Biology and Management
of
White Spruce Seed Crops
for
Reforestation in Subarctic Taiga Forests

by

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J. Alden
Institute of Northern Forestry
Pacific Northwest Forest and Range Experiment Station
U.S. Department of Agriculture, Forest Service
Fairbanks, Alaska

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PREFACE

Seed production is the most dramatic event in the life cycle of trees and is the first step in forest regeneration. Embryos of white spruce are fragile during germination, and they depend on vigorous seeds for survival and growth. Mortality of white spruce seeds and seedlings is high in northern forests because climate and microhabitat are often unfavorable for seed germination and seedling establishment. Large quantities of high-quality seed are required for natural and artificial regeneration of white spruce forests at high latitudes.

The first chapter of this bulletin describes the reproductive process of white spruce and factors that affect cone and seed production and seed quality. Knowledge of the reproduction cycle and factors that affect seed production and quality of white spruce is essential for forecasting and managing seed crops.

Evidence that white spruce is a genetically variable species in northern forests is summarized in the second chapter. This chapter includes recommendations for maintaining the gene pool of natural populations and for seed transfer in afforesting sites that do not have endemic populations. A procedure for delineating planting zones for adapted seed sources is described as an alternative for provisional seed zones that only reduce the risk of maladaptation from long-range seed transfer.

The final chapter outlines steps in harvesting white spruce seed crops and can be used as a working manual. Practical procedures are described for evaluating quality and quantity of white spruce seed crops, certifying the geographic origin of seed parents, collecting cones, and processing seeds to mainatin viability for many years.

The genetic structure of white spruce and the environment-embryology relationships that effect seed production and maturation have not been studied in detail. The need for research in the areas of genetics, biochemistry, physiology, and ecology is discussed in each chapter. The results of such research will help to improve seed yields and make the management of white spruce crops more profitable in Alaska and Yukon.

CHAPTER 1: Seed Production

INTRODUCTION

Regeneration of white spruce (*Picea glauca* [Moench] Voss) forest in subarctic climates requires abundant seed production. White spruce, like many climax tree species, has a long life cycle. It reaches sexual maturity only after a long period of juvenile growth and produces infrequent seed crops and relatively low numbers of seed. Several generations of shrub-aspen-birch succession in Alaska, and shrub-aspen-birch and lodgepole pine succession in Yukon, often precede natural regeneration of white spruce if seed is not available immediately after timber harvest or wildfire.

Although dominant seed trees of eastern white spruce (variety *glauca*) are capable of bearing more than 8,000 cones per crop (Tripp and Hedlin 1956), dominant trees of the western variety, *albertiana*, have narrower crowns and usually produce fewer than 3,000 cones even during excellent seed years (Zasada and Viereck 1970, Zasada et al. 1978). Although long-term records of seed production are not available for subarctic forests, excellent crops have been observed over wide areas every 10 to 12 years, with most stands yielding few to many cones every 2 to 3 years (Waldron 1965a, Zasada and Viereck 1970). Commercial cone collections are economically feasible about every 6 years in British Columbia (Dobbs et al. 1976). Average recovery of filled seed per cone ranges from about 20 (Tripp and Hedlin 1956, Zasada and Viereck 1970) to 34 (Nienstaedt and Teich 1972), although most white spruce cones in interior Alaska are capable of bearing 80 to 120 viable seeds each. In seed crop surveys near Fairbanks, Alaska, filled seeds per cone averaged 60 in excellent years, 11 in fair years, and 6 in poor years (Zasada and Gregory 1969). Good seed years vary widely from area to area.

The quantity and quality of white spruce seed crops depend on inherent physiological responses of seed trees to environmental events during their reproductive cycle. Some environmental events responsi-
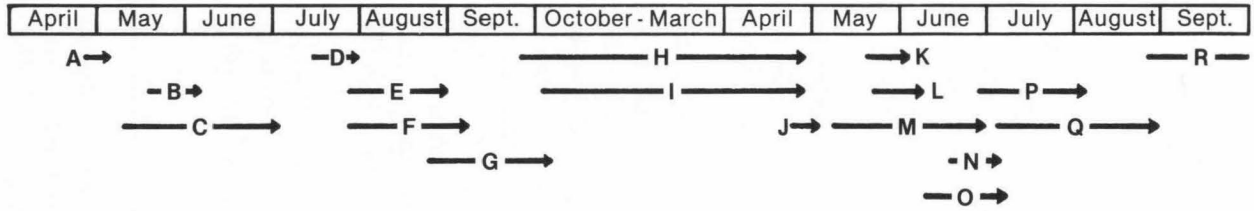
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ble for differentiation of cones occur long before flowering. Others are associated with climate during the year of seed production and affect the quantity and quality of seed after cones are produced. Management of white spruce for cone and seed production requires knowledge of reproductive processes, their response to environmental stimuli and biological agents, and physical variables that affect yield of viable seed. In this paper, I review information available for management of white spruce for seed production, although few environment-seed production responses have been studied in detail.

REPRODUCTIVE CYCLE

The reproductive process in white spruce begins with initiation of axillary buds at the end of vegetative dormancy in late April or early May and terminates with fully mature seed 15 to 17 months later (fig. 1). Abundant seed production entails many morphological, cytological, and physiological changes in the buds and cones during this period. Pollen and seed cones differentiate from axillary buds during the first summer. All microsporophylls (pollen sacs) with pollen mother cells and ovules with megaspore mother cells are initiated in the cones before dormancy. Seed-production processes during the next spring and summer include meiosis, formation of male and female gametes, flowering, pollination, fertilization, embryo development, and seed maturation. Development of seeds after fertilization in conifers is usually termed embryogenesis. Embryology refers to all reproductive processes before as well as after fertilization (Doyle 1957). Embryology of white spruce takes 1 to 2 months less in habitats with short growing seasons than in habitats with long growing seasons (Zasada et al. 1978, Owens and Molder 1979).

Differentiation of Pollen and Seed Cones

Pollen and seed cones differentiate from both terminal and axillary buds during late July after lateral shoots reach 90 per cent of their full length and all scales are initiated on the new buds (Fraser 1962, Eis 1967, Owens and Molder 1977). Pollen cones usually diffferentiate from terminal or small axillary buds on less vigorous twigs in the midcrown

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April	May	June	July	August	Sept.	October - March	April	May	June	July	August	Sept.

A→ −D→ H→ →K −R−
−B→ −E→ I→ →L −P→
−C→ −F→ J→ −M→ −Q→
−G→ −N→
−O→

A. End of vegetative bud dormancy and initiation of axillary buds.

B. Vegetative bud burst.

C. Shoot elongation.

D. Differentation of pollen and seed cones.

E. Initiation of microsporophylls.

F. Initiation of bracts.

G. Initiation of ovuliferous scales.

H. Pollen cone dormancy.

I. Seed cone dormancy.

J. Meiosis.

K. Flowering.

L. Pollination.

M. Micro- and megasporogenesis (development of male and female gametes).

N. Fertilization.

O. Seed cones become pendent and enlarge.

P. Embryo development.

Q. Seeds mature and separate from cone scales.

R. Seed dispersal.

Figure 1. Reproductive phenology of white spruce in Alaska and Yukon.

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and the lower region of the crown. Seed cones, in contrast, usually differentiate from larger axillary buds on vigorous branches or from terminal buds on less vigorous branches in the upper region of the crown. Buds that fail to differentiate into seed or pollen cones become latent, vegetative shoots, or they abort.

Mitotic activity and size of the reproductive apices in the buds increase as microsporophylls of pollen cones and bracts of seed cones are initiated in August. Initiation begins at the base of the apices and continues toward the apex. Microsporophyll initiation is complete at the end of August in British Columbia, and pollen buds become dormant in mid-September (Owens and Molder 1977). Seed cones remain active about 2 more weeks. Ovuliferous scales of seed cones are initiated in the axil of each bract in late August and September. Each scale contains two ovules in each of which a single megaspore mother cell is differentiated before winter dormancy in early October. Thus, the seed-bearing capacity of the cone is determined during the year of cone differentiation.

All microsporophylls, bracts, and ovuliferous scales are initiated before dormancy in late September or early October (Rauter and Farrar 1969, Owens and Molder 1977). This is the earliest stage at which reproductive buds or cones can be readily identified in the field and potential cone crops estimated for the next year. Fully developed reproductive buds are larger and more ovate than vegetative buds; differences between seed and pollen cone buds are less apparent. Although seed buds are found in the upper crown and are wider at the base and more pointed than pollen buds, positive identification often requires removal of the bud scales and examination of the appendages with a hand lens (Eis 1967).

Several methods of rating potential white spruce cone crops from bud or cone counts are available. The most common method used in the Pacific Northwest and Canada is a simple rating of these five criteria (adapted from Dobbs et al. 1976):

Cone crop rating	Criteria
None	No cones on trees
Very light	Few cones (< 300) on less than 25 per cent of trees
Light	Few cones on more than 25 per cent of trees
Medium	Many cones (> 300) on 25 to 50 per cent of trees
Heavy	Many cones on more than 50 per cent of trees

This method is recommended for general surveys of cone crops of white spruce in Alaska as well as in Canada. An examiner walks through the stand and estimates the number of female cone buds or seed-bearing cones on well-distributed dominant and codominant seed trees. The estimate is then standardized with cone crops from previous seasons or from nearby geographic areas.

A 10-criteria rating system (Werner 1964) has been used for predicting cone crops in Alaska, but differences between criteria are difficult to estimate and ratings are more subjective than for the reduced scale above.

A more precise method of evaluating potential white spruce cone crops has been developed by Eis and Inkster (1972) and applied by Eis (1973a). The method requires the counting of cone buds on one branch from the upper crown (third whorl) of 4 to 16 dominant seed trees until cumulative counts fall into one of five ratings in a sequential table or graph prepared for the area of interest.

Seed Formation and Development

Cytological and phenological events leading to development of mature white spruce seed have been studied in detail by Mergen et al. (1965), Rauter and Farrar (1969), and Owens and Molder (1979). Seed development is initiated with meiosis of pollen and megaspore mother cells at the end of reproductive bud dormancy in late April or early May (fig. 1). Meiosis produces four haploid microspores for each pollen mother cell and one functional megaspore in each ovule. Each microspore undergoes internal mitosis until a mature pollen grain is formed at dehiscence (rupture of the pollen sacks to release the pollen). The mature pollen grain, about 75 micrometers in diameter, produces a pollen tube and functional gamete just before fertilization (fig. 2).

The haploid megaspore contained within the nucleus of each ovule divides freely to form the female gametophyte near the time of pollination. Cell walls then develop within the female gametophyte, and one to four initial archegonial cells differentiate near the micropylar (open) end of the ovule. Other gametophyte cells differentiate into jacket cells that enclose the archegonial initials. The archegonial initials elongate for 1 to 2 weeks after pollination, then divide to produce an egg (gamete)
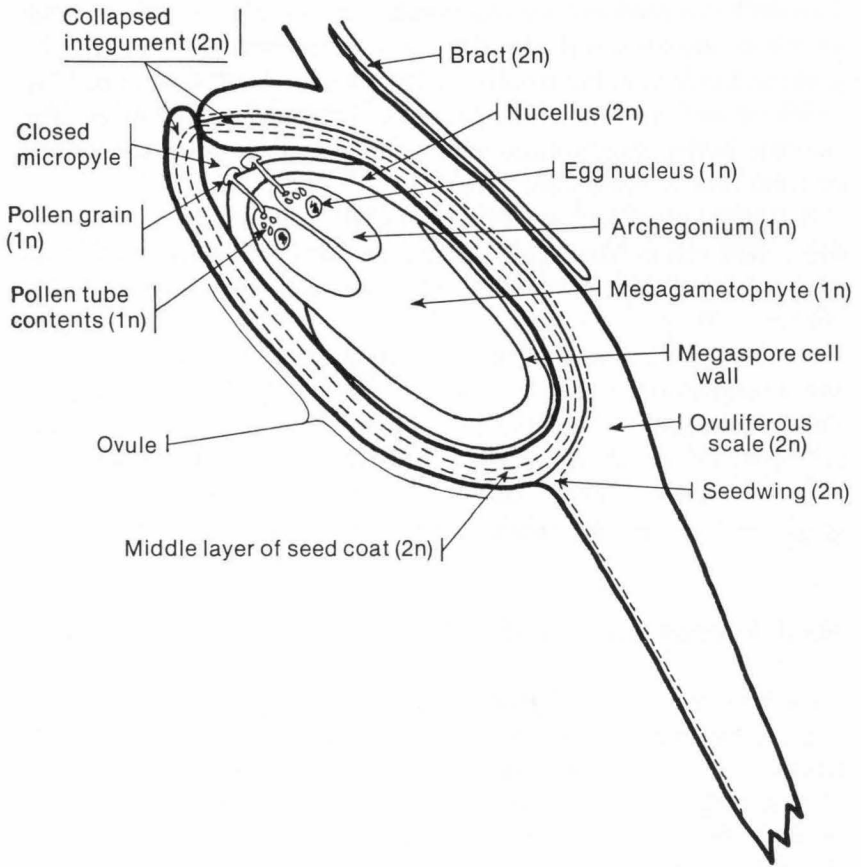
Figure 2. Diagrammatic longitudinal section of an ovuliferous scale, ovule, and female gametophyte at fertilization. One of the two fertilized eggs will abort as an early embryo. 1n = haploid cells; 2n = diploid cells.

and other cells that aid penetration of the pollen tube for fertilization (fig. 2). Rarely does more than one archegonium per ovule survive to produce an embryo after fertilization. Embryos and archegonia frequently abort, producing an empty seed.

The reproductive process of white spruce from onset of meiosis to fertilization of the egg nucleus requires from 10 weeks at low elevations to as few as 6 weeks at high elevations (Owens and Molder 1979). During this period, dehiscence of microsporophylls must be closely syn-

chronized with receptivity of the ovules for pollination. Pollen cones usually elongate and emerge from their bud scales in mid-May, 1 to 2 weeks before pollination at low elevations in Alaska (Zasada et al. 1978). Seed cones enlarge more slowly, but a few days before pollination the central region of the cone axis elongates rapidly. Seed cones emerge from their bud scales in an upright position with scales fully extended for pollination. Cone scales are longer than bracts at this time. Tips of the integument which enclose the ovule are fully extended at the micropylar opening to receive the pollen that falls between the scales and bracts (Owens and Molder 1979).

Pollination is rapid in white spruce. Natural pollination takes place during a 5-day period in late May or early June at 100 to 200 meters and 3 to 5 weeks later at elevations near 600 meters in Alaska (Zasada et al. 1978). Pollen dispersal and pollination are maximum during warm, sunny afternoons when humidity is low. Seed cones are receptive for only 3 to 5 days (Nienstaedt 1958). Only the first few pollen grains that reach the micropylar canal of white spruce are drawn into the ovule by a receding drop of moisture. Cone scales close rapidly after pollination, and the cones become pendent in about 2 weeks. The cone axis fails to elongate and the ovules are poorly developed in the basal and distal regions of the cone at pollination. For these reasons, only scales in the central half of the cone produce viable seed (Owens and Molder 1979).

After pollination, development of male and female gametes is closely synchronized for fertilization. Pollen grains deposited on the nucellus germinate about 2 weeks after pollination. The pollen tube penetrates the megaspore cell wall surrounding the female gametophyte and enters the archegonium to fertilize the egg nucleus about 1 week after germination. The pollen tube ruptures after it enters the egg cell, and the male gamete fuses with the egg nucleus to form a diploid zygote (Rauter and Farrar 1969). Fertilization occurs in late June at low elevations in Alaska when seed cones are at their maximum rate of growth (Zasada et al. 1978). The zygote undergoes several mitotic divisions to produce a proembryo which advances rapidly into the gametophyte. A small corrosion cavity develops in advance of the proembryo, and early embryo development is complete with differentiation of a root apex and hypocotyl in mid-July.

A seed coat and wing begin to develop from the integument and

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ovuliferous scale during pollination, and a separation layer forms under the ovule shortly after fertilization. The seed and its wing separate from the ovuliferous scale before embryo development is complete (Owens and Molder 1979).

Cone moisture content on a dry-weight basis decreases from 300-400 per cent in June to 25-80 per cent at seed fall in late August and early September (Zasada et al. 1978). Seventy-five to 90 per cent of all viable seed is dispersed during the following 3 months (Zasada and Gregory 1969, Zasada and Viereck 1970). Seed weight for the 1970 seed crop in Alaska averaged 0.16 gram and ranged from 0.11 to 0.25 gram per 100 seed. Average seed weight was not correlated with elevation or seed quality as measured by per cent germination of filled seed (Zasada et al. 1978). Seed maturation dates frequently vary from 1 to 2 weeks at the same geographic location in different seed years. Early stages of seed development are often 5 weeks later at high elevtaions than at low elevations. Although rate of seed development is faster at high elevations than at low elevations (Owens and Molder 1979), it is often not fast enough to produce mature seed in cold habitats with fewer than 100 days of growing season (Zasada et al. 1978). A mature white spruce seed is diagrammed in Figure 3. Note that the cotyledons are fully dif-
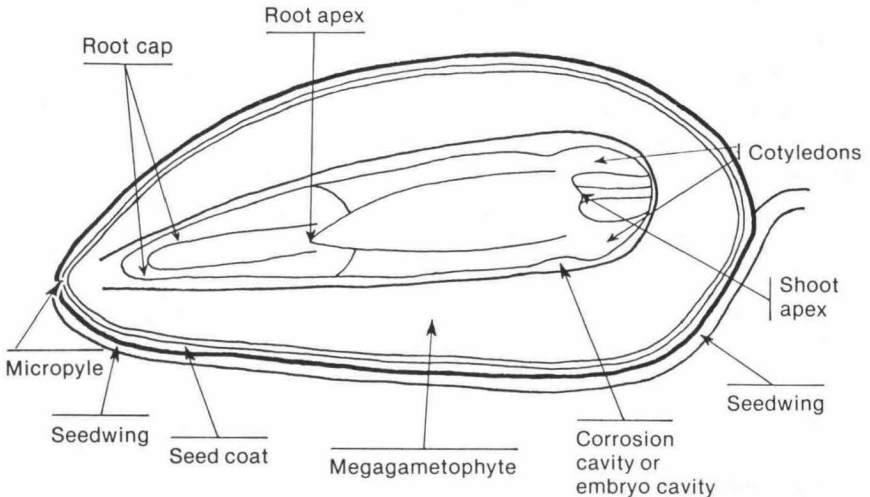

Figure 3. Diagrammatic longitudinal section of a mature seed at dispersal, showing seed coat, gametophyte, and fully developed embryo.

ferentiated, the embryo fills the embryo cavity, and the gametophyte fills the seed cavity.

Germination tests of periodic seed collections after embryos are fully developed in early August indicate that white spruce seeds continue to mature until cone moisture content declines rapidly just before seed fall. Cram and Worden (1957) found that germination increased 14 per cent, seed yield 40 per cent, and seedling production 50 per cent during 3 weeks before seed dispersal in Ontario. Zasada (1973) demonstrated that heat resistance of white spruce seed increased steadily from early August to about 1 week before seed fall in early September. During this period, moisture content of the cones decreased slowly until the seeds reached maximum heat resistance. These results indicate that metabolic processes critical for high seed vigor continue after morphological develoment of cones and seed is complete.

The biochemistry of seed development is complicated by variation in ripeness of seeds within and among trees (Jensen et al. 1967), and it has not been studied for white spruce. Studies with seeds of *Picea abies* (Jensen et al. 1967), *Pseudotsuga menziesii* (Rediske 1961), and *Abies procera* (Rediske and Nicholson 1965) have demonstrated that lipids and proteins must accumulate before maturation is complete. Energy potentials for synthesis, transport, and storage of these products in coniferous seeds have not been studied.

Germination and biochemical tests for seed vigor are time consuming and must be conducted in the laboratory. For these reasons, changes in physical characteristics such as the following are recommended criteria for estimating maturity of white spruce seeds in the field: cone moisture content (50 per cent dry weight) and specific gravity (less than 0.75) (Cram and Worden 1957); seed coat and wing color (dark brown or black), seed brittleness (breaks on cutting), and cone firmness (resists bending) (Crossley 1953); degree of embryo and gametophyte development (fills or nearly fills embryo cavity and seed, respectively) and heat sums after pollination (at least 840 growing-degree days Celsius at low elevations in interior Alaska) (Zasada 1973).

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FACTORS AFFECTING CONE PRODUCTION

Periodicity of cone crops depends on many environmental factors and genetically controlled metabolic responses. For this reason, cone crops are difficult to predict, and investigations of environmental factors that affect cone production have been the subject of several reviews (Matthews 1963, Schmidtling 1974, Puritch 1977, Bergman 1981). Production of cones and seed are major drains on metabolic resources and several years of reduced cone production are necessary to restore depleted nutrient and energy sources after an abundant seed crop. In addition, 1 or more years are necessary to restore growth of foliage and production of potential cone buds that are lost when axillary and terminal buds differentiate into cones the year before seed production.

Early (precocious) and abundant cone production are under strong genetic control in white spruce (Teich and Pollard 1973) and reduce its growth rate (Teich 1975). Precocious trees, however, have an inherent ability to grow rapidly in the absence of cone production and can be selected for wood production in habitats favorable for vegetative growth. Environmental factors critical for cone production must be managed in these habitats when seed is required for reforestation.

Investigations of weather conditions preceding cone crops have shown that a cool moist summer, a cold clear winter, and a wet spring in advance of a hot dry summer at the time of bud differentiation are prerequisites for abundant cone production in several conifers (Lowry 1966, van Vredenburch and la Bastide 1969, Eis 1973b). A mild winter and warm spring and summer without moisture stress are prerequisites for seed maturation the following year. Fraser (1958) observed that a hot dry summer with many sunny days preceded a heavy white spruce seed year in Ontario. A cool cloudy summer without moisture stress during the year of seed production may have improved seed vigor, but failed to produce a new cone crop. Excellent white spruce seed crops in interior Alaska in 1958 and 1970 were also preceded by hot dry summers in 1957 and 1969 (Zasada 1971a). Although hot dry summers promote differentiation of cone buds in July, benefits from a cool moist growing season 1 year in advance of cone differentiation are unknown.

Stress treatments such as root pruning and stem girdling or strangulation at the onset of vegetation growth are effective in promoting differentiation of cones in many species. Pruning of roots in early spring

before rapid shoot growth in June induces differentiation of cones on 10-year-old white spruce (Holst 1961). The response to root pruning and girdling may be related to moisture stress or nutrient deficiency because carbohydrates do not always accumulate in treated trees (Schmidtling 1974). Stress treatments reduce growth and increase mortality of seed trees and are probably counterproductive after the initial cone induction response is accomplished. The effects of stress treatments on seed vigor have not been studied.

Weekly or biweekly applications of the plant hormone gibberellic acid (GA_4 and GA_7) during the period of rapid shoot elongation are effective in differentiating cones for several species of *Pinacea* (Pharis 1975). Gibberellins are more effective when applied in combination with auxin and nondestructive girdling treatments. Gibberellins promote differentiation of cones on seedlings as well as on sexually mature trees, and their use has accelerated tree-breeding programs. Gibberellin treatments, however, seldom produce commercial quantities of cones, and their use is not recommended until the differentiation response of white spruce is investigated and methods of treatment are improved.

Silvicultural practices that increase tree vigor and crown size accelerate sexual maturity (Matthews 1963). Thinning modifies many environmental factors that enhance cone production and seed yields. Each factor undoubtedly has an independent effect on development of the cone crop, as well as a combined effect mediated through increased seed tree vigor and number of potential cone buds.

Mineral nutrition is an important factor in differentiation of cones, but results of fertilization trials to induce cone production vary greatly. Rainfall and other environmental factors affect the availability of nutrients and their uptake by treated trees. In addition, nutrient status of soils and seed trees is seldom investigated before fertilizer treatments are applied.

Best results are obtained from inorganic fertilizer when the deficient nutrients, especially nitrogen, are applied in combination with thinning or other cone differentiation treatments. Fertilizers should be applied at the onset of rapid shoot growth in the spring for maximum response. High concentrations of ammonium nitrate in combination with root pruning in May produced dramatic increases in the number of cones on 10-year-old white spruce (Holst 1961). Treatments were less effective in June. Sexually immature 4- to 6-year-old seedlings did not respond

to nitrogen applications in combination with drought stress and short-day treatments.

The cone differentiation response to nitrogen and moisture stress treatments is related to an accumulation of amino acids, especially arginine (Ebell and McMullan 1970, Schmidtling 1974). Nitrate is more effective than ammonium nitrogen in differentiating cones. The bud differentiation response of white spruce to different oxidation states of nitrogen has not been studied, but Durzan and Steward (1967) have shown that ammonium nitrogen, not nitrate nitrogen, increases the arginine content of white spruce seedlings in late summer.

FACTORS AFFECTING SEED QUALITY AND YIELD

Major factors that affect quality and yield of white spruce seed in subarctic climates are availability of pollen; degree of outcrossing; growing-season temperature; and attacks by pathogens, insects, and mammals on cone and seed crops.

Lack of Pollination

Viable seed yields can be highly variable because white spruce is a parthenocarpic species; that is, cones mature and produce empty seed even if their ovules are not fertilized. Thus, seed set depends on quantity and quality of pollen deposited near the micropylar canals of receptive ovules during pollination. White spruce cones flower and shed pollen during warm dry weather (Zasada et al. 1978), and pollination is rapid to avoid adverse changes in temperature and moisture. Seed cones of conifers, however, continue to develop after flowering despite abrupt changes in weather that may interfere with pollination (Bergman 1981). Rain interrupts pollination and causes premature pollen germination. Nienstaedt (1958) recovered only six filled seeds per wind-pollinated cone compared with 28 filled seed per bagged cone during a year when rain interrupted pollination of white spruce. Constant winds from one direction reduce pollination and seed set on the leeward side trees. Strong winds may accelerate pollen release before seed cones are receptive, thus reducing pollination (Matthews 1963). Finally, pollination success and seed yields depend on the number of pollen cones and the volume of pollen produced.

Self-Pollination and Inbreeding

Self-pollination and inbreeding in white spruce are natural reproductive processes that reduce seed quality and yield. Self-pollinated and inbred ovules have high abortion rates and produce inferior seeds and seedlings. High abortion of self-fertilized or homozygous embryos maintains genetic variation necessary for survival of white spruce in changing environments, but reduces seed yields. Studies of the effects of self-pollination and inbreeding on seed production and quality show that:

1. Degree of self-incompatability varies among white spruce seed trees (Mergen et al. 1965, King et al. 1970, Coles and Fowler 1976).

2. Natural barriers against self-pollination are ineffective in white spruce. White spruce trees are monoecious (individuals produce both male and female cones), seed cones reach maximum receptivity at the same time as pollen dehiscence, and seed and pollen cones overlap in the central to upper region of the crown (Nienstaedt and Teich 1972).

3. Pollen from unrelated parents has no competitive advantage over self-pollen in fertilization of white spruce ovules. Numbers of filled seed decrease and empty seed increase in direct proportion to the percentage of self-pollen deposited on receptive seed cones (King et al. 1970).

4. Self-pollination has no effect on fertilization. Reduced seed yield is caused by embryo abortion and not by failure of self-fertilization (Klaehn and Wheeler 1961, Mergen et al. 1965).

5. Self-pollination has no effect on germination rate of white spruce seed (Mergen et al. 1965, Coles and Fowler 1976), but it reduces tree survival (Ying 1978) and growth (Mergen et al. 1965, King et al. 1970, Coles and Fowler 1976) and may reduce seed dormancy and quality (Wang 1976).

These conclusions suggest that factors that affect self-pollination and inbreeding should be considered in selecting seed trees for natural and artificial reforestation. Inbreeding depends on the relationship among neighboring trees, pollen production, and distance of pollen dispersal. Family relationships exist between close neighbors in natural white spruce stands, and inbreeding effects decrease with distance between pollen and seed parents (Coles and Fowler 1976). Pollen dispersal from individual trees, however, decreases exponentially with distance (Muller 1974). For this reason, the quantity of unrelated background pollen may

be inadequate to dilute local pollen during poor seed years even in fully stocked stands, causing a higher incidence of self-pollination and inbreeding, which in turn reduces seed yield and quality (Wang 1976). Thus, many well-distributed trees capable of producing abundant pollen as well as seed should be reserved for natural regeneration after timber harvest.

Low Temperature

No information is available about the effects of low temperature on embryogenesis of white spruce, although frosts are known to cause embryo abortion and polyembryony and to reduce germination in seeds of Swedish tree species at northern latitudes (Simak 1976).

Frosts during sensitive stages of meiosis and sporogenesis cause structural changes in chromosomes and may cause sterility of pollen and ovules without evidence of freezing injury. Effects of temperature on chromosomes of haploid cells of white spruce have not been investigated, but $-2°$ to $-5°C$ induced irregularities in chromosomes of haploid cells of *Picea abies* and other conifers from high-latitude forests (Anderson et al. 1969, Jonsson 1974). Zasada (1971b) observed a 50 per cent reduction in sound seeds from a white spruce stand that was exposed to about $-1°C$ for 6 and 2 hours on successive days when cones were receptive to pollination.

Seed cones of white spruce are highly susceptible to freezing injury during pollination, but incidences of loss either have not been widely observed or have not been reported in subarctic forests. Zasada (1971b), however, reported that 96 per cent of receptive seed cones in a white spruce stand were killed or damaged during an 8-hour period when minimum temperature reached $-4°C$. Frost-damaged cones produced some sound seeds, of which 92 per cent germinated, but seed yields were much less than those from undamaged cone crops of comparable size.

Growth processes in many plants are roughly proportional to ambient temperatures between $0°$ and $30°C$ (Leopold 1964). Thus, stage of cone and seed development can be estimated for a given geographic area or ecotype from summation of the average daily temperatures above $5°C$ (growing-degree days). Pollen development and flowering of white spruce require from 120 to 150 growing-degree days at low elevations

in interior Alaska (data on file at the Institute of Northern Forestry, Fairbanks, Alaska). Seeds require an additional 625 growing-degree days after pollination to complete embryo development and about 200 more growing-degree days to reach physiological maturity at seed fall (Zasada 1973). Because low temperatures limit development of cones and seeds at high latitudes when summer temperatures are below normal, seeds from cones on south surfaces of tree crowns usually mature earlier and should be harvested in preference to seeds from cones on north exposures (Bergman 1981).

Insects, Diseases, and Mammals

Insects, pathogens, and mammals cause severe loss of white spruce cone and seed crops. Seed losses from insects alone on the Alaska Highway varied from 3-6 per cent during abundant seed years to 50 per cent or more during poor seed years (Werner 1964). Losses from disease and mammals are less serious, but inland cone rust may nearly destroy an entire seed crop in areas where conditions are favorable for widespread infection (Ziller 1974).

Insects: Excellent reviews of the life histories and feeding habits of white spruce cone and seed insects can be found in Keen (1958), Hedlin (1973, 1974), Furniss and Carolin (1977), and Hedlin et al. (1980). Most white spruce insects are found throughout the range of Engelmann and Sitka spruces as well as in subarctic spruce forests of Alaska and Yukon. White spruce cone and seed insects can be identified from feeding habits and from cone structures damaged (Hedlin 1974, Hedlin et al. 1980).

I. Insects that destroy seeds.

1. *Megastigmus piceae* Rohwer (*M. atedius* Walker), or the spruce seed chalcid, is a wasp (Hymenoptera) that inserts its ovipositor through the cone scales and deposits a single egg into each of several ovules during early summer. Each larva lives entirely in the seed and is white and U-shaped when fully developed. It overwinters in the seed and emerges as an adult after pupation in early spring. The exit hole in the seed coat is the only external evidence of injury.

2. *Mayetiola carpophaga* (Tripp), the spruce seed midge, is a tiny fly (Diptera) that lays its eggs near or in the micropylar opening during pollination. The small, yellow larva enters the ovule where it forms

a cocoon in midsummer. The pupa overwinters in the seed and emerges as an adult in late May just before pollination.

Seed infested with *Megastigmus* and *Mayetiola* spp. can only be identified by x-radiography. These insects cause relatively minor seed loss because populations are small and each larva is confined to a single seed (Tripp and Hedlin 1956, Hedlin 1974, Hedlin et al. 1980); nevertheless, occasional infestations can be severe. Hedlin (1973) found up to thirty-seven *Mayetiola* larvae per cone and a 34 per cent loss of seed in a sample from British Columbia. Seed losses are eliminated in artificial pollination programs because cones are enclosed in bags when adults emerge to lay their eggs. Application of systemic organophosphate insecticides during or just after pollination may reduce loss of open-pollinated seed; however, a *Mayetiola* egg deposited in or near the micropylar opening could conceivably interfere with pollen absorption and prevent fertilization of the ovule.

II. Insects that destroy cones and seed without external evidence of injury.

This group of insects is among the most destructive because populations reach large numbers and individual larvae feed on both cone and seeds.

1. *Hylemya (Lasiomma) anthracina* (Czerny), the spruce cone maggot, is a small fly that usually lays only one egg between the scales of each cone before it closes after pollination (Hedlin 1973, 1974; Hedlin et al. 1980). The larva feeds internally on the nearest scale, then tunnels around the cone axis in a spiral direction consuming 30 to 90 per cent of the seed during the next 4 to 6 weeks (Tripp and Hedlin 1956). The larva is white, does not have a prominent head, and is about 6 mm long when fully developed. The larvae tunnel to the surface of the cones from mid-July to late July and drop to the ground when moisture conditions are favorable. The insect overwinters in a puparium under the litter surface. The only external evidence of damage is a small exit hole in the cone long after much of the seed-bearing region has been destroyed.

2. *Laspeyresia youngana* (Kearfott), the spruce seed moth or seedworm of the order Lepidoptera, lays its eggs between cone scales that are open for pollination. The larva feeds almost exclusively on the seeds as it moves from scale to scale throughout the summer. Small larvae

bore a hole through the seed coat, and the seed contents are replaced with frass. Seeds are destroyed in pairs and often adhere to their scales after cones open in late summer. Large larvae destroy the entire seed. Each larva consumes from ten to twenty seeds, and as many as ten larvae have been found in a single cone (Hedlin 1973). The larvae are white with dark heads and up to 1 cm long when fully developed (Hedlin 1974). The larvae overwinter in the cone axis and pupate in May before the adults emerge to deposit their eggs. The pupae are tawny and 5 to 6 mm long.

3. *Dasineura rachiphaga* Tripp, the spruce cone axis midge, and *D. canadensis* Felt, the spruce cone gall midge, are common cone insects in Alaska (Werner 1964) and Yukon (Hedlin et al. 1980) but cause no direct loss of seed. The larvae are small Diptera that feed in the cone axis or scales and form cocoons in which to overwinter. The larvae pupate the following spring, and female adults lay their eggs during pollination. *Dasineura rachiphaga* lays an egg near the ovule, and the small yellowish larva tunnels into the cone axis to form a white silk cocoon. Larvae of *D. canadensis* feed in galls that are usually not near the seed and cause little damage although many scales of each cone may be infested.

Another unidentified cone scale larva that feeds on resin between cone scales has been observed in Alaska (Werner 1964). This insect may be *Asynapta hopkinsi* Felt, the cone resin midge, that is found in southeast Yukon (Hedlin et al. 1980).

Destruction of seed from insects that feed inside cones is usually complete before the damage is detected. Control measures must be initiated before eggs hatch and larvae become active feeders. Contact insecticides are ineffective because insects are protected inside the cone. Systemic organophosphate insecticides may be effective if applied during or shortly after pollination. These insecticides are translocated from the stem or foliage of treated trees to tissues of cones and seeds which become temporarily toxic to the insects. Seeds produced in tree-breeding programs can be protected by enclosing the cones in fine mesh "insect bags" after pollination. Control of insects is essential during light seed years because up to 90 per cent of the cones can be infested with one or more of the above insects (Werner 1964).

III. Insects that destroy cones and seeds with external evidence of injury.

White spruce cone and seed insects of this group are not well known in subarctic forests and apparently do not cause serious loss of seed. Several species of this group are found in Alaska and Yukon:

1. *Dioryctria* spp. are moths with large brownish larvae that feed voraciously on cones and seeds, leaving large amounts of coarse frass and webbing on the surface of the cones. *Dioryctria abietivorella* (Grote), the fir coneworm, and *D. reniculelloides* Mutuura and Munroe, the spruce coneworm, are serious pests of white spruce, but species found in Alaska have not been positively identified (Werner, pers. comm., on file at Institute of Northern Forestry). The spruce coneworm overwinters as a larva and feeds on needles and buds in the spring before it enters a cone. Pupation occurs in the cone or foliage in midsummer, and adults emerge to lay eggs in bark crevices of infested trees. Life history of *D. abietivorella* is not as well known, but larvae pupate on the ground during the summer and either overwinter in cocoons or emerge as adults which lay eggs to overwinter (Hedlin et al. 1980). The insect is particularly troublesome in controlled breeding programs because eggs, pupae, or larvae are frequently enclosed in pollination and insect bags with developing cones. Systemic insecticides provide only partial control because the insect's life cycle is highly variable.

2. Larvae of the spruce budworm, *Choristoneura fumiferana* (Clemens), a moth, feed on developing male and female cones as well as on foliage and buds of white spruce when insect populations are high (Hedlin et al. 1980). Species of spruce budworm found in Alaska and their impact on seed production are unknown. Spruce budworm has not been a serious cone and seed pest to date.

3. *Henricus fuscodorsana* (Kearfott), a cone cochylid of the order Lepidoptera, mines the cones of white spruce (Hedlin et al. 1980), causing up to 10 per cent seed loss (Keen 1958). This insect has not been reported in Alaska or Yukon.

Diseases: Inland spruce cone rust, *Chrysomxa pirolata* Wint. occurs throughout the white spruce forests of Alaska and Yukon and causes 75 to 90 per cent loss of local seed crops when cone infections become epidemic (Ziller 1974). The rust infects and kills both cones and seeds of white spruce (McBeath 1979, 1981); however, infected cones are usually killed before seeds mature. The first sign of the disease is wet

cones from secretions of pycnia (spermagonia) in early July. This is the sexual stage of the rust (Day 1972) which results in production of bright orange-yellow aeciospores on the outer surface of cone scales during late July and August. Aeciospores are binucleate diploid cells which infect leaves of the alternate hosts, *Pyrola* (wintergreen) species, a family of low evergreen herbs that survives in Alaska and Yukon. *Pyrola* species are perennial hosts in which the two haploid nuclei combine in cells of the pathogen and meiosis occurs to produce haploid basidiospores. Carried by the wind, basidiospores infect spruce cones in June and complete the life cycle of the rust.

Pyrola species also produce urediospores that infect new plants of *Pyrola* annually. Thus, the rust requires only *Pyrola* for survival, and basidiospores are always available to infect new white spruce cones. Geographic distribution and optimum environmental conditions for spread of the disease in subarctic forests of Alaska and Yukon are not fully known (McBeath 1981).

Mammals: The red squirrel (*Tamiasciurus hudsonicus*) is the only major consumer of white spruce cone crops before seed dissemination in subarctic forests. Squirrels usually initiate cutting of cones and branches containing clusters of cones in August (Wagg 1964). Cutting activity increases until seed fall, and cones are cached under deep humus, in decayed logs, or in the midden of former collections. Many cones are left scattered on the ground when crops are abundant.

White spruce seed is the primary food of the red squirrel in winter, and an average of forty to fifty cones per day is consumed by each squirrel (Brink and Dean 1966). Major caches each contain 6,000 to 8,000 cones which produce a higher percentage of viable seed than partially opened cones collected from trees late in the harvesting season (Wagg 1964).

White spruce seed from cones cached in the ground or in middens of previous squirrel collections in British Columbia may contain a high incidence of the pathogen, *Caloscypha fulgens* (Pers.) Boudier (Sutherland 1979). This fungus reduces seed quality and caused preemergence mortality of seed and seedlings. The occurrence of *C. fulgens* and *Sirococcus strobilimus* Preuss, also a seed-borne pathogen of white spruce (Sutherland et al. 1981), is unknown in Alaska and Yukon. Nevertheless, cones for commercial seed extraction should be collected from standing trees or slash in preference to squirrel caches.

RESEARCH NEEDS

Basic research and technology in seed production are important aspects of white spruce reforestation. Production of white spruce seed can be greatly enhanced by managing seed trees for cone production and seed set. Research is needed to determine environmental requirements for differentiation of cones, initiation of microsporophylls and ovuliferous scales on the cones, and differentiation of microspore and megaspore mother cells in the microsporophylls and ovules. The roles of mineral nutrition (especially nitrogen), temperature, moisture, and light in these processes have not been studied in detail for white spruce. Elucidation of the metabolic responses to environmental stimuli that mediate change from the juvenile to the sexually mature phase of development, differentiate cones, and determine periodicity of cone crops will improve management practices for cone production in white spruce.

Only 25 per cent of the seed-bearing capacity of natural cone crops produces viable seed during average seed years. Research efforts should be directed at determining the effects of low temperature and other environmental factors on each stage of embryology. Development of management practices that increase pollen dispersal and outcrossing will reduce embryo abortion and should increase seed yields of poor to average cone crops. The biochemistry and metabolic energy required for seed maturation and development of deep dormancy should be investigated to increase seed vigor and seedling survival.

Loss of white spruce seed to cone and seed insects in subarctic forests is not well known. Geographical distribution and population dynamics of each insect known to attack seed crops should be studied in detail. The effects of environmental extremes and frequency of cone crops on insect populations must be known to develop effective control measures. Effectiveness of the systemic insecticides and other environmentally safe methods of control need evaluation in field trials.

The inland cone rust is a devastating disease of white spruce cones when infection is epidemic. Geographic distribution of the disease and alternate hosts in subarctic white spruce forests should be determined. Susceptibility of hosts and environmental conditions critical for survival of the pathogen must be determined for development of hazard zones and management practices that will reduce infection levels and virulence of the disease.

Vast areas in Alaska and Yukon are capable of supporting productive white spruce forests but have lost indigenous seed sources to past fires or black spruce (*Picea mariana* [Mill] B.S.P.) and "feathermoss" succession. Seed-production technology, including harvesting techniques that result in high seed recovery without destruction of valuable seed trees, must be developed if these areas are to be reforested for future renewable-resource needs.

SUMMARY

The reproductive process of white spruce is initiated the year preceding pollination and seed maturation. Pollen and seed cones differentiate from bud primordia after all scales are formed and growth of lateral shoots is 90 per cent complete. All microsporophylls, bracts, and ovuliferous scales are initiated in the cones before dormancy in September. This is the earliest month that reproductive buds can be identified readily and surveyed in the field. Seed formation begins with meiosis in late April or early May of the next year and precedes pollen dispersal by about 2 weeks. Fertilization occurs 2 to 3 weeks after pollination, and embryo development is usually complete in early August. Cones reach maximum size in early July, but seeds continue to mature until seed fall in late August and early September.

Cone production is enhanced by hot, dry weather at the time of bud differentiation. Thinning and fertilization, especially with nitrogen, are recommended for increasing cone production. Stress treatments, such as root pruning, nondestructive girdling, and drought, promote cone differentiation but may be counterproductive in the long run. Gibberellin treatments are not recommended until the bud differentiation response of white spruce is studied and methods of application are improved.

A mild winter and warm spring and summer without drought stress are prerequisites for seed maturation in subarctic forests. Late frosts, inadequate pollen production and dispersal, self-pollination, and inbreeding reduce the yield and quality of sound seed. Low temperatures delay development of cones and seeds fail to complete maturation processes in habitats with fewer than 800 growing-degree days Celsius.

Insects, a pathogen, and a mammal are major causes of failures of white spruce seed crops in Alaska and Yukon. Four cone and seed in-

sects cause serious loss of seed, especially when cone crops are average or less. Larvae of the most damaging insects feed inside the cones and must be controlled with systemic insecticides. The inland cone rust destroys 90 per cent of local seed crops when infections are epidemic. Geographical distribution, optimum environmental conditions for spread of the disease, and control measures are unknown. The red squirrel is a major consumer of white spruce seeds but caches large quantities of cones which are readily available for collection.

Development of management practices for cone and seed production and controls for insects and disease will increase white spruce seed yields many times.

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CHAPTER 2: White Spruce Seed Zones for High Latitude Forests

INTRODUCTION

The natural evolutionary processes of gene mutation, survival of the most adapted phenotypes, and migration of genes in pollen and seed have produced many genetically different populations of the same forest tree species. Many populations have acquired precise environmental fitness from generations of natural selection in habitats that change slowly with time. Other populations, with the same outward appearance, survive in relatively unstable habitats or have only migrated to new habitats in recent geological time. These populations are still adapting to environmental change and growth, and survival rates of poor as well as precisely adapted populations often decline sharply when local seed is transferred to nonnative habitats.

JUSTIFICATION FOR WHITE SPRUCE SEED MANAGEMENT

White spruce, *Picea glauca* (Moench) Voss, occupies previously glaciated and nonglaciated habitats in subarctic forests of Alaska and Yukon. Populations native to flood-plain and warm upland sites are considered well-adapted climax or near-climax forests. Pollen records indicate that ancestors of these populations survived the Wisconsin Age (80,000 to 14,000 years B.P.[1]) and probably the Illinoian Age (250,000 years B.P.) glaciations in Yukon River watersheds (Ager 1975). Spruce forests expanded rapidly after the Wisconsin glaciation until 8500 years B.P. and then declined slightly to present distributions 6500 years ago. Thus, populations in previously glaciated areas are recent arrivals and are not likely to be as well adapted as those native to Wisconsin Age refugia.

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[1] *B.P.:* Before Present.

Regardless of evolutionary progress in adaptation, planting or direct seeding of white spruce with seed of unknown origin or environmental tolerance introduces a risk of poor survival and growth. Although little information about genetic variation of white spruce exists for subarctic forests, provenance research in low latitudes shows that different seed sources vary in rate of juvenile growth (Genys 1965; Holst 1955, 1960, 1962; King and Rudolf 1969; Khalil 1974; Nienstaedt 1969; Nienstaedt and Teich 1972; Stellrecht et al. 1974; Teich 1973; Teich et al. 1975); response to calcium nutrition (Farrar and Nicholson 1966, Teich and Holst 1974); wood density (Holst 1960, 1962; Stellrecht et al. 1974); late-season initiation of needle primordia (Pollard 1973); nuclear volume; DNA content; bud, branch, and needle morphology (Miksche 1968); optimum temperature for seed germination (Fraser 1971); in terpene biochemistry (Wilkinson et al. 1971, von Rudloff et al. 1981); and in isoenzymes (Copes and Beckwith 1977, Tsay and Taylor 1977). These studies indicate that genetic variation is associated with geographic variation and that distinct white spruce populations have evolved within broad ecological regions. The studies also show that sampling intensity must be increased to define genetic variation in survival and growth traits of both provenances[2] and ecological regions.

Electrophoretic studies of isoenzyme variation provide the best evidence that genetic variation is extensive among white spruce populations in subarctic forests. Copes and Beckwith (1977) showed that the area of natural white and Sitka spruce hybridization in southcentral Alaska is more extensive than has been previously believed and that isoenzyme variation is greater among interior white spruce provenances than among coastal Sitka spruce. Isoenzyme variation (Tsay and Taylor 1978) and terpene composition (von Rudloff et al. 1981) of white spruce provenances from glacial refugia (northern populations) are different from those of provenances in formerly glaciated regions (southern

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[2] *Provenance:* a general term for "the original geographic source of seed, pollen or propagules" (Snyder 1972).

Seed source: the locality of the stand where the seed was collected. The stand may or may not be native. Provenance of the seed collection should be recorded if the stand is non-native.

Local seed source: the indigenous geographic race at the locality in which the seedlings will be planted.

populations) in Yukon. These results support the hypothesis that glacial refugia are a center of genetic diversity for white spruce forests and that many diverse populations evolved during the postglacial period of expansion.

Variation in number and frequency of isoenzymes or other metabolic constituents of tree populations, however, has not been related to genetic differences in growth and environmental fitness. In addition, differences among provenances in wood properties and long-term survival traits such as resistance to insects, diseases, climatic extremes, and animal damage have not been investigated. For these reasons, seed-transfer rules and seed zones designed to reduce the adverse effects of seed movement should be conservative until all sources of genetic variation are well defined. Good reforestation practices require planning for seed supply in advance of timber harvest, control of seed collections, and knowledge of seed provenance (Yeatman 1976). Provenance of each seed collection should be identified to the nearest minute in longitude and latitude and to the nearest 30 meters in altitude in both Alaska and Yukon. This information should be maintained throughout the nursery phase of artificial reforestation so that plantations can be established with adapted seed sources.

The problems of seed movement and conservation of superior growth and fitness traits of well adapted natural populations must be addressed at three levels of genetic variation:

1. Variation associated with major changes in climate, physiography, soils, and competing life forms.

2. Variation associated with local environments within wide geographic regions, i.e., stand-to-stand variation.

3. Variation among trees within stands. This variation has evolved from mutation and selection in different microsites and limited gene flow from adjacent stands and trees.

Each source of variation should be managed to reduce the risk of seed movement and conserve the gene pool for desirable traits. Reforestation with local seed collections will eliminate the risk of long-range seed transfer until races of superior growth and survival are identified through provenance research. Specific information for maintaining genetic diversity among white spruce stands is unavailable. I recommend collecting seed from at least thirty well-distributed trees for each local population in order to maintain genetic diversity among trees within stands.

DELINEATION OF SEED ZONES

Seed-collection zones have been established in most forested regions of North America in order to reduce the risk of long-range seed movement. According to Snyder (1972), a seed-collection zone is a "zone of trees with relatively uniform genetic (racial) composition as determined by progeny-testing various seed sources. The encompassed area usually has definite geographic bounds, climate and growing conditions. A single geographic race may be divided into several zones."

If wide-range genetic variation is known from provenance or progeny tests, seed-collection zones can be delineated for each homogeneous ecotype; or if variation is continuous (clinal), zones can be delimited statistically as per cent change in characteristic per geographic unit in distance (Morgenstern and Roche 1969). Regression models have been developed to delimit "plantation zones" and "provenance zones" for boreal forests (Campbell 1974, Eriksson et al. 1980). Adapted provenances for a plantation zone are predicted from their geographic location, transfer distance in altitude, and survival rates at selected test sites. These models demonstrate that seed-transfer distance and plantation zones must be smaller for severe sites than for mild sites. Similar models can be developed from adaptative responses of white spruce to prescribe seed-transfer rules and delineate seed zones in Alaska and Yukon.

Campbell's procedure (Shelbourne and Campbell 1976) for seed-transfer zones is to develop a seed-transfer regression equation that predicts the pattern of clinal variation[3] in a trait of interest, e.g., survival rate, from seed-source variables. Any relevant seed-source variable such as latitude, elevation, and aspect that operates indirectly or directly in natural selection should be included in the equation. Clinal variation is determined for the trait of interest from representative provenance trials in homogeneous test regions or plantation zones. Maximum risks, e.g., death rate of nonadapted trees, are then set for each zone; and the clinal variation equation is solved for locations with adapted seed. Boundaries of the adapted sources can be plotted on topographic or climatic maps. Discontinuous environmental and racial variation underlying the clinal variation modeled in seed-transfer regressions, however,

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[3] *Clinal variation:* continuous genetic change in a trait from area to area within the species range.

may cause more or less mortality and yield than predicted. This variation must be mapped by other methods. Sites that do not conform to risk predictions should be reforested with local seed sources until superior provenances are found.

In the absence of conclusive provenance information, provisional seed zones must be delineated from ecological criteria such as climate, soils, physiography, and vegetation types. Provisional seed zones of California (Buck et al. 1970), Arizona and New Mexico (Schubert and Pitcher 1973), the Great Plains (Cunningham 1975), the Maritime Provinces Fowler and MacGillivray 1967), Ontario (Holst 1962), British Columbia (Haddock 1962, Haddock and Sziklai 1966), Alberta (Haddock and Sziklai 1966), and the Pacific Northwest have been delineated on major physiographic features within broad climatic or land-resource regions. Provisional seed zones may be designated on topographic features in regions of similar climate derived from principal-component analysis (a multivariate-statistics technique) of highly related climatic variables that determine tree survival and growth. Provisional zones should be small enough to account for major genetic differences associated with geographic variation as estimated from environmental heterogeneity of the region under consideration, and no minimum size is strictly applicable. Most provisional zones in low latitudes are limited to about 500 feet (150 meters) in altitude where topography and local climate are highly variable. Changes in zone boundaries and addition or deletion of zones can be expected when improved environmental data and information from provenance-progency research are available. Provisional seed zones will undoubtedly be revised in the future to conform with breeding zones of intensive tree-improvement programs that develop populations with highly stable performance for specific sites.

Well-prepared, provisional seed zones can be used to identify the origin of seed collections; control seed movement in artificial-reforestation programs; select breeding populations for tree improvement; stratify test regions for species, provenance, and genotype research in forest genetics; and to identify sites which give best resolution of genetic differences among provenances and genotypes. Uniform provenance-progeny test regions reduce genotype x environment interactions and increase the efficiency of selecting populations that are well adapted to all plantation sites within test regions. Grouping of habitats into zones of relatively uniform environment on the basis of provenance or genotype

x environment interaction is likely to be more effective in reducing risks of seed movement and improving yields than selecting provenances or genotypes with stable performance in a wide range of habitats (Shelbourne and Campbell 1976).

RECOMMENDATIONS FOR WHITE SPRUCE SEED MANAGEMENT

Responsibility for maintaining productivity and distribution of white spruce forests in subarctic climates must be shared by all public and private proprietors of our natural resources. The first step is good seed management in regenerating harvested forests.

1. Employ harvesting and site preparation practices that encourage natural regeneration, i.e. clearcut in narrow strips and leave adequate shelterwood overstories and seed trees (Zasada 1972). Although the seed-tree method has not been widely tested in Alaska, leave at least thirty vigorous dominant and codominant seed trees per hectare in harvest units of 30 hectares or less. Natural regeneration from numerous well-distributed trees in native stands will conserve genetic variation in survival and growth traits. The entire pool of natural variation is important for adaptation of local populations to many heterogeneous microsites and long-term changes in environment.

2. If harvested sites fail to regenerate naturally in an acceptable period of time, collect seed from thirty or more well-distributed trees per population in the harvested area for artificial reforestation. Reforestation with local seed sources will eliminate risks in seed transfer and maintain genetic integrity of indigenous populations until major levels of genetic variability can be determined.

3. If local seed is not available, collect seed from habitats with similar temperature, precipitation, and length of growing season in the same geographic or ecological region as the planting sites. Relatively homogeneous ecoregions have been described from vegetation characteristics, land form, climate, and geological history in Yukon (Oswald and Senyk 1977). These ecoregions can be used to locate white spruce populations that are adapted to sites devoid of local seed and to delimit provisional seed or plantation zones for Yukon. Ecoregions have not been described in detail for Alaska.

Wildfires, excessive harvest, and infrequent seed crops in subarctic environments of Alaska and Yukon have eliminated many indigenous white spruce populations or slowed their migration to potentially productive sites. White spruce is near the limit of its natural range in this region, and potential habitats are highly heterogeneous. Success of future afforestation programs will require rigorous adherence to seed zones and transfer guidelines. Provisional seed zones provide an interim method of locating productive white spruce provenances for off-site habitats until inherent variation associated with geographic variation is determined.

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CHAPTER 3: Seed Supply and Handling

INTRODUCTION

Artificial-reforestation programs for white spruce, *Picea glauca* (Moench) Voss, in Alaska and Canada depend on an ample supply of high-quality seed. Such seed germinates rapidly, has high germination capacity, and produces rapidly growing seedlings. Seed is most economically collected when cone crops are heavy, a large number of seeds are filled, and incidence of disease and insect and mammal predation is low. Large crops may occur only once every 10 or 12 years in interior Alaska (Zasada and Viereck 1970), and seed-collection operations should be mobilized to collect as many cones as necessary for reforestation in intervening poor seed years. Procurement of seed is usually a small cost in the total reforestation program, however, and even light seed crops should be collected when reforestation success depends on securing seed adapted to plantation sites.

EVALUATION AND MATURATION CRITERIA

Seed yields can be estimated from the average number of sliced filled seeds per cone in a representative sample of cones sliced in half lengthwise through each cone axis. A general rating of seed yield for white spruce in Alaska and Canada can be derived from average-filled-seed counts (Dobbs et al. 1976, refined by Calvert 1978):

Ave. no. sliced filled seeds per cone 3.5 mean length[1]	Estimated % filled seed recovery per cone	Seed-yield rating	Est. seed yield per hectoliter[2] of cones (kg)
> 7.0	> 75	Heavy	> 1.25
5.1 - 7.0	60 - 75	Medium (good)	0.80 - 1.25
3.1 - 5.0	40 - 59	Light (fair)	0.50 - 0.75
0 - 3.0	0 - 39	Poor	0 - 0.45

[1] Average length of white spruce cones in Alaska range from 3 to > 5 cm (Zasada et al. 1978, additional data on file at Institute of Northern Forestry). For each yield rating, increase the average filled seed count one seed for each cm average cone length > 3.5 cm.
[2] 1 hectoliter = 2.84 U.S. dry bushels, approx.

Examinations of seed yield can be made in conjunction with surveys of cone and seed development just before cone collection in August. Yield estimates from earlier surveys may be adjusted at this time for late-season seed losses from insects.

Criteria are poorly defined for determining the earliest date for cone collection and methods of handling cones and seeds. Seed vigor is reduced when cones are removed from parent trees and the seeds extracted before critical stages of development are complete (Edwards 1980). A major difficulty in collecting white spruce seeds is that maturation of cones and seeds varies from year to year, stand to stand, tree to tree, and among cones in trees. In general, white spruce cones should be collected only after the length of the embryo is 75 per cent of the length of the embryo cavity, seed coat and wings begin to darken (Dobbs et al. 1976), cone-moisture content declines to 150 per cent or less of dry weight, specific gravity is less than 0.95 (Zasada 1973), cones begin to yellow or brown, and scales begin to loosen on the earliest-maturing cones. Seeds, however, may require additional ripening in the cones after collection to achieve full vigor. This is measured by germination capacity, germination energy (time to reach a predetermined percentage of germination or rate of germination), and seedling growth (Edwards 1978, 1980). Germination characteristics determined in the laboratory are unavailable for field use during the seed-maturation period. Seed maturity in the field must be estimated from physical characteristics of the seed such as brittleness (fracturing when cut) (Crossley 1953), growing-degree days (number of degrees that accumulate above a mean daily temperature of 5 °C during the growing season) after pollination (Zasada 1973), and cone and seed characteristics described above. More research is needed to simplify maturation criteria and to determine the optimum stage of seed development for cone collection.

METHODS OF CONE COLLECTION

Methods of cone collection and handling are described in detail by Stein et al. (1974) and Dobbs et al. (1976). Most collections of white spruce cones in subarctic forests are made from felled trees and squirrel cuttings or middens. One person can collect 3 to 4 bushels (1 to

1.5 hectoliters) of cones per day from felled trees or squirrel cuttings when cone production is heavy. Trees felled for cone collection should be vigorous, salvageable, of desirable form, and from an area in need of reforestation.

Cones from squirrel cuttings remain closed and can be collected after cones have opened on standing trees. Cones collected from squirrel caches may be from trees with undesirable characteristics, however, or contain seeds infected with *Caloscypha fulgens* (Sutherland 1979) or other pathogenic fungi from surface litter. *Caloscypha fulgens* is a soilborne fungus that can kill white spruce seeds in stratification to break seed dormancy (Epners 1964). Losses are reduced in infected seed lots with naked stratification and fungicide treatments.

Less frequently, white spruce trees may be climbed or toppped and limbed for cone collection. Most white spruce cones are located in the top six to eight branch whorls, and cones can be collected easily from trees topped at 2 inches in diameter by shooting or climbing (Slayton 1969). Topping controls tree height for future cone collection, and new crowns rapidly generate from branches that grow upward on vigorous white spruce seed trees. Nienstaedt (1981) found that young white spruce seed orchard grafts produced more cones when topped 2 years before a heavy cone crop than did untreated trees. Topping might, therefore, be used to increase cone production on young white spruce seed trees in seed-production areas or orchards. It will also control tree height for easier cone collection.

Climbing white spruce trees is laborious and usually less productive for cone collection than felling or topping. Climbing should be considered only for trees that have well-developed crowns and are less than 50 feet in height.

Mechanical tree shakers have been tested for removing cones from several conifers including Engelmann spruce, *Picea engelmanii* (Parry), and Norway spruce, *Picea abies* (L). Sixty per cent of the cones from Engelmann spruce trees up to 3 feet in diameter and 125 feet in height are removed with 5 to 10 seconds of shaking (U.S.D.A. 1972). Efficiency of this method of cone removal decreases with increasing tree size, and longer shaking times increase tree damage. In addition, tree-shaking equipment is limited to roads or gentle terrain, and vegetation must be cleared around each tree to facilitate cone collection. Future application of tree shakers and other mechanical equipment for cone

collection may be restricted to well-managed white spruce seed-production areas and orchards.

SEED CERTIFICATION

The purpose of certification of forest tree seed is to ensure that the genetic identity, genetic purity, and origin of seed used in artificial reforestation programs conform to official standards (Jones and Burley 1973, Rudolf 1974). State and Federal laws for forest tree seed certification and standards adopted by the Association of Seed Certifying Agencies (A.S.C.A.) in the United States and Canada are reviewed by Rudolf (1974). Standards for certifying forest tree seed in international trade are provided by the Organization for Economic Cooperation and Development (O.E.C.D.) under the Food and Agriculture Organization of the United Nations (Jones and Burley 1973).

Minimum seed certification standards of both organizations are based on identification of exact native geographic origin of the first-generation seed parents. Certification categories are: *source-identified seed:* seed collected from natural stands or plantations of known provenance; *selected seed:* seed collected from untested superior phenotypes or untested seed orchards (a special class) of known provenance; and *certified seed:* seed produced by proven superior genotypes.

State laws in the United States and provincial laws in Canada provide seed certification for users who request the service from agencies qualified to implement A.S.C.A. and O.E.C.D. standards. Seeds are certified at the source of cone collection, at extraction and storage facilities, and in nursery operations. Seeds can also be certified as seedlings packaged for outplanting if the user requests.

Participation in certification programs by seed producers is voluntary, but demands for certified seed have usually enticed sellers to cooperate with certification agencies. The Canadian Forestry Service has procedures for certifying forest tree seed under O.E.C.D. standards (Piesch and Stevenson 1976) that are an example of services available to seed users in all parts of the world.

In the absence of seed-certification services, every nursery worker that handles white spruce seed from subarctic provenances should be sure that all containers of cones and seed are labeled, both inside and

out, with the following information: species; elevation to nearest 30 meters (100 feet); township; range and section or longitude and latitude to the nearest minute; seed zone, if available, and local name of the seed-collection area; number of seed parents; and date of seed collection. This information is necessary to select seed sources that will perform at least as well as the wild parental populations before them. All seed-source information should be maintained in permanent reforestation records for certification of future seed crops.

CONE STORAGE AND SEED EXTRACTION

White spruce seed may require ripening in the cones for complete maturation after collection. Seeds usually mature satisfactorily when cones are maintained at 5 to 15 °C and in 60 to 75 per cent relative humidity for several weeks after collection. Standard burlap sacks used for collecting cones (1.5 bushels) should be less than one-half full for air circulation among the cones and to allow space for expanding scales as the cones dry. Circulation of air at cool temperatures and moderate humidities promotes slow, uniform drying and prevents development of molds and internal heating of the cones. In the absence of controlled-environment facilities, sacked cones should be stored on racks or shelves or transferred to wire mesh trays in a well-ventilated barn or shed.

Growth rate of white spruce seedlings following seed germination rapidly declines if seeds remain in the cones after ripening is complete (Edwards 1978). Seeds should be extracted immediately after maturation and air dried in preparation for storage. More research is needed to determine optimum moisture content and temperature of the cones for seed ripening.

White spruce seeds are particularly susceptible to physiological injury from high temperature and humidity during extraction (Carmichael 1958). Seeds with an initial moisture content of 2 to 4 per cent rapidly lose vigor after a few hours at 65 °C and 30 per cent relative humidity. White spruce cones should be dried at low humidity and the lowest temperature possible for cone opening (Wang 1973). Although optimum vapor pressure gradient and temperature for drying cones have not been determined, most mature cones open satisfactorily after 8 to 16 hours at 30 to 40 °C and 20 per cent or less relative humidity. Predrying cones

with more than 20 per cent moisture content for several hours at 20 to 30 °C and low humidity will reduce seed damage and hasten cone opening at higher kiln drying temperatures.

Opened cones are tumbled or shaken to extract the seed before the wings are removed and the seed is cleaned. Cones that fail to fully open after drying can be resoaked in water for 20 minutes, redried, and retumbled to increase seed recovery. Collections with a large amount of debris may be partially cleaned with an oscillating screen scalper to remove cone parts, pitch, needles, and other contaminants that are larger than the seeds and wings (scalping).

It is difficult to remove the wings from white spruce seed, and serious damage may result from harsh rubbing to separate the wings and seed coats. Seeds are often moistened in a fine mist or soaked briefly in water to loosen persistent wings and reduce the amount of injury from mechanical rubbing. The seeds must be redried at low temperature and low humidity before they are cleaned.

A large variety of equipment is available for cleaning seeds from forest trees. Small equipment is suitable for processing most white spruce seed lots. Small seed lots are necessary to maintain the genetic integrity of local provenances and seed zones. Lowman (1975) has prepared a list of seed-processing equipment suitable for small lots, including manufacturers of kilns, dewingers, air-screen cleaners, and separators. Many seed producers use air-screen cleaners for scalping and grading (removal of dust, wings, and other debris smaller than the seeds) after dewinging, and air or gravity separators for final cleaning. Air and gravity separators remove empty seeds and particles that are the same shape and size as seeds but which have different densities and surface structures. A flow chart for processing white spruce seed is shown in Figure 1.

Seed separators are also used to sort seed into weight classes for uniform emergence and size of seedlings grown in nurseries. Each parent of white spruce seed produces a narrow range of seed weights, and entire families may be eliminated from different size classes (Hellum 1976). If white spruce seeds are sized, seedlings from different size classes should be mixed together before planting to prevent possible reduction in genetic variability as well as inbreeding problems in future generations.
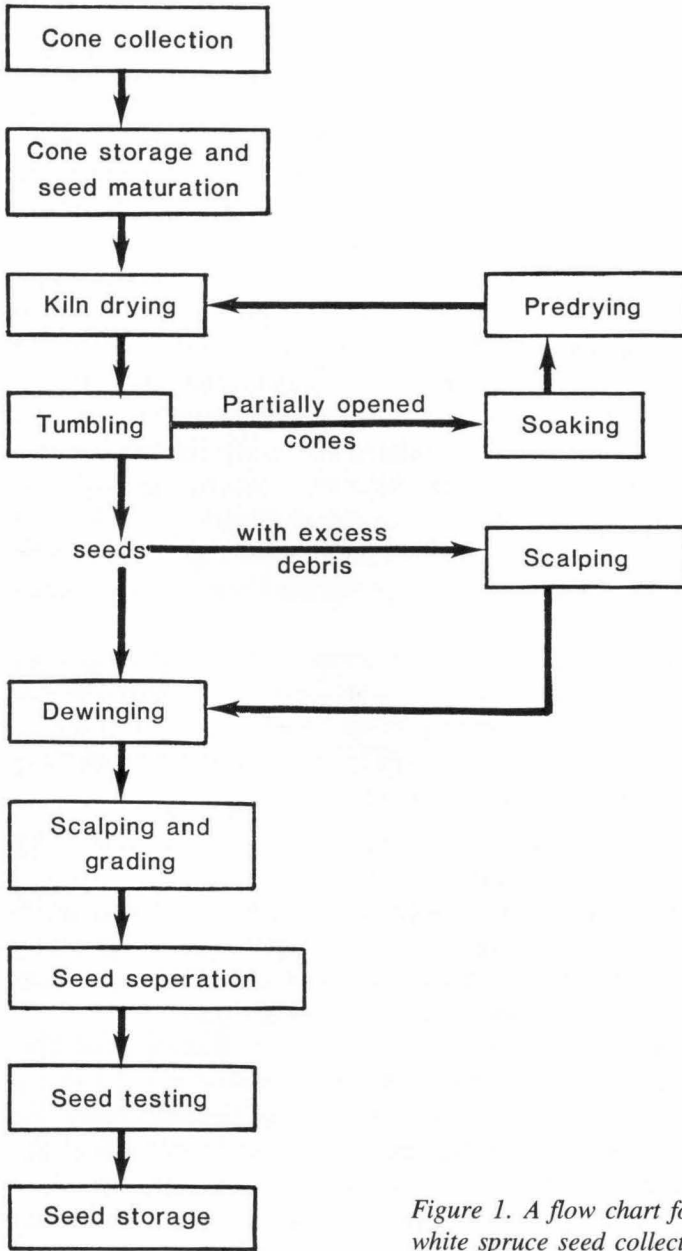
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Cone collection
      │
      ▼
Cone storage and
seed maturation
      │
      ▼
Kiln drying  ◄─────────────────────  Predrying
      │                                  ▲
      ▼                                  │
Tumbling ──── Partially opened ────►  Soaking
                   cones
      │
      ▼
seeds ──── with excess ────►  Scalping
               debris              │
      │                            │
      ▼                            │
Dewinging  ◄─────────────────────┘
      │
      ▼
Scalping and
grading
      │
      ▼
Seed seperation
      │
      ▼
Seed testing
      │
      ▼
Seed storage
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Figure 1. A flow chart for processing white spruce seed collections.

TESTING SEED

The purpose of testing seed is to estimate seed quality. Seed quality is the proportion of seed that will produce normal seedlings per unit of seed lot weight. This information is used to determine sowing rates and to control density of seedlings in nurseries and plantations that are artificially seeded. Essential parameters of seed-lot quality are percentage pure seed, seed-moisture content, number of seed per unit weight, and germination per cent in a given time, usually 4 weeks. Most commercial seed lots are purchased on the basis of pure live seed, which is a combination of percent purity and germination. Pure live seed is the proportion of seed by weight that will produce normal seedlings under standard test conditions. Seed-handling practices vary widely among nurseries, however, and results of laboratory germination tests and emergence of seedlings in the field are frequently inconsistent. Nevertheless, germination capacity and energy are principal criteria of seed quality, and germination standards for forest tree species have been established by the A.O.S.A. in Canada and the United States (Bonner 1974).

Germination tests are slow, do not reveal source or cause of seed injury, and require controlled environments for reproducible results. For these reasons, seed users and producers often use one or more of several quick tests for estimating seed-lot quality. Some quick tests useful in evaluating white spruce seed quality are:

1. Simple cutting tests to determine the percentage of firm, fully developed, insect-free seeds per seed lot.

Cut seed can be examined for embryo development and physical injury in seed processing. Cutting tests do not require special equipment or seed preparation, but sound seed estimations may exceed actual germination of white spruce seed from 10 to 30 per cent.

2. Tetrazolium color tests to estimate vigor as well as seed viability.

Seeds that are fully imbibed with water are soaked in a 0.1 to 1.0 per cent 2, 3, 5-triphenyltetrazolium chloride solution until the tetrazolium is reduced to the characteristic carmine color it becomes in normal tissue. The location and extent of normal, weak, and dead tissue are pinpointed by the color and density of the stain. Dead tissues do not stain, and weak tissues are darker than normal. Tissues weakened

from age, frost, or disease produce colors that are characteristic of the injurious agent (Moore 1973).

3. X-ray tests to determine per cent filled seed, embryo and endosperm development and detect insect injury and-seed processing damage.

Injured tissues are readily apparent in radiographs of seeds that are treated with contrasting agents such as barium chloride, silver nitrate, and vaporous halogen derivatives (Simak 1957, 1974). Contrasting agents penetrate dead or weak tissue and absorb low-energy X-rays to reveal the source and extent of injury. X-ray tests, although expensive, are quick (especially if Polaroid film is used), and nondestructive and provide a permanent record of seed characteristics.

These and other viability tests for tree seeds are reviewed by Bonner (1974). Germination energy, capacity, and initial seedling growth rates are the most reliable criteria for vigor and storage potential of white spruce seeds. Mature seeds from subarctic provenances have shallow[3] or no dormancy and no stratification requirement for germination. Fully imbibed vigorous seeds germinate rapidly after 4 to 6 days on a moist medium at 20 °C, and germination tests can be completed in 3 weeks.

STORAGE OF SEED

Both temperature and moisture must be carefully controlled to maintain high viability of tree seeds in long-term storage. Optimum conditions for storage of most tree seeds are reviewed by Stein et al. (1974) and Wang (1974). Although relationships between seed quality, seed moisture, and storage temperature are not known, tests have demonstrated that white spruce seeds remain viable for 10 to 20 years if they are maintained within critical temperature and moisture limits. Recommended storage conditions for white spruce are:

1. Moisture content.

Seeds degenerate slowly at high moisture content, and all water not essential for life processes should be removed before storage. Experience has shown that moisture content between 4 and 8 per cent of wet weight

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[3] *Seeds with shallow dormancy require little or no ripening (chilling) after harvest to complete physiological processes necessary for germination.*

is optimum for storage at temperatures between 2 and $-18\,°C$ (Stafford 1974, Wang 1974). Seeds should be dried at 25 to 30 °C and low humidity until moisture contents stabilize. White spruce seeds may be dried for 8 to 24 hours at higher temperatures if initial moisture contents and relative humidity are low, but prolonged temperatures in excess of 55 °C can be damaging (Carmichael 1958). Research is needed to determine optimum temperature and vapor-pressure gradients for drying white spruce seeds and optimum moisture-content of seeds for long-term storage.

2. Storage containers.

White spruce seeds dried for storage should be enclosed in moisture-proof containers to maintain constant moisture contents. Large seed lots are often stored in 4- to 10-mil polyethylene bags that are placed in fiberboard or metal drums to permit slow gas exchange with a dehumidified external environment. Small seed lots can be stored in glass or plastic bottles with air-tight screw caps as enclosed oxygen levels are adequate for low rates of respiration. Small seed lots sealed in two or three layers of moisture-proof polyethylene-laminated plastic conserve storage space. Each package is no larger than the seed it contains, and exchange of moisture between the seed and trapped air is minimized. Seed can be packaged in quantities that will be used at one time, or opened packages can be resealed easily for continued storage. Containers should be warmed to room temperature before they are opened to prevent moisture from condensing on seeds that will be put in storage again.

3. Storge temperature

Low storage temperature is necessary to minimize metabolic activity of seeds and prevent accumulation of water from respiration processes. White spruce seeds with 4 to 8 per cent moisture have been stored successfully for 10 to 20 years at 2 to $-18\,°C$ (Stafford 1974, Wang 1974), but optimum storage temperatures for given moisture contents are unknown. In general, seeds that tolerate drying and freezing retain viability longer at lower storage temperatures within critical temperature limits for given moisture contents (Barton 1961).

The effects of low temperature on enzyme activity and metabolism in seeds, distribution of water in seeds, and the degree of binding of water to carbohydrates, lipids, and proteins need further study to deter-

mine optimum storage conditions for white spruce seeds. Optimum storage environments may vary with age, vigor, and race or provenance of white spruce seed. More empirical research and basic research are needed to determine optimum environmental conditions, including temperature and moisture for seed maturation, seed processing, and long-term storage of seeds from white spruce provenances in subarctic climates.

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