The Selection Problem and Growth-Rhythm

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Introduction

Since variation in economic characters of our forest trees has not been proved to be caused by genetic drift, and furthermore that the variation of a number of characters both of Scots pine (Pinus *silvestris)* and Norway spruce (Picea abies) has been established to be very closely clinal (LANGLET 1936, and others), one has to take the stand-point that selection is an important factor in the development of geographic races, and often swamps the effect of gene-exchange between different populations. Few studies have been accomplished on the selection problem in forest trees. This is because of its complex nature as selection factors can operate through the whole lifetime of the tree, from the pollination of the flower until maturity. In addition trees which contribute most to the next generation by heavy seed production will also have a selective advantage which is a further complicating factor.

Uniike natural selection which is a compromise between selection for many factors, artificial selection is often truncated when operating on a few or single characteristics. Both in agriculture and in the animal sciences truncated selection through many generations has led to loss of adaptive possibilities. This is of less importance if one can control the environment. In forestry where one does not have the same degree of control over the environment, characters correlated with survival, fast growth, straight stem form, disease resistance and high wood density should be considered from the start of a selection program, in order to develop an improved forest. Each time we are confronted with a selection program, we should consider in what degree it is possible to combine the desirable character with other characters which have a selective advantage. Studies of selective characters form primarily a basis for provenance research, but it is not improbable that they will become increasingly important for the forest geneticist as the selection program proceeds within the particular provenance or geographic race, or where one starts a hybridization program with different geographic races.

Basis for the investigation

In some publications (DIETRICHSON 1961, 1963, 1964) large variability has been shown in the growth-rhythm, conditioned by provenance and the individuals within the provenance. Growth-rhythm is understood to be the time interval at which growth processes occur in the trees. The existence of large differences between different geographic races has been known for a long time, NORMAN (1883), ÖRTENBLAD (1898) with others. What has been missing in all the research up till now is an interpretation of the importance of different growth-rhythms and what they mean for height growth, stem straightness and wood quality in a given climate for different individuals and races. The international Scots pine experiment of 1938 at Matrand in Eidskog, Norway, will in the following be a biological model for such an analysis.

Based on studies of the Matrand experiment, whose location is given in table 1, it was concluded by DIETRICHSON (1961, 1964) that an unfortunate growth-rhythm which was out of phase with the climate in the experiment was the most plausible explanation for the many poor characters found in western central European races, such as low survival, damage by "Brunchorstia" defoliation and die back (Scleroderris lagerbergii GREMMEN), loss in apical dominance, decreased wood density and increased snow-break frequency, compared with northern Scandinavian races. In these studies made through investigations of cambial activity and studies of growth of the annual ring, it was made clear that cambial frost damage (fig. 1) which could easily be detected by a sudden irregularity of the wood-cells, was connected with reduced height growth. Greatly delayed late wood formation in the western central European provenances, which in some years led to incomplete lignification of the outer late wood zone was also considered to be correlated with the increased snowbreak frequency in southern races compared with the northern ones (figs. 2 *and* 3). Similarly it was shown on many research plots of Scots pine and Norway spruce that delayed late wood formation and growth cessation were also connected with low wood density, which also could be a cause for the larger frequency of snow breaks in southern provenances. In other words, trees with an unfavourable growth-rhythm would from a selective standpoint be less advantageous than trees with a growth-rhythm synchronized with the climate at the place of cultivation.

Table 1. — The provenance experiment with Scots pine of 1938, Matrand, Eidskog, Norway, 60°02' N. lat., 12°15' E. Greenwich, 110 m a. s. l. The table gives mean numbers for different characters and different sources which may be of interest for the reader. Evenly spaced and superior trees within each provenance are involved. Provenances only which are investigated in this work are shown.

No.	Provenance	N. lat.	E. Greenwich	Height a. s. l., m	Number trees	Mean tree height, m	Mean straight-ness VEEN (1953)	Mean late wood %	Mean spring frost damage	Mean autumn/winter frost damage
2	Rovaniemi	66°25'	26°36'	250	31	5.58	1.00	23.00	1.74	1.26*)
3	Sääminki	61°44'	28°55'	85	43	7.43	1.00	21.84	0.74	0.65
6	Aasnes	60°32'	12°11'	230	42	7.38	0.93	22.50	0.73	0.17
7	Svanøy	61°30'	5°07'	50	30	5.88	1.77	20.69	1.07	0.83
9	Tönnersjöheden	56°40'	13°08'	100	41	6.51	1.78	18.03	0.95	0.41
11	Vecmockas	57°03'	23°10'	80	40	7.47	1.78	14.57	0.60	0.43
17	Glen Garry	57°04'	4°55'W.	150	32	5.54	1.39	19.37	1.51	1.48
18	Hersselt (cult.)	51°03'	4°56'	20	30	6.39	3.67	19.56	1.50	0.87
20	Pförten	51°47'	14°46'	85	36	6.78	4.36	12.43	1.03	0.58
22	Cruttinen	53°41'	21°26'	120	25	7.03	2.48	14.56	1.40	1.04
24	Zellhausen	50°01'	9°00'	140	30	5.27	4.83	10.49	1.47	1.77

*) Since prov. no. 2 is extremely early in the spring, overestimation of winter frost damage is possible. The frost might have damaged the cambium just before the cell division started in the spring. (cult.) — cones harvested from plantation.

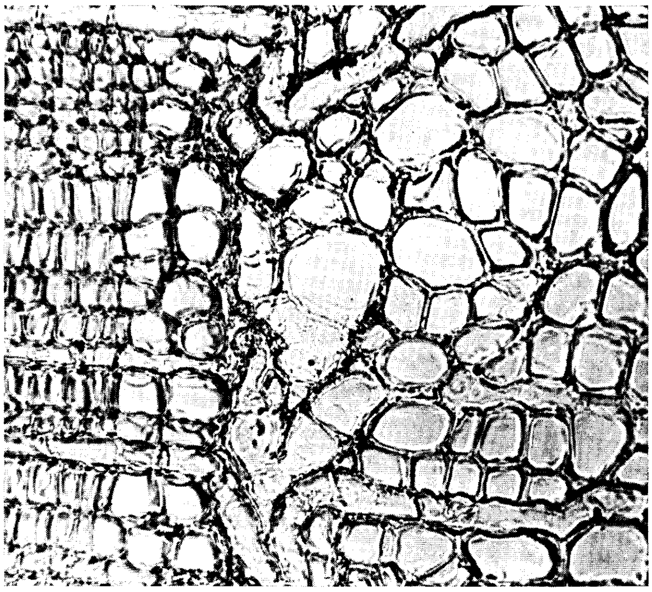

Fig. 1. — A photomicrograph, magnification 215×, of an annual ring struck suddenly by spring frost after the growth started in the spring. Provenance no. 7, Svanøy. Photo by F. Stemsrud.

The problem in the following study was to quantify the possible selective advantage for the trees of avoiding cambial frost damage. Because incomplete growth termination without subsequent frost damage appeared quite frequently it would also be interesting to quantify what this could mean for growth and stem straightness. Because it has also been demonstrated that central European Scots pine provenances in the Matrand trial showed lower wood density than northern Scandinavian races, it is of interest for further investigations to point out how well one could describe the late wood for longer periods based on a single or a few years late wood.

Methods

As in dendrochronology, which estimates the age of old timber on the basis of climatic changes and its influence on annual ring widths, one can correspondingly study anatomic characters like cambial frost damage, incomplete wood formation and changes in the late wood percentages back in time on different provenances and individuals by means of increment core-samples.

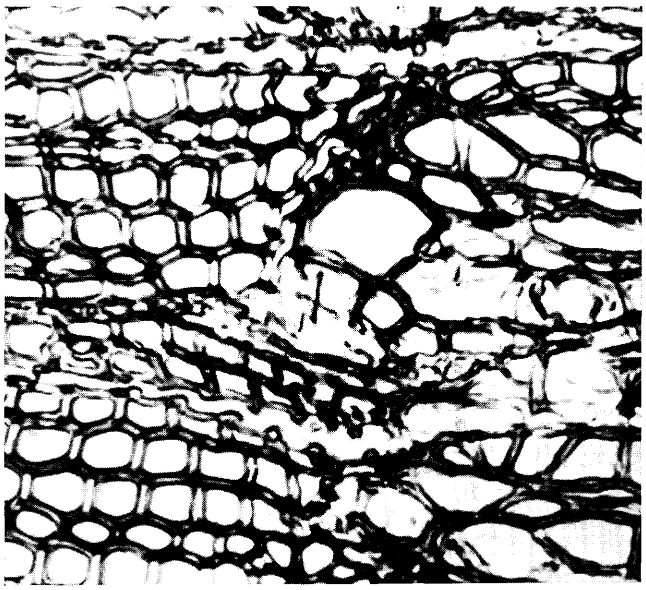

Fig. 2. — A photomicrograph, magnification 250×, of the annual ring demarcation 1954/55 of an individual from a western European provenance grown at Matrand. Note (after Mork's [1928] definition) the late wood in 1954. A weak frost has struck the cambium when it was in the annual ring demarcation. Photo by F. Stemsrud.

The core-samples in the Matrand trial were extracted in April 1963 at breast height and on the east-facing side of the trees. The samples were taken approximately ½ meter above the ground from trees which only were from 2—3 meters tall. The samples therefore vary somewhat in the number of years from the pith, but this has not been of importance for the results of this investigation.

From each core-sample, sections 30 microns thick were cut on a freezing microtome. The sections were stained red with phloroglucin and HCl and all the measurements were made under a microscope with 80 × magnification. The annual ring widths were measured and to do the same with the late wood, Mork's definition was utilized (Mork, 1928).

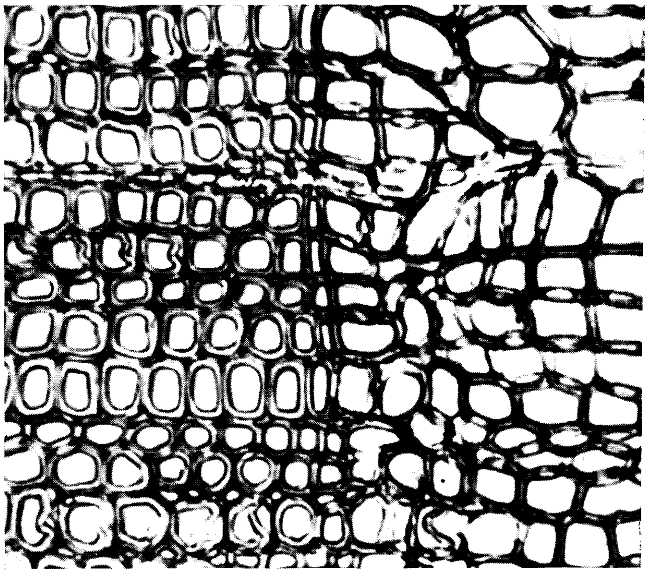

Fig. 3. — A photomicrograph, magnification 250×, of the annual ring demarcation 1953/54 on the same tree as *fig. 2*. Note that the warmer summer of 1953 has given better lignification than did the somewhat cooler summer in 1954. Photo by F. Stemsrud.

The "hidden frost damage" recorded back in time for different years is classified into two groups:

I. *Spring frost* — cambial frost damage which appeared suddenly after growth started in the spring.

II. *Autumn or winter frost* — cambial frost damage which will appear as irregular cells in the late wood or in the spring wood adjacent to the annual ring demarcation. The frost should occur before the cell division started in the spring.

Incomplete growth termination, defined as insufficient wood formation of the outer late wood zone, has been recorded for the different trees and years (*fig. 2,* see Dietrichson, 1964).

Design and Layout

The location of the Matrand experiment is given in *table 1,* and the same table summarises the data on the 11 investigated provenances. The trial is a randomised block experiment with 5 replications and was planted out in 1940 with 2 year old seedlings. An accurate description of the experiment has been given by Dietrichson (1964).

Table 2. — Temperature growth units (MORK, 1941) at Vinger and Skotterud, near the Matrand experiment.

Year	Month					Sum	Meteorological station
	May	June	Tuly	August	September		
1950	77.2	106.3	116.8	123.1	61.0	484.4	Vinger
1951	64.8	93.1	114.2	99.7	66.6	438.4	Vinger
1952	65.8	75.5	126.0	94.2	46.2	407.7	Vinger
1953	63.8	162.1	112.5	107.4	62.7	508.5	Vinger
1954	89.6	91.7	107.5	110.8	62.0	461.6	Skotterud
1955	44.7	100.1	205.1	185.1	81.3	616.3	Skotterud
1956	81.9	85.2	141.9	84.9	63.7	457.6	Skotterud
1957	57.2	97.3	135.6	109.2	50.3	449.6	Skotterud
1958	56.1	101.0	127.8	103.5	88.0	476.4	Skotterud
1959	84.6	126.8	164.5	166.5	103.1	645.5	Skotterud
1960	85.6	134.8	95.6	98.3	67.6	481.9	Skotterud
1961	68.5	121.1	119.1	92.8	73 0	474.5	Skotterud
1962	43.1	89.7	104.0	78.1	57.5	372.4	Skotterud

Because this work will not attempt to classify differences between provenances, we shall omit the details in these experiments. *Table 2,* however, describes the climate of the years 1950-62 given in temperature growth units, MORK (1941), for the different summers. Each plot of size 17×20 meters was originally stocked with 195 plants. To get samples, each plot is subdivided into 9 even squares, and the tallest tree within each subplot is selected as a sample tree. For some sources the survival was low and gave empty subplots; in such cases the next tallest tree in one of the adjacent subplots was used as the sample tree. As there were 5 replications the plan was to investigate 45 trees from each provenance, but as stated in *table 1* 115 trees are missing. This is caused by breakage of samples in the laboratory which led to incomplete sets of datas causing complications in the multiple regression analysis done on an electronic computer. The material comprised 380 trees. All the trees were measured in the autumn 1959 and the stem straightness evaluated according to a system suggested by VEEN (1953):

0 = straight tree
1 = slightly crooked, will grow straight before maturity
2 = crooked after badly healed top-break
4 = badly crooked, will never grow straight
8 = very crooked, leaning tree.

Simple and multiple linear regressions have been carried out with 3420 single observations using 9 different characteristics from each tree. The following have been chosen:

1. tree height in 1959 in meters
2. stem-straightness according to the classification of VEEN (1953)
3. mean late wood percentage 1953-62
4. number of cambial spring frost damages from 1950-62
5. number of cambial autumn or winter frost damages from 1950-62

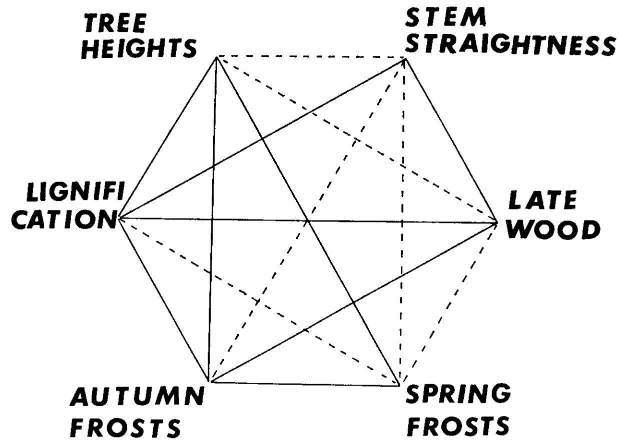

Fig. 4. — Graph indicating statistical correlations between pairs of characters in 380 trees. Values of the correlation coefficients, r above 0.133 are considered to be significant. See *table 3* for a complete listing of r values.
———— = highly significant, - - - - - - = not significant.

6. late wood percentage in 1952
7. late wood percentage in 1954
8. late wood percentage in 1957
9. number of incomplete lignification from 1950-62.

Results

In *table 3,* 36 simple correlation coefficients are given for the combinations of interest. By looking over the table, where all the coefficients have 378 degrees of freedom, the following conclusions can be drawn as all the numbers with absolute value greater than 0.133 are significant at the 1% level. See also *fig. 4.*

Tree heights

Increasing values for numbers of cambial spring, autumn and winter frost damages and incomplete lignification were correlated with height growth in the Matrand experiment. The simple correlation coefficients are: (see *table 3*) − 0.590, − 0.542 and − 0.237. Because the degrees of freedom are 378 these are all highly significant.

The multiple regression with tree height as the dependent variable and the remainder as independent variables gave:

$$y_h = 7.5493 - 0.5285x_1 - 0.3146x_2 - 0.1901x_6$$

y_h = the tree height in meters
x_1 = the spring frost damage
x_2 = the autumn and winter frost damage
x_6 = incomplete lignification.

Table 3. — Single correlation coefficients, in each case between 380 sets of observations. All correlation coefficients with absolute values larger than 0.133 are significant at 1% level. Material taken from the international Scots pine experiment of 1938 at Matrand, Norway.

Dependent variable	Independent variable								
	y_h	y_s	y_L	x_1	x_2	x_3	x_4	x_5	x_6
Tree height, y_h	1.000	−0.103	0.125	−0.590	−0 512	0.094	0.066	0.048	−0 237
Stem straightness, y_s		1.000	−0.302	−0.066	0.082	−0.315	−0.292	−0.359	0 360
Mean, late wood %, 1953−62, y_L			1.000	−0.111	−0.265	0.699	0.805	0.821	−0.284
Cambial spring frost damage, x_1				1.000	0.455	−0.097	−0.066	−0.040	0.069
Cambial autumn/winter frost damage, x_2					1.000	−0.240	−0.179	−0.203	0.213
Late wood, %, 1952, x_3						1.000	0.609	0.678	−0.357
Late wood, %, 1954, x_4							1.000	0.665	−0.290
Late wood, %, 1957, x_5								1.000	−0 367
Incomplete lignification, x_6									1.000

All the partial regression coefficients have contributed significantly to the equation with the following standard deviations and t-values:

	coefficient	st. dev.	t - value	DF
constant	b_0	0.0802	94.04***	376
spring frost damage	b_1	0.0512	−10.31***	376
autumn and winter frost damage	b_2	0.0437	− 7.20***	376
incomplete lignification	b_6	0.0526	− 3.62***	376

The multiple correlation coefficient is $R = 0.824$ and thus 67,9% of the variation in height growth has been accounted for by the three variables. *Fig. 5* gives with 3 drawings an illustration of the equation.

Discussion:

According to DIETRICHSON (1964), survival was strongly affected by provenance after the planting of the experiment in 1940. Both southern central European sources and extreme northern races had lower survival than the native ones. The western central European Scots pine provenances were severely affected by both spring and autumn/winter frost damage, while the more native and eastern central European races were less damaged. On the northern seed source (no. 2, Rovaniemi) extensive frost damage appeared (see *table 1).*

From the multiple regression it is not possible to decide upon the relative importance of spring frost versus autumn/winter frost damage. But since the simple regression equations are: $y_h = 7.29 - 0.42x_1$ and $y_h = 7.37 - 0.71x_2$, and the correlation coefficients are high (see *table 3),* it would be easy to show that spring frost damage was of least importance to height growth. In the evaluation of spring versus autumn and winter frost damage the following considerations should also be noted. Since both extreme northern as well as extreme southern races are hurt by spring frosts, there will also be an interaction between inherited growth capacity and reduction in growth caused by spring frosts.

The northern race no. 2, Rovaniemi, which has low growth capacity and high frequency of frost damage, would lead to a general overestimation of the decrease in height growth caused by spring frosts in the equation above.

RUDEN (1964) has stressed that central European provenances of Norway spruce in spite of some frost damage might outgrow northern sources due to larger growth capacity. However, as will appear from the following, the problem is rather complicated.

Stem straightness

From the simple regression coefficients in *table 3,* it can be seen that the late wood percentages given as means for the period 1953-62 for each tree, and for the different years 1952, 1954 and 1957, show significant negative correlation with the stem straightness index. This means that the trees appear more and more crooked the smaller is the late wood percentage. Of greatest importance, however, is incomplete lignification. The more frequently a tree has incomplete lignification, the more likely it is such a tree will be crooked. In this material there were no correlations between cambial frost damage and the crookedness of the tree.

A multiple regression was carried out with the stem straightness as the dependent variable. The following symbols are given:

y_s = stem straightness classified according to VEEN (1953)
x_3 = late wood percentage in 1952
x_4 = late wood percentage in 1954
x_5 = late wood percentage in 1957
x_6 = number of anual rings with incomplete lignification 1950−1962.

The equation is:

$$y_s = 2.692 - 0.012x_3 - 0.011x_4 - 0.035x_5 + 0.473x_6.$$

As seen from the function, incomplete lignification is of considerable importance in its effect on stem straigthness. This will also be apparent in the standard deviations and t-values:

	coefficient	st. dev.	t-value	DF
constant	b_0	0.217	12.45***	375
late wood percentage in 1952	b_3	0.013	− 0.99 N. S.	375
late wood percentage in 1954	b_4	0.012	− 0.88 N. S.	375
late wood percentage in 1957	b_5	0.013	− 2.59***	375
no. of incomplete lignifications	b_6	0.095	5.00***	375

Both the late wood percentage in 1952 and 1954 have not significantly contributed to improvement of the equation

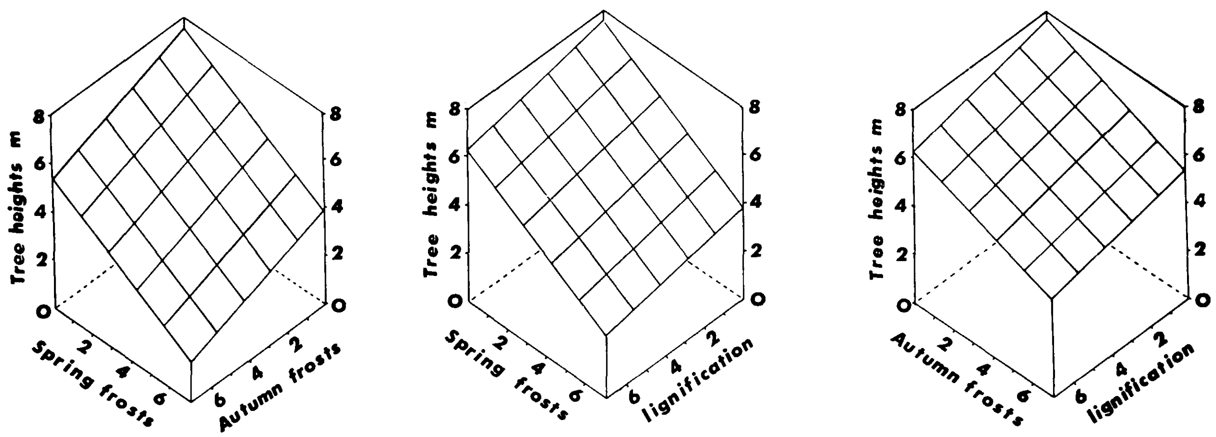

Fig. 5. — 3 graphs demonstrate the multiple regression equation between spring frost damage, autumn/winter frost damage, number of annual rings with unlignified wood, all in the period 1950—1962, and the height of the same 380 trees. The equation is given in the text.

and should be excluded. Even though this had been done, it would not change the end-result; that the multiple correlation coefficient is R = 0.664 and that 44% of the variation in stem straightness has been described by the measured anatomic characters.

Discussion:

The high correlation which has been pointed out between stem straightness and anatomic characters might be caused by the following factors: a. A weakening of the stem caused by an outer unlignified late wood zone, and therefore snowbreaks after heavy snowfalls. b. Late lignification and a dry period in the summer might have led to drooping of the annual shoot before full extension and therefore a crooked stem if repeated over many years. The latter has also been stated by ROLL-HANSEN (personal cummunication 1961). Because late lignification can be correlated with crooked growth of the Scots pine in the Matrand experiment, it ought also to be investigated whether the crooked growth of young Norway spruce in plantations established on better sites in southern Norway could also be correlated with late lignification.

The late wood in the period 1953-62

The mean late wood percentage for the period 1953-62 is correlated with the late wood percentage in the years 1952, 1954 and 1957. From *table 3* it can be estimated that 49% of the variation in the mean late wood percentage could be described by measurement of the late wood percentage in 1952. However, one obtains a better estimate by measurements of the late wood in a single year within the period: *Table 3* shows that if the annual rings from 1954 is used as "independent variable", the correlation coefficient is 0.805. The coefficient is somewhat higher if 1957's annual ring is used as "independent variable". As expected from earlier research (DIETRICHSON, 1961, 1963, 1964) increasing frequency of cambial autumn and winter frost damage and also incomplete lignification is correlated with reduction in the late wood percentage.

A multiple regression analysis has been completed with the following variables:

y_L = Mean late wood percentage in 1953-62
x_3 = Mean late wood percentage in 1952
x_4 = Mean late wood percentage in 1954
x_5 = Mean late wood percentage in 1957
x_6 = Number of rings with incomplete lignification in the period 1950-62.

$$y_L = 7.438 + 0.100x_3 + 0.274x_4 + 0.296x_5 + 0.399x_6.$$

Because both x_4 and x_5 are not independent of y_L a high correlation is expected. All factors contribute significantly as appears in the following:

	coefficient	st. dev.	t-value	DF
constant	b_0	0.368	20.20***	375
late wood per cent, 1952	b_3	0.021	4.66***	375
late wood per cent, 1954	b_4	0.020	13.41***	375
late wood per cent, 1957	b_5	0.022	13.19***	375
incomplete lignification	b_6	0.161	2.48**	375

The multiple correlation coefficient R is 0.95, and thus 89.8% of the variation in the late wood in the period 1953-62 is described by the 4 factors.

Conclusion:

The analysis show that the late wood percentage is a constant property for each tree with a large repeatability between years. By knowing the late wood percentage for a single or a few years one can predict the relative value of the late wood percentage, and with that the dry volume weight of the wood for a larger number of years.

General discussion

The results support earlier findings (DIETRICHSON, 1961, 1963, 1964) that anatomic characters are an effective tool for the forest geneticist. This is because the anatomic characters are closely related to the physiology and thus the adaptation of the trees. From many older experiments true differences between seed-sources for anatomic characters can be worked out. In the years to come the task of studying narrow sense heritability of the same physiological characteristics is important.

Table 3 gives much interesting information. In predicting all characters except for spring frost damage, incomplete lignification has contributed significantly. The correlation coefficient is often only 0.3 which only explains 9% of the dependent variable involved. This is because studies of annual rings back in time is a coarser form of analysis than the data we could obtain by studies of growth termination in the growing season. In this work incomplete lignification has discrete values. Several annual rings are therefore in spite of their late growth cessation included in the same class as northern biotypes with much earlier lignification.

With reference to cambial frost damage, there is a correlation between autumn/winter frost and spring frost damages with r = 0.455. This also supports earlier investigations of DIETRICHSON (1964), that a physiologically weak condition in the autumn in many cases is followed by a similar weak condition in the subsequent spring.

The Matrand experiment shows that frost damage barely visible in the field, has a selective role. Physiologically poorly adapted trees will drop behind in competition with the better adapted. Because the best adapted biotypes are usually the tallest, they may be the most fecund also and may contribute the most offspring to the next generation. Thus the inheritance of the same physiological characters will be a deciding factor in the rate with which new climatic races might develop by change in the selection pressure. It would be an advantage if physiological characters were strongly inherited because one could then from an indifferent population select and obtain a strong reduction in the selection pressure in the next generation against frost, which in the author's opinion could be of economic importance. The existence of genetic homeostasis has been demonstrated in wild populations other than forest trees. This is the population's protection against sudden changes in the selection pressure. If this also is the case in forest trees, one will in the long run be on the safe side to select as a starting point individuals from the best adapted population, though this will not always be the native one (see LANLGET, 1960). This population can be chosen as the population which currently in many environments appears to have the smallest aggregate selection pressure. In other words, the provenance problem is and will continue to be the frame of forest genetics.

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Summary

An investigation has been made of the relationship between different anatomic characters and economic important characteristics such as height growth, stem straightness, and wood density. The International Provenance Experiment with Scots pine of 1938 at Matrand, Eidskog, Norway has been chosen as a model for the analysis *(table 1)*.

This work is based on earlier research (Dietrichson, 1961, 1963, 1964) which has indicated that the individual variation within a geographic race for many anatomic characters often is just as large as the variation between geographic races. To study the importance of different anatomic characters which again are correlated with the growth-rhythm, both simple and multiple linear regression analysis have been made with pooled material of 11 different seed sources. *Table 3* gives the simple correlation coefficients.

By using three independent variables; the number of cambial spring frost damages, the number of cambial autumn frost damages, and the number of incomplete lignified annual rings all in the period 1950—1962, 67.9% of the variation in the height growth has been explained in a multiple regression analysis with 380 trees.

To improve the stem straightness in a climate similar to that of the Matrand experiment one should select for individuals with high late wood percentage and complete lignification. By using the late wood percentage in the years 1952, 1954, 1957 and the number of unlignified annual rings in the period 1950—1962 as independent variables, 44% of the variance in the stem straightness has been explained for the same 380 trees.

The physical explanation that trees with incomplete lignification and low late wood percentage are more crooked is undoubtly related to the snow breaks, but the possibility of an other cause has also been discussed.

An appropriate description of the late wood percentage is obtained for the period 1953—1962 by measurements of the late wood for only one year within this period. By using the late wood percentage for the years 1952, 1954, and 1957 as "independent variables" in a multiple regression, 89.8% of the variation in the mean late wood percentage 1953—1962 has been explained for 380 trees. The relative value for the late wood percentage for the particular tree compared with other trees does not change very much between years and is conditioned by the growth-rhythm.

The conclusion is that anatomic characters are an effective tool for the forest geneticist. This is because the anatomic characters are correlated with the physiology and thus the adaption of the trees. The physiologically best adapted individuals will be selected for. It has been discussed whether it will be possible to reduce the selection pressure in the following generations by selecting the best adapted trees from different kinds of populations.

Résumé

Titre de l'article: *Le problème de la sélection et le rythme de croissance.*

L'étude a porté sur la relation existant entre différents caractères anatomiques et des caractéristiques économiques importantes telles que la croissance en hauteur, la rectitude du fût et la densité du bois. L'expérience internationale de provenances de Pin sylvestre de 1938 existant à Matrand, Eidskog, Norvège, a servi de modèle pour l'analyse *(Tableau 1)*.

Ce travail est basé sur une recherche antérieure (Dietrichson, 1961, 1963, 1964) qui a montré que la variation individuelle à l'intérieur d'une race géographique est souvent, pour de nombreux caractères anatomiques, du même ordre de grandeur que la variation entre races géographiques. Pour étudier l'importance des différents caractères anatomiques qui peuvent être liés au rythme de croissance, on a utilisé sur le matériel provenant de 11 différentes sources de graines, la régression linéaire simple et multiple. Le *tableau 3* donne les coefficients de corrélation simple.

En utilisant les trois variables indépendantes: nombre de dégâts de gelée tardive sur le cambium, nombre de dégâts de gelée précoce sur le cambium, nombre d'accroissements incomplètement lignifiés dans la période 1950—1962, on trouve que 67,9% de la variation de la croissance en hauteur peut leur être rapporté dans une analyse de régression multiple portant sur 380 arbres.

Si l'on veut améliorer la rectitude du fût dans un climat analogue à celui de l'expérience de Matrand, on doit sélectionner des individus avec un pourcentage élevé de bois final et bien lignifiés. On peut rapporter pour les même 380 arbres, 44% de la variance de la rectitude du fût aux caractères suivants: pourcentage de bois final dans les années 1952, 1954, 1957 et nombre d'accroissements annuels non lignifiés dans la période 1950—1962.

On peut expliquer par les bris de neige le fait que les arbres incomplètement lignifiés et présentant un pourcentage bas de bois final sont plus tordus, mais il est possible qu'il existe aussi une autre cause.

Une description convenable du pourcentage de bois final est obtenue pour la période 1953—1962 par des mesures du bois final sur une seule année au cours de cette période. En employant le pourcentage de bois final pour les années 1952, 1954 et 1957 comme variables indépendantes dans une régression multiple, 89,9% de la variation dans le pourcentage moyen de bois final sur la période 1953—1962 peut être expliqué pour les 380 arbres. La valeur relative pour le pourcentage de bois final en ce qui concerne un arbre particulier comparé avec d'autres arbres ne change pas beaucoup suivant les années et est conditionnée par le rythme de croissance.

On peut conclure que l'étude des caractères anatomiques représente un outil efficace pour le généticien forestier; en effet, les caractères anatomiques sont liés avec la physiologie, donc l'adaptation des arbres. On sélectionnera ainsi les individus les mieux adaptés du point de vue physiologique. On a discuté le fait de savoir s'il est possible de réduire la pression de sélection au cours des générations successives, en sélectionnant dans différentes populations les individus les mieux adaptés .

Zusammenfassung

Titel der Arbeit: *Das Selektionsproblem und der Wachstumsrhythmus.*

Untersucht wurden Beziehungen zwischen verschiedenen anatomischen und ökonomischen Merkmalen, z. B. Höhenwachstum, Geradheit des Stammes und Holzdichte. Dazu ist der Internationale Fichtenprovenienzversuch von 1938

in Matrand, Eidskog, in Norwegen als Modell für eine Analyse benutzt worden (*Tabelle 1*).

Frühere Untersuchungen (DIETRICHSON 1961, 1963, 1964) hatten ergeben, daß oft die individuellen Variationen innerhalb einer geographischen Rasse bei vielen anatomischen Merkmalen genauso groß ist wie zwischen den geographischen Rassen. Um nun den Wert von mit dem Wachstumsrhythmus korrelierten anatomischen Merkmalen prüfen zu können, wurden einfache und multiple lineare Regressionsanalysen bei gepooltem Material von 11 verschiedenen Samenherkünften gerechnet. *Tabelle 3* enthält die einfachen Korrelationskoeffizienten.

Wenn 3 unabhängige Variable verwendet wurden, nämlich die Anzahl der kambialen Frühjahrsfrostschäden, Zahl der kambialen Herbstfrostschäden und Zahl der unvollständig verholzten Jahrringe während der Jahre 1950–1962, dann waren bei einer multiplen Regressionsanalyse mit 380 Bäumen 67,9% der Variation im Höhenwachstum erklärt gewesen.

Zwecks Verbesserung der Geradheit des Stammes in einem dem Versuch in Matrand ähnlichen Klima sollte man nach Individuen mit hohem Spätholzanteil und vollständiger Verholzung selektieren. Bei einer Benutzung der Spätholzprozente der Jahre 1952, 1954, 1957 und der Anzahl unverholzter Jahrringe in den Jahren von 1950 bis 1962 als unabhängigen Variablen, waren bei denselben 380 Bäumen 44% der Varianz in der Geradheit der Stämme erklärt gewesen.

Physikalisch erklärt sich der Zusammenhang, daß die Bäume mit unvollständiger Verholzung und geringen Spätholzprozenten krummer sind, zweifellos mit Schneebruch; auch andere Ursachen sind diskutiert worden.

Eine hinreichende Beschreibung des Spätholzprozentsatzes wird für die Gesamtzeit von 1953 bis 1962 erhalten, wenn nur für ein Jahr innerhalb dieser Periode Spätholzmessungen gemacht worden waren. Benutzte man die Spätholzprozente der Jahre 1952, 1954 und 1957 als „unabhängige Variable" bei einer multiplen Regression, so sind bei 380 Bäumen 89,8% der Variation der mittleren Spätholzprozente für die Gesamtzeit 1953–1962 erklärt gewesen. Der relative Wert für das Spätholzprozent bei einem Einzelbaum, verglichen mit anderen Bäumen, verändert sich nicht viel zwischen den Jahren und wird durch den Wachstumsrhythmus bedingt.

Anatomische Merkmale sind demnach für den Forstgenetiker wirksame Hilfsmittel. Der Grund dafür liegt darin, daß anatomische Eigenschaften mit der Physiologie und der Anpassungsfähigkeit der Bäume korreliert sind. Die physiologisch bestangepaßten Individuen werden selektiert. Schließlich wird diskutiert, ob eine Reduktion des Selektionsdruckes in den Folgegenerationen durch eine Selektion der bestangepaßten Bäume aus verschiedenartigen Populationen möglich ist.

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The Frequency and Abundance of Flowering in a Young Slash Pine Orchard

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There has long been an interest in the flowering behavior of forest trees as is attested by the voluminous literature on the subject. The development of seed orchards for production of improved seeds has intensified this interest and has focused attention on individual trees.

This paper presents information on flowering of grafted slash pine (*Pinus elliottii* ENGELM.). In 1956, the University of Florida began work toward establishment of a slash pine breeding orchard near Gainesville in cooperation with several forest industries of the region. Spacings of 40 × 40 feet, 35 × 35 feet, 30 × 30 feet, and 25 × 25 feet between grafted plants were used in different blocks. In 1957, a block with 15 × 15 feet spacing was added. The orchard consists of one or two ramets each of some 400 clones, with ortets in most areas of the slash pine range. Only healthy, well-established grafts were considered in this report, a total of 631 plants. These plants are now mostly over 25 feet in height and have well-developed crowns.

Counts of female strobili have been made for each plant since 1960. Accuracy of the annual counts varies with the number of strobili per plant. On southern pines, the easiest and most accurate count of new conelets can be made after rapid shoot elongation is started but before needle elongation on the fresh shoots has occurred. This procedure, however, causes one to miss flowers which have aborted earlier for any reason and would indicate effective rather than total flowering.

At the beginning of the period covered here, the grafts