Provenance and clonal variation in phenology and wood properties of Norway spruce[1])

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Introduction

Norway spruce, Picea abies (L.) Karst., has a wide natural range, and is of economic importance both within this range and as an exotic. Consequently interest in it from the genecological and tree improvement viewpoints, has been strong. The main patterns of variation, and their association with climatic variables were established early by **Cieslar** (e. g. 1899) and Engler (e. g. 1908). Langlet (1960) has been particularly interested in Norway spruce, and has periodically reviewed past work (1962, 1967). Study of the species is still very active, as is indicated by the large number of reports published on it every year (e. g. Dietrichson 1973) and by the continued establishment of provenance tests (see Vins, 1967). The present study is concerned with variation in phenology and wood properties in the Deering, New Hampshire, U.S.A. plantation of the 1938 IUFRO provenance test.

Materials

This plantation has been evaluated at various ages by Baldwin (1949a and b, 1967) and by Baldwin *et* al. (1973). The results from the numerous European and north American plantations of the same material were summarized by **Lines** (1974). There were two replications (blocks) at Deering, but sufficient funds only to adequately weed and maintain the first of these. Thus provenance measurements in this study were all made on Block I and are mainly on IUFRO provenances, but also on some non-IUFRO provenances. A few provenances were represented by two 15 X 13 tree plots in Block I (see Baldwin et al. 1973 page 99). Analysis of data from these provenances showed no differences between plot means in any of the traits studied; it was therefore considered not entirely inappropriate to assume there was no significant between blocks variance. Consequently the error term used in the analyses below is "within provenance", and is arguably a) too small, and b) less efficient an estimate of error variance than would be that from pooling with the block variance. Perhaps, therefore, the results indicate more between provenance variation than is actually present.

Further estimates of variation and genetic control of various traits were made by studying a plantation of clones of Norway spruce established by rooting of cuttings by **Farrar**[3]) in 1943, and growing in Petawawa, Ontario. There was one plot per clone, and the plantation is on a uniform site.

Methods

Detailed descriptions of the methods used for measuring height and diameter growth, and wood properties have been described elsewhere (Worrall 1970, 1973). The measurements on which the various calculations are based are as follows:

a) height increment, rate of height growth, and dates of initiation and cessation of height growth for 75 trees of 15 provenances in 1966;
b) the same as in a for 312 trees of 18 provenances in 1967, plus the height increment of 1966. Thirty five trees were common to a and b;
c) the same as in b for 64 trees in seven clones;
d) radial increment, rate of radial growth, dates of initiation and cessation of radial growth and date of initiation of latewood for 212 trees of 18 provenances in 1967. All trees were also measured as in b;
e) whole ring, earlywood and latewood specific gravities, and latewood percentage in the 1966 and 1967 increments of trees measured in d.

In addition, total height and diametex of all trees was measured. Growth rate was defined as grand period growth rate. Dates of initiation and cessation of growth were defined as the dates of completion of 5% and 95% of growth respectively. The length of the growing season was thc difference between these two dates. Since damage to the leaders was heavy, particularly in 1966, the correlation coefficients and variance components given in Table 1 are often based on a lower number of observations than indicated above.

In both the provenance and clonal material the model for the analyses of variance for between group differences, and calculation of variance components was $y_i = \mu + a_i + e$, where y_i is the value of an observation in the ith group, μ is the overall mean, a_i the deviation from this for group i, and e is the normally distributed random component: i takes the values 1 to 7 for the clones, 1 to 15 for the provenances in 1966, 1 to 18 in 1967. Since there was an unequal number of observations per group, f_i, the group variance components were computed from the between group variance minus the error variance divided by $(\Sigma f_i - \Sigma f^2_i/\Sigma f_i) / (i - 1)$, i. e. by f reduced by a simulated variance V(f) as described by Bliss (1966, page 258).

Since some measurements of the same character were repeated on each genotype, either in time, i. *e.* on the same tree in 1966 and 1967, or in space, i. e. on different ramets of the same clone, some estimates of heritability, and repeatability could be derived. Following **Falconer** (1960), the environmental variance consists of VE_s, and VE_g, which are the within individual variance due to temporary or localised circumstances, and the general environmental variance arising from permanent or non-localised circumstances (e.g. Libby's "C" effects, 1964). If V, is the genetic variance, and V, the phenotypic variance, then r, the correlation between repeated measurements is (V, $+ VE_g)/V_p$, the repeatability. This defines the upper limit of heritability and varies not only with particular characteristics, but with environmental conditions and the genetic properties of the population. This is well illustrated by the data of **Burdon** and **Harris** (1973). From the clonal material, the between clones variance divided by the between plus within clone variance is, according to some authors, an estimate of heritability (h^2), or may more correctly be called clonal repeatability.

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Table 1. — Variance components and repeatabilities for various traits.

Trait	Clones		Provenances	
	variance component % (= heritability h^2?)	repeatability r	variance component %	repeatability r
height growth init. 1966			74.9**^{a}	.87**^{b}
height growth init. 1967	.19*		56.5**^{c}	
height growth cess. 1966			39.9**^{a}	.53**^{b}
height growth cess. 1967	.59**		41.1**^{c}	
length g.s. 1966			18.7* ^{a}	.55**^{b}
length g.s. 1967	.73**		13.1**^{c}	
growth rate 1966			7.3 ^{a}	.62**^{b}
growth rate 1967	.73**		8.7**^{c}	
height growth 1966	.72**	.84**	1.9 ^{a}	.70**^{b}
height growth 1967	.72**		6.2* ^{c}	
height growth 1967/1966	.58**		27.2**^{b}	
height growth 1966 + 1967	.72**		2.7 ^{b}	
total height to 1967	.57**		34.0**^{c}	
cambial growth init. 1967			6.1* ^{d}	
cambial growth cess. 1967			8.2* ^{d}	
date init. latewood 1967			17.1* ^{d}	
length g.s. 1967			7.1**^{d}	
ring width 1966	.37**	.47**	28.5**^{d}	.50**^{d}
ring width 1967	.62**		22.1**^{d}	
ring width 1967/1966	.68**		17.1**^{d}	
ring width 1966 + 1967	.41**		22.7**^{d}	
total diameter to 1967	.69**		12.1**^{c}	
ring s.g. 1966	.51**	.64**	6.8**^{d}	.61**^{d}
ring s.g. 1967	.70**		9.0**^{d}	
earlywood s.g. 1966	.63**	.84**	14.2**^{d}	.80**^{d}
earlywood s.g. 1967	.86**		15.7**^{d}	
earlywood width 1966	.28**	.46**	2.2 ^{d}	.52**^{d}
earlywood width 1967	.51**		1.5 ^{d}	
latewood width 1966	.46**	.37**	7.4* ^{d}	.65**^{d}
latewood width 1967	.51**		9.7**^{d}	
latewood % 1966	.47**	.42**	12.4**^{d}	.52**^{d}
latewood % 1967	.33**		14.3**^{d}	

* Statistically significant at the 5% level of probability.

** Statistically significant at the 1% level of probability by F test For the clones, the base number of observations (or pairs of observations) was 64, in 7 clones, reduced to 61 for some height variables due to weevil damage. For the provenances the numbers were a 75, b 35, c 312 and d 212, again occasionally slightly reduced.

Results

The results are summarized in *Table 1*, and may be compared with those for forest trees given by Hattemer (1963), Zobel (1964) and Namkoong *et al.* (1966). Not all of the data are commented on below.

Phenology of leader growth

Many European workers have shown provenance variation in the date of bud burst, *e. g.* Langlet *op. cit.*, and have established broad high latitude and altitude to low latitude and altitude trends, the former flushing first. The trait is strongly heritable (Langner and Stern 1964) and important in relation to potential damage by late spring frosts. Breeding for late flushing date, coupled with fast growth has been suggested by Rohmeder (1952). In addition to the broad geographic trends there are provenances adapted to local climate, for instance the very late flushing north German lowlands source described by Kiellander (1956). Presumably early flushing trees either respond more quickly to the same temperature than do late flushers, or more likely have a lower threshold temperature above which metabolism occurs.

In the present study the same trend is evident, with latitude (corrected for altitude) being associated with 53% of the variation in 1966 (38 trees) and 47% in 1967 (283 trees). In similar test material assessed by Worrall and Mergen (1967), using cuttings in the greenhouse, 97% of the variation was associated with latitude. Compared to results from European tests, the range in flushing date between provenances was quite small, about eleven days. Oksbjerg (1954) showed that the range between early and late forms was reduced in warm springs, the heat sum required for flushing being obtained in a shorter time by both types. This may explain the present results, since New Hampshire has a relatively continental climate with a rapid mean temperature rise in May and June. Within provenance variation was about seven days.

Comparison of flushing dates in 1966 and 1967 gave a correlation coefficient of .87, indicating the trait may be strongly heritable. However, the clonal value for broad-sense heritability was only .19. This is perhaps because the clones were from trees that had survived the climate of Petawawa and have therefore been selected for late flushing and frost resistance. The flushing date of these clones is late, and varies little between clones. Within clone variation was small compared to within provenance variation (but in a different location), suggesting that there is more genetic control than indicated by $h^2 = .19$. Worrall and Mergen *op. cit.*, using different clonal material, reported higher heritability.

Cessation of height growth is difficult to measure (or even define) in older trees, and has usually been described in terms of bud set in seedlings. Except where lammas growth occurs, date of cessation of height growth is not critical for frost resistance. More important are the subsequent physiological processes associated with hardening off and cessation of cambial activity (Dietrichson, 1964). Bouvarel (1961) however suggested an adaptive advantage of early height growth cessation, since provenances from dry areas set buds early, before soil moisture became depleted. Provenances of many species differ in sensitivity to altered photoperiods in terms of bud set (*e. g.* Vaartaja 1959), but daylength in the field almost certainly has nothing to do with date of height growth cessation in determinate species like Norway spruce, particularly in older trees.

Table 1 shows that provenances differ in the date of cessation of height growth in both 1966 and 1967, and also there are marked clonal differences. Northern provenances cease height growth early ($100 \times R^2 = 21\%$ in 1966; 17% in 1967). Within provenance (and clone) variation is high compared to that in date of bud burst. However repeatability of the trait is quite high ($r = .53$) and the heritability from the clones was .59. Date of cessation of growth seems to be strongly genetically controlled; this fact was used elsewhere (Worrall 1970) to explain the between-provenance variation in the width of a false ring that occurred in the wood of the 1964 increment.

Interestingly, the length of the growing season is not very variable: this is because dates of initiation and cessation of height growth are correlated — early initiation is followed by early cessation. Or it may be argued that early cessation is followed by early initiation next season. This may be so for Norway spruce (Dormling *et al.* 1963) but not for sugar maple (Olmsted, 1951).

The height growth and growth rate variance components due to provenance are small or not significant, but larger for the clones. Despite large differences in 30 year total height, following the general pattern described for other plantations of the 1938 test, differences in 1966, 1967 and (1966 + 1967) height growth were minor and not correlated with total height, either within or between provenances. This is also true of the clones, and of the radial increment in provenances and clones. Evidently there are strong genotype × year (environment) interactions masking expected correlations. Otherwise the ratio of 1967 to 1966 height growth would be a constant. In fact this ratio depends strongly on provenance (but is not related to latitude) and clone. The interactions are illustrated in *Fig. 1*, for both height and radial increment in five clones. Two other explanations for the apparent anomaly (also noted by Hanover in 1963 in ponderosa pine), are possible provenance (and clone) differences in the shape of the sigmoid curve of total height on age. Rapid initial height growth may not be sustained, whereas a provenance with slow initial growth may later grow rapidly. Secondly, damage by the white pine weevil (*Pissodes strobi* Peck) has been occasionally severe — *e. g.* about 50% of trees in the provenance test in 1966, and only 1% in 1967. Damage seems to depend on genotype. For instance in 1967, three trees in the clonal plantation were attacked, and these were all in the same clone. Thus in a year of heavy infestation, growth of susceptible genotypes will be zero or even negative, whereas in a weevil free year, growth will be normal. This is how a year × genotype interaction could occur, and obscure current height — total height correlations.

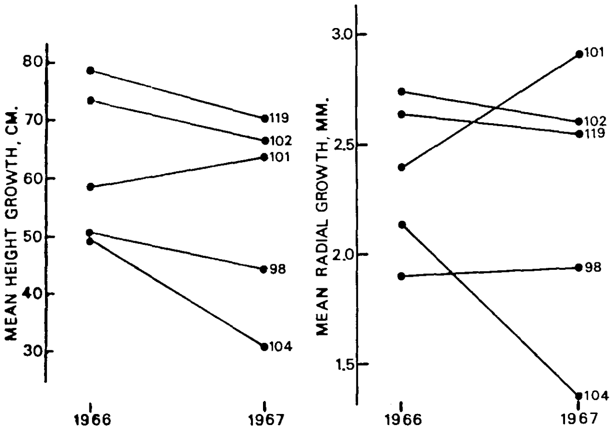

Fig 1. — Growth of five clones, showing the interaction between genotype and year.

Phenology of radial growth

Reports of variation within species are few, emphasis having been on the effects of species, sites, climates, years and silvicultural treatments. Dietrichson (*e. g.* 1964) has been concerned with activity of Norway spruce and Scots pine with particular reference to frost damage. Daubenmire (1950) and Dodge (1963) have shown provenance variation in cambial phenology of ponderosa pine, and Klem (1957) showed southern provenances of Norway spruce ceased growth later than northern ones.

Table 1 shows that differences in date of initiation of radial increment, and of latewood formation, and date of cessation (but not growth rate or amount) are associated with provenance to a minor degree. The first varies considerably less, both within and between provenances than do the other two. All three are weakly correlated to latitude (r = .14, .20 and .14 for 212 trees) with northern provenances starting and ceasing growth early, and initiating latewood early. Considering the patterns of height growth and the dependance of cambial activity on crown activity, the growth and latewood initiation relationship with latitude is expected. Early cessation of radial increment in northern provenances suggests the possible role of daylength.

Wood properties

Provenance variation in wood specific gravity is not large in Norway spruce, and within provenance variation is great enough to cause between provenance differences to be of minor importance, and make within provenance selection for specific gravity more profitable than provenance selection. Relationships with latitude similarly are very weak or absent.

Knudsen (1956) showed no provenance variation in wood specific gravity. Parrot (1960) found differences unrelated to latitude, as did Mergen[4]), in some of the material also used in the present study. Klem (1957) found that German provenances had denser wood than Norwegian ones, when grown in Norway and Sweden. Ericson (1960) showed specific gravity decreased with increasing latitude and altitude.

In the present study there were differences in specific gravity and latewood percent between provenances in both 1966 and 1967, the relationship with latitude being barely significant in 1967 only, northern sources being less dense. This significance was largely due to the fact that seed source IUFRO No. 23, from Finland, had very low density associated with a very narrow latewood band which in turn resulted from very early cessation of radial increment. Klem (1957) also used this reasoning to explain the lower density of northern provenances. Specific gravity of the earlywood was quite variable (.21—.28), and differed between provenances, but not in a way related to latitude. Latewood specific gravity was quite uniform (.58—.61) and did not differ between provenances. The correlations between the various traits in 1966 and 1967 indicate some degree of genetic control.

Heritabilities for the various wood properties in the clonal material were quite high, but less than those of Kleinschmitt and Knigge (1967) measured in the same way, and those of Kennedy (1966). The latter author used some of the same clones as used here, and studied the 1961 ring. The rather large discrepancy may be due to heritability changes with age (see Nicholls, 1967) or with environment, or Kennedy may have chosen a very uniform sample within each clone. Kennedy also included heritabilities for mechanical traits and specific gravities at various distances across the growth ring.

Summary

Differences among provenances in the Deering, U.S.A. plantation of the 1938 IUFRO test, and among clones in a Petawawa, Ontario plantation where demonstrated for many growth and wood properties of Norway spruce. These differences were usually slight when expressed as among provenance variance components. Large within provenance variation, and fairly high repeatability or heritability values suggest that for many traits, selection of individual might be more profitable than selection of provenances.

Dates of initiation and cessation of height growth were fairly strongly correlated with latitude of the provenance origin, northern provenances starting and finishing early.

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Specific gravity and percentage of latewood decreased slightly with increasing latitude in one of the two increments studied, and dates of initiation of radial measurement and latewood formation, and cessation of radial increment all were slightly earlier as latitude increased.

There were no current height growth and current diameter growth correlations with total height and total diameter at age 30 in the provenance material, or in the younger clonal material. This was attributed partly to strong year × genotype interactions.

Key words: repeatability, heritability, height increment, radial increment, specific gravity.

Zusammenfassung

Im IUFRO-Fichten-Provenienzversuch Deering, New Hampshire, U.S.A., von 1938 (*Picea abies* (L.) Karst.) sowie bei Fichtenklonen in einer Plantage in Petawawa, Ontario, Kanada, haben sich bezüglich des Wachstums und der Holzeigenschaften Unterschiede herausgestellt. Diese sind weniger groß von Provenienz zu Provenienz als innerhalb der einzelnen Provenienzen. Daraus wird der Schluß gezogen, daß die Selektion von Individuen als Ausgangsmaterial für züchterische Zwecke erfolgversprechender ist als die Selektion von Provenienzen.

Beginn und Ende des Höhenwachstums sind ziemlich streng korreliert mit der geographischen Breite des Ursprungsortes der jeweiligen Provenienz. Nördlichere Provenienzen beginnen mit dem Höhenwachstum früher und beenden dieses auch früher. Zwischen dem laufenden Höhenzuwachs und der im Alter 30 erreichten absoluten Höhe bzw. dem Durchmesser sind im Jahresgang des Höhenwachstums keine Beziehungen zu erkennen, auch nicht bei jüngerem Klonmaterial. Solche Beziehungen waren teilweise auf Jahr × Genotyp — Interaktionen zurückzuführen.

References

Baldwin, H. I.: Height growth of Norway spruce plantations. Fox Forest Notes No. 38 (1949 a). — Baldwin, H. I.: Growth and weevil damage to Norway spruce growing under aspen. Fox Forest Notes No. 45 (1949 b). — Baldwin, H. I.: Comparative results of the 1938 provenance test of *Picea abies*. XIV IUFRO Kongress, Munich. Section **22**: 782—787 (1967). — Baldwin, H. I., Eliason, E. J., and D. E. Carlson: IUFRO Norway spruce provenance tests in New Hampshire and New York. Silv. Genet. **22**: 93—114 (1973). — Bliss, C. I.: Statistics in Biology Vol. I. McGraw-Hill, New York. 558 pp. (1966). — Bouvarel, P.: Observations sur la date de l'auotement de quelques provenances françaises d'epicea. Ann. Ec. Nat. Eaux. For., Nancy **18**: 96—117 (1961). — Burdon, R. D. and J. M. Harris: Wood density in radiata pine clones on four different sites. N. Z. Jour. For. Sci. **3**: 286—303 (1973). — Cieslar, A.: Neues aus dem Gebiete der forstlichen Zuchtwahl. Centralbl. f. das Gesamte. Forstw. **25**: 99—117 (1899). — Daubenmire, R. F.: A comparison of seasonal cambial growth in different geographic races of *Pinus ponderosa*. Bot. Gaz. **112**: 182—188 (1950). — Dietrichson, J.: Proveniensproblemet belyst ved studier av vekstrytme og klima. Norske Skogsforsoksv. **5**: 499—656 (1964). — Dietrichson, J.: Abstract of papers. Meeting of IUFRO working party 2.02.11 on Norway spruce provenances. Biri, Norway, Aug. 14—20, 1973. 54 pp. (1973). — Dodge, R. A.: Investigations into the ecological relationships of Ponderosa pine in southeastern Arizona. Abstract of thesis in Dissert. Abstr. **24**: 917—918 (1963). — Dormling, I., Gustafsson, A., and D. von Wettstein: The experimental control of the life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silv. Genet. **17**: 44—64 (1968). — Engler, A.: Tatsachen, Hypothesen und Irrtümer auf dem Gebiete der Samen-Provenienz-Frage. Forstw. Centralbl. **30**: 295—314 (1905). — Ericson, B.: Studies of the genetical wood density variation in Scots pine and Norway spruce. Rapp. Avd. Skogspr. Statens Skogsforskningsinst. Stockholm, No. **4**, 52 pp. (1960). — Falconer, D. S.: Introduction to quantative genetics. Ronald, New York. 365 pp. (1960). — Hanover, J. W.: Geographic variation in ponderosa pine leader growth. For. Sci. **9**: 86—95 (1963). — Hattemer, H. H.: Estimates of heritability published in forest tree breeding research. World Consultation on Forest Genetics and Tree Improvement, Stockholm, Section 2a/3, 13 pp. (1963). — Kennedy, R. W.: Intraincrement variations and heritability of specific gravity, parallel-to-grain tensile strength, stiffness, and tracheid length, in clonal Norway spruce. Tappi **59**: 292—296 (1966). — Kiellander, C. L.: Über eine spättreibende Rasse von *Picea abies* in Schweden und eine Schwierigkeit bei der Plusbaumauswahl. Z. Forstgenet. **5**: 181—185 (1956). — Kleinschmit, J. und W. Knigge: Durch Umwelt und Erbanlagen bedingte Variation der Trockensubstanzerzeugung, Struktur und Rohdichte junger Fichten (*Picea abies* Karst.). Allg. Forst- u. Jagdzeitung **138**: 189—198 (1967). — Klem, G. G.: Kvalitetsundersokelser av norsk og tysk gran. Medd. Norske Skogsforsøksv. **14**: 285—314 (1957). — Knudsen, M. V.: A comparative study of some technological properties of Norway spruce in a provenance test. XII Congress IUFRO, Oxford 1956. No. 56/41/2, 7 pp.. (1956). — Langlet, O.: Mellaneuropeiska granprovenienser i svenskt skogsbruk. (Mitteleuropäische Fichte in Schweden, nach den Ergebnissen des internationalen Provenienzversuches von 1938.) Kungl. Skogs- och Lantbruksakad. Tidskr. **99**: 259—329 (1960). — Langlet, O.: Ecological variability and taxonomy of forest trees. *In* Tree Growth, ed. Kozlowski. Ronald, New York. 442 pp. (1962). — Langlet, O.: Regional intra-specific variousness. XIV IUFRO Kongress, Munich. Section **22**: 435—458 (1967). — Langner, W. und K. Stern: Untersuchungen über den Austriebstermin von Fichten und dessen Beziehungen zu anderen Merkmalen. Allg. Forst- u. Jagdztg. **135**: 53—60 (1964). — Libby, W. J,: Clonal selection, and an alternative seed orchard scheme. Silv. Genet. **13**: 32—40 (1964). — Lines, R.: Summary report on the IUFRO 1938 provenance experiments with Norway spruce, *Picea abies* Karst. For. Comm. Res. & Dev. Pap. No. 195, 12 pp. (1974). — Namkoong, G., E. B. Snyder and R. W. Stonecypher: Heritability and gain concepts for evaluation of breeding systems such as seed orchards. Silv. Genet. **15**: 76—84 (1966). — Nicholls, J. W. P.: Preliminary observations on the change with age of the heritability of certain wood characters in *Pinus radiata* clones. Silv. Genet. **16**: 18—22 (1967). — Oksbjerg, E.: Om udspringstid og skudstraekning i grankultur. Hedeselsk. Tidsskr. **74**: 49—55 (1954). — Olmsted, C. E.: Experiments on photoperiodism, dormancy, and leaf age and abscission in sugar maple. Bot. Gaz. **112**: 365—393 (1951). — Parrot, L.: De la variabilité genetique de la densité du bois chez l'épicea (*Picea excelsa* Link.). Ann. Ec. Nat. Eaux For., Nancy **17**: 267—334 (1960). — Rohmeder, E.: Der Jahreszeitliche Verlauf des Höhenwachstums früh- und spättreibender Fichten. Forstwiss. Cbl. **71**: 368—372 (1952). Vaartaja, O.: Evidence of photoperiodic ecotypes in trees. Ecol. Monog. **29**: 91—111 (1959). — Vins, B.: A contribution to the Norway spruce provenance research. XIV IUFRO Kongress, Munich. Section **22**: 782—787 (1967). — Worrall, J. and F. Mergen: Environmental and genetic control of dormancy in Norway spruce. Phys. Plant. **20**: 733—745 (1967). — Worrall, J.: Interrelationships among some phenological and wood property variables in Norway spruce. Tappi **53**: 58—63 (1970). — Worrall, J.: Seasonal, daily and hourly growth of height and radius in Norway spruce. Can. J. For. Res. **3**: 501—511 (1973). — Zobel, B. J.: Breeding for wood properties in forest trees. Unasylva **18**: 89—103 (1964).