VARIATION, SELECTION AND BREEDING OF CONIFEROUS TREE SPECIES: AN INTRODUCTION

by

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QUEBEC REGION, QUEBEC
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PREFACE

The literature in English dealing with variation and breeding of tree species is by and large very specialized and scattered in numerous scientific journals and books. It is difficult for anyone seeking an easily read introduction to the subject to obtain from this literature a coherent view of what it is all about. The essential unity of the subject is simply not apparent.

For this reason an effort has been made in this publication to place forest tree improvement work against the broad background of botanical science in the hope that the interrelationships of each aspect of the subject will be brought into clearer perspective, and unity given to the subject as a whole. However, a strictly academic treatment of the subject has been avoided, and examples and illustrations stemming directly from the author's research work in forest genetics and tree improvement have been included in the text.

In striving to maintain an elementary level throughout the text it has been necessary to gloss over numerous aspects of the subject. However, it is hoped that this does not seriously impair the value of the text for the purpose intended, which is to provide a coherent and easily read introduction to the important aspects of forest genetics and tree improvement research and practice. Terms which are underlined in the text are defined in the glossary. A relevant bibliography is also appended.

VARIATION, SELECTION AND BREEDING OF CONIFEROUS TREE SPECIES: AN INTRODUCTION

L. Roche

1. INTRODUCTION

It is recorded that the movement of plant seed by man from its original source began as early as 4,000 B.C., and it is not unlikely that the purposeful or unwitting selection of plants developed simultaneously. The cultivated plants of the modern world are the products of both these activities of pre-historic man and his descendants through the ages (3,8).

Man has successfully moved plant species, not only a few hundred miles from their original source, but thousands of miles. Many of the edible plants which we consider indigenous were unknown in North America a few hundred years ago. Indeed, one of the most common foods, the tomato, which originated on the slopes of the Andes, as did the potato, was practically unknown in the United States and Canada during the early 19th century. Asparagus, beets, broccoli, cabbage, cauliflower, celery, and endive, kale, lettuce, parsley, parsnips and rhubarb, all originated in those lands lying east of the Mediterranean Sea. The Far East gave us egg-plant, cucumbers and soybeans. The Middle East and India, carrots, onions and muskmelon, while Africa contributed the watermelon (8), The wild forms of all these cultivated plants, where they are still extant, are quite different from the modern cultivated forms. In some instances the wild form has disappeared from the face of the earth, for example, the ancestor of maize or corn.

With, perhaps, one striking exception, man, by selection and breeding, has produced from the wild plant forms which he found useful to his primitive existence, cultivated forms vastly superior to the wild ancestors. The one exception is the forest tree. Man has used wood from time immemorial, but the Douglas fir growing in natural stands of the Pacific Northwest is still nature's own child. The same can be said of many of the indigenous forests of Western Europe. Thus the forest tree is the only remaining plant species of major commercial importance still, for the most part, growing in its wild form.

The conversion of the wild form of a tree species to a cultivated form, possessing many characteristics desirable to man, precludes natural regeneration of existing stands, and involves the artificial propagation of improved varieties which have been obtained from these stands by selection and breeding, or by the introduction of exotics. For this reason, tree breeding is particularly applicable where artificial regeneration is practiced.

The present interest in tree breeding, therefore, is not due to academic speculations but to the fact that the transformation from old growth to second growth management, and the principles of sustained yield, have given rise to problems which can be solved only by the wise utilization of all available knowledge concerning the genetics of forest trees. Furthermore, as noted above, since all horticultural and agricultural plant species of major commercial importance are without exception the products of the plant breeder's activities, it is not surprising that one of the most valuable plant species in the world, the coniferous tree, should now be subjected to the preliminary phases of a similar process.

In contrast to many other countries where forest genetics and tree improvement is important, Canada has a large number of indigenous coniferous tree species. These species between them form a vast natural forest covering a great part of the country. As sources of raw material the species composing this great forest are fairly well characterized; their biological characteristics, however, are only now beginning to be investigated. These facts strongly influence, and rightly so, the development of forest genetics and tree improvement research and practice in Canada.

Three stages may be recognized in this development. The first is concerned with delimiting the patterns of variation within the species. The raw material is "catalogued" biologically, or put another way, an inventory is made of the gene resources of the major commercial species by genecological research, or more popularly, provenance research. At this stage appropriate steps may be taken to conserve *in situ* populations representative of diverse gene resources. The next stage is concerned with the utilization of gene resources i.e. the establishment of seed zones and seed production areas, delimited and characterized by the first stage. A third stage, which may be conducted simultaneously with the second, pertains to the improvement of gene resources by selection, breeding and progeny testing, and the mass production of the improved strains. At the present time in Canada tree improvement work is concentrated in stages one and two.

2. GENETICS AND THE THEORY OF EVOLUTION

2:1 Chromosomes and Genes

When plant or animal cells are stained with certain chemicals, long, thread-like structures become obvious in the cell nucleus. These structures which occur in pairs in definite numbers in all plants and animals are known as chromosomes. For example man has 46 such chromosomes, or 23 pairs, the potato has 24 pairs, the rat 21 and spruce species 12.

Genes are the fundamental units of inheritance. They possess highly complex chemical and physical properties, and are arranged in linear order along the chromosomes. A person has brown eyes because he possesses a gene or gene complex controlling production of a brown pigment in the iris of his eye. Similarly tree species such as white spruce (*Picea glauca*) and yellow birch (*Betula alleghaniensis*) are different from each other because they are genetically different. The individuals within each of these species will also differ genetically, though not to the extent that species differ. However, the evolutionary processes which give rise to within species variation (intraspecific variation) differ from those giving rise to between species variation (interspecific variation) only in degree and not in kind.

Genes not only influence the external appearance of an organism, they also control its internal physiological processes. Thus, because of their highly different genetic constitutions, one tree species will survive in semi-arid regions, e.g. ponderosa pine (Pinus ponderosa) while another will survive only in moist areas, e.g. Sitka spruce (Picea sitchensis). Similarly, races within a tree species will also survive and grow better in certain regions than in others, for example the coastal and inland forms of Douglas fir (Pseudotsuga manziesii).

2:2 The Breeding System and Natural Selection

During the formation of the egg cell in female organisms, and the sperm cells in male organisms, the number of chromosomes is halved, and each member of a similar pair of chromosomes will occupy different egg or sperm cells. This form of cell division which reduces the chromosome number, and gives rise to egg and sperm cells is termed meiosis. Thus the pollen produced by the male flower and the egg cells produced by the female flower on a white spruce tree will each contain 12 single chromosomes, and not 12 pairs which is the complement of all cells of this species other than sex cells. The former number is known as the haploid number and the latter as the diploid.

Many coniferous trees are self-sterile, that is they cannot inbreed, and fertilization normally occurs when pollen from one tree is blown onto the female organ of another tree of the same species (Fig. 1). The fusion of the nucleus of these two germ cells, that is sperm and egg, results in the restoration of the diploid number of chromosomes in the fertilized egg cell which is now termed the zygote. In this manner genes are contributed by both parents and fixed in new combinations in the progeny.

By a process of cell division termed mitosis the zygote develops into the embryo which is the tiny structure contained within all tree seed that finally develops into the tree. Mitosis differs from meiosis in that the diploid cells merely duplicate themselves and their chromosome complement, so that there is no reduction in the chromosome number in the cells thus formed. Thus mitotic division results in growth whereas meiosis leads to reproduction.

The number of possible recombinations of the parental genes, segregated during the formation of great amounts of sperm and eggs, is very large for a coniferous species. For example in a good seed year the seed shed by a spruce tree will give rise to seedlings no two of which are identical genetically. They will, nevertheless, be distinguishable from the seedlings of other tree species, for, though they differ from each other genetically, this difference, as already noted, is not as great as genetic differences between species. Many of these seedlings will have a genetic constitution which will allow them to survive in the environment in which they are propagated. Others will not, and will be eliminated. Thus, the random, within population variation resulting from segregation and recombination is the raw material which is acted upon by the selection pressures of the environment to produce geographic variation, that is, between population variation within the species.

The process whereby the environment "selects" individuals and eliminates others is termed natural selection. Individuals thus selected are said to be adapted to the environment in which they live. It is through the process of natural selection that species evolve, hence the word evolution.

A knowledge of the theory of evolution, therefore, which embraces both the concept of adaptation and that of natural selection, is essential to any clear understanding of variation in forest trees, and the processes of artificial selection and breeding.

Indeed, many biologists now believe that the theory of evolution is the one great unifying concept that closely knits together all the branches and experimental disciplines of biology (12). Put a little more poetically it may be said that evolution is a light which illuminates a very broad field of biological phenomena.

2:3 Inherited and Acquired Characteristics

Before discussing evolution and natural selection in greater detail it is necessary to distinguish between those environmental influences which eliminate ill-adapted individuals, and those which merely modify the external appearance of a tree. For example the external appearance of a tree may be modified to a greater or lesser degree by the environment (Fig. 2). Thus while a lodgepole pine tree (Pinus contorta) will always be distinctly a pine, it can be a scrubby or a tall one depending on its degree of exposure to strong winds, and/or other site factors. The external appearance of a tree, therefore, is the result of the interaction of the environment prevailing during its life time and its genetic make up, that is, its genotype, and is referred to as the phenotype. Put very simply: genotype plus environment equals phenotype.

Environmental influences which eliminate ill-adapted individuals and select well adapted individuals, will in the long run result in the fixation of genetically based, desirable characteristics, that is characteristics which confer a survival advantage in the population. Such characteristics are inherited. On the other hand, characteristics which are merely the result of "temporary" environmental modification such as that illustrated in fig. 2 are not inherited. Put another way, a characteristic acquired by a tree during its life time, as a result of environmental influences prevailing during that time, is not inherited.

2:4 Natural Selection and Evolution

Natural selection may be explained by the following simple analogy:

> "Suppose that from a pool of all the letters of the alphabet in large, equal abundance you tried to draw simultaneously the letters c, a, and t, in order to achieve a purposeful combination of these into the word "cat". Drawing out three letters at a time and then discarding them if they did not form this useful combination, you obviously would have very little chance of achieving your purpose. You might spend days, weeks, or even years at your task before you finally succeeded. The possible number of combinations of three letters is very large and only one of these is suitable for your purpose. Indeed, you might well never succeed, because you might have drawn all the c's, a's, or t's in wrong combinations and have discarded them before you succeeded in drawing all three together. But now suppose that every time you draw a c, an a,

or a t in a wrong combination, you are allowed to put these desirable letters back in the pool and to discard the undesirable letters. Now you are sure of obtaining your result, and your chances of obtaining it quickly are much improved. In time there will be only c's, a's, and t's in the pool, but you probably will have succeeded long before that. Now suppose that in addition to returning c's, a's, and t's to the pool and discarding all other letters, you are allowed to clip together any two of the desirable letters when you happen to draw them at the same time. You will shortly have in the pool a large number of clipped ca, ct, and at combinations plus an also large number of the t's, a's, and c's needed to complete one of these if it is drawn again. Your chances of quickly obtaining the desired result are improved still more, and by these processes you have generated a high degree of probability - you have made it probable that you will quickly achieve the combination cat, which was so improbable at the outset. Moreover, you have created something. You did not create the letters c, a, and t, but you have created the word "cat", which did not exist when you started" (37).

The selecting agent in nature is the environment, and the genes of an individual in a natural population, say a population of trees, correspond to the letters in the above analogy. Those individuals of a population with favourable gene combinations - well adapted individuals - have a survival advantage over those with unfavourable combinations - ill-adapted individuals. Thus over a period of time as a result of the selective action of the environment the population, which shares a common gene pool, is adapted to this environment.

The selective action of the environment will vary from one geographic region to another depending on differences in such factors as altitude and latitude. Consequently if a species is widespread, and occupies many diverse environments, for example, white spruce, it will vary genetically, and more or less parallel with variation in the environment. This variation within a species is termed geographic variation, and the populations thus adapted are termed geographic varieties. It is this form of variation within a tree species, which is also referred to as microevolution, that is of special interest to the forester. In time, and following isolation of the variety from the main body of the species, a new species may evolve. This is termed macroevolution.

It would be difficult to improve on the following definition of a geographic variety: "The subspecies or geographic variety is a series of populations having certain morphological and physiological characteristics in common, inhabiting a geographic subdivision of the range of the species or a series of similar ecological habitats, and differing in several characteristics from typical members of other subspecies, although connected with one or more of them by a series of intergrading forms" (39). This definition embraces both variation which is continuous and variation which is discontinuous, and, since the question of which form is predominant in a tree species is not unimportant, it is discussed in some detail in chapter 3.

In summary it may be said that there are three levels of variation in natural populations. There is individual variation that is, within population variation, resulting from segregation and recombination. A number of important characteristics of forest trees are found at this level of variation, for example wood quality. They do not confer a survival value on the tree, and are not generally subject to the selection pressures of the environment. These characteristics, therefore, are not habitat-correlated, but randomly occur in individual trees. There are, of course, many other characteristics found at this level of variation which do confer a survival value on the tree possessing them, and these characteristics are subject to the selective pressures of the environment. The second level of variation is micro-evolution by natural selection, that is, between population variation. This is the nonrandom habitat-correlated variation which characterizes populations. Characteristics at this level of variation are associated with the growth rhythm of the species, for example, times of flushing and dormancy. The third level of variation results from a combination of selection and isolating mechanisms and leads to the development of new species.

The first two levels of variation in forest trees are of considerable interest to the forester, and it is important to clearly distinguish between them. The third level of variation is primarily the concern of the evolutionist.

3. VARIATION IN FOREST TREES

3:1 The Terminology of Intraspecific Variation Patterns

A provenance is a given seed lot from one or more trees from any one part of the species distribution, and is a sample of the gene resources of the population occupying this region. Depending on the intensity of sampling, and the degree of variation within the population, this sample may adequately represent the gene pool of the population or it may be quite unrepresentative. Therefore, if seed is being collected for experimental purposes it is always wise to collect from a number of trees well scattered throughout the population. In this sense a provenance is a genetic as well as a geographic entity.

A population is a group of potentially interbreeding individuals; for example a coniferous stand in which every tree is capable of passing and receiving pollen from every other tree.

The variation pattern of any characteristic within a coniferous species may be continuous or discontinuous. That is, it may vary progressively from one environment to another, if there is a gradual transition from one environmental regime to another. If there is not a gradual transition the species may be broken up into a series of non-intergrading populations each of which exhibits the character in a different form.

If the variation pattern is discontinuous it is said to be ecotypic, and the population thus adapted is termed an ecotype. If the variation pattern is continuous it is said to be clinal, and the adapted population is termed an ecocline.

For example, the fragmented lodgepole pine populations growing in such discontinuous and diverse environments as the bogs of Lulu Island and the rocky outcrops of coastal British Columbia are likely to exhibit ecotypic variation. On the other hand white spruce populations, which are continuous in their distribution through gradually changing environments from low to high elevations and latitudes are likely to exhibit clinal variation.

3:2 Climate and Variation

The selective pressures at work in any particular environment have three principal components; these are climatic, edaphic (influences related to soil) and biotic (influences related to living organisms). Of these three, climate is by far the most important, particularly with regard to the selection and adaptation of coniferous trees. Edaphic and biotic factors also play their part, and in special circumstances can assume importance, but in most instances the climate is the basic component, for it largely determines the character of the other two. Thus whatever the technique used in the study of variation within species, the most accurate information possible of the climatic regime of the provenances selected for study is indispensable. This is particularly important in areas where there are striking differences in climate over relatively short distances.

Generally speaking the length of the growing season, which may be taken as the number of days between the average date of the occurrence of late spring frosts and early fall frosts, is closely correlated with altitude and latitude. European workers have demonstrated that an increase in altitude of 100 metres, and an increase of 1 degree of latitude will both result in the shortening of the growing season by approximately 5.5 days (40). There is little doubt that these figures are only roughly correct for Canada, for in many instances the temperature regimes expected on the basis of altitude and latitude may be reversed by such local factors as air drainage, elevation, exposure to invasions of cold air, etc. (9).

The number of days in the growing season is an important index of the climatic regime in a given area, and consequently it is closely related to the growth rhythm of the tree population occupying that area.

Another important factor of the environment which influences the growth rhythm of many plants including forest trees is the day length, or photoperiod as it is technically referred to. Day length varies with the seasons and with latitude, but at a given altitude and latitude is constant from year to year on any particular day. On the other hand the date of occurrence of late spring frosts and early fall frosts at the same location will vary from year to year. If the initiation of, say, dormancy were influenced by nothing more than temperature, then an unseasonably mild late fall, rapidly followed by freezing temperatures, would result in severe frost damage to shoots still growing because of the unseasonably high temperatures. However, if day length directly influenced the growth rhythm, then plants would go dormant when a critical day length is reached irrespective of prevailing temperatures. Plants which continued to grow after the occurrence of the average date of late fall frost would be continually cut back by frost damage, and finally eliminated from the population. In this way vital growth phases of the population are adapted to a particular photoperiod.

The interaction of day length and temperature on the growth rhythm of tree species is a complex one. Nevertheless, it may be stated that dormancy is predominantly influenced by day length and that a leaf pigment termed phytochrome, or a phytochrome-like substance, is the responsible agent. Phytochrome changes its composition under the stimulus of varying day length and thereby initiates a series of chemical processes which lead to dormancy.

There is relatively little climatic information for many of the great forested areas of Canada. Nevertheless, the information that is available, together with data concerning soil and land forms, and the distribution of plant species, is sufficient to allow the recognition of certain broad forest regions. Forest regions are ecologically distinct from each other at their centers, and consequently exert different selection pressures on populations of a single species which ranges through several regions. These regions (36) and their subdivisions (19, 20,22,23) are, therefore, important in relation to the interpretation of patterns of geographic variation in Canadian tree species, and also in relation to the occurrence of these species.

In summary, therefore, it may be said that the climatic pattern determines the genetic pattern of variation within the species. The growth rhythm of the adapted population is in phase with the surrounding climatic rhythm. This growth rhythm is genetically fixed; consequently if a provenance is transferred to an area where its growth is out of phase with the surrounding environment - for example if a provenance is transferred from low elevation to high elevation - it may not survive, and certainly will not thrive, in its alien surroundings.

In the following sections practical examples will be given illustrating the points made in the preceding paragraphs. These examples are for the most part related to the distribution and variation pattern of Canadian tree species.

3:3 Morphological Expression of Genetic Variation

Some morphological characteristics of forest trees such as absolute size and form are easily modified by the environment, that is, they are not under strong genetic control (Fig. 2). On the other hand other characteristics are under strong genetic control, and can be modified only slightly or not at all by the environment. For this reason genetic variation in the former characteristics can be measured with accuracy only when the provenances under study are brought to a uniform environment, while the latter characteristics can be studied in the natural population.

Characteristics which are under strong genetic control are related to the reproductive rather than the vegetative parts of the plant though those vegetative parts of the plant, more remote from the direct action of the environment, may also be a good expression of the genotype. One of the main reasons for the stability of the floral parts is that their growth after differentiation is always considerably less in forest trees than in any of its vegetative parts.

For these reasons, therefore, striking differences in gross morphology of forest trees in their natural habitat are seldom indicative of major genetic differences. This statement, of course, applies to populations rather than individual trees, for it is certainly not unusual to find mutant types which in gross morphology are quite different from the rest of the population. Their occurrence, however, is rare enough to render them unimportant with regard to natural selection and the build up of subspecific variation. They do, of course, provide the horticulturist with numerous ornamentals, and more rarely the tree breeder with a polyploid species, that is a species with three or more times the haploid number of chromosomes in its cells, for example the triploid aspen. Sometimes, however, a striking difference in gross morphology can reflect a genetic difference between populations occupying extensive, clear-cut climatic regions; for example the bark of the continental and coastal forms of lodgepole pine (Fig. 3).

Fig. 4 shows the extremes of the spectrum of variation in cone scale morphology in the white-Engelmann complex in British Columbia and Fig. 5 shows the relationship between an aspect of this variation and altitude. The implications of this result with regard to hybridization between white and Engelmann spruce will be discussed in the following section. For present purposes it is sufficient to note that there is a definite association between place of origin and morphology of the sample. The change in shape of the cone scale is a progressive one and reflects more or less the changing environment which runs parallel with increasing altitude.

In most instances selection in a natural population of trees involves many different genes. This will be better understood if it is recalled that the genes are in linear order along the chromosomes. Some genes are so close to each other that they are not separated during meiosis. Such genes are said to be linked. Consequently if a gene controlling a characteristic which confers a survival advantage on a tree is linked to another which controls say, shape of leaf or cone scale form, then both will be selected together. For example there is evidence that the chemical content of the needles of white and Engelmann spruce and their hybrid (21) varies in a manner similar to cone scale form illustrated in Fig. 6.

It must be noted here that the above statement concerning linkage of genes, and the implied one gene-one character relationship is a very oversimplified explanation of the actual situation. Nevertheless, there is little doubt that many non-adaptive characteristics in plant species, that is characteristics which confer no particular survival advantage on the population, are correlated with physiological processes, for example, period of dormancy, which are decidedly adaptive.

In summary, therefore, it may be said that the variation pattern in cone scale morphology referred to above, if not itself of direct advantage to spruce populations, reflects a physiological pattern of variation in these populations which enables them to survive and thrive in the varying habitats in which they are found.

The value of studies of this nature is that they provide information concerning the pattern of variation in the wild, mature populations of tree species which have undergone selection and adaptation, and possibly hybridization, in their natural habitat. In this way the scope of subsequent experimental work in immature populations in controlled and partially controlled environments is narrowed. These tests in turn narrow the scope of field tests which ultimately follow all preliminary assessments of variation in controlled and partially controlled environments.

3:4 Natural hybridization and Variation

In the last paragraph of the previous section it was implied that the variation pattern within a species may be influenced by hybridization and that a measure of the degree of hybridization can be obtained by an examination of field specimens of cones and foliage. This subject will now be examined in relation to the Canadian spruce species.

When the geographic ranges of plant species overlap, the species are said to be sympatric. If the geographic ranges do not overlap the species are termed allopatric. For example lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) are sympatric in British Columbia, while in Quebec white spruce is allopatric in respect to this species.

It is obvious that if the ranges of two species overlap, the possibility of hybridization is greatly increased; particularly if the species, unlike those referred to above, are morphologically alike and belong to the same genus. However, it is very important to note that the hybrid generation cannot successfully compete for survival in the habitats of the parental forms, for the parents will be much better adapted to their habitats than the hybrids. Consequently an ecological niche must be available to the hybrid before it can survive and colonize an area. "... This explains how species remain distinct in nature in the face of hybridization. Since the hybrids are not so well adapted as their parents to their habitats, they are weeded out by natural selection. In disturbed habitats formed by deforestation, clearing, cultivation, etc., some of the hybrids formed may have a combination of characters better adapted than their parents to the new mixture of habitats produced" (18).

The range of white spruce in British Columbia overlaps that of Engelmann. Black and white are sympatric in many areas of the boreal forest of northern Canada. Sitka and white are sympatric in the region of Hazelton in northwestern British Columbia, and possibly in other similar regions, and red and black spruce are sympatric in southern Quebec, and in the Maritimes. Therefore one of the principal requirements prerequisite to hybridization between these species is present (11,16,21,32,33,34). Now the requirement prerequisite to the successful establishment of the hybrid, that is, the availability of an ecological niche, is to a great extent met with regard to the white-Engelmann and white-Sitka hybrids. As already noted there exists a broad transitional zone between the low elevation white spruce forests, and the high elevation Engelmann spruce forests. This zone is available to the white-Engelmann hybrid. Thus the pattern of variation in cone scale morphology (Fig. 5) varies progressively from low elevation, montane white spruce forests through the hybrid form to high elevation subalpine Engelmann spruce forests. Similarly there exists a broad transitional zone along the river valleys between the coastal forests of Sitka spruce, and the Montane forests of white spruce. This zone is available to the Sitka-white hybrid. There is no such clear-cut transition zone between white spruce and black spruce in the boreal forests of northern British Columbia, and consequently it is not surprising that little evidence has been found of hybrid populations similar to that of the white-Engelmann hybrid (Fig. 5). However, this does not imply that individual black-white hybrids do not occur in northern British Columbia where these species are found together. Similarly, the black-red spruce hybrid in Quebec does not appear to have colonized a particular ecological niche intermediate between that of the parental forms. There is, however, no doubt that this hybrid occurs in Quebec.

By using graphic methods such as that represented in Fig. 5 it is possible to elucidate the variation pattern in the sympatric zones by indicating the relative proportion of each species present, and providing some evidence of degree of hybridization, if any.

In summary, therefore, it may be stated that <u>introgressive hybridization</u> affects the variation pattern within the coniferous species involved. Such hybridization does not occur independently of the processes of selection and adaptation - at least with regard to the examples given above - which operate to produce geographic variation. A natural hybrid of a coniferous species will be successful only if an ecological niche favourable to its survival is present in the general region occupied by the parental species. It is important to note that in regard to the survival of the natural hybrid the word ecological niche refers to the total environment, that is, all climatic, edaphic and biotic factors affecting the survival and colonization of the hybrid form.

With a programme of artificial hybridization it is, of course, possible to match hybrid and site. This possibility, however, is discussed in chapter 5. The discussion concerning artificial crossing in a seed orchard, given in the same chapter, is also relevant to this problem. Therefore, it is sufficient to note here that a knowledge of the genecology of each species, race or provenance involved in a crossing programme is indispensable if the hybrid progenies of each cross are to form thrifty plantations, that is, if hybrid and site are to be well matched. This knowledge is obtained by investigations such as those described above and in the following sections.

3:5 Assessment of Variation in Controlled and Partially Controlled Environments.

Physiological variation is of direct interest to the forester. He is interested in morphological variation insofar as that variation is correlated with genetically controlled physiological processes. However, a complete evaluation of these processes whether correlated with morphological characteristics or not, can only be achieved experimentally. These experiments can be conducted in a growth chamber, that is, an artificial environment over which there is complete control, in a nursery, which is a partially controlled environment, and under natural conditions in the field. To date most experiments involving studies of provenance have been conducted under the latter condition only. The provenances which are selected for study are planted in randomized and replicated blocks in an area which is selected for its ecologic homogeneity. The experiment, which is referred to as a provenance trial, is extended by selecting similar areas in different climatic zones and planting the same provenances.

In recent years attempts have been made to assess genetic differences in growth chambers and in the nursery, not to the exclusion of, but as a supplement to the field test, that is the provenance trial. There is little doubt that controlled environments will be increasingly used in the assessment of genetic variation in tree species, and in relating that variation to environmental factors at the place of origin of the material under study. The work of Dormling et al. (13) is an excellent example of the efficacy and practicality of this approach.

A nursery can be considered a partially controlled environment. For example the fertility of the soil can be enhanced and kept uniform, and an optimum moisture regime maintained. Under such conditions, and if the experiment is well replicated, and the number of provenances and individual trees in each provenance is sufficiently high, much can be learned about the genetic variability of the species in the nursery. For example, Fig. 6 shows the relationship between the growth response of 12 one-year-old provenances and the altitude at their place of origin. The pattern of variation is distinctly clinal, and it is clear that the high elevation provenances have behaved quite differently from those from low elevations. Note that the pattern of variation illustrated in Fig. 6 complements that illustrated in Fig. 5.

Fig. 7 illustrates a geographic pattern of variation in 150, 2-year-old spruce provenances in time of entering dormancy. These provenances were all grown in the same nursery on Vancouver Island in British Columbia. Nevertheless, because of the genetically determined pattern of variation resulting from adaptation to widely different environments at their place of origin these provenances differ considerably in the time they enter dormancy. High elevation provenances enter dormant first, then lower elevation, followed by those in areas of coastal influence, e.g. the Nass and Skeena River basins. The coastal provenances, which of course are Sitka spruce, go dormant last of all. The silvicultural implications of these patterns of variation in juvenile spruce populations have been discussed by Roche (34).

3:6 The Field Test

Ideally the field test, which is essentially a long term study, follows the detailed short term genecological studies discussed above. These preliminary studies provide criteria for the selection of provenances for field testing, and for the selection of climatic zones in which to test these provenances.

If the field test is replicated in several climatic zones it is possible not only to observe differences in provenances, but also to determine the differential growth behaviour of the same provenances under different climatic conditions.

Fig. 8 shows the differential growth behaviour of six, 14-year-old red spruce provenances growing at three different sites in Quebec. It will be seen that the growth of all provenances is generally more vigorous at Valcartier, and that growth of the Quebec and New Brunswick provenances is superior to that of more southernly provenances at all three test sites.

Within its temperature range, red spruce is restricted to areas where the climate is humid. Precipitation at Valcartier during the growing season is higher than at the other three test sites. It is possible, therefore, that the superior growth of the provenances at Valcartier can be explained by this important difference in climate between the three test sites.

Field tests such as this, when conducted for a period of time which will vary with species, yield definitive information concerning the adaptability of diverse provenances to the environment of the test site. This information, in conjunction with all other studies of variation within the species, is of considerable value both to the silviculturist, and the tree breeder.

In order to bring this chapter into correct perspective it is necessary to reconsider the practical aims of the studies outlined above.

It is often necessary, and sometimes desirable to transfer seed considerable distances from its source: necessary when low quantities of seed are produced in areas scheduled for planting, and desirable when more rapid growth can be obtained than is possible at the source. The silviculturist, therefore, with a large planting programme to fulfil, very frequently wishes to know the range of tolerance of a particular provenance. That is, how far from its source can seed be transferred without detriment to the survival and performance of seedlings.

Using the techniques outlined above the genecologist attempts to delimit the pattern of variation within a widely distributed species. If he achieves his objectives, he can provide seed transfer criteria for the silviculturist. He will also have "catalogued" the raw material for the tree breeder, or put another way, he will have made an inventory of the gene resources of the species. This is the first stage in the conversion of the wild forest to cultivated plantations. The second stage, described in the following chapter, deals with the utilization of the gene resources delimited and characterized by the techniques of the first stage. A third stage which may be conducted simultaneously with the second, deals with the improvement of the gene resources by selection and breeding.

In conclusion it is worth noting here that all the studies referred to in this chapter have as their objective the elucidation of habitat-correlated, genetically-based variation within species. These studies, therefore, fall into that branch of botanical science termed genecology.

Fig. 1. Male (center) and female strobili (left and right) of white spruce. Many conifers are obligatory cross pollinators, and normal quantities of viable seed are produced only when the pollen from one tree is blown on to the female strobili of another tree of the same species (30).

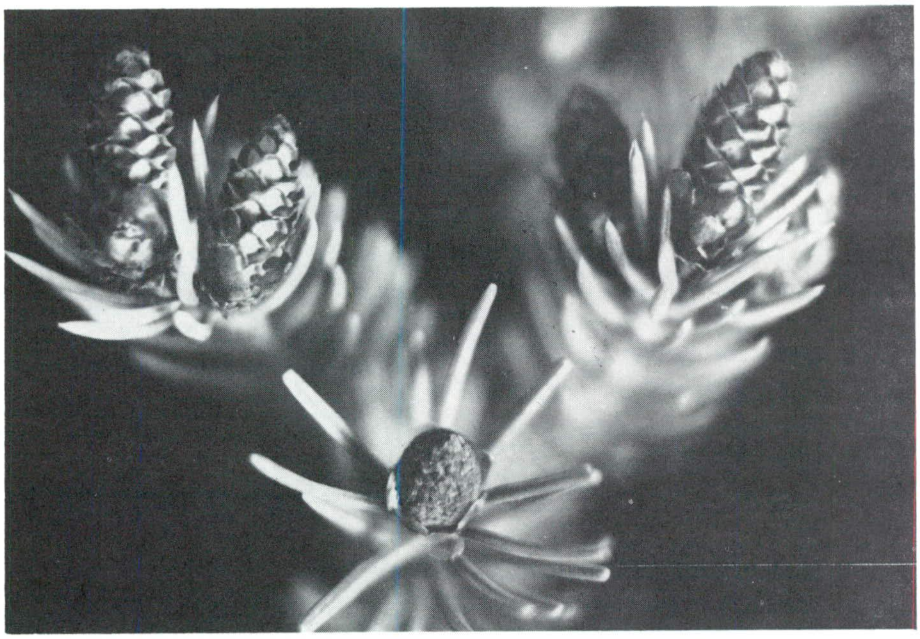


Fig. 2. (A) Coastal lodgepole pine (*Pinus contorta* ssp. *contorta*) on an exposed rocky outcrop near Whitecliff, Vancouver, B.C. Note the wind blown crown, and the generally depressed growth. (B) The same coastal form on a good site near Olympia, Washington. Note the normal growth habit in contrast to that exhibited in (A). A modified character, such as that illustrated in (A), which is the result of environmental conditions prevailing during the lifetime of the tree, is not inherited (29).


A


B

Fig. 3. (A) Bark of coastal lodgepole pine (*Pinus contorta* ssp. *contorta*) near Parksville, Vancouver Island, B.C. (B) Bark of interior lodgepole pine (*Pinus contorta* ssp. *latifolia*) near Chinook Pass, Washington. If a species is very widespread and occupies quite diverse environments, as does lodgepole pine, which is found in coastal and continental climatic regions, then a striking difference in a gross morphological character, genetically based, may be found (29).

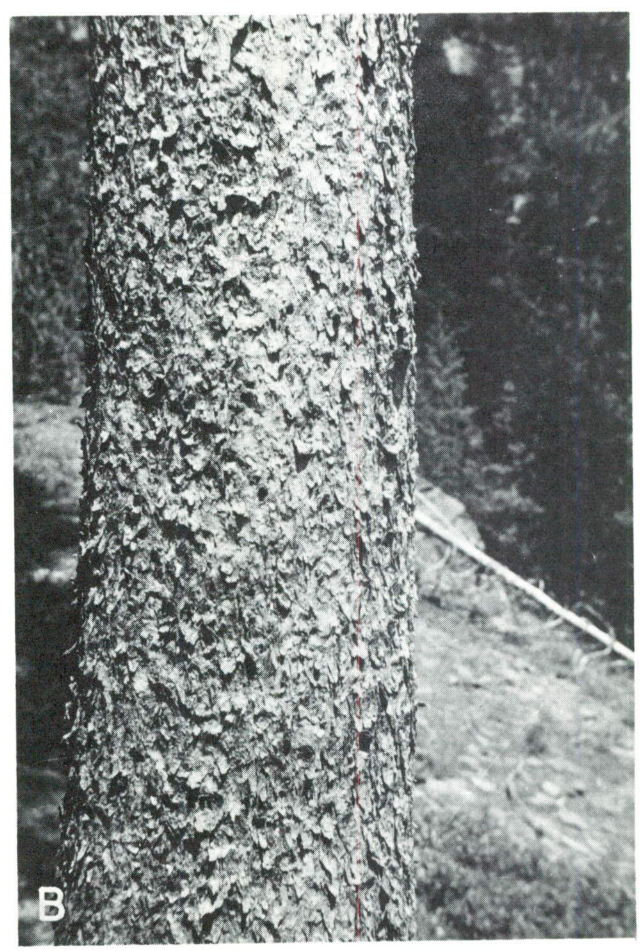


Fig. 4. The two extremes and an intermediate form of the spectrum of variation of cone scale morphology in the white-Engelmann spruce complex in British Columbia. (1) represents a white spruce population at 2,700 ft. near Williams Lake, (3) an Engelmann spruce population at 5,200 ft. near Kamloops, and (2) a sympatric population of both species at 3,300 ft. near Merrit. Although only one intermediate form is shown here it should be noted that where the species are sympatric every variation in cone scale morphology is found between the two extremes. This provides strong evidence of introgressive hybridization (32).

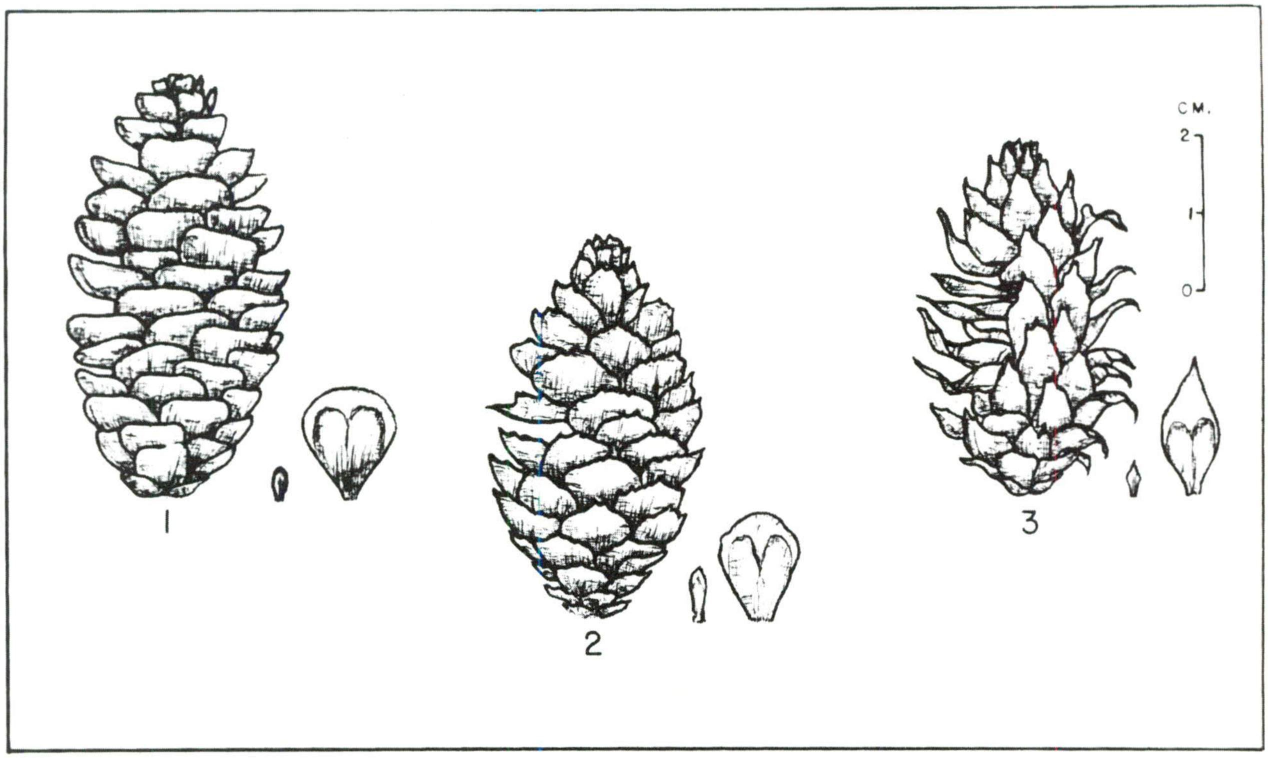

CM.
2
1
0
1
2
3

Fig. 5. Relationship between altitude and variation in cone scale morphology in the white-Engelmann spruce complex in British Columbia. Each point on the curve represents the mean of 100 cones. The pure forms of white and Engelmann spruce in British Columbia are distinct taxonomically and occupy quite distinct ecological niches. However, the intervening ecological zone is occupied by hybrid swarms, with the result that white and Engelmann spruce in British Columbia are the extreme forms of a clinal pattern of variation which ranges from low elevation montane white spruce forest to high elevation subalpine Engelmann spruce forest (32).

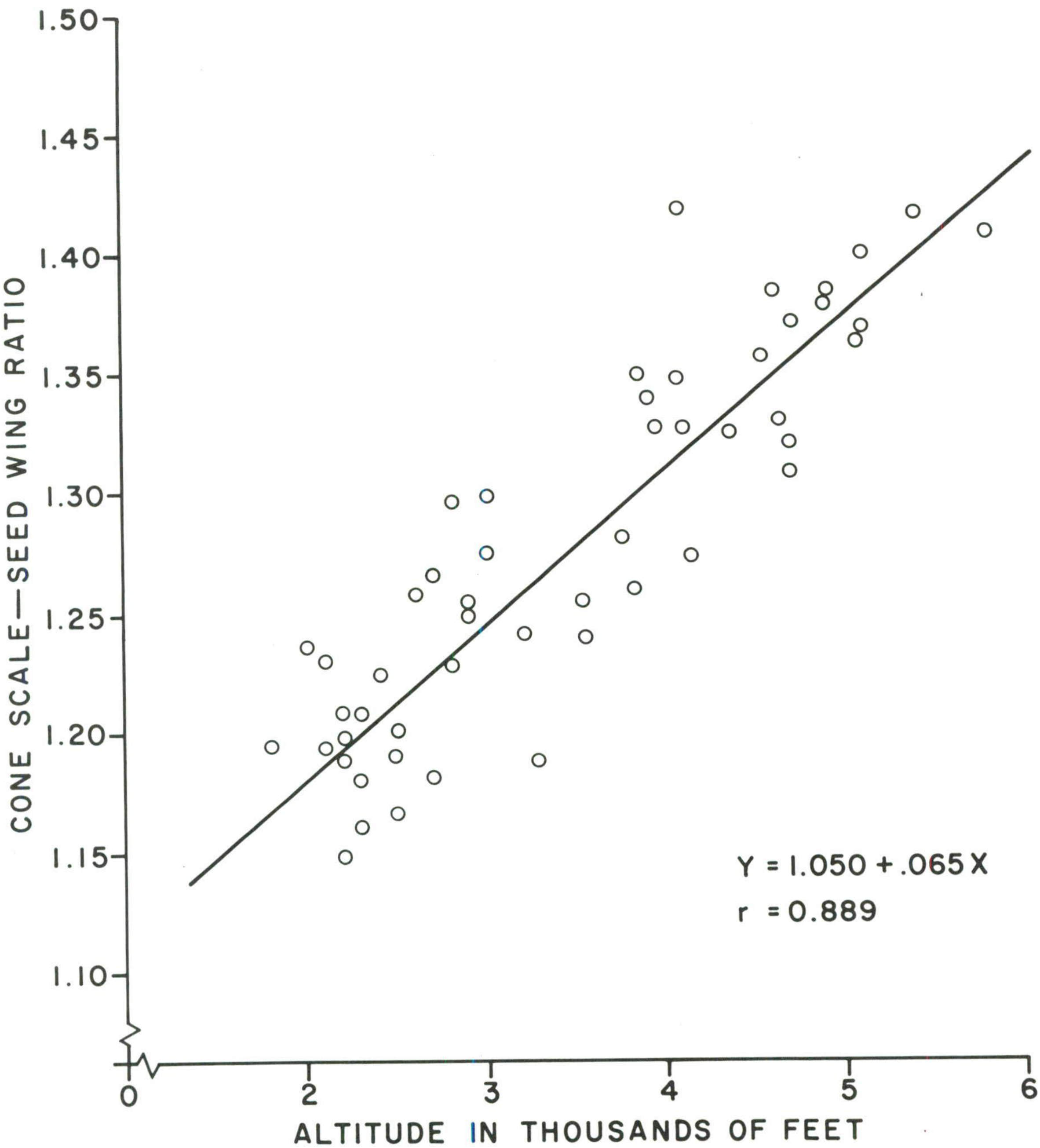
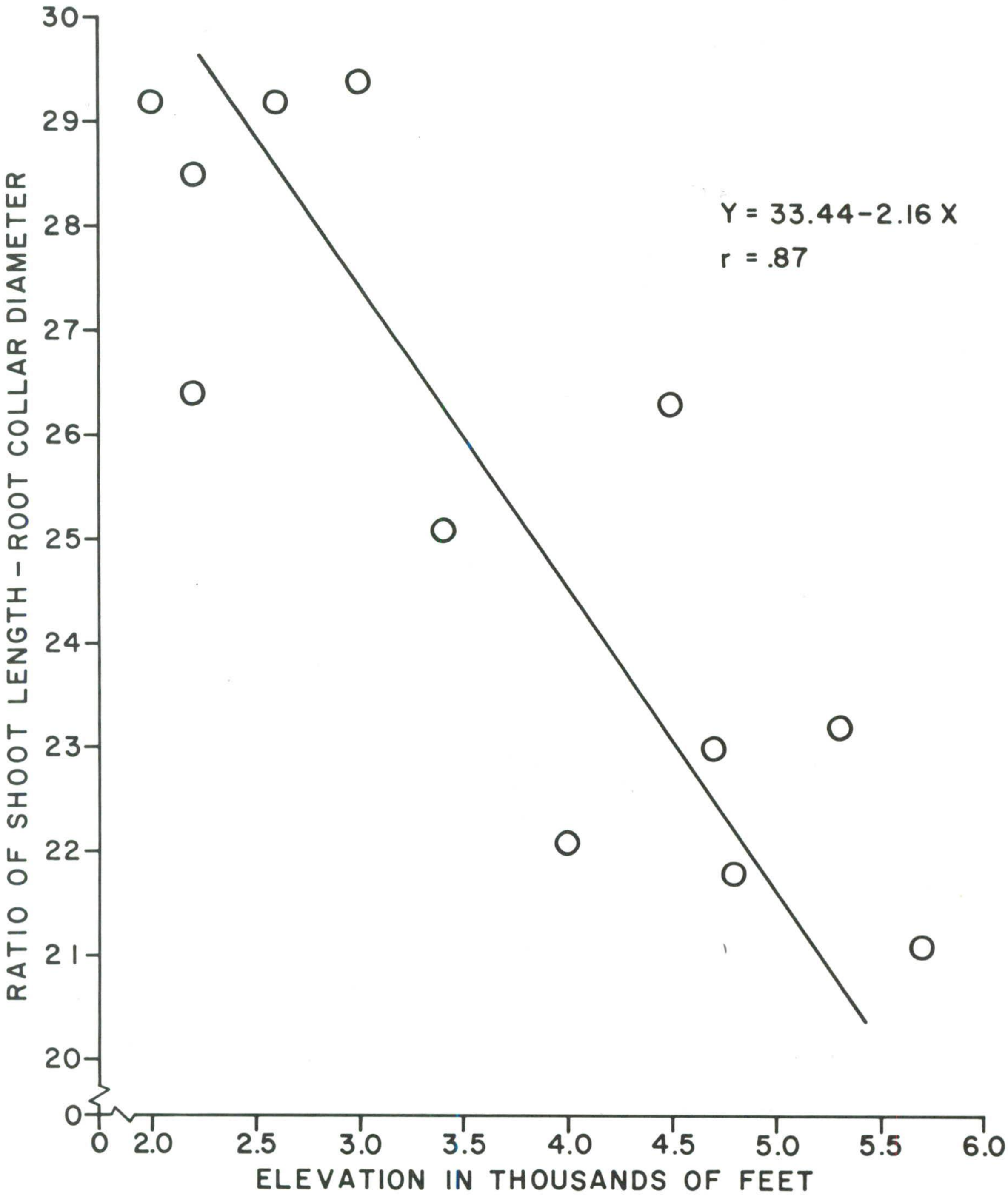

1.50
1.45
1.40
1.35
1.30
1.25
1.20
1.15
1.10
CONE SCALE—SEED WING RATIO
Y = 1.050 + .065 X
r = 0.889
0
2
3
4
5
6
ALTITUDE IN THOUSANDS OF FEET

Fig. 6. Relationship between the growth behaviour of 12 one-year-old spruce provenances grown in a uniform environment and altitude at place of origin. Each point on the curve represents the mean of 20 seedlings. Note the close relationship between growth and altitude. The high elevation provenances have the lowest shoot length/root collar diameter ratio. In white and Engelmann spruce the amount of shoot extension in a nursery during the growing season is closely related to time of entering dormancy. Those seedlings which are the first to enter dormancy produce the least growth (34).



Y = 33.44-2.16 X
r = .87
RATIO OF SHOOT LENGTH - ROOT COLLAR DIAMETER
ELEVATION IN THOUSANDS OF FEET
30
29
28
27
26
25
24
23
22
21
20
0
0
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0

Fig. 7. Relationship between the degree of dormancy on July 14, and altitude at place of origin of 150 spruce provenances grown in a uniform environment in a coastal nursery. Note that high elevation provenances go dormant first, then provenances from lower altitudes followed by those from areas of coastal influence (32).

No.	Prov. No.	Elev. in 1000 ft.	No.	Prov. No.	Elev. in 1000 ft.
1	94	0.1	76	112	2.7
2	96	0.1	77	119	2.7
3	103	0.1	78	143	2.7
4	131	0.1	79	12	2.7
5	132	0.1	80	17	2.7
6	101	0.2	81	69	2.7
7	104	0.3	82	100	2.7
8	105	0.3	83	7	2.8
9	130	0.4	84	113	2.9
10	63	0.4	85	115	2.9
11	125	0.6	86	9	3.0
12	93	0.7	87	18	3.0
13	85	0.7	88	114	3.0
14	92	0.8	89	53	3.1
15	64	0.9	90	120	3.2
16	116	1.0	91	74	3.3
17	117	1.1	92	42	3.4
18	126	1.2	93	20	3.5
19	124	1.2	94	90	3.5
20	25	1.4	95	102	3.5
21	62	1.4	96	21	3.8
22	26	1.5	97	28	3.8
23	24	1.5	98	37	3.8
24	127	1.5	99	142	3.8
25	76	1.5	100	95	4.0
26	77	1.5	101	146	4.0
27	51	1.7	102	84	4.0
28	13	1.7	103	31	4.0
29	121	1.9	104	23	4.0
30	122	1.9	105	22	4.0
31	110	1.9	106	30	4.1
32	106	1.9	107	134	4.2
33	68	2.0	108	135	4.2
34	60	2.0	109	87	4.2
35	47	2.0	110	86	4.2
36	16	2.0	111	52	4.2
37	2	2.0	112	33	4.2
38	70	2.0	113	136	4.3
39	71	2.0	114	40	4.3
40	72	2.0	115	15	4.3
41	73	2.0	116	54	4.4
42	89	2.0	117	148	4.5
43	91	2.0	118	138	4.5
44	98	2.0	119	67	4.5
45	99	2.0	120	44	4.5
46	111	2.0	121	29	4.5
47	6	2.0	122	141	4.6
48	8	2.0	123	83	4.6
49	56	2.1	124	61	4.6
50	107	2.2	125	39	4.6
51	108	2.2	126	36	4.6
52	109	2.2	127	34	4.6
53	128	2.2	128	19	4.6
54	55	2.2	129	88	4.7
55	65	2.2	130	82	4.7
56	78	2.2	131	80	4.7
57	79	2.2	132	43	4.7
58	3	2.2	133	35	4.7
59	4	2.2	134	149	4.8
60	10	2.2	135	145	4.9
61	11	2.2	136	139	4.9
62	50	2.2	137	45	4.9
63	1	2.3	138	144	5.0
64	5	2.3	139	137	5.0
65	14	2.3	140	133	5.0
66	57	2.3	141	66	5.0
67	58	2.3	142	27	5.1
68	59	2.3	143	97	5.1
69	123	2.3	144	140	5.1
70	129	2.4	145	46	5.3
71	48	2.5	146	150	5.5
72	49	2.5	147	38	5.5
73	118	2.5	148	81	5.5
74	32	2.6	149	147	5.6
75	75	2.6	150	41	5.7

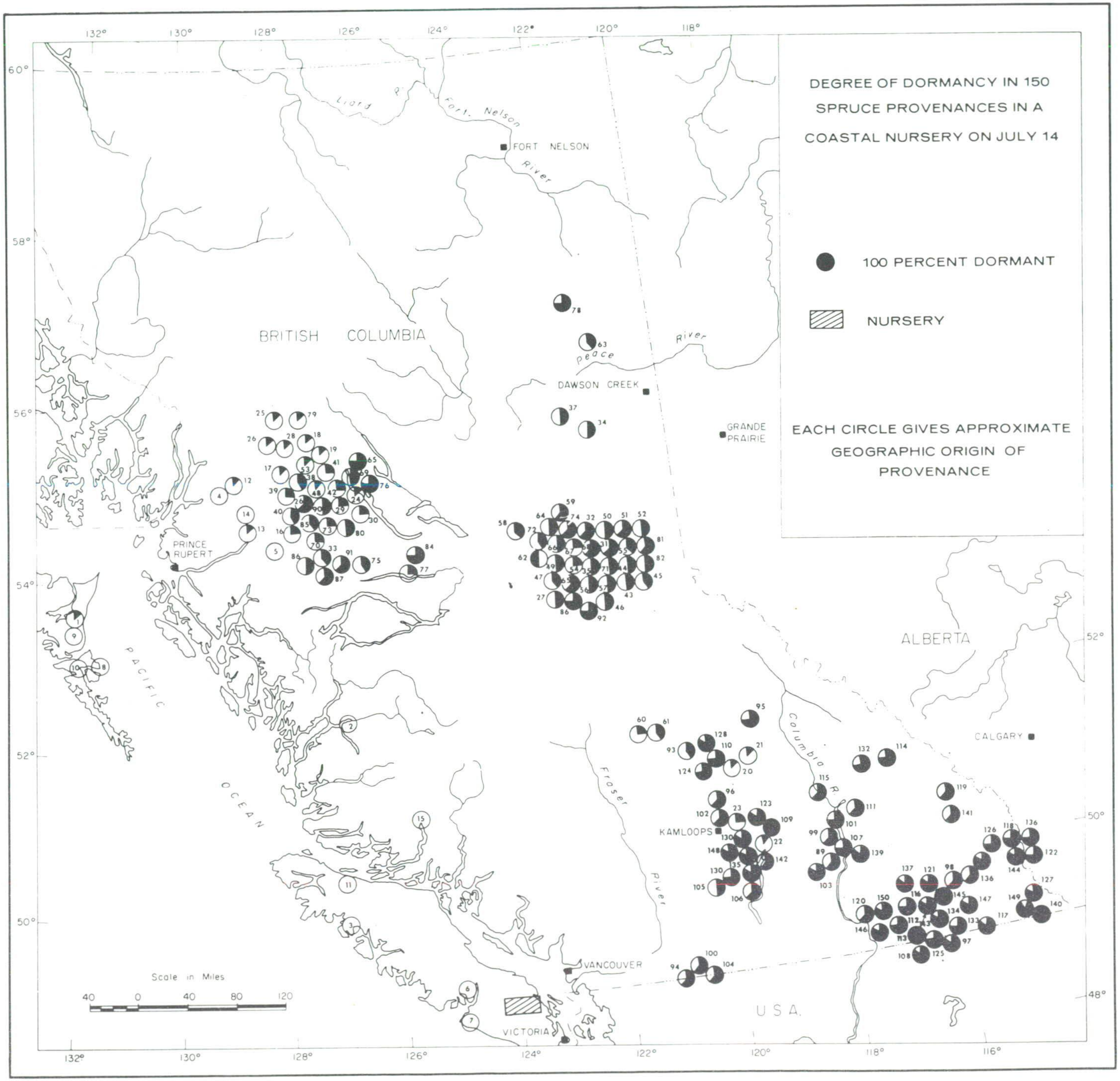


Fig. 8. Shoot extension during one growing season and total height for 6 diverse red spruce provenances at each of three test sites. Note that growth of all provenances is best at the Valcartier site, and that the northern provenances are superior in growth to the southern. (33).

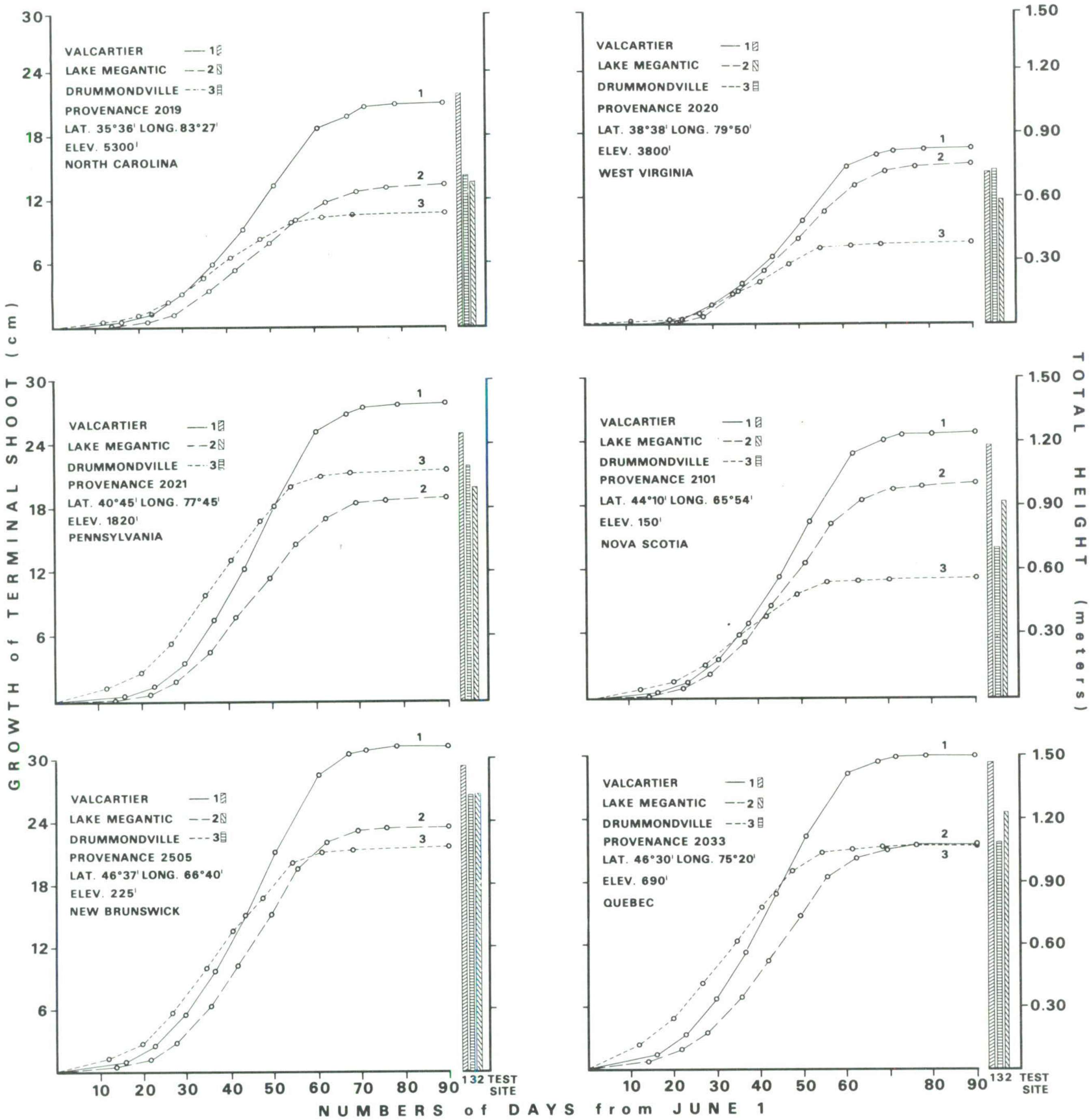
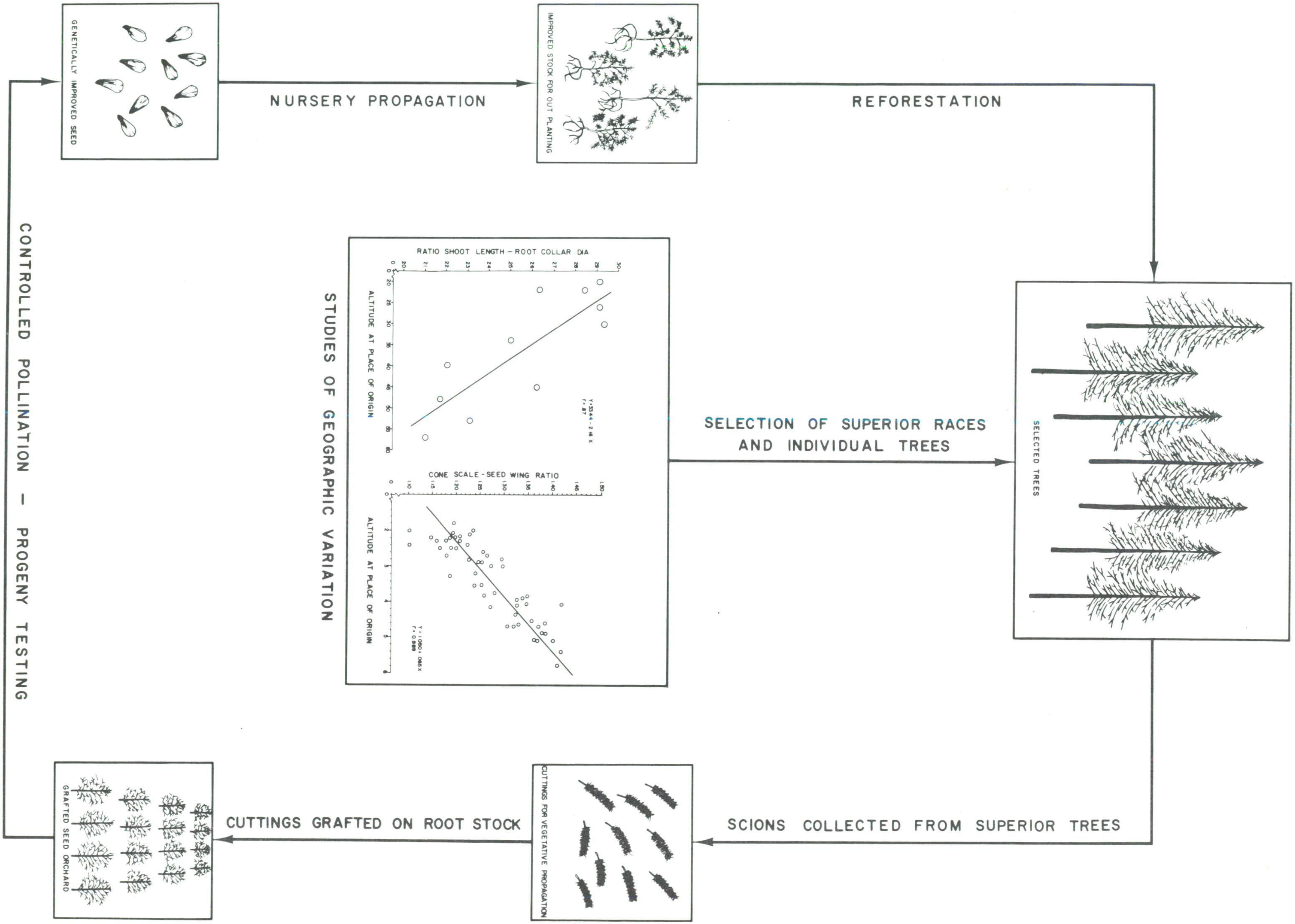

GROWTH of TERMINAL SHOOT (cm)
TOTAL HEIGHT (meters)
NUMBERS of DAYS from JUNE 1
TEST SITE
VALCARTIER — 1
LAKE MEGANTIC — 2
DRUMMONDVILLE — 3
PROVENANCE 2019
LAT. 35°36' LONG. 83°27'
ELEV. 5300'
NORTH CAROLINA
PROVENANCE 2020
LAT. 38°38' LONG. 79°50'
ELEV. 3800'
WEST VIRGINIA
PROVENANCE 2021
LAT. 40°45' LONG. 77°45'
ELEV. 1820'
PENNSYLVANIA
PROVENANCE 2101
LAT. 44°10' LONG. 65°54'
ELEV. 150'
NOVA SCOTIA
PROVENANCE 2505
LAT. 46°37' LONG. 66°40'
ELEV. 225'
NEW BRUNSWICK
PROVENANCE 2033
LAT. 46°30' LONG. 75°20'
ELEV. 690'
QUEBEC

Fig. 9. Diagrammatic representation of the steps involved in the selection and breeding of coniferous tree species. The first step in the transformation of the wild uncultivated forest into cultivated plantations possessing many characteristics desirable to man is the assessment of genecological differentiation within the species. When this is done criteria are available for selecting outstanding individual trees or populations. Such genecological investigations also provide criteria for programs of inter- and intraspecific hybridization as well as inbreeding. This is the ideal. In practice, however, breeding programs have been initiated simultaneously with genecological investigation, or even before. Frequently there are sound practical reasons for this, and local conditions rather than theoretical considerations, will often determine the development, and direction of the program. After the genecologist has "catalogued" the raw material for the tree breeder, individual trees and populations are selected for certain outstanding characteristics, and further propagated in clone banks and seed orchards. Following controlled pollination and progeny tests the genetically improved material is used for reforestation. After many years of selection, breeding and reforestation, the improved strains of forest trees will supplant the wild forms, just as hybrid corn has supplanted its primitive ancestor (31).


GENETICALLY IMPROVED SEED
NURSERY PROPAGATION
IMPROVED STOCK FOR OUT PLANTING
REFORESTATION
CONTROLLED POLLINATION – PROGENY TESTING
STUDIES OF GEOGRAPHIC VARIATION
RATIO SHOOT LENGTH – ROOT COLLAR DIA
ALTITUDE AT PLACE OF ORIGIN
CONE SCALE - SEED WING RATIO
ALTITUDE AT PLACE OF ORIGIN
SELECTION OF SUPERIOR RACES AND INDIVIDUAL TREES
SELECTED TREES
SCIONS COLLECTED FROM SUPERIOR TREES
CUTTINGS FOR VEGETATIVE PROPAGATION
CUTTINGS GRAFTED ON ROOT STOCK
GRAFTED SEED ORCHARD

4. THE UTILIZATION OF GENE RESOURCES WITHOUT BREEDING

4:1 Seed Zones

The principal objectives of a program of selecting and breeding of a tree species is to insure a seed supply that is geographically appropriate, genetically superior, and quantitatively adequate. What is geographically appropriate is determined by genecological studies. Genetically superior seed, that is, superior to the wild form in certain desirable characteristics, is obtained by selecting phenotypes exhibiting to a high degree the desired characteristics, and then estimating the heritability of these characteristics by progeny tests. A quantitatively adequate supply of improved seed is obtained by the establishment of seed orchards on a sufficiently large scale to supply the needs of a reforestation program.

Objectives two and three cannot be achieved in a short time. A very great deal of work is involved over a long period of time to achieve these objectives for even one species. Nevertheless, during the interim period, and when some information has been obtained concerning geographic variation within a tree species, a number of steps may be taken to insure that the genetic potential of each seed lot collected for reforestation purposes is fully exploited.

This work can be initiated independently of a program of selection and breeding of the species. It does not depend on such a program, and consequently, its implementation needs not be hindered if it is decided for economic or other reasons, that a program of selecting and breeding is not warranted.

The first step involves the demarcation of seed zones which govern the transfer of seed. At the present time in Canada there is not enough information concerning geographic variation within the major species warranting the demarcation of well defined seed zones. There is, nevertheless, enough information, and this information is continually accumulating, to allow the establishment of preliminary seed zones. This has been attempted by workers in the Maritimes and British Columbia (14,17).

Seed zones are based on all available information pertaining to variation within the species, and climatic differences throughout its distribution. Recommendations are made as to how far from its place of origin a provenance may be transferred without detrimental silvicultural effect. In some instances it is possible to indicate the probability of silvicultural gain by moving a provenance away from its place of origin. For example, there is evidence that certain provenances of white pine (*Pinus strobus* L.) moved north of their place of origin will grow more rapidly, and survive almost as well as local white pine (14).

The establishment of seed zones is of major importance in reforestation programs, for it is the best way of insuring that the genetic potential of the species is fully exploited by the silviculturist. Seed zones, however, are of little value if there is a chronic shortage of seed for reforestation purposes. For in such instances, and however willing the silviculturist may be in following the recommendations for a particular seed zone and species, he is unable to do so because the appropriate seed is not available for the area scheduled for planting. The answer to this problem is the establishment of seed production areas.

4:2 Seed Production Areas, and Production Seed Orchards.

If artificial regeneration is the accepted means of establishing forests, then it is simply a further rationalization of the planting program to insure an adequate supply of seed by cultural means rather than continue to depend on seed supplies from the wild uncultivated forest, a source of seed which is erratic in the extreme, and frequently low, not only in quantity but also in quality. In this regard seed production areas can yield results in a relatively short period of time. Furthermore, unlike certain aspects of tree improvement, objectives may be very sharply defined, and the relative value of the end product clearly assessed.

Seed production areas are established by selecting stands which are superior phenotypically, within the populations from which seed is required. The principal reason why seed is required from such stands is that studies of geographic variation have shown that seed from these populations is appropriate for areas scheduled for planting. The stand is thinned, with particular attention being paid to felling inferior phenotypes, and fertilized.

A basic assumption in regard to seed production areas is that the seed crop of a natural stand may be enhanced by certain treatments. There is much evidence to support this assumption. However, since the treatment applied will vary with species, a number of questions must be answered before a seed production area is established for a particular species. For example: (i) What is the optimum stand density for seed production, and how is this density attained while avoiding wind throw (ii) what fertilizer should be used, how much should be applied, and when (iii) what are the best methods of harvesting cones from standing trees without affecting the fecundity of the trees.

Seed orchards are discussed in some detail in the following chapter. It should be noted here, however, that seed orchards can be established with the sole objective of mass producing seed that is not genetically inferior, and is of the correct provenance desired for reforestation programs. Such seed orchards should be called production seed orchards in contrast to experimental seed orchards which aim at the production of genetically improved seed.

Production seed orchards, like seed production areas, are an interim measure to ensure an adequate seed supply during the long waiting period between the initiation of a breeding program and the attainment of its objective, which is the mass production of genetically improved seed.

4:3 Seed Registration and Seed Certification.

Obviously the demarcation of seed zones and the establishment of seed production areas and production seed orchards inevitably lead to seed registration. All seed collected for reforestation purposes must be fully documented as regard to origin. Precise information is required concerning the stand from which it is collected. Altitude, latitude and longitude must be accurately recorded. Information concerning the general ecology of the area is also always desirable. For example, what are the percentages of associated tree species present, and what is the aspect, slope, and condition of drainage.

As seed collecting becomes more systematized, and when agencies responsible for seed collecting and registering, plus tree selection and progeny testing, have developed sufficient competence and authority, seed registration leads inevitably to seed certification.

There are internationally recognized standards of seed certification, and in the long run no tree breeding program can be successful without full adherence to such standards. Furthermore no seed should be distributed, and called genetically improved seed, until it has fully met internationally recognized standards of testing and marketing.

In summary it can be said that the best way to utilize geographic variation in a tree species during the period between the initiation of a program of selection, breeding and progeny testing and the attainment of its objectives, is to (i) demarcate seed zones, (ii) establish seed production areas and production seed orchards (iii) maintain a seed register. Other things being equal, there is little doubt that if these three processes formed an integral part of a reforestation program for a given species dry weight per acre per annum would be increased in plantations of this species. As Zobel has pointed out "some of our greatest gains, often large enough to justify the whole tree improvement effort, have come simply by recognizing and using the proper seed source" (41).

5. THE UTILIZATION OF GENE RESOURCES BY BREEDING

5:1 Selection of Individual Trees Showing Desirable Characteristics.

Characteristics of a raw material which are considered desirable for one particular use may not be considered desirable for another. Branchiness, with its accompanying knots, is an undesirable characteristic in veneer manufacture, but, nevertheless, is of less importance in pulp and paper production.

The complete rationalization of silviculture would entail the production of diverse types of forest trees each in its way best suited to a particular industry. This is not a practical proposition at the present time, at least in those forest regions where growth is relatively slow, nor is it really desirable; for the processing industries can be relied upon to develop techniques for utilizing the raw material that is available. For example, the pulp and paper industry of the Eastern United States is now utilizing the large hardwood forests of that area. It is usually much easier to develop techniques for the manufacture of a raw material than to attempt to change the nature of the raw material in order to accommodate a particular manufacturing process. However, where the rotation period is rapid, as in the Southern United States and South Africa, it becomes more feasible to attempt to breed numerous strains for a variety of uses.

For the reasons stated above, and because of the difficulties involved in selecting for a large number of characteristics, it is likely that selection in forests of the North Temperate regions will be confined, for the time being, to five basic characteristics which are generally desirable irrespective of the final use to which the wood is put. It is assumed that selection will be confined to species which have already been subjected to genecological investigation. These five characteristics are as follows:

(i) Resistance to disease.

(ii) Good seed producer.

(iii) Rapid growth rate.

(iv) Wood of high specific gravity

(v) Straightness of stem.

It is obvious that characteristics one and two are not only desirable, but essential. There is little value in selecting for three, four and five if the species cannot be propagated cheaply, and in abundance.

Having decided what characteristics are to be selected the tree breeder makes a survey of the natural population of the species he has undertaken to improve. He then selects those individuals which are outstanding in relation to their nearest neighbours with regard to the possession of these desirable characteristics. Numerous small branchlets are taken from the upper crown of the selected trees, now referred to as plus trees, and then grafted on rootstock, that is, young trees of the same species. In this way it is possible to propagate and maintain indefinitely, numerous representatives of a single superior tree. The major steps involved in selection and propagation of plus tree material are illustrated in Fig. 9.

5:2 Propagation of Selected Material

The numerous representatives of a single tree, that is, the branchlets referred to above, are all identical genetically both with each other and the tree from which they were taken. This is in direct contrast to the progenies arising from seed collected from the same tree, no two of which, as already noted, are genetically alike. These numerous representatives of a single genotype are collectively termed a clone. Each individual of the clone, i.e. each branchlet, is termed a ramet, and the tree from which they are taken, the ortet. Following grafting on rootstock the ramet is referred to as the scion.

The clone bank is a continual source of supply of the selected material, and provides scions for the establishment and maintenance of seed orchards even when the forest tree from which the scions were taken has been felled. This is the principal function of a clone bank.

Having once established a clone bank it is possible to draw from it selected clones for the purposes of establishing a seed orchard. A seed orchard is simply an area in which the selected material is brought together, with the objective of seed production. In the long run the principal function of a seed orchard, is the production of seed which is geographically appropriate, genetically superior, and quantitatively adequate. This is possible in a seed orchard for the following reasons:

(1) The precise geographic location of the place of origin of each clone in the seed orchard is known. The phenotypic quality of the plus tree from which the clone was taken is known, and if studies such as those described in chapter 3 have been carried out, the racial characteristics of the population, of which the plus tree is a member, are also known. All this provides criteria on which to base decisions with regard to the artificial crossing of clones representing different races.

(2) Artificial crossing can be controlled with ease, and when two clones have shown good combining ability when crossed, that is have given superior progeny, the cross can be continued indefinitely. Clones which produce poor progeny, whatever the cross, can be eliminated from the seed orchard.

(3) The seed orchard can be located in a climatic region which favours seed production, and laid out in such a way that mechanical cultivation, designed to further increase seed production, is facilitated.

(4) Cone collecting is greatly facilitated due to the low position of the crown and the accessibility of every tree.

(5) Because of the ease with which their presence can be detected, and remedial measures applied, losses due to insect damage can be reduced to a very low level, or even eliminated.

The seed orchard may be established either by rooted cuttings, which is the most desirable method, or by grafting scions on root stock. The selection of either one of these methods will depend on the species rootability. Cuttings from certain coniferous tree species root very easily, while others are extremely difficult to root.

Though the vegetative propagation of plant material has been practiced for many years there are still many problems to be solved concerning the vegetative propagation of coniferous tree species. A major problem is incompatibility between scion and stock, and it is now becoming obvious that initial success in grafting a species is no guarantee of compatibility. Grafted Douglas fir which has been growing vigorously for a number of years is now exhibiting widespread incompatibility between scion and stock (28).

Vegetative propagation in forest genetics research and practice has been discussed in some detail by Nienstaedt _et al_ (25). It was concluded, and this conclusion is still valid, that "Future research must place emphasis upon studies of the physiological processes involved in graft union formation and incompatibility and in root initiation. Fundamental aspects of water relations, nutrition, and the role of hormones must be further investigated and understood, and the relationship between age and rooting must be elucidated"

For these reasons it is very important to take into account the species amenability to vegetative propagation in the early stages of a tree improvement program. If the species is not amenable to any form of vegetative propagation then it may be necessary to establish seedling seed orchards. This is done by collecting seed from each plus tree and then using seedlings in the orchard, the progenies of each tree being carefully labelled so that they are always identifiable.

There are certain fundamental differences between a seedling seed orchard and a grafted seed orchard which need not concern us here. The relative merits of both in regard to improving the species have been the subject of considerable debate. It is sufficient to note that if vegetative propagation of the selected material is not possible, then the establishment of a seedling seed orchard is a valid alternative.

5:3 Progeny Trials

Plus trees are selected because of their phenotypic superiority to the surrounding trees in a natural population. This, however, because of the variability of the natural environment, is no guarantee that the selected trees are genetically superior. For this reason all plus trees must eventually be subjected to progeny trials to determine the extent to which they are genetically superior to the average of the natural population from which they were selected. The progenies of intra- and interspecific crosses must be similarly tested.

A basic assumption of progeny trials is that when progenies of controlled crosses are grown in a uniform environment the phenotype is a good expression of the genotype. Therefore, if a particular plus tree has good combining ability, that is, if the progenies of a cross involving this tree and any other plus tree are always superior in growth and vigour it can be assumed that this plus tree is genetically superior. On the other hand if the progenies of a plus tree exhibit inferior characteristics no matter what the cross then it can be assumed that this plus tree is inferior genetically, and should be eliminated from the seed orchard.

To evaluate and select that portion of the controlled crosses showing superior characteristics, the progeny must be sown in a conventional experimental design embodying replication and randomization, both of which are essential to the assessment of experimental error.

Early assessment of progeny differences may be made in growth chambers, green houses, and in the nursery. Usually these preliminary tests are followed by field trials. The methods used, therefore, in assessing the growth differences in the progenies of controlled crosses are no different in principle to the methods used in assessing geographic variation within a tree species. The improved strain must of course, be adapted to the environment of the area being reforested. For this reason a knowledge of the genecology of the parental forms is indispensable.

5:4 Artificial Hybridization

There are two aspects of artificial hybridization, between and within species, which will be discussed separately. Between species, or interspecific hybridization involves crossing races of two distinct species, while within species, or intraspecific hybridization, is confined to crossing races of the same species.

The principal advantages of hybridization, whether between or within a species, are as follows:

(i) To increase the size of the gene pool in respect to adaptive characters so that it may be possible to extend the range of a particular provenance or species.

(ii) Desirable characteristics found in separate provenances or species, but not found in combination in any one, can be brought together to produce a strain incorporating the best characteristics of each of the parental types.

(iii) The possibility of achieving and exploiting hybrid vigor in the progeny.

Though some of the earliest work in tree improvement involved artificial hybridization, to date hybridization has not been an important part of tree breeding programs in Canada. However, it is likely to assume much more importance in the future, for the results achieved in this respect in recent years are encouraging and a stimulant to breeders on this continent (27).

Plant breeders have long observed that inbreeding or crossing closely related strains of naturally cross-pollinating plants, unusually resulted in depressed vegetative vigor in the progeny. Conversely when diverse strains of such plants were crossed the progeny was often of superior vegetative vigor. This vegetative superiority within the progeny resulting from a cross between races of dissimilar genetic constitution is termed heterosis, or hybrid vigor. It appears to result from a physiological stimulus to development which, within certain limits, increases with the genetic diversity of the parents. Put simply, the hypothesis is that the genes contributed by each parent perform single functions which individually contribute less to vegetative vigor than they do in combination in the progeny.

The method of plus tree selection is not designed to achieve a heterotic effect in the progeny of the selected trees. On the contrary, if the selected trees are concentrated in a small area in a continuous population there is likely to be a deterioration of vigor at worst, and at best the maintenance of parental vigor. For this reason it is certain that intraspecific hybridization of genetically dissimilar populations will eventually become a necessary adjunct to the method of single tree selection, and on occasion may supplant it in a tree breeding program.

Interspecific hybrids are now beginning to occupy an important position in the planting programs of many countries. The hybrid Pinus attenuata x Pinus radiata is being planted in the United States, and New Zealand, Australia and Spain have imported quantities of seed and scions from California. The hybrid Pinus rigida x Pinus taeda is supplanting the pitch pine (P. rigida) as the principal forest tree in South Korea. It greatly surpasses the pitch pine in volume growth. In Britain selection and breeding of the larches (Larix decidua and Larix leptolepis) was begun in 1950, and seed of the first generation larch (Larix x eurolepis Henry) is now being produced on a large scale in seed orchards. At the same time the hybrid Cupressocyparis x leylandii, a cross between Cupressus macrocarpa and Chamaecyparis nootkatensis, is propagated vegetatively on a mass scale. The advantage of this hybrid under British conditions is that it incorporates the rapid growth rate of the southern and the frost hardiness of the northern species. Larix hybrids are also playing an important role in reforestation programs in the Maritimes and in Quebec.

There is little doubt that a breeding programme of any tree species is incomplete if it does not include interspecific hybridization of the species to be genetically improved. Crosses between related species should always be attempted. Therefore, it is necessary for the tree breeder to build up an arboretum of those species which are of the same genus as the species he is attempting to improve genetically, and which are likely to cross with this species.

5:5 Mutation Breeding

In 1936 a triploid aspen, which grew more rapidly than diploid aspens, was discovered in Sweden. This finding generated great interest in the possibility of breeding polyploid trees. Efforts to induce polyploidy, which is exceedingly rare in conifers, by physical means such as X-ray, temperature shocks and ultrasonic treatment have not been very successful. However, the organic chemical colchicine, which is not costly and is easy to apply, effectively doubles the chromosome number. For these reasons colchicine has been widely used in attempts to produce polyploid conifers. However, while it is relatively easy to induce polyploidy in dividing cells it is not so easy to induce beneficial mutations and to devise means of perpetuating the polyploid tissue. For this reason little benefit has accrued to date from such experiments.

At the present stage in the development of forest genetics, it would appear that mutation breeding has no direct part to play in a tree breeding programme. It is obviously more profitable to concentrate on selection and breeding of desirable commercial types from the abundant variation found in natural forests, rather than from random mutants, artificially induced. Mutation breeding therefore, though it is a worthwhile field of basic research, must remain a minor adjunct to the other methods discussed here.

5:6 Inbreeding

Most commercial conifers are naturally outcrossing and self-incompatible to one degree or another. There are some exceptions, e.g. red pine (*Pinus resinosa*), but for the most part selfing is nearly always accompanied by reduced fertility and loss of vigor in the progeny. It has been shown that self-pollination in *Pinus monticola* resulted in 50 percent reduction in seed yields, though cone yields were almost identical with the cross-pollinated control. Seed germination and seedling height for the first three years were also below that of the cross-pollinated seed (7). Similar results have been obtained when other coniferous species have been selfed, and in general it can be concluded that selfing will result in a loss of vigor, and a deterioration in other characteristics in the progeny.

Most agricultural plants are annuals, and many are difficult to reproduce vegetatively. Therefore, in order to produce a desirable hybrid type it is necessary to develop pure lines by selfing. These pure lines can be maintained indefinitely and crossed each year to produce the hybrid. Trees on the other hand are perennial and there is no need to develop a pure line in order to maintain a particular genotype as is necessary in the case of an annual. Furthermore, the most important coniferous species can be maintained indefinitely by grafting or from cuttings. Thus, if the progeny of a cross between two trees has proved desirable that same cross can be repeated indefinitely, and one of the major reasons for selfing an agricultural crop does not apply in relation to forest trees.

On the basis of the results obtained with agricultural crops it is sometimes suggested that several desirable characteristics may be incorporated in a single strain of a tree species by crossing a number of pure lines, each homozygous for a particular character. There are three major objections to this practice. First it would take a considerable length of time to achieve homozygosity in a highly heterozygous coniferous tree. Secondly, outcrossing inbred lines, which will be greatly reduced in vigor as already noted, is likely to restore the vigor of the parental types only; heterosis cannot be expected. Very few of the thousands of inbred lines of agricultural crops, when outcrossed, show heterosis in a measure that makes them valuable commercially. Thirdly, in theory any variation that is obtained by inbreeding and outcrossing can be obtained by crossing alone (1).

The principal purpose of inbreeding in a tree breeding programme is to determine the degree of inbreeding depression in the species involved. It is also a useful technique for evaluating the inherent qualities of the species (26). For both these reasons it is necessary to conduct inbreeding experiments with the species which has been selected for improvement.

6. THE CONSERVATION OF GENE RESOURCES

There are many social, scientific and economic reasons why plant gene resources, including forest trees, should be conserved in situ (4,5,6,15,35). Some of the more important of these can be summarized as follows:

(i) Selection and breeding reduces genetic variation, and genetically uniform plant material is highly susceptible to attack by insects and disease.

(ii) This in turn leads to the massive use of herbicides and pesticides which have serious undesirable side effects

(iii) After a period of selection and breeding during which the genetic base is continuously being narrowed, a point is reached beyond which breeding for production and disease resistance becomes almost impossible.

(iv) If wild forms of the plant species are available they can be crossed with commercial forms to broaden the genetic base, and thus allow further improvement by selection and breeding.

(v) The perpetuation of samples of the full diversity of the world's plant and animal communities in outdoor laboratories for a wide variety of research (24).

(vi) The protection of samples of natural and semi-natural ecosystems for comparison with managed, utilized, and artificial ecosystems (24).

This kind of conservation, in relation to forest trees, becomes increasingly important if sustained yield is discarded, as has been advocated (38), and if an increasing area of land surface is denuded of forests. Even with the acceptance of sustained yield it is estimated (10) that an annual total of 500,000 acres of out-over, and burned-over forest land will not be regenerated in Canada.

The conservation of forest gene resources should not be considered as a static and negative conservation, but simply as another facet of integrated resource management (2,35). As the FAO Panel of Experts on Forest Gene Resources has pointed out "The growing public awareness of the need to reserve forest areas for recreation, watersheds, wild life refuges, and other purposes, could be harnessed to serve the joint purpose of gene resources conservation" (15).

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GLOSSARY[1]

ADAPTATION. The process of evolutionary (genetic) adjustments fitting biological groups to their environment. Often the change in structure or function itself is referred to as an adaptation.

ADAPTED. See adaptation.

ALLOPATRIC. Refers to species which do not overlap or occupy the same area.

CHROMOSOME. A microscopic, usually thread- or rod-like body carrying the units of inheritance (genes). The chromosomes are the primary constituents of the cell nucleus but are individually distinguishable only during nuclear division. Their number and form are usually constant for each species.

CLINAL VARIATION. Clinal variation results from an environmental gradient. Portions of populations exhibiting such continuous (clinal) change from one area to another preferably are not designated as ecotypes, and are more correctly termed ecoclines.

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1 This glossary is compiled with some modification principally from Snyder's Glossary for forest tree improvement workers (Snyder, E.B. 1959. Glossary for tree improvement workers, Southern Forest Exp. Sta. USDA), and Knight's dictionary of genetics (Knight, R.L. 1948. Dictionary of genetics, Chronica Botanica Co. Waltham, Mass.).

CLONE. A group of plants derived from a single individual (ortet) by asexual reproduction. All members (ramets) of a clone have the same genotype and consequently tend to be uniform.

COLCHICINE. A poisonous chemical (an alkaloid) used for multiplying or modifying the chromosomes or genes in an effort to create new types of plants.

COMBINING ABILITY. The relative ability of a biotype to transmit genes for desirable performance. General combining ability indicates a high average performance of progeny from crosses with many other parents; specific combining ability indicates that, with a certain few of the combinations, performance is better than expected on the basis of average performance. A biotype may exhibit both general and specific combining ability.

DIPLOID. Having two sets of chromosomes in the nucleus -- indicated by "2n". One half of the chromosomes are contributed by the female parent, one half by the male parent. Many higher organisms are diploid except for their sex cells and associated tissue. Similarly triploids, tetraploids, hexaploids have three, four and five sets of chromosomes respectively. All these are polyploids, that is, they have more than the diploid complement of chromosomes.

ECOCLINE. See clinal variation.

ECOLOGICAL NICHE. An environment where the factors affecting survival, reproduction, and growth combine in a way favorable to some particular biotype. Such a habitat may be discontinuous or be in an ecological gradient. Unique niches favor hybrids, mutants, etc., that might be at a disadvantage in other environments.

ECOTYPE. A race whose characteristics adapt it to a distinct habitat. Therefore, ecotypic variation is discrete or non-clinal. Some differences among ecotypes, particularly those wholly physiological, show up only when plants from different ecotypes are grown in a single environment. Ecotypes are described as climatic, edaphic, etc.

ECOTYPIC. See ecotype.

EVOLUTION. The gradual development of biological groups from prior groups as a result of the action of natural selection on hereditary variants existing in the populations.

FERTILIZATION. The union of the nucleus and other cellular constituents of a male gamete (sperm) with those of a female gamete (egg) to form a zygote from which develops a new plant. In some species, fertilization may occur months after pollination.

GENE. The unit of inheritance, which occupies a fixed position on the chromosome and which governs effects or controls the transmission and development of a hereditary character.

GENECOLOGIST. One competent in the science of Genecology.

GENECOLOGY. The study of genetically-based, habitat-correlated variation within species.

GENOTYPE. The entire genetic constitution expressed and latent of an organism.

HAPLOID. Having the reduced chromosome number, that is, having one set of chromosomes in the nucleus. This is normal in sex cells, which have only half the number of sets occurring in the diploid.

HETEROSIS. Hybrid vigor; the increased vigor of a hybrid as compared to the vigor of the parents. Heterosis is at a maximum in the first generation. Increases may occur for any measurable character such as size, fruitfulness, survival and resistance.

INCOMPATIBILITY. A failure or partial failure in some process leading to fertilization even though the egg and sperm cells are potentially functional.

INTROGRESSIVE HYBRIDIZATION. The natural infiltration of genes from one population to another through hybridization, and the successive backcrossing of the resulting hybrids to one of the parent species.

ISOLATION. The prevention of breeding among populations by interference mechanisms, e.g., seasonal differences in flowering time, or ecological separation because of different soil or habitat characteristics, genetic incompatibility, sterility, and distance.

ISOLATING MECHANISMS. See isolation.

LINKED GENES. The association of characters from one generation to the next because the genes related to these characters are grouped, or linked on the same chromosome. There are as many linkage groups as chromosome pairs. Linkage, however, is rarely complete, i.e. new combinations of linked characters can occur.

MACROEVOLUTION. The evolutionary processes which over long periods of time give rise to new species.

MEIOSIS. Nuclear division which results in the formation of sex cells each containing the haploid number of chromosomes.

MICROEVOLUTION. The evolutionary processes which currently determine geographic variation within species.

MITOSIS. Nuclear division which results in the formation of cells other than sex cells each of which contains the diploid number of chromosomes.

MUTANT FORM. The phenotypic expression of a mutation.

MUTATION. A sudden heritable change in a gene or in chromosome structure.

NATURAL SELECTION. The selection which takes place under natural conditions by reason of the death or partial inhibition of individuals less fitted to thrive under the condition obtaining.

ORTET. The one plant from which members of a clone were originally derived.

PHENOTYPE. The demonstrable characteristics of an organism; the product of the interaction of the genes of an organism with the environment.

PHYTOCHROME. A protein-like substance which changes composition under the stimulus of photoperiod, and thereby triggers physiological processes controlling growth.

PLUS TREE. A tree appearing distinctly superior to surrounding trees on the same site.

POLYPLOID. See diploid.

PURE LINE. A sexually reproducing population that is relatively pure genetically, that is homozygous, and, therefore, true breeding.

RACE. Populations within a species which exhibit general similarities discontinuous and distinct from other populations though not sufficiently so to achieve the status of a subspecies.

RAMET. An individual member of a clone.

RECOMBINATION. Combinations of genes different from the parental combinations.

ROOTSTOCK. The root-bearing plant or plant part, usually stem or root, on to which another plant is grafted. Usually referred to as stock.

SCION. Any aerial plant part, often a branchlet, that is grafted on to the root-bearing part of another plant which is called the rootstock.

SEGREGATION. The separation of genes, or of chromosomes, of paternal and maternal origin at meiosis.

SYMPATRIC. Inhabiting one and the same area.

ZYGOTE. The cell which results from union of sperm and egg.