2) Les deux types extremes A et B de feuilles se différencient d'une maniere significative par 6 caracteristiques differentes, parmi lesquelles le nombre des glandes se comporte d'une façon particulierement typique: le type A possède en moyenne 4.0 glandes par feuille, le type B n'en a en revanche que 0.1. 11 clones du type B sont demunis de toute glande!

3) I1 existe des corrélations assurees entre le nombre de glandes et 7 autres caracteristiques des feuilles.

La repartition *géographique* des types de feuilles montre que

4) le type de feuilles A, riche en glandes, représente une forme meridionale du *Populus* deltoides; en revanche, le type B, pauvre en glandes ou même sans glandes, en est une forme septentrionale.

5) Differents indices montrent finalement que les deux types principaux distingués selon des criteres de morphologie des feuilles représentent egalement différents ecotypes.

Summary

Title of the paper: *Investigations* on the *geographical* variability of *morphological* characteristics *in Populus deltoides* Bartr.

Studies on the morphological characteristics of the leaves from 50 clones of Populus *deltoides* BARTR. from 9 different states were made at the populetum of the University of Wisconsin in Madison (USA). For 10 absolutely comparable leaves from each clone, an examination and statistical analysis was made of 6 quantitative leaf characteristics and 4 character-indices. These investigations of leaf *morphology* gave mainly the following results:

1) From the entire sample it was possible to distinguish 2 distinct leaf types (A and B) as well as a less distinct and more variable type (A_b), whose partially intermediate structure indicates hybridization.

2) The 2 extreme leaf types, A and B, differ significantly in 6 characteristics. Among these, the number of glands was found to vary very typically: leaves of type A show an average of 4 glands, while leaves of type B show an average of only 0.1 glands. 11 clones of type B hsve no glands at all!

3) A significant (rank-)correlation exists between the number of glands and 7 other characteristics.

The investigations on the *geographical distribution* of the *leaf* types show that:

4) the gland-rich type A represents a southern form of *Populus* deltoides, while the gland-poor (or glandless) type B belongs to a northern form.

5) Additional factors indicate that the two principal types separated by leaf morphological characteristics also represent different ecotypes.

Literatur

(1) BROEKHUIZEN, J. T. M.: Seasonal variation in the leaf shape of some poplar clones. Institute of Forestry Research, Div. of Silviculture; Communication No. 3, 1961. — (2) Check List of Cottonwood and Balsam Poplar clonal lines, in the possession of the Maria Moors Cabot Foundation for botanical Research, Harvard University 1951 (hektographiert). — (3) Documentation OECE: Les peupliers americaines. Mission d'Assistance Technique No. 13, Paris 1951. — (4) FAO-Publ. No 12: Les Peupliers dans la production du bois et l'utilisation des terres. Rome, 1956. — (5) HARLOW, W. M., and HARRAR, E. S.: Textbook of Dendrology. New York, 1958. — (6) HEIMBURGER, C.: Communication about Poplars in Canada. Proc. 4th Internat. Poplar Congress, Annex 4, pp. 65—68, 1951. — (7) HENRY, A.: The Black Poplars. Gardeners Chronicle 1914. — (8) HESMER, H.: Das Pappelbuch. Bonn 1951. — (9) HOUTZAGERS, G.: Die Gattung Populus und ihre forstliche Bedeutung. Hannover 1941. — (10) HOUTZAGERS, G.: Les peupliers deltoides, *tremuloides* et grandidentata dans leur aire naturelle. Commission Internat. Peuplier, Rapp. cinquieme session, 1951. — (11) KENDALL, M. G.: Rank Correlation Methods. London, 1955. — (12) LITTLE, E. L.: Check List of native and naturalized Trees of the US. Agr. Handbook 41, US Dept. Agr., 1953. — (13) MAISENHELDER, L. C., and HEAVRIN, CH. A.: Silvics and Silviculture of the Pioneer Hardwoods — Cottonwood and Willow. Hektographierte Publ. des Delta Research Center of the Southern Forest Exp. Station, Stoneville/Miss. — (14) MÜLLER, R.: Gebrauchspappeln und ihre Kontrolle. Die Holzzucht, 1948. — (15) PHILLIPS, G. R., GIBBS, F. J., and MATTOON, W. R.: Forest Trees of Oklahoma. Okla. Planning and Resources Bd., 1953. — (16) POOL, R. J.: Handboolc of Nebraska Trees. Nebr. Univ. Conserv. Bul. 32, 1951. — (17) READ, R. A.: Silvical Characteristics of Plains Cottonwood. Station Paper 33, Rocky Mts. Forest and Range Exp. Station, 1958. — (18) REHDER, A.: Manual of cultivated Trees and Shrubs, hardy in North America. New York, 1960. — (19) ROI, R.: Les Peupliers et les principales essences forestieres de l'Est des Etats-Unis. Annales de l'Ecole Nationale des Eaux et Forêts et de la Station de Recherches XII, 2, (1951). — (20) SARGENT, CH. S.: Manual of the Trees of North America. Boston, 1926. — (21) SNEDECOR, G. W.: Statistical Methods. Iowa State College Press, 1956 — (22) WETTSTEIN, W.: Die Pappelkultur. Wien 1952.

Breeding for Frost Resistance

By JON DIETRICHSON*)

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In Norway, as in several other northern countries, it is important that the forest seed which is marketed gives sufficiently hardy plants. By "hardy" is understood resistant to spring, autumn and winter frosts. The objective of plant improvement — to produce a forest with a greater volume yield and of better quality than the natural forest — cannot be realised in the northern countries until we have reliable guarantees that the populations or individuals we are working with are sufficiently hardy. Since the climatic conditions vary from place to place, the direct field observations during surveys will not always provide a basis for a reliable prognosis of hardiness. This is especially dangerous if we are dealing with climstic races which are at the limits of tolerance.

Examination of wood-formation in microscopic sections appear, however, to be effective for verification of field observations.

The international Scots pine provenance experiment at Matrand, Eidskog, is situated in the south-east part of Norway, at approximately 60° N., and 130 m. above sea level. The plot, which was planted in 1940, has failed as a production experiment because a large percentage of the plants succumbed to an attack of what was presumed to be the weevil (*Pissodes* pini). The plot which is now about 20 years old, has in spite of its sparseness given some valuable information regarding variations in hardiness. 23

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provenances of Scots Pine were included in the survey. (See *table 1.)*

The plot, which had a comparatively healthy appearance until a few years ago, is deteriorating steadily due to snow break and various diseases. *Crumenula abietina* (dryness in pine buds) has been especially severe in the case of the central European pine races. The northern and Scandinavian races are still healthy, and unlike the southern ones have only to a limited extent been subject to damage by snow.

The central European Scots pine provenances differ from the Scandinavian in that they bud later in the spring. LANGLET (6) has investigated this. His results agree fully with personal observations at Matrand in 1959 and 1960.

Because the central European races at Matrand bud later than the Scandinavian, there is little likelihood of spring frost in the case of the central European Scots pine. Since it has long been known that southern provenances continue to grow later in the autumn than the northern ones, this is a factor which limits their transfer to a colder type of climate. In Norway incomplete growth and lack of maturity in the autumn leads to frost damage the following autumn or winter.

No visible damage by frost could be registered at Matrand, but examination of the wood from the most recent years, as well as the wood formation at the close of the vegetation period, revealed data which clearly graded the races according to the time of growth termination.

The problem of investigating wood formation is not new. ROMELL (13), SCHOBER (14), LADEFOGED (4), ANDERSON (1), SUNDVOR (15), and MORK (10), have all investigated wood formation, and have found variations in wood formation from year to year within one and the same tree species, as well as variations between tree species.

As far as studies of the wood's termination of growth are concerned, no attention has hitherto been paid to the different provenances within one and the same species. LANGLET (5) has shown that southern races of Scots pine have a greater moisture content in the needles in the autumn than the more northerly races. This is due to the southern races, adaptation to a warmer type of climate. A good plan is to use LANGLET's dry matter investigations as a criterium of resistance to autumn and winter frost. But anatomic investigations give us also the possibility of an actual picture of when the hidden growth ceases, and of what happen to the anatomic construction of the wood in the case of frost the following autumn or winter after incomplete growth.

The importance of the question of resistance, to us, is shown repeatedly. ROLL-HANSEN (12) has written about diseases to which forest trees in Norway were subject during 1959. Most interesting and remarkable is perhaps his reference to the damage in a 30-year-old Norway spruce plantation at Vågå, which is situated in the central part of southern Norway. The vitality of the stand, which showed good growth until four or five years ago, has since then steadily deteriorated. The tops and some of the crowns are drying, and the trees die.

ROLL-HANSEN was unable to find that the damage was due to attack by parasites. An anatomic examination revealed false annual rings. These have hitherto been assumed to be the result of drought during the period of growth. ROLL-HANSEN asserts that annual rings formed in conjunction with such droughts can have failed to reach maturity and consequently been affected by autumn frosts.

Vågå, in central Norway, belongs to Norways driest district, and has annual precipitation of 400 mm. On the other hand, this stand grew on sound and moist soil. ROLL-HANSEN himself is in doubt as to whether dryness is the primary cause, and draws attention to the provenance of the Norway spruce. It has not been possible to ascertain to which provenance the damaged Norway spruce plantation at Vågå belongs.

The damage mentioned here is not unique in Norway. We have gained experience of the variations in resistance of the provenances through observing frost damage in the nurseries. In arboreta which, in this country, are often based on imported tree species, representatives are found for varying types of hardiness. It will often happen that the tops or the entire tree dry up. If only the top dies, a side branch will soon grow in its place. The result will be a crooked trunk, often with a double top. In some cases there will be no such visible sign, the trees just decline, and it is easy for parasits to gain a foothold. Reports have been received from Finland, which has older provenance experimental plots than Norway, of unsatisfactory experience with several central European Norway spruce provenances.

JOACHIM (2) has done work in connection with frost damage to *Populus*. He shows how trees are retarded of diseases caused by frost. Both large and small trees are affected.

LADEFOGED (4) investigated, as previously mentioned, a number of tree species in Denmark. As well as differences between the species, he found that increasing annual ring width gave proportionately increased growth period.

OKSBJERG (11) measured the reach of the Norway spruce shoots and found that the growth period increased proportionately with the length of shoot. In Norwegian forest nurseries it has long been experienced that excessive fertilising renders the plants more liable to damage by autumn frosts. If we accept the hypothesis that good growth also implies a long period of growth, this means:

1) Late termination of growth incurs the risk of autumn frost.

2) A southerly provenance gives late termination of growth.

3) High site class gives late termination of growth.

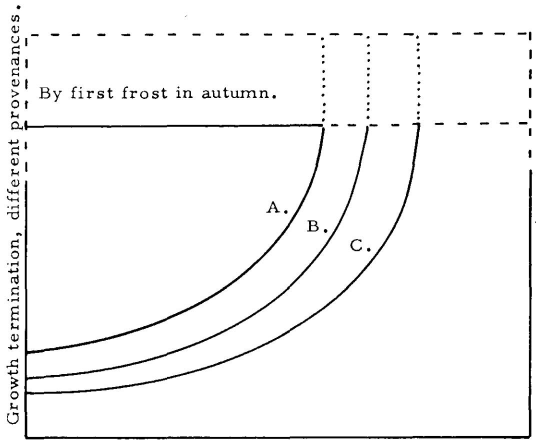
4) Thinly stocked forest gives later termination of growth because increasing annual ring width.

5) The annual ring width and the length of the top shoots alter with the age of the tree and give variations in termination of growth.

As these points will show, the problem of resistance to frost is a complicated one. Damage by frost during autumn or winter can be determined by the summer climate, the time of the first autumn frost, the minimum temperature and the temperature variations the following winter. All these factors vary from year to year. The coldest summer combined with the coldest winter during the period of rotation of the stand must be decisive for the choice of climate race.

As mentioned, consideration must also be given to the plants' most susceptible period and the site class on which the trees grow.

If we ignore the influence of photoperiodicity on the termination of growth, LANGLET (7), it is shown by, i. a. LADEFOGED (4) that the temperature has an influence on the termination of growth. MORK (8), has shown that temperature is a decisive growth factor. He has investigated how the growth of Norway spruce shoots varies with the temperature. It is therefore quite obvious that cold summers with



Decreasing frost resistance.

Fig. 1.

insufficient aggregate warmth for a given provenance also result in this provenance being poorly matured. This makes damage by frost possible.

Fig. 1 shows how different climatic races with declining hardiness defined as resistance to autumn and winter frosts, will react in three different climates, designed as A, B and C. A indicates the coldest, C the warmest and B something between the two. The determination of these lines of regression will give us information about the different climatic races general resistance or susceptibility to frost in the future.

In the international Scots pine provenance experiment at Matrand, a study has been made of the termination of growth. Interesting data has come to light after the collection of samples of the current annual rings for 1959 and 1960 in the different provenances. On the 12th August 1959 I collected between 3 and 15 samples for each provenance shown in *table 1*. Samples were taken of three individuals in each repeat. The sample trees chosen at random from amongst the prevailing trees in each square. The samples were cut from the east side of the trees, and comprised at all times the 14th year from the pith.

By means of cutting a section of each individual sample, using freezing technique on a microtome with a section

Table 1

Provenances No.	Provenances Locality	North lat.	East long.	Altitude *m*	No. replications
1	Inari	68°40'	27°37'	140	2
2	Rovaniemi	66°25'	26°36'	250	5
3	Saaminki	61°44'	28°55'	85	5
4	Tynset	62°22'	10°48'	550	3
5	Målselv	69°06'	18°50'	75	1
6	Åsnes	60°32'	12°11'	230	5
7	Svanøy	61°30'	5°07'	50	5
8	Voxna	61°20'	15°31'	200	5
9	Tønnersjøheden	56°40'	13°08'	100	5
11	Vecmokas	57°03'	23°10'	80	5
14	Talmacel	45°40'	24°08'	600	5
17	Glen Garry	57°04'	4°55' W	150	4
18	Hersselt (cult.)	51°03'	4°56'	20	5
19	Diever (cult.)	52°51'	6°21'	10	5
20	Pförten	51°47'	14°46'	85	5
21	Göddenstadt	52°59'	10°50'	75	5
22	Cruttinen	53°41'	21°26'	120	5
23	Elmstein	49°20'	7°57'	325	5
24	Zellhausen	50°01'	9°00'	140	5
48	Vitsand	60°23'	12°55'	175	3
49	Axamo	57°46'	14°03'	225	1
53	Mustejki	54°08'	24°25'	130	1
—	Skjåk	61°52'	8°10'	400	14

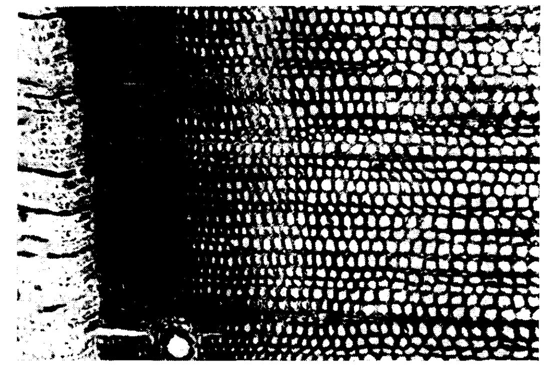


Fig. 2. — Nearly terminated growth. August 12, 1959. Provenance Skjåk, Norway. Informations *table 1*. Photo F. STEMSRUD.

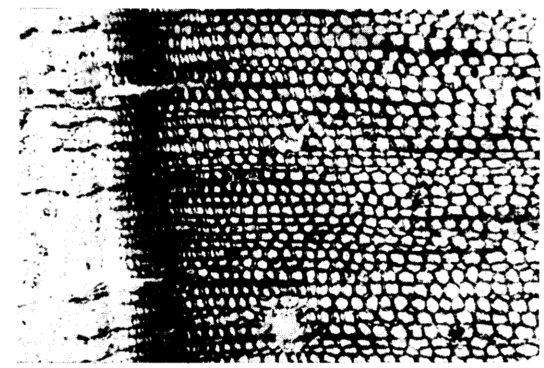


Fig. 3. — Annual ring still growing August 12, 1959. Provenance 19, Diever, Holland. Informations *table 1*. Photo F. STEMSRUD.

thickness of 20 micron, and subsequently colouring the section red with phloroglucin and HCL, I was able to see under the microscope whether the growth had stopped. *Fig. 2* shows a picture of what the wood should look like when the cambium is in its dormant state during winter. *Fig. 3* shows an annual ring which is still growing.

Terminated growth is defined as the stage where the current year's summer wood is fully grown, and the formation of secondary thickness-increment of the summer wood is complete up to the cambium zone.

Examination of the different provenances on the 12th August 1959 showed that only the most northerly provenances had reached the completed growth stage. The remaining provenances were still growing, according to the definition. For the purpose of grading the provenances, the summer wood was defined in accordance with measurements given by MORK (9). Summer wood as a percentage of annual ring width at 12th August 1959 is used as a comparison. The results are seen in relation to the observations published by LANGLET (6) regarding the dry matter percentage in the needles in the same provenances in the corresponding Swedish survey. *Fig. 4* shows the line of regression. The correlation coefficient is 0.4. The averages of the provenances are included.

We see that the westerly central European races have the lowest percentages of summer wood. The result suggested that, apart from having differences between Scandinavian and central European races, there were also differences between those from the east and west of the continent. Provenance No. 24 from Zellhausen showed irregular wood formation as a result of hidden frost. This was present in several repetitions. *Fig. 5* shows a micro-picture of annual ring transition 1958-1959 from a tree in this provenance. It is probable that the climate in 1958 has been inadequate to allow of full maturity being reached in the

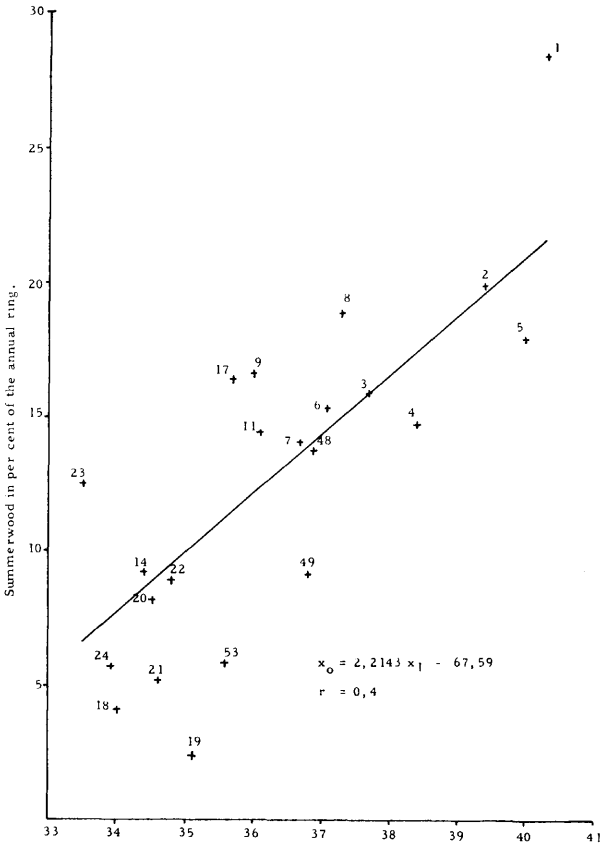


Fig. 4. — Relative termination of growth by measurement of the summerwood, August 12, 1959. 440 growth units.

provenance from Zellhausen. Individual cambium cells have been damaged, resulting in irregular wood. *Picture No. 6* of a provenance from Skjåk, which was used as a standard in the survey, shows that termination of growth is not tangentially regular. The growth here is practically completed on 12th August 1959, but certain cells are still not lignificated. It is possible that such retarded termination of growth in the case of individual cells has caused unsatisfactory maturing of the corresponding cambium cells, which have consequently frozen and led to picture 5.

In many cases we will not find irregular cells of this type, because either segments or the entire circumference of the trunk suffer damage by frost. The first circumstance will lead to the destruction of the tissue followed by splitting

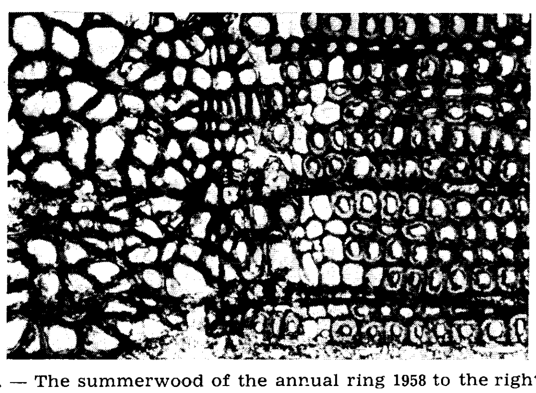


Fig. 5. — The summerwood of the annual ring 1958 to the right. The springwood 1959 to the left. Frostinjury have probably disordered the cells in the springwood. Provenance 24, Zellhausen. Informations *table 1.* Photo F. STEMSRUD.

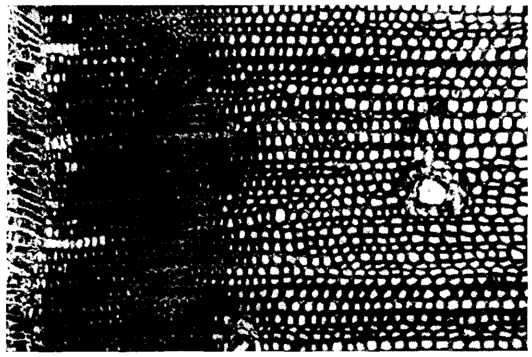


Fig. 6. — The annual ring nearly terminated growth. Some rows of cells still not lignificated. Provenance Skjåk, Norway. Informations *table 1.* Photo F. STEMSRUD.

of the trunk, while the latter will result in the death of the tree or its top.

Collecting samples only once during the autumn is not a wholly satisfactory method, because there is considerable variation in the summer wood percentages even when the growth is fully completed. In 1960, therefore, termination of growth was followed up by the taking of samples at intervals from the beginning of July to the beginning of October. The summer of 1960 was cold in relation to the summer of 1959. A meteorological station, Skotterud, which lies about 6 km. from the international Scots pine provenance experiment, served as a basis for the definition of growth units, according to MORK (8). The growth unit is the growth effect realised when the mean temperature of the six warmest hours of the day are 8^0 C. The growth unit for each day can be gauged approximately by taking the temperature at 2 P. M. *Fig. 7* shows the growth units for the international Scots pine provenance experiment at Matrand during the last 11 years, calculated from 1st May to 30th September each year.

The summer of 1959, which was warm, allowed full termination of growth for all the central European Scots pine

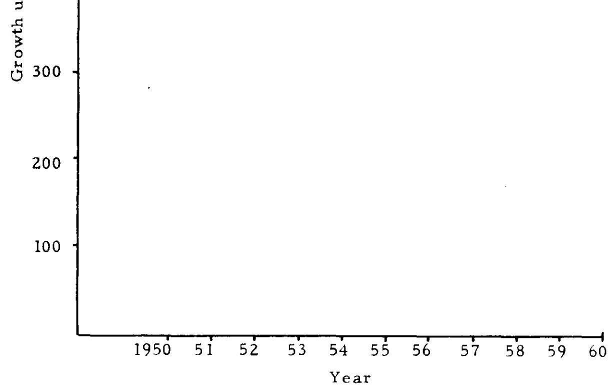


Fig. 7. — Growth units, after E. MORK (1941). The international Scots pine test, Matrand, Norway.

Table 2

	Provenance	Succession of termination of growth different trees 1960					
1	Inari	1	1	-	-	-	-
2	Rovaniemi	2	3	5	-	-	-
3	Saaminki	2	2	-	-	-	-
4	Tynset	2	2	-	-	-	-
5	Målselv	2	2	-	-	-	-
6	Åsnes	3	3	5	-	-	-
7	Svanøy	2	2	-	-	-	-
8	Voxna	2	2	5	-	-	-
9	Tønnersjøheden	4	5	5	5	-	-
11	Vecmokas	5	3	7	6	-	-
14	Talmacel	5	5	5	5	7	-
17	Glen Garry	5	5	5	5	5	-
18	Hersselt (cult.)	5	7	7	7	6	-
19	Diever (cult.)	7	7	6	7	6	7
20	Pförten	7	7	5	7	6	-
21	Göddenstadt	7	7	6	6	7	-
22	Cruttinen	5	6	5	5	6	-
23	Elmstein	4	5	7	7	7	-
24	Zellhausen	7	7	6	7	-	-
48	Vitsand	3	3	-	-	-	-
49	Axamo	4	5	-	-	-	-
53	Mustejki	4	4	-	-	-	-
—	Skjåk	5	3	-	-	-	-

No. succession	Wood formation terminated
1	July 20th.
2	Aug. 7th.
3	Aug. 30th.
4	Sept. 8th.
5	Sept. 19th.
6	Oct. 4th.
7	Not terminated 1960.

species. In 1960, the summer was so cold that on the western central Scots pine provenances termination of growth was not reached. The eastern central European races reached full termination of growth before the onset of winter, but as might be expected, ceased growing later than the Scandinavian races. In 1960 the number of specimen trees had to be limited, compared with 1959. Only two individuals from each provenance were examined in the case of the Scandinavian provenances, while five individuals were examined from each of the central European. *Table 2* shows termination of growth dates for the various races of Scots pine.

We see here that provenance 17 from Glen Garry in Scotland falls in the same class as the eastern central European races as far as resistance is concerned. *Fig. 8* shows a histogram of the degree of significance in relation to the provenance from Glen Garry. The result must be interpreted as showing that there is no demonstrable difference

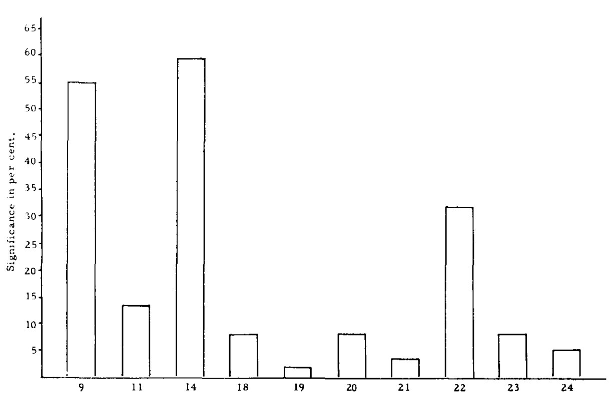


Fig. 8. — Termination of wood formation 1960. Significance levels in comparison with Scots pine from Glen Garry, Scotland. Based on probability.

in resistance between provenances 9, 11, 14 and 22 and 17. The western continental races 18, 19, 20, 21, 23 and 24 are, however, less resistant. This result is in agreement with the investigations made with Norway spruce *(P. abies)*, Langlet (7). He shows that the Polish spruces cease growing earlier in the autumn than the more westerly races.

If we look at *fig. 7*, it will be seen that the years 1956, 1957 and 1958 have all been poor climatically. Studies of the annual rings on a number of trees cut during thinning operations in the autumn of 1960 showed that the summer of 1957, which was the coldest of these years, had given full termination of growth neither for the western nor the eastern central European races. There is, therefore, reason to assume as a further working hypothesis, that a climate which gives less than 450 growth units is in the minimum even for the eastern central European races of Scots pine investigated. In addition to this, a climate giving 500 growth units is in the minimum for the western central European races.

As previously mentioned, there is no direct evidence of damage as a result of frost in the Matrand research plot, but retrospective measurement of the top shoots of the nine highest trees in each square of each provenance could, however, indicate a reduction of the height increment in relation to the Scandinavian races. This reduction has been apparent from 1956 up to the present. The central European races, which at first had the strongest growth, are now outdistanced by the more northerly Scandinavian races.

The international Scots pine research at Matrand, Eidskog. proves that one should be very careful in basing conclusions on quite young research projects. There is no doubt that southern provenances in general are more vigorous in growth. But if the limit of tolerance for resistance is exceeded, this is at the expense of growth vigour in relation to the native breeds. The problem of establishing how much warmth the various provenances must have to complete growth is therefore very important in the northern countries. I have undertaken a number of investigations with young plants of various tree species, to find out more about this.

In the autumn of 1958, I gathered Norway spruce seed from a number of plantations in south-eastern Norway. The plantations, which dated from the beginning of the century, have grown well. The unknown origin has given rise to much speculation as to the provenance. Many have assumed that these were examples of the successful application in Norwegian forestry of central European climatic races. Klem (7) investigated two of these stands in connection with dry pulp production, and found that they had more dry pulp than the Norwegian climatic races. This provided a new reason for the use of central European provenances in Norwegian forestry.

During the summer of 1959, seeds from the assumed Norwegian-German stands were sown in an experiment, for the purpose of studying the growth-rhythm of these stands. The seeds were sown in boxes filled with well-mixed forest soil from the Norwegian Forest Research Institute, Vollebekk. Two repeats were made of each seed sample. As a comparison, sowings were made from provenances from Harz 520 m. above sea level and 220 m. above sea level, and autochthon Norwegian stands.

On the 21st October 1960, three individuals were selected at random from the 2-yearly plants, with the object of studying growth termination. By using the procedure followed for Scots pine, it could be established that of the

Norway spruce plants, which originated directly from the Harz district, only 1 in 7 of those investigated had terminated growth in accordance with the previous definition. The result reveals that the descendents of the investigated Norwegian-German stand are more resistant than the imported Harz provenances, even from the imported selected trees at 520 m. above sea level.

The result of this little investigation encouraged me to continue. In the first half of November 1960, therefore, I gathered a quite large material from different Norwegian forest nurseries. The samples included not only Norway spruce, but also *Pseudotsuga taxifolia, Tsuga heterophylla, Picea sitchensis* and *Larix* spp.

The investigations showed that a number of the more southerly races had not succeeded in terminating growth during the summer of 1960. *Fig. 9* shows a histogram, giving some of the results obtained for Norway spruce.

The incomplete termination of growth in 1960 has not led to great damage by frost in Norwegian forest nurseries, but there are also instances of various provenances of *Pseudotsuga taxifolia* from Washington and Oregon being badly damaged by frost in their 4th year of life, after previously having survived in the coastal regions of southern Norway. Anatomic investigation of these provenances revealed a very low degree of maturity. As the winter of 1960/61 was warmer than is normal in Norway, this shows that the limiting factor as a rule is summer temperature and not winter temperature. In this we must disregard the coastal regions, where the winter temperature seldom falls below —5° C to —10° C.

In the north of Norway at Sandnessjøen, lat. 66° N., right on the coast, the Norwegian Forest Research Institute has a production plantation of Norway spruce. The existing stand is about 40 years old. Its origin is said to be southern Norway. During measurement of the stand in 1960, increment cores were collected to determine the course of production.

When the measurements were taken, the observer discovered that the Norway spruce, according to the definition of summer wood, had seldom succeeded in forming any of this.

This proves that the coastal climate, because of its mild winters, enables southern races to grow without being subject to frost damage. On the other hand, it is very probable that southern races cultivated at the limit of what they can tolerate, will give reduced dry pulp production.

The investigation here shows that the problem of resistance is complicated, but that even in experiments when the plants are young we can obtain relative values for resistance, defined in accordance with the termination of growth of the wood. That the growth of wood proceeds normally and is built up in accordance with its ultimate purpose is something which cannot be ignored by forest tree breeders.

In many provenance research projects, perhaps especially in northern countries, the foreign provenances are often attacked by diseases of various types. It is probable that this is due to the different growth rhythms of the various races. Hidden frost damage has a retarding effect on growth, and impairs resistance to diseases. Often we persuade ourselves that special hybrids or provenances are less resistant to diseases, but it is perhaps a question of whether the primary factor is not the difference in the growth rhythm of the various races and hybrids. If this is so, we can form an opinion of the likelihood of a successful result in practical forestry even while the plants are small.

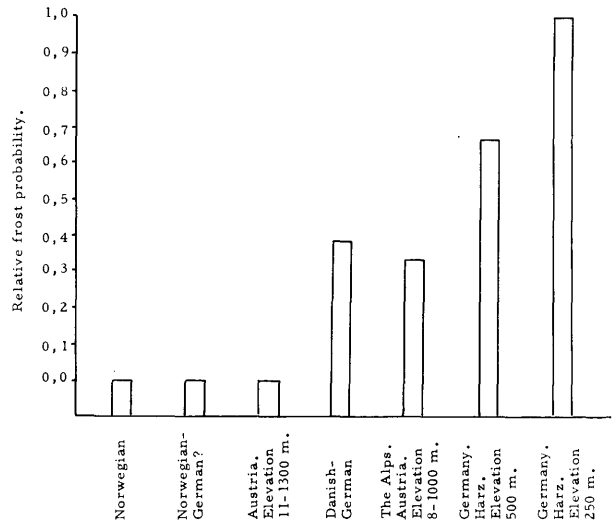


Fig. 9.

Summary

In Norway, as in several other northern countries, it is important that the forest seed which is marketed, gives sufficiently hardy plants. By "hardy" is understood resistance to spring, autumn and winter frost.

The international Scots pine provenance experiment from 1938 at Matrand, Norway *(table 1)*, has been studied concerning the growth rhythm. The growth start in the spring has been investigated by observations of the budding. The results agree fully with observations made by Langlet (6). Because the central European races at Matrand bud later than the Scandinavian, their is little likelihood of spring frost in the case of the central European Scots pine *(Pinus silvestris)*. Since it has long been known that southern provenances continue to grow later in the autumn than the northern ones, this is a factor which limits their transfer to a colder type of climate. Lack of maturity in autumn leads to frost damage the following autumn or winter.

No visible damage by frost could be registered in the provenance experiment at Matrand. But examination of the wood from the most recent years, as well as the wood formations at the close of the vegetation period by means of microscopic sections, revealed data which clearly graded the races according to the time of growth termination. Terminated growth is defined as the stage where the current years summer wood is fully grown, and the formation of secondary thickness-increment of the summer wood is complete up to the cambium zone.

Studies in the years 1959 and 1960 gave a result which showed that western continental races stopped growing later in the autumn than the provenance no. 17 from Glen Garry and the eastern continental races. In 1960 the climate was colder than 1959. In the warm summer 1959 all the races reached maturity, but in 1960 only the Scandinavian and the eastern continental races included the provenance from Glen Garry terminated growth. Studies of the wood from 1957 which had even a colder climate than 1960 had not given full termination of growth neither for the western nor the eastern central European races.

Retrospective measurement in the Matrand test of the top shoots of the nine highest trees in each square of each

provenance could indicate a reduction of the height increment in relation to the Scandinavian races. This reduction has been apparent from 1956 up to the present. The central European races, which at first had the strongest growth are now outdistanced by the more northerly Scandinavian races.

The international Scots pine research at Matrand, proves that we should be very careful in basing conclusions on quite young research projects. There is no doubt that southern provenances in general are more vigorous in growth. But if the limit of tolerance for resistance is exceeded, this is at the expense of growth vigour in relation to the native breeds.

Anatomic investigations on small plants of Norway spruce *(Picea abies)*, Douglas fir *(Pseudotsuga taxifolia)*, Western hemlock *(Tsuga heterophylla)*, Sitka spruce *(Picea sitchensis)* and different *Larix* spp., showed that a number of the more southerly races had not succeeded in terminating growth during the summer of 1960. A low degree of maturity does not always lead to frost damage. In the Norwegian coastal regions, there are examples where more southerly races of Norway spruce grow well without reaching full maturity in the autumn. In the coastal regions mentioned, the winter temperature seldom falls below -5^0 C. to -10^0 C.

It is probable that southern races cultivated at the limit of what they can tolerate, will give reduced dry pulp production.

The investigation shows that the problem of resistance is complicated, but that even in experiments when the plants are young, we can obtain relative values for resistance, defined in accordance with the termination of growth of the wood.

Zusammenfassung

Titel der Arbeit: *Züchtung auf Frostresistenz.*

In Norwegen, wie in mehreren anderen nördlichen Ländern, ist es wichtig, daß man aus Handelssaatgut ausreichend frostharte Pflanzen anziehen kann. Unter „frosthart" verstehen wir widerstandsfähig gegen Früh-, Spät- und Winterfröste.

Der Internationale *Pinus silvestris*-Provenienzversuch aus dem Jahre 1938 in Matrand Norwegen *(Tabelle 1)*, wurde hinsichtlich des Wachstums-Rhythmus untersucht. Der Wachstumsbeginn im Frühjahr wurde durch Knospenbeobachtungen festgestellt. Die Ergebnisse stimmen mit den Langletschen Beobachtungen (6) völlig überein. Weil die mitteleuropäischen Rassen in Matrand später austreiben als die skandinavischen, ist bei ihnen die Wahrscheinlichkeit von Spätfrostschäden recht gering. Da es schon seit langem bekannt ist, daß südliche Herkünfte ihr Wachstum im Herbst länger fortsetzen als nördliche, stellt dieses Verhalten eine Begrenzung des Eindringens in kältere Klimaregionen dar. Die fehlende Verholzung im Herbst führt zu Frostschäden im darauf folgenden Spätherbst oder Winter.

Im Provenienzversuch Matrand waren keine sichtbaren Frostschäden festzustellen. Jedoch führten mikroskopische Untersuchungen des in den letzten Jahren gebildeten Holzes und auch der Holzbildung am Ende der Vegetationsperiode zu Befunden, nach denen die Rassen hinsichtlich ihres Wachstumsabschlusses klar abgestuft werden konnten. Wachstumsabschluß wird als Stadium definiert, in dem das Spätholz des laufenden Jahres voll ausgebildet und die Ausbildung des sekundären Dickenwachstums des Spätholzes bis zum Kambium abgeschlossen ist.

Untersuchungen der Jahre 1959 und 1960 führten zu dem Ergebnis, daß bei westlichen kontinentalen Rassen der Wachstumsstop später im Herbst eintrat als bei der Provenienz Nr. 17 aus Glen Garry und bei den östlichen kontinentalen Rassen. 1960 war das Klima kälter als 1959. Im warmen Sommer 1959 schlossen alle Herkünfte ihr Wachstum ab, 1960 jedoch nur die skandinavischen, die ostkontinentalen und die Provenienz Glen Garry. Untersuchungen des 1957 gebildeten Holzes, ein Jahr in dem es noch kälter war als 1960, ergaben, daß weder bei den westlich- noch bei den östlichkontinentalen Rassen das Wachstum abgeschlossen worden war.

Verfolgt man im Versuch Matrand das jährliche Höhenwachstum der neun höchsten Stämme jeder Provenienz und jeder Wiederholung zurück, so stellt sich eine Reduktion der Trieblänge im Vergleich zu den skandinavischen Provenienzen heraus. Dieses Nachlassen war von 1956 bis zum Untersuchungsjahr zu beobachten. Mitteleuropäische Herkünfte, die anfangs am kräftigsten wuchsen, werden nun von den nördlicheren skandinavischen Rassen übertroffen.

Der internationale Kiefernversuch in Matrand macht klar, daß man in der Aufstellung grundsätzlicher Schlußfolgerungen aus jungen Versuchsanstellungen zurückhaltend sein sollte. Ohne Zweifel sind südliche Provenienzen generell wüchsiger. Falls jedoch die Toleranzgrenze der Resistenz überschritten wird, geschieht das auf Kosten der Wüchsigkeit im Vergleich zu den einheimischen Populationen.

Anatomische Untersuchungen an Sämlingen von *Picea abies, Pseudotsuga taxifolia, Tsuga heterophylla, Picea sitchensis* und verschiedenen *Larix*-Arten ließen erkennen, daß eine Anzahl südlicher Herkünfte während des Sommers 1960 ihr Wachstum nicht abgeschlossen hatten. Unvollständiger Wachstumsabschluß führt jedoch nicht immer zu Frostschäden. In der norwegischen Küstenregion findet man Beispiele dafür, daß südliche Herkünfte von *Picea abies* Gutes leisten, ohne völligen Wachstumsabschluß im Herbst zu erreichen. In den erwähnten Küstenpartien sinkt die Temperatur selten unter $—5^0$ bis $—10^0$ C ab.

Wahrscheinlich werden an der Grenze ihrer Kältetoleranz angebaute südliche Rassen eine geringere Produktion von Trockencellulose aufweisen.

Die Untersuchungen zeigen, daß das Frostresistenzproblem verwickelt ist, daß man jedoch selbst bei Experimenten mit jungen Pflanzen Relativwerte der Resistenz in Anlehnung an den Wachstumsabschluß des Holzes erhalten kann.

Résumé

Titre de l'article: *Sélection pour la résistance au froid.*

En Norvège, ainsi que dans plusieurs autres pays nordiques, il est nécessaire que les graines mises sur le marché donnent naissance à des plants suffisamment rustiques. Par »rusticité«, on entend la résistance au froid de printemps, d'automne et d'hiver.

Le rythme de croissance des arbres a été étudié dans la plantation comparative internationale de provenances de pin sylvestre établie en 1938 à Matrand, Norvège *(tableau 1)*. Des observations sur le débourrage ont permis de connaître le départ de la croissance au printemps. Les résultats concordent avec ceux obtenus par Langlet (6). Les races de l'Europe centrale débourrent plus tard à Matrand que les races scandinaves; il est donc peu probable que ces provenances de pin sylvestre d'Europe centrale souffrent de

gelées printanières. On sait depuis longtemps que les provenances méridionales poursuivent leur croissance plus tard à l'automne que ne le font les provenances septentrionales; ce fait limite donc leur transfert dans un climat plus froid. Le mauvais aoûtement conduit à des dégâts de gelée à l'automne ou à l'hiver suivant.

Aucun dégât de gelée n'a pu être observé dans l'expérience de provenances à Matrand. Mais l'examen microscopique du bois des dernières années et de la formation des cellules à la fin de la période de végétation a permis de classer les provenances suivant l'époque où elles arrêtent leur croissance. La croissance est considérée comme terminée lorsque la formation du bois d'été de l'année est achevée et que l'épaississement secondaire du bois d'été est complet jusqu'à l'assise cambiale.

Les études faites en 1959 et 1960 ont montré que les races d'Europe occidentale arrêtent leur croissance plus tard à l'automne que la provenance n⁰ 17 de Glen Garry et que les provenances d'Europe orientale. En 1960, le climat fut plus froid qu'en 1959. Après l'été chaud de 1959, toutes les provenances se sont aoûtées, mais en 1960, seules celles de Scandinavie et d'Europe orientale, avec celle de Glen Garry, ont achevé leur croissance. L'étude du bois de 1957, année plus froide encore qu'en 1960, a montré qu'aucune des provenances d'Europe occidentale ou orientale n'avait pu achever sa croissance.

La mesure rétrospective dans l'expérience de Matrand des pousses terminales des 9 plus grands arbres dans chaque parcelle unitaire a révélé une réduction de la croissance en hauteur pour les provenances scandinaves. Cette réduction s'est manifestée depuis 1956. Les races d'Europe centrale, qui avaient au début la plus forte croissance, sont maintenant distancées par les races scandinaves plus septentrionales.

Cette expérience internationale de pin sylvestre de Matrand prouve que nous devon être très prudents dans les conclusions tirées d'expériences très jeunes. Il est certain que les provenances méridionales en général ont une croissance plus forte. Mais si la limite du seuil de résistance est dépassée, c'est la vigueur de croissance qui en souffre.

Des études anatomiques de jeunes plants d'épicéa *(Picea abies)*, Douglas *(Pseudotsuga taxifolia)*, Tsuga de l'Ouest *(Tsuga heterophylla)*, épicéa de Sitka *(Picea sitchensis)* et différentes espèces de mélèze, ont montré qu'un certain nombre des types méridionaux n'ont pu achever leur croissance au cours de l'été 1960. Un aoûtement incomplet ne se traduit pas toujours par un dégât de gelée. Dans les régions côtières de Norvège, on connaît des cas où des races d'épicéa méridionales poussent très bien, bien qu'elles s'aoûtent imparfaitement à l'automne. Dans ces régions, la température hivernale tombe rarement au-dessous de -5^0 C à -10^0 C.

Il est probable que des races méridionales cultivées à la limite de leur résistance au froid donneront une production de matières sèches réduite.

Ces recherches montrent que le problème de la résistance est complexe, mais que, même dans les expériences sur de jeunes plants, nous pouvons obtenir des estimations relatives de la résistance, celles-ci étant définies d'après l'achèvement de la période de croissance.

Literature

(1) ANDERSON, S. O.: Om tidpunkten för den årliga diametertilväxtens avslutande hos tall och gran. (On the date of completion of annual diametral growth in pine and spruce.) Statens Skogforskningsinstitut, Medd. B 43 nr. 5, 1—27 (1953). — (2) JOACHIM, H. F.: Frostschäden an der Gattung *Populus*. Forst und Jagd 8, 458—461 (1958). — (3) KLEM, G. G.: Kvalitetsundersøkelse av norsk og tysk gran. (The Quality of Norway Spruce *[Picea abies]* of Norwegian and German Origin.) Medd. Norske Skogforsøksvesen nr. 48, B. XIV, 290—314 (1957). — (4) LADEFOGED, K.: The Periodicity of Wood Formation. Kgl. Danske Videnskabernes Selskab. Biol. skr. 7, no. 3, 98 p. (1952). — (5) LANGLET, O.: Studier över tallens fysiologiska variabilitet och dess samband med klimatet. (Studien über die physiologische Variabilität der Kiefer und deren Zusammenhang mit dem Klima.) Medd. f. Statens Skogsforsøksanstalt 219—470 (1936). — (6) LANGLET, O.: A Cline or not a Cline — a Question of Scots pine. Silvae Genetica 8, 13—22 (1959). — (7) LANGLET, O.: Mellaneuropeiska granprovenienser i svenskt skogsbruk. (Mitteleuropäische Fichte in Schweden, nach den Ergebnissen des internationalen Provenienzversuches von 1938.) Kungl. Skogs- och Lantbruksakademiens Tidskrift 99, 259—329 (1960). — (8) MORK, E.: Om sambandet mellom temperatur og vekst. Undersøkelser av de daglige variasjoner i granens høydevekst. (Über den Zusammenhang zwischen Temperatur und Wachstum. Untersuchungen der täglichen Variationen des Höhenzuwachses.) Medd. Norske Skogforsøksvesen nr. 27. B. VIII, h. 1, 1—89 (1941). — (9) MORK, E.: Granvirkets kvalitet særligt med sigte på slip og celluloseved. Papir-Journalen 16, 54—58 (1928). — (10) MORK, E.: Om sambandet mellom temperatur, toppskuddtilveksten og årringens vekst og forvedning hos gran. (On the relationship between temperature, leading shoot increment and the growth and lignification of the annual ring in Norway spruce *[Picea abies]* [L.] KARST.) Medd. fra Det norske Skogforsøksvesen nr. 56. B. XVI. H. 4, 229—261 (1960). — (11) OKSBJERG, E.: Om udspringstid og skudstrækning i grankulturer. Hedeselskabets Tidsskrift 75, 49—55 (1954). — (12) ROLL-HANSEN, F.: Melding om sykdommer på skogstrærne i Norge i året 1959. (Annual Report on Forest Diseases in Norway 1959.) Medd. Norske Skogforsøksvesen nr. 57. B. XVI, h. 5, 339—349 (1960). — (13) ROMELL, L. G.: Växttidundersökningar å tall och gran. (Recherches sur la marche de l'accroissement chez le pin et l'épicéa durant la periode de végétation.) Medd. från Statens Skogsforsöksanstalt. H. 22, 45—124 (1925). — (14) SCHOBER, R.: Zum jahreszeitlichen Ablauf des sekundären Dickenwachstums: Untersuchungen im Lehrforstamt Kattenbühl. Allg. Forst- u. Jagdztg. 122, 81—96 (1951). — (15) SUNDVOR, T.: Noen undersøkelser over når tykkelsestilveksten innstilles hos lauvtrærne om høsten på Vestlandet. (Some Observations on the Date of Cessation of Cambial Activity in Deciduous Trees in Western Norway.) Blyttia 14, 122—125 (1956).