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RESEARCH at the Institute of Forest Genetics

NORTH CENTRAL FOREST EXPERIMENT STATION
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FOREWORD

Forest genetics research was begun in the late 1920's in the Lake States. Farsighted men, such as Carlos G. Bates, Paul O. Rudolf, and Joseph H. Stoeckeler, established major studies with both pine and spruce – studies we use in large measure in our research even today, 40 years later.

The second phase began in the early 1950's with the installation of the first major cooperative genetics study in the United States. Paul Rudolf saw clearly that large scale cooperative efforts are essential if we are to harvest the full benefits of our studies. With State conservation departments and universities he began the Lake States Jack Pine Study, which became the pattern for similar efforts across the nation. This has culminated in the NC-51 Cooperative Regional Research Project involving 12 States and two USDA Forest Service Experiment Stations. Without doubt, the NC-51 is the largest cooperative forest genetics project in the world.

The genetics research at the Lake States Forest Experiment Station (now North Central) obtained project status in 1955 and moved to Rhinelander, Wisconsin, in 1957, where a period of program development and establishment of experimental plant material got underway. We are now at a turning point in our program; before us are more penetrating studies of this plant material, and the actual breeding of new strains in close cooperation with the National Forests in the Lake States. This is an appropriate time to review our work and results over the past years.

The entire staff at the Institute contributed material for this report. It was assembled by Richard M. Jeffers, who subsequently has had sole responsibility for revision, updating, and reviews. It is fitting, therefore, that his name appear on the title page.

This summary is intended as a source of information for forest managers and scientists. We have attempted to present the pertinent facts without going into detail. For those interested in details, a list of Institute publications is included at the end of the report. Beyond that, the staff at Rhinelander is available to answer inquiries.

HANS NIENSTAEDT
Chief of Laboratory

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RESEARCH AT THE INSTITUTE OF FOREST GENETICS, RHINELANDER, WISCONSIN

Richard M. Jeffers

The Institute of Forest Genetics was formally opened June 6, 1957, by the North Central (then Lake States) Forest Experiment Station. The main facility of the Institute is a 10,000-square-foot building containing laboratories, offices, controlled-environment growth rooms, and a library. Facilities are available for pollen extraction, microscopy, photography, tissue culture, and chemical analyses. The laboratory-office building is supplemented by a 2,400-square-foot greenhouse, with an attached headhouse. Two combination coldframe-shade houses provide for care of plants in an environment somewhat less severe than outdoors.

The Institute is ideally located for experimental work. It is immediately adjacent to the Hugo Sauer Nursery, which is operated by the Wisconsin Department of Natural Resources. Nursery facilities, therefore, are readily available to staff members for nursery tests and growing seedlings for field plantings. Several test plantations and three National Forests are within 2 hours driving time of Rhinelander. Planting sites for long-range evaluation of test trees throughout the Lake and Central States are necessary. These sites are provided by the National Forests, State agencies, universities, and private organizations.

The Institute was established to centralize the Station's research effort in forest genetics and tree improvement. Studies carried on by the Station since as early as 1928 have showed that genetic improvement is a promising means of increasing the quality and quantity of timber products. However, it was also obvious from the early work that a more intense and fundamental research program was necessary to meet the production goals of the northern forest section of the United States.

The need for increasing the productivity of the forest lands in the north central United States is great. The projected increase in demand for timber products (80 percent by the year 2000) will necessitate full production from all of our forest land. Yet, nearly 60 percent of the forest sites in this region are presently unsuited for the species growing on them.

Planting or seeding of productive sites with genetically improved tree seed, seedlings, or cuttings offers opportunities for increasing future yields of forest raw materials. The Institute of Forest Genetics is dedicated to research that will make possible the production of improved trees for reforesting all feasible areas.

Originally only one project, the Forest Genetics Project, was located at the Institute; today there are four: Forest Genetics, Pioneering Research, Radiobiological Studies of Northern Forest Communities, and Maximum Fiber Yield. This publication will present only the work of the Forest Genetics Project during its first 12 years.

OBJECTIVES OF FOREST GENETICS RESEARCH

Two ways of increasing wood production have long been recognized by foresters: (1) improving the stocking of merchantable tree species, and (2) managing the stands so the most desirable species and most valuable trees make up the harvest. A third related, but less widely demonstrated, way of increasing wood production is to develop and grow genetically better trees than those we now have.

Genetics is the study of similarities and differences between related individuals—the magnitude of the differences, the frequency of variants, and their control. It includes studies of the cells and cellular processes and factors of the environment causing the similarities and differences. Tree improvement is the practical extension of forest genetics. It includes selection of superior trees and races of trees, sexual or vegetative mass production of these selections, and further improvement through actual tree breeding.

The purposes of the research program at the Institute of Forest Genetics are to:

1. Increase knowledge of the genetic constitution and variation in the populations of several forest tree species.

2. Develop guidelines that will enable tree breeders to plan realistic and efficient tree-breeding programs.

3. Breed trees for local use in pilot operations.

WORK PROGRAM

In the 12-year period since the Institute was founded, the work program has steadily grown. It has been directed to include the following areas of research:

1. Seed-source testing
2. Species hybridization
3. Heritability testing
4. Radiation research
5. Genetics of disease and pest resistance
6. Tree improvement
7. Plant introduction
8. Vegetative propagation, including basic studies of root initiation and differentiation in cuttings
9. Cell biology

Most work has been concentrated on white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), and yellow birch (*Betula alleghaniensis*). In addition a large number of other native and exotic genera and species are being studied less intensively. The Institute cooperates on many of its studies with universities and experiment stations throughout the world.

Studies set up in the past 12 years by the Institute have produced some results already, but data will accumulate much more rapidly from now on. Since 1957 approximately 130 technical and nontechnical articles have been published on work conducted at the Institute. The following pages summarize studies in progress and results obtained to date.

SEED SOURCE STUDIES

To determine the improvement that can be expected in a breeding program, the amount and nature of adaptive genetic variation existing in a species must be known. There is no way of examining a natural stand of trees and determining how much of the observed variation is genetic. Some of the variation is undoubtedly due to environmental factors.

Only in seed source studies can genetic and environmental factors be distinguished. Such studies involve collecting seed from stands in more than one area, usually from many sources throughout the species range, planting all of this seed in separate plots in one nursery, and field planting in different environments. The study will usually include evaluation of the seed, nursery investigations of the seedlings, field establishment, and evaluation and measurement of the planted trees for many years.

Seed source studies have been underway at the North Central Forest Experiment Station for over 30 years and have yielded much valuable information.

Red Pine

More red pine has been planted in the Lake States than any other species. Its easy establishment, few diseases and insects, and high utility as a lumber and pulping species have made it valuable. Hence, red pine was one of the first species to be subjected to seed source and progeny tests in the Lake States.

RED PINE SEED SOURCE STUDY—SUPERIOR NATIONAL FOREST

One of the Station's oldest studies is a red pine seed source and individual tree progeny test. One set of plantations was established in 1931 with 37 seed sources and individual tree progenies, and a second in 1933 with 140 seed sources and individual tree progenies. Originally, plantations were established in at least three localities in the Lake States, but fire, drought, and other causes reduced the number of plantings to one, located near Ely, Minnesota, on the Superior National Forest.

Evaluation of the 1931 planting at age 18 showed significant differences among seed sources and progenies in survival, average height, average diameter, basal area per acre, and cubic volume per acre. In general, trees from northern Minnesota, northeastern Wisconsin, and adjacent southern Upper Michigan sources performed better than those from central and northwestern Wisconsin, Lower Michigan, and New England sources.

Evaluation of the 1933 planting gave similar results at age 23, with the best 20 percent of the sources and progenies (cubic-foot volume) coming from Minnesota, northern Wisconsin, and Upper Michigan. The average total height was 19.6 feet, and the unpeeled volume per acre was 341 cubic feet (the range was from 8 cubic feet to 910 cubic feet).

A plantation of red pine containing 50 of the same sources that were used in the Superior National Forest planting was established in northwestern Pennsylvania in 1937. At the end of the tenth growing season, significant differences in tree height growth among sources were noted. Trees from Upper Michigan, northern Wisconsin, and Minnesota sources had significantly poorer height growth than those from central Wisconsin and Lower Michigan sources. The similar results from these two widely separated plantings show that red pine from Minnesota, northern Wisconsin, and Upper Michigan do differ from central Wisconsin and Lower Michigan red pine. And, in general, trees from sources nearest the planting sites did better than those from more distant sources. However, trees from distant sources occasionally may out-perform the local source, indicating that some genetic variation exists in red pine, although it is a comparatively homogeneous species (Rudolf 1965a).

In 1964 a more intensive evaluation of 69 individual tree (open-pollinated) progenies was made. For the preliminary analysis, the progenies were arranged by region according to the seed collection zones suggested by Rudolf (1959a). Analyses showed significant differences among individual progenies in height, d.b.h., and survival. Height growth rates of the different progenies were relatively uniform; trees from the poorest source grew at a rate of 1.14 feet per year, while those from the best source grew at 1.36 feet per year. Regional differences, however, were significant for survival only.

Progenies from climatic zones differing greatly from that of the planting site appear to be more variable than progenies from climatic zones similar to the planting site, suggesting that some genotypes interact with the environment more strongly than others.

Marked differences in tree form were noted. Some progenies were tall with small diameters, while others were intermediate in height with large diameters.

On the basis of the data analyzed we can expect genetic gains of 3 to 4 percent in rate of height growth. This would mean an increase in board-foot yield of approximately 9 percent at rotation age (Nienstaedt 1965a). This increase is more than enough to provide 4 to 6 percent interest on all development costs, particularly if improved seedlings are planted on the best sites (Lundgren and King 1966).

Jack Pine

Jack pine occupies large acreages in the Lake States, and it is an economically important species. In 1967, 569,000 cords of jack pine pulpwood were consumed in the Lake States, second only to aspen. It fills an important ecological niche because of its rapid juvenile growth on relatively infertile soils.

Jack pine presents some problems for the foresters: growth rate varies widely among seed sources, its form is often poor, and it is susceptible to a number of disease and insect enemies. However, it appears to be extremely variable and flowers early; therefore, it should have a great potential for genetic improvement. For these reasons, several studies were begun to determine the type and magnitude of variation present in the species and the possibility of breeding better strains.

LAKE STATES SEED SOURCE STUDY

The first jack pine seed source study was initiated by the Station and the University of Minnesota in 1951. Seed was collected from 29 jack pine stands in Minnesota, Wisconsin, and Michigan. Each collection was made from dominant and codominant trees in a stand considered good for the area. Seedlings from all 29 stands were grown in State nurseries in Wisconsin and Minnesota, and in 1954 the 2-year-old seedlings were field-planted in 17 locations in the Lake States. In each planting the test seed sources were compared with a local source.

After 10 years of growth, trees in 11 of the plantations were measured; the mean tree height of the plantations varied from 9.6 feet on the

Chippewa National Forest in northern Minnesota to 15.2 feet on the Marinette County Forest in northeastern Wisconsin. Trees in the six plantings in northern Wisconsin were the tallest, and trees in two plantings in northern Minnesota and two in Lower Michigan were the shortest. The greatest range in total tree height among sources was present in a Washburn County, Wisconsin, planting; trees from the shortest source (Minnesota) were 25 percent shorter than the plantation mean, while trees from the tallest source (Lower Michigan) exceeded the mean by 17 percent. In general, trees from Lower Michigan seed sources performed best throughout Michigan and Wisconsin, and trees from north-central Minnesota sources did best in the northern Minnesota plantings.

In nine of the 11 plantings trees from the commercial nursery sources were shorter than those from the test sources by 12 to 28 percent. In almost all of the plantings, trees from the test source closest to the planting site outgrew the commercial nursery stock (King 1966).

Jack pine often exhibits "late-growth" or second flushing during a single growing season. This second flushing may occur only on the terminal (lammas growth) or the laterals (prolepsis), or a combination of both, causing the tree to develop a crooked stem and other undesirable characteristics. A study of the nature and extent of these abnormalities in jack pine, utilizing the 29 seed sources in six of the field plantings, was conducted over three successive growing seasons.

The frequency of occurrence of lammas growth, prolepsis, and their combinations varied significantly among seed sources in all the plantations studied. It is clear that both lammas growth and prolepsis are under strong genetic control. Because of the undesirable results of this type of growth, seed collection from trees exhibiting lammas growth and prolepsis or in stands with a high frequency of these growth types should be avoided (Rudolph 1964).

RANGEWIDE SEED SOURCE STUDY

A study including seed sources representing the entire range of jack pine was initiated in 1962 at the Institute of Forest Genetics. This study was designed to determine the patterns of variation in jack pine over its entire natural distribution in Canada and northern United States, and to increase knowledge and understanding of jack pine evolution and migration.

Ninety-two seed collections, the majority of which were supplied by the Petawawa Forest Experiment Station, Ontario, Canada, were included in the nursery phase of the study. Ninety of these collections were subsequently field-planted in northern Wisconsin in 1965 for further evaluation. Measurements taken during a 5-year period in the nursery showed much variation among sources in tree height growth, fall needle coloration, stem color, female strobili abundance, insect incidence, and wood quality.

Some of the most significant findings to date relate to wood quality. At the end of the fifth growing season in the nursery, 34 of the original 92 sources were selected for measurements of tracheid length and specific gravity. Stem samples were taken from the center of the lowest 1964 internode (jack pine is multinodal). The entire cross-section (1964, 1965, and 1966 wood) was used for specific gravity determination, but only the outermost portion of the 1966 summerwood for tracheid length determination.

The results were as follows:

1. Tracheid length and specific gravity of 3-year-old wood differed significantly among seed sources.

2. There were strong *positive correlations* between mean seed source tracheid length, diameter inside bark, and annual height growth in jack pine at this age. There were strong *negative correlations* between mean seed source specific gravity and tracheid length, diameter inside bark, and annual height growth.

3. Because the seed sources were diverse, the genetic variation among stands was much greater than the variation within stands.

4. Trees from Michigan, Minnesota and Wisconsin seed sources had the highest growth rate, longest tracheids, and lowest specific gravity, while those from northern Canada and eastern Nova Scotia sources had the lowest growth rate, shortest tracheids, and highest specific gravity.

5. Tracheid length estimated from young jack pine may be a good indication of mature-tree tracheid length when the sources have great genetic diversity. Specific gravity of 3-year-old

Figure 1. — Jack pine variation in a plantation in northern Wisconsin containing trees from seed sources throughout the species range. After 8 years from seed the mean tree height from the New Brunswick source being evaluated exceeded the mean tree height from the Nova Scotia source in the foreground by nearly 200 percent.

wood, on the other hand, probably will not be useful in predicting the specific gravity of mature trees (King 1968).

In future experiments, these results will be compared with results from older trees. If the correlations are high, the time required for an effective program to improve these characters can be greatly reduced.

SEED COLLECTION RECOMMENDATIONS

The following seed collection recommendations for the Lake States can be made:

1. Collect seed only from better-than-average stands.

2. In Lower Michigan plantings, use only seed collected in Lower Michigan.

3. In Wisconsin and Upper Michigan, collect seed from Lower Michigan and mix the Lower Michigan seedlings with seedlings from local stands.

4. In Minnesota, collect seed from selected stands near the planting site (King 1966).

Racial Variation in White Spruce

White spruce seed was collected in 1955, 1956, and 1957 from 29 locations throughout the natural range of the species. Seed from each lot was sown at Rhinelander, Wisconsin, in the spring of 1958 and the seedlings transplanted in 1960. In 1962, trees from 28 of the seed sources were field-planted in 17 locations from North Dakota to New Brunswick, representing a range in latitude of 42° to 48° N. All sources were evaluated during the first, second and fourth year in the nursery and after five growing seasons in the field. Over 30 measurements of vigor and taxonomic characters were made on the nursery material. The field measurements included survival, total height, annual height growth, and number of branches.

Survival in nearly all plantings exceeded 80 percent. With the exception of three sources from Alaska and one from the Yukon Territory, the different seed sources varied little in tree survival. Tree height growth, however, differed significantly among sources after 5 years in the field. The tallest planting at Grand Rapids, Minnesota, had a mean tree height of 36.3 inches. Trees from a Montana source were the shortest in this plantation, with an average height of 15.7 inches, and those from an Ontario source were the tallest (55.2 inches). The average height of trees from two local seed sources (those nearest the planting site) was 48.2 inches.

Analysis suggested that seed sources from the southeastern portion of the species range – the Lake States, southern Ontario, a portion of Quebec, and New England – produced trees relatively well adapted to all of the test sites, and some

Figure 2. – White spruce variation in a plantation at Grand Rapids, Minnesota, containing trees from seed sources throughout the species range. The trees are 13 years from seed; after 5 years in the field the total heights, in percent of the plantation mean, of the sources shown here were: New Hampshire (right) 119; Alaska (last 2 trees in 4-tree plot, lower center) 45; Minnesota (upper center) 128; Minnesota (left) 137. The best source in this planting was from Beachburg, Ontario. Its height was 153 percent of the plantation mean, and exceeded the average of the two Minnesota sources in the photo by 14 percent.

were growing better than the average for the plantation. Trees from the more northern sources were poorly adapted to the planting sites and had slow overall growth. The one outstanding seed source in this study was from Beachburg, Ontario. Without exception, seedlings from this source were above average on all sites and superior on the best sites. At Grand Rapids, Minnesota, their growth exceeded the plantation average by 52 percent and the average of seedlings from two local sources by 14 percent. It is interesting to note here that a Douglas, Ontario, seed source, in another older study, still maintains a 22 percent superiority in tree height growth over seven other sources after 29 years in a plantation in northern Wisconsin, and an approximate advantage of 16 percent over the local white spruce seed source (King and Rudolf 1969).

The data suggest that white spruce from the entire southeastern region of the species, and southeastern Ontario and southwestern Quebec in particular, may provide excellent breeding stock for the area encompassing the test plantings. Simply introducing the Beachburg-Douglas, Ontario provenance in some of the areas in which tests were conducted would result in direct improvement (Nienstaedt 1969a).

Natural Variation in Yellow Birch

A study of natural variation in yellow birch was initiated at the Institute in 1963. Seed lots collected from 55 sources throughout the species range were sown in the spring of 1965 and the resulting seedlings were transplanted to the Rhinelander nursery in the summer of 1965. The average height of trees from the 55 sources at the end of the third growing season was 47.8 cm., ranging from a low of 29.3 cm. for a Tennessee source to a high of 63.6 cm. for a Lower Michigan source. Height was not correlated with latitude, longtitude, length of growing season, annual precipitation, average January temperature, or average July temperature of the seed sources. Although seedlings from the northern sources showed some tendency to be thicker than those from the southern ones, diameter was only weakly correlated with latitude and length of growing season. Thus, the variation in height and diameter of yellow birch appears to be random, at least in the seedling stage.

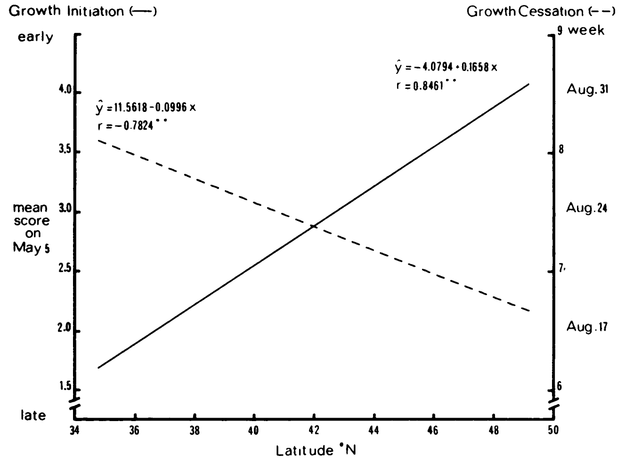

Figure 3. — Yellow birch exhibits a gradual north-south trend, or clinal variation, in growth initiation and cessation at the Rhinelander, Wisconsin nursery. The regression lines show the relationship between growth initiation and cessation and latitude of seed origin. In general, trees from northern sources start flushing and stop growing earlier than those from southern origins. Data are based on 2-year-old trees measured in the fall of 1966 and spring of 1967.

These early results suggest that much potential growth may be lost if the wrong seed source is used in a yellow birch planting. The importance of seed origin was apparent in the great differences in the performance of seedlings from different sources within the same State or Province. For example, the height differences between seedlings from the best and the poorest seed sources amounted to 32 percent for Wisconsin, 55 percent for Michigan, 28 percent for Quebec, and 44 percent for Nova Scotia. Growth rate of seedlings originating from areas relatively close to each other often differed greatly. Thus, one New Hampshire source produced seedlings 19 percent taller than those from a source 40 miles north. Similarly seedlings from one Lower Michigan source were 29 percent taller than those from a source 70 miles away in the Upper Peninsula (Clausen and Garrett 1969).

The apparent random variation in height and diameter growth of yellow birch may, in part, be due to individual tree variation. Catkin and fruit characteristics have already been shown to vary greatly among individual trees within a stand (Clausen 1968a), and similar growth differences may exist. To determine whether the great height variability observed in this study might be due to the fact that the seed lots used were a mixture from about 10 trees per stand, a study of 199 individual tree progenies representing 21 stands located throughout the natural range of yellow birch is now in progress.

Yellow birch, in contrast to its random variation in height and diameter, exhibits a gradual north-south trend, or clinal variation, in growth initiation and cessation at the Rhinelander, Wisconsin, nursery. In general, trees from the northern sources start flushing and also stop growing earlier than those from southern ones (Clausen 1968b). Times of flushing and growth cessation, however, do not appear to be related to total height.

Trees from early-flushing sources are likely to be damaged by late spring frosts, while those that continue growth until fall are susceptible to injury from early fall frosts. Trees from all 55 seed sources showed some degree of winter injury after their second winter in the nursery. Although the percentage of injured trees was often high, the damage was normally light in most of the northern and eastern sources. Most severely damaged were seedlings from the Ohio, Indiana, Virginia, Kentucky, and Tennessee sources. Of the southern group, only the North Carolina and Georgia seedlings from high elevations were relatively frost resistant (Clausen and Garrett 1969). This again illustrates the importance of selecting the right seed source for a particular climate.

On the basis of these early tests, the local yellow birch seed source may not be best. The local source was among the five poorest after 2 years in the Rhinelander nursery. It improved somewhat at the end of the third year, but was still poorer than the other four Wisconsin sources. Current indications are that the largest improvement in this species will come from progeny-tested individual trees selected in provenances within fairly large regions.

Interregional Provenance Study of Eastern White Pine

Eastern white pine seed collected from 17 sources representing the species range was sown in the Toumey Nursery, Watersmeet, Michigan, in 1958. In the spring of 1960 the 2-0 stock was transplanted to the Hugo Sauer State Nursery near Rhinelander, Wisconsin. Subsequently 2-2 stock was field-planted in Minnesota, northern Wisconsin, Upper Michigan and Lower Michigan. These four plantations were evaluated after 5 years in the field. No seed source or group of sources was consistently better than the others in the nursery or in all field plantings. Trees from the Appalachian sources started out well in the nursery and were among the best in the Lower Michigan planting. These sources showed the greatest susceptibility to winter injury and therefore did not do well in the more severe climate of northern Wisconsin and Minnesota. On the other hand, trees from an Ontario source were tallest in Minnesota but below average in Lower Michigan. The ranking by height of the seed sources growing in Lower Michigan was similar to the ranking of the same seed sources growing in southern Illinois, Indiana, Ohio, and North Carolina. However, there is little resemblence to the ranking of the same seed sources being grown in Wisconsin and Minnesota. The results show that trees from white pine seed sources react strongly to the environment, suggesting that many stands must be tested to locate enough superior sources of seed for reforestation in the Lake States.

For the more severe climates of northern Minnesota, northern Wisconsin and Upper Michigan, seed should be obtained from stands in areas where the mean January temperature is less than 20° F. This includes white pine stands in all of Minnesota, Wisconsin, Upper Michigan, and the northern parts of Lower Michigan and Ontario. For planting in southern and western Lower Michigan, southern Appalachian seed sources offer enough promise to warrant further investigation. In the meantime, foresters in the Lake States should use seed from stands no more than 100 miles from the planting site (King and Nienstaedt 1968, 1969).

Other Seed Source Studies

Other seed source studies underway at the Institute include Scotch pine, tamarack, balsam fir, northern white-cedar, Engelmann spruce, and Norway spruce.

INHERITANCE STUDIES OF WHITE SPRUCE

Seed source studies provide information on the total variation within the species. Heritability studies involve individual tree progenies and provide specific information on the inheritance of desirable tree characteristics. Together, seed source and heritability studies guide tree breeders in the choice of an efficient breeding program. Like the seed source studies, these studies involve testing under a variety of environmental conditions. The test plants are derived from open-pollinations or from controlled pollinations in which both the male and female parents are known.

The objectives of the white spruce heritability studies are:

1. To determine the magnitude and nature of genetic variation among individual white spruce trees.
2. To determine genetic correlations between desirable characteristics such as vigor, height growth, form, branchiness, and wood quality.
3. To determine juvenile-mature tree correlations. These are especially important to the tree breeder as they can materially shorten the period between breeding generations.
4. To provide breeding arboreta for crossing tests between trees of known parentage.

Heritability studies in white spruce were started at the Institute in 1962. Twenty-eight mature white spruce trees growing in northeastern Wisconsin, northern Minnesota, and the Upper Peninsula of Michigan were selected and measured. Open-pollinated seed from these parents was sown in the Hugo Sauer State Nursery at Rhinelander, Wisconsin, in the fall of 1963. After four growing seasons in the nursery total and current height growth of the 2-2 seedlings were measured.

The average annual height growth of the parents was strongly correlated with the growth of their respective progenies ($r = 0.80$), indicating that trees making the greatest average annual growth produce the fastest growing seedlings (Jeffers 1969). All of the parents used in this study have been grafted and are established in breeding arboreta and clonal tests at the Institute.

Another study has shown that superior growth of selected individuals in the nursery at 4 years can be maintained for at least 7 years in the field (King *et al.* 1965). If the superior growth of progenies from selected fast-growing parents is maintained to rotation age, considerable increases in yield can be achieved and these increases will more than offset the added costs of seed collection.

Figure 4. — One-year-old white spruce planting in northern Wisconsin containing 90 open-pollinated, half-sib families from selected white spruce trees growing in the Lake States and Ontario, Canada.

Figure 5. — Field evaluation of 8-year-old grafted clones of selected early-and late-flushing white spruce. Late-flushing clones have been damaged less by late spring frosts and also have grown faster than early-flushing clones. The taller grafts are from a late-flushing clone and the shorter grafts are from an early-flushing clone.

Controlled pollinations were made in 1964 utilizing four female parents and six different pollen parents for a total of 24 full-sib (both parents known) families. In 1965, eight pollen parents were crossed with three additional females and seed was collected from 20 of these combinations. Therefore, the Institute has seed or seedlings of 44 full-sib families. By 1972, it is anticipated that this number will be increased to nearly 100 full-sib families. These families will then be used as breeding material in the further development of faster growing white spruce varieties.

A white spruce study was also initiated in 1962 to develop a variety that would be less susceptible to damage from late spring frosts. In a white spruce plantation near Rhinelander, it was noted that date of spring growth flush varied among individual trees by as much as 3 weeks. Nine early-flushing and 16 late-flushing individuals were selected, grafted, and established in a clonal planting near Lake Tomahawk, Wisconsin. Subsequent observation of these clones indicated that the late-flushing clones avoided damage from late spring frost, grew at a faster rate during a shorter growing season, and often ended up producing greater annual height growth than the early-flushing clones.

In 1967 pollen from early-flushing, late-flushing, and randomly selected individuals was crossed on 10 of the original and three additional selections (nine late-flushing and four early-flushing). The seedling progenies were grown for 1 year in the greenhouse and then moved into controlled environment rooms at the Institute. Flushing date and growth rate have been observed in the progeny, and flushing has been shown to be under strong genetic control (heritability estimates have reached $h^2 = 0.705$). It has been estimated that the risk of late spring frost under northern Wisconsin conditions might be reduced 40 to 50 percent (Nienstaedt and King 1969).

Heritability studies are also underway in Jack pine. These studies are discussed in detail in the next section.

DISEASE AND INSECT RESISTANCE BREEDING

The destructive effect of forest pests on timber production is well known. In 1962 it was estimated that 42 percent of the annual sawtimber mortality in the United States – about 2.4 billion cubic feet – was caused by insects and disease. The breeding of pest-resistant varieties of forest trees is one promising method of reducing losses from insects and disease.

Individual jack pine trees vary in susceptibility to a variety of insect and disease organisms, such as the white-pine weevil (*Pissodes strobi* (Peck)), red-headed pine sawfly (*Neodiprion lecontei* (Fitch)), needle rust (probably *Coleosporium asterum* (Diet.) Syd.), jack pine needle cast (*Hypodermella ampla* (Davis) Dearn.), bark beetles (*Pityophthorus* spp.), eastern pine-shoot borer (*Eucosma gloriola* Heinrich) and eastern gall rust (*Cronartium quercuum* (Berk.) Miyabe ex. Shirai) (King 1971, King and Nienstaedt 1965).

Figure 6. – Destruction of current-year shoots in jack pine resulting from attack by the eastern pine shoot-borer, Eucosma gloriola. *Variation in jack pine susceptibility to this insect and several other pests appears to be related to seed source. Individual trees have been selected in seed source tests on the basis of white pine weevil and shoot-borer incidence, clonally propagated, and used in controlled pollinations to study inheritance of pest resistance in jack pine.*

Jack pine needle cast, caused by the fungus *Hypodermella ampla* Dearn., causes defoliation of jack pine. Twenty-nine seed sources of jack pine in three plantings in Michigan's Upper Peninsula and northeastern and south-central Wisconsin were found to differ in susceptibility to the fungus. The differences remained constant from year to year and from environment to environment, indicating they have a direct genetic basis (King and Nienstaedt 1965).

The general approach in the study of pest resistance at the Institute is as follows: first, parents are selected from seed sources that have shown variation in pest incidence. This should insure genetic variation in the progenies. Occasionally, parents are selected from natural stands, but only where pest incidence has been severe enough to suggest that undamaged trees did not escape pest infestation by accident. Selection

Figure 7. – Controlled pollination in jack pine utilizing parents selected on the basis of susceptibility or resistance to the white pine weevil. Progenies produced from the pollinations will be used to study the inheritance of white pine weevil resistance.

of parents is followed by grafting to establish breeding arboreta. The parents are crossed with several pollen-tester parents to produce full-sib families. These families of progeny will then be tested for pest resistance, providing the basis for a new cycle of selections. As an example, controlled pollinations were made in 1968 and 1969 using 24 clones as female parents and six other trees as male parents. All were selected for their relative resistance or susceptibility to the white pine weevil. The crosses will yield 144 full-sib families with which to study the inheritance of variation in white-pine weevil resistance.

This approach has the following advantages: (1) it indicates the degree to which genetic pest resistance is transmitted through the seed parent and pollen parent (narrow-sense heritability), (2) it provides material for studying the underlying causes of resistance, and (3) it provides inheritance data on other economically important characteristics of jack pine.

Thus far 45 trees have been selected within nine seed sources on the basis of white-pine weevil and eastern pine-shoot borer incidence. In 1965 and 1966 the selected parents were grafted. The grafts are now located in a breeding arboretum near Lake Tomahawk, Wisconsin. Six additional trees have been selected for use as pollen parents and grafted in 1970.

Trees that were selected in the Institute's seed source studies for eastern pine-shoot borer inci-

Figure 8. — Exotic spruces in the Institute's spruce arboretum. The species being observed is Picea asperata *from China. At the left is* P. omorika *from Serbia in Yugoslavia, and in the right foreground is* P. glehnii *from Japan. Twenty-nine species of spruce are being tested at Rhinelander.*

dence were grafted in 1966, and the grafts were field-planted in 1968. These grafts will also be used in controlled pollinations as soon as they begin to bear female strobili.

As indicated previously, not all selections are made in seed source test plantations. In 1961 a severe outbreak of jack-pine budworm (*Choristoneura pinus* Freeman) occurred in Douglas County, Wisconsin. In some of the infested stands a few undamaged survivors remained. In the fall of 1961 open-pollinated seed was collected from 10 undamaged trees and one severely defoliated tree. In February 1966 the 10 selected trees were grafted and the successful grafts were field-planted in 1968 at our breeding arboretum near Lake Tomahawk, Wisconsin.

Similarly, 13 trees were selected for studies of pine tortoise scale (*Toumeyella numismaticum* (Pettit and McD.) in a Polk County, Wisconsin, jack pine plantation severely attacked between 1959 and 1961. The selections were grafted in 1966 and the grafts field-planted in 1968.

THE INSTITUTE ARBORETUM

The introduction of exotic tree species is usually a part of any complete forest genetics program. Introduced species will sometimes grow faster and straighter or produce more wood than the species native to the area. Some of these adapted species serve a purpose in forest economics not readily served by a native species.

The Institute not only tests exotic species for their adaptability to this area, but studies hybridization between exotic and native species. The role of interspecific hybridization in tree improvement is discussed in the next section. To facilitate hybridization and other phases of the Institute program, substantial collections of exotic *Betula* and *Picea* species have been assembled at or near the Institute (tables 1 and 2). The

Table 1. — Exotic Betula *species and varieties in tests at or near the Institute of Forest Genetics*

Species and variety	Seedlings	Grafts
Subsection *Acuminatae*:		
Betula maximowicziana Reg.		X
Subsection *Costatae*:		
B. albo-sinensis var. *septentrionalis* Schneid.		X
B. delavayi Franch.		X
B. ermani Cham.	X	X
B. ermani var. *subcordata* (Reg.) Koidz.		X
B. forrestii (W. W. Sim.) Hand.-Mazz.		X
B. grossa Sieb. & Zucc.	X	
B. lenta L.	X	X
B. nigra L.	X	X
B. raddeana Trautv.		X
Subsection *Albae*:		
B. cordifolia Reg.	X	
B. davurica Pall.		X
B. minor (Tuckerm.) Fern.	X	
B. obscura Kot.	X	
B. occidentalis Hook.	X	
B. pendula Roth	X	X
B. pendula var. *dalecarlia* (L.) Schneid.		X
B. pendula var. *fastigiata* (Clemenceau) K. Koch		X
B. pendula var. *gracilis* Rehd.		X
B. pendula var. *purpurea* (Andre) Schneid.		X
B. pendula var. *tristis* (Beiss.) Schneid.		X
B. pendula var. *youngii* (Th. Moore) Schneid.		X
B. platyphylla var. *japonica* (Miq.) Hara	X	
B. populifolia Marsh.	X	X
B. pubescens Ehrh.	X	X
B. pubescens var. *urticifolia* (Loud.) Schelle		X
B. pubescens forma *aurea*		X
B. tortuosa (Ledeb.) Schneid.	X	
B. turkestanica Litvin.		X
Subsection *Nanae*:		
B. glandulosa Michx.	X	X
B. humilis Schrank		X
B. nana L.	X	X
B. ovalifolia Rupr.	X	
B. pumila var. *glandulifera* Reg.	X	X
B. tatewakiana Ohki & Watanabe	X	
Natural hybrids:		
B. x *jackii* Schneid.		X
B. x *purpusii* Schneid.		X
B. x *sandbergii* Britt.		X

Table 2. – Exotic Picea *species and varieties in tests at or near the Institute of Forest Genetics*

Species and variety	Seedlings	Grafts
Subsection Eupicea:		
Picea abies (L.) Karst	X	X
P. abies cv. acrocona (Fries) Krü.		X
P. abies var. viminalis (Alstroem) Fries		X
P. asperata Mast.	X	X
P. bicolor (Maxim.) Mayr.	X	X
P. bicolor var. acicularis Shiras. and Koyama	X	
P. glauca var. albertiana (densata) (S. Brown) Sarg.	X	
P. glehnii (Fr. Schmidt) Mast.	X	X
P. koyamai (koraiensis) Shiras.	X	X
P. maximowiczii Reg.	X	
P. obovata Ledeb.	X	
P. orientalis (L.) Link	X	X
P. polita (Sieb. and Zucc.) Carr.	X	X
P. retroflexa Mast.		X
P. rubens Sarg.	X	
P. schrenkiana Fisch. and Mey.	X	X
P. smithiana Boiss.	X	
P. wilsonii Mast.	X	
Subsection Casicta:		
P. engelmannii Parry	X	
P. jezoensis (Sieb. and Zucc.) Carr.	X	X
P. jezoensis var. hondoensis (Mayr.) Rehd.	X	
P. likiangensis var. balfouriana (Rehd. and Wils.) Cheng		X
P. montigena Mast.		X
P. pungens Engelm.	X	
P. purpurea Mast.		X
P. sitchensis (Bong.) Carr.	X	
Subsection Omorika:		
P. breweriana S. Wats.	X	
P. omorika (Pancic) Purkyne	X	X
P. spinulosa (Griff.) Henry	X	
Taxonomic status not known:		
P. chihuahuana Martinez	X	
P. mexicana Martinez	X	X
P. morrisonicola Hayata	X	

birch collections represent 26 species from four subsections of the genus, nine named varieties of these species, and three natural hybrids. European, Asian, and North American species are represented. Also included are the four species native to northern Wisconsin. Twenty-seven species of spruce and five named varieties have been assembled. Two species native to northern Wisconsin are included in the collection.

To develop successful hybrids both parents much be at least reasonably well-adapted to the climate where the hybrids are to be grown. Hybrids between California lodgepole pine and Wisconsin jack pine, for instance, are a total failure in the Lake States (Rudolph and Nienstaedt 1962). Hybrids between *Pinus monticola* and *P. strobus* have also shown poor adaptation.

To find exotic species able to survive and grow at least moderately well in the severe climate of northern Wisconsin, small-scale seed source studies have been initiated, particularly in spruce. The species involved are *Picea engelmannii, P. rubens, P. omorika, P. orientalis,* and *P. jezoensis.* Large scale tests of *P. abies* have been started more recently. Grafted trees established with scions from mature trees cannot be used to evaluate climatic adaptation. For example, young *Picea omorika* seedlings at Rhinelander suffer severely from winter drying, while grafts with the needle structure of mature trees suffer little or no injury. The time of flushing becomes later with age. Grafts of scions from mature trees will, therefore, show less spring frost injury than seedlings.

INTERSPECIFIC HYBRIDIZATION

Species hybridization has played a major role in tree improvement. Hybrid poplar and larch have been widely used and are favored by forest managers in many parts of the world. The efforts to produce new hybrids involving species in many genera continue. In the following pages, our studies of species crossability in the genera *Picea* and *Betula* will be discussed.

The objectives have been (1) to determine if (or how well) the species within each genus cross with one another and (2) to determine the evolutionary relations among the species. This objective is based on the theory that closely related species generally will cross more readily than those more distantly related.

Spruce Hybridization

Fifty-two combinations of spruce species have been attempated (table 3). Eight species, of which three are North American, were used as female parents, and 15 were used as male parents. Two of the taxonomic subsections – *Eupicea* and *Omorika* – were represented by the species used as females. The third subsection – *Casicta* – was represented among the males.

Twenty-seven crosses produced seedlings. Of these, 12 were crosses between species in the subsection *Eupicea*, six involved species in *Eupicea* and *Omorika*, and nine were crosses between subsections *Eupicea* and *Casicta*. One attempted cross between *P. omorika* subsection *Omorika*) and *P. likiangensis* (subsection *Casictoa*) failed.

Ten of the successful crosses, as far as we know, have not been reported in the literature. Many of these have yielded only a few seedlings and we have not been able to design adequate tests that would enable us to verify hybridity. Of the six crosses for which replicated tests could be made, the following four appear to be verified hybrids: *P. glauca* x *P. maximowiczii*, *P. omorika* x *P. glauca*, *P. mariana* x *P. abies*, and *P. mariana* x *P. pungens*. Two crosses – *P. glauca* x *P. abies* and *P. mariana* x *P. montigena* – are doubtful hybrids; they show significant differences in a few characteristics, but cannot be established as hybrids with certainty.

Table 3. – Crossing patterns in the genus Picea, *IFG crosses 1956-1966*

	Male parent																	
	Eupicea									Casicta					Omorika			
Female parent	abies	asperata	glauca	koyamai	mariana	maximowiczii	orientalis	retroflexa	schrenkiana	jezoensis	likiangensis	montigena	pungens	sitchensis	omorika	Total	No. of combinations	Comb.-seedlings
Eupicea abies		5 3 ?	2 0				1 0				2 1 ?				2 0	12 4	5	2
asperata	3 2		1 0								1 0				1 0	6 2	4	1
glauca	15 5 ?	12 3 +		3 0		6 1 N +	9 2	2 1 N	5 1	6 2 +	1 1 N +	12 7 N	6 4	4 4 +	14 3 N +	95 34	13	12
koyamai		3 2	9 0		1 0		1 0				1 1 N				1 0	16 3	6	2
mariana	4 2 N +	4 0	4 0				4 0					3 1 N ?	2 1 N +		2 2 +	23 6	7	4
orientalis	1 1	2 0	1 0		1 0						1 0					6 1	5	1
rubens		4 0	1 0		6 0		2 1		6 0						2 1	21 2	6	2
Omorika omorika	1 1 N	2 0	8 4 +		3 1 +				1 0		2 0					17 6	6	3
Total	24 11	32 8	26 4	3 0	11 1	6 1	17 3	2 1	12 1	6 2	8 3	15 8	8 5	4 4	22 6	196 58		
No. of combinations	5	7	7	1	4	1	5	1	3	1	6	2	2	1	6		52	
Comb.-Seedlings	5	3	1	0	1	1	2	1	1	1	3	2	2	1	3			27

Key: Number of attempts → 3 (left) ← ; Attempts resulting in seedlings ← 1 (right); N ← Combination not previously reported; + ← Hybridity of seedlings substantiated; ? ← Hybridity of seedlings not fully substantiated.

Figure 9. — One of two promising spruce hybrids produced at the Institute, a cross between black spruce and Serbian spruce from Yugoslavia, is indicated by the arrows on the right. At 8 years of age from seed the total height growth of the hybrid exceeded that of the native parent species (arrows on the left) by 20 percent.

Two crosses are particularly interesting from a tree improvement standpoint. In 1959 we crossed *P. mariana* growing near the Institute with *P. omorika* of unknown origin growing at the Morton Arboretum, Lisle, Illinois. In 1968 when the resulting trees were 8 years old from seed, their average heights were:

P. mariana x *P. omorika*	2.50 m.
P. omorika x *P. mariana*	2.21 m.
P. mariana control	1.99 m.

P. mariana x *P. omorika* exceeded the native parent species by 20 percent and is a well-formed, promising tree. The reciprocal cross, *P. omorika* x *P. mariana,* is taller than the native black spruce, but is variable and some trees have poor form.

The *P. omorika* x *P. glauca* cross was made in 1964. Seedlings were forced in the greenhouse in 1966 and planted in the nursery in 1967. In the fall of 1968 they measured:

P. glauca	204 mm.
P. omorika x *P. glauca*	286 mm.
P. omorika x *P. glauca*	228 mm.
P. omorika x *P. glauca*	278 mm.
P. omorika x *P. omorika*	237 mm.

Thus, the best hybrid was 40 percent taller than the native parent; furthermore, while *P. omorika* was susceptible to frost injury in the fall, the hybrid showed little injury. The injury percentages were as follows:

	P. glauca	P. omorika x P. glauca	P. omorika x P. omorika
Normal top development	71.2	61.8	8.3
Dead terminal	.0	4.4	85.0
Lateral shoot in dominant position	28.8	33.8	6.7

Additional crosses and studies of the hybrids are necessary before results can begin to shed any light on the evolutionary history of the genus *Picea*. In the meantime, two promising hybrids have been developed. They will be repeated using selected *P. glauca, P. mariana,* and *P. omorika* parent trees.

Birch Hybridization

To study compatibility in *Betula*, crosses have been made among 12 birch species belonging to three subsections of the genus (table 4). Seven species are North American and five are exotic. In all, 110 interspecific combinations were attempted between 1962 and 1968. Each combination has been repeated several times, bringing the total number of attempts to 423 and individual crosses to about 900.

Crossability has been verified for 20 of the 28 combinations reported in the literature; only six attempted combinations were unsuccessful. An additional 84 new combinations were attempted and some degree of success was reached in 50 of these. Because many of the crosses produced only a few seedlings, we have not been able to verify hybridity of these. Most crosses are now being studied to determine which have yielded true hybrids.

B. nigra, B. ermani, and *B. papyrifera* were generally more successful as female parents than they were as male parents. On the other hand, *B. lenta, B. pendula, B. pubescens* and *B. pumila* performed better as male parents. Three species, *B. alleghaniensis, B. populifolia,* and *B. glandulosa,* were equally successful as female or male parents.

Table 4. — Crossing patterns in the genus Betula, *IFG crosses 1962-1968*

Female parent species and ploidy	Male parent* Costatae nig 2X	len 2X	erm 4X	all 6X	Albae pen 2X	pop 2X	pub 4X	pap 4-6X	Nanae gla 2X	hum 2X	nan 2X	pum 4X	Number of attempts Total	Succ.	Number of combinations Total	Succ.
Costatae																
nigra 2X		6 2 N	7 5 N	11 1 N	15 9 N	9 2 N	7 3 N	15 1 N	5 1 N	1 0		5 1 N	81	25	10	9
lenta 2X	3 0			1 1	4 0	2 0	1 0	2 0					13	1	6	1
ermani 4X	10 2 N	8 2 N		5 0	9 4 N	2 1 N	5 4 N	3 1 N	3 0	2 2 N	1 0	6 5 N	54	21	11	8
alleghaniensis 6X	12 1 N	4 1	2 1 N		6 0	4 1 N	1 1 N	9 4	3 1 N			2 1	43	11	9	8
Albae																
pendula 2X	9 1 N	3 0		3 1		6 1 N	6 0	10 4	1 0			2 1	40	8	8	5
populifolia 2X	3 1 N	3 1	3 1 N	1 1 N	3 2 N		3 1 N	2 1	1 1 N			2 2 N	21	11	9	9
pubescens 4X	2 1 N	1 0		1 1	2 1	5 1 N		2 1	2 1 N	1 0		1 1 N	17	7	9	7
papyrifera 4-6X	7 5	5 2	3 1 N	7 5	4 3	4 1	3 2		3 0			3 1	39	20	9	8
Nanae																
glandulosa 2X	8 0		1 0	3 0	7 0	7 0	4 2 N	7 0			1 0	2 0	40	2	9	1
humilis 2X	2 0	1 0	1 1 N	2 1 N	2 0	2 0	2 1 N	2 1 N	2 0			1 0	17	4	10	4
nana 2X	3 1 N	1 0	2 0	1 0	2 0	3 1 N	2 1 N	3 0	3 1 N			2 0	22	4	10	4
pumila 4X	7 0	3 0	2 1 N	5 0	3 1 N	4 1 N	5 1 N	3 1	3 0	1 1 N			36	6	10	6
Attempts																
Total	66	35	21	40	57	48	39	58	26	5	2	26	423			
Successful	12	8	10	11	20	9	16	14	5	3	0	12		120		
Combinations																
Total	11	10	8	11	11	11	11	11	10	4	2	10			110	
Successful	7	5	6	7	6	8	9	8	5	2	0	7				70

*Names of species used as male parents are abbreviated but listed in the same order as under female species.

Key: Number of attempts. → 3 1 ← Number of successful attempts.
N ← Combination not previously reported.

Species belonging to the same subsection presumably are more closely related to each other than to members of other subsections, so one might expect greater crossability within than between subsections. So far, this does not appear to be the case in *Betula*. Crosses with *Costatae* as female parents and *Albae* as male parents were generally more successful than crosses within either *Costatae* or *Albae*. Similarly, crosses within *Nanae* were less successful than crosses between female *Nanae* and male *Albae*.

The birches represent a polyploid series with chromosome numbers ranging from 2n = 28 (diploid) to 2n = 84 (hexaploid). Results indicate that in interspecific crosses between parents of similar ploidy, crossability appears to increase with increasing ploidy, as it does in certain other plant genera; e.g., *Solanum*.

Early evidence indicated that crosses between low ploidy females and high ploidy males were most successful (Clausen 1966). Although there are exceptions, this appears to be a general pattern in *Betula*.

Differences between reciprocal crosses are common. Seed from the cross *B. ermani* x *B. pumila* had 75 percent germination, while the riciprocal cross produced few germinable seed; both species have the same sumber of chromosomes. In most cases, the difference in success of reciprocal crosses appears to be due to differences in ploidy levels of the parents. The success of crosses has also been shown to vary with the individual trees used as parents (Clausen 1966). Apparently interspecific compatibilities depend not only on the species themselves, but also on the compatibility of the individuals involved in the cross.

RADIATION GENETICS AND RADIOBIOLOGY

Radiation resulting from fallout and natural background sources is of particular concern to the forester. Because of their longevity, trees may be continuously exposed to low-level radiation over many decades. It has been estimated that in forest trees, the natural background radiation may be responsible for 40 to 50 percent of all genetic changes that occur. Also, the threat of whole forests being exposed to high dosages of ionizing radiation from nuclear disasters makes knowledge of the biological effects of radiation on forest trees important. From a more practical viewpoint, radiation can be used to induce genetic changes. As such, it is potentially a valuable tool (1) in producing marker genes for basic tree genetic studies and (2) in producing additional variability for tree improvement programs of species with limited natural variation.

It is within this frame of reference that the Institute of Forest Genetics at Rhinelander was assigned responsibility for radiation research within the Forest Service. The broad, long-term objectives of the project are as follows:

1. The fundamental study of acute and chronic gamma irradiation effects on forest trees.
2. The development of radiation as a possible tool in genetic studies of forest trees.
3. A comparison of the responses of trees to gamma radiation with responses to other types of radiation and chemical mutagens.
4. The induction of mutations useful in a tree improvement program.

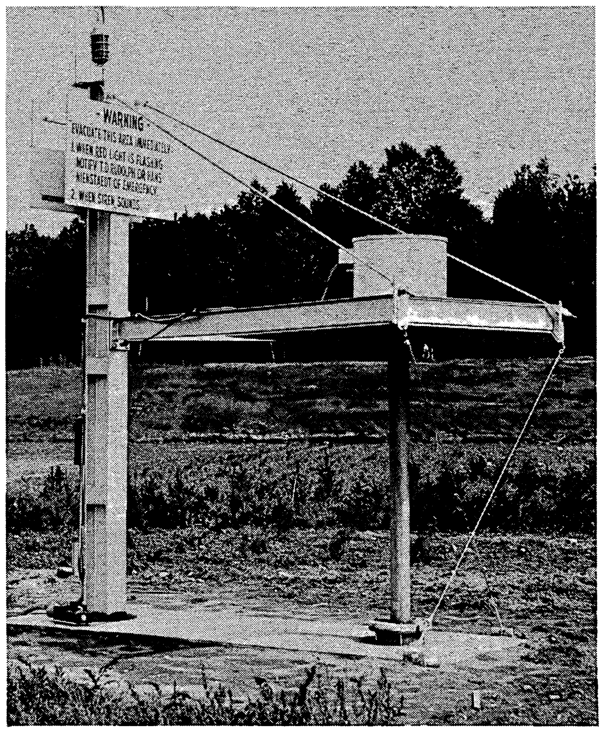

Figure 10. — Gamma field radiation source support and operating mechanism. The radioactive source capsule, containing 1,500 curies of Cesium ¹³⁷, is elevated in the tube to a position just below the sky shield to irradiate tree seedlings planted in the area around the source.

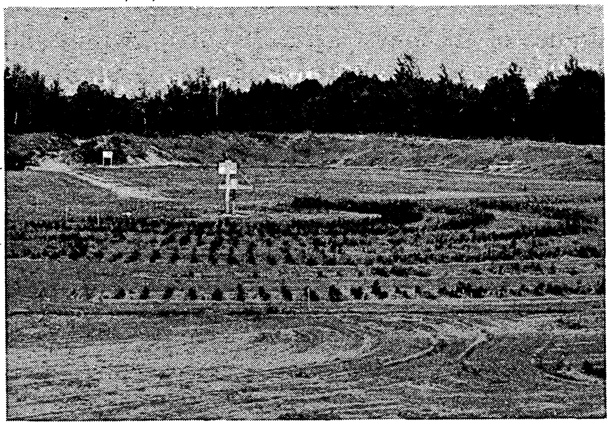

Figure 11. — Plots of various tree species are arranged in arcs around the gamma source.

For this research, two major sources of gamma radiation were installed in 1965. The first is a 6.5-acre gamma radiation field in which a 1,500 curie source of Cesium 137 (^{137}Cs) is exposed in the center for 20 hours each day from about April 15 to October 15 each year. The other is a self-contained gamma irradiator containing 260 curies of ^{137}Cs used for irradiation of seeds, pollen, small seedlings, and cuttings.

Some radiation research was conducted by the North Central Forest Experiment Station as early as 1951, when jack pine seed was irradiated with 1,000 and 4,000 Roentgens (R) of X-rays.[1] The response to the X-rays was tested under nursery conditions and in the field. At 4,000 R no seedlings survived beyond 1 year of age. At 1,000 R seedling survival was approximately 30 percent of control survival after 2 years. The LD_{50} (the exposure resulting in 50-percent mortality) decreased as the seedlings aged — 2,025 R at 40 days, 1,710 R at 130 days, and 700 R at 14 months. Irradiated jack pine also showed a low reproductive capacity — about 10 percent after cross-pollination, and less than 5 percent after self-pollination. Thus, the effects of seed irradiation in jack pine, and probably other conifers, cannot be fully evaluated in the first generation — at least two generations are required (Rudolph 1967).

[1] *This work was done in cooperation with Dr. Scott S. Pauley (now deceased), who then was on the staff of the Maria Moors Cabot Foundation for Botanical Research at Harvard University.*

The jack pine seed X-irradiation studies have resulted in some additional important findings. More than 30 trees carrying genes for chlorophyll deficiencies and other genetic markers were discovered. Genetic segregation ratios were determined for these easily identifiable characteristics (Rudolph 1966a), and the parent trees are now being studied further to more fully assess their usefulness in modes of inheritance and other basic genetic studies.

Much of the radiation research thus far has been devoted to studying the relative radiosensitivity of gymnosperm seeds and seedlings. Soaked seeds of eastern larch, Norway spruce, white spruce, black spruce, red pine, jack pine, lodgepole pine, Scotch pine, and northern white-cedar were irradiated with ^{137}Cs gamma rays in two experiments at exposures ranging from 150 to 38,400 R. Seed radiosensitivity varied among species by a factor of more than four. Norway spruce, white spruce, and Scotch pine were the most sensitive species, and jack pine the most resistant. The average LD_{50} exposure for all endpoints studied varied between 2,300 R for the most sensitive species to 10,500 R for the most resistant. The more than fourfold differences in seed radiosensitivity were found to be unrelated to differences in nuclear volume, chromosome volume, and DNA (deoxyribonucleic acid) content of these species. The seed sensitivity pattern showed no relation to predicted seedling and mature plant sensitivities for the same species (Rudolph and Miksche 1970).

Relative radiosensitivity of gymnosperm seedlings was studied in seven species: eastern larch, white spruce, black spruce, jack pine, lodgepole pine, red pine, and northern white-cedar. The seedlings were irradiated when the seedcoats were shed on half of the seedlings. Gamma ray exposures ranged from 150 to 3,600 R. Shoot dry weight 50 days after treatment showed the greatest radiosensitivity, with a D_{50} (50 inhibition exposure) ranging from 195 to 380 R for the seven species. The number of leaves at 50 days and survival and shoot dry weight at 130 days had consistently higher D_{50} exposures, ranging from 400 to 750 R. Seedling and seed radiosensitivity in the same populations were not closely correlated, nor was seedling sensitivity related to predicted mature plant sensitivity. Seedling sensitivity was, however, related to

DNA content but not to other nuclear variables. These results further point out the variation in radiosensitivity among stages of the gymnosperm life cycle (Rudolph 1971).

A preliminary study showed that white spruce pollen irradiated with gamma ray exposures up to 800 R and applied to nonirradiated female strobili stimulated seed yield (Rudolph 1965). A followup study that included pollen exposed to 16 levels of gamma radiation showed that viable seed yield apparently was stimulated at pollen exposures below 1,500 R. However, a significant decrease in yield of filled seed was noted at pollen exposures above 3,000 R. The yield of filled seed and seed viability indicated an LD_{50} ranging between 4,500 and 9,500 R for the three pollen lots studied. This contrasts with an average LD_{50} of 400 R for white spruce seedlings and about 2,500 R for seed. Less than 1 percent of the seed produced was filled and viable at the 19,200 R exposure, and none was filled or viable with pollen exposed to 28,800 R (Rudolph 1969). Thus, a total lethal dose for white spruce pollen appears to be about 20,000 R.

The radiation research at the Institute is currently being expanded to include a comprehensive study of the response of natural northern forest communities to gamma radiation. The new research will include studies ranging from cell biology to general forest ecology. The program will include several seasonal exposures of northern forest communities as well as one long period of chronic irradiation. Support will be provided by the Atomic Energy Commission and the USDA Forest Service. In addition, a wide variety of research in the project will be undertaken by university cooperators.

VEGETATIVE PROPAGATION RESEARCH

Vegetative propagation (propagation of a plant by asexual means) provides a way to maintain the genetic identity of an individual. It has, therefore, found wide use in forest tree improvement work. The techniques are used for preserving and multiplying valuable tree germ plasm, in analyzing inheritance, establishing breeding arboreta and seed orchards, and in various research projects where it is desirable to use clonal material.

Research at the Institute includes (1) basic studies of the physiology of root initiation and differentiation, (2) production of plantlets through rooting of cuttings, and (3) improvement of grafting techniques.

Rooting Research

Vegetive reproduction of forest trees from cuttings would simplify production of clones for tree breeding and forest genetics research. However, this is still impractical because cuttings of many desired species (particularly older trees) do not root easily enough. To gain an understanding of the physiology of adventitious root initiation, basic studies of root formation on cuttings were initiated. Hormonal control of root initiation, the action of indole-3-acetic acid, benzyladenine, and gibberellic acid in particular, is under study. A dual approach is being used in studying the regulation of nucleic acid and protein metabolism at the cellular level in adventitious root initials: (1) semiquantitative histochemical and cytochemical techniques, such as microautoradiography, and (2) quantitative biochemical analyses of tissues from cuttings in various stages of root initiation. This approach will be continued until a clearer understanding of the hormonal control of adventitious root initiation has been obtained. With this new knowledge we hope to be able to develop economic and efficient rooting techniques.

Production of Plantlets by Rooting of Needle Fascicles

In 1960 a study was initiated to develop jack pine plants by rooting needle fascicles. The terminal buds were removed on 2- and 5-year-old jack pine seedlings in early July at about the time elongation had ceased. By September, buds had developed in many of the needle fascicles. The needle bundles were treated with 0.1 percent and 0.8 percent indole butyric acid (IBA), and placed in a sand medium. Best rooting – 70 percent – was on fascicles from 2-year-old plants when propagated under 20-hour photoperiods in a heated rooting medium, and treated with 0.1 percent IBA. Fascicles from the older plants and those receiving other treatments gave poorer results. Fascicles without large preformed buds fail to form shoots although they may form roots (Rudolph and Nienstaedt 1964).

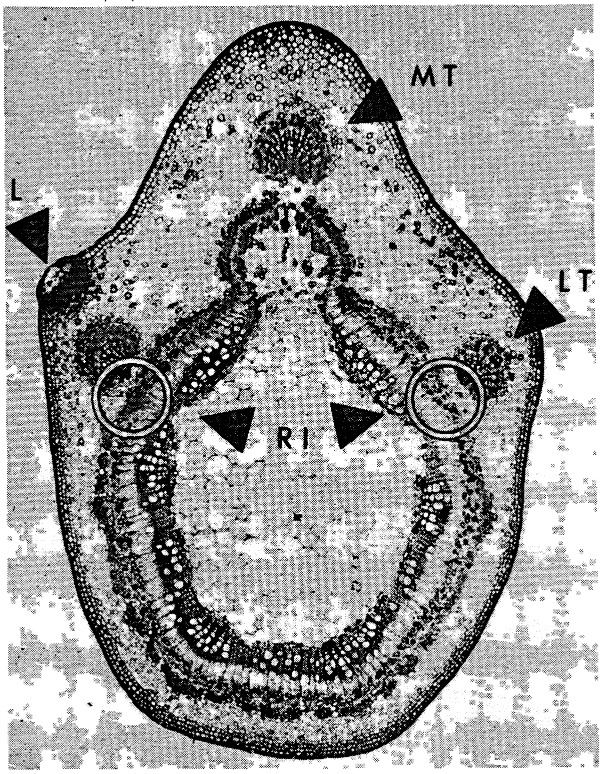

Figure 12. — Transverse section through a node of brittle willow showing the proximity of developing lenticel (L), lateral leaf trace (LT), medium leaf trace (MT), and root initials (RI). Brittle willow has been used to study adventitious root initiation because root primordia always develop at specified locations.

The results of this study showed that jack pine plants can be propagated successfully from rooted needle fascicles provided the fascicles are taken from young plants and possess well-developed buds before they are placed in the rooting medium. The ability to propagate individual trees by rooting needle fascicles provides a useful technique for isolating somatic mutations in studies concerned with induced mutations.

Grafting Research

Standard grafting techniques (Nienstaedt *et al.* 1958) work well with spruce, pine, fir, and birch. Side grafting on potted root stock, forced in the greenhouse in late winter and early spring, will give excellent results for most species. Research at the Institute has, therefore, been concentrated on developing methods for extending the grafting season.

Greenhouse grafting can be performed successfully in September on potted stock using standard grafting techniques; the grafts are maintained on long-day photoperiods for 4 to 6 weeks after grafting, then transferred to short-day conditions for a few weeks, and finally to cold storage for 6 to 8 weeks of chilling (Nienstaedt (1959c). Exposure to 40° F. during this period fulfills chilling requirements. The plants can then be returned to the greenhouse where they will start growing in 3 to 5 weeks.

In the field, best results have been obtained from the middle of May to the first week in June, with grafting near the base of the previous year's leader. The best time is just when the bud scales break, before any substantial elongation of the new shoots has taken place. Small tests in the nursery on 6- to 7-year-old plants have demonstrated that earlier grafting is possible. We grafted as early as the last week of March and until the first week of May with good results. The survival ranged from 90 to 100 percent, and subsequent growth was excellent.

Grafting on potted root stock in an open lathhouse has been successful as early as the last week of March. Success was 80 to 90 percent about the middle of April. Grafting did not become unsatisfactory until the scions began to show activity.

Another field study has shown that scion material from 30- and 60-year-old trees can be grafted successfully from the middle to the end of July. The grafts were made at the base of the leader on 8-year-old plantation-grown trees. Near the end of the third summer after grafting, survival for the 30- and 60-year-old scion material was 63 and 50 percent for grafts made on July 17, 33 and 30 percent for grafts made on July 31, and 13 and 27 percent for those made on August 14. All grafts done after August 14 failed completely (Nienstaedt 1965b).

CELL BIOLOGY

The cell biology program is relatively new at the Institute of Forest Genetics. As a field of study, it is essentially an extension of cytology that developed from the convergence of cytology with other fields of biological research, particularly genetics, physiology, and biochemistry. The investigation of the cell as the primary unit of biological organization is the objective of cell biology, as it is with cytology, but the problems of the cell are approached at all levels of organization from molecular structure to cellular differentiation.

Examples of research that fall within the general objectives are: physical and chemical aspects of cellular and intercellular structure, biosynthesis with reference to cell growth, reproduction and differentiation, mechanism of meiosis and mitosis, cell cycles, membrane function, interactions between cells in tissues or in culture, environmental relations and adaptations, interactions between genome and cytoplasmic factors, functional role of subcellular particles, and regulation of cellular processes.

Some results of the cell biology program are described in the following pages.

Cycle Time

Cycle time is defined as the time necessary for a cell to begin and terminate nuclear division. The cycle time of a forest tree species is important to the researcher because the time required for a cell to divide has a direct bearing upon growth rate. The cycle time is also an important factor in determining the plant radiosensitivity.

There are several stages during a cycle of cell division: G_1 (resting), S (DNA synthesis), G_2 (resting), and mitosis. The quantity of DNA (deoxyribonucleic acid) doubles during the course of division and the levels are notated by 2C, intermediate, and 4C amounts, corresponding to G_1, S, and G_2, respectively.

Using seeds of a northeastern Wisconsin seed source, the miotic cycle time of jack pine (*Pinus banksiana*) was determined with the use of tritiated thymidine as a labeled DNA precursor. The extent of the labeling was determined using liquid emulsion autoradiography. Beta particles emitted from the tritiated thymidine reduce the silver grains of the photographic emulsion. The number of labeled cells (prophase stage) scored, when plotted over a time course, yields the cycle time. The estimated duration of the mitotic cycle of *Pinus banksiana* was 25.7 hours. The time intervals of interphase were found to be: G_1, 15.3; S, 7.6; and G_2, 1.4 hours (Miksche 1967b).

The most important finding was the long G_1 period of 15.3 hours. This may be an important factor related to the high radiosensitivity of gymnosperms. Cells in G_1 (interphase) yield chromosome type aberrations that ultimately result in a greater loss of genetic material than losses due to chromatid aberrations originating in late S or G_2 phases.

Figure 13. — Jack pine chromosomes observed during the prenuclear stage in ovule development. Twelve chromosomes are visable on each side of the anaphase figure shown here. Apparent bands on some chromosomes are artifacts produced during slide preparation.

Physical and Chemical Aspects of Cellular and Intercellular Structure

Experiments were conducted to determine the variation in nuclear volume and DNA per cell among 13 coniferous species. We also determined the correlation between nuclear volume and DNA, and tried to establish a relationship between these factors and the distribution of the species.

Feulgen microspectrophotometry and biochemical analysis were used to estimate the amount of DNA per cell. Prepared slides were also used to measure the nuclear volumes of root meristems. Nuclear volume among the 13 species varied by a factor of 11.3, while DNA per cell varied by a factor of 3.2. The correlation between absolute amounts and cytophotometric estimation of DNA and nuclear volume was high, with a correlation coefficient of 0.81. The large amounts of DNA per cell compared with most dicotyledons suggests that conifers contain an excess of DNA, because it is highly unlikely that conifers contain more genetic information than other plants.

Nuclear size (and DNA per cell) may have an adaptive value in the ecological sense. In the species studied, those with small nuclear volumes tended to have a wider distribution (Miksche 1967a).

The response of white spruce shoot apices to chronic gamma irradiation has been investigated (Cecich and Miksche 1970). It was found that the volume of the apical initial and central mother cell zones changed during the growing season. Apices were extremely radiosensitive when these zones were the largest in size.

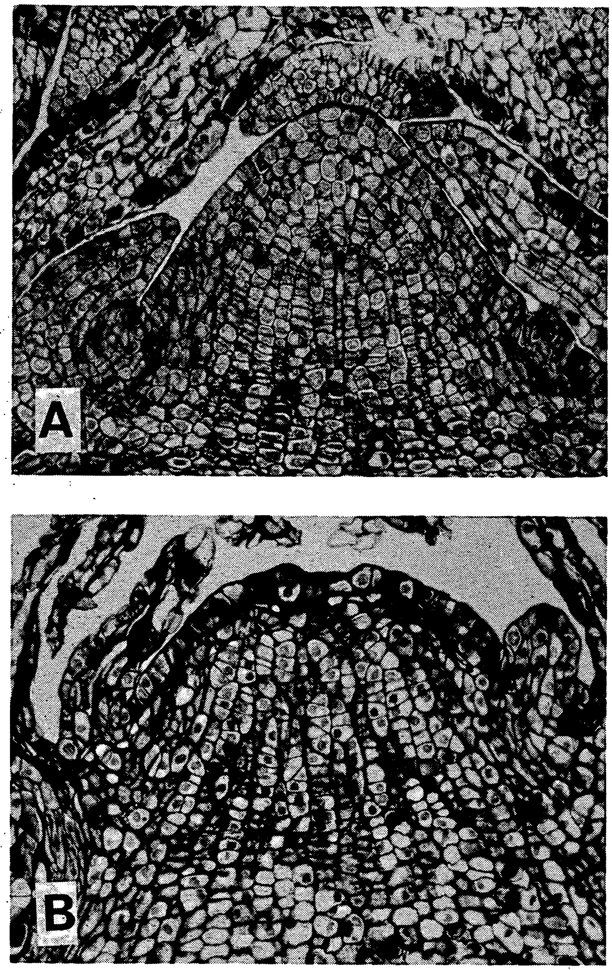

Figure 14. — Response of white spruce shoot apices to chronic gamma irradiation: (A) cone-shaped apex of nonirradiated white spruce during early July; (B) indented apex — a typical response after exposure to 15 and 30 Roentgens of Cesium ^{137}/20-hour date during late June and early July.

Environmental Relations and Adaptation

A study was conducted to determine the amount of intraspecific variation in DNA per cell among different seed sources of jack pine (*Pinus banksiana*) and white spruce (*Picea glauca*). The amount of DNA per cell was established chemically and cytophotometrically for 17 seed sources of *P. glauca* and cytophotometrically for 11 sources of *P. banksiana*. The DNA Feulgen absorption per cell varied from the lowest to the highest amount by factors of 1.6 and 1.5 for *P. glauca* and *P. banksiana*, respectively. Intraspecific variation of histone was similar to the observed DNA variation. There was also a significant positive correlation between the amount of DNA and the nuclear volume within species.

A regression analysis between DNA per cell and latitude showed that *Picea glauca* has eastern and western populations series.

Another objective of the study was to determine the relationship between DNA per cell and the growth rate in white spruce. Measurements of taxonomic characteristics have suggested that eastern sources are different from western sources. The study of the relationship between DNA and height growth gave similar results. Seedling height in the western provenances varied inversely with DNA content; that is, seedlings from seed sources with low DNA per cell displayed greater growth. The eastern sources did not display the inverse relationship between DNA amount and 2-year growth (Miksche 1968a).

Differentiation and Metabolic Activity in the Apical Meristem of Sugar Pine

Germinating seeds and seedlings were used to determine the relative metabolic activities of the different regions in the vegetative shoot of sugar pine (*Pinus lambertiana*) (Fosket and Miksche 1966a).[2] Seedlings were selected for morphological examination and histochemical study at 5, 8, 10, 13, and 16 days after planting. At 5 days the shoot apical meristem consisted of a relatively

[2] *Research carried out at Brookhaven National Laboratory under the direction of the U.S. Atomic Energy Commission. Paper published after Miksche was employed by the North Central Forest Experiment Station.*

homogeneous population of cells. After 8 days, four distinct cytohistological zones could be recognized: (1) the apical initial zone, (2) the central mother cell zone, (3) the peripheral zone, and (4) the rib meristem. Needle primordia were also evident at this time.

The pattern of histochemical staining for acid phosphatase (AP) activity was closely correlated with the development of the cytohistological zones in the apex. By the fifth day after planting, AP activity was relatively more intense in the potential apical initial and central mother cell zones than in the other two potential zones. After 8 days, when cytohistological zonation was evident, the pattern of AP activity was reversed; the most intense activity was noted in the peripheral zone; but almost no activity was observed in the apical initial zone and the central mother cell zone. The apical meristem of the 16-day-old seedlings exhibited high AP activity in the peripheral zone only during the early stages of needle primordia initiation.

The distribution of cytoplasmic and nuclear protein-bound sulfhydryl (SH) groups and succinic dehydrogenase (SD) activity were also closely correlated with cytohistological zonation. At 5 days protein-bound SH was distributed rather uniformly and SD activity was observed throughout the apex. By the eighth day, the four zones contained differential quantities of protein-bound SH, and the apical initial and central mother cell zones exhibited differentially greater levels of SD activity.

TREE IMPROVEMENT STUDIES

Purpose of Tree Improvement Research

The application of forest genetics in practical forestry is accomplished by planting genetically improved nursery stock in the forest. Trees in future forests will be faster growing, of better quality for specific end products, and will utilize the sites on which they are planted much more effectively than do most trees in present stands.

The results of many studies reported here, such as seed source studies, can be applied immediately by the managing forester, nurseryman or tree-improvement forester. The studies of heritability, compatibility, and vegetative propagation, however, need to be interpreted and enlarged in order to become usable. The Institute's tree improvement program is oriented toward this objective.

Seed Collection Zones

The use of the proper seed source was interpreted by P. O. Rudolf in 1959. He proposed seed collection zones based on: (1) a summation of normal average daily temperature per year above 50° F. ("growth degrees"), and (2) mean January temperatures (Rudolf 1959a). Twenty-year growth of 119 red pine seed sources and individual tree progenies substantiated his proposed seed collection zones.

Individual Tree Selection

In any forest stand individual trees vary considerably as to growth rate, crown size, branch angle, and resistance to insects and diseases. Until the progenies of a tree are evaluated for these traits, it cannot be ascertained whether the traits can be transmitted. However, as shown by the white spruce and jack pine studies described previously, many traits are under strong genetic control and the nurseryman should collect seed from superior individuals.

In addition to securing seed from selected trees, scions can be collected from them and grafted to rootstock of the same species, and the graftings set out in seed orchards. The trees in the seed orchard that are contributing favorable characteristics to the next generation can be determined by making crosses, and the poorest trees can be rogued out.

Several selection guides have been produced at the Institute describing traits that are probably under strong genetic control in economically important species. A guide for 11 Lake States species was developed first (Rudolf 1956b), followed by a guide for 17 shelterbelt species (Dawson and Read 1964), and later by a guide for the selection of superior phenotypes of yellow birch (Clausen and Godman 1967).

Selection can also take place in nursery beds. Clausen (1963c) found that the size of plants of *Betula pubescens* and *B. pendula*, after 9 years in the field, was directly related to the initial size of nursery stock. Height and diameter of the trees still reflected the original classification into large, medium, and small seedlings. Similarly, King *et al.* (1965) found that white spruce seedlings selected for superior nursery performance maintained their height growth advantage over average 2-2 nursery stock after seven growing seasons in the field.

Seed Production Areas

Seed production areas consist of the *best trees* in the *best stands* of a species within the *best geographic* area. In other words, superior stands of a species are upgraded by removing undesirable trees and are treated for early and abundant seed production. Rudolf (1959d, 1961, 1962b) studied the possibilities of seed production areas for red pine, jack pine, eastern white pine, white spruce, and black spruce, and set standards for their development, estimated yield, spacing between trees, optimum age for seed production, maintenance measures, and cost of seed. Seed production areas are intended to serve until seed orchards become established.

Stimulation of Jack Pine Seed Production

It was found that flowering and seed production of jack pine seedlings under greenhouse and nursery conditions could be stimulated to occur sooner and more often than under natural conditions. Female strobili developed on as many as two-thirds of 23-month-old seedlings and one-fourth of 17-month-old seedlings when good growing conditions were provided. These frequences contrast sharply with the 0.3 percent flowering on 3-year-old seedlings grown under normal commercial nursery conditions (Rudolph 1966b). The ability to reduce the time between sexual generations in jack pine to less than 3 years (including the period required for seed maturation) gives the forest geneticist a chance to make research progress akin to that of the geneticist working on annual plant species.

Economics of Tree Improvement

Tree improvement as a forest practice must be considered, along with other forest practices such as timber stand improvement and fertilization, as a means of raising forest productivity. Lundgren and King (1966) described a method for evaluating the potential benefits of tree improvement programs. They showed that under "long-term" and "short-term" programs, both red pine and jack pine management could be improved economically.

Forest Seed Quality Control

One of the urgent needs of nurserymen the world over is the assurance of the quality of seed they are purchasing. The place of origin (including latitude, longtitude, and altitude), the year of seed collection, and the germination and purity of the seed are of vital importance. The need for standardizing State and Federal laws and international policies in relation to seed quality has been of primary concern to researchers at the Institute. In all, there have been 17 publications dealing exclusively with the work being done on upgrading seed quality, standardizing seed testing, and providing adequate labeling (Nienstaedt 1968; Rudolf 1962a,b, 1964a,c,d, 1965b,c,d, 1966e,f, 1967a; SAF Seed Certification Subcommittee 1961, 1963a,b; SAF Tree Seed Committee 1964a,b). Much of the work described has been done by the Society of American Foresters, the Organization for Economic Cooperation and Development of the United Nations, and the International Crop Development Association.

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