as well as on older material enhances its value.

Annual rhythm and hardiness

Regressions of survival after ten years in a harsh climate on annual rhythm of provenances showed that a very accurate estimate of the relative hardiness can be obtained by measurement of the rhythm. Up to 96 per cent of the variation in survival could be accounted for by the regressions.

Annual rhythm of the single tree and the relationship to height

Regression analyses showed a relationship between height and rhythm for the single tree within the provenance. If this relationship has a genetic base there is a potential gain from selection among trees within a provenance.

The influence on annual rhythm of latitude and altitude of seed source

There is a complicated interaction between altitude and latitude of seed source. It was concluded that a transfer of seed one degree of latitude to the south is equal to a corresponding transfer into higher elevation by some amount that is unique for every combination of latitude and altitude. In general the rhythm varied with latitude and altitude in a similar way to survival. An exception was the trait bud-setting which was affected more by altitude than other traits.

The influence by an additional unit of altitude increases towards timberline.

The rule used hitherto, that one degree of latitude should be equal to one hundred meters of altitude, does not apply to the material investigated here. These results show that 200—500 m to each degree of latitude would be a more accurate figure.

The use of annual rhythm in progeny testing

The results show that the relative hardiness may be estimated by measurement of the annual rhythm of fairly young seedlings. If methods are further improved, a measurement of the mean character of the population and the variation among its individuals should make it possible to predict which climate an artificially-produced population would be adapted to provided that the progeny test contained a series of standard provenances with known origin. It was suggested that complete knowledge about the potential production of tested progenies could not be obtained unless a description of the rhythm could be the base for estimated loss of production resulting from the lack of adaptation by the individual tree to the testing environment.

ACKNOWLEDGEMENTS

An important part of the material used in this study originates from a provenance test series which was designed by professor Eric Stefansson. He has permitted me to use his data from a revision in 1960, for which I thank him.

The field work was paid for by the Swedish fund "Fonden för Skoglig Forskning" and most of the data processing and work with the manuscript was done at the Canadian Department of Fisheries and Forestry, Calgary, Alberta.

LITERATURE

BALATINECZ, J. J., Forward, D. F. & Bidwell, R. G. S. 1966: Distribution of photoassimilated $^{14}CO_2$ in young Jack pine seedlings. Can. J. Bot., 44, pp 362—365.

BRACH, E. J. & MASON, W. J. 1965: A stable multivibrator for measuring impedance of plant leaves and stems for evaluating of winter hardiness. Can. J. Bot., 43, 8, pp 995—997.

DIETRICHSON, J. 1961: Breeding for frost resistance. Silvae Genetica, 10, 6, pp 172—179.

— 1964a: Proveniensproblemet belyst ved studier av vekstrytme og klima (The provenance problem illustrated by studies of growth rhythm and climate). Medd. Norske Skogsf. Vesen, 19, 71, 5, pp 501—656.

— 1964b: The selection problem and growth rhythm. Silvae Genetica, 13, 6, pp 174—184.

— 1968: Klimaskader, vekstrytme og höjdeutvickling (Climatic damage, growth rhythm and height development). Medd. Norske Skogsf. Vesen, 88, 2, pp 141—158.

ENEROTH, O. 1926: Studier över risken vid användning av tallfrö av för orten främmande proveniens (A study on the risks of using in a particular district pine-seed from other sources). Medd. Stat. Skogsf., 23, pp 1—58.

FENSOM, D. S. 1963: The bioelectrical potentials of plants and their functional significance. Can. J. Bot., 41, pp 831—851.

HAGNER, M. 1966: Metoder för bestämning av härdigheten hos svensk tall samt en studie över härdighetens nedärvning (Methods for evaluation of hardiness of pine from Sweden and a study of the inheritance of hardiness). M. Sc. thesis (in Swedish), Royal Coll. For. Stockholm.

— 1969: Thermal mapping of conifer seedlings—a useful method in pathological and physiological research. Zeitschr. f. Pflanzenphysiologie, 61, 4, pp 322—331.

LADEFOGED, K. 1952: The periodicity of wood formation. Biol. Skr. Danske Vidensk. Selskab, 7, 3.

LANGLET, O. 1936: Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Medd. Stat. Skogsf., 29, pp 219—470.

— 1959: A cline or not a cline—A question of Scots pine. Silvae Genetica, 8, 1, pp 13—22.

— 1968: Om klimatiskt betingade gränser för förflyttning av tallprovenienser till skogsodlingsplatser i Norrland (On climatic limits for transfer of Scots pine provenances for silviculture in northern Sweden). Sveriges Skogsv. Förb. Tidskr., 6, pp 503—532.

LEVITT, J. 1956: The hardiness of plants. (Academic Press) New York.

MERYMAN, H. T. 1966: Cryobiology. (Academic Press). New York.

MORK, E. 1941: Om sambandet mellom temperatur og vekst. Medd. Norske Skogsf. Vesen, 8, pp 1—89.

NEILSON, R. 1966: Puncture technique for marking xylem internally. Faculty For. Univ. Toronto.

OKSBJERG, E. 1954: Om udspringstid og skudsstraekning i grankulturer. Hedeselskapets Tidskrift, 75, pp 49—55.

RUDEN, T. 1960: Rassenforschung und Pflanzenzüchtung in der norwegischen Forstwirtschaft. Sborn. Csl. Akad. Zemed. Ved (Lesn.), 6, 33, pp 651—662.

SCHOTTE, G. 1923: Tallfröets proveniens — Norrlands viktigaste skogsodlingsfråga. Medd. Stat. Skogsf., 20, pp 305—400.

SCHÜTT, P. 1962: The selection of fast growing *Pinus silvestris* seedlings from a long-day provenance. Silvae Genetica, 11, 2, pp 39—42.

SINYUKHIN, A. M. & RUTKOVSKII, I. V. 1965: Practical applications of an electrophysical method of recording the vitality of woody plants. (UDC 581.1.03.036) Fiziologiya Rastenii, 13, 2.

STEFANSSON, E. & SINKO, M. 1967: Försök med tallprovenienser med särskild hänsyn till norrländska höjdlägen (Experiments with provenances of Scots pine with special regard to high-lying forests in northern Sweden). Stud. For. Suecica 47.

TRALAU, H. 1958: Beiträge zur Kenntnis der Variabilität der Fichte. III Farbcharakteristika. (Variability in Spruce. III Colour characteristics). Phyton, Buenos Aires, 11, 1, pp 63—74.

TUMANOV, I. I., KRASAVCEV, O. A. & HVALIN, N. N. 1959: Increasing the frost resistance of Betula verrucosa and Ribes nigrum to −253°C by hardening. (For. Abstr. 21 No 215). Dokl. Akad. Nauk. SSSR, 127, 6.

WAISEL, Y. & FAHN, A. 1965: A radiological method for the determination of cambial activity. Physiologia Plantarum, 18, 1, pp 44—46.

WARDROP, A. B. 1957: The phase of lignification of wood fibers. Tappi, 40, pp 225—243.

WIERSMA, J. H. 1963: A new method of dealing with results of provenance tests. Silvae Genetica, 12, 6, pp 200—205.

WILNER, J. KALBFLEISCH, W. & MASON, W. J. 1960: Note on two electrolytic methods for determining frost hardiness of fruit trees. Can. J. Plant Sci. 40, pp 563—565.

WILNER, J. 1961: Relationship between certain methods and procedures of testing for winter injury of outdoor exposed shoot and roots of apple trees. Can. J. Plant Sci. 41, pp 309—315.

WOLTER, K. E. 1968: A new method for marking xylem growth. Forest Science, 14, 1, pp 102—104.

Sammanfattning

En genekologisk undersökning av årsrytmen hos *Pinus silvestris* L.

Introduktion

Proveniensforskningen i Skandinavien och Finland har visat att den genetiskt betingade härdigheten hos plantmaterialet är av avgörande betydelse för våra planteringar med tall. Det är därför av stor vikt för framtida proveniensforskning och skogsträdsförädling att en mätning av unga plantors relativa härdighet kan genomföras.

Avsikten med denna undersökning var att finna lätt uppmätbara karaktärer, som speglar årsrytmen hos varje enskilt träd, samt att studera rytmens samvariation med härdigheten hos fältprövat material. Avsikten var vidare att undersöka vilka av ursprungsortens parametrar, som bäst samvarierade med härdigheten.

Material

Studierna har utförts på tallplantor i tre olika åldrar i avsikt att utarbeta metoder för uppskattning av årsrytmen, vilka kan tillämpas både i plantskolor och i fältförsök.

I ett proveniensförsök i Björkvattnet, Jämtland, följdes artonåriga träd. Detta försök ingick i en serie på fem, förlagda till skilda områden mellan 59:e och 66:e breddgraden i Sverige. Samtliga försök innehöll delar av samma plantmaterial. I ett annat försök i denna serie, förlagt till ett område med synnerligen strängt klimat, Bäckstrand, varierade överlevnaden starkt och här erhölls den verkliga klimatiska härdigheten hos de prövade provenienserna (Stefansson & Sinko, 1967) (tabell I, II, figur 1).

I en plantskola i mellersta Norrland, latitud 62, studerades 64 provenienser treåriga omskolade plantor och 48 provenienser tvååriga oomskolade plantor. Båda dessa proveniensserier hade insamlats i Sverige (tabell III, IV).

Metoder

Fältmetoder

Följande metoder prövades:

Lignifieringen i stamvedens perifericeller i september. Frekvensen av lignifierade/olignifierade celler registrerades (figur 2) (Ladefoged, 1952; Wardrop, 1957; Dietrichson, 1961, 1964a).

Skottskjutningen följdes genom fyra skilda mätningar under säsongen, dvs. före och efter skottskjutningen samt två gånger under sträckningsperioden. Vid databehandlingen användes den relativa skottlängden vid andra mätningen samt den relativa förlängningen mellan de två mätningarna i mitten av säsongen (Dietrichson, 1964a).

Barrlängden på ett terminalskott uppmättes i mitten av sträckningsperioden och jämfördes med de fullbildade barren på det skott som utvecklats föregående år (Langlet, 1959).

Knoppsättningen hos plantskoleplantorna registrerades som en frekvens av plantor med synlig terminalknopp.

Barkfärgen på nybildade skott övergår i augusti från klargrön till mörkbrun. Den beskrevs efter okulärbedömning i en 5-gradig skala, där 5 representerade materialets brunaste och 1 dess grönaste färg (Hagner, 1966; Stefansson & Sinko, 1967).

Torrsubstanshalten i nybildade barr bestämdes genom ugnstorkning under 4 timmar i 105°C (Langlet, 1936).

Elektrisk resistens mättes med en relativt enkel apparat, som konstruerats för detta ändamål. Två stålelektroder infördes med 5 mm mellanrum i kambievävnaden strax under cotyledonerna på tvååriga plantor på ett sådant sätt att elektriciteten leddes parallellt med ledningsbanorna (Wilner *et al.*, 1960; Wilner, 1961; Brach & Mason, 1965).

Statistiska metoder

De flesta analyserna har utförts i datamaskin med ett standardprogram för stegvis regressionsanalys. Med hänsyn till att de biologiska förlopp som studerats företrädesvis har krökta samband infördes variablerna i enkel och kvadrerad form. I de multipla regressionerna, i vilka latitud (L) och altitud (A) ingick som oberoende variabler, kunde komplicerade samspel förväntas, varför variablerna även infördes transformerade på följande sätt: LL, AA, AL, A/L, L/A, 1/L, 1/A.

Resultat och diskussion

Genom en serie regressioner studerades förhållandet mellan proveniensernas överlevnadsprocenter efter 10 år i Bäckstrands-försöket, där det stränga klimatet förorsakat stor avgång, och den årsrytm som kunnat fastställas genom mätningar på plantor i Björkvattnet-försöket. Det konstaterades att upp till 97 procent av variationen i överlevnad kunde förklaras av sambandet med årsrytmen (tabell 1, figur 3).

Detta innebär med andra ord att man t. ex. genom en okulärbedömning av barkfärgen på 144 individer per proveniens med nära 100-procentig säkerhet kan beräkna den härdighet som avgör proveniensernas överlevelseförmåga i fält.

Årsrytmen hos plantmaterial i tre olika åldrar jämfördes genom regressionsanalys med latituden och altituden för proveniensernas hemorter. Med undantag av lignifieringen i Björkvattnet-materialet och elektrisk resistens hos de tvååriga plantorna konstaterades starkt signifikanta samband med latituden (tabell 2, 3, 5, figur 4, 5, 6, 7, 9, 10, 11, 12). Endast i två fall var sambandet med altituden signifikant nämligen för torrsubstans och knoppsättning hos tvååriga plantor (tabell 3, figur 17, 18).

Samvariationen mellan årsrytm, överlevnadsprocenter och geografiska parametrar hos ursprungsorten bekräftar Langlets (1936) resultat, som visade att en genetisk anpassning till det lokala klimatet har skett hos tall. De likartade sambanden mellan årsrytm och ursprungsort i de skilda planteåldrarna visar att den relativa härdigheten eller klimatanpassningen kan bedömas redan på unga plantor.

För att söka klarlägga om rytmen samvarierade i högre grad med någon annan faktor än med latituden, utfördes en korrelationsanalys på barkfärg, latitud, altitud, vegetationsperiod (antal dagar med temp. $\geq +6°C$) och kontinentalitet (temp.skillnad juli—januari) (tabell 6). Både på 18-åriga och 2-åriga plantor visade latituden den största korrelationen med barkfärgen. (Jfr Langlet, 1936.)

Av detta förhållande kan man sluta sig till att skottskjutningscykeln och förändringen i barkfärg, lignifiering och torrsubstans är starkt anpassade till fotoperioden på ursprungsorten (=latituden), medan tidpunkten för knoppanläggningen hos tvååriga plantor dessutom är avpassad efter den klimatfaktor som förändras med höjden över havet.

En bedömning av prövade metoder gjordes med ledning av de statistiska resultaten och med hänsyn tagen till de praktiska svårigheterna i samband med mätningarna. Barkfärgsbedömningen kom därvid att te sig som den bästa, eftersom man härigenom snabbt erhåller värden för enskilda träd utan laboratorieanalyser och utan att göra anatomiska ingrepp på plantorna. Denna metod kan dessutom lika väl användas på både 2-, 3- och 18-åriga plantor. Elektrisk resistens visade sig vara den sämsta metoden.

Sambandet mellan höjd och rytm hos träd inom proveniens undersöktes i Björkvattnet inom följande tre provenienser: Muodoslompolo (247 träd), Lövånger (51 träd) och Söråker (182 träd) (figur 15). Signifikanta regressionssamband konstaterades vilka visar att sambandet såvida det har ett genetiskt ursprung bör ge möjlighet till förädlingsvinster genom selektion för rytm inom proveniens (figur 16).

Samspelet mellan latitud och altitud visade sig vid studium av årsrytmen avvika från det som tidigare antagits (tabell 3, figur 17, 18) (Schotte, 1923; Eneroth, 1926; Langlet, 1936 Ruden, 1960; Wiersma, 1963; Langlet, 1968). För att utreda om detta mönster överensstämde med variationen i verklig härdighet, infördes överlevnadsprocenterna, vilka registrerats i fem av fältförsöken i den 18-åriga serien, (Stefansson & Sinko, 1967) såsom beroende variabler i multipla regressionsanalyser (tabell 7, figur 19—23). Den verkliga härdigheten visade ett variationsmönster motsvarande det hos torrsubstanshalten och undersökningen bekräftade att en breddgradsförändring snarare motsvaras av 200—500 meters altitudförändring än av det värde på 100 meter som man tidigare antagit gälla. I verkligheten ökar höjdlägets relativa inflytande mot trädgränsen och samspelet är så komplicerat att betydelsen av en breddgradsförändring troligen är specifik för varje kombination av breddgrad och höjdläge.

Ett studium av årsrytmen vid avkommeprövning borde öka förutsättningarna för tidiga och korrekta slutsatser beträffande avkommornas härdighet och tillväxt, under förutsättning att en serie ursprungsdokumenterade provenienser ingår i fältförsöken samt att sådana metoder användes som möjliggör beräkning av rytmen hos såväl populationer som individer. Härigenom skulle hänsyn kunna tagas till bristande anpassning hos populationen samt till populationens inre spridning i anpassning. Ytterligare forskning krävs för att skapa lämpliga metoder för bedömning av enskilda trädindividers årsrytm.

Framtida studier av årsrytmen bör kunna effektiviseras betydligt genom utnyttjandet av modern teknik, t. ex. inom följande områden: Colourimetri (Tralau, 1958), Elektrisk potential (Brach & Mason, 1965; Sinyukhin & Rutkovskii, 1965; Fensom, 1963), värmestrålning (Hagner, 1969), radioisotopi (Waisel & Fahn, 1965; Balatinecz *et al.*, 1966).

Tables

Tab. I. Data concerning provenance field tests and nursery test site.

Age	Name	Environment	Lat °N	Long °E	Alt m	Grow seas[a]	Cont[b] °C	Rep[c]	Prov[d]	Design[e]
18	Suodok	pasture	66°14′	20°25′	150	119	30.0	5	21	Yates
18	Bäckstrand	forest	65°04′	16°26′	500	99	26.0	4	17	Fisher
18	Brattfors	forest	64°31′	18°24′	310	122	24.5	5	21	Yates
18	Björkvattnet	forest	63°26′	16°02′	460	121	27.0	4	21	Fisher
18	Laxå	forest	59°00′	14°35′	100	165	19.5	5	21	Yates
2	Sundmo	nursery	63°30′	16°30′	250	131	25.5	1	48	—
3	Sundmo	nursery	63°30′	16°30′	250	131	25.5	1	64	—

a Number of days per year with a mean daily temperature above 6°C.
b Temperature difference July mean—Jan mean.
c Number of replications.
d Number of provenances tested.
e Experimental design: Yates = Yates incomplete blocks. Fisher = Fishers complete randomized blocks.

Tab. II. Eighteen-year-old trees. Data concerning environment of seed source, annual rhythm and survival after ten years in field.

	Lat.[a]	Alt.m	Grow[b]	Cont.[c]	Bark[d]	Needl[e]	Shoot[f]	Xylm[g]	Surv.[h]	Drym[i]
Muodoslompolo	68.07	275	102	28.2	4.20	66.4	63.3	08.85	—	40.88
Lainio	67.58	325	112	29.1	4.06	61.3	66.1	06.10	—	41.61
Kompelusvaara	67.05	210	111	27.0	3.64	54.4	54.8	10.85	93.4	41.79
Björkfors	65.92	030	125	28.0	3.55	56.7	—	08.60	91.2	40.74
Moskosel	65.87	340	113	26.0	3.45	53.0	—	11.35	89.6	40.29
Norrsele	65.60	360	111	24.4	3.20	52.9	46.1	10.90	87.9	41.11
Nordanås	65.75	420	112	25.0	3.26	50.0	—	08.20	91.9	39.90
Kolerträsk	65.57	275	117	27.5	3.24	51.0	—	07.40	88.4	39.93
Svanmyren	64.62	350	121	25.0	2.70	46.9	39.3	10.50	—	40.29
Brännberg	65.77	100	124	27.8	2.73	51.5	—	09.50	75.7	39.43
Lövånger	64.37	012	129	23.1	2.65	48.2	—	10.90	68.7	39.33
Laxbäcken	64.63	345	120	25.0	2.56	40.3	40.2	08.20	66.5	39.77
Junsele	63.78	250	131	26.6	2.34	40.8	36.8	07.50	44.1	39.55
Ramsele	63.53	250	131	25.5	2.27	40.8	39.1	07.10	56.4	39.02
Hede	62.41	409	120	25.0	2.07	35.9	—	07.75	45.7	39.68
Söråker	62.53	075	140	23.0	1.81	35.3	36.9	13.30	30.5	39.26
Ånge	62.50	170	138	25.0	1.74	40.0	35.0	15.00	11.5	38.67
Mora	61.00	200	141	23.1	1.09	34.5	25.6	14.60	—	37.52
Håbol	59.00	140	159	19.5	—	32.9	34.3	12.45	01.8	36.75
Laxå	59.03	090	160	19.8	—	29.4	—	—	—	—
Käringboda	58.90	050	167	19.5	—	34.3	—	—	—	—

a Degrees and decimals. *b* Number of days with mean temp above +6°C. *c* Continentality, temp diff July mean—Jan mean. *d* Bark colour mean 5/8, 23/8, 27/8. *e* Needle length 9/7 in per cent of full. *f* Shoot length 16/6 in per cent of full. *g* Xylem, per cent not fully lignified cells 1/10. *h* Per cent survival 10 years after planting at Bäckstrand. *i* Per cent dry matter of needles 15/10. *d, e, f, g, i* = data obtained at Björkvattnet 1965.

Tab. III. Two-year-old seedlings. Data concerning environment of seed source and annual rhythm measured in the nursery.

Lat[a]	Alt[b]	Grow seas[c]	Cont[d]	Bark[e]	Shoot[f]	Shoot[g]	Drym[h]	El[i]	Xylm[j]	Bud[k]
55.83	038	182	17.2	0.34	21.0	34.0	27.88	—	30.75	002
56.25	050	182	17.5	0.33	—	—	—	—	—	002
56.85	008	189	17.5	0.69	21.0	36.0	29.20	25.85	29.75	018
57.50	209	161	18.8	0.71	23.5	39.0	28.44	—	31.05	036
57.25	018	174	17.2	0.49	21.5	33.5	27.19	—	33.25	025
58.05	165	166	18.8	0.31	—	—	—	—	—	011
58.75	060	169	19.5	0.30	14.5	35.0	28.81	24.86	18.90	000
59.13	160	165	19.6	0.81	30.0	33.0	30.16	—	15.15	064
60.17	290	149	22.1	0.74	24.0	37.5	29.86	—	13.20	020
60.07	050	157	20.9	0.67	19.5	31.5	30.16	27.11	13.40	035
61.08	415	145	22.2	1.13	—	—	—	—	—	013
61.00	150	150	21.3	0.96	—	—	—	—	—	096
62.50	700	100	22.2	1.02	39.5	20.5	32.76	—	10.25	007
62.08	560	110	23.7	0.87	33.7	26.3	32.13	—	07.80	004
62.50	450	132	25.0	0.73	—	—	—	—	—	115
62.50	370	132	25.0	1.23	—	—	29.96	22.56	—	188
62.50	350	130	25.1	0.73	—	—	—	—	—	106
62.50	376	132	25.0	0.85	—	—	—	—	—	112
62.50	350	132	25.0	0.73	—	—	—	—	—	022
62.90	330	130	22.0	0.98	—	—	—	—	—	208
62.55	220	135	23.7	0.78	37.0	25.5	31.18	—	12.35	114
62.50	100	135	23.5	0.69	33.5	37.5	30.51	23.15	09.95	029
62.58	050	139	22.0	0.71	27.0	29.5	30.97	—	08.95	047
63.00	425	133	23.5	0.89	—	—	—	—	—	032
63.33	370	130	22.0	0.89	—	—	—	—	—	081
63.50	250	120	24.5	0.98	40.0	27.5	31.21	—	07.05	096
63.50	130	131	23.5	0.76	—	—	—	—	—	112
63.50	135	131	23.5	1.25	38.0	30.5	32.66	—	10.00	130
64.47	500	111	24.2	1.49	50.0	25.5	33.49	—	07.60	056
64.47	260	127	25.3	1.31	43.5	22.5	32.91	—	09.30	073
64.50	080	128	24.0	0.98	40.0	26.0	30.88	—	11.60	145
65.50	530	117	25.6	1.91	38.8	19.5	36.05	—	08.35	007
65.93	420	111	24.6	1.57	44.5	26.5	33.68	22.29	09.10	077
65.62	210	124	26.7	1.68	43.0	17.0	32.00	—	08.20	088
65.87	015	127	27.5	2.39	57.5	21.5	34.00	22.54	09.15	260
66.00	440	111	25.9	2.33	—	—	—	—	—	035
66.05	300	110	28.0	2.50	—	—	—	—	—	122
66.05	280	110	28.0	2.51	60.0	19.0	35.01	—	06.60	139
66.48	150	120	28.2	2.23	63.0	22.5	34.43	—	08.40	208
66.50	050	120	28.1	1.88	53.0	22.0	34.59	23.00	07.75	300
67.50	320	108	29.0	2.43	—	—	—	—	—	108
67.50	350	098	27.0	3.38	46.5	21.3	35.95	22.03	09.70	062
67.27	250	112	27.5	2.84	61.0	19.0	34.55	—	06.80	034
67.30	200	112	28.0	2.78	52.0	18.5	35.61	—	07.05	132
67.05	145	112	27.5	2.40	—	—	—	—	—	103
68.00	390	096	27.6	3.70	48.6	21.0	38.94	24.36	06.95	200
68.00	260	100	28.6	3.02	46.5	23.8	36.81	—	08.70	150
68.00	360	100	28.0	2.83	—	—	34.01	—	—	106

a Degrees and decimals. *b* Meters above sea level. *c* Number of days per year with temp above +6°C. *d* Continentality, temp diff July mean—Jan mean. *e* Bark colour mean 4/8, 16/8. *f* Shoot length 15/6 in per cent of full. *g* Shoot elongation between 15/6 and 8/7 in per cent of full. *h* Dry matter content of needles 15/10. *i* Electrical resistance of stem 26/10. *j* Xylem, relative number of unlignified cells 30/9. *k* Relative figure for per cent seedlings with buds. Sum of observations 12/7, 20/7, 29/7.

Tab. IV. Three-year-old seedlings. Data concerning seed source and annual rhythm measured in the nursery.

Lat[a]	Alt[b]	Xylm[c]	Bark[d]
65.50	250	—	1.97
66.50	250	—	3.03
67.50	250	—	3.50
65.50	050	—	2.80
65.50	150	—	1.77
66.50	050	—	3.23
66.50	150	—	3.23
66.50	325	—	2.83
66.50	375	—	3.00
66.50	425	—	3.43
66.50	475	—	3.17
66.50	525	—	2.70
67.50	150	—	3.43
67.50	325	—	3.53
67.50	375	—	2.67
67.67	410	—	3.00
68.50	250	—	3.20
68.50	300	—	3.27
65.50	325	—	3.23
64.50	375	26.4	2.63
64.50	250	26.4	2.13
64.50	050	32.1	1.87
64.50	150	36.7	2.00
64.50	325	32.1	2.33
64.50	425	30.1	2.27
64.50	475	35.5	2.83
65.50	325	29.2	2.23
65.50	375	28.2	2.00
65.50	425	25.2	2.90
65.50	475	24.7	2.63
65.50	525	22.1	2.80
62.50	250	38.8	1.73
63.50	250	34.4	1.83
62.50	150	43.9	1.73
62.50	325	44.2	1.43
62.50	375	43.9	1.50
62.50	425	41.7	1.87
63.50	050	40.0	2.00
63.50	150	38.0	2.07
63.50	325	32.1	1.70
63.50	375	37.7	1.80
62.50	475	51.1	1.83
62.50	550	41.0	1.60
63.50	425	45.1	1.53
61.00	250	67.3	1.37
60.00	375	68.5	1.30
60.50	050	65.7	1.07
60.50	150	63.6	1.03
60.50	250	60.6	1.23
60.50	425	66.7	1.03
60.50	525	62.8	1.20
60.50	575	60.7	1.37
61.50	050	60.3	1.53
61.50	325	64.0	1.30
61.50	375	61.6	1.17
61.50	425	66.1	1.27
61.50	475	66.1	1.30
61.50	525	71.7	1.33
61.50	575	64.1	1.33
61.50	625	67.7	1.23
62.50	575	67.3	1.27
62.50	625	63.2	1.40
60.50	350	59.5	1.20
60.50	450	57.7	0.97

[a] Degrees and decimals. [b] Meters above sea level. [c] Xylem, relative number of unlignified cells. A mean of measurements 4/9 and 28/9. [d] Bark colour 18/8.