branch thickness as a ratio to stem thickness at the measuring point, and branch length as a ratio of total height.

4. There was an association among high branch number, light branch size (thickness and length), and flat branch angle — in contrast to low branch number, heavy branch size (thickness and length) and steep-angled branches. Genetic relationships were established for a fine-branching form type and were shown to be positively associated with stem volume.

5. Path-analysis demonstrated that 42% of the additive genetic variation in stem volume could be accounted for by the additive genetic variation in branch number.

6. A negative genetic correlation is demonstrated between height and bole taper. Strong positive genetic correlations exist between bole taper and branch number, and bole taper and branch thickness. Higher bole taper exists where more wood is shifted from the bole to branches.

7. Multi-trait selection for the improvement of form and growth traits can accentuate the positive association of the fine-branching form type of profuse/light/flat branches with stem volume. Selecting key traits (branch number, proportional branch thickness, and knot index) in the tree-form-complex, along with stem diameter, can favourably affect all traits. Selecting for diameter on its own can improve form, but is not as effective as multi-trait selection for pursuing a fine branching form type.

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Effect of Geographical Transfer on Growth and Survival of Jack Pine (Pinus banksiana Lamb.) Populations

By C. Mátyás[1]) and Chr. W. Yeatman[2])

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Summary

Heights and mortality at age 15 were analysed in Ontario tests of a range-wide provenance experiment.

The analysis confirmed that the between-sources variaton pattern of height growth in jack pine populations is shaped by thermo- and photoperiodic effects. The geographical pattern is latitudinally clinal but weakly expressed.

For calculating the response regression surface, the variable "ecological distance" was introduced as a measure of environment change for the transferred sources. The

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developed model illustrates a generally observable trend of superiority (or at least equal performance) of sources transferred moderately northward as compared to the local source. The existence of obvious adaptation to harsher conditions as the local is interpreted as "adaptation lag".

Mortality caused by maladaptation and predicted performance of transferred populations was used to propose safe limits of transfer.

Key words: *Pinus banksiana,* geographic variation, provenance, response modelling, adaptation.

1. Introduction

Detailed survey of the adaptive behaviour of populations is essential for the delineation of breeding zones and scientific regulation of forest planting-stock trade. The phenotypic response of a population to changed environmental conditions may be described by reaction norm functions (e. g. height growth as a function of latitude of the planting location). The development of response models has been initiated to express the effect of various ecologically important environmental factors on growth and survival (CAMPBELL, 1974; ERIKSSON et al., 1980; KUNG and CLAUSEN, 1984; RAYMOND and LINDGREN, 1986; MÁTYÁS and YEATMAN, 1987; and others). In the present study the modelling of genetic variation in height and mortality was attempted aimed at defining limits of safe transfer distances for seeds and plants.

2. Description of the experiments and the data base

An all-range jack pine source study covering Canada and the Lake States was initiated by M. J. HOLST (Petawawa National Forestry Institute, Ontario, Canada). Between 1958 and 1962, seeds from 99 locations were collected throughout the whole range of the species.

Seed lots were sown at Petawawa in 1964 and the plants were distributed in 1966 among 12 planting locations across Canada (HOLST, 1967). The populations were planted mostly in 10-tree row plots. The present study deals with an analysis of height data at age 15 (measured in 1978) in 8 tests across Ontario. Basic data are listed in *table 1.* Height and survival data were collected and summarised by C. W. YEATMAN. From among the original set of sources 56 were analysed in detail, originating mainly from Ontario, western Quebec and adjacent areas in the United States (*Figure 1*).

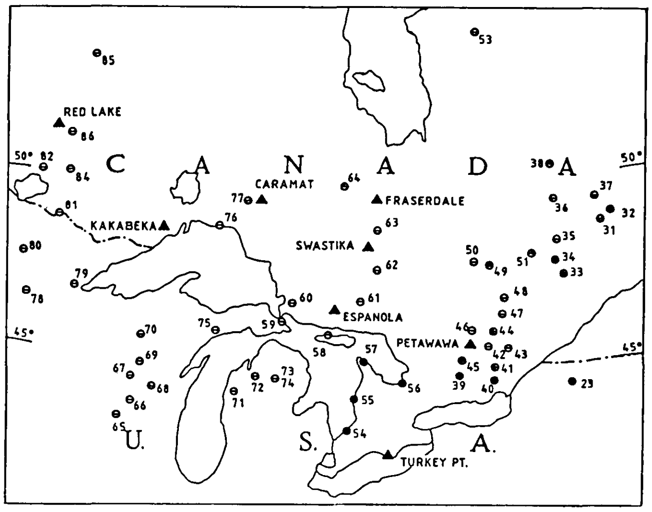

Figure 1. — Jack pine sources analysed in the study. Circles denote the origin of the seed lots. Sources with filled circles were identified as outliers. The location of the 8 Ontario experiments are indicated by triangles.

For practical reasons only plot averages were used for the analysis of 15-year heights. Survival of sources showed great differences, especially on difficult sites. Sources with high mortality and damages caused by winter injury and/or *Scleroderris* cancer could not be meaningfully compared with others. Therefore only sources with above 50% survival were used for height growth analysis. The data of the Espanola experiment were omitted because of some obvious errors in the planting design. Turkey Point data were also excluded from response regression calculations as the site is outside the natural range of the species.

The test locations were carefully selected as typical jack pine sites. Accordingly, all tests are situated on sandy soils of varying fertility. For quantification of the local growth potential, height of the local (autochtonous) source was introduced. Although "local height" is not free from random effects, comparisons have shown that it is at least as valid as any group average.

The aim of the study was first of all to obtain information on the limits of safe transfer, i. e. to evaluate performance of populations originating from ecologically reasonable distances. For modelling these moderate effects the incorporation of observations indicating strong height depression due to excessive transfer (e. g. planting Michigan sources in Northern Ontario) was considered inpractical.

Observations qualified as depressed due to extreme northward transfer were identified by centroid clustering, and removed from the data pool.

In addition, the data sets included a number of isolated outlier populations of weak growth which do not fit into

Table 1. — Main data of the Ontario test locations of the all-range jack pine experiment series.

Location	Heat sum (growing degr. days 5°C<)	Latitude (decim.)	Number of analysed proven- -ances	reps	Analysis of 15 yr. height Expt. mean	F value*
Petawawa	1900	45.8	98	9	632.7	27.4
Turkey P.	2200	42.8	81	7	552.4	22.9
Swastika	1450	48.0	68	10	545.5	9.9
Fraserdale	1360	49.7	57	10	481.9	7.3
Espanola	1520	46.7	34	8	363.0	4.0
Caramat	1360	49.6	37	8	490.7	9.7
Kakabeka	1500	48.2	70	6	502.6	8.6
Red Lake	1520	51.0	43	8	442.2	7.2

*) of between provenance component

the variation pattern of the other sources. Prior to analysis these sources were identified by comparison of their height performance at various locations. Sources were classified as depressed outliers and were eliminated only if indirect evidence of genetic depression could be traced in Holst's stand descriptions (see *Figure 1*).

3. Methods of statistical analysis

Mean heights of provenances at all locations were subjected to multiple regression calculations to determine the combination of ecological factors which accounted for most of the observed variation in height growth at a given test location. The variables tested were precipitation, latitude and heat sum of the origin of sources and of the test locations, the height of the local provenance (as an indicator for the test site potential) as well as squares and crossproducts of the above.

The number of variables had to be limited to facilitate modelling. The minimum number of variables was determined by Mallows' Cp statistic (Mallows, 1964).

3.1 Introducing ecological distance as an index for transfer effects

Transfer of plants to test locations with substantially different environments results in reduced adaptation to the new conditions. The environmental change for every source planted at a given location may be expressed as a difference between the ecological parameters of the test location and of the site of origin. The local source would, then, have 0 value at any test location. The differences take on negative values in case of the sources transferred towards cooler or more northern environments and positive ones in the opposite direction. This variable is regarded as "ecological distance" or ecodistance (Mátyás and Yeatman, 1987).

Analyses described in section 4 confirm that latitude and heat sum are the decisive ecological parameters with respect to both growth and survival. To obtain the required positive or negative values for ecological distance, the differences of latitude (DLAT) and heat sum (DHEAT) were calculated as follows:

DLAT = SLAT — LLAT and
DHEAT = LHEAT — SHEAT, where

SLAT and SHEAT is the latitude and heat sum of the source origin;
LLAT and LHEAT is the latitude and heat sum of the test location.

As latitude and heat sum (sum of "growing" degree days above 5° C) are correlated, so are their differences. If the differences are subjected to principal component analysis, the first component will account for most of the variation. It can be used therefore to express the ecological distance between origin and planting site.

The variable "ecological distance" is the first principal component for latitude and heat sum differences. (Entering only two variables into the principal component analysis keeps the index easy to interpret).

3.2 Modelling effects of limited transfer

The arrangement of source height averages by any ecological parameter (latitude or heat sum of origin, ecodistance) results in curvilinear pattern which may be described by quadratic equations for every experiment. The series of regression curves over the different test locations define a quadratic surface which can serve for modelling the reaction norm of populations.

To model height, quadratic polynomial regressions were used. The "response surfaces" may be depicted as contour plots. The height of the "local" source (an index of the test site potential) and the ecodistance of transfer were entered as independent variables. Average source height was the dependent variable. The equation for the response regression is:

$$z_{ij} = \beta_0 + \beta_1 x_{ij} + \beta_2 y_j + \beta_3 x^2_{ij} + \beta_4 y^2_j + \beta_5 x_{ij} y_j + \varepsilon$$

where:

z_{ij} is the height of the i-th source at the j-th location
x_{ij} is the ecodistance of the i-th source, calculated for the j-th location
y_j is the height of the "local" source at the j-th location
β_0 to β_5 are estimated parameters and
ε is the residual error of fitting to the regression surface.

3.3 Mortality analysis

Populations displaying less than 50% survival were regarded as complete failures, regardless of the growth of the surviving trees, and had to be dealt with separately. The analysis was limited to an estimation of the probability of failure of a source as a function of the ecological distance. A more detailed analysis of survival differences was found impractical because of the assumed high proportion of errors and bias affecting the number of surviving plants (initial plant size, microsite differences, human error effects etc.).

4. Results

Of the investigated environmental parameters an optimum combination of 7 variables was found to explain 86% of the variation of the provenance mean heights (see *Table 2*). The examination of the variables confirms that

Table 2. — Optimum combination of environmental factors determining the provenance mean height (multiple regression analysis of 7 Ontario test data).

Variable	Signif. (%)
Source latitude, linear	0.1
- - , quadratic	0.1
- heat sum, linear	0.1
- - , quadratic	0.1
Test location latitude, linear	10.0
- - , heat sum, linear	10.0
Height of local population, linear	0.1
Attained r^2 value	0.855

Table 3. — Statistics of the calculated response regression equations (6 Ontario experiments without Turkey Pt. and Espanola).

	Linear	Quadratic	Crosspr.	Total	M.S. contribution of variable	
	r^2 components			r^2	Ecodistance	Local Height
Absolute heights (cm)	0.83***	0.08***	0.0	0.91***	63,279***	300,441***
Relative heights (%)	0.38***	0.23***	0.02**	0.63***	1,406***	304***
Significance: ** = 1 %; *** = 0,1 % level						

latitude (effect of photoperiod) and heat sum of the source as well as the height of the local source determine most of the observed variation. Local growth potential seems to be characterized much better by local height than by latitude and heat sum values. The significance of the squared components indicates the curvilinear character of the relationship.

Heat sum and latitude were incorporated in the response model through the variable "ecological distance" (see section 3). According to the principal component analysis for heat sum and latitude differences, the first principal component, that is the "ecological distance" of sources, accounts for 93.6% of the variation.

4.1 Effects of limited transfer

The results show a high degree of linearity for absolute hight response, determined by the dominance of local height effects (*Table 3*). The quadratic component is small (below 10%) and the crossproduct effect (interaction) is virtually missing.

When using relative height data (as percent of the local) the linear component of local height is disregarded and quadratic effects are strong. Significant crossproducts indicate location x source interaction effects, but their relative magnitude remains low.

The images of the regression surfaces exhibit a characteristic pattern. For the 6 Ontario experiments (*Figure* 2) the equation of the regression surface is

$$Z = 529.5 - 85.6\ X^2 - 0.85\ Y^2 + 0.0956\ XY$$

(for explanation of variables see previous section)

The surface forms a ridge, the "crest" indicating the origin of source attaining the (theoretically) best height growth. If the local sources performed best, the maximum had to appear at O ecodistance. This is true only for the best sites with the greatest local height in the milder part of the range. Towards the less productive (more northern) environments, characterised by decreasing local heights (y axis on *figure* 2), the maximum appears at increasingly negative ecodistance values to about —1.5. Negative ecodistance stands for northward transfer, thus the sites with relative growth maximum lie generally north from the site of origin. That is, non-autochtonous sources transferred from the south seem to surpass the local provenances (until the appearance of increased mortality). The northward shift of the theoretical maximum is observable on all test sites. The phenomenon is interpreted as the proof for the possible superiority in growth potential of transferred populations over the local ones.

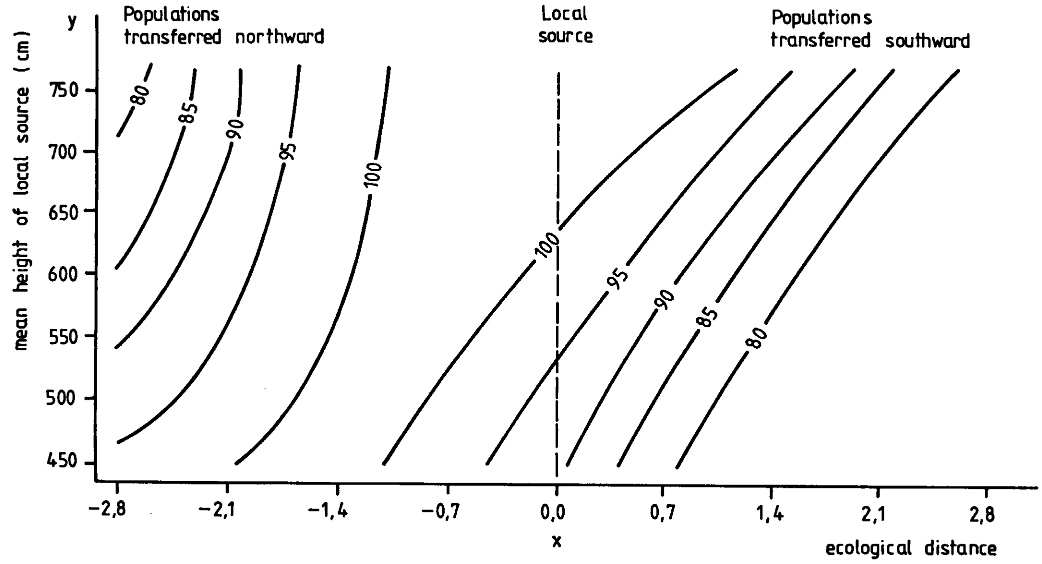

Figure 2. — Contour plot of the relative source heights (calculated from 6 Ontario tests) expressed as percents of the local height. Excessively transferred sources exhibiting marked growth depression were excluded.

4.2 *Ecodistance and mortality*

Sixteen sources exhibited mortality of over 50% at one or more locations, mostly in connection with serious damage by winter injury or diseases. Without further examining the reasons of mortality, its occurrence was related to respective ecodistances. *Figure 3* shows the regression between the probability of mortality over 50% and ecodistance.

A 50% probability for planting failure was found at ecodistance —2.21, 5% at —0.92. The latter value corresponds roughly to a northward transfer over 2 degrees of latitude and causing a loss of 300° C degree-days of heat sum (see *Figure 4*).

Tolerance to geographical transfer seems to be source-specific, but there seems to be no direct connection between phenotypic stability and extreme transfer tolerance. The minium and maximum values for the first appearance of excessive mortality (over 50%) among the investigated sources were observed at ecodistances —1.34 and —2.69 (sources #47 and 66, respectively).

5. Discussion

5.1 *Thermo- and photoperiod, and height growth of jack pine populations*

The importance of the temperature conditions for the adaptation of northern — boreal tree species was recognised already more than 100 years ago (Langlet, 1971). Temperature is the most critical limiting factor to growth and survival at higher latitudes of continents in the northern hemisphere. Thermal gradients shape adaptive response patterns not only for growth, but also for cold hardiness and disease susceptibility (Sarvas, 1972/1974; Morgenstern, 1978; Yeatman, 1984).

Growth chamber studies with the all-range jack pine sources revealed, that the height growth and dry matter production differences between sources correlated best with the heat sum of the place of origin (Yeatman, 1966; Giertych and Farrar, 1962) Correlations between seedling height in the nursery and heat sum of origin were established by many other researchers (Holst, 1969; Skeates, 1979). In the juvenile stage (age 17 to 19) height and volume of Ontario jack pine sources correlated best with heat sums (Holst and Yeatman, 1961), less with summer temperatures.

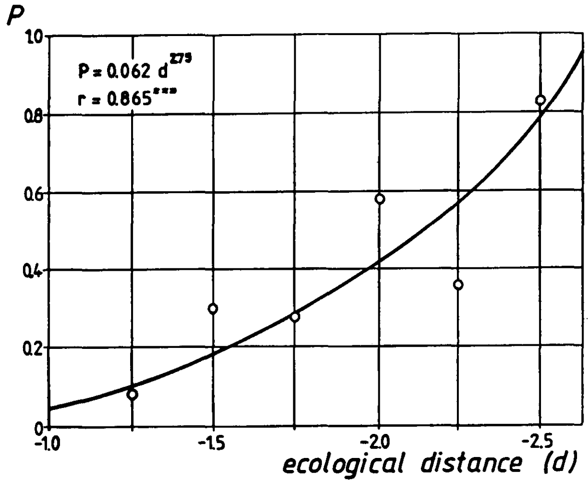

Figure 3. — Probability of excessive (> 50%) mortality due to long distance transfer, as function of the ecological distance (d). Data for 7 Ontario tests, grouped by ecodistance classes.

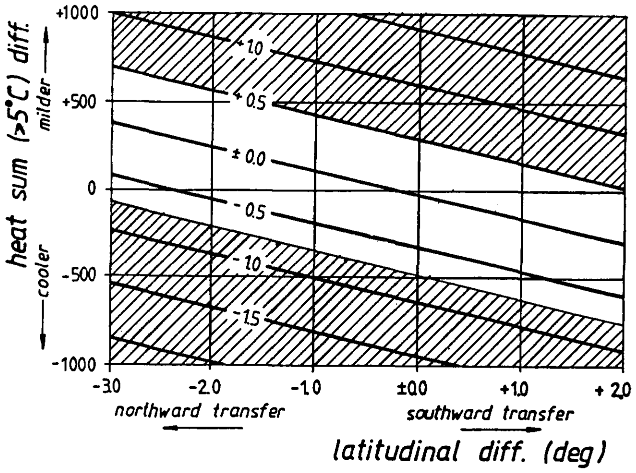

Figure 4. — Graph of "ecological distance" values (on isolines) derived from latitudinal and heat sum differences between the locations of origin and the planting sites. The shaded area represents distances outside the limits of safe transfer.

One may agree with Morgenstern (1978) that various aspects of the thermoperiod are subcomponents of the same effect. There are no substantial differences using growing degree days at various threshold levels, length of the frost-free period or summer temperatures etc.

The effect of photoperiod (latitude) is normally confounded with thermal effects. The importance of daylength in the adaptation process was demonstrated relatively recently (Langlet, 1936; Vaartaja, 1959). Strong latitudinal effects were reported also in jack pine source tests (Giertych and Farrar, 1962; Rudolph and Yeatman, 1982).

In the present study up to 80% of the total height variation was accounted for by thermo- and photoperiodic effects. On the other hand, precipitation plays a subordinate role. This may be explained first of all by the relative insensitivity of the species to moisture conditions and by the fact that moisture deficit is, at least from the climatical point of view, a factor of limited importance in Northern Ontario (Chapman and Thomas, 1968).

5.2 *Adaptive variation pattern of height growth of jack pine populations*

The discussed model of the reaction norm of height growth suggests a continuous, clinal variation which was observable at all test sites. The clinal character of variation was already observed by Schoenike (1976) and Jeffers and Jensen (1980), first of all for the southern part of the range, while Rudolph and Yeatman (1982) stated that clines associated with climate are less valid in the harsher boreal zone. From the gathered information this statement may be verified in the sense that the expression of geographical clines becomes less accentuated in harsh environments, at the same time the effects of site × genotype interactions increase with maladaptation of the transferred sources.

The clinal gradient in growth is not very steep and there are only few instances where geographically adjacent sample populations show significantly different behaviour. This indicates large distances of effective gene exchange of the order of 50 km to 100 km. This is supported by results of Yeatman (1975) and Canavera (1975).

5.3 Utilization of the model for the definition of safe transfer distances

As both the present study and many other experiments confirm correlations between ecological conditions at the site of origin and performance at the planting location, it seems reasonable to utilize transfer effects to regulate trade of forest reproductive material and to optimize tree breeding activities.

Optimum zone sizes based on response functions are described by Raymond and Lindgren (1986) and Raymond and Namkoong (1990). These concepts presume symmetrical responses to either northward or southward transfers and — for the sake of simplicity — work mainly with latitude.

In this paper the gliding transfer limit concept is followed, which considers permissible transfer distances. To predict transfer effects, ecological distance and mortality effects are utilized.

If the permissible transfer effect is defined as maximally 5% loss in height growth (compared to the local population), the model proves that within +0.5 and —1.0 ecodistance a transferred population will display comparable growth.

Regarding mortality caused by northward transfer, the 5% probability limit for serious losses lies at ecodistance —0.92. Combining the two methods of calculation, safe limits of transfer for the investigated area may be proposed as

+0.5 ecological distance for southward transfer, and
—0.75 ecological distance for northward transfer.

These values may be directly utilized for delimiting the acceptable range of suitable seed sources for a given location by using the ecodistance graph presented in *Figure 4*.

6. Adaptation lag as a source for suboptimality of natural populations

Although local sources are always among the top-ranking ones and they are significantly inferior in height only at the Caramat test location, it is also true that non-local sources growing equally well, or even slightly better as the local one appear at all test sites, causing a shift in the predicted origin of the theoretically best source, mostly towards the south (see *Figure 2*). This phenomenon was noticed for a large number of different species, as for the southern pines in the U.S. (Wells, 1969), for lodgepole pine (Rehfeldt, 1988), for Scots pine (Mátyás, 1989), and even for some hardwoods like red maple (Townsend, 1974), white and green ash (Roberds et al., 1990; Wells, 1986) and black walnut (Kung and Clausen, 1984). It has to be regarded as a systematic feature of adaptation and could be defined as "adaptation lag" (Mátyás, 1989, 1991). For a boreal species one might consider recent climatic changes and migration effects leading to non-optimality of local populations. A more general explanation however has to be sought in the constraints of the adaptation process as defined by Fisher (1958).

Another interesting feature of the adaptation process is the relative flatness of the clinal variation pattern, a surprising insensitivity to changing ecological conditions, at least in the geographical sense (Elevational clines are in comparison much steeper: see Rehfeldt, 1988). There are a number of factors limiting the effect of adaptation; effective migration of genes and superiority of heterozygotes are presumably the most important. Artificial regeneration itself (i. e. the outplanting of an experiment) may change the conditions of optimum fitness in a sense that the advantage of local (autochtonous) populations diminishes. From another viewpoint, this idea is supported by life cycle studies (Eriksson and Lundkvist, 1986).

The maintenance of a high level of genetic heterogeneity at the expense of growth and yield has no doubt evolutional advantage under natural conditions. In addition, long-term provenance experiments show the importance of survival or hardiness, which may improve the ranking of local sources as compared to excessively transferred populations at later stages of stand age. Approaching the northern limits of distribution, the importance of hardiness and stress tolerance increase at the expense of hight growth potential. Accordingly, the described northward shift of the site of maximum relative productivity ("mode environment") disappears and may be even reversed; in northern Sweden southward transferred Scots pine populations were superior to local ones (Eriksson et al., 1980; Prescher, 1986). Similar effects were observed by Roberds et al. (1990) for white ash.

These facts caution against the exclusive judgement of adaptation on the basis of dry matter production.

7. References

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Buchbesprechungen

Proceedings of the meeting of IUFRO — WP S2.02-21 on "Actual problems of the legislation of forest reproductive material and the need for harmonization of rules at an international level. Gmunden/Vienna — Austria, June 10. to 14. 1991. FBVA-Berichte Nr. 65. By J. Nather (Editor). 1992. Österreichischer Agrarverlag, Wien. 168 pages. öS 200.—.

The proceedings of IUFRO working party "Legislation of Forest Reproductive Material" on "Actual problems of the legislation of forest reproductive material and the need for harmonization of rules at an international level" held in Gmunden/Vienna, Austria, June 10. to 14., 1991, contain a collection of 21 articles and the conclusion from the final discussion and the technical session. The proceedings are divided into 6 sections: Implementation of rules for forest reproductive material; principle for classification of forest reproductive material; clonal forestry; categories of forest reproductive material; special problems on seed certification and quality standards; forest policy and law on forest reproductive material. The papers cover the actual problems which influence the legislation of forest reproductive material including the need for harmonization of rules at an international level. The participants agreed that breeding methods are developing rapidly and international rules should not obstacle this development. M. Liesebach (Großhansdorf)

Bakterienviren. Von S. Klaus, D. H. Krüger und J. Meyer. 1992. Gustav Fischer Verlag, Jena und Stuttgart. ISBN 3-334-60353-9. 300 Seiten mit 144 Abbildungen und 29 Tabellen. DM 128,—.

Die Entdeckung der in Bakterien lebenden Viren (Bakteriophagen) geht auf Twort (1915) und D'Herelle (1917) zurück. Die moderne Phagenforschung begann in den dreißiger Jahren und wurde seit etwa 1940 intensiv betrieben. Die Molekularbiologie hat ihre Entwicklung der Phagenforschung zu verdanken. Die Grundlagen der modernen Genetik, die Aufklärung der Nukleinsäurestruktur, der Mechanismen von Rekombination, Replikation und Genexpression wären ohne den Beitrag der Phagenforschung nicht denkbar. Inzwischen wurden einige Tausend versechiedene Phagen isoliert und analysiert. Einige von ihnen wurden besonders intensiv bearbeitet und sind für genetische Untersuchungen unverzichtbar. Die Literatur über Phagen umfaßt inzwischen viele Tausend Arbeiten, darunter auch umfangreiche Übersichtsreferate. Das vorliegende Buch gibt aber erstmals in deutscher Sprache einen Gesamtüberblick über das Thema für "Nichtphagologen". Hierzu ist der Stoff in einen allgemeinen und einen speziellen Teil untergliedert. Die allgemeinen Kapitel informieren über die Bakterienzelle als Wirtsorganismus, die Physiologie der Phagenvermehrung, die Lysogenie, die Phagengenetik, die Phagen-Taxonomie und schließlich die Bedeutung der Phagen für Medizin, Fermentationsindustrie und Virusforschung. Im speziellen Teil werden ausgewählte Phagenvertreter ausführlich beschrieben. Ein abschließendes Kapitel ist der Verwendung von Phagenvektoren in der Gentechnik gewidmet. Den einzelnen Kapiteln sind Hinweise auf weiterführende Literatur angefügt. Das Buch ist darüber hinaus gut illustriert und allen biologisch interessierten "Nichtphagologen" als Informationsquelle zu empfehlen. B. R. Stephan (Großhansdorf)

Illustrierte Flora von Mitteleuropa. Band I. Teil 3. Gramineae. Lieferung 6. 3., völlig neubearbeitete Auflage. Von G. Hegi. Bearbeitet von H. J. Conert. 1992. Verlag Paul Parey, Berlin und Hamburg. ISBN 3-489-52520-5. Seite 401 bis 480 mit 38 Abbildungen und 2 Tafeln. DM 45,—.

Von der in einem Umfang von 8 Lieferungen geplanten dritten, völlig neubearbeiteten Auflage des Gramineen-Bandes des "Hegi" liegt jetzt die 6. Lieferung vor. Die hohe fachliche Qualität dieses Standardwerkes über die mitteleuropäische Flora zeigt sich auch bei dieser Lieferung: genaue umfassende Beschreibungen der Arten und ihrer Variabilität, detaillierte Hinweise auf allgemeine Verbreitung und Vorkommen im Gebiet, auf Cytologie und Inhaltsstoffe, auf Nutzen und Verwendung, auf Krankheiten und Schädlinge, sowie auf wichtige Literatur. Mit Hilfe von eingehenden Bestimmungsschlüsseln können Arten und Unterarten sicher identifiziert werden. Jede Art ist zudem durch sehr gute, detailgenaue Zeichnungen vom Gesamthabitus sowie durch für die Identifizierung wichtige Einzelmerkmale dargestellt. Behandelt werden in dieser Lieferung aus der Unterfamilie der Pooideae 9 Gräser-Gattungen. Außer den in Mitteleuropa natürlich vorkommenden Arten werden auch zahlreiche adventiv auftretende Arten behandelt. — Es bleibt zu hoffen, daß die restlichen Lieferungen des Gramineen-Bandes in kürzeren Zeitabständen erscheinen als die bisherigen.

B. R. Stephan (Großhansdorf)

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