VEGETATIVE AND SEXUAL PHENOLOGY, REPRODUCTIVE DYNAMICS AND BUD DIFFERENTIATION IN A CLONAL SEED ORCHARD OF WHITE AND BLACK SPRUCE

BY

Conor O'Reilly

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Lakehead University
School of Forestry

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ABSTRACT

To evaluate the importance of phenology and strobilus production in a clonal seed orchard of white and black spruce, 14 clones of each species represented by 4 ramets each, were selected from the Mattawin seed orchard, Thunder Bay District, Ontario. The times of flushing of the terminal buds of the leaders and 4 lateral branches were determined using an index of vegetative bud and shoot development. Dates of growth cessation were determined at 95 percent of shoot elongation. An index was used to score stages of pollen release and female receptivity of black spruce. Counts were made of male and female strobilus production per ramet in black spruce. The time of reproductive bud differentiation, in two clones of black spruce, was estimated to be mid-July after viewing dissected buds under a dissecting microscope and epimicroscope. Analyses of variance showed significant differences among clones in times of flushing and growth cessation of the leaders and lateral branches of white and black spruce, and significant differences in times of pollen release and female receptivity in black spruce but not white spruce. However, few clones were significantly different from each other using Duncan's NMR test. Generally there was a small range in clonal mean dates for these characteristics, perhaps because the clone ortets all originated from the

same northern seed zone. Early-flushing black spruce clones produced the greatest leader extension. Peak pollen release and female receptivity coincided in most clones, thus increasing the probability of selfing. An analysis of variance of the number of female strobili per ramet and an analysis of covariance of the number of male strobili per ramet, using ramet height as covariant, showed significant clone differences. A few clones produced the largest number of strobili, especially in male strobilus production. Heavy male strobilus producing clones were not necessarily heavy female strobilus producers. The genetic composition of the progeny was estimated from: 1) the daily stages of pollen release and female receptivity, and 2) the number of male and female strobili per clone. A few clones were the largest contributors to the genetic composition of the progeny; the timing of pollen release and female receptivity had little effect on these estimates. The total percentage of selfed-crosses was estimated at 11 percent, although the individual clone rates of selfing varied from 1 to 25 percent.

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INTRODUCTION

The establishment of clonal seed orchards of white spruce (Picea glauca (Moench) Voss) and black spruce (Picea mariana (Mill.) B.S.P.), from selected plus trees, has been carried out in most provinces, mainly with the objective of increasing volume yield (Morgenstern et al. 1975). It appears that an increasing percentage of the planting stock will originate from seed collected from such seed orchards. However, there have been few studies on clone differences in many important characteristics in these orchards, such as vegetative and flowering[1] phenology, and male and female strobilus production. In addition, there have been no studies on the timing of reproductive bud differentiation in both species for northern Ontario. Information on these factors would be useful for better seed orchard management.

Clone differences in the timing and duration of flowering and strobilus production affect the genetic composition of the progeny (Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). No studies have estimated the effects of these factors on the genetic composition of the progeny in seed orchards of white and black spruce. Small clone differences would be of little importance; however, large differences have important implications for the tree

[1] "Flower" is used in the sense of a "determinate sporogenous shoot"(Jackson and Sweet 1977). Flower and strobilus are used interchangeably throughout text.

breeder as most of the gamete contributions may originate from a few clones. These factors may also affect the degree of selfing. In addition, determination of clone flower production, its timing, and the estimates of the genetic composition of the progeny can be combined with other information, such as desirable physical traits, in clone selection. For example, a clone might be removed if its time of flowering was not well synchronized with the other clones, or if it produced too few or too many strobili. Removal would be easier to decide on if it was also shown that the clone was less than average in some vegetative characteristics (e.g., growth rate), based on progeny tests.

The main objectives of this study were to investigate: (1) the timing and duration of pollen release and female receptivity, and total male and female strobilus production over one year, in a clonal seed orchard of white and black spruce and: (2) to estimate the genetic composition of the seed based on clone differences in the timing and duration of flowering, and clone differences in male and female strobilus production.

A secondary objective of this study was to evaluate the range in flushing and growth cessation dates among clones of white and black spruce. This information is important in seed orchard management for a few reasons. The vegetative phenological characteristics of flushing and growth cessation are important identifiable stages in forest growth

rhythms (Sarvas 1968, Nienstaedt 1974, Owens et al. 1977). In addition, these characteristics are under strong genetic control in most forest trees and may influence the amount of growth produced in a growing season (Nienstaedt 1974). Therefore, clone dates of flushing and growth cessation can be related to the amount of growth in that growing season. Further, the time of flushing can be related to the time of pollen release and female receptivity. Also, as the time of flushing may affect the amount of frost damage to a tree, selecting for late-flushing genotypes may be an effective method of reducing the probability of damage, especially in white spruce (Nienstaedt and King 1969, Sutton 1969, Nienstaedt 1972, 1974; Nienstaedt and Teich 1972, Stiell 1976, Wilkinson 1977, Morgenstern 1978). Therefore, information on the range of flushing dates between clones of white spruce is necessary for selecting late-flushing white spruce clones. Black spruce flushes later than white spruce, even on similar sites and when located within a few metres of each other, and therefore it suffers little from late spring frosts (Fraser 1966).

Another objective of this study was to estimate the time of reproductive bud differentiation in white and black spruce in the same seed orchard. Knowing the approximate time of flower bud differentiation is important in estimating the optimal time for the application of flower stimulants (Puritch 1972, Sweet 1975, Owens and Molder 1976, 1977a, 1977b, 1977c, 1979a; Pharis 1976, 1979); this

information may be useful for increasing cone production in seed orchards. Flower stimulants might be applied only to clones with a record of poor strobilus production. The time of reproductive bud differentiation coincides with the completion of lateral shoot elongation in white spruce (Owens and Molder 1977a) and other species (Owens and Molder 1976, 1979a). Therefore, a reliable external indicator of the time of reproductive bud differentiation might be the cessation of shoot elongation. Bud differentiation is used here to denote "that short morphogenetic phase when the developmental pathway of an apex becomes determined, and can be identified anatomically" (Owens and Molder 1976).

Although the approximate time of reproductive bud differentiation has been determined for white spruce (Eis 1967, Owens et al. 1977) and black spruce (Eis 1967) in British Columbia, there have been no similar studies in the rest of these species range in North America. This information is lacking especially for flowering phenology and flower production.

The results of this study may answer some of the following questions : do the earliest flushers cease growth first? Do early-flushers produce the greatest amount of leader growth? Are early-flushers also first to release pollen or to reach receptivity? Some of these relationships have direct practical implications, e.g., if we select for late-flushing white spruce types, do we also select for

rapid growth? Also, these results may support or refute some physiological relationships; e.g., does a clone producing large numbers of strobili also produce less leader growth due to competition for available photosynthate between vegetative and reproductive sinks?

LITERATURE REVIEW

Vegetative Phenology

Flushing

Since time of flushing has an adaptive value to spruce populations, and as both white and black spruce grow in diverse sites, genetic differences in flushing times of spruce populations have been commonly observed (Nienstaedt 1974, 1976; Wright 1976). Genetic patterns of variation in flushing time, as well as other characteristics, have been demonstrated by provenance trials for several conifers.

The range-wide pattern of genetically based variation in flushing has not yet been demonstrated in white spruce, although such a pattern has been demonstrated in black spruce (Morgenstern 1969a, 1969b, 1978), and several other species including sitka spruce (Picea sitchensis (Bong.) Carr; Burley 1966a), and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco; Irgens-moller 1968).

Morgernstern (1969a, 1978) analysed populations of black spruce and concluded that the temperature regieme of seed origin accounted for the greatest amount of variation in the time of budbreak; photoperiod accounted for only a small proportion of this variance. Morgenstern (1969b,

1978) found that variation in time of budbreak was clinal. It is likely that white spruce also has a clinal pattern of variation in the time of flushing since it does for many other characteristics (Nienstaedt and Teich 1972), and the clinal pattern is most common in north temperate trees (Nienstaedt 1976). Nicholson (1969) reported variation in the time of budbreak among provenances of white spruce, but he did not relate the differences to the environment of seed origin.

Just as there is considerable variation in time of budbreak between provenances, there is also much variation in the time of budbreak between individual trees of a stand. Variation in the time of budbreak between individual trees is largely due to genetic factors; this variation has been demonstrated in progeny trial experiments in white spruce (Nienstaedt and King 1969, Nienstaedt and Teich 1972), black spruce (Morgernstern 1969a, 1978), and other species (Nienstaedt 1974, 1976).

The date of budbreak varied as much as 21 days between 25 grafted clones of white spruce (Nienstaedt and King 1969). The grafts were taken from a plantation of unknown seed source growing in northeastern Wisconsin. In another study, the largest difference between four trees in a stand of white spruce near Chalk River, Ontario was only 5 days (Yeatman and Venkatesh 1974). Pollard and Ying (1979) studied flushing of six half-sib families from each of four

white spruce stands located in southeastern Ontario. They found no significant differences between stands, although highly significant differences occurred among families within stands. Wilkinson (1977) reported a range of twelve and nineteen days in a two year observation of the time of budbreak of individual white spruce seedlings. However, differences of only 3.5 and 5 days were found between the means of the seedling families in the same study.

Various physical traits are related to flushing date, although no definite pattern emerges. Nienstaedt and King (1969) found that late-flushing white spruce clones were 42 percent taller, had 50 percent greater daily growth rates, and had only 16 percent as many frost injured buds. However, Nienstaedt (1972) found a negative correlation between date of flushing and height growth among the progeny of nine late-flushing female parental clones. Wilkinson (1977) found a negative correlation between time of budbreak and shoot length among seedlings of white spruce.

The mean date of budbreak in a range-wide provenance trial of 121 seedling families of black spruce differed by 23 days in one study (Morgenstern 1969b) and 11 days in a later study (Morgenstern 1978). Sixty-one percent of the total variance in the time of budbreak in the former study was accounted for by provenance variance, and eight percent by family variance; both variances were significant at the 0.001 level. Dietrichson (1969, 1971) reports a similar

variance for flushing time among seedling provenances of black spruce planted in Norway. No other detailed studies on flushing in black spruce have been completed, and none have considered clonal flushing.

There are conflicting reports in the literature concerning the time of flushing in lateral branch buds. Fraser (1962, 1966) reported that flushing occurred first in the terminal bud of the leader of black and white spruce trees, and shortly after, flushing occurred in the lateral branch buds in a basipetal direction. However, Langlet (1960, In Nienstaedt and King 1969) suggested that the lowest buds in the crown flush first. It is not clear if these apparently conflicting reports are due to age, species, genetic, or environmental differences. However, Nienstaedt (personal communication) indicates that the lowest branches will flush first because the microenvironment is warmer close to the ground. Also, flushing time is delayed by as much as two to three weeks as tree age increase (Nienstaedt and King 1969).

Time of budbreak is a function of cumulative spring temperature and the genetic constitution of the tree (Sarvas 1967, 1972; Nienstaedt and King 1969, Nienstaedt and Teich 1972, Nienstaedt 1974, 1976; Yeatman and Venkatesh 1974). Cool springs delay flushing more in late-flushing trees than in early-flushing trees (Nienstaedt and King 1969). However, the actual breaking of dormancy is unaffected by

spring temperature; the breaking of dormancy is determined by the interdependent action of winter chilling and spring photoperiod (Owens et al. 1977). The end of vegetative bud dormancy was determined in the last study by the mitotic frequency in the median 10 percent of median longitudinal sections of bud apices.

Additional environmental factors are secondary in their effects on budbreak. Nienstaedt (1966) hastened budbreak by increasing the photoperiod in seedlings that had received insufficient chilling. However, the effect of photoperiod on budbreak has not been demonstrated other than its effect as a factor compensating for chilling (Nienstaedt 1974). The effect of increased photoperiod in the study of Nienstaedt (1966) may have been to cause an early break in dormancy, as the end of dormancy is determined by the interdependent action of winter chilling and spring photoperiod (Owens et al. 1977). In coastal Douglas-fir, Campbell and Sugano (1975) showed that an increased period of chilling and photoperiod resulted in a larger response to temperature. This response results in increased rates of budburst at all temperatures (Campbell and Sugano 1975).

There are many general references to date of flushing of white and black spruce throughout their ranges. In these studies, flushing times were usually recorded on the terminal leader or upper branch buds. Most studies have dealt with mature stands and individual trees throughout

their range.

White spruce flushed in mid-May at Chalk River, Ontario (Fraser 1962) at Keene, New Hampshire (Kienholz 1934) in Maine (Baldwin 1931), near Stephenson, New York (Cook 1941) and in Northeastern Minnesota (Ahlegren 1957). Flushing occurred in late-May in Michigan according to one report (Rowe 1955). Owens et al. (1977) reported flushing in late May and early-June in two consecutive years of observation near Prince George, B.C. Helum (1967) noted flushing of the terminal leader buds of white spruce seedlings in late-May and early-June in Alberta. Late-flushing clones of white spruce flushed in late-May to early-June, and early-clones in mid-May over a four year period near Rhinelander, Wisconsin (Nienstaedt 1972).

Black spruce flushed between late-May and early-June at Chalk River, Ontario (Fraser 1966), and Maine (Baldwin 1931). Flushing occurs a few days later in the Lake States, where Heinselman (1957) noted that it occurred during the first two weeks of June. Horton and Lees (1961) reported flushing on about June 1 in Alberta. Flushing is usually several weeks later in black spruce than white spruce even on trees growing on similar sites (Fraser 1966). Black spruce flushed five to ten days later than white spruce in Manitoba and Saskatchewan (Rowe 1955). A similar time differential has been reported in Minnesota (Le Baron 1948).

Growth Cessation

Time of growth cessation, like flushing, is an adaptive characteristic of trees to their environment (Nienstaedt 1974, 1976; Wright 1976). The general patterns of genetic variation have been shown in provenance trials. The magnitude of the genetic variation in the time of growth cessation is generally larger, and more uniform, than that of flushing (Nienstaedt 1974). Trees from southern or low altitude seed sources which have evolved in milder climates, are last to set bud in the fall (Nienstaedt 1974). This response has been shown, to some extent, in provenance trials of a number of species including white spruce (Roche 1970), black spruce (Morgenstern 1969a, 1969b, 1978), sitka spruce (Burley 1966a, 1966b), and Douglas-fir (Irgens-Moller 1958, 1967, 1968).

There is little information on genetic variation in time of growth cessation among individual trees and clones (Nienstaedt 1974). A difference of approximately three weeks in the time of growth cessation seperated the earliest from the latest of 25 white spruce clones observed by Nienstaedt and King (1969). These clones originated from one plantation stand of unknown seed origin. The range changed little from year to year, and repeatability from year to year had a correlation exceeding 0.84 (23 df) in all cases (Nienstaedt 1974). Morgenstern (1969b) found significant differences in the time of growth cessation

between seedling families of black spruce, although 84 to 90 percent of the total variance was accounted for by provenance variance and only 1 percent (approx.) by family variance, significant at the 1 and 5 percent level, respectively.

The time of shoot growth cessation may be related to shoot length. Nienstaedt and King (1969) found a strong correlation (R= 0.71, 24df) between shoot length and growth cessation among clones of white spruce. Roche (1970) also found a strong correlation between time of bud-set and total growth among seedling provenances of white and engelmann spruce (Picea engelmannii Parry ex. Engelm.) provenances in British Columbia.

Based on observations made in 1968 near Rhinelander, Wisconsin, Nienstaedt and King (1969) found that selected late-flushing white spruce clones ceased growth in early-July, and the early-flushing clones ceased growth in late-June; thus, the length of the growth period was approximately the same for both types.

Photoperiod is considered the major factor in the control of growth cessation (Kramer 1943, Fraser 1952, 1962, 1966; Nienstaedt 1974, Owens et al. 1977). Daylength was positively correlated with time of growth cessation in one study of black spruce (Morgenstern 1969a). Southern provenances of most species, when they are moved north, respond to the increased daylength by growing longer into

the fall in spite of low temperatures; the result may be injury from frost (Nienstaedt 1974). However, most species show much scatter around the regression line when date of growth cessation is plotted against photoperiod (Nienstaedt 1974). Therefore, other factors may also affect the the time of growth cessation; temperature regime was considered the most important secondary factor in black spruce (Morgenstern 1969a, 1978). Other environmental factors may influence the time of growth cessation. Severe plant water stress, due to low precipitation and high summer temperature, may result in early growth cessation, as reported for white spruce (Nienstaedt 1957). Growth cessation may also be affected by nutrients (Kozlowski 1963, Kozlowski and Winget 1964). However, the role of nutrients in the control of growth cessation is unclear.

Many studies make general references to the date of growth cessation, usually of the terminal leader or upper branch shoots, of individual trees or stands throughout the ranges of white and black spruce.

White spruce growth cessation occurs between mid-June and early-August depending on location. Growth cessation occurred in mid-July at Chalk River, Ontario (Fraser 1962), towards the end of July in New York (Cook 1941), and the upper Michigan peninsula (Nienstaedt 1957), and in early-August near Prince George, B.C. (Owens et al. 1977). White spruce growth cessation occurs as early as mid-June in

the prairie provinces, where low precipitaion and high summer temperatures induce severe plant water stress (Nienstaedt 1957).

There have been few reports on the time of growth cessation in black spruce. Black spruce shoot growth cessation occurred at the end of July at both Chalk River, Ontario (Fraser 1962), and Keene, New Hampshire (Kienholz 1934). Black spruce shoot growth terminated about two weeks later than white spruce of similar size, located within 10 metres of each other on the same site (Fraser 1962, 1966).

Flowering Phenology

Time of flowering, like time of flushing and growth cessation, is probably an adaptation to the local environmnent (Sarvas 1969, 1973; Stern and Roche 1974). While genetic differences in flowering time between populations have been determined in provenance trials, few such provenance trial studies have been completed which relate population differences in time of flowering to the environment of seed origin. Eriksson (1977) found a relationship between time of flowering (dependent variable) versus latitude, altitude, and distance to sea (independent variables) in provenances of lodgepole pine (Pinus contorta Dougl. ex Loud.) in Sweden. Polk (1966) noted clear differences between the time of flowering between

provenances of Scots pine (Pinus sylvestris L.) planted in Michigan. However, Polk (1966) did not relate these differences to environment of seed origin, although a phenological gradation among sources was noted from north to south and east to west, with sources from the far north and those from the southeast being first to release pollen and reach receptivity. There have been no similar studies in white or black spruce.

There have been few reports on individual tree variation in the time of flowering in white and black spruce, and less on the genetic component of this variation. Nienstaedt (1958) noted differences in the time of female strobilus receptivity between individual trees of white spruce at Rhinelander, Wisconsin. There have been no reports on individual tree and clonal variation in time of flowering in black spruce. Nonetheless, there are many reports of individual tree and clone differences in the time of flowering in other species.

Wasser (1967) noted differences in the stages of male and female strobilus development, including pollen release and female receptivity, between clones of shortleaf pine (Pinus echinata Mill.) and loblolly pine (Pinus taeda L.) in Virginia. The most detailed studies on flowering phenology have been conducted in seed orchards of Norway spruce (Picea abies (L.) Karst.) and Scots pine in Sweden (Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). These studies

showed highly significant differences between clones in the time of flowering of both species, suggesting a large genetic component. Sarvas (1967) suggested that the genetic factors accounted for about 85 percent of the total variance of flowering time in closed stands in southern Finland; no data or species were mentioned.

As has been shown for flushing, temperature appears to be the most important factor affecting the time of flowering of a genotype (Sarvas 1967, 1968; Winton 1964, Owens and Molder 1977a, 1977b, 1979a, 1979b, 1980). However, the breaking of dormancy in reproductive buds, as in vegetative buds, is determined by the interdependent action of winter chilling and spring photoperiod (Owens and Molder 1979a, 1979b). Tiren (1935, In Anderson 1965) noted a strong connection between the spring temperature, especially in May, and flowering time. Wind, rain, and humidity, contribute to variability in flowering times; however, these factors have an effect of short duration, and tend to be local in importance (Sarvas 1967, 1968, 1970). There is a strong relationship between time of flowering and latitude in longleaf pine (Pinus palustris Mill.), shortleaf, and loblolly pine (Dormann and Barber 1956). The time of flowering occurred 10 to 15 days later in the spring for each 2 degrees of latitude in a northerly direction (Dorman and Barber 1956). The pattern of flowering noted in that study was probably largely due to environmental factors, especially temperature, which vary with latitude. However,

genetic factors probably also played a role; the effect of this factor would have to be confirmed by a provenance trial.

There are many general reports on dates of flowering of black and white spruce throughout their ranges. White spruce flowers for a short period in May (U. S. Dept. Agr. 1948), June (Can. Dept. North. Affairs 1961), or July (Hustich 1950) depending on geographical location and climate. Flowering occurred between May 25 and May 30 near Ely, Minnesota (Nienstaedt 1957). From other observations in the same area over a five year period, pollen release and female receptivity varied between May 12 and June 1 (Nienstaedt 1957). Time of flowering also varies with latitude and elevation. Flowering occurred from May 25 to May 27, at low elevations (135 m), and was three to five weeks later at higher elevations (600 m or higher) in interior Alaska (Zasada et al. 1978). Owens and Molder (1979a) reported pollination occurring on May 26 at low elevations, and on June 9 at high elevations at Prince George, B.C. in 1975, and on May 21 and May 31 at low elevations at Pince George, and Smithers respectively in 1976. Male and female flowering times overlap, and are completed within three to five days (Wright 1953, Nienstaedt 1957, 1958; Nienstaedt and Teich 1972, Sutton 1969).

There are few reports on the flowering times in black spruce. Black spruce flowers in mid-May in the Lake States (Heinselman 1957) and about June 1 in northern Ontario (Vincent 1965). Black spruce shed pollen about nine days later than white spruce at the same location in Minnesota (Winton 1964).

Number of Strobili

There have been few detailed studies on flower production, and most studies have concentrated on female flower or seed-cone production. The methods of evaluation of flower and cone production in these studies were often crude, althogh suitable for general observations of flower production and annual periodicity at the stand and population level. There are even fewer studies on flower and cone production in white and black spruce.

Much of the variability in flower and cone production can be attributed to genetic factors (Wright 1953, Nienstaedt and Jeffers 1970, Nienstaedt and Teich 1972, Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). There is also large variability between years, sites, geographic location. (Anderson 1965). The effect of these factors, alone and in combination, on flower and seed production is very complex (Anderson 1965).

Variation in flower and cone production between populations, resulting from genetic sources, have been estimated in provenance trials. Teich and Pollard (1973) amd Teich (1975) reported differences in cone production among white spruce provenances, based on the frequency of cone bearing trees. However, these investigators did not relate the differences to the environment of seed origin. Eriksson (1977) found differences in the number of male and female strobili between provenances of lodgepole pine in Sweden. A strong relationship (R^2= 0.84) existed between the number of female strobili (dependent variable) and latitude, altitude, and distance to coast (independent variables), of provenance seed origin (Eriksson 1977). There was no similar relationship found for the number of male strobili. There is also much variablility in strobilus production between individual trees and clones. Nienstaedt and Jeffers (1970) studied seed-cone production in a white spruce clone collection in Rhinelander, Wisconsin. They found significant differences in seed cone production among clones (0.005 level) and replicates (0.05 level) at first count and among clones (0.05 level) but not among replicates at the second count, three years later. Nienstaedt (1980) reported differences in cone production between clones in both top-pruned and untreated ramets of white spruce; the data were not tested statistically for clone differences. Cone production may also be related to tree growth. Nienstaedt and Jeffers' (1970) data suggest that the slower

growing clones were the most prolific cone producers.

Eriksson et al. (1973) and Jonsson et al. (1976) conducted detailed studies of flower production and phenology in seed orchards of Norway spruce and Scots pine in Sweden. Eriksson et al. (1973) found highly significant clone differences between clones of Norway spruce in the production of both male and female strobili. Jonsson et al. (1976) reported large clone differences in male and female strobilus production between clones of Scots pine. Koski (1975) studied pollen production in seed orchards of Scots pine in Finland. It is not clear if total pollen production varied between clones, although a strong relationship existed between pollen production and both ramet diameter at breast height, and total height (Koski 1975). Eliason and Carlson (1969) made total counts of female flowers and cones on all trees in an open grown Norway spruce stand in New York, over a seven year period. Twenty-one trees ("coners") of the 109 trees produced more than 90 percent of the total cones every year with the exception of one, over the first five years of very light cone production. The "coners" produced 42 and 58 percent of the total cones in the other two years of very heavy and medium light cone production, respectively. Overall, the "coners" produced 49 percent of the total cones over the seven year period.

There have been many less detailed studies of flower and seed cone production, mainly in natural stands, of a number of tree species including white spruce. Zasada et al. (1978) noted differences in seed cone production between individual trees and stands of white spruce in Alaska. In that study, counts were made of the cones on one side of 15-16 trees in each stand using a telescope. Using binoculars, Lindgren et al. (1977) estimated cone production in Norway spruce stands all over Sweden. Their study showed large differences in cone production between stands, especially between those in northern and southern Sweden; the latter produced the most strobili. Wright (1953) visually classified annual flower and cone production from 0 (none) to 5 (very heavy) of open grown Picea species, including white and black spruce, in the Pennsylvania area. The number of trees observed was not given, although differences in flower and seed-cone production between trees were observed. Sarvas (1963, 1968) studied mainly stand production of male and female strobili of Norway spruce and Scots pine in Finland. In both studies, the number of male strobili was estimated based upon the amount of male strobilus residue falling to the ground after flowering and then related to pollen production by regression techniques. The number of female strobili was estimated based upon an annual count on some stand sample trees. The number of male and female strobili differed between stands and between trees within stands (Sarvas 1963, 1968). The differences

between stands apparently were largely due to differences in stand height; the number of strobili increased with an increase in the stand dominant height (Sarvas 1963, 1968).

A high proportion of the regional variability in seed production in a species is environmental rather than genetic in origin (Sweet 1975). Most of the environmental factors which influence flower production are important in the differentiation and development of reproductive buds. The most important factors affecting the development of reproductive buds after differentiation are physiological and/or climatic in origin (Sweet 1973, 1975).

Furthermore, loss of reproductive buds and strobili due to insects, fungi, birds, mammals, and diseases may be high especially in seed orchards (Dinus and Yates 1975). Extent of damage to reproductive buds and strobili due to these factors is largely dependent on location, type of damaging agent, and the extent of artificial protection (Dinus and Yates 1975).

Reduction in the number of reproductive buds and strobili due to physiological and/or climatic factors can occur at two stages of development: (a) during the period between differentiation and anthesis, and (b) during the period between anthesis and seed maturity (Sweet 1975).

(a) Loss during the period between differentiation and anthesis: Much flower loss results from the abortion of structures with floral potential or from the reversion of reproductive buds to the vegetative state (Owens 1969). A continued period of favourable climatic conditions, especially a high summer temperature, is important in the normal development of reproductive buds and strobili (Fraser 1962, 1966; Mathews 1963, Andersson 1965, Bronbo 1970, Jackson and Sweet 1972, Sweet 1975, Lindgren et al. 1977). In addition, spring and fall frosts may cause a reduction in cone crop potential (Andersson 1965, Sweet 1975, Lindgren et al. 1977, Calvert 1979).

(b) Loss during the period between anthesis and seed maturity: During the period in which pollen germination, fertilization and seed development occurs, loss of potential seed may take place at a number of different developmental stages and in a number of different ways (Sweet 1975).

Ovule abortion has been reported for a number of tree species as a factor in reducing potential seed set (Sarvas 1962, 1968; Sweet 1975, Owens and Molder 1980). Generally, the ovules that first abort are those which are not pollinated (Sweet 1975). Inadequate pollen production for effective pollination has been reported in Norway spruce and other species in Finland with the result that up to 40 percent of the ovules may fail to develop (Sarvas 1968, 1970). Poor pollination has also been reported for western

larch (Larix occidentalis Nutt.; Owens and Molder 1979a), and sitka spruce (Owens and Molder 1980). There may be heavy potential seed loss also due to the drop of developing flowers and cones (Brown 1970, Sweet 1975). Sweet (1975) suggested that two factors largely account for this drop: (i) a high incidence of ovule abortion due the low number of effective pollinations; and (ii) competition between developing flowers, and between flowers and vegetative shoots, for carbohydrates, mineral nutrients, and water.

After fertilization, potential seed production may be reduced due to embryo abortion. High levels of embryo abortion may occur after self-fertilization where abortion has an adaptive function (Sweet 1975). However, abortion can also occur due to unfavourable environmental conditions such as frost and insect damage (Mathews 1963, Andersson 1965). Sarvas (1962, 1968) gave figures for embryo abortion in Finland of 14 percent for Scots pine and 20 to 40 percent for Norway spruce.

Years of abundant flower and cone crops in forest trees are cyclic in nature (Andersson 1965, Bronbo 1970, Grano 1973, Lindgren et al. 1977, Zasada et al. 1978, Calvert 1979), and good cone crops are least frequent in northern environments (Sarvas 1968, Lindgren et al. 1977, Zasada et al. 1978). Heavy cone crops of white spruce are produced every 2-6 years (Nienstaedt and Teich 1972). Black spruce is a more prolific and consistent producer of cones than

white spruce (Harlow and Harrar 1968). Morphological, physiological, and environmental factors probably interact to cause periodicity in flowering (Calvert 1979).

The role of morphology is important in species which bear their reproductive structures in terminal twig positons such as white spruce and Norway spruce (Jackson and Sweet 1972, Lindgren et al. 1977, Calvert 1979). These species do not have as many available locations for flower production the year following a good crop; thus light crops follow heavy crops (Andersson 1965, Fraser 1966, Grano 1973, Lindgren et al. 1973, Zasada et al. 1978). The presence of a cone crop has also been shown to affect the differentiation and development of flower buds in some species for physiological reasons. During years of cone production in balsam fir (Abies balsamea (L.) Mill.; Morris 1951, Powell 1977) and Douglas-fir (Owens 1969, Allen and Owens 1972), new shoots tend to be short, and few bud primordia develop. The minimum period between good crops in these species is thus two years (Morris 1951, LaBastide and Van Vrendenburch 1970, Powell 1977). The environmental factors affecting cone differentiation and the factors affecting subsequent development all interact in their effect on the periodicity of flower and cone crops.

Differentiation and Early Development of Reproductive Buds in White and Black Spruce

Bud differentiation in the Pinaceae occurs in late summer prior to the onset of the dormant winter period. Phenoloical patterns of bud differentiation have been elucidated for several species using different technical approaches.

Black spruce buds become differentiated in early-August near Chalk River, Ontario (Fraser 1966). In that study, reproductive buds were recognized by using serial longitudinal sections of black spruce buds taken periodically throughout the growing season. Eis (1967) suggested that black and white spruce reproductive buds differentiate at the time of lateral shoot growth cessation which occurs in late-July in interior British Columbia. Eis (1967) estimated the time of reproductive differentiation based on observations of generative activity in the apices of dissected buds, although the first recognizable reproductive buds were not evident until mid-August. Fraser (1966) and Eis (1967) described stages of reproductive bud development from the time of earliest recognition until activity ceased (dormancy). No other studies report on the timing of reproductive bud differentiation and development in black spruce.

The actual timing of bud differentiation has been determined more accurately using detailed anatomical and histochemical methods. To determine when apical differentiation occurs, Owens and Molder (1977a) suggested the use of several criteria, such as changes in mitotic activity, apical size, shape, and zonation, and absence of ergastic substances in the pith. In conifers, the most useful criterion varies with the species (Owens and Molder 1977a). These criteria have been used in a number of west coast conifers, including white spruce (Owens and Molder 1977a), sitka spruce (Owens and Molder 1976), western larch (Owens and Molder 1979a), pacific silver fir (Abies amabilis (doug.) Forbes; Owens and Molder 1977d), yellow cedar (Chamaecyparis nootkatensis (D. Don) Spach.; Owens and Molder 1974a), and western hemlock (Tsuga heterophylla (Raf.) Sarg.; Owens and Molder 1974b). Most of these studies have been briefly reviewed by Owens and Molder (1977e). The times and patterns of reproductive bud differentiation are different in most of the above species (Owens and Molder 1977e). However, within the genus Picea, sitka spruce (Owens and Molder 1976) and white spruce collected in British Columbia (Owens and Molder 1977a), are similar in the timing and pattern of reproductive bud differentiation and subsequent development (Owens and Molder 1977e).

Owens and Molder (1977a) described the time of reproductive bud differentiation in white spruce growing at a few locations in B.C. as follows. In late-July, a marked increase in mitotic frequency occurred in differentiating reproductive apices resulting in changes in apical size, shape, and zonation. Leaf, bract, and microsporophyll initiation began at about August 1. Differentiating reproductive apices had fewer darkly staining phenolic compounds and ergastic substances than did vegetative apices at the same stage of development. Similar apical changes occurred in trees from other sites and other years. The onset of microsporophyll, bract, and leaf initiation varied from one to two weeks within a tree and between trees. Ovuliferous scale initiation began in late-August. Fraser's (1962) observation of reproductive bud development in white spruce, from early-August onward, was similar to those of Owens and Molder (1977a). There have been no similar detailed studies of black spruce.

Termination of lateral shoot elongation appears to coincide with reproductive bud differentiation in black spruce (Eis 1967), white spruce (Eis 1967, Owens and Molder 1977a), and sitka spruce (Owens and Molder 1976). Also, differentiation of reproductive buds in white spruce (Owens and Molder 1977a) and sitka spruce (Owens and Molder 1976), occurs after all bud scales have been initiated.

Reproductive bud differentiation in conifers does not appear to result from a unique floral stimulus; instead differentiation is the culmination of a series of developmental stages, each sequentially determined by a hormonal and nutritional balance at the initiation site and at the appropriate time (Jackson and Sweet 1972). This balance may be modified by environment (Owens and Molder 1976), although the exact mechanism of the interaction between environmental and endogenous factors is not well understood (Mathews 1963, Anderson 1965, Bronbo 1970).

Transition from Juvenility to Sexual Maturity

There is usually a juvenile stage during which plants will not reproduce (Jackson and Sweet 1972). Large genetic differences exist between species, provenances, and clones, both in the age at which maturation is attained and in the age at which the first flowers are normally initiated (Zimmerman 1972). Teich and Pollard (1973) and Teich (1975) reported differences in precocity between white spruce provenances from central and eastern Canada. The age at which flowering in a tree is initiated is also influenced by environmental factors (Mathews 1963).

Warmer climates hasten the onset of flowering, and trees on southern slopes may flower and fruit before trees on northern slopes (Mathews 1963). Mathews (1963) cites a

number of studies which report that trees in sunny positions, in the open or on edges of plantations, attain reproductive status earlier in life than those grown in a closed stand or in shade.

Pharis (1979) discussed the role of gibberellins (GAs) in attaining the flowering state. He suggested that in the juvenile plant the GAs are preferentially used for vegetative purposes; thus, sexual maturity occurs when there are enough GAs left over. Precocious flowering has been successfully stimulated in the Cupressaceae (Pharis et al. 1965, Pharis and Morf 1967, Hashizume 1973, Pharis 1977), Taxodiaceae (Hashizume 1973, Pharis 1977) and Pinaceae (Ross and Pharis 1976, Pharis and Ross 1976), with exogenous applications of GAs.

Environmental factors

The effect of envirironmental factors on flowering in forest trees has been extensively studied and reviewed (Mathews 1963, 1970; Anderson 1965, Bronbo 1970, Jackson and Sweet 1972, Sweet 1975, Lindgren et al. 1977). Most of the environmental factors considered in these studies, affect the differentiation and development of reproductive buds, and few have been shown to affect only the differentiation process. It appears that many of these factors affect both processes, and that the complexity of flowering makes it difficult to isolate the effects of one

factor (Anderson 1965).

The principal environmental factors affecting flower bud differentiation are: temperature, light, water supply, and nutrition. The effects of these factors have been summarized as follows:

(a) Temperature: A certain minimum accumulated heat requirement is necessary for reproductive bud differentiation, probably higher than that for vegetative buds (Fraser 1962, 1966; Mathews 1963). Warm weather during the summer, especially in June and July, favours the differentiation of reproductive buds in black spruce (Fraser 1958, 1966), white spruce (Fraser 1958, 1962), and Norway spruce (Tiren 1935, In Bronbo 1970; Lindgren et al. 1977). Usually black spruce is a more prolific and consistent producer of flowers than white spruce (Harlow and Harrar 1968). The specific differences in flowering of the two species might be due to differences between species in the time of bud formation (Fraser 1966). Black spruce forms its buds in late-June when air temperatures are consistenly higher; thus, regular reproductive bud differentiation would be favoured (Fraser 1966). Reproductive buds in white spruce, however, differentiate earlier in the growing season and probably only in years when the May-June temperatures are above a certain unknown threshold value (Fraser 1966).

(b) Light and Photoperiod: There have been many general reports on the influence of light on flowering. It is usually edge trees, open grown, or dominant trees in a stand that flower most abundantly (Mathews 1963, Anderson 1965, Bronbo 1970, Sweet 1965). These results suggest that increased light intensity may favour the differentiation of reproductive buds, although perhaps indirectly. However, the effect of photoperiod on flower bud differentiation in most conifers is inconclusive and is confounded with light intensity. A southward move of a provenance may promote flowering (Lindgren et al. 1977); although this response may be largely due to other factors, such as change in temperature regime (Bronbo 1970). Increasing day length may exert an enhancing effect on flowering (Pharis et al. 1977) simply by increasing the total amount of photosynthetically useable light or through a truly photoperiodic (i.e. phytochrome-mediated) mechanism (Pharis and Kuo 1977). Reproductive bud differentiation occurs at approximately the time of shoot growth cessation in white spruce (Eis 1967, Owens and Molder 1977), black spruce (Eis 1967), and sitka spruce (Owens and Molder 1976). Since shoot growth cessation appears to be largely influenced by photoperiod (Fraser 1952, 1966; Owens et al. 1977), reproductive bud differentiation may also be influenced by photoperiod (Jackson and Sweet 1972). However, as in light availability, the effect of photoperiod on bud differentiation may be indirect.

(c) Water supply: Different species may react differently to drought or excessive moisture (Bronbo 1970). Van Brendenburch and LaBastide (1969) and LaBastide and Van Vrendenburch (1970) showed that a wet March and a sunny warm and dry summer the previous year are important to an abundant cone crop the following year in Douglas-fir and other species in the Netherlands. Lindgren et al. (1977) suggested that high precipitation may have had a negative effect on reproductive bud differentiation in Norway spruce in Sweden. However, as higher temperatures were associated with low precipitation, it was difficult to interpret the effect of low precipitation alone (Lindgren et al. 1977). Grano (1973) found that the seed yields of 17 loblolly pine trees growing in southern Arkansas were highest when abundant spring rain and a relatively dry summer preceded flower formation. Ebell (1967) promoted flowering in potted Douglas-fir grafts in a controlled environment by drought treatment the previous year.

(d) Nutrition: A high rate of carbohydrates as compared to available nitrogen (C/N) are believed to promote reproductive differentiation (Kramer and Kozlowski 1960). However, a number of researchers have been successful in increasing reproductive activity by applying N (Shoulders 1968, Hare 1978, Hare et al. 1979). Sweet and Hong (1978) increased cone production in Monterey pine (Pinus radiata D. Donn) after exogenous applications of N. They suggested that in Pinus, N application increases crown size, and thus

the the number of sites where cones may be initiated. Similarly, Bronbo (1970) concludes that it is difficult to isolate the effect of fertiliser on flower differentiation from the general effect on tree vigour.

Endogenous Factors

Cells of the apical meristem are believed to direct the production of enzymes which catalyze the various chemical reactions that determine the form of the fully differentiated cell (Pharis and Owens 1966). The exact mechanism by which a meristem is stimulated to become a flower is not known (Pharis and Owens 1966). Auxins, GAs, and cytokinins may all be involved in bud differentiation (Mathews 1963).

A high auxin level may be involved in female flower development, and a lower level with male flower development in Pinus (Jackson and Sweet 1972, Sweet 1975). However, the role of auxin in the differentiation of reproductive buds is unclear.

GAs mediate or influence many different growth and development processes in conifers, including reproductive bud differentiation (Pharis and Kuo 1977). At least 51 different endogenous GAs have been identified in many tissues from a wide variety of coniferous species (Pharis and Kuo 1977). Different GAs have different effects, and it is probable that plants regulate growth and differentiation

by controlling the level and type of endogenous GA (and other hormones) (Pharis 1979). Many attempts have been made to correlate endogenous GA levels with flowering stage in plants subjected to cultural treatments which sometimes stimulate flowering, such as, starvation, nitrogen or phosphorous fertilization, girdling or strangulation, root pruning, drought stress, and nitrate fertilization (in Douglas fir) (Pharis 1979). When Cupressus arizonica Greene was induced to flower by low nitrogen nutrition, changes were apparent in the levels of endogenous GAs (Kuo 1973, In Pharis and Kuo 1977). Low nitrogen also caused a shift in the endogenous GAs from those of a polar nature to GAs of a relatively non-polar nature (Kuo 1973, In Pharis and Kuo 1977). Another method used to investigate the role of endogenous GAs in flowering is through the use of growth retardants before exogenous GA3 application. Using this technique on Cupressus arizonica, Pharis and Kuo (1977) found a positive correlation between the number of strobili induced and the amount of GA3 extractable from the tree. They suggested that exogenous GA3 supplements endogenous levels if it is assumed that the growth retardant has no effect on the action of applied GA3. Pharis and Kuo (1977) concluded that the presence of sufficient amounts of the appropriate GA appears to be the limiting factor in sexual differentiation of lateral primordia.

MATERIALS AND METHODS

Site

The Mattawin seed orchard is located in the Fort William unit of the Thunder Bay Forest District, site region 4W (48° 23', 89° 80'). The seed orchard is approximately 10 ha (25 acres) in area, including roads and fire guards. The orchard is surrounded by an even-aged jack pine (Pinus banksiana Lamb.) stand. It contains grafted trees made from scions obtained from mature (greater than 30 years) white and black spruce plus trees selected in Ontario Ministry of Natural Resources site region 3400 (3W) (Appendices 1, 2). All scions were grafted onto white spruce rootstock.

The seed orchard consists of 36 blocks evenly divided between the two species (Figure 1). Each block is approximately 0.2 ha (0.5 acres) in size. The blocks are designated by year of plantation (Figure 1). Each block contains 12 clones represented by 12 ramets each outplanted at a 3.6 x 3.6 m (12 x 12 ft.) spacing. Locations of clonal ramets were random with the constraint that no ramets of the same clone be adjacent. The first blocks were planted in 1966 and the last in 1972. There are 100 clones in total, 61 of black and 39 of white spruce. Some clones are represented in many blocks while other clones are not.

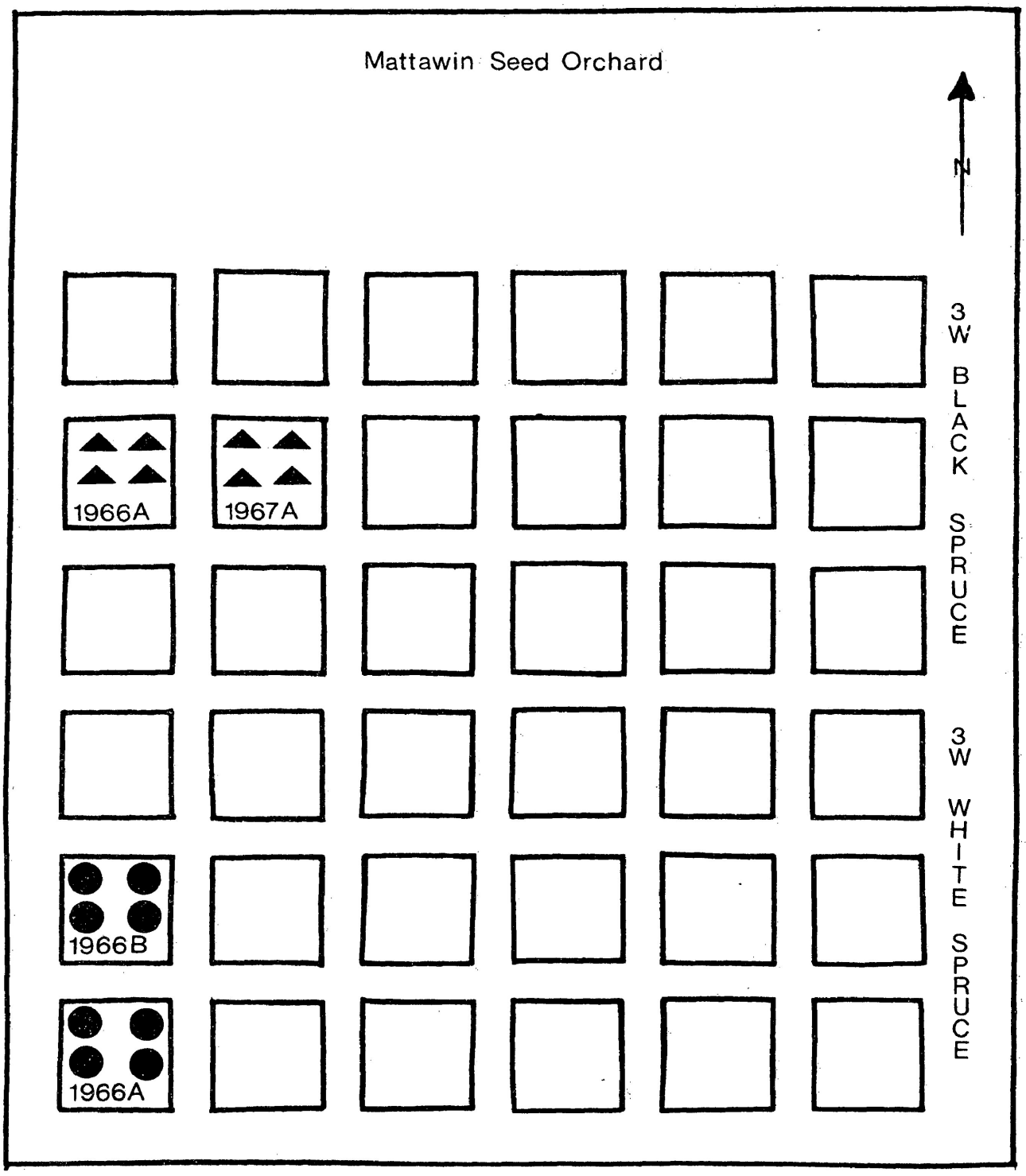


Figure 1. Block lay-out and location of white spruce (●) and black spruce (▲) blocks used.

Number of Clones and Selection Procedure

Fourteen clones each, of white and black spruce, were selected from the older blocks which were most likely to produce flowers. The origin of the clone ortets are shown in appendices 1 and 2. Four healthy, vigorous ramets were selected to represent each clone, two white spruce blocks 1966A and 1966B and two black spruce blocks 1966A and 1967A (Figure 1). Initially, block 1966B of black spruce was selected; however, this block was generally less vigorous than the others, so black spruce block 1967A was substituted.

The selected ramets were tagged, and numbered between 1 and 112 for ease of further observation. The tags were placed on the terminal shoot of a lateral branch in the fifth whorl down from the leader, on the west side of each ramet.

Temperature Data

Temperature has been determined as the most important factor in the timing of flowering and flushing (Sarvas 1968, 1972; Winton 1964; Owens et al. 1977). Therefore, accumulated temperature, as degree-days, may be more important as a reference point than calendar dates for the occurrence of these events (Sarvas 1962, 1963, 1965, 1967,

1968, 1972; Nienstaedt and King 1969, Nienstaedt 1972, Eriksson et al. 1973; Jonsson et al. 1976).

Daily temperature was recorded continuously by a hygrothermograph (Model G-450; R. Fuess, Berlin-Steglitz), located in a Stevenson screen near white spruce block 1966B (Figure 1). Temperature recording began in early spring 1979 (April 28) before any accumulated degree-days had taken place and continued until well after all clones had ceased shoot elongation (September 12).

The mean daily temperature was calculated as the average of the 12 temperature readings at two hour intervals on the hygrothermograph monitor sheet. Degree-days were calculated according to the formula $T = \sum_{n=1}^{m}(tm-5)$, where T is the temperature sum with a threshold value of $+5^{\circ}C$, n is the number of days with a mean temperature greater than $+5^{\circ}C$, and tm is the mean temperature of the nth day (Sarvas 1965) (Appendix 3).

Vegetative Phenology

A. Flushing

Flushing Data Collection

Many recent phenology studies use an index, in which identifiable stages of bud and shoot development are scored periodically in the field (Borodina 1968, Nienstaedt and King 1969, Nienstaedt 1972, Yeatman and Venkatesh 1973, Pollard and Ying 1979). This method is likely to be more accurate and objective than simply recording flushing as one event (Fraser 1962, 1966). Therefore, the index of Nienstaedt and King (1969) was used in this study (Table 1). This index covers 6 stages of bud and shoot development, from a score of 6 when the bud is in a winter condition, to a score of 1 when the shoot begins to elongate. To facilitate repetitive data collection, the following shoots were tagged on each selected ramet: (1) leader, the largest leader if multiple leaders existed; and (2) 4 vigorous lateral branches, 5 whorls down from the leader, facing north, south, east, and west.

The terminal bud of the leader and terminal bud of the four tagged lateral branches were scored every 2-3 days using the index of Nienstaedt and King (1969) (Table 1). The leader scores and the average score of the four lateral branches were plotted against scoring date for each ramet.

Table 1. Index of vegetative flushing and early shoot development.[1]

Condition	Score
Buds in winter condition	6
Buds just beginning to swell	5
Buds swelling	4
Buds green	3
Needles completely free of bud scales	2
Shoot beginning to elongate	1

1 After Nienstaedt and King (1969).

The date at which flushing (score "3") occurred was interpolated from these graphs for all ramets. However, sometimes flushing was recorded on an observational date. In this situation, graphs were not constructed, as the dates were directly recorded. Direct recording of flushing dates occurred frequently with the leader scores, as there was only one leader bud score at each date whereas the lateral branch score was the average score of four buds sometimes at slightly different stages of development.

The time of flushing of the leader and the average time of lateral branch flushing of each ramet was recorded as the number of days from May 1st and June 1st for white and black spruce, respectively. Different starting dates were used for white and black spruce as some clones of the former flushed in May while all clones of the latter flushed in June. A single reference date of May 1 was used when both species were compared, as in the Tables. The flushing dates per ramet were arranged by clone number and species for data analysis. Degree-days corresponding to these dates were also arranged by clone number.

B. Shoot Elongation and Growth Cessation Data Collection

Shoot elongation is largely controlled by temperature (Owens et al. 1977). Degree-days were used to show the influence of temperature on shoot elongation during the extension period. In contrast, the time of shoot growth cessation is largely determined by photoperiod (Kramer 1943, Fraser 1952, 1962, 1966; Nienstaedt 1974, Owens et al. 1977). Therefore, the time of shoot growth cessation was recorded by date only; degree-days were not used.

Growth cessation is frequently recorded as the time at which bud set occurs (Morgenstern 1969a, 1969b, 1978; Nicholson 1969), although bud set is difficult to determine (Nicholson 1969, Sarvas 1972). Other studies refer to growth cessation as the time at which shoot elongation is complete (Fraser 1962, 1966; Perry et al. 1966). Growth cessation can be recorded as the time at which a predetermined percentage (often 95%) of shoot elongation is complete (Nienstaedt and King 1969). One hundred percent of shoot elongation was not used as the last 5 percent (approx.) of elongation takes place over a relatively long period for all trees. Thus, clone differences in the time of growth cessation would be difficult to detect at 100 of shoot elongation.

Beginning July 2nd, shoot elongation of all tagged vegatative buds was measured every 4-6 days. Shoot elongation of the leader and average elongation of the four lateral branches were plotted against date. Date of growth cessation in the leader and the average date of growth cessation in the 4 lateral branch shoots was calculated graphically by interpolation, as the time at which 95 percent of shoot elongation had taken place.

The numbers of days to growth cessation of the leaders and the lateral branches of all ramets, arranged separately by species and clone number, were used for analysis.

A problem was encountered in determing date of growth cessation in white spruce. Growth cesation had already taken place in the lateral branch shoots of all white spruce clones at the time of first measurement, on July 2. Growth cessation was expected to occur in these shoots during early-July, but not to have occurred before early-July (Owens et al. 1977). However, growth cessation had not occurred in the leaders of white spruce.

Leader elongation of 13 white spruce clones (one clone was omitted due to leader damage to all ramets) and 14 black spruce clones and average shoot elongation of the four lateral branches of 14 black spruce clones, were averaged for each species and plotted against measurement date -- the number of days from May 1. Similar graphs were constructed using degree-days corresponding to measurement date. The

graphs were constructed to show the relative rate and duration of shoot elongation of the leaders of white and black spruce and of the leaders and lateral branches of black spruce in the Mattawin seed orchard in 1979. For leader and lateral branch elongation, the following simple regression equations were fitted: (i) linear, $Y= a+bX$; (ii) exponential, $Y= Ae^{b}$; (iii) allometric, $Y= aX^{bx}$; (iv) Logarithmic, $Y= a+b\ (Ln\ X)$; where Y= shoot elongation, X= degree-days or date, a and b= regression constants, and Ln= natural log.

Total shoot length data of the leaders of all ramets were recorded separately by clone number and species. These data were used mainly for correlation analyses, in which mean times of leader flushing and growth cessation, and the mean number of strobili per ramet per clone, were related to mean clone leader length.

The average duration of the growth period, from the time of flushing to growth cessation, was calculated in two ways for each clone: (1) the number of days and (2) degree-day accumulation. The duration of the growth period versus shoot length per clone was then subjected to simple linear correlation analysis.

C. Data Analysis

(i) Flushing

An analysis of variance of the number of days and degree-days to flushing, as a complete random design, was carried out to test for significant differences between clones in the time of flushing of (1) the leaders of white and black spruce and (2) the average of the four lateral branches. A completely randomized design was assumed because of original block design (completely random), although selection of the clone ramets was not random. However, the criteria on which the selection of clone ramets was based, were not related to vegetative or flowering phenology. Clone ramets were selected based on tree vigour.

Duncan's new multiple range (NMR) test was carried out to determine which clones were significantly different from each other in flushing degree-day requirements. All Duncan's NMR tests were carried out at the 0.05 level of significance. This test was done separately for the leader and the lateral branches and for both white and black spruce. Duncan's NMR test was used because it is easy to apply; it takes into account the number of treatments (clones); it permits decisions as to which differences are significant and which are not whereas the F test permits no such decisions when F is significant; it uses a set of significant ranges, each range depending upon the number of

means in the comparison (Steel and Torrie 1960).

(ii) Shoot Elongation and Growth Cessation

An analysis of variance of the number of days to growth cessation of the leaders and the average of the four lateral branch shoots of white and black spruce, as a complete random design, was carried out to test for significant differences between clones. The analysis of variance of growth cessation of the leader of white and black spruce had unequal replication due to pathogen damage and leader breakage. Many white spruce leaders were twisted and were difficult to measure accurately. The twisting only occurred in the leaders of white spruce, and may have been due to mild frost damage (Nienstaedt, personal communication).

Duncan's NMR test was carried out to determine which clones were significantly different from each other in the time of growth cessation of the leaders of white and black spruce and the average of the four lateral branch shoots of black spruce. Kramer's (1956, In Steel and Torrie 1960) procedure for unequal replication was used in Duncan's NMR test of leader growth cessation in white and black spruce.

An analysis of variance of leader length of white and black spruce was carried out to test for significant differences between clones. Simple linear correlation

analyses were carried out, to relate leader length to leader flushing data, date of growth cessation, and the number of strobili per clone when clone differences were significantly different.

Flowering Phenology

A. Data Collection

(i) Pollen Release

The time of pollen release can be accurately recorded by using an automatic pollen registering apparatus. These samplers are useful especially for measuring stand or population phenology (Sarvas 1962, 1963, 1967, 1968, 1972; Basset 1964, Grano 1966, 1973; Zasada et al. 1978) or in a seed orchard (Jonsson et al. 1976). However, wind and rain may adversely affect the accuracy (Sarvas 1967, 1972), and it does not discriminate between pollen release of individual trees and strobili (Eriksson et al. 1973, Barnes and Mullin 1974, Jonsson et al. 1976, Zasada et al. 1978).

An index of male strobilus development and pollen release as used by Polk (1966), Wasser (1967) and Borodina (1968) appears to be more flexible, as it discriminates between pollen release of individual trees and strobili, and is less affected by wind and rain. An index was used in

this study similar to those of Polk (1966), Wasser (1967) and Borodina (1968) (Table 2). This index consists of 7 stages of microstrobilus development from a score of 7 when the buds are in a winter condition, to the stages when increasing (4), maximum (3), and decreasing (2) amounts of pollen are being released from the microsporangia, and lastly a score of 1 when all pollen release has terminated and the strobilus is beginning to shrivel.

Ten black spruce male buds were located and tagged as close as possible to the fifth whorl down from the leader on each ramet as soon as positive identification was made. These buds were so selected to reduce within tree variability (Polk 1966, Nienstaedt, personal communication), and were numbered from 1 to 10 on each ramet. However, some ramets had no male or fewer than 10 male strobili. Black spruce clone 393 bore no male strobili on any of its ramets used in this study.

The male strobili tagged above were scored every 2-3 days on all ramets over the period of male strobilus development and pollen release until all pollen had been released, using the index presented in Table 2.

All stages of male strobilus development and pollen release were observed and scored, although only the stages of pollen release were used in data analysis and presentation. The important stages of male strobilus development covering pollen release were converted to

Table 2. Index of reproductive bud and strobilus development.

Female	Score	Male
Buds in winter condition	7	Buds in winter condition
Buds swollen	6	Buds swollen
Strobili emerge, but are closed and largely covered by bud scales	5	Strobili emerge - sometimes covered by bud scales. No pollen release
Strobili partially receptive (50 percent assumed). Some cone scales are open and others are beginning to open	4	Pollen release begins. Some cone scales are open (50 percent assumed)
Strobili are fully receptive (100 percent assumed). Most cone scales are open	3	Maximum pollen release. Most cone scales are open (100 percent assumed). A pollen cloud can be seen after shaking the strobilus
Strobili partially perceptive (50 percent assumed). Cone scales are closing	2	Little pollen release. Many of the cone scales are fully open and no pollen remains. Some pollen is released from other microsporophylls (50 percent assumed)
Strobili not receptive. Cone scales have closed completely	1	No pollen release. Strobili begin to shrivel up and fall off

percentage pollen release scores as follows: the scores of 4, 3 and 2 were designated to represent 50, 100 and 50 percent rates of pollen release, respectively. It was assumed, using this method, that 50 or 100 percent of the microsporangia of an observed strobilus were releasing pollen depending upon the score it received. Zasada et al. (1978) made similar assumptions when observing white spruce strobili in Alaska.

Percentage pollen release on any scoring date for each ramet was calculated as the average score of the 10 strobili observed. Ramets bearing less than 10 strobili were not used. The average percentages of pollen release of each ramet on all observation dates were arranged by clone number for analysis.

(ii) Female Receptivity

Accurate determination of the time of female strobilus receptivity would require a series of controlled pollinations (Nienstaedt 1958). Conducting a series of controlled pollinations would be impractical in observing a large number of trees.

Various indexes have been used, in which identifiable stages of megastrobilus development and receptivity are scored periodically as in flushing and male phenology

observations (Cumming and Righter 1948, Polk 1966, Wasser 1967, Borodina 1968, Eriksson et al. 1973, Jonsson et al. 1976, Danials 1978). The index method has the advantage in that many strobili can be easily and quickly observed. This advantage makes the method suitable for observing a large number of clones in a seed orchard (Eriksson et al. 1973, Jonsson et al. 1976), and thus was used in this study (Table 2). The index consists of 7 stages of megastrobilus development, from a score of 7 when the buds are in a winter condition, to the stages of increasing (4), maximum (3), and decreasing (2) receptivity, and lastly a score of 1 when the strobilus is no longer receptive (Table 2).

When positive identification was possible, 10 black spruce megastrobilus buds were selected in, or close to, the third whorl down from the leader of each ramet. These buds were tagged and numbered from 1 to 10, and were so located within the crown to reduce within tree variability in the stages of megastrobilus development and receptivity (Polk 1966, Nienstaedt, personal communication).

The tagged megastrobilus buds on each ramet were scored every 2-3 days throughout the period from bud swelling and receptivity, to the non-receptive stage using an index similar to Polk (1966), Wasser (1967), and Borodina (1968) (Table 2).

Although 7 stages of megastrobilus development and receptivity were observed (Table 2), only the stages of receptivity were used in data analysis and presentation. These stages of female receptivity were used because they are the stages when pollination is possible. The scored stages of megastrobilus development of 4, 3 and 2 were designated to represent 50, 100 and 50 percent receptivity, respectively. It was assumed, using this method, that 50 or 100 percent of the megasporangia of an observed megastrobilus were receptive to pollination depending on developmental score.

Percentage female receptivity of each ramet was calculated on any scoring date as the average of the 10 observed strobili. Ramets bearing less than 10 female strobili were not used. The average percentage stages of female receptivity per ramet were then arranged by scoring date for each clone to facilitate further analysis.

B. Data Analysis and Presentation

Graphs were constructed to demonstrate the average progress of pollen release and female receptivity of all black spruce clones observed. Average percentage pollen release of 12 clones and receptivity of 14 clones of black spruce was graphed against degree-days and date.

Additional graphs were constructed showing the cumulative progress of pollen release and female receptivity based on the average of 12 clones for pollen release and 14 clones for female receptivity. This calculation was carried out by expressing the average percentage pollen release on each observational date or corresponding degree-day sum, as a percentage of the total accumulation of these scores. In this fashion, the last observational date of pollen release and female receptivity would equal 100 percent. The same simple regression equations were fitted to these data points as in shoot elongation where Y= cumulative percentage score, and X= degree-days or date.

Graphs of percentage pollen release and female receptivity of each ramet versus date were constructed for all clones. The points on these graphs were joined by straight lines. For each ramet, the date at which 50 percent pollen release and female receptivity occurred on the ascending and descending part of the curves were recorded by ramet and clone. Thus, there were two dates for each ramet, one representing 50 percent at the beginning and the other 50 percent at the end of pollen release and female receptivity. The average of these two dates was taken as the date at the midpoint of pollen release or female receptivity for each ramet. The midpoint dates of pollen release and female receptivity were calculated for all clones as well as corresponding degree-days.

The average dates and degree-days at the midpoints of pollen release and female receptivity were separately subjected to an analysis of variance to test for significant differences between clones. As in flushing, growth cessation, and shoot length analysis, a completely random design was assumed. The analysis of variance had unequal replication due to too few strobili on some ramets.

Degree-day requirements for pollen release and female receptivity were subjected to Duncan's NMR test, using Kramer's (1956, In Steel and Torrie 1960) procedure for unequal replication, to determine which clones were significantly different from each other.

Separate graphs of date versus percentage female receptivity were made for all ramets of a few arbitrarily selected clones assuming that all scores of receptivity using the index (Table 2) indicate 100 percent receptivity. These graphs were constructed to see if it made any appreciable change in the shape of the curves compared with the curves constructed assuming two different levels of receptivity, thus increasing the inherent error if the assumptions made in constructing the graphs were incorrect. However, the shape of the curve changed little, resulting only in a more rapid increase and decrease in flowering progress, and an extension in the duration of maximum receptivity. Overall, the results arrived at by using the method described earlier would not be much affected by a

more liberal interpretation of female receptivity, especially as the relative differences between ramets and clones should be similar.

Reproductive Dynamics

A. Number of Strobili

Data Collection

A knowledge of the average time of flowering of clones in a seed orchard is of limited use in estimating its effect on genetic makeup of the progeny unless the number of strobili involved are known (Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). Therefore, an estimate was made of black spruce strobilus production per ramet and clone in this study.

The number of female strobili were counted on all ramets of the clones used in the phenology study. The number of male strobili were counted on the same ramets, except those having more than 1 200 strobili (approx.). An estimate of the number of strobili on ramets bearing more than 1 200 strobili was made due to the time it took to make total counts. In addition, total counts with such large numbers may have a large associated error due to strobilus double counting and strobilus drop before time of count.

Strobilus counts on ramets having less than 200 strobili (approx.) were difficult as they required much time to locate the few strobili scattered throughout the crown. Also, there was always a possibility of missing strobili due to strobilus drop after pollination. The above problems were less likely with ramets having between 200 and 1 200 strobili as they bore their strobili relatively evenly distributed throughout the crown, and previous strobilus drop could be easily recognized by the cone scars.

The number of strobili was estimated, on ramets bearing more than 1 200 strobili, as follows: the number of strobili on two arbitrarily chosen branches of a whorl was averaged and multiplied by the number of branches in that whorl; the number of srobili per whorl was thus calculated and summed for all whorls of each ramet; these totals were recorded by clone number. The same procedure was conducted on all whorls of all ramets being estimated. This method was similar to the method used previously by Nienstaedt (1980). It is assumed that the estimate falls within 25 percent of the true value, and it may be expected that the error per clone would be lower (Eriksson et al. 1973, Jonsson et al. 1976).

The number of male strobili was stratified into classes of 200 mainly because many of the counts were estimated, and because of the number of problems associated with counts on ramets having less than 200 strobili. Therefore, the number

of male strobili was stratified into classes as follows: 10 to 200 strobili = 1, 200 to 400 strobili = 2, etc. The error associated with this method should be small because of the large range in the number of male strobili (from 0 to more than 7 000 per ramet). In addition, handling the data was made simpler.

The number of female strobili per ramet and the stratification class numbers for male strobili per ramet were arranged separately by clone number.

At the field, it was noticed that the tallest ramets appeared to carry the greatest number of male strobili. Therefore, the heights of all tagged black spruce ramets were measured using a height measuring pole. The heights of all ramets, to the nearest tenth of a metre, were recorded by clone number.

Data Analysis

The number of female strobili per ramet was subjected to an analysis of variance to test for significant differences between clones. The number of male strobili per ramet (stratification numbers) was subjected to an analysis of covariance to release the effect of height. Thus, differences between clones in the number of male strobili, without the effect of height, could be evaluated.

The numbers of male and female strobili per ramet per clone were graphed against mean ramet height per clone. It is biologically probable that the number of strobili increases with an increase in the size of the tree crown (Eriksson et al. 1973). Thus, the number of strobili may increase faster than linearly by height (Eriksson et al. 1973). Therefore, as well as the simple regression equations as used on the data of shoot elongation, cumulative pollen release and female receptivity, the following transformations were tested: (i) Log-Log: Log Y= a+blog X, (ii) square root: square root of Y= a+bX, where Y= number of male or female strobili, X= mean ramet height per clone, and a, b= regression constants.

B. Gamete Contributions and Genetic Composition of the Progeny

Information on the timing and duration of pollen release and female receptivity, and the number of male and female strobili per clone, can be combined to estimate the genetic composition of the progeny. An estimate was made of the genetic composition of the progeny of a sample of 12 black spruce clones in the Mattawin seed orchard based on one year's observation, using a method similar to Eriksson et al. (1973) and Jonsson et al (1976). Two clones were omitted, clone 283 due to incongruous pollen release

results; the average index score for pollen release in this clone decreased and then increased again whereas the scores should only reduce with time. This error probably occurred during field data collection. Clone 393 was omitted due to lack of male strobili.

In order to calculate the genetic composition of the progeny, an estimate was made of the clone contributions to the pollen cloud.

The Pollen Cloud

The daily clone contributions to the pollen cloud was calculated as follows:

1) For each clone, the mean number of male strobili per ramet (Table 19) was expressed as a percent of the total summation of mean number of male strobili per ramet of all clones (Table 23).

2) The percentage number of male strobili per ramet per clone (Table 23) was multipled by the percentage stage of pollen release (Table 17) of that clone for each day; it was assumed that the percentage stage of pollen release determined on a sample of 10 strobili from each ramet in a clone was representative of all strobili in that clone. These calculations gave relative measures of the pollen contributions of a clone for each day. The percentage

stages of pollen release for all clones on intermediate days, when no field observations were made, were interpolated from the graphs of clonal percentage pollen release (Appendix 4).

3) The relative daily measures of pollen contribution from each clone were expressed as a percentage of the summation of all clones' relative contributions for that day. These daily percentage values of the clonal contributions to the pollen cloud were tabulated by date and clone number.

The Genetic Composition of the Progeny

The genetic composition of the progeny was estimated using the information on the daily percentage clone contributions to the pollen cloud (Table 27), the daily clone percentage stage of female receptivity (Table 18), and the percentage number of female strobili per clone (Table 23).

To get relative measures, clonal percentage stage of female receptivity (Table 18) was multiplied by the percentage contribution of pollen from each clone for all days during the full period of female receptivity. An example of this calculation is shown for clone 288 in appendix 5. These relative numbers were summed up for all

days for every combination of clones. The total sum of each clone as a male contributor (far right column, appendix 5) to a female parental clone was then divided by the total summation of all male contributions to this female parent (lower right corner, appendix 5). This calculation was done for each clone as a female parent, giving the proportional contribution of all male parental clones to each female parental clone. These proportions were multiplied by the percentage number of female strobili per ramet for each parental clone (Table 23). The percentage clone composition of each possible crossing combination, thus obtained, was tabulated indicating the male parental contributions horizontally, and the female parental contributions vertically (Table 28).

By adding the rows and columns in Table 28, the percentage contribution of the clones to the progeny as male (columns) or female (rows) parents was obtained. The average of the percentage values of one clone as a male and female parent, expresses the genetic contribution of a clone in the filial generation. This calculation was done for all 12 clones.

The total percentage of selfed-pollinations was calculated from the same Table by adding the numbers on the diagonal from upper left corner to lower right corner.

Differentiation and Early Development of Reproductive Buds in White and Black Spruce

Careful observation of dissected buds using a dissecting microscope can be an accurate method of estimating the time of reproductive bud differentiation in white and black spruce (Eis 1967). Therefore, the time of reproductive bud differentiation was estimated in this study using this technique.

Selection of Study Material: White spruce clones 287, and 305, and black spruce clones 288, and 303 were selected. These clones were arbitrarily chosen based on vigour and visible evidence of past cone crops.

Two branches, one from the upper and middle crown, likely to produce female and male buds respectively, were taken weekly from one ramet in each clone from July 9, until August 30, 1979. One more collection was taken on September 13. This collection period was considered to cover the full range of reproductive bud differentiation and later development. A healthy ramet was chosen arbitrarily from each selected clone in white spruce blocks 1966A, and 1966B, and black spruce blocks 1966A and 1967A (Figure 1); these are the same blocks as used in the phenology and cone production study. A different ramet from each of the four clones' 12 representative ramets was usually chosen at each collection.

In the laboratory, most 1979 shoots were removed from each branch and fixed in formalin-acetic-acid-alcohol (FAA) (Johansen 1940).

Beginning with the latest samples, buds were dissected under 70 percent ethanol using a Zeiss dissecting microscope. Selected stages of vegetative and reproductive bud development were stained in acid fuchsin, and prepared for photomicrography according to the technique described by Sattler (1968). These buds were photographed using a Zeiss epimicroscope equipped with Leitz Ultropak objectives fitted with immersion attachments. Kodak high contrast copy film was used to record the stages of development.

A few buds at selected stages of development were prepared for the scanning electron microscope (SEM). SEM photographs were made to determine the usefulness of the technique in this type of study.

In preparation for the SEM, dissected buds were placed in 100 percent ethanol for about two hours. The buds were then taken through a series of increasing concentrations of amyl acetate, immersed for about ten minutes in each solution. Finally, the bud samples were taken though two changes of 100 percent amyl acetate, for about ten minutes each. Immediately after, the specimens were dried to the critical point using CO_2 (Hyat 1974).

The dried sprecimens were mounted on SEM stubs using silver dag. The buds were coated with gold before being placed in the SEM vacuum tube. The photographs were taken using Kodak plus X-film.

RESULTS

All flushing, shoot elongation, and flowering data, were analysed based upon both degree-days and dates. However, to avoid duplication, all statistical tests and graphs are presented using only degree-days. Generally, degree-days gave the most consistant results, although the differences between the two methods were small. Dates are used in the text, while dates and corresponding degree-days are presented in the Tables. Shoot growth cessation data were analysed using dates only as the time of growth cessation is largely determined by photoperiod (Kramer 1943, Fraser 1952, 1962, 1966; Nienstaedt 1974, Owens et al. 1977).

Vegetative Phenology

A. Flushing

Mean clone flushing dates of the terminal bud of the leaders began on May 31 and ended on June 9 in white spruce (Table 3) and began and ended on June 12 and 17, respectively, in black spruce (Table 4). Mean clone flushing dates of the lateral branch buds began on June 1 and ended on June 7 in white spruce and began and ended on June 11 and 21, respectively, in black spruce. Mean date of

Table 3. Average degree-day requirements and corresponding number of days to flushing for the terminal bud of the leader and lateral branches of 14 clones of white spruce[1].

Leaders				Lateral branches			
Clone no.[2]	Clonal flushing degree-day requirements	Days to flushing	Standard deviation of number of days to flushing	Clone no.[2]	Clonal flushing degree-day requirements	Days to flushing	Standard deviation of number of days to flushing
	Degree-days	Number of days from May 1	Number of days		Degree-days	Number of days from May 1	Number of days
282	66.8	31	1.3	262	67.9	32	2.5
630	73.2	33	1.9	282	79.4	34	3.2
389	74.2	33	1.7	389	88.8	36	0.6
262	75.6	33	1.6	261	90.8	36	2.2
305	81.8	35	1.5	289	93.4	36	1.9
395	82.9	35	1.9	270	93.9	37	0.5
261	88.8	36	2.1	306	93.9	37	0.5
286	94.4	37	1.7	287	94.4	37	1.7
289	94.5	37	1.9	305	94.9	37	0.0
306	95.4	37	1.5	630	95.4	37	1.5
397	104.0	38	3.6	397	98.1	37	2.3
287	104.7	38	1.5	395	99.1	37	2.1
270	109.4	39	0.0	286	101.7	38	2.1
281	114.4	40	2.0	281	105.4	38	2.2
Mean	90.0	36			92.7	36	

[1] Clones not significantly different from each other in flushing degree-day requirements, using Duncan's NMR test (at 0.05 level), are sidescored with a continuous line.

[2] Clones are ranked according to flushing degree-day requirements.

Table 4. Average degree-day requirements and corresponding number of days to flushing for the terminal bud of the leader and lateral branches of 14 clones of black spruce[1].

Clone no.[2]	Leaders			Clone no.[2]	Lateral branches		
	Clonal flushing degree-day requirements	Days to flushing	Standard deviation of number of days to flushing		Clonal flushing degree-day requirements	Days to flushing	Standard deviation of number of days to flushing
	Degree-days	Number of days from May 1	Number of days		Degree-days	Number of days from May 1	Number of days
283	126.6	43	0.6	283	125.3	42	0.5
492	126.6	43	0.6	393	129.2	43	0.0
393	127.9	43	0.5	492	130.6	43	0.8
386	129.4	43	1.0	387	136.2	43	1.9
284	130.3	42	4.1	490	143.9	44	0.5
387	137.1	44	1.3	288	147.6	45	0.6
490	142.7	44	2.1	284	147.8	44	5.0
290	144.9	44	1.0	386	154.5	45	0.8
288	151.3	45	0.5	491	158.2	45	0.5
491	169.4	46	2.2	290	167.6	46	0.0
304	172.7	47	1.3	291	179.0	47	0.8
291	175.9	47	1.3	304	184.4	48	0.6
384	182.1	48	0.6	384	186.6	48	0.5
303	190.0	48	1.3	303	216.0	52	1.0
Mean	150.5	45			157.6	45	

[1] Clones not significantly different from each other in flushing degree-day requirements, using Duncan's NMR test (at 0.05 level), are sidescored with a continuous line.

[2] Clones are ranked according to flushing degree-day requirements.

flushing of both leader and lateral branch buds of all clones was June 5 and 14 for white and black spruce, respectively. Clones of white and black spruce are ranked in Tables 3 and 4 according to flushing degree-day requirements. The corresponding number of days to flushing for each clone is also given.

An analysis of variance was performed on flushing degree-day requirements for the leader buds of white spruce (Table 5) and black spruce (Table 6) and the average of the lateral branch buds of white spruce (Table 7) and black spruce (Table 8). Differences between clones were highly significant in all tests (0.01 level). Clonal mean degree-day requirements not significantly different from each other, using Duncan's NMR test, are sidescored with a continuous line in Tables 3 and 4. Generally, Duncan's NMR test showed that many clones were not significantly different from each other, especially that of lateral branch flushing in white spruce (Table 3). For example, the white spruce clones could probably be divided into three groups based on Duncan's NMR test of leader flushing: Clones 282-262, 305-306, 397-281. However, only the earliest (Clone 262) and the latest (Clone 281) flushing clones of white spruce are demonstrated to be significantly different from the other clones on the basis of lateral branch flushing (Table 3). Black spruce clones might be roughly divided into two groups on the basis of flushing in the leader buds: clones 283-288, 491-303 (Table 4). Black

Table 5. Analysis of variance of leader flushing degree-day requirements in white spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	11 400.9	878.0	8.4
Within clones	42	4 375.2	104.2	
Total	55	15 776.1		

Table 6. Analysis of variance of leader flushing degree-day requirements in black spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	27 199.1	2 092.2	8.3
Within clones	42	10 569.4	251.7	
Total	55	37 768.5		

[1] $F_{0.01,\ 13/42} = 2.59$

Table 7. Analysis of variance of lateral branch flushing degree-day requirements in white spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	4 572.2	351.7	3.1
Within clones	42	4 807.9	114.5	
Total	55	9 380.1		

Table 8. Analysis of variance of lateral branch flushing degree-day requirements in black spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	35 824.6	2 755.7	13.1
Within clones	42	8 841.4	210.5	
Total	55	44 666.0		

[1] $F_{0.01,\ 13/42=2.59}$

spruce clones would be difficult to divide into groups based on flushing of the lateral branch buds (Table 4).

The white and black spruce clones leader flushing degree-day requirements were significantly correlated with lateral branch flushing degree-day requirements (Figure 2). The correlation coefficient was highly significant in black spruce (0.01 level) but less so in white spruce (0.05 level) (Figure 2). Generally, these relationships show that flushing time in the leader differs little from that in the lateral branch buds for both species, although there is some scatter around the regression lines, especially in white spruce.

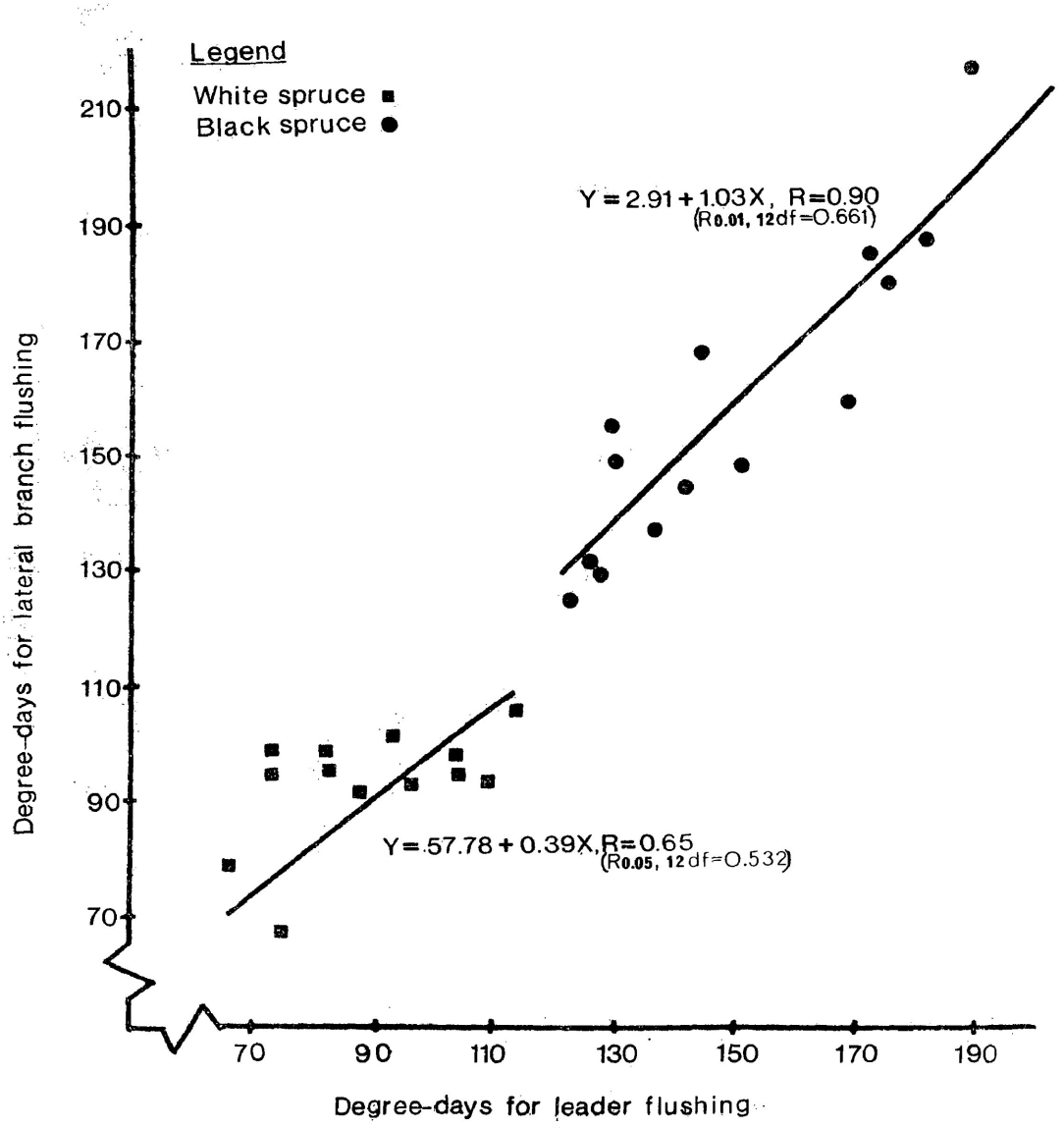


Figure 2. Degree-day requirements for leader flushing versus lateral branch flushing of white and black spruce.

B. Shoot Elongation and Growth Cessation

(i) Shoot Elongation

The mean length of shoot elongation of the leaders of 13 white spruce and the leaders and the lateral branches of 14 black spruce clones on each measurement date are graphed against degree-days (Figure 3). The logarithmic equation $Y= a+b (Ln X)$ gave the highest R value for these data points, where Y= length of elongation (mm), Ln= natural logarithm, X= degree-days, and a and b= regression constants (Figure 3). The correlation coeffecients for these relationships were significant at the 0.01 level for the leaders of white and black spruce but not for the lateral branches of black spruce. Average shoot length at time of flushing was not known. Nevertheless, reference values of shoot elongation were calculated for the average flushing times of white and black spruce, assuming that approximately 30 percent of total shoot elongation had taken place at this time (Owens et al. 1977). A discontinuous line was used to indicate elongation that had taken place between flushing and first measurement (Figure 3).

Fifty-eight percent of total shoot elongation of the leaders of white spruce had taken place at time of first measurement, on July 2, while 55 and 82 percent of leader and lateral branch shoot elongation, respectively, of black spruce had taken place at time of first measurement, on July

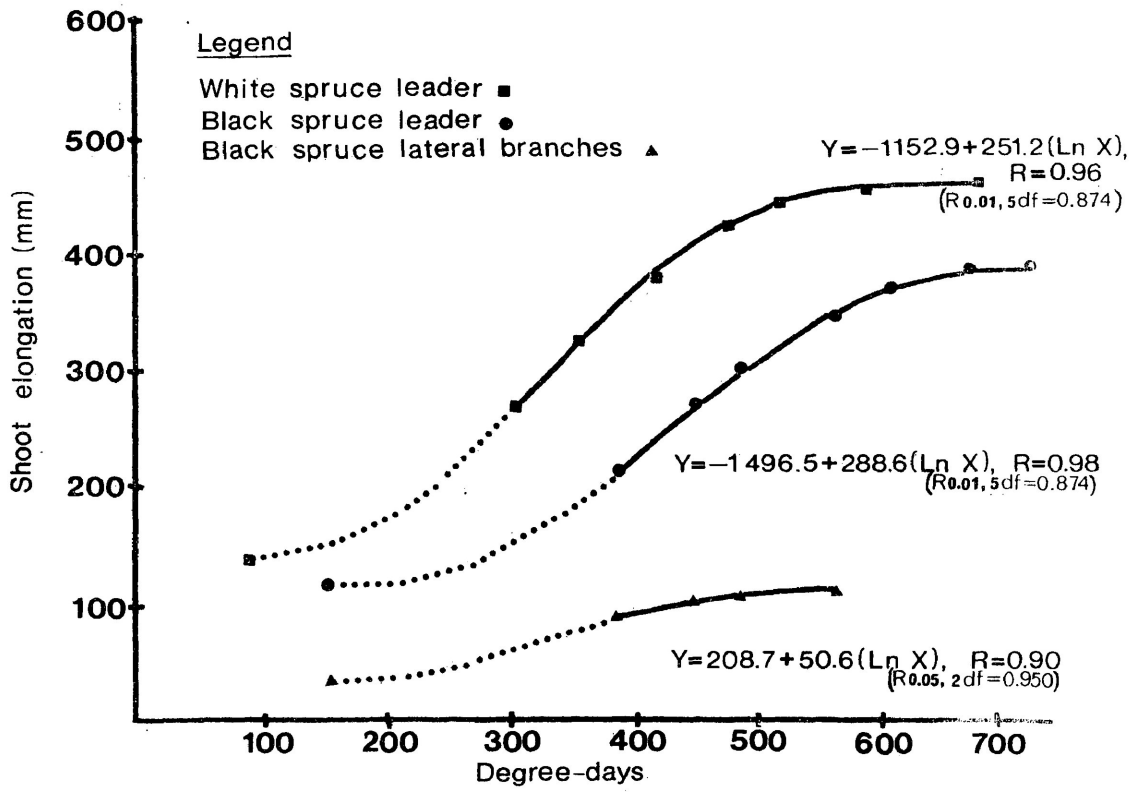


Figure 3. Degree-days versus shoot elongation of the leaders of white and black spruce and the lateral branch shoots of black spruce.

9 (Figure 9).

Leader growth of white spruce exceeded that of black spruce at any degree-day sum (Figure 3). However, leader growth of white spruce tapered off before that of black spruce (Figure 3). Most black spruce lateral branch elongation had taken place by the time of first measurement.

The duration of the period of leader elongation in black spruce clones, using degree-day accumulation and number of days from flushing to growth cessation, versus mean ramet leader length per clone, was subjected to a linear correlation analysis. The correlation coefficient was not significant: degree-days, R= 0.22, 12 df; number of days, R= 0.42, 12 df.

Average total length of the leaders of white spruce (457 mm) was greater than that of black spruce (388 mm) (Figure 3). Clone differences in leader length of white spruce were not significant using an analysis of variance (Table 9), while in black spruce clone differences in leader length were significant at the 0.05 level (Table 10). Mean leader length per clone is presented in Table 11 (white spruce) and Table 13 (black spruce).

Mean leader flushing degree-day requirements per clone of black spruce (Table 4) were plotted against mean leader length (Table 13). The linear correlation coefficient (R= -0.57, 12 df) was just significant at the 0.05 level

Table 9. Analysis of variance of total leader length of white spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	12	136 037.0	11 336.4	1.50[NS]
Within clones	24	181 481.4	7 561.7	
Total	36	317 518.4		

[1] $F_{0.10,\ 12/24} = 1.83$, NS = not significant

Table 10. Analysis of variance of total leader length of black spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	120 938.0	9 302.9	2.16
Within clones	35	150 509.8	4 300.3	
Total	48	271 447.8		

[1] $F_{0.05,\ 13/35} = 2.04$

(R0.05, 12 df= 0.532) (Figure 4). Generally, the earliest flushing clones produced the greatest leader extension.

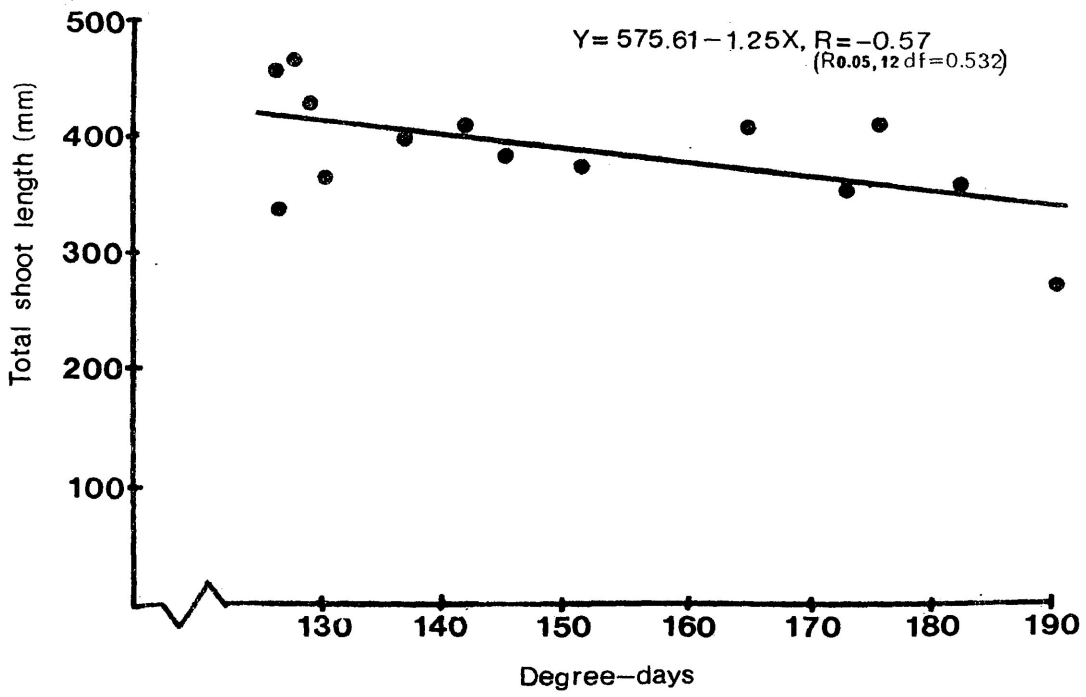


Figure 4. Regression of clone flushing degree–day requirements versus total clone leader length for black spruce.

(ii) Growth Cessation

Growth cessation of the leaders of the white spruce clones occurred between July 12 and July 23 (Table 11), encompassing a range of 12 days, inclusive. The mean date of growth cessation of the leaders of the 13 white spruce clones was July 17 (Table 11). Table 11 ranks the times of growth cessation of the individual white spruce clones, and gives the corresponding average leader lengths. Clone differences in the times of leader growth cessation of white spruce were only significant at the 0.10 level using an analysis of variance (Table 12). Duncan's NMR test showed that few white spruce clones were significantly different from each other. Therefore, in this case, clones not significantly different from each other were not sidescored by a continuous line in Table 11. Clone differences in leader length were not significant using an analysis of variance (Table 9). Therefore, no correlation analysis was carried out between time of growth cessation versus leader length. In addition, linear correlation analysis carried out between the time of leader flushing (Table 3) and the time of growth cessation (Table 11) showed no significance ($R = 0.40$, 11 df).

Growth cessation in the leaders of the black spruce clones occurred between July 21 and July 30 (Table 13), which is a range of 10 days, inclusive. The mean date of leader growth cessation of the 14 black spruce clones was

Table 11. Mean number of days to growth cessation and mean leader length of white spruce.

Clone no.[1]	Growth cessation		Leader length	
	Days to cessation	Standard deviation	Total[2] length	Standard deviation
	Days from May 1	Number of days	mm	mm
306	73	1.2	400.2	58.2
389	73	1.9	393.8	55.4
289	73	2.7	351.0	49.6
282	77	0.1	407.5	57.8
395	78	2.0	459.3	75.2
261	78	8.6	499.0	149.1
305	78	0.9	463.0	30.6
630	79	2.1	457.3	65.7
270	79	6.0	429.8	141.3
281	81	0.5	512.0	106.2
287	81	6.5	476.0	119.0
286	82	1.1	587.0	18.4
397	84	1.1	507.0	35.6
Mean	78		457.1	

[1] Clones are ranked according to number of days to growth cessation.

[2] Analysis of variance showed that clone differences were not significant (Table 9).

Table 12. Analysis of variance of white spruce leader growth cessation based on number of days from May 1.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	12	407.2	33.9	2.02
Within clones	24	402.3	16.8	
Total	36			

[1] $F_{0.10,\ 12/24} = 1.83$

Table 13. Mean number of days to growth cessation and mean leader length of black spruce.

Clone no.[1]	Growth cessation		Leader length	
	Days to cessation	Standard deviation	Total length	Standard deviation
	Days from May 1	Number of days	mm	mm
283	82	3.9	457.3	108.5
284	82	0.9	362.0	18.4
492	84	3.5	339.5	94.2
384	85	1.4	352.3	51.6
387	86	3.1	403.5	74.6
288	86	1.7	375.8	21.3
491	88	2.8	407.8	41.1
490	88	5.1	411.5	103.9
304	89	2.2	354.7	31.6
291	90	3.1	407.5	40.7
303	90	0.8	273.3	46.1
290	90	3.2	384.8	93.5
386	91	2.3	429.3	41.1
393	91	0.6	466.7	38.8
Mean	87		387.6	

[1] Clones are ranked according to number of days to growth cessation.

July 26 (Table 13). Table 13 ranks the times of growth cessation of the leader of the individual black spruce clones and gives the corresponding mean total leader length. Times of leader growth cessation of black spruce showed significant differences between clones at the 0.01 level using an analysis of variance (Table 14). Duncan's NMR test showed that most clones were not significantly different from each other. As in white spruce, clones not significantly different, using this test, are not sidescored by a continuous line (Table 13). Time of leader growth cessation per clone (Table 13) was not significantly correlated with leader length (Table 13) and time of flushing (Table 4), using simple linear regression: leader length, R= 0.04, 12 df; flushing, R= 0.32, 12 df.

Growth cessation of the lateral branches of black spruce clones occurred between July 10 and 15, a range of only 6 days, inclusive (Table 15). The mean date of lateral branch growth cessation was July 12 (Table 15). Table 15 ranks the clones of black spruce according to the time of lateral branch growth cessation. Times of black spruce lateral branch growth cessation showed significant differences between clones at the 0.05 level using an analysis of variance (Table 16). Duncan's NMR test showed that few clones were significantly different from each other. For this reason, clones not significantly different from each other are not sidescored in Table 16.

Table 14. Analysis of variance of black spruce leader shoot growth cessation based on number of days from June 1.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	432.1	33.3	4.45
Within clones	35	261.4	7.5	
Total	48	693.5		

[1] $F_{0.01,\ 13/35} = 2.67$

Table 15. Mean number of days to growth cessation of the lateral branch shoots of black spruce.

Clone no.	Days to cessation	Standard deviation
	Days from May 1	Number of days
288	71	1.3
283	72	1.6
490	72	1.2
492	72	1.3
290	72	1.4
303	72	1.1
491	73	0.5
291	73	1.8
384	74	1.9
304	74	0.5
393	74	1.1
386	74	1.1
387	75	2.5
284	76	3.9
Mean	73	

[1] Clones are ranked according to number of days to growth cessation.

Table 16. Analysis of variance of black spruce lateral branch growth cessation based on number of days from June 1.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	96.3	7.4	2.51
Within clones	42	124.0	3.0	
Total	55			

[1] $F_{0.01, 13/42} = 2.39$

Time of growth cessation and flushing are probably mutually independent events, although the controlling genetic and physiological factors may be related. Therefore, only simple linear regression tests were carried out to see if early flushing clones were also early in their time of growth cessation, and similarly to see if time of leader growth cessation was correlated with lateral branch growth cessation. Time of lateral branch flushing of the black spruce clones (Table 4) was not significantly correlated with time of lateral branch growth cessation (Table 15) ($R = 0.03$, 12 df). In addition, time of lateral branch growth cessation (Table 15) was not significantly correlated with time of leader growth cessation (Table 13) ($R = 0.05$, 12 df).

Flowering Phenology

Maximum pollen release and female receptivity of all black spruce clones occurred on June 10. Pollen release and female receptivity began on June 4 and ended on June 15 for the former and June 18 for the latter, a range of 13 and 16 days, respectively (Figure 5). Tables 17 and 18 show the percentage progress of pollen release and female receptivity of the individual clones throughout this period. Percentage pollen release and female receptivity are graphed against degree-days in Figure 5. These graphs show that the percentage progress of pollen release and female receptivity is rapid. Also, the shape of the graphs closely resemble a normal distribution, although this was not tested statistically (Figure 5).

Figure 6 shows the cumulative percentage progress of pollen release and female receptivity of all black spruce clones versus degree-days. These curves closely resemble the typical growth curve (cf. Figure 3). The superimposed pollen release and female receptivity curves were almost identical; thus, only one curve is used to represent both pollen release and female receptivity. As in shoot elongation (Figure 3), the logarithmic equation $Y= a+b\ (Ln\ X)$ gave the highest R value for cumulative pollen release ($R= 0.93$, 6 df) and female receptivity ($R= 0.86$, 6 df), where Y= cumulative pollen release or female receptivity, Ln= natural logarithm, X= degree-days, and a and

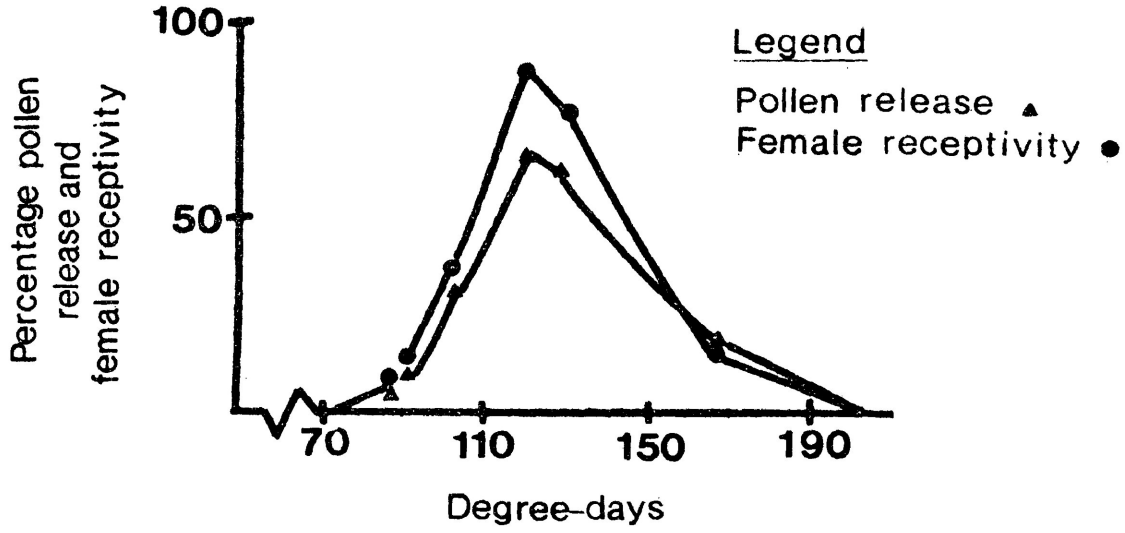


Figure 5. Average percentage pollen release and female receptivity of all black spruce clones versus degree-days.

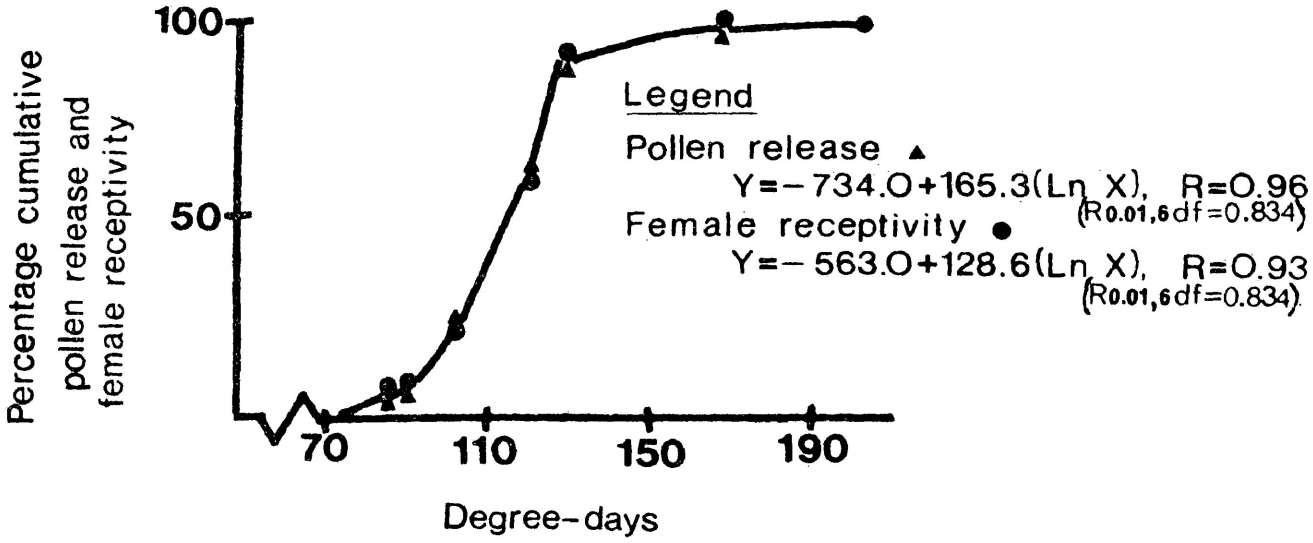


Figure 6. Cumulative percentage pollen release and female receptivity of all black spruce clones versus degree-days.

Table 17. Daily percentage pollen release of black spruce clones.

Date (June)	4[1]	5[1]	6[2]	7[1]	8[2]	9[2]	10[1]	11[2]	12[1]	13[2]	14[2]	15[1]	16[2]	17[2]	18[1]
Clone no.															
288					12	24	36	49	61	55	50	45	30	17	
303				2	13	24	35	50	65	62	60	58	32	17	
304				8	23	41	58	59	80	66	51	35	23	12	
384					23	46	69	82	95	73	51	29	20	9	
386	10	24	47	67	75	85	95	66	30	24	17	12	8	4	
387	8	19	33	45	61	78	95	66	35	24	13				
284	18	28	59	100	86	72	63	28							
290	7	10	23	35	53	72	90	66	40	27	15				
291						18	55	72	88	73	58	43	28	14	
490		5	15	25	39	55	72	63	56	37	18				
491	11	17	24	28	43	57	70	57	43	28	13				
492	12	19	42	66	62	58	55	42	26	18	10				

1 Clonal mean percentage pollen release on observational dates.

2 Clonal mean percentage pollen release on intermediate dates, interpolated from clone pollen release graphs (Appendix 4).

Table 18. Daily percentage female receptivity of black spruce clones.

Date (June)	4[1]	5[1]	6[2]	7[1]	8[2]	9[2]	10[1]	11[2]	12[1]	13[2]	14[2]	15[1]	16[2]	17[2]	18[1]	19[1]
Clone no.																
288	8	25	40	59	72	85	100	82	64	42	22	3	2	1		
303	3	3	3	3	15	28	40	55	68	65	63	60	43	27	10	5
304	4	11	16	23	44	67	91	95	100	73	42	9	8	5		
384					22	45	69	84	100	75	62	29	18	11		
386		21	41	67	75	87	100	72	40	32	23	13	8	5		
387		15	30	45	63	81	100	75	50	43	37	33	22	12		
284	35	50	75	100	92	85	78	70	63	42	22					
290	6	10	22	35	52	70	90	89	78	52	25					
291				3	30	59	90	94	100	80	62	43	28	14		
490	4	6	16	29	51	75	99	99	99	72	47	19	13	7		
491			12	28	50	75	98	86	75	51	25					
492			20	43	52	62	73	85	99	67	32					

1 Clonal mean values on observational dates.

2 Interpolated values from clonal percent receptivity graphs (Appendix 4).

b= regression constants (Figure 6). The most rapid phase of pollen release and female receptivity occurred between 90 and 130 degree-days (approx.) (Figure 6).

Overall, the graphs of percentage pollen release and female receptivity (Figure 5), and the cumulative progress of these scores (Figure 6), show that pollen release and female receptivity of all black spruce clones were well synchronized.

Differences between clones in degree-day requirements at the midpoints of pollen release and female receptivity were highly significant using an analysis of variance (Tables 19, 20). Duncan's NMR test showed that many clones were significantly different from each other in degree-day requirements for pollen release and female receptivity (Table 21). Clones not significantly different from each other are sidescored with a continuous line in Table 21.

Table 21 ranks the black spruce clones according to mean degree-day requirements to reach the midpoints of pollen release and female receptivity (Appendix 4); this Table also shows corresponding dates of pollen release and female receptivity. Midpoints of pollen release and female receptivity periods were reached on June 8 by the earliest clones and on June 13 by the latest clones. Thus, a difference of only 5 days separated the first from the last clones for both pollen release and female receptivity. The mean date of pollen release and female receptivity of all clones was June 10 (Table 21).

Table 19. Analysis of variance of degree-day requirements for pollen release.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Clones	11	3 503.6	318.5	10.4
Within clones	27	830.5	30.8	
Total	38	4 334.1		

[1] $F_{0.01,\ 11/27} = 3.00$

Table 20. Analysis of variance of degree-day requirements for female receptivity.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Clones	13	1 837.6	141.4	33.8
Within clones	31	129.8	4.2	
Total	44	1 967.3		

[1] $F_{0.01,\ 13/31} = 2.79$

Table 21. Pollen release and female receptivity of black spruce clones based on degree-day requirements and date.[1]

Male			Female		
Clone no.[2]	Clonal degree-day requirements	Mean date (June)	Clone no.[2]	Clonal degree-day requirements	Mean date (June)
284[3]	109.4	8	393[3]	107.2	8
492	111.1	8	386	116.0	9
386	116.0	9	284	116.0	9
387	118.1	9	288	118.1	10
290	120.2	10	387	120.2	10
491	120.2	10	283	120.2	10
490	123.2	11	491	121.5	10
384	127.9	12	290	122.1	10
291	129.2	12	492	123.1	11
304	133.5	12	490	124.0	11
288	138.4	13	384	124.0	12
303	140.2	13	291	126.6	11
			304	127.9	11
			303	140.2	13
Mean	124.0	10.6		121.9	10.3

1 Mean degree-days and date at the midpoints of pollen release and female receptivity.

2 Clones are ranked according to mean degree-day requirements.

3 Clones not significantly different from each other, using Duncan's NMR test, are sidescored with a continuous line.

Degree-day requirements for pollen release by clones were graphed against degree-day requirements for female receptivity by clones in Figure 7. Generally, clones releasing pollen at a relatively late date were also late in reaching receptivity, although the correlation is not very significant (R= 0.64, 10 df) (Figure 7).

Degree-day requirements per clone for lateral branch flushing (Table 4) were moderately correlated with degree-day requirements per clone for pollen release (R= 0.69, 10 df) and female receptivity (R= 0.78, 12 df) (Figure 8). Generally, the latest flushing clones were also latest in releasing pollen and in reaching female receptivity (Figure 8).

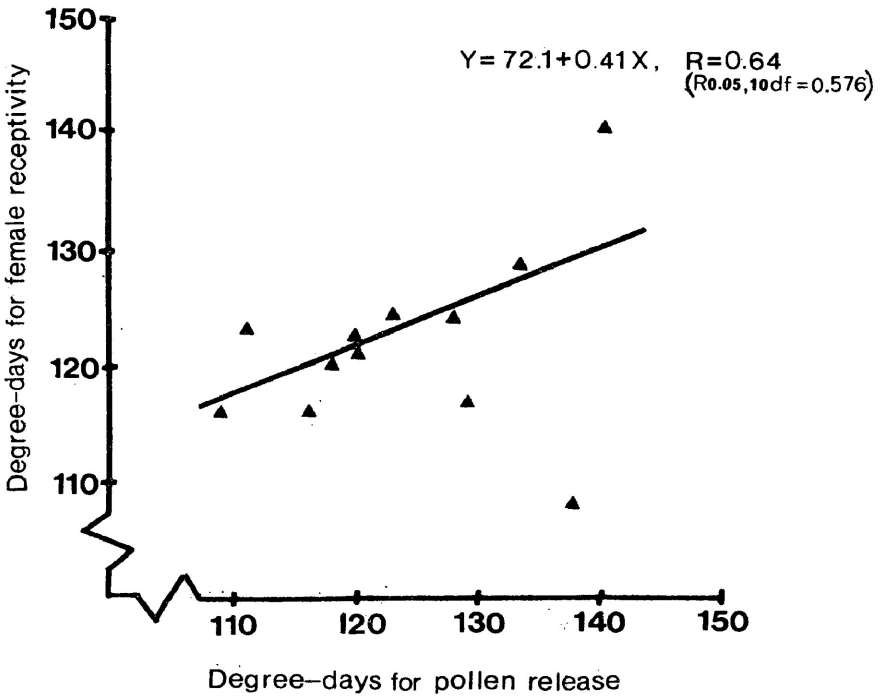


Figure 7. Mean degree-day requirements for pollen release versus mean degree-day requirements for female receptivity of 12 black spruce clones.

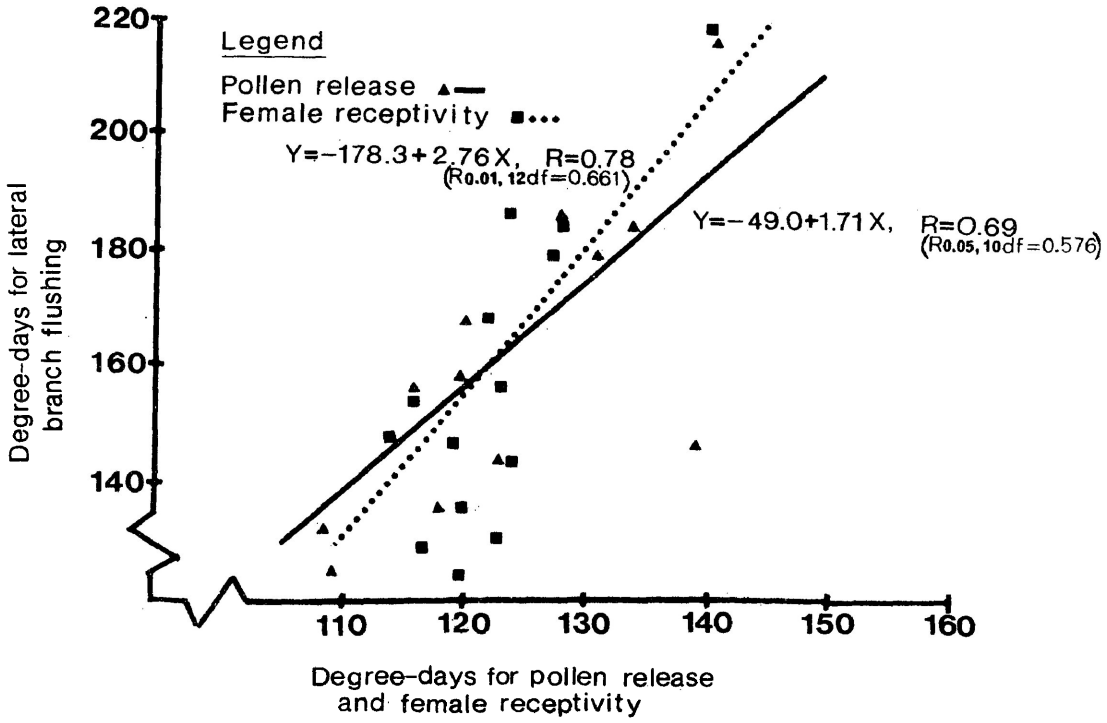


Figure 8. Mean degree-day requirements for pollen release and female receptivity versus degree-day requirements for lateral branch flushing in black spruce clones.

Reproductive Dynamics

A. Number of Strobili

The mean numbers of male and female strobili of black spruce clones are shown in Table 22. The mean number of male strobili per ramet ranged from 0 (Clone 393) to 4 550 (Clone 288), and the mean number of female strobili per ramet ranged from 12 (Clone 393) to 178 (Clone 492) (Table 22). The mean number of male and female strobili per ramet of all clones was 1 030, and 75, respectively (Table 22). Number of strobili per ramet per clone is expressed as a percentage of the total number of strobili produced by all clones in Table 23. Two clones, 288 and 290, bore about 55 percent of all the male strobili (Table 23). This trend is less pronounced in female strobilus production where four clones, 492, 288, 386, 290, bore almost 52 percent of the strobili (Table 23).

The linear correlation coefficients for the relationship between the number of male ($R= -0.12$, 12 df) and female ($R= -0.35$, 12 df) strobili versus leader length were not significant.

The mean number of male strobili per ramet per clone was plotted against mean ramet height per clone. The linear equation provided the best fit for this relationship and was significant at the 0.05 level ($R= 0.60$, 12 df; Figure 9).

Table 22. Mean number of male and female strobili per ramet and mean ramet height per clone of black spruce.

Clone no.	Mean ramet height	S.D.[1] of height	Mean number of male strobili per ramet (X200)	S.D.[1] of the number of male strobili	Mean number of female strobili per ramet	S.D.[1] of the number of female strobili
	M	M				
288	4.73	0.26	22.75	8.85	122	50.00
303	3.13	0.17	4.00	3.56	87	143.22
304	3.87	0.21	0.75	0.50	90	44.54
384	3.99	0.58	2.75	0.96	45	16.44
386	4.34	0.47	4.75	2.06	119	92.02
387	3.77	0.45	1.50	1.73	27	32.34
393	4.49	0.37	0.00	0.00	12	5.45
283	3.92	0.23	2.25	1.89	46	61.56
284	2.95	0.15	1.00	0.00	19	9.85
290	4.14	0.17	13.00	1.63	91	23.11
291	3.41	0.49	7.25	3.86	90	24.58
490	3.99	0.27	2.25	0.96	94	38.51
491	3.32	0.13	1.00	0.82	25	13.45
492	3.21	0.21	3.75	3.10	178	80.07
Mean	3.81		5.15		74.6	

[1] S.D. = Standard deviation.

Table 23. The percentage number of male and female strobili per clone for 14 clones of black spruce.

Clone no.	Male	Female
288	35.13	12.33
303	6.18	8.80
304	1.16	9.11
384	4.25	4.59
386	7.34	12.08
387	2.32	2.74
393	0.00[2]	....[1]
283	....	....
284	1.54	1.88
290	20.08	9.21
291	11.20	9.13
490	3.47	9.54
491	1.54	2.51
492	5.79	18.09
Total	100.00	100.00

[1] These clones had no male components in the calculation of the genetic composition of the progeny (Table 28); thus, they were omitted from this calculation.

[2] This clone was excluded as it was not used later in the calculation of the genetic composition of the progeny (Table 28) due to incongruous results in the pollen release data.

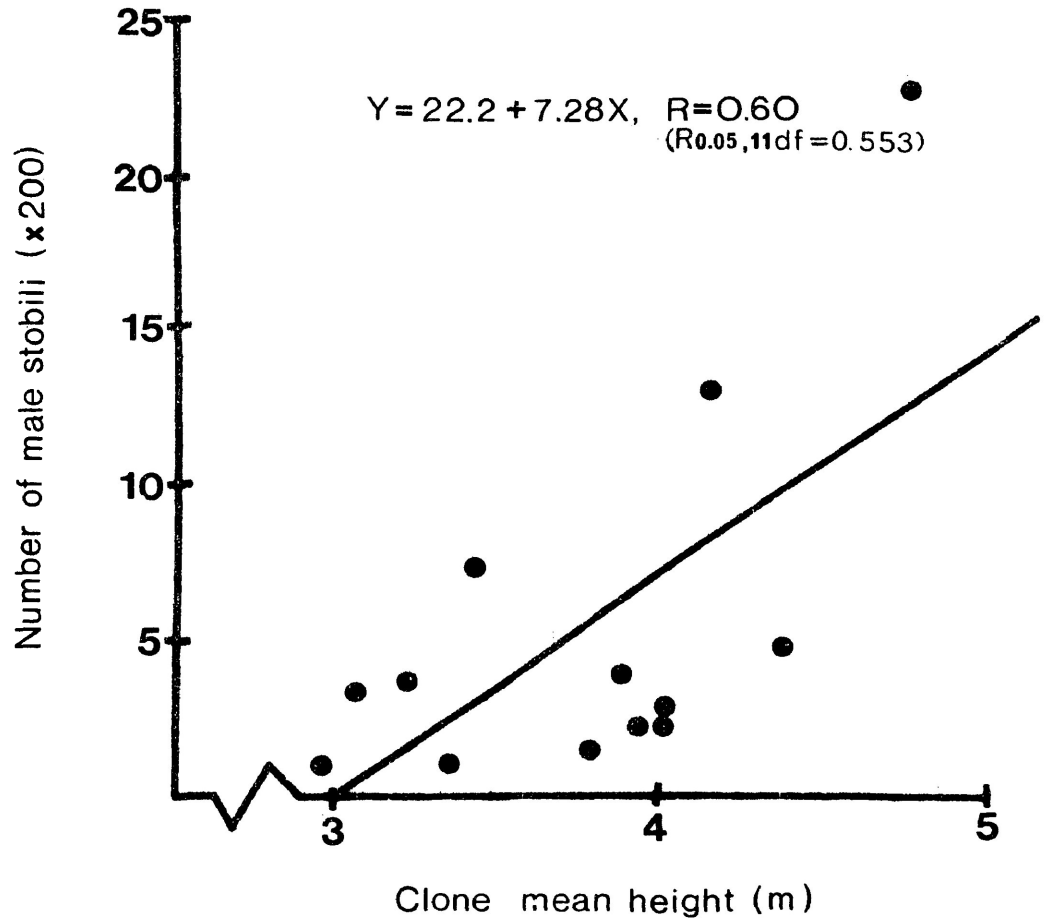


Figure 9. Mean number of male strobili per ramet per clone of black spruce versus mean ramet height per clone.

However, the number of female strobili was not related to mean ramet height per clone (R= 0.07, 12 df). Generally, the taller clones bore more male strobili than the shorter clones (Figure 9; Tables 22, 23). For example, the tallest clone (Clone 288, mean height= 4.73m) had an average of 4 500 strobili (approx.) per ramet (Table 22). The shortest clone (Clone 284, mean height= 2.95m) had an average of less than 200 strobili per ramet (Table 22). Nevertheless, there is much variability between clones. For example, Clone 291 which had a mean ramet height of 3.41m had an average of 1 450 male strobili per ramet whereas clone 386 which had a mean ramet height of 4.34 had an average of only 950 strobili (Table 22).

The linear correlation coeffecient (R= 0.40, 12df) of the relationship between the number of male strobili per ramet per clone versus the mean number of female strobili per ramet per clone was not significant.

An analysis of covariance was carried out on the number of male strobili per ramet to release the effect of height (Table 24). Clone differences in height were significant at the 0.01 level using an analysis of variance (Table 25). Differences between clones in the number of male strobili were significant at the 0.01 level before and after adjustment for height (Table 24). However, the reduction in the F ratio due to the effect of height was small, as F before adjustment for height was 18.2, and 15.1 after

Table 24. Covariance analysis of the number of male strobili per ramet in black spruce.

Source	Unadjusted				Adjusted			
	Degrees of freedom	Sums of squares YY	XY	XX	Degrees of freedom	Sums of squares	Mean square	F[1]
Clones	12	1 926.9	93.4	12.7				
Within clones	39	343.9	18.4	4.3	38	265.9	7.0	
Total	51	2 270.8	111.8	17.0	50	1 536.7		
Difference for testing adjusted clonal means					12	1 270.8	105.9	15.1

F^2 before adjustment: (1 926.9/12) (343.9/39)=18.2

Regression coeffecient b = 18.4/4.3 = 4.24

[1] Adjusted. F0.01, 12/38=2.69
[2] Unadjusted. F0.01, 12/39=2.67

Table 25. Analysis of variance of ramet height (m) in black spruce.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Between clones	13	15.2	1.169	12.3
Within clones	42	4.0	0.095	
Total	55	19.2		

[1] $F_{0.01, 13/42} = 2.59$

(Table 24). Therefore, the number of male strobili per ramet were not adjusted for height using the covariance formula for adjustment.

Differences between clones in the number of female strobili per ramet showed significant differences at the 0.01 level using an analysis of variance (Table 26). There was less variation between clones in the number of female strobili per ramet than in the number of male strobili per ramet as shown by the lower F value for female strobili.

Table 26. Analysis of variance of the number of female strobili per ramet of black spruce clones.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F[1]
Clones	13	118 841.7	9 141.7	2.67
Within clones	42	143 795.3	3 423.7	
Total	55	262 638.0		

[1] $F_{0.01,\ 13/42} = 2.59$

B. Gamete Contributions and Genetic Composition of the Progeny.

The percentage daily composition of the pollen cloud on each day from the beginning of pollen release (June 4) to the end of pollen release (June 18) is shown in Table 27. These daily percentage values were calculated on the basis of each clone's daily stage of pollen release (Table 17), and its percentage number of male strobili (Table 23). However, the percentage contribution to the pollen cloud of each clone is also dependent on the number of other clones releasing pollen on that day. This result occurs because the daily percentage contribution to the pollen cloud must total 100 percent for all clones releasing pollen on that day. For example, clone 386 contributes an average of 25 percent over the first 4 days of pollen release (Table 27), although it bore only 7 percent of the total number of male strobili (Table 23). Overall, clones 288, 386, 290, 291 and 492 had the highest percentage contributions to the pollen cloud. Clones 386, 290 and 492 predominated in the early stages, and clones 288 and 291 in the later stages of pollen release (Table 27). The other clones had much smaller daily contributions to the pollen cloud (Table 27). Although some clones are early or late, there is considerable overlap in the timing of pollen release, especially between June 8 and 13 (Table 27).

Table 27. Daily percent clone contributions to the pollen cloud of 12 black spruce clones.

Date (June)	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Clone no.															
288					14	19	21	30	39	42	48	59	60	63	
303				1	3	3	4	5	7	8	10	14	11	11	
304				1	1	1	1	1	2	2	2	2	2	2	
384					3	4	5	6	7	7	6	5	6	4	
386	21	29	26	25	18	14	12	8	4	4	3	3	3	3	
387	5	7	6	5	5	4	4	3	1	1	1				
284	8	7	7	8	4	3	2	1	0						
290	41	33	35	35	35	33	30	23	14	12	8				
291						5	10	14	18	18	18	18	18	17	
490		3	4	4	4	4	4	4	4	3	2				
491	5	4	3	2	2	2	2	2	1	1	1				
492	20	17	19	19	12	8	5	4	3	2	2				

The daily percentage clone contributions to the pollen cloud (Table 27), the daily percentage stage of female receptivity (Table 18) and the percentage number of female strobili (Table 23) were combined to estimate the genetic composition of the progeny (Table 28). The percentage clone composition of each possible crossing combination, using this method, is shown in Table 28. The male parental contributions are indicated horizontally and the female parental contributions, vertically in Table 28.

The percentage contribution of each clone as a male parent (summation of individual columns) is shown in the bottom row of Table 28. These percentages represent each clone's contribution to the filial generation as a male parent. Each clone's contribution as a male parent depended on its daily percentage pollen contribution to the pollen cloud (Table 27), the percentage stage of receptivity (Table 18), and the percentage number of female strobili of the female parents (Table 23) that were receptive during its period of pollen release. The total percentage contribution of each clone as a female parent (summation of individual rows) is given in far right column of Table 28. These total female percentages are the same as those for the percentage number of female strobili per clone (Table 23). No change occurs in this percentage as the method used assumes that the same proportional percentage of female strobili were fertilized, unless it became receptive too early or too late for any crossing to occur. However, lack of overlap between

Table 28. Percentage contribution of each possible crossing combination to the progeny of 12 black spruce clones.

Male clone no.	288	303	304	384	386	387	284	290	291	490	491	492	
Female clone no.													Sum of female contributions
288	2.611	0.491	0.135	0.499	1.678	0.452	0.369	3.335	1.013	0.459	0.241	1.048	12.331
303	3.599	0.703	0.147	0.492	0.545	0.142	0.066	1.204	1.322	0.217	0.091	0.272	8.800
304	2.618	0.489	0.123	0.464	0.904	0.256	0.163	2.035	1.056	0.322	0.149	0.530	9.109
384	1.655	0.314	0.072	0.265	0.318	0.094	0.040	0.804	0.656	0.145	0.060	0.167	4.590
386	2.588	0.497	0.133	0.471	1.675	0.445	0.371	3.246	0.953	0.440	0.228	1.034	12.081
387	0.699	0.136	0.033	0.120	0.329	0.089	0.068	0.666	0.262	0.095	0.047	0.196	2.740
284	0.314	0.060	0.018	0.060	0.302	0.077	0.074	0.547	0.188	0.068	0.042	0.202	1.882
290	2.260	0.419	0.112	0.430	1.071	0.300	0.215	2.320	0.917	0.344	0.167	0.651	9.206
291	3.257	0.622	0.140	0.515	0.668	0.194	0.089	1.632	1.265	0.282	0.112	0.346	9.122
490	2.791	0.526	0.127	0.482	0.941	0.265	0.171	2.105	1.102	0.329	0.152	0.550	9.541
491	0.651	0.120	0.032	0.124	0.271	0.078	0.051	0.621	0.264	0.095	0.043	0.159	2.509
492	4.809	0.898	0.241	0.891	1.931	0.537	0.374	4.282	1.962	0.677	0.300	1.188	18.090
Sum of male contributions	27.852	5.275	1.313	4.813	10.633	2.929	2.051	22.797	10.890	3.473	1.632	6.343	100.001

pollen release and female receptivity was not a problem here (Tables 17, 18). The percentage daily clone contributions to the pollen cloud and the percentage stage of female receptivity only affects the male composition of the progeny (Table 28).

The percentage gamete contributions of each clone to the progeny as both a male and female parents are shown in Table 29. These percentages are the summations of each clone's crossing combinations as a male parent (bottom row Table 28) and female parent (far right column, Table 28). For example, clone 288 contributes 27.852 percent as a male parent (far right column, first row) and 12.331 percent as a female parent (bottom row, first column, Table 28). These values are summarized for each clone in Table 29. The average of these two values for each clone gives the clone's percentage composition of the progeny in the filial generation (Table 29, Column A). For clone 288, the average percentage clone composition of the progeny= 27.852 (male contribution) + 12.331 (female contribution) divided by 2= 20.09 percent (Table 29, Column A).

Five clones, 288, 290, 492, 386 and 291 contribute approximately 70 percent to the genetic composition of the progeny: 80 percent (approx.) as male parents and 61 percent (approx.) as female parents (Table 29, Column A). Two clones, 288 and 290, together contribute 55 percent (approx.) of all the male parental contributions (Table 29).

Table 29. The percentage male and female gamete contributions, the average percentage genetic composition of the progeny, and the percentage selfing per clone, of 12 black spruce clones.

Clone no.	Gamete contributions		Average percentage genetic composition of the progeny		Percentage selfing
	Female	Male	A[1]	B[2]	
288	12.33	27.85	20.09	23.73	21.17
290	9.21	22.80	16.00	14.65	25.20
492	18.09	6.34	12.22	11.94	6.57
386	12.08	10.63	11.36	9.71	13.87
291	9.13	10.89	10.01	10.17	13.87
303	8.80	5.28	7.04	7.49	7.99
490	9.54	3.47	6.51	6.51	3.45
304	9.11	1.31	5.21	5.14	1.35
384	4.59	4.81	4.70	4.42	5.77
387	2.74	2.93	2.84	2.53	3.25
491	2.51	1.63	2.07	2.03	1.71
284	1.88	2.05	1.97	1.71	3.93
Total	100.00	100.00	100.00	100.00	108.13
Mean	8.33	8.33	8.33	8.33	9.01

[1] Average percentage composition of the progeny based on the average of male and female gamete contributions (from Table 28).

[2] Average percentage composition of the progeny based on the average of the percentage number of male and female strobili per clone (Table 23).

If panmixis were achieved, each clone would contribute 8.33 percent (100/12= 8.33 percent, denominator= number of clones) to the progeny. Most clones do not equal or exceed this amount (Table 29). However, two clones, 288 and 290, exceed this figure by a large degree (Table 29). Generally, the results show that the genetic composition of the progeny is heavily weighted by a few clones (Table 29).

Another method can be used to approximate the percentage clone composition of the progeny. This method simply averages the percentage values of male and female strobili per clone (Table 23). These averages are included in Table 29 (Column B) for comparison, and they correspond closely to the values calculated by summing of gamete contributions (Column A).

Clones 288, 290, 492, 291, and 386 remained the largest gamete contributors, as in the the more complex method (Table 29), contributing about 60 percent (approx.) to the clone composition of the progeny. The contribution of clone 288 to the progeny is slightly larger when estimated using this method (23.73 percent) than using the more complex method (20.09 percent) (Table 29). The other clones change little in magnitude and the ranking order of all clones remains unchanged except for clones 386 and 291 which are interchanged (Table 29).

Overall, the timing and duration of pollen release and female receptivity had little effect on the genetic composition of the progeny using the more complex method (Table 28). Clone differences in male and female strobilus production had the most important effect upon the genetic composition of the progeny.

The total percentage of selfed-pollinations was 10.69 percent, calculated by adding the numbers on the diagonal from the upper left corner to lower right corner in Table 28. The percentage selfing would be 10.44 percent if only the number of male and female strobili per clone (Table 23) reflected the gamete contributions of each clone. This percentage was calculated by multiplying the percentage number of male by the percentage number of female strobili for each clone (Table 23), summing these values for all clones, and dividing by 100. If panmixis was assumed, 8.33 percent selfing would be expected.

The average percentage selfing per clone was calculated by expressing each clone's percentage of selfed-pollinations as a percentage of the total gamete contributions of that clone as a female parent (Table 28). Thus, each selfing value per clone is adjusted such that clone differences in female strobilus production are not included, which was not the case for the total percentage of selfed-pollinations above. These values were calculated for each clone and are presented in Table 29. The average percentage selfing per

clone varied from 25.20 (Clone 290) to 1.35 (Clone 304) percent, although the average of all clone values was 9.01 percent (Table 29). This large range in percent selfing per clone were mainly due to clone differences in male strobilus production; the heaviest male strobilus producers had the largest percentage values of selfing (Table 29).

Differentiation and Early Development of Reproductive Buds of White and Black Spruce

The time of reproductive bud differentiation could not be estimated in white spruce as few reproductive buds were found among the 200-300 white spruce buds dissected. Female bud development in black spruce was followed on clone 303 and male bud development on clone 288, as there were few male buds found in collections from the former and few female buds from the latter.

Female Buds: Generally, female buds were found on vigourous shoots in the upper part of the crown, and at any position except the terminal. Frequently, female buds occurred in the distal part of the previous year's shoot increment, although clusters of female buds were occasionally noted in the proximal part of this shoot, partly surrounded by last year's bud scales. Female buds sometimes occurred in a terminal position on the less vigourous shoots.

The earliest stage of female bud recognition was on August 7, 1979 (Figure 10); this date is one week later than that of male bud recognition. At this stage, a number of bracts can be seen proximally on the bud axis. The next collection (August 15) was at a similar stage of development. Rapid initiation of bract primordia occurred acropetally thoughout August (Figures 10, 11). The later

stages of female bud development showed a small increase in the number of initiated bracts compared with that shown in Figure 12. However, the bracts had increased in size and were similar in stage of development to the more proximal bracts in Figure 11.

Ovuliferous scales were first recognized in the middle of August (Figure 11). The ovuliferous scale appears to be initiated in the axil of a bract (distal portion, Figure 11). Ovuliferous scale development continues until they are approximately the same size as the bracts (middle portion, Figure 11). Then, rapid bract development resumes, resulting in the ovuliferous scale being overgrown by the bract (proximal portion, Figure 11). All ovuliferous scales in the later collections were similar in stage of development to the most proximal in Figure 11.

Male buds: Male buds occur mostly in the lower part of the crown. Male buds were found often on shoots borne on the lower side of the main axis of a branch, and rarely within the last two to three annual growth increments.

The earliest stage of male bud recognition was on July 30, 1979 (Figure 12). This bud was considered male, based on the shape of the apex as well as its frequent occurence in bud samples from the lower part of the crown. This male bud apex (Figure 12) was more pointed, being relatively narrower and longer than a potential vegetative and female reproductive buds (Figure 15) collected on the same date.

Thus, male reproductive buds were recognized one week before vegetative or female reproductive buds.

The first microsporophylls were visible in the next collection on August 7. Rapid, acropetal microsporophyll initiation proceeded throughout August. Figure 13 shows a male bud on August 15, at which time most microsporophylls had been initiated. However, a few stages of microsporophyll development are visible on this bud (Figure 13). Towards the base of the apex, an early stage of microsporophyll initiation can be seen as a small primordium, while a slightly later stages of microsporophyll development can be seen proximally (Figure 13).

Most microsporophylls have been initiated by late August and early September (Figure 14). Figure 14 is an SEM photograph of a male bud collected on September 13. At this stage of development, the microsporophylls have increased in size compared with the earlier collection date (Figure 13).

Vegetative bud development: Figure 15 shows an SEM photograph of a bud which was not confirmed as either vegetative or reproductive. However, this bud is probably vegetative since these were by far the most common type collected. As in reproductive buds, leaf primordia are initiated acropetally throughout August (Figure 17). The vegetative bud shown in Figure 16 has a similar number of primordia as the female and male buds shown in Figures 11 and 13.

Most leaf primordia had been initiated by the last collection date (September 13; Figure 17). This bud is considerably smaller and broader than the reproductive buds shown in Figures 11, 13, and 14.

Figures 10-17. Stages of development of male, female, and vegetative buds of black spruce.

Figure 10. Side view of a female reproductive bud collected on August 7, 1979, showing the apex (A), and recently initiated bracts (B).

Figure 11. Top side view of a female reproductive bud collected on August 22, 1979. Located distally along the cone axis: the apex (A), recently initiated bract (B) (to right in Figure), and a later stage of development with an ovuliferous scale (OS) in the axil of the bract (B). Located in the centre along cone axis: bract (B) and ovuliferous scales (OS) at an intermediate stage of development, both are approximately the same size. Located proximally along cone axis: bract (B) and ovuliferous scale (OS) at later stages of development; the ovuliferous scale is small and barely visible in the axil of the large bract which has overgrown it.

Figure 12. Top side view of a suspected male bud collected July 30, 1979, showing a large apex (A), and bud scale (BS). The apex is pointed and relatively narrow at the base.

Figure 13. Top side view of a male bud collected August 15, 1979, showing the apex (A), distally, a recently initiated microsporophyll (M), and proximally, a later stage of microsporophyll (M) development.

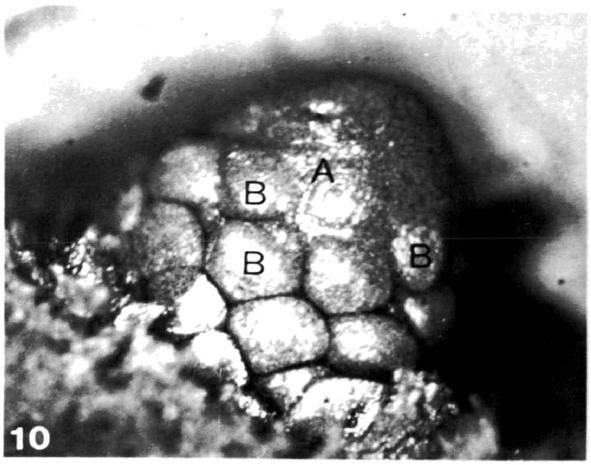
Figure 14. Scanning electron micrograph of a male bud collected September 13, 1979, showing many well developed microsporophylls (M). Scale is indicated on Figure.

Figure 15. Scanning electron micrograph of a vegetative or female repoductive bud collected July 30, 1979, showing a large apex (A), recently initiated primordia (P) (leaf or bract) at base of apex, and inner bud scales (BS). Scale is indicated on Figure.

Figure 16. Top side view of a vegetative bud collected August 29, 1979, showing the apex (A) and many leaf primordia (LP).

Figure 17. Top side view of a vegetative bud collected September 13, 1979, showing small apex (A) and many well developed leaf primordial (LP).

Figures 10-13, 16, 17, x 40.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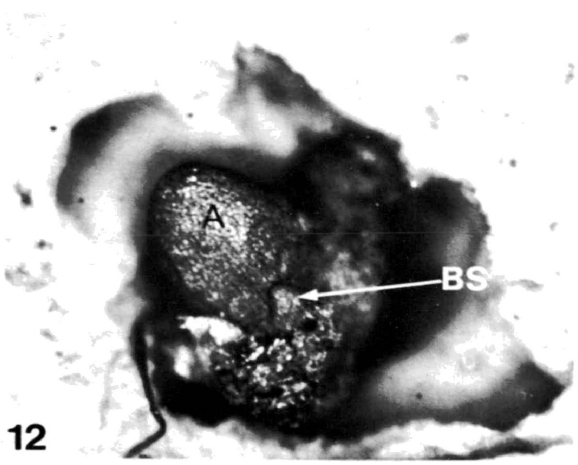
B
B
B
10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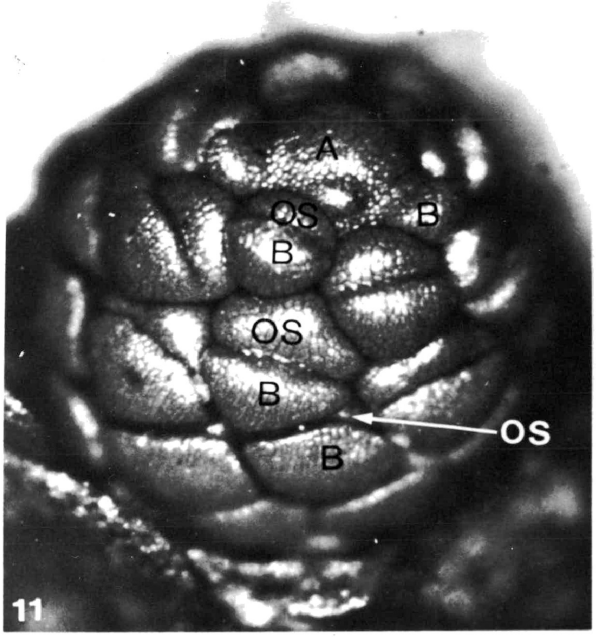
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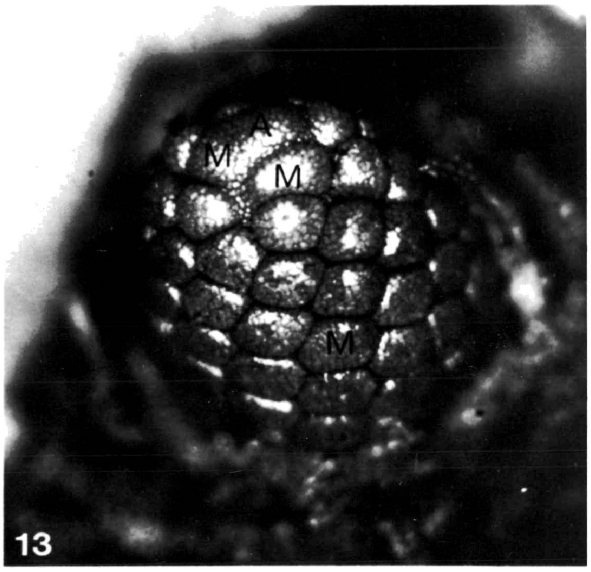
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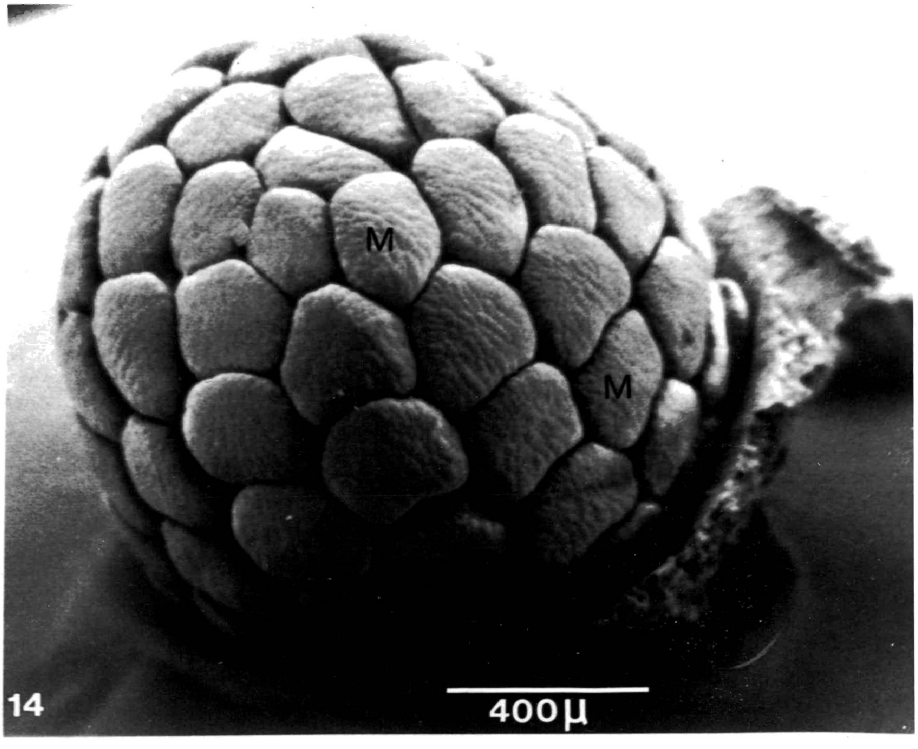
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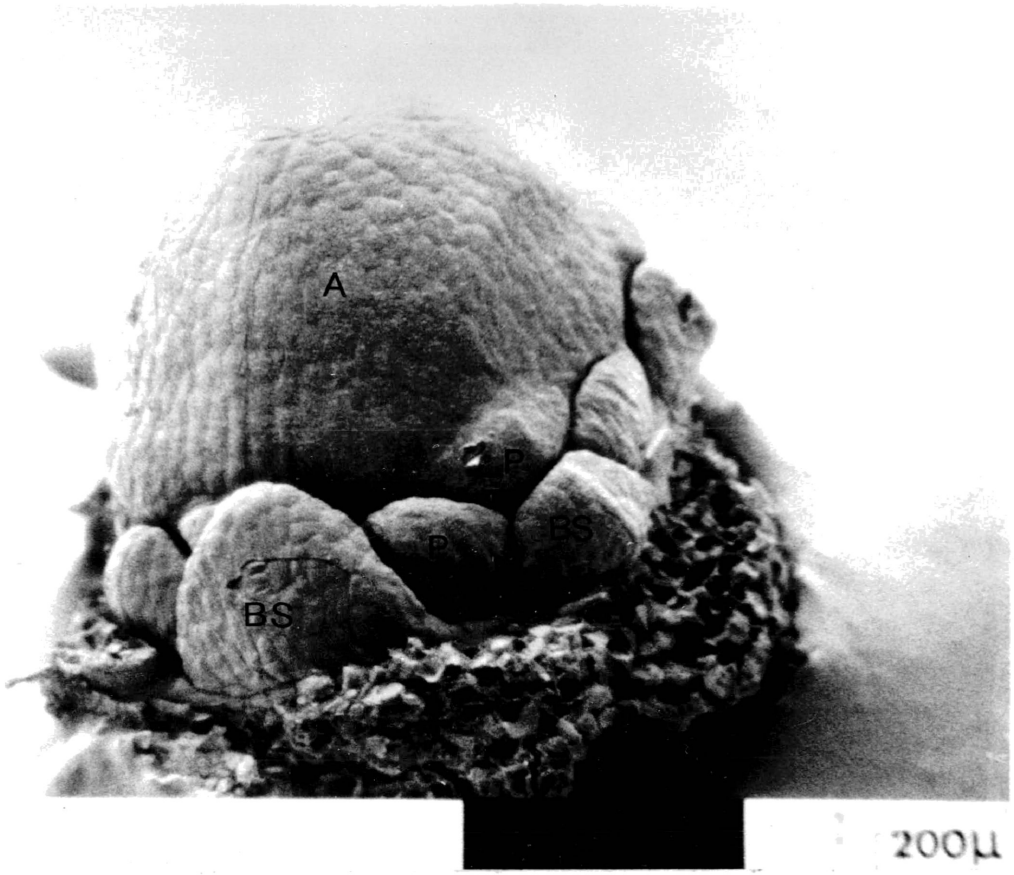
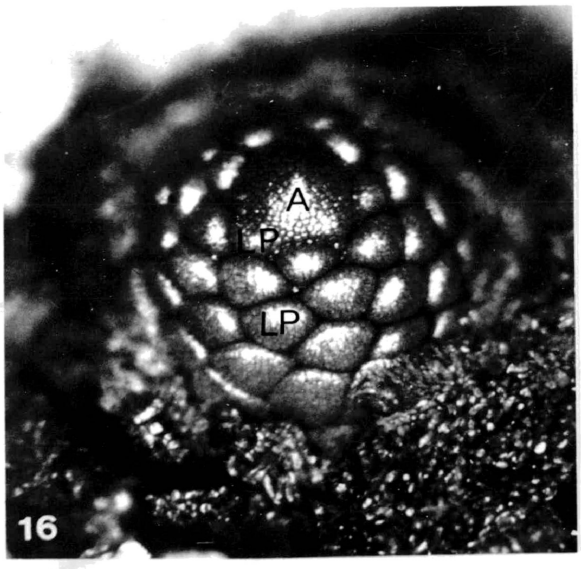
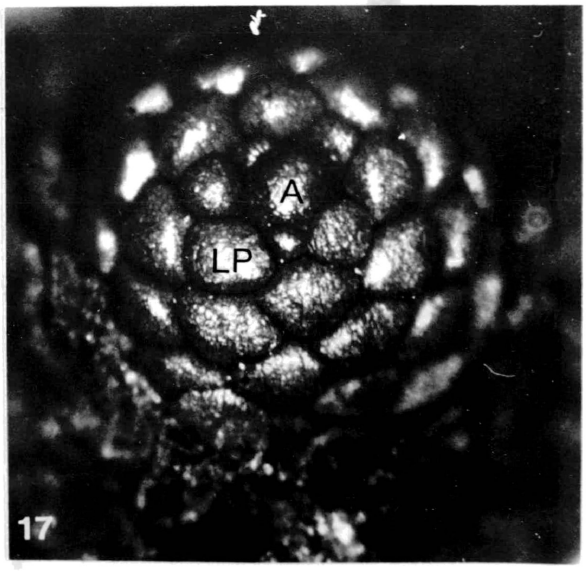


15

200μ



16



17

DISCUSSION

Vegetative Phenology

Flushing

Highly significant differences between clones were found between the time of flushing of the leaders and lateral branches within both white and black spruce (Tables 3, 4). These results support other studies suggesting that the time of flushing in both species is under strong genetic control (Nienstaedt and King 1969, Dietrichson 1969, Nienstaedt 1972, 1974; Ying and Bagley 1974, Wilkinson 1977, Pollard and Ying 1979). Heritability estimates for flushing time are generally high, especially for white spruce, where they varied between 0.228 to 0.910 in a number of studies (Nienstaedt and King 1969, Yeatman and Venkatesh 1974, Wilkinson 1977). Much less is known of heritability of flushing in black spruce, although it appears to be similar to white spruce. In the one study of black spruce, heritability of flushing was estimated at 0.73 (Dietrichson 1969).

Selecting for late-flushing genotypes may be an effective method of reducing the probability of frost damage, especially in white spruce (Nienstaedt and King 1969, Nienstaedt 1972, 1974; Wilkinson 1977). However, the

range in average flushing dates between clones of white spruce was 10 and 8 days for the leaders and lateral branches (Table 3), respectively, compared with a range of 21 days among clones (Nienstaedt and King 1969), and 12-19 days among seedlings of white spruce (Wilkinson 1977) in other studies. However, differences of only 3.5 to 5 days were found between the means of the seedling families in the latter study. The 21 day range in flushing time observed by Nienstaedt and King (1969) reflect the extreme ranges between selected early- and late-flushing white spruce clones. For the clones included in this study, however, the small range in flushing dates suggests that selection for late-flushing types might be difficult to achieve even if flushing heritability is high. Nevertheless, Yeatman and Venkatesh (1974) concluded that selection for late-flushing white spruce trees would be effective, due to the high heritabilities, although differences between the earliest and latest parental trees was about 4 days. If selection for late-flushing types is to be carried out in northern Ontario, flushing heritability estimates need to be verified and the range in flushing times should be determined over a number of years observation and with a greater number of clones that are more representative of the whole of northern Ontario.

The range in average flushing times between clones for the leaders and lateral branches of black spruce were 6 and 11 days, respectively. There is no published information on

the range of flushing dates among individual trees of black spruce, although such information exists for seedling provenances of the species (Morgenstern 1969b, 1978; Dietrichson 1969, 1971). Successful selection for late-flushing black spruce trees may be carried out (Dietrichson 1971); however, this necessity may not arise as it flushes later than white spruce, and thus suffers less from late spring frosts (Fraser 1966).

Temperature has been determined as the most important factor in controlling flushing time (Sarvas 1967, 1972; Nienstaedt and King 1969, Nienstaedt 1974, 1976; Yeatman and Venkatesh 1974). Temperature data, as degree-days, have been used in many studies of flushing in predicting these events (Nienstaedt and King 1969, Nienstaedt 1972). However, degree-days only marginally increased the F ratio in the analysis of variance of flushing in white and black spruce compared with corresponding accumulated number of days. This result may have occurred for a number of factors. The range in flushing dates between clones was small, and as temperature is positively correlated with date, the differences in degree-day accumulations between dates, and consequently between clones, would have been small. Owens et al. (1977) found that the best relationship between temperature sums and early stages of vegetative bud and shoot development in white spruce, including flushing, could be expressed by using the breaking of bud dormancy as starting date and a base temperature of 5

degrees celsius for the calculation of the temperature sums. However, the date of bud dormancy breaking (cf. p 10) was not known for white and black spruce in this study. Other environmental factors may also have contributed to this small range in flushing dates. Spring of 1979 was cooler than normal for the Thunder Bay region (Appendix 3). Thus, the resulting increased duration of chilling and photoperiod may have caused a more rapid flushing response in all clones once temperatures rose in the spring; this theory is supported by the results of Nienstaedt (1966), and Campbell and Sugano (1975). Also, clones that originate from a northern environments, as in this study (Appendices 1, 2), tend to differ less in their times of flushing (Sarvas 1967, 1969).

Mean degree-day requirements were 90 and 150 for white and black spruce, respectively, while the individual clone values varied from 67 to 114 for the former, and from 127 to 190 for the latter (Tables 3, 4). These flushing degree-day requirements for white spruce are less than half those reported among clones of white spruce at Rhinelander, Wisconsin (Nienstaedt and King 1969), although they were a little closer to the degree-day requirements recorded for flushing of the progeny from several of the same clones grown in a cool growth room (Nienstaedt 1972). Nienstaedt (1972) also found that the lowest degree-day requirements were recorded in the year with the coolest spring, and the latest recorded date for flushing; this explaination may

account for the low degree-day requirements for flushing of white and black spruce in this study. There is no published data on flushing degree-day requirements in black spruce.

The mean date of flushing for both the leaders and laterals was June 5 for white spruce and June 14 for black spruce; these dates are a little later than those reported in other studies (Baldwin 1931, Kienholz 1934, Cook 1941, Ahlegren 1957, Heinselman 1957, Horton and Lees 1961, Fraser 1962, 1966; Helum 1967, Nienstaedt 1972, Owens et al. 1977). Location differences in date of flushing may reflect variation between locations in average genetic, latitudinal, and environmental factors. However, some of the differences are probably due to annual environmental fluctuations. For example, due to the late spring of 1979, the dates of flushing reported for white and black spruce in this study are probably later than average for the Thunder Bay region (Appendix 3).

The average time of flushing of the leaders of both white and black spruce clones in this study occurred at approximately the same time as flushing in the lateral branches. This result does not support either of two other reports from the literature. Fraser (1962, 1966) found that the leader of white and black spruce trees flushed first, and shortly after, flushing occurred in the lateral branches in a basipetal direction. Langlet (1960, In Nienstaedt and King 1969) suggested that the lowest buds in the crown of a

tree flushed first and the leader flushed last. The lateral branch buds observed in this study were from the fifth whorl down from the leader and thus may not have been low enough in the crown to detect differences in flushing times between the leader and lateral branches.

Shoot Elongation and Growth Cessation

In northern provenances of Picea, the phase of rapid shoot elongation is short (Sarvas 1965); this observation was true of white and black spruce (Figure 3). The average duration of the period of active elongation of the leaders was similar for both white and black spruce (about 50 days). The leaders of white spruce flushed earlier and growth was more rapid than in black spruce, reaching an average total length of 457 mm compared with 388 mm for black spruce. Lateral branch flushing of black spruce occurred at the same time as leader flushing, but elongation was less rapid, tapering off in mid-July, and only reaching an average total length of 110 mm. Lateral branch growth of white spruce was complete at time of first measurement (July 2). These observations on the growth period of the leaders of white and black spruce and lateral branches of black spruce were similar to those reported in other studies at Chalk River, Ontario (Fraser 1962, 1966). The specific differences in leader growth patterns reported here for white and black

spruce may be partly because white spruce begins physiological activity at lower temperatures than black spruce (Fraser 1966).

The early-flushing black spruce clones produced the greatest leader growth (Figure 4); however, the correlation coefficient (R= -0.57, 12df) was low and was just significant at the 0.05 level. A similar analysis was not attempted on white spruce as differences in leader length between clones were not significant. In contrast, Nienstaedt and King (1969) found significant, but positive, correlations between flushing time and leader length among clones of white spruce at Rhinelander, Wisconsin. Nienstaedt (personal communication) suspects that these results were due to higher average daily temperatures during the grand period of growth of late-flushing clones. However, in a later study, negative correlations were found between flushing time and height growth in the progenies from several of these clones (Nienstaedt 1972). Similarily, Wilkinson (1977) reported low or negative correlations between date of budbreak and leader length among white spruce seedlings growing in Maine.

It may be possible to select for early-flushing black spruce clones to get improved growth rates as the early-flushing clones produced the greatest leader extension. The relationship between leader flushing and growth, however, needs to be determined more accurately over

a number of years, and using more clones. Heritability estimates would have to be determined for both time of flushing and leader growth.

Clone differences in the time of growth cessation of the leaders of white and black spruce, were significant at the 0.10 and 0.01 level, respectively, and the lateral branches of black spruce at the 0.01 level. The relatively low level of significancee in white spruce, perhaps, was affected by shoot damage resulting in less accurate elongation measurements, and reduced replication when badly damaged leaders were ommitted from the test. Nevertheless, the results generally support the theory that growth cessation is under strong genetic control, as shown in earlier studies of both white spruce (Nienstaedt and King 1969) and black spruce (Dietrichson 1969). However, Duncan's NMR test showed that few clones were significantly different from each other.

The range in number of days between the earliest and latest clones to cease leader growth in white and black spruce was 12 and 10 days, respectively, and 6 days for the lateral branches of black spruce. These ranges for the leaders of white and black spruce were a little larger than that reported for flushing, but less than that reported for lateral branch flushing of black spruce in this study. In one study of white spruce (Nienstaedt and King 1969), the range of growth cessation dates between the earliest and

latest clones varied from 19-23 days over a 4 year period of observation. Early-flushing clones also terminated growth first; thus, the period of growth was similar for the early and late-flushing clones (Nienstaedt and King 1969). Irgens-Moller (1966a) also found a positive relationship between flushing date and date of growth cessation in four Douglas-fir provenances. In contrast, dates of leader growth cessation were not significantly correlated with dates of flushing in either white or black spruce in this study. This result means that the early-flushing clones were not necessarily early in date of growth cessation. It is possible that the relationship between time of flushing and time of growth cessation would be clearer if the ranges in the dates of flushing and growth cessation were larger, and if a greater number of clones was included. There is no published information on the range of growth cessation dates in black spruce.

Clone dates of leader growth cessation were not significantly correlated with dates of lateral branch growth cessation per clone. A significant correlation might be expected for this relationship if growth cessation is under strong genetic control. This result may be due to the small range in lateral branch growth cessation dates, and the small number of clones included in the study.

Unlike time of flushing, dates of growth cessation of the leaders of the black spruce clones were not significantly correlated with mean leader length per clone in this study. A similar relationship was not investigated for white spruce as differences in leader length between clones were not significant, possibly due to leader damage. In contrast, Nienstaedt and King (1969) found significantly positive correlation between dates of growth cessation and shoot elongation in clones of white spruce. In sitka spruce, variation in the time of growth cessation, which was as large as 3 months, had a significant effect on height growth among seedling families of that species, while time of flushing probably had little effect (Burley 1966).

Neither the duration of the growth period of the leaders of the black spruce clones, nor degree-day accumulation over this period for each clone, were significantly correlated with mean leader length per clone in this study. In contrast, Nienstaedt and King (1969) found a highly significant correlation between mean clonal elongation and length of the growth period among selected late-flushing white spruce clones. They suggested that differences in leader length between clones may be largely due to clone differences in rates of leader growth, as the average lengths of the growth period were the same for both types. This explanation may account for the differences in leader length length among clones of black spruce (Table 13). However, the early-flushing black spruce clones had

the largest leader extension even though flushing was not well correlated to total extension. Thus, the earlier flushing of these clones may have resulted from the faster rates of extension. A parallel observation was shown in one study of white spruce (Owens et al. 1977). These relationships could not be studied in white spruce in this study as clone differences in leader length were not significant.

Average date of lateral branch growth cessation of all black spruce clones occurred on July 12, which is 14 days before cessation of leader growth. In contrast, average flushing dates of the leader and lateral branches were the same (Tables 3, 4). The differential in the time of growth cessation between the leader and fifth whorl lateral branch shoots is similar to that reported for black spruce in another study (Fraser 1966). Lateral branch growth had terminated in white spruce prior to first measurement date. This result suggests that lateral branch growth in white spruce probably ceased at the end of June, which roughly aggrees with the observations of Fraser (1962), but is earlier than that reported for the upper branch laterals at Prince George, B.C. (Owens et al. 1977). The earlier cessation of extension growth in the lower branches compared with the leader in another study of black spruce (Fraser 1966) was attributed to partial shading from the upper branches with consequent lower photosynthetic capacity. Hormone gradients, especially auxin concentrations may also

play a role in the control of this phenomenon (Fraser 1952, 1958, 1962). Shading was probably not a factor in controlling lower branch cessation in this study as all ramets were open grown. Leader apical control probably played a role in the earlier cessation of lateral branch growth; however, the mechanism of apical control is not well understood (Kramer and Kozlowski 1960). Nienstaedt (personal communication) suggests that lateral branches cease growth earlier because 1) their microenvironment is warmer and 2) their primordial shoots are shorter, hence requiring less time for expansion.

Mean dates of leader growth cessation occurred on July 17 and July 26 in white and black spruce, respectively (Tables 13, 15). These dates were close to those reported in a number of earlier studies (Kienholz 1934, Cook 1941, Nienstaedt 1957, Fraser 1962, 1966; Nienstaedt and King 1969, Owens et al. 1977). This time differential in growth cessation between the two species is a little less than the two weeks reported for white and black spruce at a similar site and location near Chalk River, Ontario (Fraser, 1966).

As in flushing, there appears to be great similarity in the time of growth cessation of white and black spruce throughout their ranges. The small differences in growth cessation dates may be due to the small latidudinal and environmental variations between locations sampled.

Flowering Phenology

Differences in clone dates at the midpoints of pollen release and female receptivity of black spruce were highly significant in this study using an analysis of variance. These results support the theory that the timing of pollen release and female receptivity are under strong genetic control in black spruce, as in other species (Wright 1953, Wasser 1967, Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). Athough the analyses of variance showed that clone differences in the times of pollen release and female receptivity of black spruce were highly significant, Duncan's NMR test showed that many clones were not significantly different from each other (Table 21). This result was probably because all the clone ortets came from the same seed zone; thus, clone differences in the times of flowering are likely to be small.

There was a small range, of only 6 days, between the earliest and latest black spruce clones in reaching the midpoints of pollen release and female receptivity (Table 21); this range was the same as that found for leader flushing. The range in dates at the midpoints of pollen release and female receptivity reported here for black spruce clones are a little less than those found for Scots pine (Jonsson et al. 1976, Eriksson 1977), and Norway spruce (Eriksson et al. 1973, Eriksson 1977) in Sweden, although clone differences in those studies also represented

wide provenance variation as the Scots pine clones were of Swedish and Finnish origin and the Norway spruce clones were of French, German, and Swedish origin. The small range reported here for black spruce is in agreement with the theory of Sarvas (1970) who suggested that seed orchards composed of clones originating from northern locations would differ less in their times of flowering. The range in flowering times reported for southern pines is usually much greater than that for northern species (Wasser 1967, Dorman 1976).

The results of this study are based on a single year of observation and the range in flowering times for black spruce might be greater (or less) in other years for a number of reasons. Reproductive development, like vegetative bud and shoot development, is strongly temperature dependent in white spruce (Owens et al. 1977, Owens and Molder 1979a), and other tree species (Sarvas 1965, 1968, 1970, 1972; Eriksson et al. 1973, Jonsson et al. 1976). Therefore, as in flushing, the late spring of 1979 in the Mattawin seed orchard may have caused a more rapid flowering response in all black spruce clones; therefore, a reduced range in clone flowering times may have resulted. Although the range in dates of flowering and the average date of flowering for all clones may vary from year to year, the relative order of ranking of the clones would probably remain unchanged as shown for Scots pine in Sweden (Jonsson et al. 1976).

The overall average progress of either pollen release or female receptivity of all black spruce clones had a shape close to the normal distribution (Figure 5), while the cumulation of these scores had the shape of a typical growth curve (Figure 6), when plotted against degree-days. Responses of pollen release and female receptivity to the temperature sum were similar in other species (Sarvas 1965, 1968, 1970; Eriksson et al. 1973, Koski 1975, Jonsson et al. 1976). The relationship between cumulative pollen release or female receptivity versus degree-days might be expected if the response of pollen release and female receptivy to temperature is similar to that of shoot elongation.

Although the individual clones differed in their times of pollen release and female receptivity, the graphs of the average progress of pollen release and female receptivity of all clones showed that the times of maximum pollen release and female receptivity coincided (Figure 5). This result is desirable as the probability of effective pollination is maximized. However, clones that were early in releasing pollen also tended to be early in reaching receptivity (Figure 7). These observations are similar to those made on other species (Nienstaedt 1958, Sarvas 1970). However, Eriksson et al. (1973) reported that female receptivity passed its maximum before the time of peak pollen release in most clones of Norway spruce in Sweden. As the times of pollen release and female receptivity of the black spruce

clones coincided (Figure 7), the probability of self-pollination is maximized (Sarvas 1970).

The times of lateral branch flushing of black spruce were strongly correlated with the times of pollen release and female receptivity; late-flushing clones were also late in the times of pollen release and female receptivity. The average time of pollen release and female receptivity for all black spruce clones (Table 21) preceded the average time of flushing of the leader and lateral branches by 3 and 4 days, respectively. Pollen release in black spruce preceded flushing by a few days in another study in northeastern Minnesota (Winton 1964). Thus, flushing and flowering times are closely related in black spruce, as in other species (Polk 1966, Ying and Bagley 1974, 1976). These results support the theory that flushing and flowering times respond similarly to environmental factors. This finding may have some practical applications. For example, it may be possible to determine flowering synchronization based on flushing phenology, although this method requires verification over a number of years before firm conclusions can be made.

Reproductive Dynamics

Number of Strobili

This study showed large, and highly significant, clone differences in the total production of male and female strobili of black spruce in 1979. This observation supports the theory that fecundity in black spruce is under strong genetic control, as shown for white spruce (Nienstaedt and Jeffers 1970, Teich and Pollard 1973, Teich 1975), and other conifer species (Wright 1953, Puritch 1972, Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). However, the number of male and female strobili per ramet was very variable, especially for the number of female strobili (Table 22). Thus, environmental factors have contributed largely to the differences in strobilus production between the black spruce clones in this study.

A few clones, especially in male strobilus production, produced the greatest number of strobili (Table 22). For example, clone 288 produced 35 percent of the male and 12 percent of the female strobili. If panmixis were assumed, each clone would contribute about 8 percent each of male and female strobilus production. The results indicate that male and female strobilus production per clone may deviate largely in any one year from the level necessary to achieve panmixis. Clone mean levels of male strobilus production were larger than levels of female strobilus production

(Table 22); this result is particularly important as there have been few studies of male strobilus production in black spruce. Similarly, Jonsson et al. (1976) found that clone mean levels of male strobilus production in Scots pine were larger than levels of female strobilus production. These difference may have occurred because male strobili are produced more abundantly by all clones at an older age (Jonsson et al. 1976); the seed orchards in that study were outplanted about 10-12 years before the counts were made. The black spruce clones were outplanted in the Mattawin seed orchard 12-13 years before this study was undertaken. Differences in male strobilus production are important in a seed orchard as they influence total pollen production, and ultimately, the relative contributions of each clone to the seed crop.

A low linear correlation was found between mean ramet height per clone and the mean number of male strobili per clone in black spruce (Figure 9). Consequently, height made only a small reduction in the F ratio using an analysis of covariance (Table 24). In one study of Norway spruce, Eriksson et al. (1973) found a significant correlation between the square root of the mean number of male and female strobili per ramet and mean ramet height per clone. Eriksson et al. (1973) suggested that the square root transformation was the best fit for this relationship because crown size, and thus number of positions available for strobili to form, increases faster than linearly by

height. However, the square root transformation did not give a better fit for the relationship between male strobilus production and height for black spruce (Figure 9).

In contrast to male strobilus production, there was no significant correlation between the number of female strobili per ramet per clone and mean ramet height per clone for the black spruce clones used in this study. This result is similar to that found in one study of loblolly pine (Grano 1973). In white spruce, Nienstaedt and Jeffers (1970) noted that the clones derived from the slower growing ortets were the most prolific cone producers. As in male strobilus production, Eriksson et al. (1973) found a significant correlation between the square root of the mean number of female strobili per clone and mean ramet height per clone.

In this study, although the number of male and female strobili were not significantly correlated with leader length, a general negative relationship can be seen in the data. As vegetative and reproductive sinks compete for available photosynthate (Kramer and Kowlowski 1960), it might be expected that heavy strobilus producing clones would have less leader extension. It is probable that the relationship between the number of male and female strobili per clone versus mean ramet height and mean leader length in black spruce would be clearer in a year of heavier cone production, over a number of years observation, and if more

clones were included.

Strobilus production in 1979 was probably a year of moderate production for black spruce and the results of this study may not be adequate to judge if poor female strobilus producers should be removed from the clonal seed orchard. Most conifer tree species show a cyclic pattern of flower and cone production (Anderson 1965, Sarvas 1968, Lindgren et al. 1977, Calvert 1979). Black spruce produces good crops of seed cones every 4-5 years and white spruce every 2-6 years (Calvert 1979). Nevertheless, many studies have shown that differences between trees in cone production can be largely attributed to genetic factors and that poor producers in one year are consistently poor in other years (Wright 1953, Eliason and Carlson 1969, Nienstaedt and Jeffers 1970, Nienstaedt and Teich 1972, Eriksson et al. 1973, Jonsson et al. 1976, Eriksson 1977). Therefore, it is likely that heavy black spruce cone producers in the Mattawin seed orchard in 1979 (e.g. clone 288) will be also heavy cone producers in other years, although the differences between clones may be less in a year of heavy cone production, as shown between individual trees of Norway spruce (Eliason and Carlson 1969). The present study gives a clear picture of the amount of cone production, and the differences between clones in cone production, that can occur in one year in a seed orchard of black spruce in Northwestern Ontario. The most important result was the large differences between clones in male strobilus

production which are not necessarily tied to female production levels.

Gamete Contributions and Genetic Composition of the Progeny

The results of this study with black spruce clearly show that a few clones, out of 12 selected for study, are the largest contributors of gametes to the progeny. For example, 20 and 16 percent of the progeny originated from clones 288 and 290, respectively-- a total of 36 percent. This observation has important implications for the tree breeder, as much of the seed produced in 1979 would be genetically similar, with the large gamete contributions from two clones.

A method that calculated the genetic composition of the progeny based on only the number of male and female strobili per clone gave similar results to the method which included the influence of phenology. The number of male and female strobili per clone was the main factor affecting the genetic composition of the progeny as the small phenological differences between clones in 1979 had little effect. Similar results were found for Norway spruce (Eriksson et al. 1973, Eriksson 1977) and Scots pine (Jonsson et al. 1976, Eriksson 1977) in Sweden after 2 and 3 years of observations, respectively. Differences between clones in flowering times may be larger and, therefore, more important

in their influence on the genetic makeup of the progeny for black spruce in other years, and for other species, especially southern pines (Wasser 1967, Dorman 1974, Lill and Sweet 1977, Fashler and Sziklai 1980, Fashler and Devitt 1980). However, information on clone flowering times in black spruce may be more important if planning the time for carrying out supplemental or controlled pollinations (Cumming and Righter 1948, Sluder 1977, Danials 1978).

The total percentage of selfed-pollinations was estimated at less than 11 percent in this study. The number of male and female strobili per clone was the most important factor affecting this estimate of selfing. The timing of pollen release and female receptivity had little effect on the percentage selfing, as shown by the small differences when the percentage selfing was estimated based only on the number of strobili per clone. Eriksson et al. (1973) found similar results for Norway spruce, but calculated a lower percentage selfing of just less than 7 percent.

The average percentage self-pollination of all clones was 9 percent for black spruce (Table 29). This figure is lower than that for total percentage of selfed-pollinations as it excludes between-clone differences in female strobilus production. However, the percentage selfing of the individual clones varied from 25.2 to 1.4 percent (Table 29). Clones that produced the greatest number of male strobili had the highest rates of selfing. The

percentage selfing estimates given here refer to self-pollination; however, the percentage of resulting self-fertilizations can not be estimated. Estimating the amount of self-fertilization is also more difficult because some clones may be more self-fertile than others (King et al. 1970, Hadders 1972, Hadders and Koski 1975). Nevertheless, the selfing figures presented here are probably good estimates of the selfing potential in a seed orchard of black spruce. The large range in the selfing estimates of the individual black spruce clones suggests that the incidence of selfing may be high on good male strobilus producers (Table 29). The effect of selfing is often reflected in a greater number of empty seeds, and a lower percentage of viable seeds, due mainly to a high frequency of embryo abortions (Sarvas 1962, King et al. 1970, Hadders and Koski 1975). However, more than 50 percent of the embryos originating from self-fertilization are viable in many species within the Pinaceae (Hadders and Koski 1975). Selfed-seed often have increased mortality and reduced rates of growth compared with cross-pollinated seed in many species within the Pinaceae (Fowler 1965, Franklin 1970, 1971; Koski 1973, Hadders and Koski 1975), including white spruce (Mergen et al. 1965). Also, a number of authors have indicated that selfing may be greater in the lower part of the female bearing crown due to the proximity of male strobili (Hadders 1971, Hadders and Koski 1975). Nevertheless, one study of white spruce showed that the

proximity of male and female strobili in the crown did not significantly change the rate of selfing (Millard 1981).

There may be a few ways of overcoming the problems associated with high rates of selfing on a per clone basis. To adjust for the female contributions, an equal number of cones from each clone can be used at time of seed collection. However, adjusting for the male component is not so simple. This problem may be partly overcome by monitoring male strobilus production, or more simply, removing less seed-cones from heavy cone producing clones if it is shown that heavy cone producers are also heavy male strobilus producers. Nevertheless, the results of this study showed no significant correlation between the number of male and female strobili per clone.

In calculating the percentage selfing in this study, it was assumed that outcross pollen had no advantage over self-pollen prior to fertilization, as previously shown for white spruce (King et al. 1970). The proportion of selfed-seed produced by a clone is directly proportional to the amount of self-pollen in the pollen cloud (King et al. 1970); this relationship was assumed for black spruce here.

The method used in this study to estimate the genetic composition of the progeny was based on certain assumptions. The assumptions made in this method were: airborne pollen of each clone had the same probability of reaching ovules of the receptive strobili of each clone; no incompatibility

existed between clones; no fertilizations were effected by pollen originating from outside the orchard and from the remaining 48 clones; all clones were self-fertile; the amount of pollen available was not a limiting factor once pollen release had begun; the number of ferilizations each day was proportional to the number of female strobili and to their stages of receptivity; each female strobilus had an equal number of ovules. Additional assumptions were made in order to estimate the clone contributions to the pollen cloud: the estimate of the number of male strobili was statistically correct; the amount of pollen contributing to the pollen cloud was the same for all microsporangia releasing pollen; each microstrobilus had an equal number of microsporangia; all pollen grains had the same viability and spent an equal length of time in the pollen cloud. Most of the above assumptions were based on two other similar studies (Eriksson et al. 1973, Jonsson et al. 1976). Many of these assumptions cannot be supported or refuted. However, some of these assumptions need elaboration concerning the present study.

There are some limitations to the method used in this study in calculating the gamete contributions and genetic composition of the progeny. One large limitation of this method is that the results are based on only one year's data, and the periodic nature of good cone and seed crops, which are especially pronounced in the north, have been well documented for many tree species (Wright 1953, Andersson

1965, Grano 1973, Lindgren et al. 1977). In addition, the results are based on a sample of 12 clones from a total of 60 of black spruce clones planted in the Mattawin seed orchard. However, most of the unsampled clones, and unsampled ramets of the observed clones represented in the other blocks, would probably have had relatively low contributions to the progeny due to the spatial arrangement of blocks (Figure 1) and high ramet mortality. Also, the other blocks were younger and were likely to produce less pollen. Thus, the results of this study probably do approximate actual composition of the black spruce progeny.

The assumption that each female strobilus produces an equal number of ovules was not verified, and it is conceivable that significant variation in numbers may have existed in the observed trees. Actual counts of white spruce seeds have shown that the total number of seed per cone may vary from 59 to 109 among clones (King et al. 1970). If the black spruce clones of this study show similar variation, then the calculated contributions of each clone to the progeny will be altered.

The most important limitation may be that the method assumes the amount of pollen available is sufficient to allow pollination of the same maximum number of ovules for all female strobili. The quantity of pollen in the pollen cloud may not have been sufficient at all times during the pollination period; this limitation may be hold especially

at the beginning and end of the pollen release period (Eriksson et al. 1973). One study in Monterey pine (Lill and Sweet 1977) showed that the most heavily pollinated cones were those which were receptive when maximum pollen was available. However, the time of pollen release may have been more important in that study, as the total period of receptivity of the five clones was 5 weeks compared with about 15 days for the 12 black spruce clones (Table 18). In the present study, adequate pollen may have been produced only during the period of maximum pollen release, from June 7 to 13 when more than 40 percent of the microsporangia were releasing pollen (Figure 5). Although low seed-set is caused frequently by low pollen production, it is caused also by late frosts and non-synchronous flowering times (Sarvas 1968, Nienstaedt and Jeffers 1970, Denison and Franklin 1975, Owens and Molder 1979a, 1980).

The use of the index for scoring stages of pollen release may be critized also. A strobilus was determined as fully opened when a large pollen cloud was observed after shaking an individual strobilus. However, this method may be biased as the pollen release may have been caused by the vibration, and there might have been no spontaneous natural release of pollen (Eriksson et al. 1973). Nevertheless, it is likely that any bias was uniform from clone to clone, and that the relative differences between ramets and clones remained similar.

In this study, some pollinations were probably effected by pollen originating from outside the orchard. Nevertheless, the probability of this event occurring should have been low as the seed orchard was surrounded by a nearly pure stand of jack pine.

Some of the assumptions with regard to female receptivity may be biased also. The index of female receptivity, similar to pollen release, was based on observations of cone external morphology. Accurate determination of the stages of female receptivity are more critical than those for pollen release as they determine when pollination may actually occur, whereas pollen release is only the physical release of pollen from the microsporangia. An index of receptivity was used in this study because it is easy to use with a large number of trees, and it is likely that external morphological characteristics, especially the angle of the bracts, are closely related to the stages of receptivity (Cumming and Righter 1948, Polk 1966, Wasser 1967, Borodina 1968, Eriksson et al. 1973, Jonsson et al. 1976, Sluder 1977, Daniels 1978). The angle of the bract may act as a physical barrier to pollen entry, as the larger this angle is, the more likely that pollen will sift into the micropyle. In addition, when this angle closes, there is no possibility for pollen entry.

Maximum receptivity, which is the period when most pollinations are likely to occur on a given strobilus, varies with the genus or species because of differences in pollination mechanisms (Doyle 1945, Dogra 1964, Owens et al. 1980a, 1980b). Pollination mechanisms, or the structure of the ovule tip and the process by which pollen is taken into the micropyle, have been described to some extent for most genera within the Pinaceae (Doyle 1926, Doyle and O'Leary 1935, Doyle and Kane 1943, McWilliam 1958, Barner and Christianson 1960, 1962; Allen 1963, Lill and Sweet 1977, Owens and Molder 1979b, 1979c, 1980; Owens et al. 1980a, 1980b). There is no published information on the pollination mechanism in black spruce, although it is probably similar to that of lodgepole pine and of other Picea species (Owens, personal communication). Owens dissected and observed female cones of lodgepole pine throughout the pollination period in order to relate external morphology to receptivity. The process from the time of full cone emergence until the end of receptivity took about 10-12 days, but cones were most receptive for only the middle of this period. In the early stage of receptivity, pollination drops formed first at the base of the cone and progressed toward the tip over about 4 days. This period was the most receptive stage, and was followed by about 2 days when a few pollination drops were present only in the distal part of the cone. Then, the scales began to thicken, sealing the space between the scales at the end

of receptivity. The pollination mechanisms in Monterey pine (Lill and Sweet 1977) and Pinus kesiya Royle ex. Gordon (Pattinson et al. 1969) appear to be similar. Since no female cone dissections were made on black spruce in this study, the stages of female receptivity may not have been defined accurately. Nevertheless, it is likely that the stages of female receptivity scored closely approximated the actual stages based on the descriptions given by Lill and Sweet (1977) and Owens (personal communication). These studies generally describe periods of increasing, maximum, and decreasing receptivity, which approximate the scored stages of partial, full and partial receptivity, respectively (Table 2). It is expected that if any error existed, all such errors would be uniform throughout the seed orchard. Overall, the relative differences between ramets and clones would probably have remained similar, even if the stages of receptivity were determined more accurately.

If the pollination mechanism in Picea is similar to lodgepole pine (Owens, personal communication) and Monterey pine (Lill and Sweet 1977), it can be expected that the first arriving pollen does not have an advantage over late pollen in black spruce. The method of calculation of clonal gamete contributions makes this assumption (Table 28). Pollinations were expected to occur at random as influenced by the stages of receptivity, with no weighting given to early pollen. In Monterey pine, Lill and Sweet (1977) found

that late arriving pollen, provided it lands on the micropylar arms, may have as good an opportunity of reaching the micropyle as early arriving pollen. In lodgepole pine, pollen applied when pollination drops were most abundant were preferentially taken in (Owens, personal communication). A little of the earlier pollen that landed on the micropylar arms also was taken in when the drop finally was exuded, but no pollen was taken in after the final withdrawal of the drop. However, controlled-pollinations were most effective in the earlier stages of receptivity in white spruce (Nienstaedt 1958), slash pine (Pinus elliottii Engelm.; Franklin 1974), and Douglas-fir (Owens et al. 1980). The results of Nienstaedt (1958) and Franklin (1974) do not support the findings of Lill and Sweet (1977) and Owens (personal communication), although all species described have similar pollination mechanisms (Doyle and O'Leary 1935, Owens, personal communication). However, the early stages of receptivity recognized by Nienstaedt (1958) and Franklin (1974) may have been the stages of maximum receptivity when pollination drops were most abundant as described by Owens (personal communication).

Differentiation and Early Development of Reproductive Buds in Black Spruce

An estimate of the time of reproductive bud differentiation in black spruce in the Mattawin seed orchard in 1979, can be made based on the results of this study and information from the more detailed studies in two other Picea species, white spruce (Owens and Molder 1977a) and sitka spruce (Owens and Molder 1976).

Male and female reproductive buds of black spruce were identified at the end of July and beginning of August, respectively (Figures 10, 12). These times closely correspond with the time of first reproductive bud recognition in black spruce at Chalk River, Ontario (Fraser 1966). In studies of other species, reproductive buds of white spruce (Fraser 1962, Owens and Molder 1977a), and sitka spruce (Owens and Molder 1976), were identified at comparable stages of development to the black spruce buds in this study. Differentiation of reproductive buds occurred in late-July in white spruce collected near Prince George, B.C. (Owens and Molder 1977a), and in mid-July in sitka spruce collected near Kelsey Bay, B.C. (Owens and Molder 1976); leaves, bracts, and microsporophylls were recognized in the buds of both species at the end of July, approximately 2-3 weeks later. Ovuliferous scales of black spruce were recognized in late-August in this study, at Chalk River, Ontario (Fraser 1966), and also in white spruce

near Prince George, B.C. (Owens and Molder 1977a). Generally, black spruce early reproductive bud development appears to be similar to sitka spruce and even more so to white spruce. Therefore, the timing and pattern of reproductive bud differentiation of black spruce may be similar to white and sitka spruce. These three species are similar in that both male and female buds can form by the transition of previously vegetative apices or from newly-initiated, axillary apices (Fraser 1962, 1966, Owens and Molder 1976, 1977a). In addition, apices of the three species pass through a stage of bud scale initiation before they initiate leaves, bracts, or microsporophylls (Owens and Molder 1977a).

Differentiation of black spruce reproductive buds in this study probably occurred in mid to late-July, which is about two to three weeks before the reproductive buds were recognized, as was shown for sitka and white spruce (Owens and Molder 1976, 1977a). Eis (1967) suggested that reproductive buds of black and white spruce differentiate in late-July in B.C. Eis (1967) used a dissecting microscope as in this study, but did not observe the actual stages of differentiation. In fact, Eis did not identify reproductive buds with certainty until mid-August. The approximate time of reproductive bud differentiation in black spruce given here and that of Eis (1967) are probably good estimates.

Black spruce may be similar to white spruce (Owens and Molder 1977a), in that through much of its range, shoot elongation ends and reproductive bud differentiation occurs at about the same time, during the last half of July. About 95 percent of lateral branch shoot growth in black spruce was complete by mid-July in this study. However, the remaining 5 percent of shoot growth took place from mid to late-July. Shoot growth cessation also occurred in mid to late-July at Chalk River, Ontario (Fraser 1966), and in late-July in B.C. (Eis 1967).

If the time of cessation of lateral branch growth coincides with the time of bud differention, as shown previously for white spruce (Owens and Molder 1977a) and sitka spruce (Owens and Molder 1976), it may be expected that black spruce buds would differentiate after white spruce buds. Fraser's (1966) results, and the results of this study, showed that apical growth of white spruce begins and terminates before that of black spruce at a similar site and location. The time of bud differentiation, therefore, may have occurred later than that indicated here for black spruce. However, the estimated time of cone differentiation given here covers a two to three week period from mid to late-July, and reproductive bud differentiation in black spruce may occur in the latter portion of this period, about one week after cone differentiation in white spruce at the same site.

This study provides information concerning the critical period for attempting to induce cones in black spruce. Attempts at flower induction, e.g., application of gibberelins, are most successful when applied at, or shortly before, the time of reproductive bud differention (Puritch 1972, Sweet 1975, Owens and Molder 1976, 1977a, 1977b, 1977c, 1979; Pharis 1976, 1979; Sweet and Krugman 1977). This period would be in the first 2-3 weeks of July in the Thunder Bay region. An external indicator for treatment application might be based on shoot elongation as suggested for white spruce (Owens and Molder 1977a); however, the use of this method requires further study.

Male buds were identified approximately one week before female buds based upon differences in the size and shape of the apex, and their frequent occurence in samples from the lower part of the crown. The results of this study do not allow any conclusions to be made as to why male buds were recognized before female buds. This result may have occurred for a few reasons. Actual time of male bud differentiation may precede female bud differentiation as in western hemlock (Owens and Molder 1974a), western red cedar (Thuja plicata Donn.; Owens and Pharis 1971), and yellow cedar (Owens and Molder 1974a). However, in white spruce (Owens and Molder 1977a) and sitka spruce (Owens and Molder 1976), no differences were found in the time of differentiation between male and female reproductive buds. Black spruce is likely to be more similar to other Picea

species. However, as the male and female buds in this study were from different clones, differentiation times may reflect clone differences. The onset of microsporophyll, bract, and leaf initiation was shown to vary between and within trees from one to two weeks in white spruce (Owens and Molder 1977a), and from two to three weeks in sitka spruce (Owens and Molder 1976). Owens and Molder (1976) could not ascertain if the differences in the time of initiation was due to variation in the time of bud differentiation between and within trees or to the subsequent rate of development.

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Appendix 1. Origin of clone ortets.

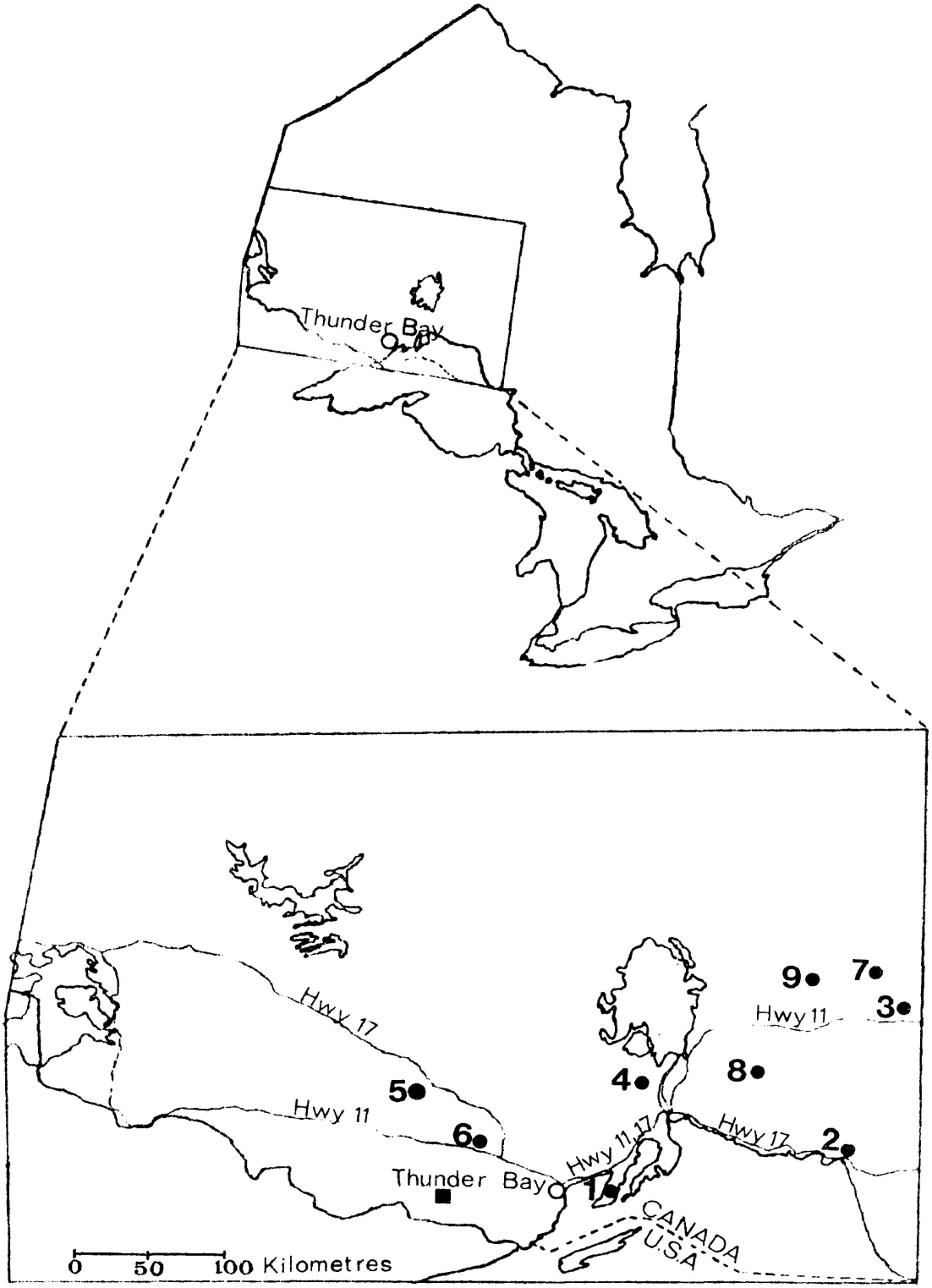
White spruce

Clone no.		Map location[1]	Mattawin block no.
261	Port Arthur, Sibley	1	1966 A
262	Port Arthur, Sibley	1	1966 A
270	Geraldton, Marathon	2	1966 B
281	Geraldton, Marathon	2	1966 A
282	Geraldton, Pagwa	3	1966 A
286	Port Arthur, Black Sturgeon Lake	4	1966 A
287	Port Arthur, Black Sturgeon Lake	4	1966 A
289	Port Arthur, Black Sturgeon Lake	4	1966 A
305	Geraldton, Pagwa	3	1966 B
306	Geraldton, Pagwa	3	1966 B
389	Geraldton, Kimberley Clark, Pagwa	3	1966 A
395	Geraldton, Kimberley Clark, Camp 57	3	1966 A
397	Geraldton, Kimberley Clark, Camp 57	3	1966 A
630	Kenora, Sherwood Lake Road	5	1966 A

Black spruce

288	Port Arthur, Black Sturgeon Lake	4	1966 A
303	Port Arthur, Abitibi	6	1966 A
304	Port Arthur, Abitibi	6	1966 A
384	Geraldton, Kimberley Clark, Club Lake Road	7	1966 A
386	Geraldton, Kimberley Clark, Club Lake Road	7	1966 A
387	Geraldton, Kimberley Clark, Club Lake Road	7	1966 A
393	Geraldton, Kimberlay Clark, Camp 35	8	1966 A
283	Geraldton, Kimberley Clark, Camp 35	8	1967 A
284	Geraldton, Kimberley Clark, Camp 35	8	1967 A
290	Port Arthur, Black Sturgeon Lake	4	1967 A
291	Port Arthur, Black Sturgeon Lake	4	1967 A
490	Geraldton, Leonard Lake	9	1967 A
491	Geraldton, Leonard Lake	9	1967 A
492	Geraldton, Leonard Lake	9	1967 A

[1] See appendix 2.



Appendix 2. Origin of clone ortets (●) (Location numbers are listed in appendix 1) and location of seed orchard (■).

Appendix 3

Temperature data, Mattawin seed orchard, 1979.

Temperature data 1979, Mattawin seed orchard.

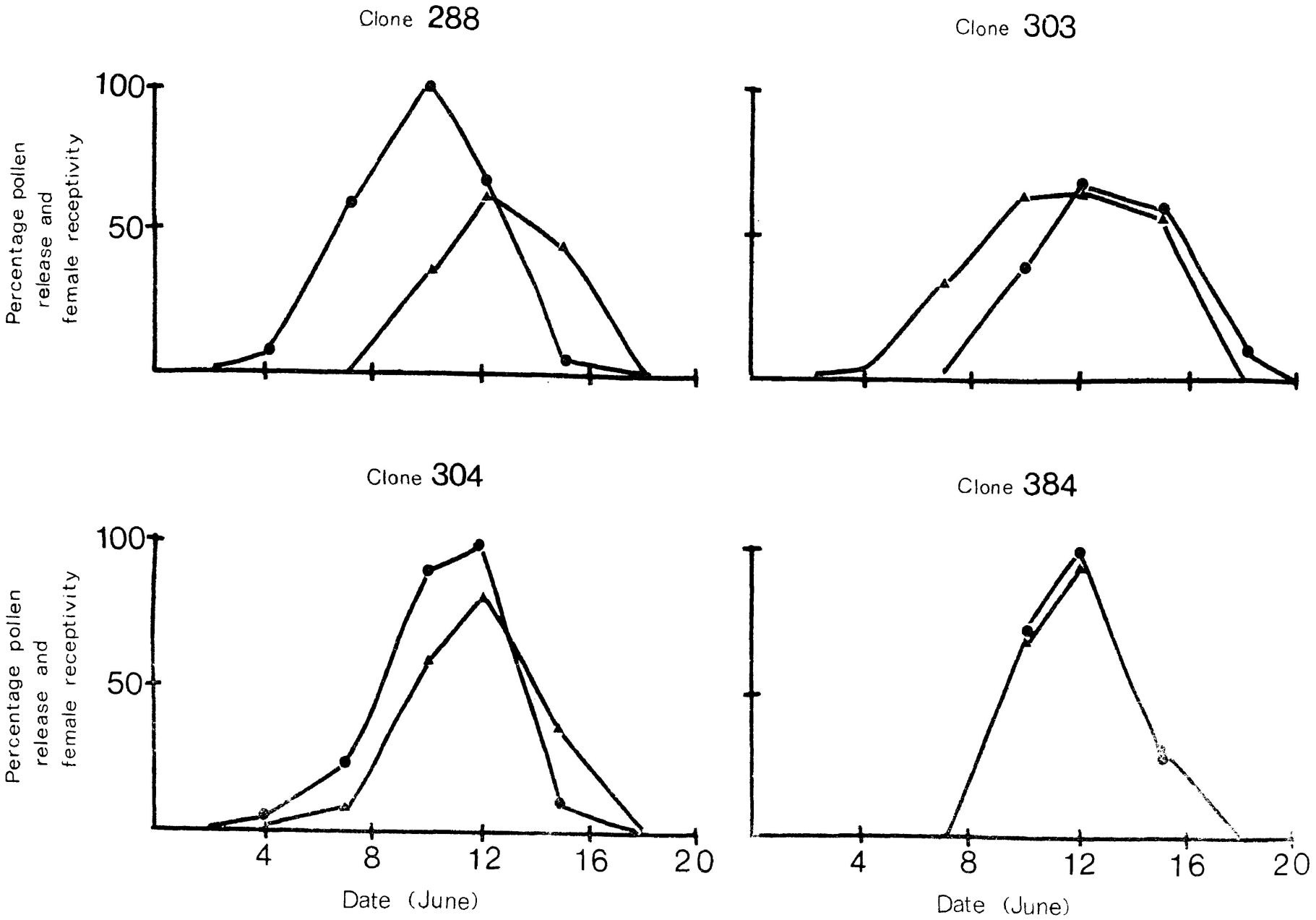
Day	Month	Number of days from May 1	Mean temperature (°C)	Degree-days per day	Cumulative degree-days
28	4		0.1	0	0
29	4		-0.2	0	0
30	4		-1.5	0	0
1	5	1	-1.0	0	0
2	5	2	2.3	0	0
3	5	3	0.6	0	0
4	5	4	-1.0	0	0
5	5	5	-1.6	0	0
6	5	6	-3.1	0	0
7	5	7	1.3	0	0
8	5	8	3.1	0	0
9	5	9	-0.1	0	0
10	5	10	1.7	0	0
11	5	11	4.4	0	0
12	5	12	4.7	0	0
13	5	13	6.1	1.1	1.1
14	5	14	3.1	0	1.1
15	5	15	3.9	0	1.1
16	5	16	8.8	3.8	4.9
17	5	17	17.3	12.3	17.2
18	5	18	10.4	5.4	22.6
19	5	19	4.0	0	22.6
20	5	20	2.5	0	22.6
21	5	21	6.0	1.0	23.6
22	5	22	5.0	0	23.6
23	5	23	5.0	0	23.6
24	5	24	6.9	1.9	25.5
25	5	25	9.2	4.2	29.7
26	5	26	10.8	5.8	35.6
27	5	27	9.3	4.3	39.8
28	5	28	12.4	7.4	47.1
29	5	29	11.3	6.3	53.4
30	5	30	12.6	7.6	61.0
31	5	31	9.5	4.5	65.5
1	6	32	8.9	3.9	69.4
2	6	33	10.4	5.4	74.9
3	6	34	11.3	6.3	81.2
4	6	35	10.6	5.6	86.8
5	6	36	8.9	3.9	90.7
6	6	37	9.2	4.2	94.9
7	6	38	12.9	7.9	102.7
8	6	39	11.7	6.7	109.4
9	6	40	11.6	6.6	116.0

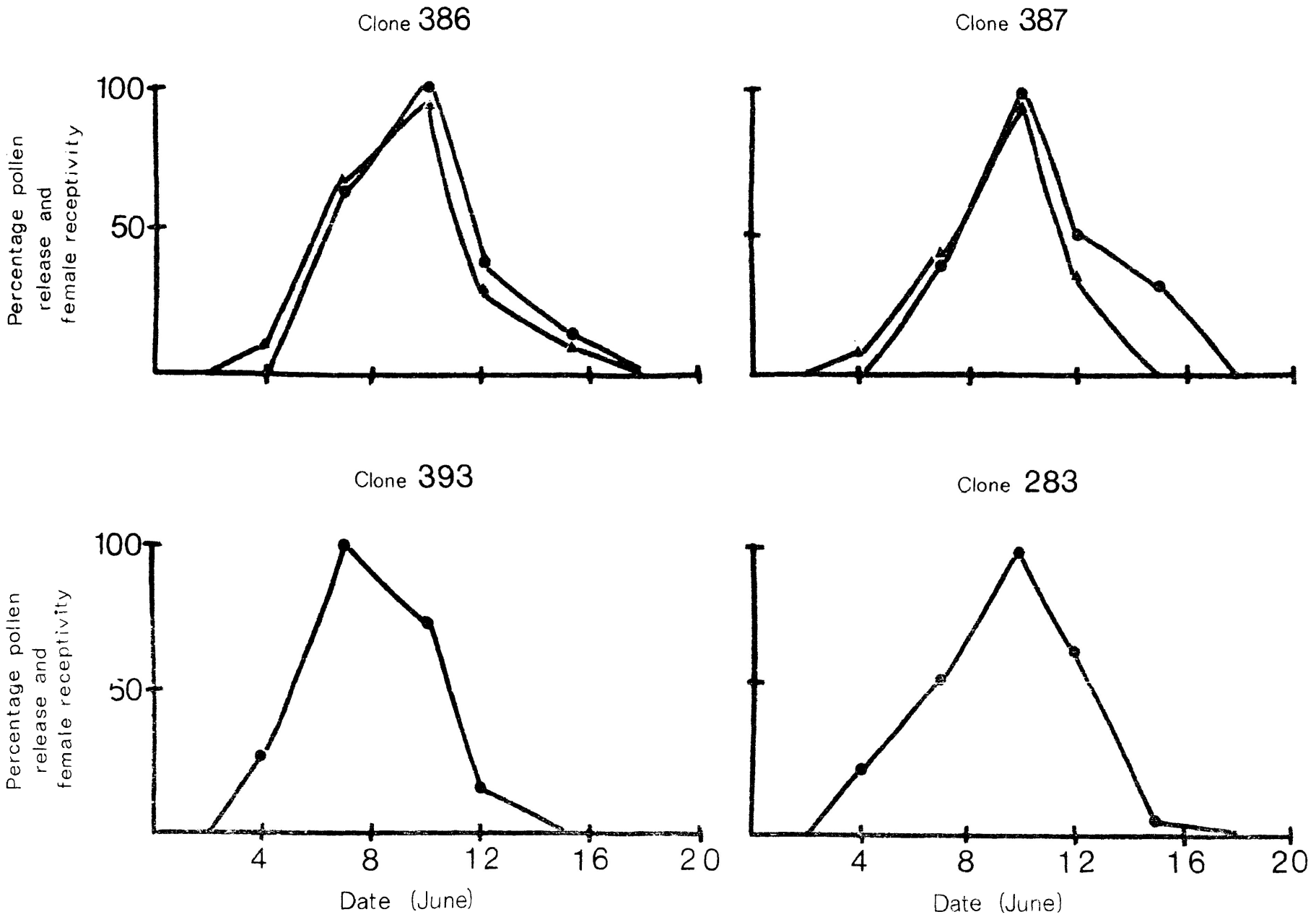
Day	Month	Number of days from May 1	Mean temperature (°C)	Degree-days per day	Cumulative degree-days
10	6	41	9.2	4.2	120.2
11	6	42	8.8	3.8	124.0
12	6	43	10.2	5.2	129.2
13	6	44	16.0	11.0	140.2
14	6	45	19.9	14.9	155.0
15	6	46	17.6	12.6	167.6
16	6	47	17.2	12.2	179.8
17	6	48	14.1	9.1	188.9
18	6	49	10.7	5.7	194.6
19	6	50	12.9	7.9	202.5
20	6	51	14.8	9.8	212.3
21	6	52	11.3	6.3	218.6
22	6	53	7.2	2.2	220.8
23	6	54	8.4	3.4	224.2
24	6	55	13.5	8.5	232.7
25	6	56	14.4	9.4	242.2
26	6	57	14.4	9.4	251.6
27	6	58	17.7	12.7	264.3
28	6	59	11.8	6.8	271.1
29	6	60	15.7	10.7	281.8
30	6	61	15.7	10.7	292.7
1	7	62	14.2	9.2	301.7
2	7	63	12.5	7.5	309.2
3	7	64	14.0	9.0	318.2
4	7	65	14.4	9.4	327.5
5	7	66	18.6	13.6	341.2
6	7	67	16.5	11.5	352.7
7	7	68	15.9	10.9	363.6
8	7	69	19.2	14.2	377.8
9	7	70	20.5	15.5	393.3
10	7	71	20.0	15.0	408.3
11	7	72	21.4	16.4	424.7
12	7	73	20.3	15.3	440.0
13	7	74	19.6	14.6	454.6
14	7	75	15.7	10.7	465.3
15	7	76	12.1	7.1	472.4
16	7	77	14.0	9.0	481.4
17	7	78	15.5	10.5	491.9
18	7	79	16.7	11.7	503.6
19	7	80	18.0	13.0	516.6
20	7	81	23.1	18.1	534.7
21	7	82	14.2	9.2	543.9
22	7	83	19.9	14.9	558.8
23	7	84	20.6	15.6	574.4
24	7	85	16.1	11.1	585.5
25	7	86	15.6	10.6	596.1

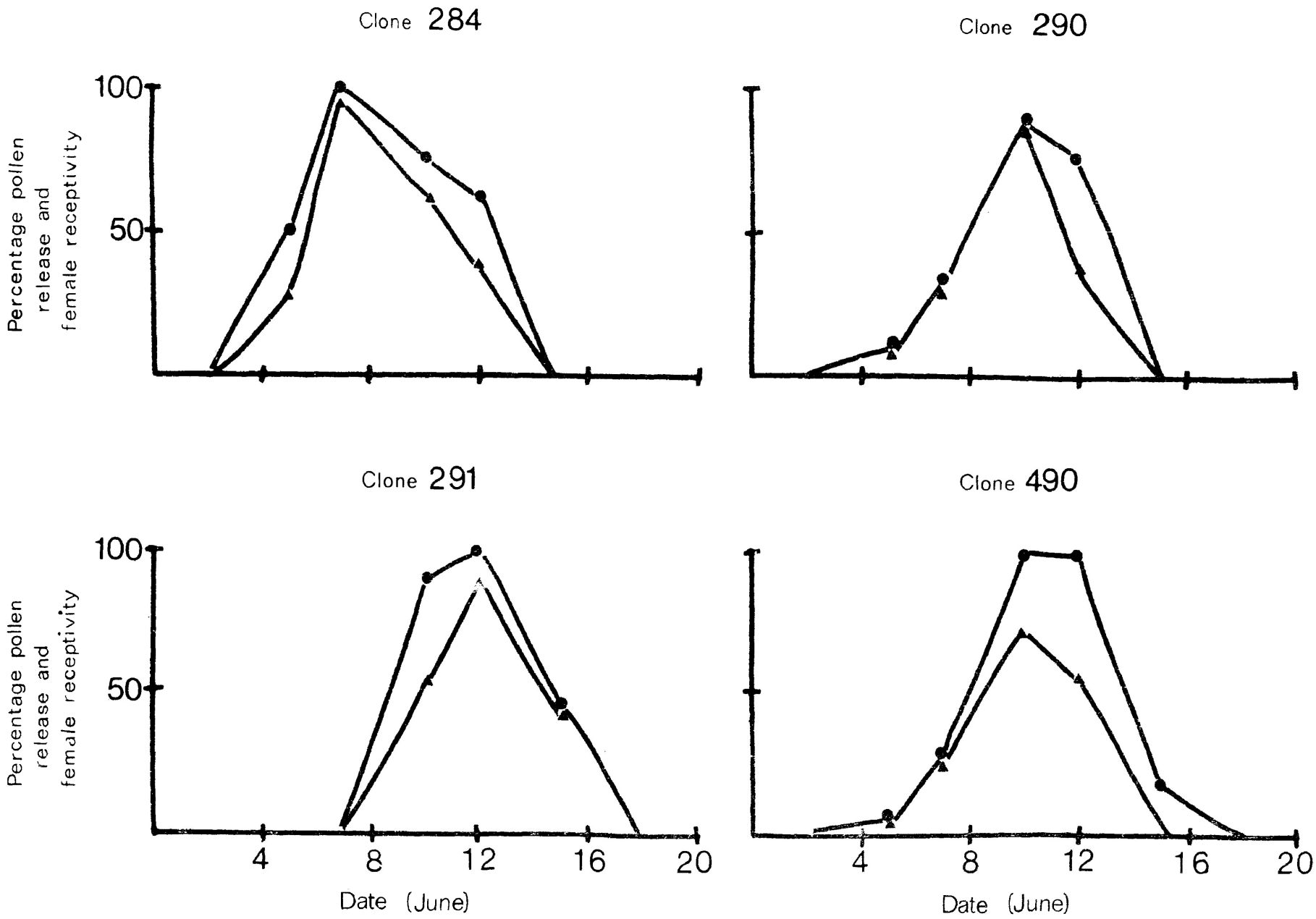
Day	Month	Number of days from May 1	Mean temperature (°C)	Degree-days per day	Cumulative degree-days
26	7	87	13.9	8.9	605.0
27	7	88	16.2	11.2	616.2
28	7	89	19.0	14.0	630.2
29	7	90	14.3	9.3	639.5
30	7	91	16.0	11.0	650.5
31	7	92	15.6	10.6	661.1
1	8	93	19.9	14.9	676.0
2	8	94	16.6	11.6	687.6
3	8	95	14.2	9.2	696.8
4	8	96	15.0	10.0	706.8
5	8	97	12.6	7.6	714.4
6	8	98	18.9	13.9	728.3
7	8	99	12.6	7.6	735.9
8	8	100	12.1	7.1	743.0
9	8	101	12.0	7.0	750.0
10	8	102	10.0	5.0	755.0
11	8	103	12.8	7.8	762.8
12	8	104	11.0	6.0	768.8
13	8	105	8.4	3.4	772.2
14	8	106	8.6	3.6	775.8
15	8	107	11.6	6.7	782.5
16	8	108	14.8	9.8	792.3
17	8	109	17.5	12.5	804.8
18	8	110	17.1	12.1	816.9
19	8	111	15.2	10.2	827.1
20	8	112	16.6	11.6	838.7
21	8	113	14.5	9.5	848.2
22	8	114	14.2	9.2	857.4
23	8	115	11.4	6.4	863.8
24	8	116	14.1	9.1	872.9
25	8	117	10.9	5.9	878.8
26	8	118	9.6	4.6	883.4
27	8	119	13.9	8.9	892.3
28	8	120	17.0	12.0	904.3
29	8	121	11.4	6.4	910.7
30	8	122	6.3	1.3	912.0
31	8	123	11.9	6.9	918.9
1	9	124	13.8	8.8	927.7
2	9	125	9.7	4.7	932.4
3	9	126	16.9	11.9	944.3
4	9	127	17.5	12.5	956.8
5	9	128	11.1	6.1	962.9
6	9	129	10.0	5.0	967.9

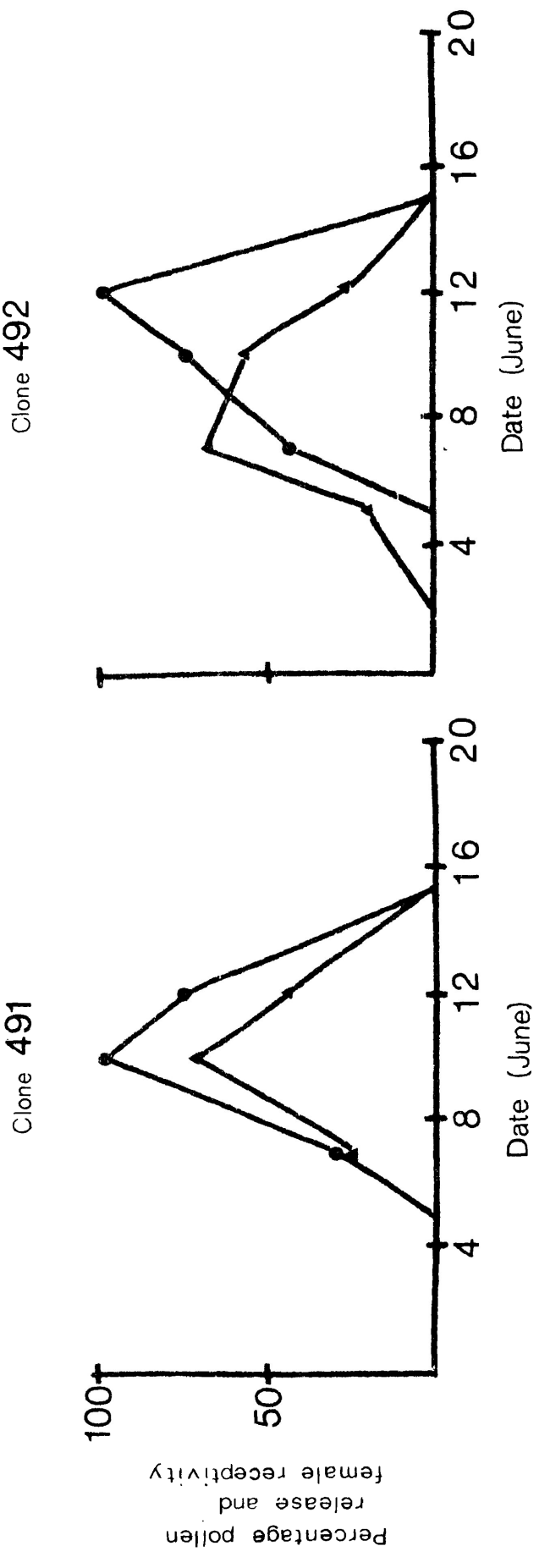
Appendix 4

Percentage pollen release (▲) and female receptivity (●) versus date for the individual clones of black spruce.


Clone 288
Clone 303
Clone 304
Clone 384
100
50
Percentage pollen release and female receptivity
4
8
12
16
20
Date (June)


Clone 386
Clone 387
Clone 393
Clone 283
Percentage pollen release and female receptivity
100
50
4
8
12
16
20
Date (June)


Clone 284
Clone 290
Clone 291
Clone 490
100
50
Percentage pollen release and female receptivity
4
8
12
16
20
Date (June)


Clone 491
Clone 492
Percentage pollen release and female receptivity
100
50
4
8
12
16
20
Date (June)

Appendix 5

Example calculation: Relative measures of the genetic composition of the progeny (Clone 288).

Female clone no.: 288

Male clone no.		Date (June)	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total relative contributions of each clone as a male parent
		Percentage female receptivity	7.5	25.0	40.0	58.8	72.0	85.0	100.0	82.0	63.8	42.0	22.0	2.5	2.0	1.0	
288	A[1]		0	0	0	0	14	19	21	30	39	42	48	59	60	63	
	B[2]		0	0	0	0	1 008	1 615	2 100	2 460	2 486	1 764	1 056	147	120	63	12 819
303	A		0	0	0	1	3	3	4	5	7	8	10	14	11	11	
	B		0	0	0	59	216	255	400	410	446	336	220	35	22	11	2 410
304	A		0	0	0	1	1	1	1	1	2	2	2	2	2	2	
	B		0	0	0	59	72	85	100	82	127	84	44	5	4	2	664
384	A		0	0	0	0	3	4	5	6	7	7	6	5	6	4	
	B		0	0	0	0	216	340	500	492	446	294	132	12	12	4	2 449
386	A		21	29	26	25	18	14	12	8	4	4	3	3	3	3	
	B		157	725	1 040	1 469	1 296	1 190	1 200	656	255	168	66	7	6	3	8 239
387	A		5	7	6	5	5	4	4	3	1	1	1	0	0	0	
	B		37	175	240	294	360	340	400	246	64	42	22	0	0	0	2 220
284	A		8	7	7	8	4	3	2	1	0	0	0	0	0	0	
	B		60	175	280	470	288	255	200	82	0	0	0	0	0	0	1 810
290	A		41	33	35	35	35	33	30	23	14	12	8	0	0	0	
	B		307	825	1 400	2 056	2 520	2 805	3 000	1 886	893	504	176	0	0	0	16 372
291	A		0	0	0	0	0	5	10	14	18	18	18	18	18	17	
	B		0	0	0	0	0	425	1 000	1 148	1 147	756	96	45	36	17	4 970
490	A		0	3	4	4	4	4	4	4	4	3	2	0	0	0	
	B		0	75	160	235	288	340	400	328	255	126	44	0	0	0	2 251
491	A		5	4	3	2	2	2	2	2	1	1	1	0	0	0	
	B		37	100	120	117	144	170	200	164	64	42	22	0	0	0	1 181
492	A		20	17	19	19	12	8	5	4	3	2	2	0	0	0	
	B		150	425	760	1 116	864	680	500	328	191	84	44	0	0	0	5 142
		Total relative contributions of all male clones															60 528

[1] Daily percent composition of the pollen cloud for each clone.

[2] Daily percent composition of the pollen cloud x the percentage female receptivity of clone numbered at top.