DO NOT REMOVE

TREE IMPROVEMENT — PROGRESSING TOGETHER

AMÉLIORATION DES ARBRES UN EFFORT COOPÉRATIF

PROGRESSING TOGETHER

C.T.I.A. A.C.A.A.

TRURO, N.S. - 1987

CANADIAN
TREE IMPROVEMENT
ASSOCIATION

PROCEEDINGS

TWENTY-FIRST MEETING
PART 2

TRURO, NOVA SCOTIA
AUGUST 17 - 21, 1987

ASSOCIATION
CANADIENNE
POUR L'AMÉLIORATION
DES ARBRES

COMPTES RENDUES

VINGT-ET-UNIÈME CONFÉRENCE
2e PARTIE

TRURO, NOUVELLE-ÉCOSSE
DU 17 AU 21 AOÛT 1987

EDITORS/RÉDACTEURS
E.K. MORGENSTERN
T.J.B. BOYLE

PROCEEDINGS

OF THE

TWENTY-FIRST MEETING

OF THE

CANADIAN TREE IMPROVEMENT ASSOCIATION

PART 2:

SYMPOSIUM ON

TREE IMPROVEMENT-PROGRESSING TOGETHER

HELD IN

TRURO, N.S.

AUGUST 17-21, 1987

EDITORS:

E.K. MORGENSTERN & T.J.B. BOYLE

Part 1. Minutes and Members' Reports

Distributed to Association members and to others on request to the Editor, C.T.I.A./A.C.A.A., Chalk River, Ontario, Canada, K0J 1J0

Part 2. Tree Improvement-Progressing Together

Distributed worldwide to persons and organizations actively engaged or interested in forest genetics and tree improvement.

Additional copies of this publication are available from:

Editor C.T.I.A./A.C.A.A.
Canadian Forestry Service
Petawawa National Forestry Institute
Chalk River, Ontario, K0J 1J0

Produced by
Canadian Forestry Service,
for the
Canadian Tree Improvement Association,
Ottawa, 1988

COMPTES RENDUS

DE LA

VINGT ET UNIÈME CONFÉRENCE

DE

L'ASSOCIATION CANADIENNE POUR L'AMÉLIORATION DES ARBRES

PARTIE 2

COLLOQUE SUR

AMÉLIORATION DES ARBRES - UN EFFORT COOPÉRATIF

TENUE À

TRURO (N.-É.)

DU 17 AU 21 AOÛT 1987

RÉDACTEURS:

E.K. MORGENSTERN & T.J.B. BOYLE

Partie 1. Procès-verbaux et rapports des membres

Distribué aux membres de l'association et aux autres sur demande au rédacteur, A.C.A.A./C.T.I.A., Chalk River (Ontario) Canada, K0J 1J0.

Partie II. Amélioration des arbres - un effort coopératif

Distribué à l'échelle mondiale aux personnes et aux organisations activement engagées ou intéressées à la génétique forestière et à l'amélioration des arbres.

Des exemplaires de cette publication peuvent être obtenus à l'adresse suivante:

Rédacteur A.C.A.A./C.T.I.A.
Service canadien des forêts
Institut forestier national de Petawawa
Chalk River (Ontario) K0J 1J0

Publié par le
Service canadien des forêts
pour
l'Association canadienne pour
l'amélioration des arbres,
Ottawa, 1988

PROCEEDINGS OF THE TWENTY-FIRST MEETING OF THE CANADIAN TREE IMPROVEMENT ASSOCIATION

With the compliments of the Association

Enquiries may be addressed to the authors or to Mr. J.F. Coles, Executive Secretary, C.T.I.A./A.C.A.A., c/o Ontario Tree Improvement Council, Johnston Hall, University of Guelph, Guelph, Ont. N1G 2W1.

IF YOUR ADDRESS ON THE LABEL IS INCORRECT OR INCOMPLETE, PLEASE RETURN CORRECTION SLIP BELOW

Others interested in receiving Proceedings, notice of meetings etc. may return the slip to be listed as Corresponding Members (Canadian) or be placed on the mailing list for the Proceedings only (libraries, institutions, foreign addressees). If you no longer wish to receive these Proceedings, please check "delete" and return the completed slip to the Editor.

The Twenty-second Meeting of the Association will be held in Edmonton, Alberta, August 14-18, 1989. Speakers will be invited to address the topic of "Test results and their application in tree improvement". Canadian and foreign visitors are welcome. Further information will be distributed in the winter 1988 to all members and to others on request. Enquiries concerning the 22st Meeting should be addressed to: J.I. Klein, Canadian Forestry Service, Northern Forestry Centre, 5320-122 Street, Edmonton, AB T6H 3S5.

To:
T.J.B. Boyle, Editor, C.T.I.A./A.C.A.A.
Canadian Forestry Service
Petawawa National Forestry Institute
Chalk River, Ontario K0J 1J0
CANADA

PLEASE PRINT

Name: *Prof.* *Ms.*
Dr. *Mr.* ....

Address: ....

....

.... *Postal Code* ....

Please check one: *Correction*

New addressee

Delete from C.T.I.A. mailing list

Signed ....

COMPTES RENDUS DE LA VINGT ET UNIÈME CONFÉRENCE DE L'ASSOCIATION CANADIENNE POUR L'AMÉLIORATION DES ARBRES

Don gracieux de l'association

Les demandes de renseignements peuvent etre adressées aux auteurs ou à J.F. Coles, Secrétaire général, A.C.A.A./C.T.I.A., c/o Ontario Tree Improvement Council, Johnson Hall, University of Guelph, Guelph, Ont. N1G 2W1.

SI VOTRE ADRESSE EST INEXACTE OU INCOMPLÈTE SUR L'ÉTIQUETTE, S.V.P. RETOURNEZ LA FICHE DE CORRECTION CI-DESSOUS

Ceux qui seraient intéressés à recevoir les comptes rendus, les avis de réunions, etc., sont priés de retourner la formule pour être ajoutés à la liste de membres correspondants (Canadiens), ou à la liste d'envoi pour les comptes rendus seulement (bibliothèques, institutions, destinataires à l'étranger). Si vous ne désirez plus recevoir ces comptes rendus, veuillez cocher <<rayer>> et retourner la formule remplie au rédacteur.

La vingt-deuxième conférence de l'association aura lieu à Edmonton, en Alberta, du 14 au 18 août 1989. Des orateurs seront invités à adresser le sujet de <<Résultats d'expériences et les applications à l'amélioration des arbres>>. Les intéressés au Canada et à l'étranger sont les bienvenus. Des renseignements supplémentaires seront distribués au cours de l'hiver de 1988 à tous les membres et à tous ceux qui en feront la demande. Si vous avez des questions à poser concernant la 22^e^ conférence, veuillez les adresser au: Canadian Forestry Service, Northern Forestry Centre, 5320-122 St., Edmonton, AB T6H 3S5.

À: *T.J.B. Boyle, rédacteur, A.C.A.A./C.T.I.A.*
Service canadien des forêts
Institut forestier national de Petawawa
Chalk River (Ontario) K0J 1J0

LETTRES MOULÉES

Nom: *M. Mme* ....

Adresse: ....

....

.... *Code postal* ....

S.V.P. cocher une seule case: *Correction*

Nouveau destinataire

Rayer le destinataire de la liste d'envoi de l'A.C.A.A.

Signé ....

ACKNOWLEDGMENTS

On behalf of the Canadian Tree Improvement Association, I gratefully acknowledge the following agencies for their generous support to the 21st biennial meeting:

Nova Scotia Department of Lands and Forests
Canadian Forestry Service - Maritimes (Federal
    Technology Transfer Project)
Bowater Mersey Paper Co. Ltd.
Scott Worldwide Inc.
Stora Forest Industries
Minas Basin Pulp and Power Co.
Maritime Farm Supply Ltd.
Plant Products Co. Ltd.
Ropak CanAm Ltd.
Nova Scotia Agricultural College

I would also like to extend thanks to the members of the '86-87 executive who made my term as Chairman a rewarding, yet painless experience: Kris Morgenstern (symposium), Howard Frame (local arrangements), Jim Coles (Executive Secretary), Kit Yeatman (Treasurer) and Tim Boyle (Editor). Special recognition must also be given to the other members of the Planning Committee for the 21st meeting whose extraordinary efforts made for an extraordinary meeting: Ted Bulley, Penny Chapman, Don Fowler and Brian White. Thanks are also due to Bill Selkirk and Barb Ballantyne of Petawawa National Forestry Institute for the completion of the Proceedings and for organizing and editing the French abstracts, respectively.

T.J. Mullin, Chairman

CONTENTS/TABLES DES MATIÈRES

INVITED PAPERS/CONFÉRENCIERS INVITÉS

VOLUNTARY PAPERS - ABSTRACTS/CONFÉRENCIERS VOLONTAIRES - RÉSUMÉS

APPENDICES/ANNEXES

CONFÉRENCIERS INVITÉS

INVITED PAPERS

THE STATUS OF PROVENANCE RESEARCH IN CANADA

Cheng C. Ying[1] and E.K. Morgenstern[2]

[1] Research Branch, Ministry of Forests and Lands, Victoria, B.C.
V8W 3E7

[2] Faculty of Forestry, University of New Brunswick, Fredericton, N.B.
E3B 6C2

ABSTRACT

Between 1940 and 1992, approximately 900 ha of provenance experiments will have been established in the 10 provinces of Canada, involving 27 coniferous and 12 deciduous species. British Columbia leads in provenance test area established (301 ha), followed by Ontario (215 ha) and Quebec (209 ha). Establishment peaked in the 1970-1974 period and is now declining. Maintenance and measurement of some older key experiments will continue. Of particular interest is the trend in survival which may lead to further modification of seed and breeding zones. Much useful information has become available for the major species but for species of minor importance experimental results are scarce. Some of these species are now becoming more important in reforestation than they have been in the past.

It is concluded that provenance research is making important contributions to silviculture and tree improvement as well as to our understanding of the basic biology of the species.

RÉSUMÉ

De 1940 à 1992, environ 900 ha servant à des tests de provenance auront été établis dans les 10 provinces du Canada; ces expériences auront porté sur 27 essences de conifères et 12 de feuillus. La Colombie-Britannique arrive en tête dans ce domaine avec 301 ha et devance l'Ontario (215 ha) et le Québec (209 ha). Le nombre d'hectares établis a atteint un sommet dans la période 1970-1974 et il est maintenant en voie de déclin. Le maintien et la mesure de certaines anciennes expériences fondamentales se poursuivront. La tendance de la survie est particulièrement intéressante puisqu'elle permettra peut-être de modifier davantage les graines et les zones de reproduction. On dispose maintenant d'informations très utiles sur les principales espèces, mais très peu sur les résultats d'expériences effectuées sur des espèces de moindre importance. Certaines de ces espèces deviennent maintenant plus importantes dans le reboisement qu'elles ne l'ont été dans le passé.

On conclut que les tests de provenance apportent une contribution importante à la sylviculture et à l'amélioration des arbres et nous permet de mieux comprendre la biologie fondamentale des espèces.

INTRODUCTION

The importance of the geographic origin of seed to reforestation has long been recognized in Canada. Sixty years ago A.C. Thrupp pointed out the need for "scientific seed collection" in an article in the Forestry Chronicle. He referred to the tremendous range of environments occupied by such species as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), Ponderosa pine (Pinus ponderosa Laws., and red oak (Quercus rubra L.), and reported large differences in hardiness and growth of various seed sources when observed in the nursery. Adaptation to environment should be recognized (Thrupp 1927). Between 1942 and 1945 Dr. Carl Heimburger established the first provenance test plantations of Norway spruce (Picea abies L. Karst.) and white spruce (Picea glauca (Moench) Voss) at the Petawawa Forest Experiment Station (now Petawawa National Forestry Institute) in Ontario. The first graph showing a relationship between height growth of white spruce on the one hand and latitude and summer temperature at the place of origin on the other, was developed from data obtained from one of these plantations (Holst 1955). Following an intensive period of provenance research undertaken by Mark Holst and his associates at Petawawa, Yeatman and Morgenstern (1979) stressed the importance of seed source variation in silviculture and tree breeding. Fowler (1979b) surveyed accomplishments and the need for additional research during the next 10 years.

This paper will review the present state of provenance research, discuss the pattern of geographic variation in native and exotic species as recognized today, and the impact of results on silviculture and tree breeding.

PRESENT STATUS OF PROVENANCE RESEARCH

Survey Results

A questionnaire was sent to each province to gather the following statistics: number of provenances tested, number of tests and hectares (ha) established, and year of establishment. Results received indicated that tabulation of accurate numbers of provenances was not possible because identification of the relevant variables was not uniform. However, we found that the area of experiments established is a good indication of the status of provenance research. This information is recorded in Figures 1 and 2, and Tables 1, 2 and 3.

Provenance research in Canada started in the late 1930's and gained momentum in the mid-1950s (Fowler 1979b). Mark Holst was the driving force for about 20 years following his arrival at Petawawa in 1950. Establishment of long-term field tests increased steadily, peaked in the mid-1970s, and still continues but at a reduced rate (Figure 1). According to the survey, only Alberta and Quebec plan to establish a substantial number of tests in the next five years (1988-1992). British Columbia, Ontario and Quebec are the leading provinces (Figure 2). Many of the tests east of the Rocky Mountains were organized by Petawawa National Forestry Institute in cooperation with the provinces and regional research centres of the Canadian Forestry Service.

As expected, provenance research has been focused on the major native conifers, black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce, and Sitka spruce (*P. sitchensis* (Bong.) Carr.), Douglas-fir, jack pine (*Pinus banksiana* Lamb.), and lodgepole pine (*P. contorta* Dougl.) (Table 1). Considerable attention was devoted to some exotics: Norway spruce, Scots pine (*Pinus sylvestris* L.), and European larch (*Larix decidua* Mill.) (Table 1). Experiments with deciduous species are a recent event and limited in scope (Table 2). Across Canada, the total area of experiments already established and planned for the next five years adds up to about 900 ha.

Variation Patterns by Species

Black spruce. The pattern of geographic variation is predominantly clinal in seedling phenology and growth behavior (Morgenstern 1969a, 1969b, Pollard et al. 1975), a response to natural selection along the gradients of daylength and temperature (Morgenstern 1978). The expression of this pattern was much weaker in field tests at ages 9 to 15 years from seed (Boyle 1985, Fowler and Park 1982, Khalil 1984). Boyle (1985) attributed these differences to growth behavior: free growth is the predominant component in leader elongation of young seedlings whereas in older trees, growth potential is largely predetermined. Khalil (1975b) found that geographic variation in Newfoundland is related to regional temperature, a pattern which he described as ecotypic. An overall evaluation of the range-wide study at age 15 based on 29 experiments in the United States and Canada is currently underway. Survival differences are beginning to emerge in some experiments but need to be followed over a longer time period (Morgenstern and Villeneuve 1987).

Over much of its range and particularly in boreal climates, black spruce occupies a broad range of sites from bogs to uplands. Many of the pure stands on the fertile upland sites originated after fire and are replaced by more tolerant species or become mixed stands in the course of succession (Heinselman 1957). The question whether edaphic ecotypes exist, therefore must take species ecology into account and this has not always been done. Results of a variety of studies provide little evidence for edaphic ecotypes although stand-to-stand differences exist (Morgenstern 1969b, Fowler and Mullin 1977, O'Reilly et al. 1985).

Red spruce. Red spruce (*Picea rubens* Sarg.) received very early attention in investigation of geographic variation with the expectation that populations in unglaciated areas would be of high genetic diversity and would offer the potential to expand the climatic and edaphic range of the species (Heimburger and Holst 1955). Results from field tests based on samples from the whole range indicated weak population differentiation, inferiority to black spruce or their hybrids in growth and survival, and, therefore, a very low potential of success in silviculture based on clear-cutting and planting (Morgenstern et al. 1981). Another test series with samples from Maine and New Brunswick demonstrated a random pattern of variation independent of geoclimatic variables (Dr. D.P. Fowler, pers. comm.). In Newfoundland the growth of red spruce is inferior to native species and introduction is not warranted (Hall 1986a).

White spruce. The early provenance tests established from late 1950s to mid 1960s identified very productive seed sources in southeastern Ontario, e.g., Beachburg (Lat. 45.7°N, Long. 76.8°W) and Peterborough (Lat. 44.1°N, Long. 78.0°W) (Nienstaedt 1969, Teich 1973, Khalil 1974, Teich et al. 1975). However, in Newfoundland the fast growing Ontario sources had below average survival at 25 years from seed (Hall 1986b). Provenance samples involved in these early studies were usually small and concentrated In Ontario and Quebec. The pattern of geographic variation across the whole range of this species is not yet fully understood (Nienstaedt and Teich 1971). The recently established regional and range-wide experiments with systematic sampling will fill this information gap (Ying 1980, Murray and Cheliak 1985).

Evidence from studies of chemosystematics, cone morphology and seedling phenology points to a major division of the range at approximately 95°W. This hypothesis is supported by the assumption of glacial refugia in the Yukon Valley and Appalachian Mountains. Within each division variation is clinal along latitudinal gradients (Nienstaedt and Teich 1971). Studies using hierarchal sampling within limited geographic areas showed high tree-to-tree variation and low stand-to-stand variation in growth (Dhir 1976), seedling phenology (Pollard and Ying 1979a, 1979b), and cone morphology (Khalil 1975a).

In contrast to black spruce, there is evidence for edaphic ecotypes in white spruce in eastern Canada (Teich and Holst 1974, Murray and Skeates 1985).

Sitka spruce. A clinal pattern of variation south-to-north and coast-to-inland Sitka spruce has been well established. Provenances of northern and inland origins flushed earlier, had a shorter duration of shoot elongation and less volume growth, but were more winter hardy than southern and coastal provenances (Pollard et al. 1975, Falkenhagen 1977, Illingworth 1978b). Seed sources of the Oregon-Washington coast planted on northern Vancouver Island outgrew the local source by 40% in total height in 10 years (Ying, unpublished data). This pattern of clinal variation is most obvious along the Pacific 'fog belt', but become complicated from outer coast to inland by increasing environmental complexity and introgressive hybridization with white and Engelmann spruce (Picea engelmannii Parry) (Fowler and Roche 1975). Introgression of white spruce increased the winter hardiness but decreased the growth potential of Sitka spruce (Ying and Morgenstern 1982).

Sitka spruce seems to offer little promise in other regions of Canada (Khalil 1977) although it is an important plantation species in many other countries, Britain in particular (Roche and Fowler 1975).

Englemann spruce and spruce complex in interior British Columbia. Engelmann spruce hybridizes freely with white spruce wherever they are sympatric (Roche 1969, Fowler and Roche 1975). In British Columbia, in silviculture they are treated as a single species complex - interior spruce. Our understanding of the geographic variation of interior spruce is largely derived from Roche's (1969) genecological study at the nursery stage and in subsequent field tests of the same material. Elevation of seed source was the dominant geographic variable determining genetic differentiation; high elevation sources completed shoot elongation and entered dormancy earlier, and produced less dry matter than low elevation sources. Clinal variation with latitude was weak although growth behavior of northern sources was similar to that of high elevations. Provenance performance in field tests after 15 years showed a similar trend associated with elevation (Jaquish et al. 1984).

Jack pine and lodgepole pine. Both are closely related genetically and natural hybridization occurs where their ranges overlap, i.e. in north-central Alberta and between the Peace and MacKenzie Rivers in the Northwest Territories (Rudolph and Yeatman 1982). The natural range of lodgepole pine is limited to Alberta and British Columbia whereas jack pine is distributed from the Atlantic Coast to the Northwest Territories. Both species received the most comprehensive study among our native pine species (Table 1).

Geographic variation in jack pine is characterized predominantly by a clinal pattern across its range (Rudolph and Yeatman 1982). This pattern is associated with latitude (photoperiod) and length of growing season. Heat sum (degree days) at seed origin is the most important environmental variable explaining the response among seed sources (Yeatman 1974). Adaptive traits such as growth behavior, phenological events and winter hardiness showed stronger clinal trends than branching habit, foliage color, seed yield, and tolerance of insects and diseases (Rudolph and Yeatman 1982). Hierarchal analysis revealed little stand-to-stand genetic differentiation and much variation among families within climatic regimes (Yeatman 1975).

Lodgepole pine provenance studies have been concentrated in British Columbia and a comprehensive provenance test program was organized in 1960. Sharp geographic differentiation occurred along the coast-interior division resulting in distinct differences between the coastal and interior forms of the species, which were classified by Critchfield (1980) as P. contorta ssp. contorta (shore pine) and P. contorta ssp. latifolia (Rocky Mountain pine). They differ not only in gross morphology, but also in less obvious features such as leaf anatomy. Coastal provenances can be readily distinguished in the nursery and field tests by their shorter, thicker and darker green foliage and susceptibility to frost (Illingworth 1971, 1975, Ying and Illingworth 1986). A high number of stomata per square millimetre of needle surface is an important adaptive trait associated with coastal sources. A strong north-south clinal pattern along the Pacific Coast was evident in growth, autumn frost damage and other traits, but became less discernable in the interior where the complex interplay of mountains, the maritime air from the Pacific and cold air from the Arctic tend to obscure north-south environmental gradients and the associated pattern of variation (Illingworth 1975).

Long-term field tests exist mainly in interior British Columbia where lodgepole pine is a major commercial species. Provenance response to environments throughout the interior of the Province indicated broad regional patterns, a strong influence of elevation of seed origin, and weak provenance x site interaction (Illingworth 1978c, Ying et al. 1985, O'Reilly 1986, Yanchuk 1986). The main distinguishing features of sources from different geographic regions are:

Geographic region	Features
Pacific coast	Least hardy (repeated winter damage)
Coast-interior transition	Susceptible to frost and disease
Yukon and northern B.C.	Susceptible to disease, slow growing
Central and southern B.C.	Hardy, large variation in growth and tolerance of disease (high elevation sources slow growing and susceptible to disease).

Red pine. Red pine (Pinus resinosa Ait.) is known for its genetic homogeneity (Fowler and Heimburger 1969a). Field tests confirmed this low genetic variability, but a latitudinal pattern of geographic variation can still be detected (Park and Fowler 1981) and use of wrong sources can result in substantial loss in productivity (Roller 1968, Klein 1976).

White pine. Both eastern white pine (P. strobus L.) and western white pine (P. monticola Dougl.) have been very valuable timber species in Canada for a long time. More work has been done in Canada with eastern than with western white pine. Even so, only very few samples of eastern white pine have been taken in Ontario and Quebec where the range extends into boreal regions. Both species exhibited less genetic variability than other species with a similar ecological range and they were marked by extreme phenotypic plasticity. Provenance samples of eastern white pine covering 13 degrees of latitude, 30 degrees of longitude and 2300 m of elevation showed little differences in winter hardiness, although a broad latitudinal cline was detected in growth (Fowler and Heimburger 1969b). Similarly, sampling of parts of the range of western white pine failed to detect geographic, ecological, or elevational patterns of differentiation (Rehfeldt and Steinhoff 1970, Steinhoff 1981). Three broad latitudinal zones could be delineated only from samples representing the entire range, approximately 20° latitude (Rehfeldt et al. 1984).

Coastal Douglas-fir. Douglas-fir, the most important timber species in the coastal region, has been planted in British Columbia since 1930. Systematic provenance research in British Columbia began and a network of field tests was established between 1969 and 1975. Populations exhibited a broad pattern of geographic variation parallel to major climatic gradients from maritime to subcontinental areas. Beyond these major trends, provenance variation was only weakly correlated with environmental and ecological factors indicating no discernible pattern of local adaptation (Illingworth 1978a, Ying, unpublished report). Provenances from northeastern Washington were fast growing and showed remarkable stability over a wide range of environments.

Other native species. We know very little about geographic variation of the true firs, the larch species and most of the deciduous species. Systematic provenance testing of some of these species has been initiated in recent years, e.g. the true firs, tamarack, and some of the deciduous species (Tables 1 and 2). No doubt we will learn more about them as time goes on. Because of limited resources, we cannot expect to develop comprehensive field experiments for species with low commercial value.

Exotic species. Provenance testing of exotic species has been undertaken mostly in eastern and central Canada. Norway spruce is the most widely planted exotic conifer and has been most extensively tested, but none of the tests sample the entire elevational and latitudinal range in systematic fashion. For descriptions of the variation pattern we must therefore go to European investigators (Schmidt-Vogt 1977). Fowler (1979a) points out that this species encounters biotic agents in North America not found within its natural range, particularly the white pine weevil (Pissodes strobi Peck) and spruce budworm (Choristoneura fumiferana Clemens). In the colder continental climates of central Canada winter drying of provenances from milder areas (low-elevation areas of western Europe) is also a serious problem. In spite of these problems, experiments indicate a potential of certain provenances to outgrow white spruce on carefully selected, slightly acid sites, particularly in the Maritime provinces which are within the temperate zone (Fowler 1979a). In the boreal and extreme continental areas of Canada, Norway spruce introduction is probably not justifiable (Klein 1977).

Scots pine from the Soviet Union was tested in Canada and results showed that the northern Ukraine and southern Russia is a region of potential seed sources (Teich and Holst 1970). In the Prairie Provinces there was extensive insect and disease damage resulting in poor form in later ages (Klein 1979) but in Ontario and Quebec a number of good stands exist which regenerate naturally.

Japanese larch (Larix leptolepis (Sieb. et Zucc.) Gord.) and European larch and their hybrids were tested extensively. Japanese larch showed high variation among provenances but there was no geographic pattern related to latitude, longitude or elevation (Park and Fowler 1983). Assessments of plantations of both species and hybrids in eastern Canada indicated yields of 7 to 14 m^3 per ha per year on good sites, which could be further augmented by a selection program (Park and Fowler 1983, Vallée and Stipanicic 1983). Two recent workshops in Ontario and New Brunswick have summarized the information on variation in the genus Larix Mill. and of prospects for breeding (Graham et al. 1983, New Brunswick Forest Research Advisory Committee 1986).

DISCUSSION

This review has shown that geographic variation received very early attention in tree improvement but that early tests were exploratory in nature involving small numbers of provenances, typically 30 or less, and often were not replicated.

Our information on geographic variation is largely derived from the newer test established since about 1955 in eastern Canada and after 1960 in western Canada. These newer tests were carefully designed with extensive and systematic provenance samples, e.g. the cooperative range-wide tests of jack pine, black spruce and white pine organized by Petawawa National Forestry Institute, and the lodgepole pine, coastal Douglas-fir and Sitka spruce provenance tests established by the B.C. Forest Service.

The degree of geographic differentiation varies with species: red pine and both western and eastern white pine showed little geographic differentiation even though ecological magnitude within their natural range is comparable to that of many other species. Most species, however, exhibited clinal patterns parallel to environmental gradients. Clinal differentiation is expected from natural selection, but the degree of parallelism in clinal trend varies from species to species, and also from one part of the species range to another. For example, Sitka spruce and shore pine exhibited a high degree of parallelism following the north-south gradient along the Pacific Coast. This north-south parallelism was not as obvious in coastal Douglas-fir, although the type occupies a similar range of environments. From coast to inland, the increasing complexity of environmental gradients tended to obscure this parallelism in clinal trends in both Sitka spruce and lodgepole pine (Illingworth 1987 b, c, Ying et al. 1985). Provenance test results seem to indicate low parallelism in clinal trends (broad regional variation) in most conifers. Predictability of provenance performance would be high with species showing a high degree of parallelism, which would render the task of seed zone delineation and control of seed transfer much simpler.

Despite the fact that the newly established tests usually involve large provenance samples, often over 100, the samples are far from adequate to unravel variation patterns within regions. Different adaptive patterns of variation could have evolved within a limited geographic area (Campbell 1987). Although we now have an idea of major geographic trends there is still a long way to go before we fully understand the underlying evolutionary processes and adaptive mechanism in relation to regional and local environments.

Furthermore, most tests are too young to determine survival tends over a whole rotation period. Studies of Douglas-fir pursued over a 60-year period indicate that decimation of non-adapted sources began after age 30 (Silen 1978). Long-term studies of several species in Europe underline the critical role of survival. At greater age, stocking may control volume production more strongly than height (Campbell 1974, Oleksyn and Giertych 1984). It is therefore important to maintain existing experiments for several more decades so that survival can be followed and seed zone boundaries be adjusted as new information becomes available.

SILVICULTURAL IMPACT

The results of provenance research are being used in several ways in silviculture. In British Columbia, the existing seed zones based on ecological classifications have been revised according to the geographic variation patterns derived from provenance tests of lodgepole pine and interior spruce (Anon. 1987). These new zones and guidelines for seed transfer provide the framework for decision on selection of seed sources, parent-tree selection and seed orchard planning (Lester et al. 1988). Provenance test results are also used to guide seed collection and distribution in the Maritime Provinces and in Ontario, and to develop breeding zones (Murray and Skeates 1985, Boyle 1985, Fowler 1986). In Quebec, stands designated for cone collection are chosen on the basis of available provenance test results, and regulations are frequently updated (Y. Lamontagne, pers. comm.).

In reforestation, after a choice of species has been made, selection of the best available seed sources comes next. The most tangible impact of provenance testing is the identification of productive seed sources. A few of the better known examples are the Ottawa Valley white spruce, coastal Douglas-fir from northwestern Washington, and Sitka spruce from the Oregon-Washington coast. By planting these productive sources on the right sites, increases in wood production can be substantial, e.g. 40% in volume over a local source by planting Oregon-Washington Sitka spruce on Vancouver Island (Ying, unpublished data).

Time is the most valuable ingredient in research with tree species. Despite many compromises in design and sampling of the older provenance tests (Fowler 1979b), they are very valuable. Genetic variation in certain traits takes many years to develop. Tremendous variation among provenances of Sitka spruce was observed in the ability to deter and recover from weevil (*Pissodes strobi* Peck) attack (Ying, 1986), of Sitka and coastal Douglas fir to recover from deer browsing, and of lodgepole pine to overcome frost injury. Much of this information will be lost when assessment is limited to growth and survival. Such old tests are also invaluable for interdisciplinary research, e.g., assessment of site specific productivity, study of plantation ecology, and impact of intensive silviculture on wood density.

Other, more intangible benefits of provenance research are the experience gained in seed collection and raising of nursery stock, which can be used to improve silvicultural practices, particularly of lesser known species.

CONCLUSIONS

This review has presented the major facets of variation in our most important species. After 45 years of work a much better understanding exists of basic species biology, and this knowledge has been applied to improve methods of silviculture and tree improvement. At the same time, the development of more comprehensive reforestation programs involving a greater variety of species is calling for investigation of additional species, e.g. yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) and red cedar (*Thuja plicata* Donn) on the west coast and some hardwood (deciduous) species in eastern Canada. As Tables 1 to 3 indicate, experiments with species of the genus *Abies* L. and several hardwoods have been recently established and early results are available.

Beyond this, it is necessary to recognize the fact that we have few results that allow final conclusions. We are too optimistic if we rely on field experiments that are only 10 to 20 years old and if we limit our attention to tree height. Particularly when seed sources have been moved considerable distances, changes in ranking are still taking place and slowly declining survival can be expected to influence volume production. The maintenance and continued observation of the major experiments is therefore required.