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FLOWERING CHARACTERISTICS OF *PINUS SYLVESTRIS* L. WITH SPECIAL EMPHASIS ON THE REPRODUCTIVE ADAPTATION TO LOCAL TEMPERATURE FACTOR

MÄNNYN (PINUS SYLVESTRIS L.) *KUKKIMISOMINAISUUKSISTA, ERITYISESTI KUKKIMISEN SOPEUTUMISESTA PAIKALLISEEN LÄMPÖILMASTOON*

Min-Sup Chung

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HELSINKI 1981

Arvi A. Karisto Oy:n kirjapaino
Hämeenlinna 1981

PREFACE

This present study was carried out during 1976–1980 under the supervision of Professor P. M. A. TIGERSTEDT, Ph.D., with the field guidance of Dr. Veikko KOSKI and with financial support from the Department for International Development Co-operation, Ministry for Foreign Affairs of Finland, for the study courses in forest genetics at the Department of Plant Breeding, Faculty of Agriculture and Forestry, University of Helsinki. In this connection the author wishes to express his sincere appreciation to Professor P. M. A. TIGERSTEDT, for the preparation of valuable study courses and all possible study facilities during this study, Dr. Veikko KOSKI for the excellent field guide and discussions on Scots pine flowering, and to the staff of the Department of International Development Co-operation, Ministry for Foreign Affairs of Finland for the financial support for this study in the form of a scholarship since the fall of 1975.

Special appreciation is expresses to Professor Max. HAGMAN, Dr. at the Department of Forest Genetics, Finnish Forest Research Institute, who furnished the study materials for the observation of Scots pine flowering, seed development and the discussions on this matters. Discussions on phenological studies with Mr. Jouni MIKOLA at this same Department were also very useful for this study. The author also wants to extend his acknowledgement to the staff of Punkaharju Tree Breeding Station of the above Institute who aided the author in many ways during the field observation and plastic-house experiment. Particulary the help of Mr. Pauli VÄRTINEN and Mr. Pentti MANNINEN was indispensable for the completion of the field work.

Greatful acknowledgement is made to Professor Paavo YLI-VAKKURI, Dr., the former Head of the Department of Silviculture, Faculty of Agriculture and Forestry, University of Helsinki, Professor Matti LEIKOLA, Dr., the Head of the same Department at present, who prepared and led the study courses in silviculture. Sincere appreciation is also extended to Professor Liisa SIMOLA and to Assistant Professor Niina VALANNE at the Department of Botany, Faculty of Science of the same University, for the study courses in plant physiology. The author also wants to extend his appreciation to Dr. Olavi LUUKKANEN, who is now an acting Professor at the Department of Botany, Faculty of Science of the same University, for the advice and aid during the previous study in silviculture.

The author wishes to express his sincere appreciation to Professor HYUN, Sin-Kyu, Dr., and the staff of the Institute of Forest Genetics in Suweon, Republic of Korea, for their encouragement for this study in Finland.

Many thanks are due to Mr. Donald NEVILLE for correcting the English in this thesis, Miss Sisko SALMINEN for drawing figures, and to Miss Anja KORPELAINEN for the typing.

Finally, the author wishes to give thanks to his wife KIM, Jae-Il, for her devoted assistance in the field and laboratory work during this study.

Helsinki, January 1981

AUTHOR

CONTENTS

1. INTRODUCTION

The motive of this present study originated from the attempt to find answers to questions which presented themselves during the earlier observations made by the author (unpublished) between 1971–1975 on the pine flowering in a hybrid seed orchard. The hybrid seed orchard was established with seedlings of *Pinus rigida* Mill. and *Pinus taeda* L. in 1959 aiming at hybrid seed production and is located in the southern part of the Republic of Korea. The flowering time of parental species as well as the individual trees of the species in the hybrid seed orchard fluctuated almost every year. The parental species showed different flowering behavior in each year and the time difference of flowering between the two species, approximately six to seven days, on an average, effectively isolated each other reproductively even though the flowering time of a few late flowering *Pinus taeda* L. (male strobili) and early flowering *Pinus rigida* Mill. (female strobili) individuals partially overlapped in some years.

1.1. Flowering and seed development in forest trees as an implement of reproduction and regeneration

As for its reproductive function, flowering and seed development is one of the most important parts of the life cycle in forest trees. The process leading to the development of flower*1 and seed in pine species display several sequential stages including 1) differentiation of floral initials, 2) the growth and development of floral initials into flower bud followed by flowering and pollination, 3) cell division in the megaspores and enlargement of the megagametophytes, 4) fertilization, 5) growth and differentiation of embryos and the subsequent development up to mature seed and cones. If the floral initials of Scots pine were supposed to be formed during August in the northern hemisphere as WAREING (1958) and KUPILA-AHVENNIEMI et al. (1980) reported (see also DUFF and NOLAN 1958, MERGEN and KOERTING 1957, and SACHER 1954 for other pine species) it would take approximately two years and four months to accomplish the full process of the reproductive cycle from the differentiation of floral initials up to seed maturity in southern Finland. In additon to this long-time requiring development for the completion on one reproductive cycle the reproductive growth shows an annual cyclic development in accordance with the changes of seasonal climatic patterns as SARVAS described elsewhere (SARVAS 1967 a and b).

Most of the studies on tree flowering and seed development have been conducted for the practical implications in silviculture and forest tree breeding as the demand of genetically improved forest tree seeds increases with the increasing tendency towards comprehensive silvicultural management followed by the extensive exploitation of forest for forest industry. Studies on flowering and seed development have also been conducted from the botanical and physiological point of view, for instance, FERGUSON (1901 a, b, 1904), DUFF and NOLAN (1953, 1958), SACHER (1954), MERGEN and KOERTING (1957), WAREING (1958), HASHIZUME (1959, 1969) and others.

The significance of flowering as a reproductive function in forest trees lies not only in the provision of seeds for production of planting stocks in regeneration but also, more greatly, lies in genetic improvement of forest trees. Genetic improvement through gene recombination in forest trees is possible only by sexual reproduction by way of flowering at present.

Recently much effort has been directed to forest tree breeding work in many countries of the world mainly applying plus tree selec-

*1: In this thesis the term "flower" is adopted for the developing strobili of gymnosperms as JACKSON and SWEET (1972) defined a flower simply as "a determinate sporogenous shoot". cf. HILLMAN (1963 p. 1) for the definition of flower. See also KRAMER and KOZLOWSKI (1960).

tion and the subsequent establishment of seed orchards for mass production of genetically improved seeds (cf. FEILBERG and SØEGAARD 1975). However, many problems have risen in the course of seed orchard establishment such as location, design, size of the seed orchards, propagation of parent materials, flowering, pollination dynamics, pollen contamination from surrounding stands, seed development, genetic constitution of the seeds, seed orchard management and protection etc. Among these problems, flowering, seed development, and the genetic constitution of the seeds become major subjects of study for forest tree physiologists, geneticists and tree breeders. A great number of studies have been carried out on flowering, seed development and seed or cone yield in conifer species, for instance WRIGHT (1953), SARVAS (1955, 1957, 1962, 1968), BARNER and CHRISTIANSEN (1960), ANDERSON (1965), WASSER (1967), ELIASON and CARLSON (1969), HAGMAN (1972), ERIKSSON et al. (1973). KARRFALT (1975), KOSKI (1975, 1980) KOSKI and TALLQVIST (1978), JONSSON et al. (1976), PEDERICK and BROWN (1976), BHUMIBHAMON (1978), etc.

1.2. Population structure in natural forest ecosystems

The genetic structure of a population is determined by the breeding system of the species and natural selection under specific environmental conditions. STEBBINS (1958 and 1974, p. 38) suggested that the opitimal genetic system of long-lived organisms which have both evolutionary success and the potential for further diversification is characterized by cross-pollination and high recombination rates, particulary in stable habitats. STERN (1972) stated that the interplay between genetic systems of populations and environments might often result in the establishment and preservation of high genetic variance or polymorphism. He also assumed that there must be modes of natural selection leading to genetic diversity rather than to genetic uniformity.

TIGERSTEDT (1973, 1974 a, b, and 1979) found in his isozyme studies that marginal *Picea abies* population retain plenty of genetic variation in spite of very strong natural selection and low population densities. He (ibid) has also determined the gene frequencies in some allozyme systems which agreed astonishingly well with the Hardy-Weinberg equilibrium. He interpreted this fact as a consequence of balancing selection.

A great genetic diversity with respect to morphological and physiological characteristics was also found even in the colonizing species with a mating system involving predominantly self-fertilization (ALLARD 1965). This fact implies that an inherent genetic variability exists, even in some of the predominantly self-pollinated colonizers, irrespective of the advantage of genotypic uniformity for colonization. Therefore, ALLARD (ibid) considered that most individuals that are successfully and predominantly self-pollinating species are heterozygous to some extent and thus they are presumably capable of contributing fine adjustments to the habitat through the segregation of better adapted types. The same author (ALLARD 1965) also found that even a little out-crossing is an important factor keeping the predominantly self-pollinating Lima bean populations from becoming highly uniform and interpreted that the situation was due to the higher relative selective values of the hybrids.

ALLARD and WORKMAN (1963) observed that selective values fluctuate widely from year to year and in many cases the advantage of heterozygotes over homozygotes is apparently associated with stressed environments. This fact indicates that the selection pressure exerted on a population is not a single factor but a multiple complex of factors operating through different population mechanisms at different times. Therefore, it is generally expected that the selective values of various genotypes in a population would vary relative to one another in response to the different environmental conditions in different times of a year or different years. Various selection pressures may be exerted on a population at almost the same time during the growing seasons or separately in different growing seasons or years, one year favoring one genotype and the other years favoring another. These various selective forces operating simultaneously or independently whether they are directional (the direction of selection may change during different growning seasons or years) or diversive, appear to render the population structure more polymorphic than uniform in spite of the great stablizing selection pressure within a population favoring intermediate types (refer to GRANT 1967 p. 213–215. METTLER and GREGG 1969 p 106–113, and TIGERSTEDT 1969 for the mode of selection).

Population structure can be changed gradually by mutation, migration and selection but usually by the interaction of these factors. The mutation rate appears to be very small (WRIGHT 1975 p. 18). Therefore, in many cases, the effect of mutation on the change of gene frequency in populations may be small. However, if the mutation is a recurrent and adaptive one to a changing environment, it can be a source of variation in the population and may provide alternative genes in the following generations.

Migration is one of the important factors affecting the change in genetic structure of a population. Migration at seed stage appears to be ristricted to a few tens of meters, at best, to a few hundred meters from the parent trees in most conifer species under normal climatic conditions (STERN and ROCHE 1974 p. 50–57). A relatively long-distance seed dispersal was reported in *Pinus radiata D. Don.*, although the number of seeds found at this distance was very small (BANNISTER 1965). Migration at the gamete stage (pollen) seems to be relatively effective as compared to the zygotic stage (seed). KOSKI (1970 a, 1974) reported occasional or recurrent long-distance pollen dispersion although most of the pollen reaching the receptive female strobili comes from the nearest neighboring individuals within a subpopulation (see also SARVAS 1967 c, WANG et al. 1960, WRIGHT 1953). The immigration of male gametes to a population can often be an important factor affecting the gene frequencies of a population, as also found in introgressive species hybridization (FORREST 1979).

Selection is one of the most dominating factors that affect the gene frequency of a population and occur at various developmental stages of an organism or a population with differential intensities and modes in time and space according to the stages. Selection usually occurs in association with other factors such as mutation and migration both in natural or new colonizing and transferred habitats. Adaptation or the flexibility of plant populations to local environment, particularly to the climatic rhythms of the natural habitats, appears to be one of the most important factors determining the fitness values of the populations or individuals under the selective pressures of changing environment or at different transferred places (DIETRICHSON 1961, 1964 a, 1964 b, 1968 a, 1968 b, 1969 a, 1969 b, 1971, EICHE 1966, EICHE and ANDERSSON 1974, LANGLET 1967).

1.3. The aim of study

In Finland, the majority of northern plus tree seed orchards were established, apart from the original localities of selection, in the south of the seed utilization area for safe and increased seed production (cf. SARVAS 1970 a) in central and southern Finland. However, the problems that would be caused by the distant north-south transfer in relation to flowering and seed development were not studied extensively. The ideal condition for the northern plus tree seed orchards in central and southern Finland would be synchronous flowering of the individual trees or clones within the seed orchards and at the same time reproductive isolation of the seed orchards' trees from trees of the surrounding stands.

The aim of the present study is to investigate the inherent characteristics of Scots pine flowering and the seed development as well as the factors controlling or affecting the floral development in relation to its practical implications in seed orchard establishment. The major questions concerned in this study are;

1) Is the progress of reproductive cycle of Scots pine adapted mainly to local temperature factor?
2) Does the development of floral organs up to flowering in the spring mainly depend on the time-temperature factor as SARVAS (1967 a, 1972) reported?
3) To what extent is the physiological reproductive isolation (cf. SARVAS 1970 a) possible by the north-south transfer?
4) How do the flowering characteristics of pine species affect the seed development and the genetic structures of the resulting seeds?

2. MATERIALS AND METHODS

The study materials were the flowers, cones and seeds of Scots pine plus tree clones in the clone bank established in 1958 and 1968 at Punkaharju Tree Breeding Station (61° 48′ N, 29° 19′ E, 80 m a.s.l. mean annual local temperature sum Σ T +5° C (cf. SARVAS 1967 a, 1970 a, 1248 ± 27° C), of the Finnish Forest Research Institute. The clones are from 73 different localities throught Finland including two foreign localities. The localities were grouped into 23 geographic regions and on a greater scale into three clonal groups namely northern (N), central (C) and southern (S) clones according to the mean annual temperature sums above +5° C (cf. SARVAS 1967 a, SOLANTIE 1976) of the original localities where the plus tree clones were selected (Fig. 1, Tab. 1). The classification of the three clonal groups are as follows:

N clones: clones that are from the localities belonging to annual temperature sums between 560° and 1000° C.

C clones: clones that are from the localities belonging to annual temperature sums between 1001° and 1199° C

S clones: clones that are from the localities belonging to annual temperature sums between 1200° and 1280° C

2.1. Observations for floral development

Female flowering was observed for three consecutive years from 1976 to 1978 on the same grafts (in most cases) of the same clones. An average of 32 female strobili from two grafts in each clone, at the height of 2 m above ground level, in each northern, southern eastern and western aspects of tree crown were observed in 1976. However, on the average 28 and 16 female strobili from one (mostly) or two grafts in each clone were observed in 1977 and 1978 respectively, in the same way as in 1976. The number of clones observed for male and female flowering is presented in Table 2.

In most cases, the same clones were sampled in every observation year for the observation of male flowering. Many of them were the same clones used for the observation of female flowering. The sampling fluctuation for the observation of male flowering was mainly due to the yearly fluctuations of the abundance of male flowering in the sampled clones.

Pollen shedding, as a way of male flowering measurement, was recorded in three steps by visual observation, the beginning, the maximum and the last day of shedding on one tree as a whole. In addition to this visual observation on pollen shedding seven registering pollen catch meters (cf. KOSKI 1970 b, SARVAS 1967 a) were installed to measure the effective pollen dispersion at three different sites in 1976 and 1977. Two registering pollen catch meters were located at about 6 m above ground level in a clone bank established in 1958 (sample stand 1), two at about 7 m above ground level in a clone bank established in 1968 (sample stand 2) and the other three at 21 m above ground level in an about 100-year old natural Scots pine stand (sample stand 3). In addition to these pollen catch meters two more registering pollen catch meters were installed at 2 m height in sample stand 3 in 1978.

The cellulose acetate bands with the trapped pollen grains on their vaseline coated surfaces that were placed inside of the registering pollen catch meters to be exposed to a certain period (6-days) of dispersing pollen clouds were collected and stored in protective cardboard cases before pollen counting by microscope. Just before microscopic observation the vaseline surface of the band was sprayed with Nobecutan spray*2 to fix and protect the creamy surface of vaseline with the trapped pollen grains from pollen contamination, and to improve the legibility of the band. After drying, the band was sprayed

*2: Liquid acryl spray for sugery.

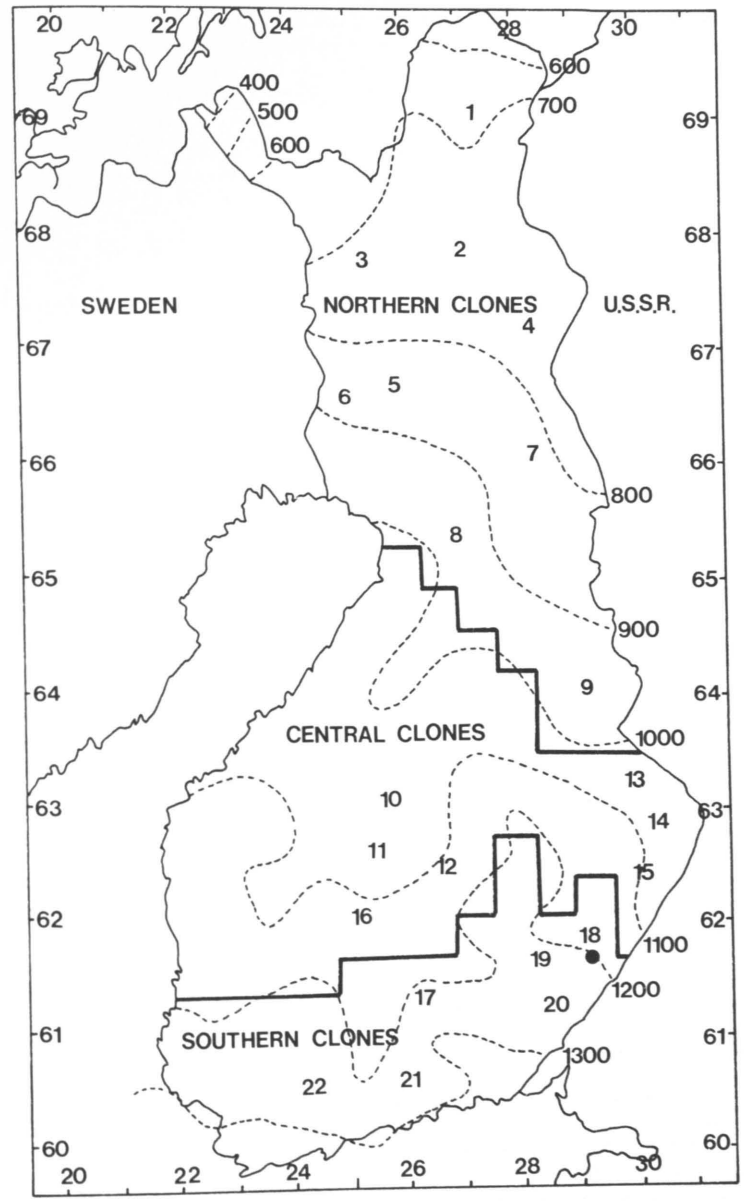

Fig. 1. Distribution of clonal regions (localities) throughout Finland
——— = boundaries between clonal groups
– – – – – = isograms of mean annual temperature sums (d.d.) above + 5°C
● = location of Punkaharju clone bank.
Localities are also presented in Arabic numbers.

Table 1. Locality numbers and the clonal orgins on the map (Fig. 1).

Clonal group	Locality No.	Name of locality	No. of clones
N	1	Inari	15
	2	Sodankylä	21
	3	Kittilä, Muonio, Kolari	10
	4	Savukoski, Pelkosenniemi, Salla	10
	5	Rovaniemi, Rovaniemi mlk.	14
	6	Pello, Yli-Tornio, Tervola	12
	7	Kuusamo, Posio	9
	8	Pudasjärvi	7
	9	Kuhmo	5
Sum			103
C	10	Kannonkoski, Konginkangas, Karstula, Viitasaari, Pihtipudas, Kivijärvi	24
	11	Saarijärvi, Pylkönmäki, Äänekoski	35
	12	Joroinen, Rautalampi	6
	13	Pielisjärvi	13
	14	Ilomantsi, Eno	15
	15	Kiihtelysvaara	7
	16	Jämsä, Korpilahti, Keuruu, Petäjävesi, Kuorevesi, Kuhmoinen	9
Sum			109
S	17	Suomenniemi, Hartola, Sysmä, Padasjoki, Mäntyharju, Heinola, Asikkala, Lammi, Vanaja	20
	18	Kerimäki, Punkaharju	7
	19	Sulkava	9
	20	Taipalsaari, Ruokolahti	15
	21	Savitaipale, Valkeala, Sippola, Pornainen, Virolahti	10
	22	Kalvola, Tammela, Pyhäjärvi, Janakkala, Yläne, Lohja, Inkoo	23
	23	Exotics from Norway and England	8
Sum			92
Total			304

again with absolute ethyl alcohol to improve the transparency before microscopic observation. A total of sixty microscopic fields consisting of five microscopic fields on each fraction at two-hour intervals on each day were examined to count the pollen grains on the band.

Two plastic-houses were built on 12 May (plastic-house No. 1) and on 17 May (plastic-house No. 2) 1978 to observe flowering responses to different temperature regimes. Each plastic-house contained five grafts of different clones planted in 1968. Nine of them were northern clones and one was a central clone.

The size of the plastic-house was 5 m × 25 m × 4,7 m in its width, length and height respectively. Each plastic-house was equipped with one door and four openings on both the northern and southern sides near ground

Table 2. The number of clones observed for male and female flowering.

Observation year	Year of Clone Bank Estab.	Clonal group and the No. of clones observed				Remarks
		N	C	S	Sum	
1976–1978	1968	103	109	92*3	304	♀
1976	1958	6	7	5	18	♂
	1968	36	18	46	100	
	Sum	42	25	51	118	
1977	1958	17	19	14	50	
	1968	18	13	35	66	
	Sum	35	32	49	116	
1978	1958	22	24	17	63	
	1968	7	20	49	76	
	Sum	29	44	66	139	

*3: 8 exotic clones were included in the S clonal group

level to control the temperature through natural ventilation by adjusting the size of the openings. Temperatures were recorded by installing thermographs in the center of the plastic-houses at the height of 2,2 m, about the same level as of the observed female strobili.

All of the male and female flowering outside were observed once a day and the time of observation was recorded at approximately one to two hour intervals. Later the observed flowering times were converted into period unit (p.u., cf. SARVAS 1972) sums of flowering. However, the female flowering in the plastic-houses was recorded three times a day at about 8, 12 and 16 o'clock, because the development of female strobili as well as the progress of p.u. was very rapid due to the high temperatures in the plastic-houses during the sunny days.

2.2. Seed development

A total of 16 mature cones per clone were collected in late April and November 1978, for the cones developed from 1976 and 1977 flowering respectively at about the same level and directions as in the observations on female flowering. The cones were from the same clones (mostly from the same grafts of the clones) comprising of 63 N, 44 C and 55 S clones for which the female flowering was recorded earlier in the clone bank established in 1968.

In addition to this, cones were also collected from 13 clones in the neighboring clone bank established in 1958. The seeds were extracted manually after drying the cones in an drying oven at 40–45° C for two to five days immediately after the cone collection and later 50 seeds in each clone were photographed by soft x-ray transmission equipment.

Observation on the conelet abscission was made during June 2nd-5th 1979 for the conelets developed from the 1978 flowering of the clones for which the female flowering was recorded. On the average, 153 of either normally developing or abscissed conelets per clone were recorded for 29, 28 and 28 of early, intermediate and late flowering clones respectively to observe the differences in the proportion of conelet abscission.

The major parts of the statistical analysis were made by a computer at the university computor center and the rest of the miscellaneous calculations were carried out with a Hewlett Packard -67 electronic calculator.

3. RESULTS

3.1. Female flowering

3.1.1. The development of a female strobilus and the receptive interval

According to externally visible characteristics the developmental stage of Scots pine female flowers were classified as follows:

Stage 1–1: Initial protruding stage of flower bud (Fig. 2–1).

Stage 1–2: The stage with a considerably swollen flower bud which is still enclosed entirely within the flower bud scales (Fig. 2–2).

Stage 2–1: Initial protruding stage of female strobilus out of flower bud scales (Fig. 3–1).

Stage 2–2: A further development of stage 2–1, most upper part of the ovuliferous cone scales are exposed to the air at this stage. The growth of the floral axis is conspicuous from this stage (Fig. 3–2).

Stage 2–3: About a half of the ovuliferous cone scales are exposed to the air and bracts are considerably developed but still erect at this stage (Fig. 3–3).

Stage 3 : All or most of the fertile ovuliferous cone scales are exposed to the air and some of the bracts are reflected at this stage (Fig. 4). The axis of the strobilus is approximately parallel to the axis of the shoot on which the strobilus is located. The base part of the cone axis (peduncle) is considerably elongated at this stage.

Stage 4–1: The exposed ovuliferous cone scales in the air begin to open, making fissures between the cone scales from the lower part of the developing strobilus, immediately thereafter, they would permit pollen grains to enter the ovule (Fig. 5–1). The base part of the cone axis starts to bend down forming a larger angle to the shoot axis about at this stage in normal years.

Stage 4–2: Ovuliferous cone scales are fully open with a maximum possibility of pollination, in some cases, even the intact micropyles can be seen from outside of the fissures at this stage without the aid of a magnifier but with careful visual observation (Fig. 5–2). The elongation growth of both conelet axis and scales is conspicuous at this stage.

Stage 5 : The fissures start to close as the ovuliferous cone scales grow conspicuously in thickness. No more pollen grains can enter into the ovules from outside of the closed conelet scales after this stage (Fig. 6–1). At this stage the conelet axis meets the shoot axis with a considerably larger angle which will finally become approximately parallel in a reverse direction from the beginning of its development to the axis (Fig. 6–2).

The flower bud of a female strobilus in Scots pine protrudes (Stage 1–1) out of the scales of the growing shoot apex around late May in southern Finland, about two to three weeks prior to flowering. But in some extreme cases, particularly abnormally early flowering northern clones or very late flowering southern or exotic clones, the

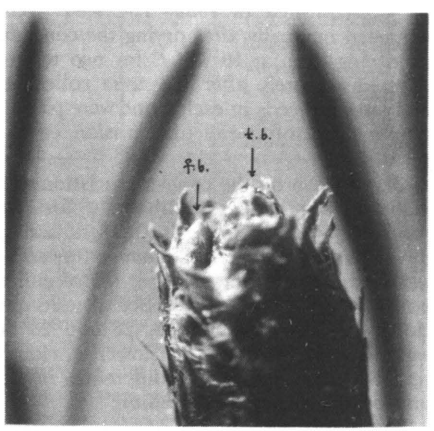

Fig. 2–1. Stage 1–1.
f. b. = flower bud.
t. b. = terminal bud.
l.b. = leaf bud.

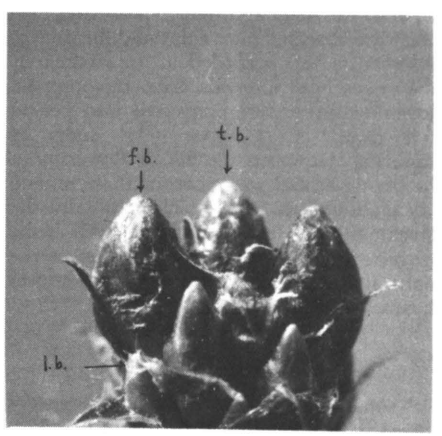

Fig. 2–2. Stage 1–2.

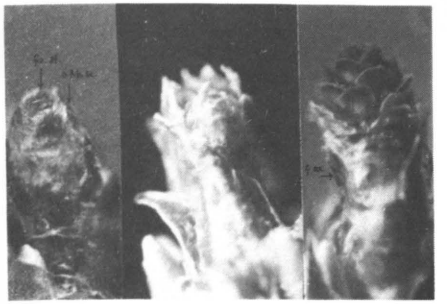

Fig. 3–1 Stage 2–1

Fig. 3–2 Stage 2–2

Fig. 3–3 Stage 2–3

fe. St. = Protruding female strobilus.
o. f. b. Sc. = Outer flower bud scales.
f. ax. = floral axis.

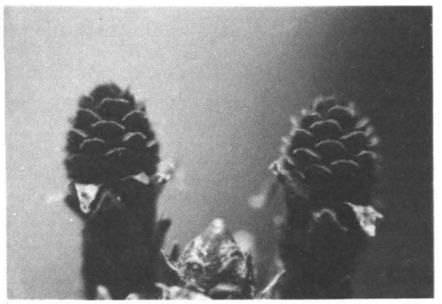

Fig. 4–2. Stage 3.

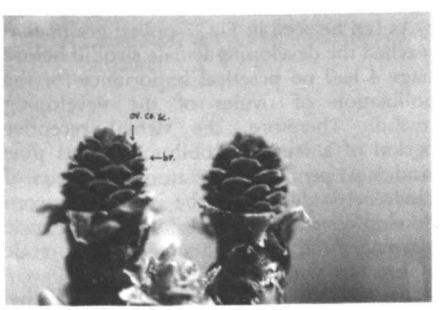

Fig. 4–1. Stage 3
ov. co. sc. = ovuliferous cone scale.
br. = bract.

Fig. 5–1. Stage 4–1

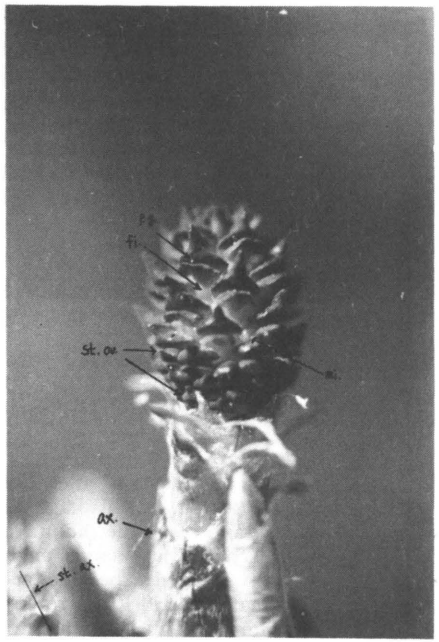

Fig. 5–2. Stage 4–2

p. g. = pollen grain on the surface of ovuliferous cone scale.
fi. = open fissure between the ovuliferous cone scales.
st. ov. = sterile ovuliferous cone scales.
mi. = micropyle exposed to the air.
ax. = basal part of conelet axis.
st. ax. = shoot axis.

protrusion of female flower buds commences in early May or in early June, respectively. In spite of this larger differences in the beginning of developmental stage 1–1, usually the floral development in most of the investigated clones except the extremely early or late flowering clones reached stage 4 at about the same time in early or in the middle of June within a rather shortly defined period (for a few days) depending on the climatic conditions of the flowering years. Other types of flowering characteristics in Scots pine are described elsewhere (SARVAS 1962, WAREING 1958).

To determine the virtual receptive interval of a female strobilus, 57 strobili of N clones were sampled and pollinated artificially without bagging according to the different developmental stages (Stages 1–4) of the strobili in 1977. Later, as soon as the pollinated strobili reached stage 5, they were collected and examined under a dissecting microscope to calculate the proportion of pollinated ovules.

Fig. 6–1. Stage 5
Ovuliferous scales are closed.

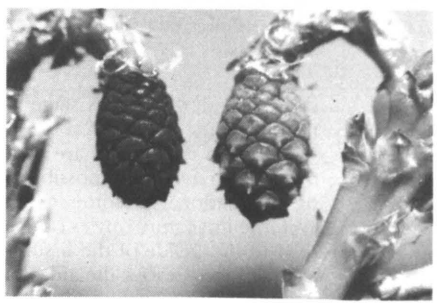

Fig. 6–2. Stage 5
Final stage of the first year's development.

As can be seen in Fig. 7 pollen grains that reached the developing female strobili before stage 4 had no practical importance for the pollination of ovules of the developing strobili. Therefore, the virtual receptive period of a female strobilus on Scots pine (and most probably, also in other species of Pinaceae) is defined as the interval between developmental stage 4–1 (ovuliferous scale opening) and stage 5 (ovuliferous scale closing) from now on.

In 1976 and 1977 the female strobili that reached developmental stage 2–1 were recorded and later converted into the time of actual receptivity by the calculation of the temperature sum difference between the two stages determined by separate precise observations on the development of female strobili from stage 2–1 to stage 4–1. The average temperature sum required for the development from stage 2–1 to stage 4–1 was 44.2 ± 8.1 degree days (d.d.). In 1978, the developmental stage 4–1 was recorded as the sign of the beginning of the receptive period.

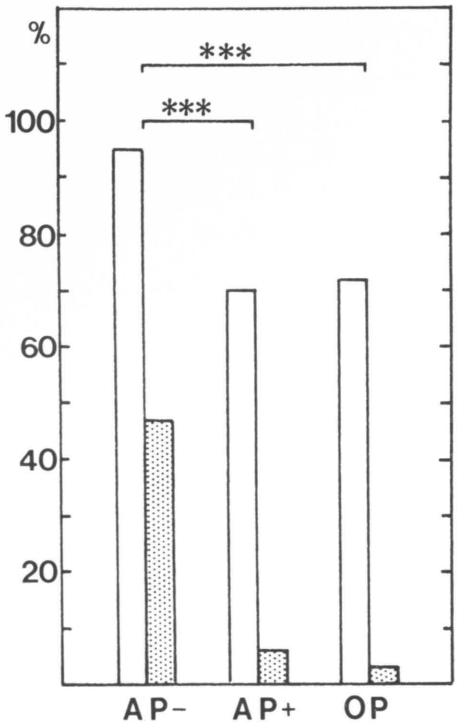

Fig. 7. Percentage of pollinated micropylar cavities in artificially and in open pollinated strobili.
AP– = Artificial pollination after flowering and subjected to open pollination
AP+ = Artificial pollination just before flowering and subjected to open pollination
OP = Open pollination
□ = Pollinated micropylar cavities
□ = micropylar cavities with 11 or more pollen grains
*** = significance at 1 % level (t-test with pooled variance)

3.1.2. The time and p.u. sums of female flowering

Developmental stage 4–1 is considered to be the beginning of flowering and the receptive interval, or else as the flowering period in a narrow sense, while in a broad sense flowering includes all of the developmental stages of the reproductive organs.

The time of female flowering showed a wide range of variation throughout the three different observation years as well as between different clones in the same year. In this respect the time scale appears to be a fluctuating parameter for the measurement of flowering in Scots pine. In general, the flowering follows the fluctuation of meteorological conditions, particularly the temperature factors, in each year. The meteorological conditions in each of the three observation years were not identical.

The earliest flowering was recorded on May 30th in 1978 in northern clones and the latest one was on June 20th in 1976 in central clones. However, most of the clones flowered during the later half of early and the earlier half of the middle of June (6–16) in 1976 and 1977 respectively. The flowering in 1978 was much earlier than in the previous two years and appeared to be rather exceptional, probably due to the lack of late frost just before flowering in this year.

The flowering p.u. sums (calculated from the beginning of the year) of the different clonal groups in 1978 were also much smaller than the other two years. This was somewhat unexpected in view of the results obtained in the two previous years.

The p.u. sums and times of flowering in different clonal groups are listed in Table 3.

The northern clonal group as a whole is distinctly different from central or southern clonal groups in its flowering p.u. sum (Figs. 8, 9 and 10, Tables 4, 5 and 6). However, the clones from locality 9 (Kuhmo) of the northern clonal group, which is located near the border line between the northern and central clonal groups, showed somewhat different flowering behavior in different years from the same northern clonal group as can be seen by comparing tables 4, 5 and 6. Some clones from the locality flowered as early as northern ones and the others as late as southern ones. The flowering behavior of clones from locality 8 (Pudasjärvi), which is also located close to

Table 3. The flowering times and p.u. sums of different clonal groups at Punkaharju clone bank (61° 48′ N, 29° 19′ E, 80 m a.s.l.)

Clonal group	Year	Earliest flowering clone	Mean ± sd	Latest flowering clone	Mean p.u. sums for flowering
Northern	1976	June 2nd	June 11 ± 2.4	June 16th	6548 ± 265
	1977	" 6th	" 8 ± 1.1	" 11th	6657 ± 295
	1978	May 30th	" 1 ± 1.0	" 4th	5925 ± 200
Central	1976	June 9th	June 14 ± 2.0	June 20th	6785 ± 241
	1977	" 7th	" 9 ± 1.2	" 13th	6989 ± 369
	1978	May 31st	" 2 ± 1.3	" 5th	6230 ± 234
Southern	1976	June 9th	June 14 ± 1.8	June 18th	6792 ± 201
	1977	" 8th	" 10 ± 0.7	" 15th	7198 ± 400
	1978	May 31st	" 3 ± 1.2	" 6th	6367 ± 245

p.u. sums are calculated from the beginning of the corresponding years.

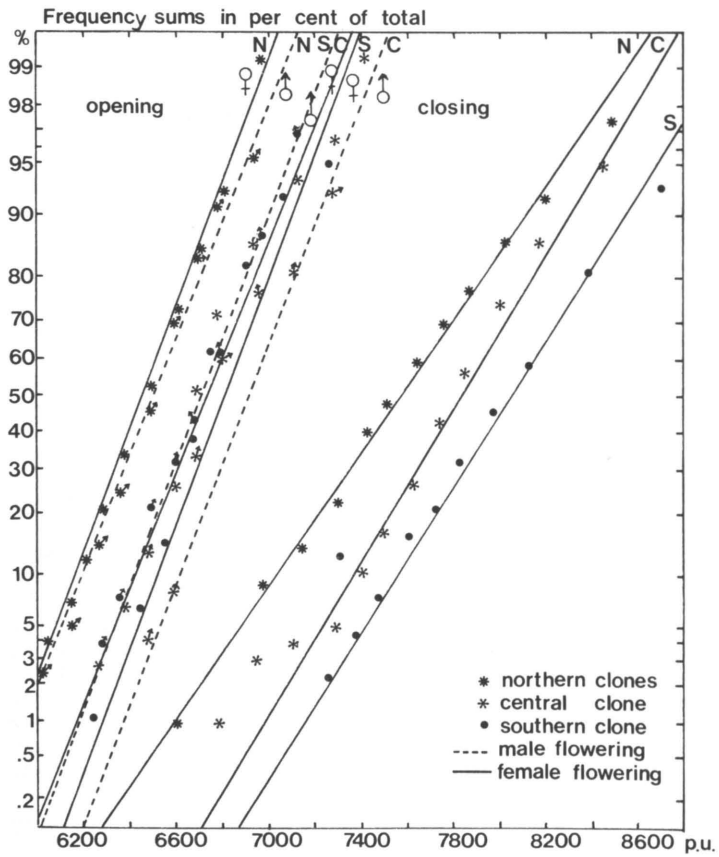

Fig. 8. The distribution of frequency sums of the male and female flowering in relation to p.u. sums at Punkaharju clone bank (61° 48′ N, 29° 19′ E. 80 m a.s.l.) in probability-net paper. Flowering in 1976. Abscissa: p.u. sums in even scale. Ordinate: Gauss integral. All lines have been drawn free-hand.

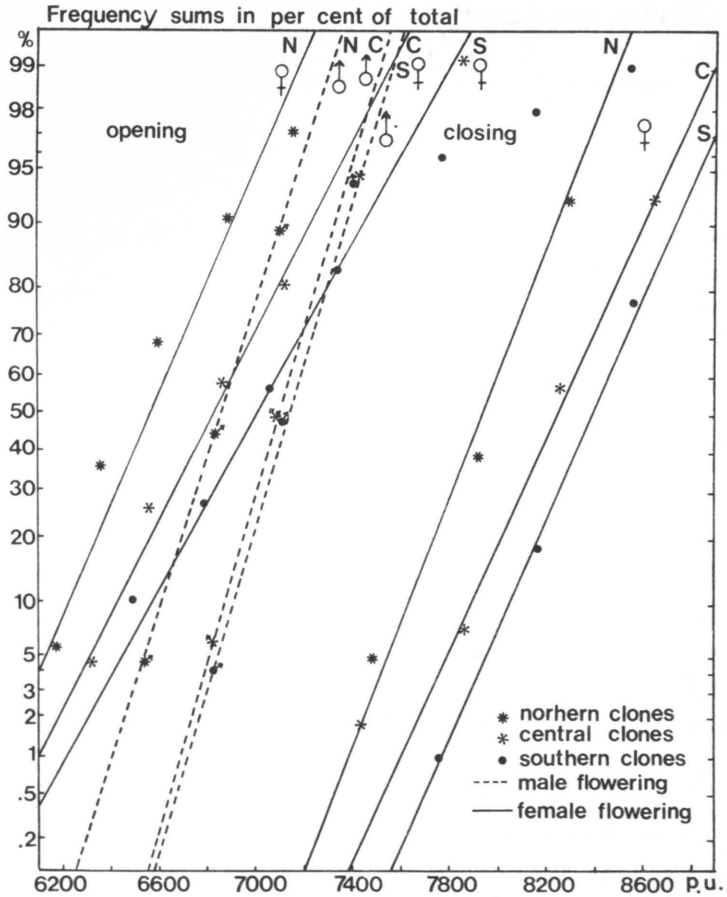

Fig. 9. The distribution of frequency sums of the male and female flowering in relation to p.u. sums at Punkaharju clone bank (61° 48′ N, 29° 19′ E, 80 m a.s.l.) on probability-net paper. Flowering in 1977. Abscissa: p.u. sums in even scale. Ordinate: Gauss integral. All lines have been drawn free-hand.

the boundary between the northern and central clonal regions, showed similarity to the clones from locality 9 in 1976 and 1977 (Tables 4 and 5). The flowering behavior of the clones from these two transitional localities were somewhat different in 1978, when there was no late spring frost during the time of active floral development. In 1978, the clones from locality 8 behaved like northern clones while those of locality 9 did not (Tab. 6). The clones from locality 18, the same place where the investigated clone bank is located, flowered earlier than clones from some of the central or southern localities.

Generally, the earliness or lateness of flowering in the obseved clones was significantly correlated to both the local temperature sums above +5° C and the vegetation period throughout the distribution range of Finland. The smaller the local d.d. sums (or shorter the vegetation period) of the clonal origin the earlier (or at samaller p.u. sums) the female flowering. However, the correlations between local d.d. sums and the

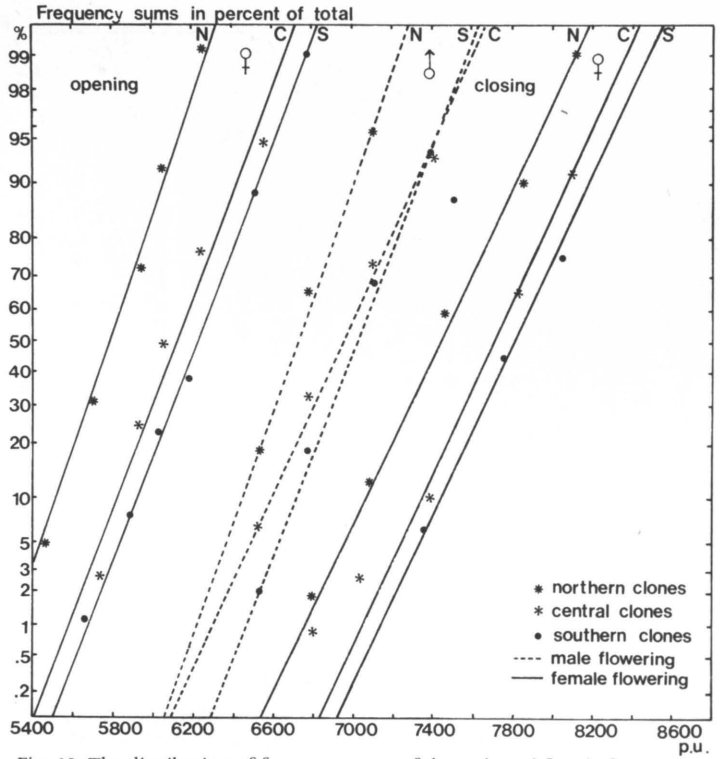

Fig. 10. The distribution of frequency sums of the male and female flowering in relation to p.u. sums at Punkaharju clone bank (61° 48′ N, 29° 19′ E, 80 m a.s.l.) in probability-net paper. Flowering in 1978. Abscissa: p.u. sums in even scale. Ordinate: Gauss integral. All lines have been drawn free-hand.

earliness of female flowering was relatively poor within central or southern regions in 1976 and 1978 (Tab. 7). In most cases, the early flowering clones flowered early and vice versa during the three observation years. That is the earliness or lateness in flowering of the clones was significantly correlated between different years (t = 17***---21*** for entire Finland).

The receptive interval of female strobili also showed a year to year variation (Tab. 8) such as in flower opening. In 1976, the receptive intervals ranged from 991 p.u. in locality 8 to 1494 p.u. in locality 18. In general, northern and central clones had smaller receptive p.u. intervals than southern ones in 1976 (Tab. 8). The receptive period of female strobili in this year lasted for, on an average, 8--9 days in time scale. A smaller receptive interval does not always mean a shorter receptive period in time scale because the temperature conditions during female flowering can readily alter the time duration of the receptive period. For instance, a receptive interval of 1000 p.u. can be passed within three days at high temperature while the same receptive p.u. interval would require eight to nine days at low temperature conditions.

The receptive p.u. intervals in all clonal groups in 1977 and 1978 were larger than those in 1976 except for the southern clones between 1976 and 1977 (Tab. 8). The average receptive period in time scale lasted approximately 4 days in 1977 with a larger receptive p.u. interval and a shorter time duration than that of 1976. The receptive period in 1978 lasted approximately 6 days in time scale. The extent of receptive p.u. intervals between

Table 4. Differences in p.u. sums for flowering between clonal origins (localities) at Punkaharju clone bank (61°48′ N, 29°19′ E, 80 m a.s.l.) in 1976.

Locality	flowering p.u. sum and the rank (from the earliest)
1	6439 (1)
2	6565 (6)
3	6550 (5)
4	6540 (3)
5	6486 (2)
6	N 6546 (4)
7	6595 (7)
8	6601 (8)
9	6737 (13)
10	*** *** ** ** *** *** * 6809 (18)
11	*** ** ** ** *** ** * 6777 (15)
12	* 6723 (11)
13	* C 6730 (12)
14	** ** * * *** ** 6818 (19)
15	* 6604 (9)
16	*** *** ** *** *** *** * * 6958 (22)
17	*** *** ** ** *** *** * 6834 (20)
18	* 6662 (10)
19	** *** ** *** *** ** * ** * 6888 (21)
20	** ** * ** *** ** * * S 6786 (16)
21	* ** 6753 (14)
22	*** ** ** ** *** ** * * * 6792 (17)
23	*** *** *** *** *** *** ** ** ** *** * *** ** ** * ** 7077-
Locality	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

significance (t-test)
* = 5 % level
** = 1 % level
*** = 0.1 % level

Locality 23 (exotics) is excluded in ranking

northern and southern clones was reversed in 1978 from that of 1976 (Tab. 8).

Generally the receptive period in 1976 was long lasting in time duration, yet accumulated smaller p.u. intervals. On the other hand, the receptive period in 1977 was of short time duration with intermediate p.u. intervals. The receptive period in 1978 was intermediate in time scale with the largest receptive p.u. intervals of the three years.

3.2. Male flowering and pollen shedding

3.2.1. Male flowering

Male flowering usually begins a little later than female flowering on the same tree and in the same population as a whole. This protogynous flowering characteristic of Scots pine (and probably in most of the other anemophilous plant species) enables the female strobili to be pollinated sufficiently during their relatively short flowering season. However, there were some exceptions to this rule at the individual level depending on the meteorological conditions during the floral development in different years. In 1976, 33.3 %, 41.7 % and 72.4 % (about 51 % of the total observation) of the observed northern, central and southern clones respectively, male strobili flowered earlier than the females. In 1977, only 18.5 % (9.8 % of the total observation) of southern clone male strobili flowered earlier than female ones and none of the northern or central clone male strobili flowered earlier than the females at the individual level. On the other hand, none of the male strobili in the observed clones flowered earlier than the females at the individual level

Table 5. Differences in p.u. sums for flowering between clonal origins (localities) at Punkaharju clone bank (61°48′ N, 29°19′ E, 80 m a.s.l.) in 1977.

Locality	flowering p.u. sum and the rank (from the earliest)
1	6540 (1)
2	6739 (7)
3	6600 (4)
4	6598 (3)
5	N 6574 (2)
6	6607 (5)
7	6706 (6)
8	6786 (9)
9	** * ** 6982 (15)
10	*** * ** ** *** ** 6969 (14)
11	*** * ** ** *** ** * 6989 (16)
12	** * * ** ** 6968 (13)
13	** * * ** * C 6925 (11)
14	*** * ** ** *** ** 6959 (12)
15	* * 6802 (10)
16	*** *** *** *** *** *** ** * * * * * 7304 (22)
17	*** *** *** *** *** *** ** * * 7184 (18)
18	* * 6779 (8)
19	*** *** *** *** *** *** *** ** * * * ** 7257 (20)
20	*** *** *** *** *** *** ** ** * * * * S 7239 (19)
21	*** *** *** *** *** *** * 7124 (17)
22	** ** ** ** ** 7267 (21)
23	* ** ** * ** * 7653-
Locality	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

significance (t-test)
* = 5 % level
** = 1 % level
*** = 0.1 % level

Locality 23 (ecotics) is excluded in ranking

(when the male flowering time was determined by the developmental stages at which the average or maximum pollen shedding condition was reached one tree as a whole) in 1978. Moreover, in most of the clones, male strobili flowered and shed pollen considerably later (3–4 days) than the occurence of female flowering in the same clones in 1978. This fact indicates that the male and female strobili of Scots pine may have different developmental requirements and thus respond differently to various environmental factors and conditions. Therefore, the timing in the flowering of Scots pine "chasmogamy" or "dichogamy", does not appear to be an inherent but rather a flexible character of this species at the individual level, that can be altered according to the external factors and the conditions during the development of floral organs.

In 1976, the male flowering pattern was distinctly different from the other two years due to unfavorable climatic conditions (particularly temperature and rainfall) during the active floral development and flowering. Central clones flowered slightly earlier than southern clones. This was because a higher proportion of younger trees (about 10-year old) flowered earlier under the open-crown system in the southern clonal group than in the central clonal group that had a higher proportion of older grafts (about 20-year old) in the selected samples. In this year older grafts with a closed-crown system flowered significantly later than the younger ones in the same clonal group. The time of male flowering and the p.u. sums of the three clonal groups for each year are graphically illustrated in Fig. 11.

Table 6. Differences in p.u. sums for flowering between clonal origins (localities) at Punkaharju clone bank (61°48′ N, 29°19′ E, 80 m a.s.l.) in 1978.

Localities	flowering p.u. sum and the rank (from the earliest)
1	5815 (1)
2	5964 (7)
3	5909 (5)
4	6001 (8)
5	5901 (4)
6	N 5898 (3)
7	5869 (2)
8	5948 (6)
9	* * ** ** * ** * 6175 (11)
10	*** *** *** ** *** *** *** *** 6223 (15)
11	*** *** *** * *** *** *** ** 6206 (12)
12	** *** *** ** ** ** *** ** C 6290 (17)
13	*** ** ** * ** ** *** * 6217 (14)
14	*** *** *** ** *** *** *** ** 6212 (13)
15	* * * * * * 6149 (10)
16	*** *** *** *** *** *** *** *** * * * 6398 (20)
17	*** *** *** *** *** *** *** *** * 6354 (18)
18	* * * * * * * 6148 (9)
19	*** *** *** *** *** *** *** *** *** * ** ** * ** * ** 6472 (22)
20	*** *** *** *** *** *** *** *** * * * * * 6395 (19)
21	** ** ** * ** ** ** * S 6279 (16)
22	*** *** *** *** *** *** *** *** *** * ** *** * ** ** ** 6424 (21)
23	*** *** *** ** *** *** *** ** * 6429-
Localities	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

significance (t-test)
* = 5 % level
** = 1 % level
*** = 0.1 % level

Locality 23 (exotics) is excluded in ranking

Table 7. Correlation between local d.d. sums and female flowering within clonal regions and the entire Finland.

Clonal group \ Year	n	Correlation coefficient, r 1976	1977	1978	Remarks
N	103	0.25*	0.24*	0.28**	significance at
C	109	0.03	0.06	0.07	* = 5 % level
S	84*4	0.12	0.31**	0.15	** = 1 % level
entire Finland	296	0.44***	0.54***	0.64***	*** = 0.1 % level

*4: exotic clones were excluded

Table 8. Mean receptive p.u. intervals of the three clonal groups at Punkaharju clone bank in three observation years.

Clonal group	n	Mean p.u. intervals 1976	1977	1978	Remarks
N	103	1143 ***	1513 ***	1671	significance at
		***			* = 5 % level
C	109	1148 ***	1464 ***	1631 *	** = 1 % level
		***			*** = 0,1 % level
S	84*5	1356	1446 **	1595	
		***			

*5: exotic clones were excluded

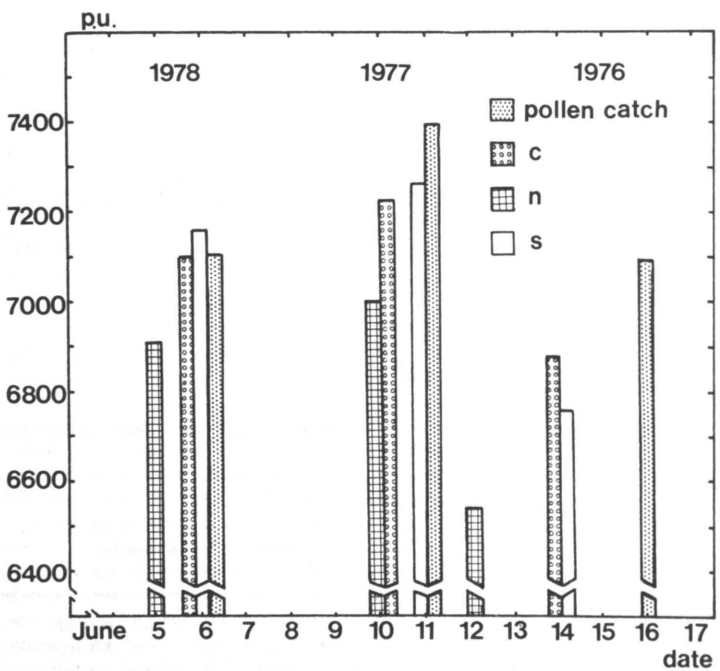

Fig. 11. Date of male flowering at Punkaharju clone gank (61°48′ N, 29°19′ E, 80 m a.s.l.) and the corresponding p.u. sums for clonal group. P.u. sums is claculated from the beginning of the year up to around 13.00 o'clock of the flowering date.

3.2.2. Pollen shedding and pollination

The frist pollen catch by the registering pollen catch meters was recorded on June 1st in 1978 and on June 3rd both in 1976 and 1977, however, a few pollen grains were caught as early as the 23rd of May in 1976. The sampling of pollen by the registering pollen catch meters lasted until July 2nd, June 25th and June 21st in 1976, 1977 and 1978 respectively, and some pollen grains were caught on those days which means the pollen shedding lasted more than one month, 23 and 21 days in those years respectively.

The date of maximum pollen dispersion determined by the amount of pollen grains caught in the registering pollen catch meters did not always coincide with the maximum male flowering of the visual observation during the three observation years. Only in 1978, maximum male flowering of the whole clonal group coincided with the maximum pollen catch as registered by the pollen catch meters. The time difference between maximum male flowering and maximum pollen dispersion appeared due to weather conditions, particularly, wind and air humidity during the male flowering periods.

In pollen dispersion the pollen vector; wind is one of the most important factor determining the direction, distance and the quantity of pollen. If the wind velocity is very weak, most of the shed pollen appears to move downwards. For instance, on June 5th 1978, one of the relatively warm and calm days, about a 1.6 times higher pollen catch was recorded at a height of 2 m than one of 21 m (about the same height of tree crown) in sample stand 3. On the next day, when the weather was warm and moderately windy (maximum pollen catch was recorded on that day), the situation was reversed, that is, approximately a 1.5 times higher pollen catch was recorded at a height of 21 m than that of 2 m by the same pollen catch meters.

The amount of total and effective pollen catch (cf. SARVAS 1962 p. 38) of the whole population (in this case the effective pollen catch of the whole population was denoted as the total effective pollen catch during the female flowering and calculated based on the receptive period of the female strobili in the population as a whole from the average time needed to reach developmental stage 4 minus one standard deviation up to the average time needed to reach stage 5 plus one standard deviation, that is from stage 4−1 s.d. to stage 5+1 s.d.) in 1976 was much higher than those of 1977 and 1978 but the percentage of effective catch from the total in 1976 was much less than those of 1977 and 1978. In other words the pollen dispersion in 1976 was rather wide spread for a longer period while the pollen dispersions in 1977 and 1978 were concentrated during the receptive period of female strobili (Tab. 9). However, all the maximum pollen shedding dates came just in the midst of the receptive periods of the female strobili in the population as a whole during the three observation years. In general, the female strobili received more pollen grains in the decreasing order of northern, central and southern clones during their receptive periods in 1976 and 1977, however the situation was reversed in 1978 flowering.

The average number of pollen grains in the micropylar cavity was 2.9 (Actual number should be larger than this one because the number of pollen grains totaling more than 11 in a micropylar cavity could not be counted properly and thus it was regarded as 11 in this investigation). The distribution of pollen grains in the micropylar cavity did not follow the Poisson distribution as SARVAS (1962) had already reported (Fig. 12). It gave significantly higher values in the lowest and highest ends of the pollen grains in the micropylar cavities from the Poisson distribution.

In spite of the large amount of pollen catch registered by the pollen catch meters in sample stand 2 about 15*6 (Fig. 31) to 25 %*7 (average of the investigated samples in Fig. 12) of the micropylar cavities of the fertile ovules remained emply without pollination. This may be most porbably due to the partially predominant pollination of the ovules facing the prevailing windward side. Up to the optimum level of the effective pollen catch as

*6 and *7: Actual pollination – the entrance of pollen grains into the pollen chamber – will probably be a little higher than these percentages because two or three pollen grains (these are the average number of pollen grains that enter the pollen chamber (cf. SARVAS 1962)) having entered pollen chamber resulting in an empty micropylar cavity by the time it had been observed. The pollen chamber cannot be observed by a simple optical examination with a dissecting microscope.

Table 9. Pollen dispersion and the pollen catch by registering pollen catch meters. Pollen grains/mm².

Sample stand	Age years	Year	Total catch	Effective catch	% of effective catch	% of effective catch to total catch		
						N	C	S
No. 1	about 20	1976	3658	2205	60	70	56	55
		1977	2739	1929	70	73	65	56
		1978	2094	1859	89	82	89	90
Mean			2830	1998	71			
No. 2	about 10	1976	2940	1810	62	72	57	55
		1977	1670	1212	73	76	67	59
		1978	1231	1078	88	83	88	88
Mean			1947	1367	70			
No. 3	about 100	1976	4669	2567	55	71	49	46
		1977	2559	1996	78	80	72	63
		1978	1980	1814	92	84	92	94
Mean			3069	2126	69			

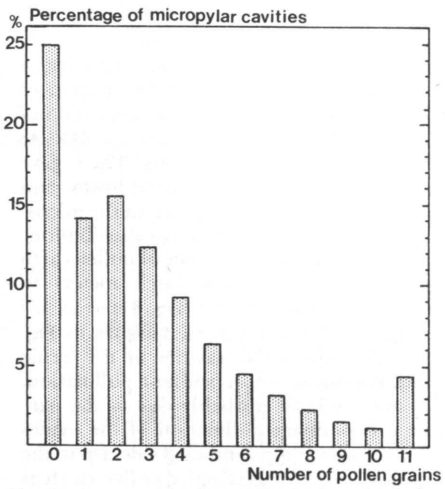

Fig. 12. Amount of pollen grains in the micropylar cavities of open-pollinated female strobili. About 25 % of the investigated micropylar cavities are remained unpollinated. (Mean of 224 strobili from 15 clones.)

registered by the pollen catch meters (about 700 grains per square millimeter) the percentage of pollinated micropylar cavities increases gradually until it approaches 80 %. Above this level of pollen catch the percentage of pollinated micropylar cavities increases only slightly regardless of the considerable increase of the effective pollen catch.

It is most probable that when most of the micropylar cavities have already been pollinated to a certain level, the pollen grains reaching the female strobili after that time have less of a chance to pollinate the rest of the empty micropylar cavities on the leeward side of the strobili than repollinating the ovules on the prevailing windward side that had already been pollinated with some pollen grains by that time. The percentage of pollinated ovules in relation to the effective pollen catch under open pollinated conditions is presented in Fig. 13.

3.3. Estimation of the starting point of new year's floral development

As the p.u. sum was calculated cumulatively from the beginning of the new calendar year and not from the beginning of the new year's floral development*8, the yearly flowering p.u. sums of different populations appear to

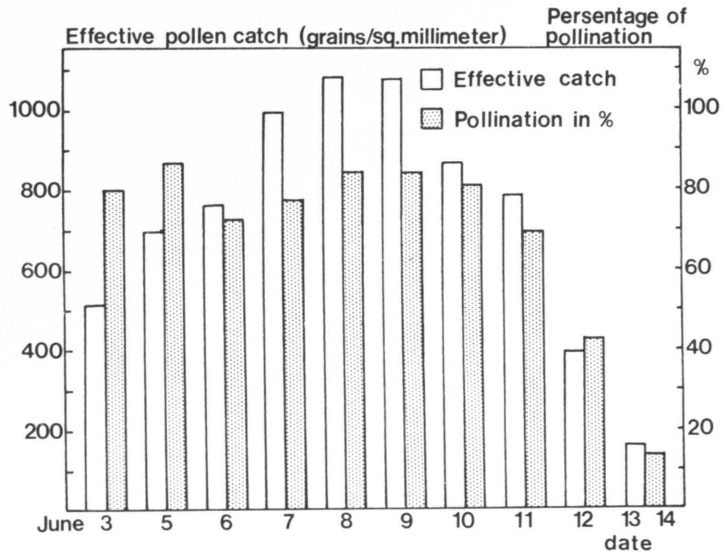

Fig. 13. Effective pollen catch according to flowering date and the percentage of pollinated micropylar cavities. (Mean of 244 strobili from 15 clones.)

Differences between the treatments (1 % level).

June 5 and June 6.
June 6 and June 8, June 9.
June 11 and others except June 6 and June 7.
June 12 and others.
June 13 and others.

fluctuate between the years. Therefore, to determine the approximate active period for flowering (A.P.F; the p.u. sum required for floral development from the beginning point up to flowering) of each population (locality), an attempt was made to estimate the starting point (S.P.) of new year's floral development by reverse calculation of p.u. sum from the flowering point (F.P.) of each population in each year. This starting point may not be indentical to zero point of phase change of the population of Sarvas' physiological clock model. According to SARVAS (1974), the zero point is in the fall of the previous year of flowering but not in the spring of the flowering year.

The estimation of the starting point of floral development requires the following assumptions;

(1) The new year's floral development should follow the p.u. scale which is depending on temperature and time factors.

(2) The developmental stage of floral organs of a population in each year should be the same at the beginning of new year's floral development so that an identical p.u. sum is required from the starting point up to flowering in each year.

(3) The progress of p.u. sum and the time (T) from the starting point (S.P) up to flowering of a population fortunately did not deviate notably during the 3 years under observation. That is, $T_{76} \simeq T_{77} \simeq T_{78}$ (cf. Fig. 14) where T_{76}, T_{77} and T_{78} are the time lapses from starting point to flowering in 1976, 1977 and 1978 respectively.

Figures 14 and 15 illustrate the method of estimation of the starting point by reverse calculation of p.u. sum from the flowering point in each year. In these Figures, $APF_{76} = APF_{77} = APF_{78}$ under the above assumption (2), and if $T_{76} \simeq T_{77} \simeq T_{78}$ during the three observation years, the reverse calculation of p.u. sum starting from the flowering point (F.P.) in each year will converge to one point at S.P. as shown in Fig. 15. However, under conditions for $T_{76} \neq T_{77} \neq T_{78}$, $T_{76} \simeq T_{77} \neq T_{78}$, $T_{76} \neq T_{77} \simeq T_{78}$ or $T_{76} \simeq T_{78} \neq T_{77}$, the reverse calculation of p.u. sum starting from the F.P. will not converge to one point but may meet at two or three different points around the S.P. of new year's floral development as exemplified in Figures 16 and 17.

In Fig. 16 the reverse calculation of the p.u. sum was started as if the F.P. in 1976 was about 500 p.u. smaller (earlier in time) and in

*8: The term "new year's floral development" is used for the following year's floral development after the initiation of floral organs.

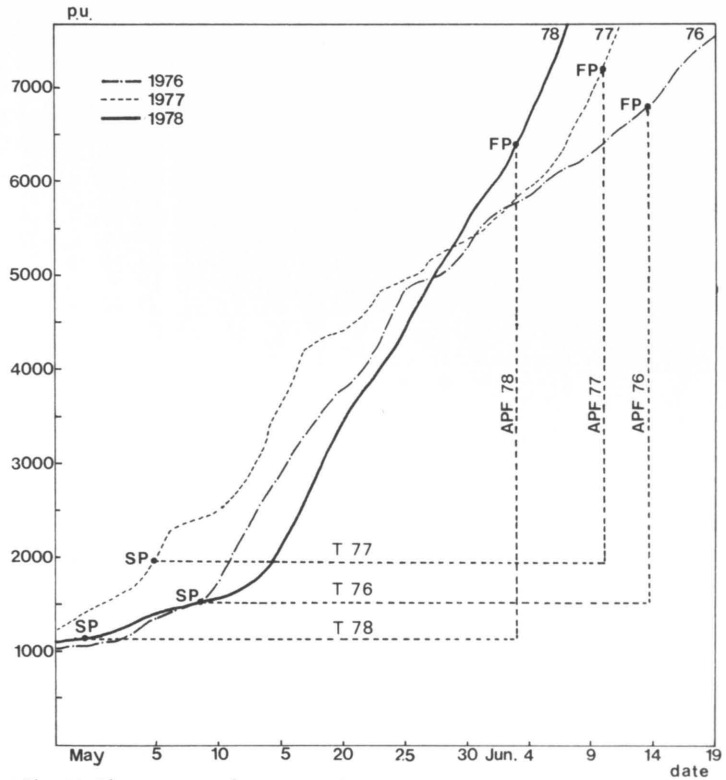

Fig. 14. The progress of p.u. sums during the periods of floral development in 1976–1978. The starting points (S. P.) of floral development of locality 20 (Taipalsaari) were estimated by reverse calculations of. p.u. sum from the flowering points (F.P.) in each year (see text for the illustration).
A.P.F. = Active period for flowering
T = Time lapse from S. P. to F. P.

1978 was 170 p.u. larger (later in time) than those of the observed values of the control[*9] (Locality 20). Thus they intersect the originally estimated p.u. sum of A.P.F. (active period for flowering, 5265 p.u. in this case) in Fig. 16 four days later (T_{76}) and four days earlier (T_{78}) than the estimated time when adjusted to a common F.P. ($T = T_{77}$). When comparing the uppermost pairwise intersection of the lines, they meet at three different points. The intersection of P_{76} - P_{77} (P = the progress of p.u. sum in a year) lines is less reliable than the other points because the P_{76} and P_{77} lines are very close to each other. Thus, if we ignore the P_{76} - P_{77} intersection and choose the P_{76} - P_{78} and P_{77} - P_{78} points as the approximate S.P. of the new year's floral development, they deviate about 160–180 p.u. (approx. 3 %) from the control (L. 20).

Fig. 17 was drawn according to the same method as in Fig. 16 but the reverse calculation was started at a p.u. about 400 and 430 larger (later in time) than the observed values for the flowering p.u. sums of 1976 and 1977 to adjust to a common flowering point ($T = T_{78}$). In this case T_{76} and T_{77} deviate one day

*9: Locality (L) 20 was used as a control or a standard for comparisons.

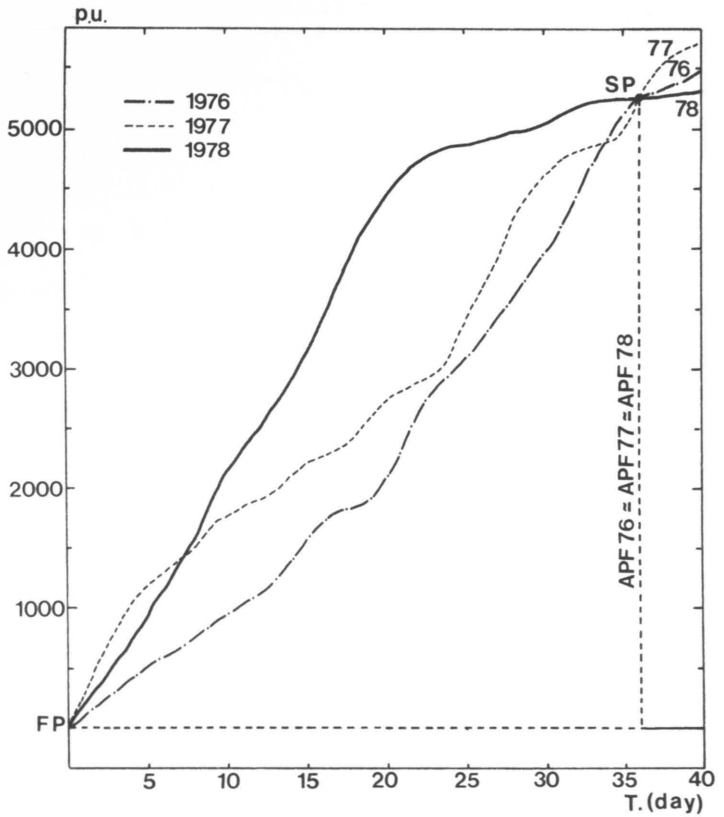

Fig. 15. An example of the convergence of reverse calculations of p.u. sum from the flowering points in each year when A. P. $F._{76} \simeq$ A.P.$F._{77} \simeq$ A.P.$F._{78}$ and $T_{76} \simeq T_{77} \simeq T_{78}$ (L. 20, Taipalsaari). In this case T_{78} was slightly smaller than T_{76} or T_{77}, but the three lines of reverse calculations of p.u. sum closely converged to one point (for the abbreviations see Fig. 14).

with negligible differences in p.u. on each side of the control (L. 20) indicating that estimates using the reverse calculation method do not appear to deviate significantly from the original estimation under natural conditions in the three years of observation.

Among the locality groups examined in this way, clones from localities 16 (central Finnish origin), 19, 20 and 22 (all are south Finnish origin) converged almost exactly to one point (Figures 15 and 18). This fact indicates that the progress of p.u. sum and time from starting to flowering in the three observation years agreed well for the southern clones. In addition, most of the southern trees follow almost exactly the p.u. scale for their female flower development under southern Finnish climatic conditions.

However, the reverse calculation of all the northern and most of the central localities did not converge to one point. Lines of P_{76} and P_{77} intercept the P_{78} line independently and meet at a higher p.u. sum above the P_{78} line (Figures 19 and 20). This fact seems to indicate that the floral development in 1976 and 1977 required higher p.u. sums than that of 1978 and/or the progress of p.u. (P.) and time (T.) during the floral development of the

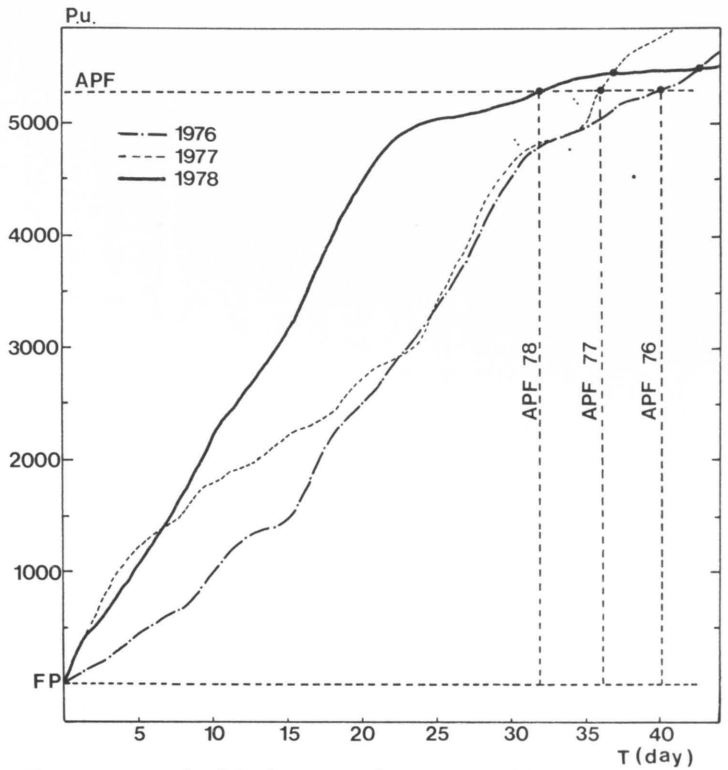

Fig. 16. An example of the divergence of intersections of the reverse calculations of p.u. sum from the flowering points in each year when $T_{76} \neq T_{77} \neq T_{78}$. The calculations were made as if the F.P. in 1976 and 1978 respectively (except 1977) were 500 p.u. smaller and 170 p.u. larger than the observed values for the flowering of locality 20. In this case, the lines of the progress of p.u. sums (reversely calculated) intercepted the line of A.P.F. independently and intersected each other at higher p.u. sums, 1976–1977 lines forming one point and 1977–1978 lines forming another. The deviation of estimated p.u. sums for the S.P. in this way were about 160–180 p.u. (approx. 3 %) from the original estimate (for the abbreviations see Fig. 14).

northern and central clones in those years deviated considerably from year to year.

Another attempt was made to test whether the new year's floral development of the different locality groups start in a regular manner and in a sequential order with certain p.u. intervals during the three observation years. The flowering p.u. sums of locality 20 (Taipalsaari, one of the nearest population from the observation area) in each year were chosen as standards and subtracted from the corresponding years' flowering p.u. sums of other localities. Thus, if the northern clones start floral development earlier and central and southern clones follow with consistent and regular p.u. intervals, characteristic to each population during the three observation years, the differences in flowering p.u. sums between the localities in each year must be constant under the assumption (2) (cf. page 25). For intance, $PL_{20} - PL_1$, (1976) = $PL_{20} - PL_1$, (1977) = $PL_{20} - PL_1$, (1978), where PL_1 is

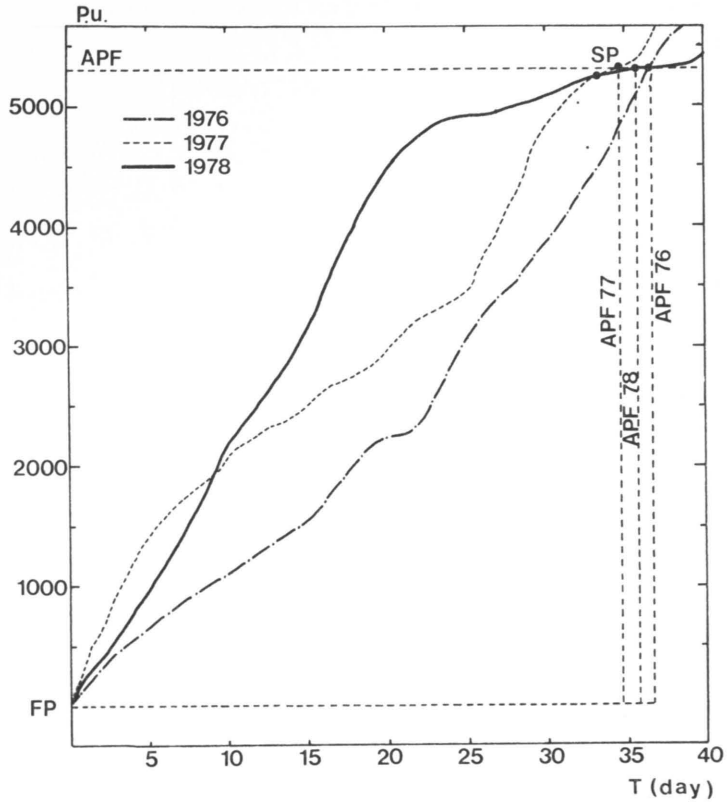

Fig. 17. Another example of the divergence of intersections of the reverse calculations of p.u. sum from the F. P. in each year when $T_{76} \neq T_{77} \neq T_{78}$. The reverse calculations were made as if the flowering points in 1976 and 1977 respectively were 400 and 430 p.u. larger than the observed values. In this case, the estimated starting points did not deviate considerably from the original estimate in Fig. 15.

the flowering p.u. sums of locality 1 and PL_{20} is the flowering p.u. sums of locality 20 (standard) in each year and 1976–1978, the flowering years. However, this condition is not met in most of the cases as can be seen in Fig. 21. The differences in flowering p.u. sums within and between locality groups from the standard in each year indicate that the new year's floral development between the different locality groups may not start in a regular manner with constant p.u. intervals (probably the starting order may be approximately the same). It seems as if floral development may also be affected by various physiological stress conditions.

It appears that the differences in flowering p.u. sums between standards (L. 20, southern clones with longer active period) and northern or central clones (with relatively shorter active periods) originate from the differences in (1) the p.u. sums of starting points for the new year's floral development and (2) the active periods for flowering (A.P.F.) between the locality groups. For instance, suppose that a southern clonal group has an A.P.F. of 5.300 p.u. and a northern clonal group of 4.900 p.u. Then the flowering p.u. sums of the southern and northern clonal groups would be; p.u. sums at starting point (P.S.P.) for the southern clones +5,300 p.u . . . . (1)

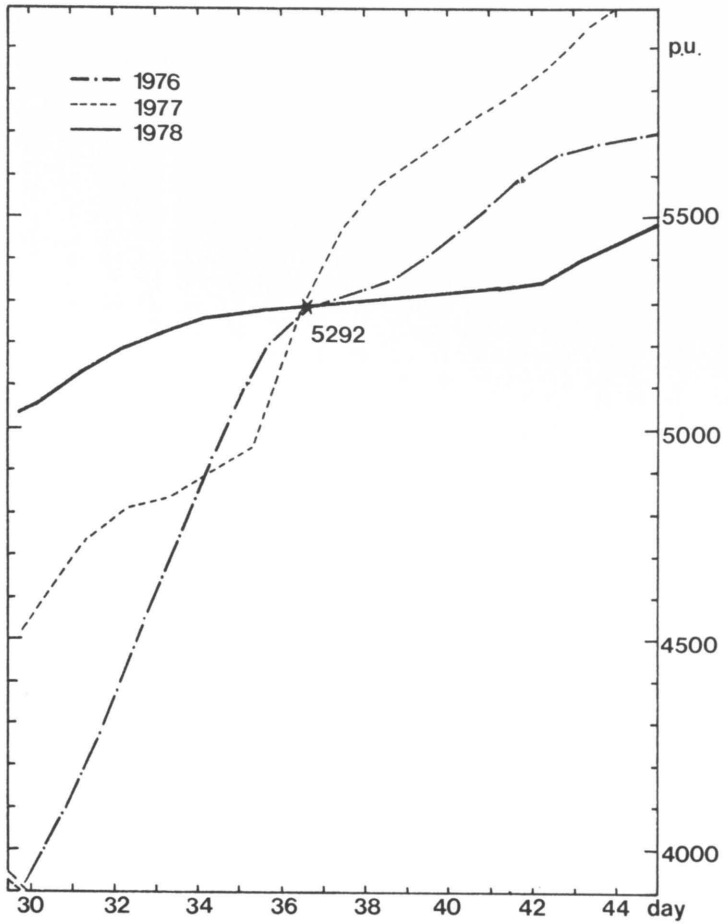

Fig. 18. The convergence of reversely calculated p.u. sums from the flowering point observed over three years under natural conditions at Punkaharju clone bank. Kalvola population (locality 22). Ordinate: reversely calculated p.u. sums from the flowering point. Abscissa: time scale in days from the flowering point.

and P.S.P. for the northern clones +4,900 p.u . . . (2).

Thus, if we assume that the southern and northern clonal groups started floral development at 1,500 and 1,000 p.u. sums in 1976, the flowering p.u. sums for the southern and northern clonal groups would be;

1,500 p.u. + 5,300 p.u. = 6,800 p.u . . . . (3)

and 1,000 p.u. + 4,900 p.u. = 5,900 p.u . . (4)

However, if the P.S.P. were 2,000 and 1,100 p.u. for the southern and northern clonal groups in 1977, the corresponding flowering p.u. sums for the southern and northern clonal groups would be;

2,000 p.u. + 5,300 p.u. = 7,300 p.u. . . . (5)

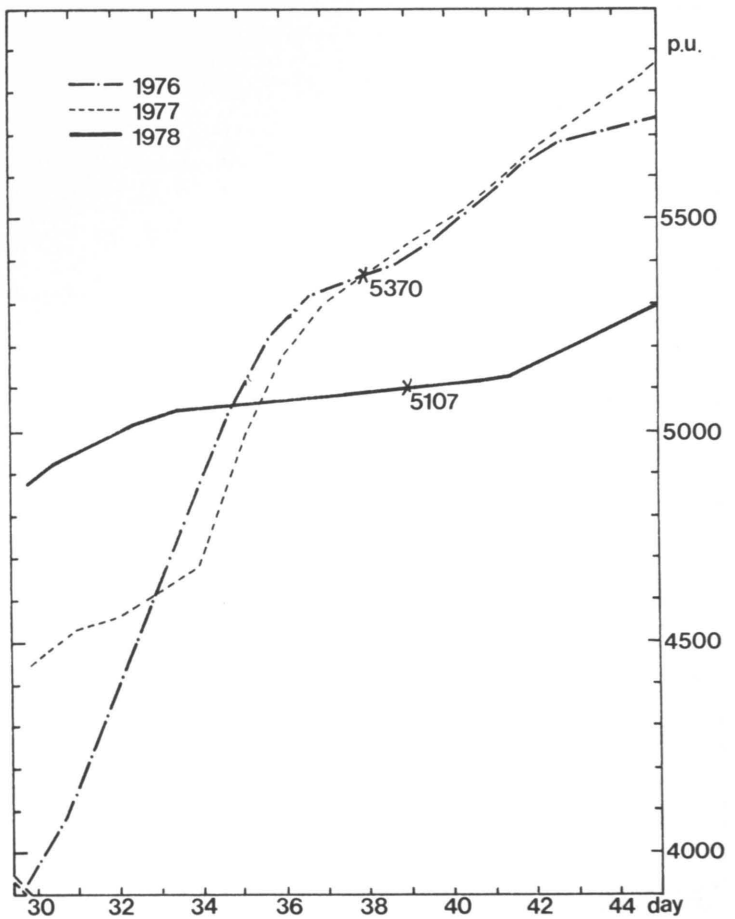

Fig. 19. The convergence of reversely calculated p.u. sums from the flowering point observed over three years under natural conditions at Punkaharju clone bank. Viitasaari (locality 10). Ordinate: reversely calculated p.u. sums from the flowering point. Abscissa: time scale in days from the flowering point.

and 1,100 p.u. + 4.900 p.u. = 6,000 p.u . . (6)

From exanples (3), (4) and (5), (6), we obtain the differences in flowering p.u. sums of 900 and 1,300 p.u. between the southern and northern clonal groups in 1976 and 1977 respectively. This calculation clearly shows how the p.u. sum at starting point of floral development of a population in a year affect the flowering p.u. sum in that year. That is, the difference in active period for flowering (A.P.F.) between the two localities was only 400 p.u. (5,300–4,900), but the differences in flowering p.u. sums were 900 and 1,300 p.u. in 1976 and 1977 respectively in these examples.

On the basis of the above mentioned estimations, the starting points of new year's floral development must be located on the segment of the line for p.u. sum, northern

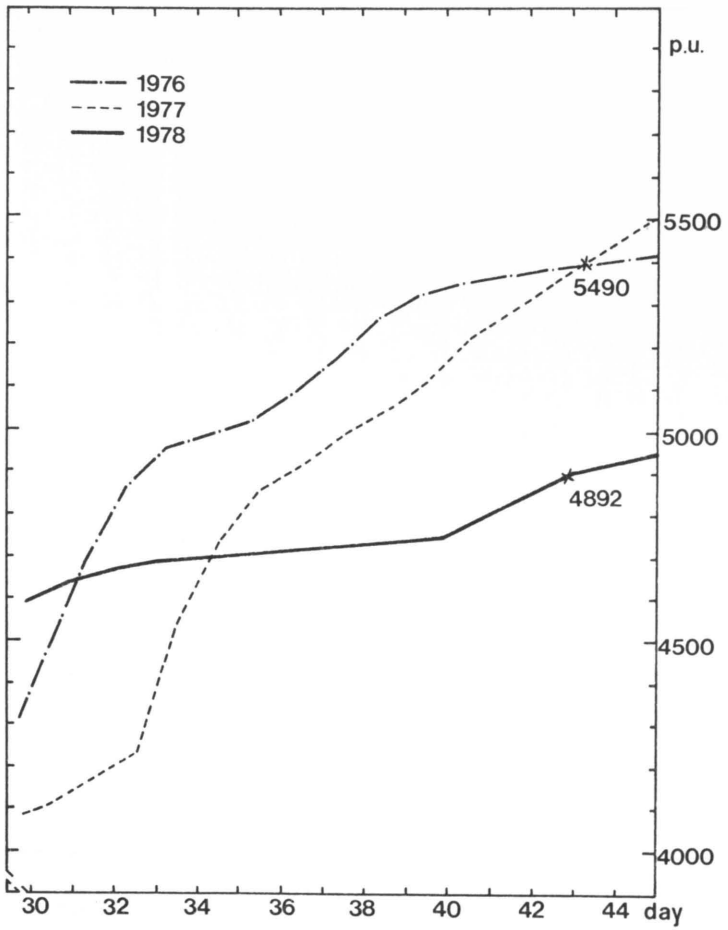

Fig. 20. The convergence of reversely calculated p.u. sums from the flowering point observed over three years under natural conditions at Punkaharju clone bank. Inari population (locality 1). Ordinate: reversely calculated p.u. sums from the flowering point. Abscissa: time scale in days from the flowering point.

clones start in the low and southern clones in the high end of the segment, so that the difference in p.u. sum at two starting points correspond to (F.P.S. of S. – A.P.F. of S.) – (F.P.S. of N – A.P.F. of N.), where F.P.S. is the flowering p.u. sum, A.P.F. is the active period for flowering and N, S. the northern and southern clonal group. For a numerical example, from examples (3) and (4) the difference in starting p.u. sum between the southern and northern clonal groups will be, (6,800 p.u. – 5,300 p.u.) – (5,900 p.u.– 4,900 p.u.) = 500.

The positions of the estimated starting points of southern and some of the northern and central localities (estimated by reverse calculation) are presented in Fig. 22. In comparing Figures 21 and 22, the segment of the progress of p.u. sum between late April and early May for 1977 starting points

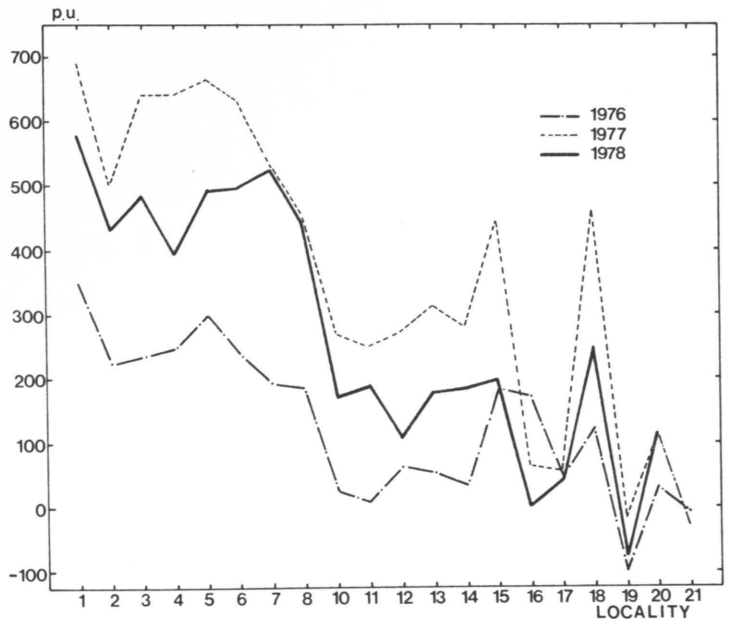

Fig. 21. The difference in p.u. between the flowering p.u. sums of locality 20 and the other localities in each year.

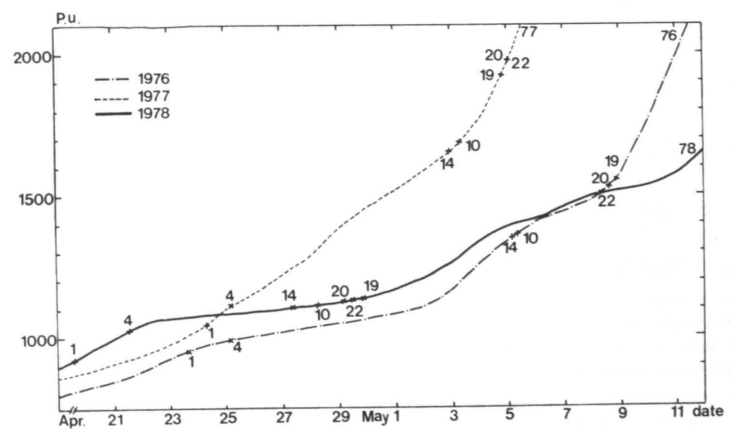

Fig. 22. The estimated starting points of new year's floral development on some localities by reverse calculations of p.u. sums from the flowering points of the localities. Numbers 1–22: the locality numbers.

indicates that the estimation of starting points in this year by the reverse calculation coincides approximately with those of the differences in flowering p.u. sums between the standard (L. 20) and the others (particularly the northern clones) in each year.

The estimated starting points in 1978 are located on the segment of the line for p.u. sum in late April with small differences in p.u. intervals (100–200 p.u.) between the northern and southern localities (Fig. 22). This fact seems to indicate that the differences in flowering p.u. sums between the standard (L. 20) and those of the northern localities in this year (Fig. 21) are mostly based on the differences in A.P.F.

The differences in flowering p.u. sums between the standard (L. 20) and the northern localities in 1976 (Fig. 21) were in most cases smaller than the estimated p.u. sum differences in A.P.F. between the standard (L. 20) and the northern localities (on an average, the difference was approximately 350 p.u.). Therefore, if we interpolate the A.P.F. of northern localities with that of the standard (L. 20) starting from the respective flowering points (Fig. 23) the lines of A.P.F. paradoxically indicate as if the starting points of northern localities were slightly later (larger in p.u. sum) than that of the standard which is a

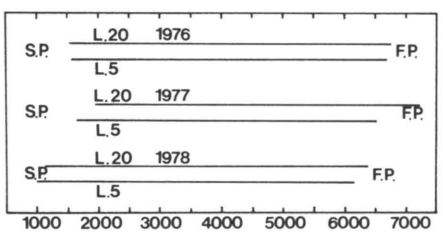

Fig. 23. The estimated starting points (S. P.) of locality 5 (lower lines) when the active periods of flowering for locality 5 were interpolated starting from the flowering points (F.P.) with those of the locality 20 (upper lines) in each year.
The S. P. of locality 5 (northern clones) in 1976 comes later (or at higher p.u. sums) than that of the locality 20 (southern clones), which is the most improbale fact under natural conditions in southern Finland. This fact clearly indicates that the floral development of the northern clones in 1976 were affected by other factors than the p.u. scale.
Scale: p.u. (abscissa)

southern locality. This fact clearly indicates that the floral development of northern clones in 1976 required much lager p.u. sums than those of original active periods for flowering. In other words, the floral development of northern clones in this year was affected by other factors. In a detailed examination of the starting points (estimated) and the flowering p.u. sums of the localities, there are indications that the flowering of northern and central clones in 1976 and 1977 were delayed to some extent probably through stress conditions by late spring frosts which occurred during the most active period of floral development of those clones. The low-temperature that appears to induce the stress condition leading to the delay of floral development was lower than +2° C lasting more than 2–3 hours at the time of female flower flushing.

The estimated starting points of the new years's female flower development in Scots pine in the observation area usually come around late April to early May when the progress of p.u. sum rises steadily and rapidly. The temperature recordings during late April and early May between 1965–1974 years showed a similar tendency of temperature rise as found in the three observation years. The estimation of the starting point of new year's floral development in this study is based only on three years of observations on flowering. Therefore, further studies are required to estimate a more precise value and to prove the validity of the estimation. Most probably, with repeated observations of flowering on the same populations, and with the estimation by reverse calculations of flowering p.u. sums, we can find the approximate starting point of new year's floral development of each population.

3.4. Flowering in the plastic-houses

When the plastic-houses were built on May 12th (No. 1) and May 17th (No. 2), some of the clones had already protruded visible female flower buds from the growing shoots, however no strobili were flushing by that time. The p.u. sums reached approximately 1,600 and 2,400 when the plastic-houses No. 1 and No. 2 respectively were completed. The weather conditions during the floral development in the plastic-houses were relatively fine (mostly clear days) until flowering on May 25th–28th in the plastic-houses. However, the trees in plastic-house No. 1 experienced temperatures as low as −3.1° C and the low-temperature condition (below +2° C), that appeared to delay floral development at a certain critical developmental stage, lasted for about 7 hours during the second night (May 13–14) in plastic-house No. 1. This low-temperature condition did not appear to affect the floral development remarkably as the floral development had not reached a sensitive stage by that time.

The low-temperature conditions below +2° C came again in the early mornings of May 24th and 25th (only in the plastic-houses, not outside) when many of the clones in the plastic-houses had reached the most critical developmental stage of the female strobili that was readily affected by continuous low-temperature conditions lasting more than 2 hours below +2° C (Table 11).

The development of female strobili in the plastic-houses was very rapid in accordance with the rapid progress of p.u. under high temperature conditions during the day time. In most cases, the flowering of female strobili (opening of ovuliferous cone scales) began at the same time or just after the flushing of female strobili out of the flower-bud scales. Under natural conditions, usually the female strobili of northern clones began to flower after the strobili were sufficiently exposed to the air, when the flower-bud scales were almost or completely removed from the strobili.

In many cases the clones in the plastic-houses flowered at higher p.u. sums than the controls (of the same clones) outside the plastic-houses. The flowering p.u. sums of those clones inside and outside of the plastic-houses are listed in Table 10.

The higher p.u. sums for flowering in the plastic-houses appeared to be a result of the disturbance of floral development in the plastic-houses by the stress of critical low-temperature during the active cell division of the floral organs. Therefore, the temperature conditions and the developmental stages of

Table 10. Female flowering p.u. sums inside and outside (natural conditions) of the plastic-houses at Punkaharju clone bank.

Plastic-house	Clone No.	Flowering p.u. sum (M± sd)		Difference in		t-value
		plastic-house	control	p.u.	%	
No. 1	p.121	6441±321	6121±349	+320	5.2	3.2***
	p.141	6252±197	6032±183	+220	3.6	3.8***
	p.156	6090±234	5944± 79	+146	2.5	2.4*
	p.174	5855±101	6026±185	−171	2.8	4.1***
	p.206	5889±130	5855±130	+ 34	0.6	0.8
Mean		6105	5996	+109	1.8	
No. 2	k.1003	6332±281	6447±249	−115	1.8	1.4
	p. 6	6549±271	5834±129	+715	12.3	9.9***
	p. 14	6041±238	5885±120	+156	2.7	2.5*
	p. 26	6313±239	5892±146	+421	7.1	6.6***
	p. 68	6412±279	5790±129	+622	10.7	8.4***
Mean		6329	5970	+359	6.0	
Total mean		6217	5983	+234	3.9	

p.u. sums are calculated from the beginning of the year up to flowering.
* = 5 % level ** = 1 % level *** = 0,1 % level p = northern clone k = central clone

Table 11. Low-temperature conditions in the mornings of May 24th and 25th inside and outside of the plastic-houses.

Date and conditions	May 24		May 25	
	min.temp.	duration below +2°C	min.temp.	duration below +2°C
Plastic house No. 1	−0.4°C	4.5 hrs	1.0°C	3.5 hrs
" No. 2	0.0 "	4.0 "	1.2° "	2.0 "
Control (outside)	+1.8 "	1.5 "	3.1° "	–

female strobili at the time of low-temperature stress were thoroughly studied to elucidate this phenomenon and the results are listed in Tables 11 and 12. In the phenological study, the floral development on female strobili almost reached flower developmental stage 2 – the time of female strobili flushing – at the time of critical low-temperature stress. In other words, the low-temperature conditions came just before or, in some cases, at the same time as flower flushing in the plastic-houses.

The temperature conditions in the plastic-houses were much higher (usually 28–30° C, in some cases as high as 35° C) during the day and slightly lower during the night, than those outside.

In comparing the Tables 10–12, it can be seen that in all of the clones that reached p.u. sums of 3900–4200 from S.P. for their floral development, the floral development was affected by the low-temperature stress. In all

Table 12. P.u. sums from the estimated starting point of floral development on each clone at the time of low-temperature stress.

plastic-house	clone No.	p.u. sums from s.p. May 24	p.u. sums from s.p. May 25	Remarks
No. 1	p.121	4149	4505	underlined parts are the most highly affected ones by low-temperature stress.
	p.141	4213	4570	
	p.156	4276	4633	
	p.174	4221	4578	
	p.206	4330	4686	
No. 2	k.1003	3758	4126	compare with Table 10
	p. 6	3969	4337	
	p. 14	3916	4284	
	p. 26	3934	4302	
	p. 68	4018	4386	
control in all (outside) clones		3400	3500	

cases, except for clone p. 174, the clones that were subjected to low-temperature stress (particulary at developmental stages with 3900–4200 p.u. from the S.P.) experienced delayed floral development by about 150–700 p.u. This means that clones subjected to low-temperature stress (below +2° C for 3.5–4.5 hours) flowered at higer p.u. sums (about 150–700 p.u.) than the controls. In the case of clone p. 174, the flowering was enhanced by about 170 p.u. in the plastic-house. This can not fully be understood and explained at this time with limited knowledge on the effect of low-temperature on flower development. The only explanation is that the female strobili of clone p. 174 flowered evenly and almost at the same time both in the plastic-house or outside, hence yielding a high t-value in the statistical treatment.

In the case of clone p. 206, the floral development had already passed the critical stage at the time of low-temperature stress in the plastic-house. Therefore, this clone flowered at about the same p.u. sums both inside and outside of the plastic-house. For clone k. 1003, the development of female strobili had reached a sub-critical stage at the time of the first low-temperature conditions on May 24th and it reached a critical stage by the time of the second low-temperature condition on May 25th. However, this clone flowered at about similar p.u. sums (no statistical difference) both inside and outside of the plastic-house. This fact may indicate the induction of resistance through previous exposure to the same kind of stress at a sub-critical stage.

3.5. Seed development

3.5.1. Variation in number of cone scales

There was great variation in the total number of cone scales and potentially fertile scales between different clones. The mean number of cone scales ranged from 32 ± 5 to 76 ± 5 for the total and from 12 ± 2 to 27 ± 3 for the potentially fertile scales. The number of total and fertile cone scales was related to the local mean annual temperature sums (or to the length of growing season) of the clonal origins within Finland. The clones from warmer regions (with larger mean annual temperature sums) had a smaller number of total and potenitally fertile cone scales than those of the colder regions (with smaller mean annual temperature sums). When the regressions of the number of cone scales on the local mean annual temperature sums were calculated the regression equations are;

$$Y = -0.025X + 83.339$$

($t=-9.70^{***}$, df=175) for the total cone scales and

$$Y = 0.012X + 55.814$$

($t = -6.50^{***}$, df = 173) for the potentially fertile ovules (fertile scale × 2).

Generally, the clones that had a larger number of total cone scales had the larger number of potentially fertile scales. However, the proportion of fertile to total cone scale decreased with the increasing number of total cone scales (Fig. 24). When the total number of cone scales were assorted into 10 classes with 5 scale intervals from the smallest to the largest, the calculated regressions of the number of potentially fertile ovules and the percentages on the total number of scales are;

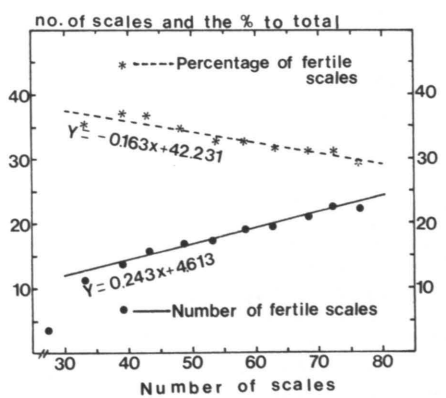

Fig. 24. Regressions of the number and the percentages of fertile scales on total number of cone scales. Abscissa: number of total cone scales. Ordinate: Left = % of fertile to total cone scales, Right = number of fertile scales.

$$Y = 0.243X + 4.613$$

($t = 17.24^{***}$, $df = 8$) for the number of fertile scales and

$$Y = -0.163X + 42.231$$

($t = -6.75^{***}$, $df = 8$) for the percentages on the total number of scales.

The number of total and potentially fertile scales and the percentage of fertile to the total scales in early (mostly northern origin), intermediate (mostly central, including some of southern and a few northern origins) and late (mostly southern origin) flowering clones are presented in table 13.

3.5.2. Variation in seed setting

The data were studied in detail by the analysis of pooled variances or covariances in order to determine whether there were differences in seed setting between the three clonal groups, and within and between the two flowering years.

The number of seeds (clonal average) per cone between the clones also showed a wide range of variation ranging from a minimum of 5 to a maximum of 43 seeds, depending on the clones. Generally, the number of seeds per cone increased as the number of potentially fertile ovules increased. The regression equations for the number of seeds on the number of fertile ovules are;

$$Y = 0.478X + 4.946$$

($t = 4.81^{***}$) and

$$Y = 0.693X + 0.052$$

($t = 7.09^{***}$) for the seeds developed from the 1976 and 1977 flowering respectively. However, when the clones were assorted according to flowering time, the clones of the early flowering group did not show any significance in the regression coefficient b ($t = 2.02$, $p = 0.055$; and $t = 1.03$, $p = 0.323$ for the seeds developed from the 1976 and 1977 flowering respectively) while the other intermediate (Fig. 25) and late flowering (Fig. 26) groups showed significance in the b. coefficients for the seeds developed from both flowering years ($t = 3.00^{**}$, $t = 5.73^{***}$ in late flowering clones and $t = 3.30^{**}$, $t = 6.08^{***}$ for the intermediate flowering clones, for the seeds developed from the 1976 and 1977 flowering respectively).

Table 13. The number of total and potentially fertile cone scales and the percentage of fertile scales to the total cone scale in early (E), intermediate (I) and late (L) flowering clones.

Clonal group	n	No. of cone scales and the percentage: Total scale	fertile scale	% of fertile scale	Remarks
E	29	63.2±7.2	20.7±2.5	32.9	significance level *= 5 %
I	117	58.1±8.8	18.6±2.9	32.3	**=1 %
L	29	51.6±9.0	17.5±2.5	34.3	*** = 0.1 %
Total mean	175	57.9±9.1	18.8±2.9	32.7	t-test by pooled variance

data based on the cones developed from 1977 flowering

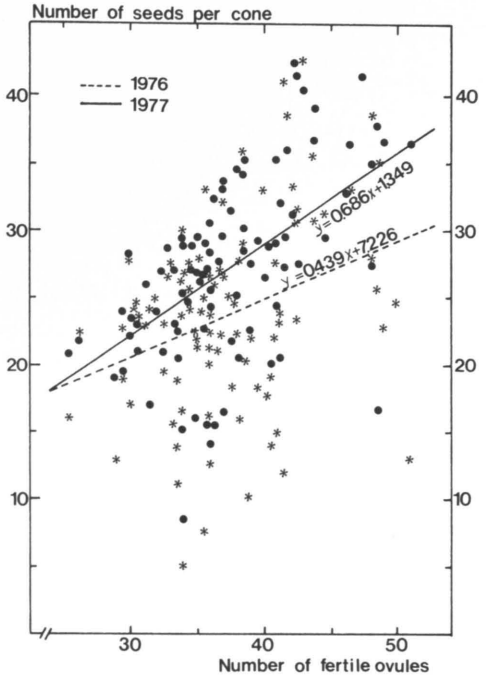

Fig. 25. Regression of seed setting on the number of potentially fertile ovules. Intermediate flowering clones.

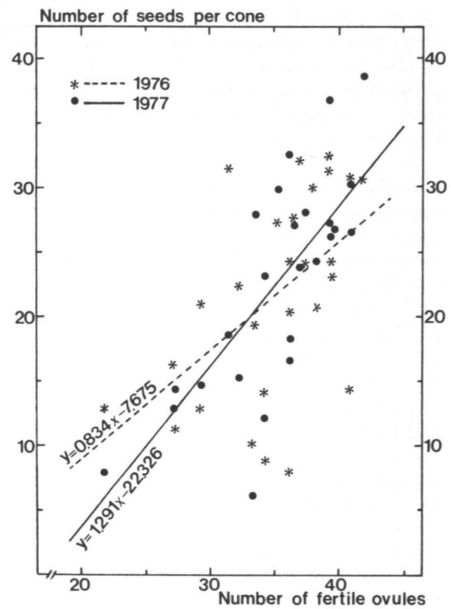

Fig. 26. Regression of seed setting on the number of potentially fertile ovules. Late flowering clones.

The regressions in the early flowering group showed that the seed setting in this group was not related to the number of potentially fertile ovules. In other words, the pollination of the female strobili in the early flowering clones did not meet a proper condition and thus fluctuated considerably during the two flowering years.

In the analysies of covariances, the slopes and the elevations of the regression lines of seed number on the number of the potentially fertile ovules within the clonal groups were not statistically different between the two flowering years except for the elevation of the regression lines in the intermediate flowering group (Fig. 25). The elevation of the regression line for the seed setting from the 1977 flowering in the intermediate flowering group was significantly higher than the elevation from 1976 ($F = 12.92^{***}$, $df = 1, 181$).

The elevation of the regression line of the whole group for the seed setting from 1977 flowering was also significantly higher than the one from 1976 ($F = 13.85^{***}$, $df = 1,291$), while the slope was not. This means that the seed setting from 1977 flowering of the intermediate flowering group or the three groups as a whole was higher than that of from 1976, while the increasing tendency of seed setting in line with the increasing number of potentially fertile ovules was not significantly different.

However, there were differences in the slopes of the regression lines between the groups. The late flowering clones had higher regression line slopes than those of the intermediate flowering clones in both years ($F = 5.30^{*}$ and $F = 5.57^{*}$ for 1976 and 1977 respectively, Figs. 25 and 26). The late flowering clones also had higher regression line slopes than that of early flowering clones but the significance was found only between the regression lines for the seed setting from 1977 flowering ($F = 5.76^{*}$). This fact indicates that the female strobili of the late flowering

clones had pollinated effectively in proportion to the increasing number of fertile ovules or else, only well pollinated female strobili in proportion to the increasing number of fertile ovules developed into mature cones in the late flowering clones.

In spite of the differences in the number of potentially fertile scales and the slopes of regression lines between the clonal groups, there were no statistical differences in the mean number of seeds per cone produced by the three clonal groups except for one case. Only the intermediate flowering clones produced significantly larger number of seeds per cone than the late flowering one in the cones developed from 1977 flowering. In this respect, the number of seeds per cone appeared to be counterbalanced by the offsetting factors that affected the number of seed developed per cone among the groups during the observation years. That is, the early flowering northern clones had a larger number of fertile ovules with a smaller probability of pollination (or poorer ability of seed development) under natural conditions in southern Finland. On the other hand, the intermediate and late flowering clones had a smaller number of potentially fertile ovules with a higher probability of pollination wich would eventually affect the seed development through the well-timed male and female flowering within the whole population.

The percentages of developed seed to fertile ovules ranged from 16.2 % to 100.0 % and showed yearly fluctuations between the clonal groups and between the same individual clones. The intermediate flowering clones appear to have the highest probability of pollination or seed development during the two flowering years in relation to the potentially fertile ovules as compared to the early or late flowering clones. This seems to be due to the fact that the intermediate flowering clones consisted of the majority of the population and hence usually formed the highest pollen density within the population while the female strobili of those clones reached the most receptive stages under natural conditions.

The number of seeds (empty and filled) and the percentages to fertile ovules are presented in Table 14.

In spite of the higher number of effective pollen catch registered by pollen catch meters in 1976 (1810 grains/ mm^2) than in 1977 (1212 grains/mm^2) (Tab. 9), more seeds and higher percentages of seeds to fertile ovules per cone were found in the cones developed from 1977 flowering. This fact indicates the significance of pollen density at the right time of the receptive period of female strobili and the quality of the pollen.

In 1976 the male and female flowering was spread over about two weeks from the earliest to the latest flowering individuals, and the pollen density was high during the earlier and later part of the receptive period of the majority of female strobili. Moreover, frequent rain disturbed pollen dispersion while the majority of the clones were flowering. On the other hand, the male and female flowering as well as the pollen dispersion in 1977 was concentrated within a week and the pollen density was very high when the majority of the female strobili were most receptive. There was no rainfall which would disturb pollination during the most effective pollen despersion in 1977. Only some of the earliest and latest flowering clones appeared to have received insufficient pollen for good seed development in 1977. Therefore, it was expected that the seed development from 1977 flowering in Scots pine would be much better than the ones developed from 1976 flowering, although the total amount of flowering and the pollen density was much smaller than in 1976. The number of filled seeds per cone, the percentages of filled seeds to fertile ovules and the percentages of filled to the total number of seeds are presented in Table 15.

In comparing the early and late flowering groups the pollination and seed development in 1976 appeared to favor the late flowering group, while the pollination in 1977 was about the same in both groups. The early flowering clones (mostly northern origins) apparently had a lower percentage of filled to total number of seeds in both years than any other clonal groups.

3.5.3. Conelet absicission

The conelet abscission observed in early June 1979 for the developing conelets from the 1978 flowering ranged from a minimum of 1.7 % to a maximum of 60.2 % between individual clones. As was expected from the characteristics of the male and female flowering in 1978 described in 3.1. and 3.2., the early flowering clones generally showed significantly higher percentages of conelet abscission at the beginning of the June of the year following flowering with smaller sized and greyish brown color while the normally developing cones were large and green. However, a few clones in the early flowering group showed as low percentages of conelet abscission as in the late or intermediate flowering groups. On the other hand, in spite of the pine flowering in 1978 favoring the pollination of the late and intermediate

Table 14. The number of seeds and the percentages to fertile ovules per cone in early (E), intermediate (I) and late (L) flowering clonal groups.

Clonal group	n	No. of seeds 1976	No. of seeds 1977	% of seed to fertile ovules 1976 (%)	% of seed to fertile ovules 1977	Remarks
						significande level
E	28	23.8	26.6	57.8	65.0	
				*	*	*=5 %
I	92	23.6	27.0	63.6	72.3	**=1 %
		**	*	***	*	
L	27	21.6	22.9	61.1	64.0	*** = 0.1 %
Total mean	147	23.3	26.2	62.1	69.4	t-test by pooled variance
		***		***		

Clones that had insect-damazed cone (or cones) were excluded.

Table 15. The number of filled seeds per cone, the percentages of filled seeds to the number of fertile ovules and the percentages of filled to the total number of seeds in early (E), intermediate (I) and late (L) flowering groups.

Clonal group	n	No. of filled seeds 1976	No. of filled seeds 1977	% of filled seed to fertile ovules 1976	% of filled seed to fertile ovules 1977	% of filled to total seeds 1976	% of filled to total seeds 1977	Remarks
								significance level
E	28	16.8	21.5	40.8	52.5	69.6	80.4	
		*	*	*	*	**	**	
I	92	19.5	24.6	52.4	65.9	82.7	90.2	* = 5 %
		***	*	***	*	**	**	** = 1 %
L	27	19.0	21.2	53.6	59.0	87.2	92.0	*** = 0.1 %
Total mean	147	18.9	23.4	50.4	62.1	81.1	88.7	t-test by pooled variance
		***		***		***		

Clones that had insect-damazed cone (or cones) were excluded.

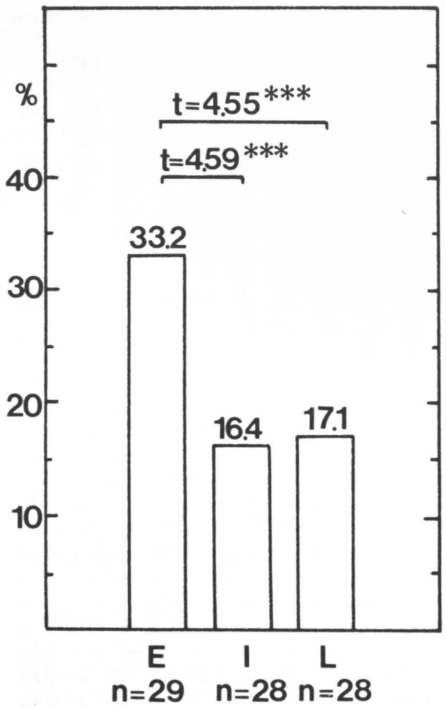

Fig. 27. Percentages of abscissed conelets developed from 1978 flowering in early (E), intermediate (I) and late (L) flowering clones.
n = The number of clones observed

flowering clones, conelet abscission exceeding 42 % was observed even in some of the late and intermediate flowering clones. This seemed to indicate that there were some other factors affecting cone development in addition to sufficient pollination of female strobili.

There was no significant differences in conelet abscission between the intermediate and late flowering groups. The differences in conelet abscission between the groups are presented in Fig. 27.

4. DISCUSSION

4.1. The adaptation of trees' reproductive cycle to local temperature factor

Its is generally known that plants growing in boreal and temperate zones are adapted not only to their specific local climates but also to the overall seasonal variation of the climatic conditions in that they grow and carry out their generative functions during the favorable seasons and they pass the unfavorable seasons in the state of dormancy. The timing schedule of a plant's development, that is the release from dormancy, and the plant growth and reproductive development during the favorable seasons and the entrance into dormancy as the unfavorable season approaches, must be adjusted to the seasonal rhythm of the local climate. Particularly, the development of reproductive organs in accordance with the seasonal variation of climatic conditions is essential for the success of reproduction and regeneration in forest trees.

According to SARVAS (1967 a and b) the annual course of development is composed of numerous sequences of physiological events which commence in spring when the daily mean temperature exceeds +5° C and it forms a closed cycle. The development is controlled by the thermal factor, and each stage of the closed cycle of a given tree species passed through in the main part of its range at a certain portion of annual temperature sums specific to the species. For instance, according to Sarvas' model, the physiological events of reproductive development in *Pinus sylvestris* L. are usually achieved at the following portions of the local mean annual temperature sums above +5° C; that of meiosis 5,2 %, that of anthesis 17,3 %, that of syngamy 31,0 % and that of seed maturation 77 % of the corresponding years of the development (SARVAS 1967 a, b). These proportions are consistant within the distribution range of a given tree species where the reproductive adaptation to temperature factor is optimal, except in the northern and southern transitional and marginal areas. The result of the adaptation of the active period to local climate in the whole range of the species often shows a strong north-south genetic gradient of the active period (LANGLET 1959, SARVAS 1969, 1970 a and b).

According to this rule, trees transferred from colder regions with shorter growing seasons to a warmer region with a longer growing season are expected to grow, develop floral organs and end the active cycle earlier than those transferred from warmer regions or the local trees as LANGLET (1967) stated by citing Linsser's work. In this present study, as far as floral development of Scots pine during the flowering season is concerned, the Linsser's principle is generally confirmed. Particularly, the reproductive adaptation of Scots pine to local temperature factor appeared to be pronounced (Answer for the question (1) in page 7). The earliness of flowering expressed in the period unit sums are significantly correlated with the local temperature sums of the origin of selection ($r = 0.44---0.63^{***}$). This tendency was most pronounced in 1978 when there was no low-temperature stress that usually affects the floral development at a certain critical stage (cf. 3.3.). This fact indicates that the trees from colder regions are adapted to develop their floral organs efficiently with smaller temperature sums to achieve their reproductive cycles under the climatic conditions of shorter growing seasons in those localities except that the northern marginal zones where the trees reproductive cycles cannot fully be adapted to the local temperature factor (SARVAS 1966, 1967 a, 1970 a).

The development of female flowers from the new year's initiation of their growth until flowering appeared almost entirely to depend on the temperature and time factor (Answer for the question (2) in page 7), that is the p.u. scale, as shown in the estimation of the starting points of new year's floral development (cf. 3.3.). The development of male strobili also appeared to mainly depend on the p.u. scale. In this case, however, the convergence of reversely calculated p.u. sums

from the flowering points (pollen shedding) of the three observation years was rather poor and thus appeared that the p.u. sums for pollen shedding from the starting point of the new year's floral development fluctuate slightly from year to year. This is most probably due to the time lapse between the male floral development up to readiness to pollen shedding (fully developed stage of male strobili and the actual pollen shedding of which the situation cannot be found in female flowers).

In male flowering, air humidity influences pollen shedding by controlling evaporation of water from the exothecium cells surrounding the anthers and thereby influencing their opening. In other words, the development of male floral organs up to the readiness to pollen shedding depends mainly on the p.u. scale while the actual pollen shedding from that stage is often influenced, to a certain extent, by air humidity as well as the air temperatures (SARVAS 1962). The development of male floral organs may also have a higher subsceptibility to external factors such as low-temperature stress that will cause a delay of floral development. However, the fluctuation seems to correspond to a very small portion of the total annual temperature sums. Therefore, anthesis usually started when the temperature sums reached approximately the same proportion of the local annual temperature sums. BOYDAK (1977) also obtained a very similar result from the observations on male flowering of Scots pine in Turkey where the southern marginal Scots pine population is located. The corresponding percentages of temperature sums for anthesis are 14.5 and 15.0 % of the local annual temperature sums, which are 2.3–2.8 % less than the 17.3 % in southern Finland near the northern marginal Scots pine population.

Temperature sums is generally known to be one of the dominating environmental factors governing the new year's growth initiation, growth and development in plants (IRGENSMOLLER 1957, MANDY and KARPATI 1958, NIENSTAEDT 1974, PAULEY and PERRY 1954, PERRY 1971, ROCHE 1970, SARVAS 1967 a, 1972, 1974, STERN and ROCHE 1974 p. 15).

Therefore, temperature sum is often used for the prediction of growth and development in crops (ARNOLD 1960, BROWN 1975, HOLMES and ROBERTSON 1959, MAJOR and JOHNSON 1975, PARTRIDGE 1947) and forest trees (BOYER 1973, 1978, SARVAS 1967 a, 1967 b, 1969, 1970 a, 1970 b, 1972, 1974). A number of methods and threshold values were employed by various researchers for the calculation of temperature sums.

Although temperature factor appears to play a major role for new growth, the initiation points of new years floral development of the Scots pine clones from various localities could not be fully explained only with the temperature factors including p.u. sums, d.d. sums or single thereshold temperatures for the initiation. In the estimation of the points of new year's floral development, the locality groups showed a general order of early through late initiation or small through large flowering p.u. sums in the three observation years, but not exactly the same order every year. This fact indicates that the initiation of new year's floral development may not entirely dependent only on temperature factor but other factor (or factors) may be involved in this physiological event. SARVAS (1972 p. 72) had already stated the "zero point problem on the cycle intervals of the active period" which he was not able to determine easily by any single temperature factor before he (1974) further developed a cycle model on the development of active and dormancy cycle in woody species.

However, even the lately developed Sarvas model, which is based only on a temperature and time factor explains only partially the following phenological event observed during this present study. That is, grafts of a northern Scots pine clone which was transferred from 69° 13′ N), latitude to the observation area 61° 48′ N), partially, but not all of an individual (graft) or even the female strobili on the same terminal buds (which means the new growth initiation is extremely localized), developed female strobili up to the developmental stage 2 (flushing stage, cf. Fig. 3) in late fall and thus usually experienced frost-damage during the cold winter. Some of the female strobili in this clone also developed up to developmental stage I (Fig. 2) with varying degrees by the late fall but were covered with dense resin and the strobili flowered very early in the following spring. However, a major part of the female strobili in the clone developed and flowered somewhat later than the abnormally early flowering strobili of the same clone but somewhat earlier than the other northern clones.

Many of the northen Scots pine clones, but not all, which were transferred from 66–69° N latitude to the observation area also showed a similar trend of abnormal female flowering in early spring with varying degrees of developmental stages. In certain cases the degree of development of female strobili was not consistent even in the same level of a growing shoot of the abnormally early flowering northern clones. If the initiation of new floral growth was manipulated solely by temperature factor, the new growth of floral organs would have been rather regular with small variation. However, the variation was very great even within an individual graft by showing that the latest developing strobili reached the developmental stage 3 while the earliest developing strobili reached the final stage of the first year's growth (stage 5) from flowering. The abnormal and irregular flowering behavior of northern clones transferred to the south gives the impression that the initiation of new floral development in the buds seems to be manipulated by growth regulators of which the production translocation and the level can be extremely localized (in the tissues of a bud) and also can be modified through an interaction between environmental factors such as temperature and light as shown bud-burst in Douglasfir (CAMPBELL and SUGANO 1975). The northern Scots pine clones in southern Finland usually start to form resting buds in early summer (from late June to early July) and expand the buds up to their full size of the overwintering stage during August. The low night temperatures during late August and early September might have acted as a chilling effect upon the newly formed and expanded buds which were ready to start to grow by external stimuli by that time. Therefore, it is assumed that the chilling effect by low night temperatures during late summer might have enhanced the production of growth promotors in the buds of northern clones (presumably also in the needles) while the shorter photoperiod compared to the native one would have enhanced the production of growth inhibitors in the needles (COOPER 1963). It is also expected that a large amount of growth inhibitors would have been produced in the needles and translocated to bud tissues and scales at the time of bud formation. In this way in the apical meristem tissues of the buds where the growth promotors overruled the level of translocated growth inhibitors for new growth initiation new growth of floral organs would have started in the buds, while the meristem tissues of buds where the level of translocated growth inhibitors exceeded the level of growth promotors would have remained dormant, as described by NITSCH (1963).

Hormonal regulation of growth and dormancy is comprehensively reviewed and discussed by WAREING and SAUNDERS (1971). The photoperiodic effect on growth cesassion or bud expansion growth as shown in various experiment under controlled or modified environments from those of natural ones may be caused through alteration of the levels of growth regulators by the modified photoperiods. The interaction between light and temperature factor on plant growth and development is also reported on various species (ASHBY and HELLMERS 1959, HEIDE 1974 a, b, REYNOLDS and THOMPSON 1973, ROBERTS and MAIN 1965, WENT 1945, 1957, 1978), however, the degree of interaction appears to be dependent on plant species and closely related to the plant adaptation to those factors and the mechanism of natural selection.

In short, tree growth and development is generally adapted to the environmental factors of the natural habitats, and it usually proceeds in harmony with the seasonal changes of climatic conditions such as temperature, light and rainfall. During the active growth phase, the tree's reproductive and vegetative growth appears to be mainly dependent on a temperature and time factor, as it was reported by SARVAS (1967 a, 1972, 1974) for reproductive development and by HARI and LEIKOLA (1974) on vegetative development. This is because the seasonal course of development of trees in the northern temperature zones is mainly adapted to the most limiting temperature factor for tree growth in those areas (LANGLET 1967). However, the transition phase or the cycle shift from one phase to the other appears to be affected by various environmental factors and the interactions of those factors such as temperature and light (photoperiod) or in

certain cases, moisture conditions (such as dry season or severe drought during active growth period) and nutritional status (YOUNG and HANOVER 1978).

4.2. Biological stresses and ecological aspects of adaptation

Trees that remained in the present natural ecosystems appear to be the product of long-term natural selection, which favors those best adapted, both vegetatively and generatively, to the environments. However, tree populations seems to be confronted with various biological stresses particularly when transferred out of their native habitats, and in some cases even under natural habitat conditions.

Of the biological stresses (cf. LEVITT 1972), low temperature conditions during the trees' active period frequently affect the growth and development of trees. Late or early frost injuries frequently occur in late spring or early fall respectively, when tree provenances are transferred to regions where the length of growing seasons are distinctly different from those of their natural habitats (HEIKINHEIMO 1949). The discordance of rhythm between the growth of the transferred populations and the new environments seems to cause these kind of frost injuries.

In this present study low-temperature stress imposed upon the actively developing female strobili appeared to delay the floral development. Unfortunately, the mechanism of low-temperature action of the female flower development could not be clearly elucidated at this time. The low-temperature stress may simply decrease the developmental rates of all or partial metabolic processes in floral organs, or totally arrest the floral development for a short period at certain low-temperature sensitive stages by disturbing the metabolic process itself. In some cases the low-temperature stress may result in the production of toxic substances in its metabolic processes which would finally lead to a temporary inhibition of the development or the abortion of floral organs.

Usually the developing Scots pine female strobili appears very sensitive to low-temperature at the time of flower flushing (developmental stage 2–1). This seems to be the most active stage of cell division or elongation for the necessary energy of flushing out of the tightly-covered flower bud and for the rapid growth. Usually the development of female strobili is very rapid from this stage until flowering, provided that the temperature is warm during floral development up to flowering (under natural conditions this warm period appears to be very common during active floral development in the natural habitat).

The developmental stage 2–1 of Scots pine at the experimental site (Punkaharju) was reached in late May in the case of northern tree populations, and in early June in the case of central and southern tree populations in normal years. Under natural conditions the p.u. sum from the starting point usually reaches 3900–4200 at the time of flushing. In view of the writer's experience on chromosome investigation, active mitotic cell division (particularly metaphase) was most frequently observed in the proximal parts of the newly developing needles at the time of leaf flushing. The time of leaf flushing and the female flower flushing are well in accordance with each other.

The rapid development of floral organs and the above mentioned facts indicates that cell division must be very active in the female floral organs at the time of flushing. Low-temperature stress in these actively dividing cells at the time of flower flushing must be very hazardous and therefore the low-temperature might have disturbed the metabolic processes of floral development, including cell divisions. Various studies on the effect of low-temperature on meiotic cell division in conifer species are reported (ANDERSSON et al. 1969, CHIRA 1964, 1965, 1967, CHRISTIANSEN 1960, EKBERG et al. 1968, 1972, ERIKSSON 1968 a, b, 1970, ERIKSSON et al. 1970 a, b, and JONSSON 1974).

In most cases, low-temperature induced chromosomal irregularities during the meiosis of PMC would lead to the production of defective pollen or complete death of the male flower bud (ANDERSSON 1969, CHIRA 1967, ERIKSSON 1968 b, 1970, ERIKSSON et al. 1970). CHIRA (1967) reported that MI (metaphase I) – AI (anaphase I) and MII-AII of PMC in *Pinus edulis Englm.* were highly sensitive to low-temperatures.

ERIKSSON (1970) reached the same conclusion in his study on meiosis and pollen formation in *Larix* in that the developmental phases up to the insensitive stage and from this stage to TII (telophase II) except interphase were highly sensitive to low temperatures. This fact indicates that the actively dividing phases within a relatively short period, when the chromosomes are fully enlarged – metaphase to anaphase – are the most sensitive stages to external hazardous factors such as low-temperatures, radioactive radiations, or chemicals.

The critical temperatures for the induction of chromosomal irregularities appear to vary species to species and may be modified under different conditions. CHIRA (1967) reported that three hours' exposure to +3° C caused irregularities in PMC of *Pinus edulis Engelm.* CHRISTIANSEN (1960) reported that pollen sterility reached 100 and 87 percent in *Pinus nigra Arn.* and *Pinus sylvestris L.* respectively due to low-temperature conditions below 0° C for a 15-day period during the sensitive part of meiosis. JONSSON (1974) observed a high percentage of degeneration in developing P.M.C. in *Picea abies (L.) Karst.* exposed to −7.8° C. She also observed that chromosomal irregularities at TI. MII, AII and TII increased when the developing P.M.C. were treated at −5° C for three days. ANDERSSON et al. (1969) suggested that the critical temperature responsible for the induction of chromosomal irregularities in the meiosis of P.M.C. ranges from about −2° . . . −4° C in *Picea abies (L.) Karst.* to a few degrees above 0° C in other conifer species.

In this present study, the critical temperature for the delay of female flower development at mitotic phase appeared to be −1.4°. . .+2° C in Scots pine. The minimum temperature recorded during the most low-temperature sensitive developmental stage was −1.4°C. Therefore the critical low-temperature that would eventually destroy the developing female strobili could not be observed during the three observation years. ERIKSSON et al. (1973) reported that 35 % of the labelled female strobili for flowering observation in Norway spruce were frost-damaged during the night, when the temperature dropped to −3° C. No visible frost damage on developing female strobili (at the time of flushing) occurred at a temporal low temperatures of −1.4° C in Scots pine. Usually longer than two hours exposure to lower than +2° C at the low-temperature sensitive stage appeared to delay the development of female strobili in Scots pine. Low-temperatures between +2° C and +3° C may also delay the development of developing female strobili at the low-temperature sensitive stage, if the duration of exposure is prolonged for more than two hours.

At early stages of development, particularly when the new year's developing female floral initials are covered by the terminal bud scales of the shoot, they appeared to be considerably frost hardy. For instance, at the beginning of new year's floral development, when the estimated p.u. sum from the starting point reached 200, floral initials tolerated temperatures as low as −9.8° C and they developed normally up to later stages. This fact implies that the responses of floral organs to low-temperature stress is different according to the developmental stages. Occasionally, abortion of developing female strobili was observed just before or after flowering only in certain clones. However, the cause of flower abortion was not yet known, whether it is due to the low-temperature stress or clone specific genetic factors.

Previous low-temperature experience of trees just before the low-temperature sensitive stage may induce an elastic tolerance or elastic resistance of the trees. On the contrary, high temperature conditions just before the low-temperature sensitive stage may cause a decisive frost injury or greater delay of flower development by pushing up all the developing cells to the most critical stage at the same time. In supporting the effect of previous thermoexperience CHIRA (1964) reported that three days exposure at −4° C caused damage to P.M.C. during prophase I - - telophase I but to a lesser extent during the second meiotic division in *Taxus bacata L.* EIGA (1972) reported that pretreatment of low-temperature (usually subfreezing temperature) increased the frost hardiness in the seedlings of *Abies sachalinensis Fr. Schm.*

In most cases the development of the annual cycle in tree populations seems to coincide well with the corresponding seasonal climatic rhythms in their natural habitats. The growth and development appears to be relatively slow in its initial stages, when the climatic

conditions are comparatively unfavorable for rapid growth and development, and it becomes more rapid as the growth and development proceed to the final stage as the climate becomes warmer and warmer. The growth and development of southern trees at the experimental site (Punkaharju) reach the maximum stage usually just after the late frost period (late May- - -early June in the observation area) has passed. The climate after this late frost period is usually very warm and favorable for tree growth and development. Flowering and pollination is completed during this relatively short and most favorable time with minimum frost risks. This appears to be an avoidance adaptation of the natural populations to the seasonal rhythms in their natural habitats.

On the contrary, the northern tree populations begin to grow and develop floral organs somewhat earlier than southern populations and reach the stages of maximum growth and development before the late frost period in southern Finland. Therefore, the northern tree populations are frequently subjected to low-temperature stress caused by late spring frost in southern Finland. However, no visible late frost damages were found in the newly growing shoots or developing female strobili in the years of frequent late frost, 1976 and 1977. Only the delay of female flower development could be found by the measurement of flowering p.u. sums. The northern tree populations appears to have resistance adaptation to a certain limit of low temperatures. Actually, the female strobili of northern tree populations showed a considerably thickened growth in their ovuliferous cone scales while they were exposed to low-temperatures (−1.4° . . . +2° C) during the active developmental stages. In the case of newly growing needles, the upper exposed parts have already developed a fairly thickened and cutinized waxy surface and the lower (proximal) relatively succulent parts are covered by a waxy fascicle sheath at the time of leaf flushing. The needle structure of Scots pine itself, that is, thick-walled epidermis with heavy cuticle and deeply sunken stomata with overarching subsidiary cells, and sclerified fibrous hypodermic layers, which occur beneath the epidermis, may play an important role in frost hardiness.

HEIKINHEIMO (1949) reported that spring frost frequently injured northern spruce races in southern Finnish experimental sites proportionally more than the southern ones due to the fact that the buds of the former open at lower temperatures and consequently earlier in the spring than those of the latter. His observations on late frost injury in Norway spruce is well in accordance with the present study on late frost stress in Scots pine flowering, though the low-temperature conditions in this study did not damage but only appeared to delay floral development during the two observation years. Serious spring forst damages, at least in floral organs, on the northern trees in southern Finland cannot be excluded in the years of severe late spring frost.

It is generally known that more southern provenances or geographic races of Scots pine and Norway spruce retain their faster growing characteristics than those of the more northern populations even after they are transferred slightly north of their original localities in the north of central Europe. This is most probably due in part to the fact that the trees of southern origins flush later than those of local populations in the transferred regions and hence they avoid the biological stress of late frost more safely and effectively use the most favorable warmer period for their growth and development that usually is followed by late frost in the more northern regions. In this case the limiting factors for the south-north transfer will be the stresses of early frost in the fall and winter frost. However, south-north provenance transfers appear to be disadvantageous in northern Sweden, where the climatic conditions are often harsh and unfavorable for tree growth. In northern Sweden, north-south transfers of Scots pine populations, within the limits of their growing season zones are not significantly different, generally show a higher degree of hardiness and survival rate and hence higher overall wood production than the local ones. On the contrary, in most cases, south-north transfers showed inferior survival rates and lower overall wood production per hectare in spite of the superior growth rate of the few surviving individuals (EICHE and ANDERSSON 1974, ERIKSSON et al. 1976) This fact may again indicate the difference in adaptive strategies between vegetative and reproductive cycles and at the same time the effective gene flow from the south to the north in Sweden.

The adaptive strategy of the vegetative cycle is not for maximum growth but maximum survival. The adaptive strategy of the reproductive cycle is not maximum survival nor maximum growth but maximum reproduction. Maximum growth is required in competition, which will complement the fitness value of the vegetative cycle. The integration of these adaptive strategies endows the adaptive value of the local population, which involves various kinds of compromise between these factors. Therefore, in certain cases a local population may not be one of the best growing, surviving or reproducing but may be one of the optimally adapted to some of those factors in the local climatic conditions. The effective gene flow from the south to the north may also reduce the survival rate of the seedlings of the following generations in the local climatic conditions.

The genetic adaptation of tree populations to local climate, particularly, the seasonal changes of climatic factors in the natural habitats is very important from the practical point of view in silviculture and forest tree breeding. When silvicultural practice and tree breeding aim at a stable and fast growing tree populations by minimizing the biological stresses in a given site and environment, the growth rhythm of trees in relation to the seasonal rhythimic changes of local climatic conditions must frist be considered. Of the climatic factors temperature, light (quality, intensity and day length) and precipitation appear to be the most important component (CAMPBELL and SUGANO 1975 and 1979, MORGENSTERN 1969).

Many researchers emphasized the prime importance of temperature factor (minimum and maximum temperatures or growing season in terms of number of days that exceed threshold temperatures above 0° C or +5° C etc.) in relation to plant adaptation in temperate zones (LANGLET 1967, SARVAS 1967 a, 1969, 1970 a, 1972, 1974).

RUBY (1964) reported that the characteristics of Scots pine showed an overall pattern of greater temperature effects in the northern (colder regions) and greater precipitation effects in the southern (warmer regions where the temperature is less limiting than precipitation for tree growth and reproduction under natural conditions) ranges of the species distribution. This fact may indicate that the adaptation of plants to local climate is more closely related to the most limiting factor for plant survival, growth and reproduction. It has also been demonstrated that photoperiods have a crucial effect in the regulation of shoot growth, particularly at seedling stage, under controlled or modified conditions from those of natural environments of the trees habitats (VAARTAJA 1954, 1959, WAREING 1950 a, b, 1951 and others) although they often interact with temperature factors (EKBERG and DORMLING 1979, HEIDE 1974 a, b, MALCOLM and PYMAR 1975). It appears that the photoperiodic response for tree growth cannot easily be detected under natural habitat climatic conditions and therefore, in most cases, tree growth appears to be mainly dependent on temperature factor (HARI and LEIKOLA 1974, SARVAS 1967 a). This may be due to the fact that the natural tree populations have already been well adapted to and selected for the regularly changing photoperiod as well as the fluctuating temperatures during growing seasons by allocating the periods of shoot growth, bud formation, tissue and organ differention which is usually associated with bud extention growth. Therefore, under natural habitat conditions, the natural photoperiods during the fast developing phase of natural tree population may not decisively alter the normal shoot growth until the preformed growth primordia in the buds during the previous year complete their growth. Thus tree growth within this active growth period usually shows a temperature dependence. However, if the temperature during the active shoot growth period is unfavorable so as to delay the shoot growth until late in the growing season exceeding the photoperiodically preadapted shoot growth period, the shorter day-length after that time may decisively affect the shoot growth to insure an early bud set for a proper tissue and organ differentiation of the newly formed buds and the safeguard against adverse environments.

The strategic allocation of shoot elongation growth and bud formation, tissue and organ differentiation period and the resulting tree growth in the tree species with monopodial growth behavior within the growing season

can be inferred and illustrated schematically in the following way (Fig. 28). Tree growth is usually affected by the climatic conditions in two consecutive years (HEIDE 1974 b, MIKOLA 1962) during (1) bud formation, tissue differentiation and bud expansion, (2) active shoot growth period in the following year. Suppose that there are three types of tree populations that have distinctly different growth patterns in a given site and environment namely trees with (1), a short active period (S), (2), a growth rhythm optimally allocated for the growth season (O), and (3), a long active period (L) as shown in Fig. 28 a. The S trees have an excessive growth period for tissue differentiation and expansion of the buds but a short shoot growth period that can fulfill only 80 % of the growth potential that had already been formed and laid down in the buds in the previous year. On the contrary, the L trees have too long a shoot growth period so as to limit the tissue differentiation and bud expansion growth to only 90 % of the growth potential. However, the trees that have allocated the shoot and bud growth periods optimally within the growing season will develope and grow by 100 % of both the shoot and bud growth potential. The integrated final shoot growth will be 80, 100 and 90 % of the growth capacity of the S, O and L tree populations respectively, provided that the genetically determined growth potentials are the same in those tree populations. In this situation the O tree population will naturally be selected for during the developmental stage of severe competition.

During the years of cool summers, even the O trees may not fully develop the buds up to the maximum growth potential because the tree growth may lag until late in the growing season so as to limit the time for bud growth (Fig. 28 b, OC). On the contrary, during the years of warm summers the L trees will complete shoot growth earlier than on average years (because the development of predetermined growth initials will be completed in a shorter period at higher temperature conditions) and thus have enough time for bud differentiation and expansion growth up to its full growth potential. The resulting shoot growth of the following year will be 100 % of the genetically determined growth potential (Fig. 28 b, LW).

If the O trees are transferred to a northern latitude where the growing season is shorter*[10] than the natural habitat, the trees may grow until late in the growing season due to the lower temperatures and longer day-length during the growing season. However, if the shoot elongation growth lasts too long until late in the growing season, the differentiation of bud tissues and bud expansion growth will be limited as shown in Fig. 28 C (ON). The consequence of limited bud tissue differentiation and bud expansion growth in

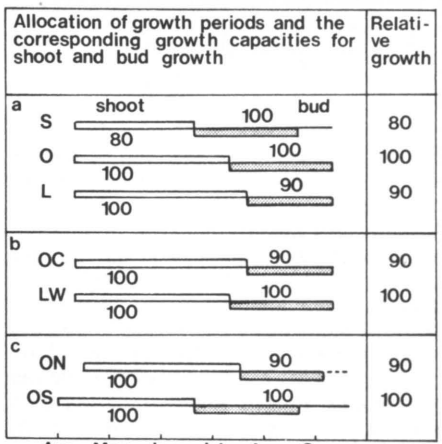

Fig. 28. (a) Strategic allocation of growth periods between tree populations with short active period (S.), optimum active period (O.) and long active period (L.) for shoot and bud growth and the resulting relative tree growth in a given site and environment. (The genetic growth potential of S.O.L. trees are considered to be the same under optimum climatic conditions.)

(b) The modification of growth patterns by changing environments in the same site and the resulting relative tree growth. O.C.: O. trees in cool summers. L. W.: L. trees in warm summers.

(c) The modification of growth patterns by transfers of optimally adapted population in a site to the north (O.N.) and to the south (O.S.) from the original site and the resulting relative tree growth.

▭ = shoot growth
▨ = bud growth
—— = meteorological growth period

a year is limited shoot growth in the following year. The north-south transfer (Fig. 28 c, OS) may affect the tree growth in a different manner from that of south-north transfer. The transferred trees usually start to grow early*[11] and also cease shoot growth early in the growing season (DUNBERG 1979 a, HEIKINHEIMO 1949) due to the smaller growth potential of the northern trees of which the growth can be achieved in a relatively shorter biological growth period at warmer conditions and the shorter photoperiod that often enhances the cessation of shoot growth in the transferred southern region. The effects of photoperiod on tree growth and development have been studied by many research workers (DORMLING et al. 1968, DOWNS 1958, 1962, DOWNS and BORTHWICK 1956, EKBERG and DORMLING 1979, ERIKSSON et al. 1978, HEIDE 1974 a, b, IRGENS-MOLLER 1957, LEIKOLA 1970, McCREARY et al. 1978, NIENSTAEDT and OLSON 1961, ROCHE 1970, VAARTAJA 1954, 1959, WAREING 1948, 1950 a, b, 1951, 1953, 1954, 1956, WAREING and BLACK 1958, WAREING and LONGMAN 1959). In general, tree growth will be favored by warmer temperatures and a longer meteorological growing season in a north-south provenance transfer. On the other hand the shorter photoperiod during the growing season in the south will limit the shoot growth of the transferred trees from the north. The reverse will be the case in a south-north transfer. That is, tree growth will be favored by longer day-length but lower temperature conditions and a shorter meteorological growing season will limit tree growth in south-north transfer.

The question as to whether the tree growth will be enhanced or suppressed by the north-south or south-north transfer depends on the trees' adaptation and the extent of responses to environmental factors that greatly affect tree growth and which factor affects the tree growth greater than the others by the transfers. The environmental factors often interact with one another in plant gorwth and development. In this connection LAUDE (1953) reported a prominent example of plant *(Poa scabrella)* adaptation to local environment and the response to major external factors – temperature, water and day-length – for its seasonal growth and development. Trees of different origins often respond differently to modified photoperiods or temperature conditions from those of their natural ones in their growth behavior (CALLAHAM 1962, DÖRMLING et al. 1968, DOWNS 1958, 1962, DOWNS and BORTHWICK 1956, HÄBJORG 1978, HEIDE 1974 a, b, IRGENS-MOLLER 1957, NIENSTAEDT and OLSON 1961). JENSEN and GATHERUM (1965) reported that height growth in Scots pine seedlings at 13.3° C was greater than that of at 21.7° C at 16- and 20-hour photoperiods but not a 12-hour photoperiod. This fact indicates that, in certain cases, tree growth in Scots pine can be enhanced by a south-north transfer that is usually associated with cooler temperatures and longer photoperiods during the active growth period. On the other hand, it has been reported that the rate of shoot growth in Norway spruce was increased with increasing temperatures in long-day conditions (HEIDE 1974 a). Under natural conditions the tree growth within the genetically determined growth potential depends mainly on the inate growth rhythm and temperature (HARI and LEIKOLA 1974) and the total tree growth is more closely related to the rate of growth during the fast shoot elongation growth period than the total length of the growth period in a year (JENSEN and GATHERUM 1965).

Late spring frost or early fall frost and winter frost are also important factors that affect the tree growth in north-south or south-north transfers. Frost damages are usually caused by the discordance of trees inate growth rhythm and the seasonal rhythm of transferred regions (DIETRICHSON 1964 a, b, 1969 a, b, EICHE 1966, EICHE and ANDERSON 1974, HAGNER 1970 a, b, c). A successful transfer of tree species or tree provenances can be made within the range that the seasonal rhythm of climate does not seriously affect the inate growth rhythm of the transferred tree species or provenances. LARCHER (1978 p. 222) introuduced LANGLET's (1936) study concerning the temporal co-ordination of climatic rhythm

*[10]: The south-north transfer is generally but not always accompained by shorter and cooler growing season.

*[11]: There are also exceptions, cf. CAMPBELL and SUGANO 1975 and 1979, GIERTYCH 1972.

and the rhythm of growth in trees.

Altitudinal transfers of tree populations also give similar results as in latitudinal transfers, but there seems to be complicated interactions between the seed sources, the transfer distances, elevation or locations (HAGNER 1970 a, ERIKSSON et al. 1976).

HEIKINHEIMO (1949) suggested that the biologically safe distance of south-north provenance transfer would be 200–300 km and 200 km for Norway spruce and Scots pine respectively, and 100–150 km for north-south transfer of those two species for silvicultural purpose.

Studies on the growth rhythm of forest trees have been conducted in Scandinavian countries through provenance transfer or species introduction and recognized the importance of growth rhythm for future tree improvement in relation to adaptation (DIETRICHSON 1964 a, b, 1968 a, b, 1969 c, 1971, EICHE 1966, ERIKSSON et al. 1976, HAGNER 1970 a, b, c, HEIKINHEIMO 1949, LANGLET 1960). The significance of photoperiodic responses of forest trees is also realized and many researchers emphasized the implications of photoperiodic responses for forest tree beerding in relation to tree growth (EKBERG et al. 1979, ERIKSSON 1979, HEIDE 1974 a, b, NIENSTAEDT and OLSON 1961, PAULEY 1958) and frost or disease resistance (ARONSSON and ELIASSON 1970, BERVAES et al. 1978, CHRISTERSSON 1978, DIETRICHSON 1968 a, b, 1969 a, b, HAGNER 1970 a, b, c, KIELLANDER 1970, McGREARY et al. 1978). The responses of trees to differential temperatures between day and night which can be altered by the transfers may also be important in some tree species as studied by HELLMERS (1962, 1967), HELLMERS et al. (1970), KRAMER (1957, 1958), KRAMER and KOZLOWSKI (1960) and LARSON (1967).

The latitudinal transfers of tree population may also affect the flowering of trees (DUNBERG 1979 b, SARVAS 1970 a). In this present study, most of the northern Scots pine clones in the observation area (north-south transferred) produced a lot of female strobili (also abundant male strobili in some clones) at graft age 8–10 during the observation years. This abundant flowering of northern clones in the south may be due to the fact that the northern trees ceased shoot growth early in the mid-summer as illustrated in Fig. 28 c and thus the newly formed buds of northern clones usually met very favorable climatic conditions with abundant photosynthesis for the initiation and differentiation of reproductive organs as well as the vegetative organs in the developing buds. Temporal water stress during the active shoot growth period may result in an early cessation of shoot growh by lowering the auxin level through the increase of auxin oxidative enzyme activity (DARBYSHIRE 1971). The early cessation of shoot growth by the water stress may lead to abundant flowering as it has been reported that low summer precipitation was often associated with abundant flowering in the following year (EBELL 1967, HOLMSGAARD 1972, HOLMSGAARD and OLSEN 1966, LINDGREN et al. 1977, MATTHEWS 1955, TIRÉN 1935). However, it must be emphasized that the effect of water stress on floral induction would not be direct but indirect through an early resting bud formation, that is, aftereffects. If the water-stress conditions were prolonged until the time of bud tissue differentiation and bud expansion growth, not only the normal differentiation of vegetative parts but also the reproductive organs would have been distrubed. In supporting this inference, DUNBERG (1979 a) reported that water stress was detrimental to flower induction of Norway spruce and that abundant watering was a prerequisite to stimulate flowering at high temperatures.

In conclusion, as GOLDSCHMIDT (1934) stated "The decisive biological fact is that the normal life cycle of the form has to be in tune with the seasonal cycle of nature", tree growth and development in unision with the seasonal rhythm of climate is very important for normal growth and reproduction. Plant growth and development in tune with the climatic rhythm not only affects the plant survival and reproductive functions but also the growth rate and competitive ability of an individual or of a tree population in the biomass.

4.3. Gene flow as a consequence of flowering time

In Scots pine usually the female strobili become receptive before the individual's own pollen begins to shed in the years of normal meteorologic conditions. Therefore, the probability of pollination of female strobili is maximized for pollen sources reaching receptive female strobili. The protogynous flowering behavior in Scots pine renders a directional gene flow within and between subpopulations or sometimes even between populations.

In earlier work KOSKI (1970 a) reported that a fraction of trees with a so-called short active-period have the preference in the pollination of trees that are close to the mean and that they in turn have the preference in the long-period fraction of pollination in subpopulations. However, the tendency is reversed within a greater framework in that the gene flow is from the trees with longer active period to those of relatively shorter ones due to the trend of flowering time being earlier in the south and relatively later in the north.

In this present study the same tendency of directional gene flow is confirmed. Under natural Finnish climatic conditions the gene flow is from the earliest flowering individual trees to the sequentially later flowering ones within subpopulations or interbreeding populations. This is because usually the male flowering of earlier flowering trees and the female flowering of later flowering trees is synchronized.

Under natural conditions the reverse gene flow form the intermediately early flowering trees (that is from the population mean) towards the earlier flowering trees can frequently be recognized within populations if the pollen density of the early flowering trees themselves and of foreign pollen sources is not sufficient (due to their small number) to pollinate receptive female strobili of earlier flowering trees up to the maximum possible pollination levels (80–85 % of receptive ovules of a strobilus). The unpollinated ovules of the early flowering trees will then be pollinated by the successively later flowering trees, which usually form a higher pollen density due to larger number of flowering individuals, than the former.

The gene flow within populations is also greatly affected by the aspects and the velocity of wind during the male flowering time (SARVAS 1962). However, it is generally known that the wind blows from the south to the north during the pine flowering season in Finland. The mating probalility between individuals within a population in the course of directional gene flow can be modified according to the differences between male and female flowering at population and individual levels in different years. A conspicuous example can be seen in Fig. 29. In 1976, the difference between male and female flowering was not great. Therefore, the magnitude of gene flow was expected to be rather gradual and stepwise from the slightly earlier flowering to the later flowering individuals. On the contrary, the difference between male and female flowering in 1978 was great and almost all of the female strobili reached receptivity before male flowering. Therefore, it is expected that a mass gene flow took place from the early flowering individuals to the whole range of flowering individuals except for those that flowered latest.

In considering the flowering behavior and pollination mechanism of Scots pine, the early flowering individuals in a population have a greater possibility of self-pollination than those of the later ones. The early flowering individuals also have a greater possibility of cross-pollination by the pollen sources from other populations provided that the conditions for a relatively long-distance pollen dispersion are met. In this case the early female flowering trees are foreign pollen acceptors.

KOSKI (1970 a) reported that flowering usually begins earlier in the regions, where the growing season is longest and begins progressively later in regions with an increasingly shorter growing season. That is, flowering begins earlier in the warmer southern regions and gradually proceeds to the northern cooler regions of Finland. Furthermore, the amount of pollen production, which is one of the most important factors for optimum pollination, decreases when moving northwards (SARVAS 1962 and 1968). The prevailing wind during the flowering season blows from the south (or southwest) to the north (or northeast). All these factors render the gene flow easily from the south to the north of Finland. A mass of pollen clouds from the south may travel from a few tenths up to several kilometers (or even occasionally a few hundred kilometers) to the north under Finnish climatic conditions (KOSKI 1970 a). The female strobili of the most northern

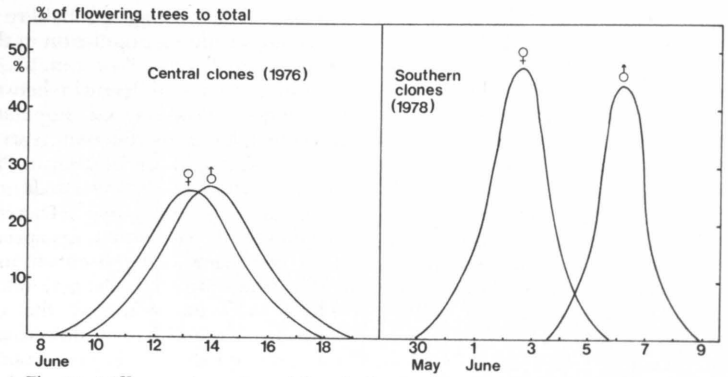

Fig. 29. Difference in male and female flowering time at Punkaharju clone bank in 1976 and 1978. Left: Male and female flowering of central clones in 1976. Right: Male and female flowering of southern clones in 1978.

populations may reached maximum receptivity, when the pollen clouds from the south arrive, while the male flowering of the northern population itself has not yet begun. As a result, the southern pollen has the maximum possibility for pollination of the northern populations' female strobili. In this case the gene flow will be from the intermediate or late flowering trees of the south to the early flowering trees of the north according to the distance of pollen migration. Now the progenies of early flowering foreign pollen acceptor individuals of the northern population release male gametes, half of which are of foreign origin, within the population in the following generation. That means the early flowering individuals in a population usually receive the foreign male gametes and release the foreign gametes within the population in the following generation through their progenies.

In relation to the direction of gene flow within and between populations (or subpopulations) and its mechanism, a gene flow model is presented in Fig. 30.

The directional gene flow from the south to the north of Finland may have taken place in two ways: 1) occasional relatively long distance direct gene flow, 2) indirect gene flow through neighbor bridging populations.

Evidence of gene flow from the south to the north within Finland can be found in monoterpene studies (HILTUNEN 1976, HILTUNEN et al. 1975 a, b, and TIGERSTEDT et al. 1979). According to the authors, there is a clinal variation in the gene frequency of recessive low 3-carene allele (c) from a low value in the south to a high one in the north. Furthermore, there is a tendency of artificial plus tree selection for high 3-carene phenotype (CC or most probably Cc), which signifies strong influence of southern tree characteristics in northern Finland (TIGERSTEDT et al. 1979). The vigorous growth capacity of southern

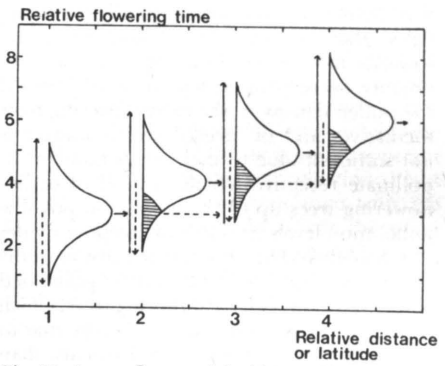

Fig. 30. A gene flow model within and between populations. Normal curve indicates the frequency distribution of flowering trees from the earliest to the latest and the shaded parts indicate the proportion of foreign pollen acceptors. Ordinate: Relative flowering time. Abscissa: Relative distance or latitude.

trees originated by gene flow may be favored for plus tree selection in the north. In considering the natural selection that favors the 3-carene recessive allele in the cold northern climatic conditions (TIGERSTEDT et al. 1979) the gene flow from the south to the north may be stronger than which can be seen in the evidence found in monoterpene studies. All evidence indicates that the directional gene flow from the south to the north of Finland is a strong and recurring event over long periods covering many generations.

However, there appears to be discontinuity of monoterpene content (particularly in 3-carene and pinene), though it is a cline as a whole from the south to the north in Finland, at 63°-64° N latitude. SARVAS (1969 and 1970 a) also reported that annual development of the reproductive cycle in Scots pine and Norway spruce does not strictly follow the local heat factor in the marginal and transitional zones of the species distribution range. The discontinuity may be due mainly to the interruption of effective gene flow in the transition area.

In case of introgressive species hybridization (particularly in the aneromophic species) in the regions where the species are sympatrically distributed, the gene flow will be from the early flowering species to the late flowering ones, just the same as found in this present study of Scots pine. The sequence of gene flow at the individual level between the two species will follow the same rule as mentioned before.

The pollination mechanism of anemophilous conifer species – that is a greater probalility of pollination is given to the pollen grains reaching the strobili from every wind direction and the pollination accomplished by the pollen successively reaching the receptive strobili at different times in accordance with the development of female strobili of an individual tree and the sequential directional gene flow within and between individuals and populations appear to be the fundamental and major force of recombining and releasing heterozygosity of the tree species (Answer for the question (4) in page 7). Upon these heterozygous population structures, various factors, such as heterozygote superority, density and/or frequency dependent selection etc. reinforce to maintain heterozygosity of the tree populations.

4.4. Practical implications of flowering characteristics of Scots pine in relation to seed orchards establishment

The major aim of north-south transfer of Scots pine plus tree clones for seed orchards establishment is to ensure the regular and normal seed development that usually cannot be achieved every year in the north due to harsh climate, as well as for the increase of flowering in the south (SARVAS 1970 a). There is no question that the north-south transfer of Scots pine clones would improve the conditions for successful seed development. The average percentages of filled seeds of northern Scots pine clones in north Finland were 11 % in the poor seed year of 1971 and 54 % in the good seed year of 1972, while the average percentage of filled seeds of northern Scots pine clones at Punkaharju (the same clone bank where this present observation was made) in southern Finland is 93 % for the seeds collected in 1976 (BHUMIBHAMON 1978). However, the percentages of filled seeds of early flowering clones (mostly northern clones) that developed from the flowering of 1976 and 1977 were 70 % and 80 % respectively (Tab. 15). These results indicate that the seed development was apparently favored by the north-south transfer. In this respect, the establishment of northern clone seed orchards south of the seed utilization area is quite reasonable. Abundant female flowering of northern Scots pine clones at a young graft age in the observation area (southern Finland) was observed, however, reports on direct comparison on the flowering of the same clones in the north and in the south are lacking.

One of the major problems of north-south transfer in the establishment of northern clone seed orchards is pollen contamination by the local populations of the same species in the transferred area. To estimate the cross-pollination between the local and the transferred populations, mating probabilities and the percentages of pollen contamination were calculated in the following way. Mating probabilities between the southern local population (the tree population of locality No. 22 is considered to be the southern local population) and the other populations were calculated on the basis of flowering obser-

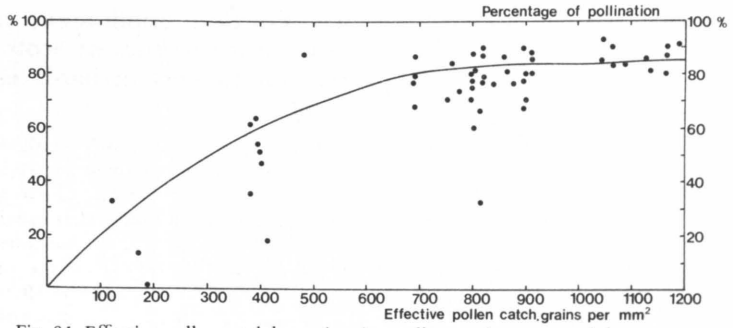

Fig. 31. Effective pollen catch by registering pollen catch meters and the percentages of pollinated micropylar cavities of the ovules. (Curve is drawn free-hand.)

vation in 1978 and on the data for the pollination of ovules in relation to effective pollen catch by the registering pollen catch meters (Fig. 31). In 1978, there were no signs of low-temperature stress that would delay the floral development during the flushing stage of female strobili. The calculations were made on the assumption that,

(1) an equal and evenly distributed number of clones from each pair of population groups (local population; locality No. 22 and one of the other populations) were planted in the south Finland where the climatic condition is similar to the flowering observation area in this study.

(2) the number of male gametes*[12] produced per clone is the same for all clones and the pollen dispersion within a clone is in proportion to 0.4, 1.0 and 0.7 one day before, on the maximum and one day after maximum male flowering one tree as a whole, respectively (the calculation of the ratios of pollen dispersion were based on the visual observation of male flowering and pollen catch in 1977, when the proportions of pollen catch one day before and after the maximum male flowering were distinct and easy to determine). The number of and the effective pollen catches are supposed equal to the average of the three-year observations.

(3) the number of female gametes produced per clone is the same.

(4) the probability of pollination follows (a) the "first come first served rule", and (b) the adopted values in Fig. 31 in relation to the effective pollen catch by the registering pollen catch meters.

Three factors were involved in the calculation of pollination of the different pollen sources (local and the transferred populations) on the recipient female flowers (transferred population);

(1) the proportion of female flowering (F) on each day (transferred clones).

(2) the proportions of pollen grains (G) shed and dispersed on each day in each locality group (local and transferred clones). (The male flowering of clones of which the male flowering was not recorded during the observation years due to poor or lack of male flowering, was estimated by the average difference of flowering intervals between female and male flowers. The average difference was 748 ± 280 p.u. (average of 48 clones)).

(3) the probability of pollination (P) by the amount of shed and dispersed pollen on each day from each locality group in relation to Fig 31.

The proportions of pollination by the different pollen sources on the recipient female strobili is the product of the three factors. If we use the abbreviations L. (with corresponding arabic numbers of the locality numbers) and S. for the transferred localities and southern local population (locality 22) respectively, we can formulate the probability of pollination on the first day of effective pollen shedding in the following ways.

*[12] Actually the number of gametes appear to be different depending on the origin and individual clones (BHUMIBHAMON 1978). However, the same number of male gametes were used in this calculation because specific data on those populations are lacking.

$$1LL_{11} = FL_1 \times GL_1 \times P_{11} \text{ and}$$

$$1LS_{11} = FL_1 \times GS_1 \times P_{11}$$

$1LL_{11}$ denotes the proportion of pollinated female strobili of transferred population locality No. 1 by the pollen grains of the same population on the first day of pollen shedding. (The arabic subscripts denote the dates or combinations of date.)

$1LS_{11}$ denotes the proportion of pollinated female strobili of transferred population locality No. 1 by the pollen grains of the local population S (locality No. 22) on the first day of pollen shedding from either or both of the local or transferred populations.

FL_1 denotes the proportion of female strobili of transferred clones having reached receptivity up to the first day of pollination (usually female strobili reach receptivity earlier than pollen shedding of the same tree or the same population in Scots pine).

GL_1 and GS_1 denote the proportion of pollen grains on the first day of pollination shed and dispersed from transferred (locality NO. 1) and southern local populations respectively.

P_{11} denotes the probability of pollination on the first day by the sum of pollen grains shed and dispersed from both local and transferred populations.

The next day, if the strobili were not pollinated up to the most probable upper limit of open pollination: 80--85 % (cf. Fig. 31), the rest of the unpollinated ovules will be pollinated by the pollen grains shed on the second day. Thus the proportion of pollination of the same strobili by the pollen grains of southern local population on the second day ($1LS_{12}$) will be:

$$1LS_{12} = FL_1 \times GS_2 \times P_{12}$$

($1LL_{12} \ldots 1LL_{13} \ldots$ that is the probability of pollination within the transferred population will not be formulated because the major interest in this study is the probability of cross-pollination between the transferred and local populations). Where GS_2 is the proportion of S (local) pollen grains on the second day of pollination, and P_{12} is the probability of pollination on the unpollinated ovules by the pollen grains on the second day of pollination.

In this way on the following third day and so forth until the same strobili will be successively pollinated up to the most possible upper limit of pollination. The calculation formulae for the proportion of pollination of the successive days are:

$$1LS_{13} = FL_1 \times GS_3 \times P_{13}$$

$$1LS_{14} = FL_1 \times GS_4 \times P_{14}$$

$$\vdots$$

$$1LS_{1m} = FL_1 \times GS_m \times P_{1m}$$

When FL_1 reaches the upper limit of pollination on the m^{th} day from the first day of pollination, the total proportion of pollination of the female strobili ($1LS_1$) will be:

$$1LS_1 = 1LS_{11} + 1LS_{12} + LS_{13} + \ldots 1LS_{1m}$$

The female strobili of transferred clones which flowered on the second day (FL_2) of effective pollen shedding will be pollinated by the same rule. Hence the proportions of pollination will be:

$$1LS_{22} = FL_2 \times GS_2 \times P_{22}$$

$$1LS_{23} = FL_2 \times GS_3 \times P_{23}$$

$$\vdots$$

$$1LS_{2n} = FL_2 \times GS_n \times P_{2n}$$

$1LS_{22}$ is the proportion of pollination on the first day of flowering of FL_2 (the second day of from the pollination of first flowered female strobili of the population) and P_{22} is the probability of pollination on that day. $1LS_{23} \ldots 1LS_{2n}$ and $P_{23} \ldots P_{2n}$ follow the same rule up to the maximum possible level of pollination of FL_2 reached on n^{th} day from the first pollination of FL_2. Thus:

$$1LS_2 = 1LS_{22} + 1LS_{23} + \ldots 1LS_{2n}$$

In the same way:

$$1LS_3 = 1LS_{33} + 1LS_{34} + \ldots + 1LS_{3q}$$

$$1LS_4 = 1LS_{44} + 1LS_{45} + \ldots + 1LS_{4r}$$

and so forth.

Then the total proportion of cross-pollination of the female strobili of locality 1 ($1LS_t$) will be:

$$1LS_t = 1LS_1 + 1LS_2 + \ldots + 1LS_e$$

($1LS_e$ is the proportion of cross-pollination of the last flowering female strobili.)

In this way, the proportion of cross-pollinations ($2LS_t$, $3LS_t \ldots 21LS_t$) between the southern local population (pollen source) and the transferred populations (female gamete sources, locality No. 2, 3, . . 21) were calculated and presented in Fig. 32.

The proportion of pollen contamination was also calculated in the same assumption and the same way as in the calculation of mating probability, but the seed orchards of transferred clones were considered to be surrounded by the southern local population (locality No. 22), and 54 % of pollen migration rate (SARVAS 1967 c) from the surrounding stand was adopted in this calculation (Fig. 32).

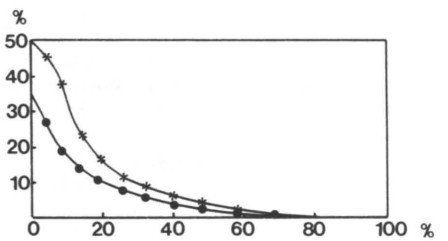

Fig. 32. Probability of cross-pollination between populations from different origins with different local temperature sums (upper line) and the percentage of pollen contamination of seed orchard when the rate of pollen migration from surrounding stand was assumed to be 54 % (lower line). The maximum probability of pollination between two populations is considered to be 0.5 when the difference in local temperature sums is zero, because, when the flowering time between the two populations is the same the female strobili of the transferred population will be pollinated equally by the pollen from the same population (50 %) and the southern local population (50 %). If a late flowering population is transferred to a place where the early flowering trees are common, the probability of cross-pollination of the female strobili of the transferred population by the local pollen will exceed 50 % because the local pollen will reach the receptive female strobili of transferred population earlier.

If we calculate the mating probability or the proportion of pollen contamination in the same way as above but use locality No. 16 (central clones) as the southerly located local population instead of locality No. 22 (southern clones) we expect approximately the same values as in Fig. 32, because the clones from this locality flower as late as most of the southern clones. Actually locality No. 16 is located in central Finland where most of the northern and central clone seed orchards are located. The calculated local temperature sum is 97 d.d. smaller than that of locality No. 22. The reason why the clones from this area flower late is not known yet. If we consider that 10 % of the pollen contamination of the produced seeds in a transferred seed orchard is permissible, the north-south transfer should be made to the extent of increasing, through the transfer, local temperature sums by about 20 % from that of clonal origin (Answer for the question (3) in page 7). However, the same goal can be achieved with smaller temperature sum differences between the clonal origin and the place to which the transfer is being made by choosing a place where the late flushing trees are common, as in locality No. 16.

SARVAS (1970 a) and KOSKI (1975) also estimated the probability of cross-pollination between the tree populations which have different active periods in terms of local temperature sums. Direct comparison between the values estimated by the above authors and that of in this study (Fig. 32) is difficult because of the differences in observation materials, places and calculation methods. However, the values in this study appear to be slightly higher than those estimated by the above authors.

The genetic consequences of reproductive isolation based on the reproductive adaptation to the local temperature factor appears to be very effective if the difference of local temperature sums (usually express in active period, cf. SARVAS 1967 a, 1970 a, 1972, 1974) made by the transfer exceeds approximately 30 % of the temperature sums of the clonal origin (Fig. 32). Judging from the results in this study, the responses for flowering in each clone or population, in relation to temperature factors of the origins in the observation area, shows clone or population specific characteristics which means a strong genetic control of flowering. The genetic determination of flowering appears to function through thresholds determined as a consequence of adaptation and natural selection in the developmental path of given environments.

However, it must be emphasized in connection with the physiological isolation (SARVAS 1970 a) that, in most cases, the isolating mechanism is not merely by the absolute difference in the time of female flowering in one population and male flowering of the other populations but by the differences in pollination time within and between populations because the receptivity of female strobili in one population (for example early flowering northern clones) usually lasts until the maximum male flowering of the other populations (for example late flowering southern clones). Therefore, in most cases, a complete reproductive isolation of one population of a species from others merely by the differences in flowering time through the transfer to one place is a rare event except between very early and very late flowering clones or populations unless,

(1) the time differences between female flowering of a population and male flowering of the other population is longer than the receptive period of the female strobili of the former population, or

(2) effective pollination up to the upper limit of open pollination is achieved within the population before the foreign pollen from the surrounding population reach the receptive female strobili of the population.

In any case, under natural Finnish climatic conditions complete elimination of background pollination in Scots pine seed orchards apperas to be difficult due to the reasons mentioned before. Moreover, ovules of the female strobili that become receptive one or two days later than the peak day of male flowering of the seed orchard cannot usually be pollinated up to the maximum level of open pollination by the seed orchard's pollen source and thus the remaining unpollinated ovules are subjected to background pollination. In this respect, to eliminate pollen contamination or selfing, clones for which flowering time deviates considerably from the population mean must not be included in a seed orchard. For the same reason, it is also recommendable to use the clones originating from a limited geographic area in establishing a seed orchard.

As mentioned before, the decisive factors affecting the pollination of Scots pine are the relative time of flowering between male and female and the receptive period, the quantity of pollen and the conditions of pollen vectors that would influence the pollen dispersion and the migration rates. The pollen contamination in a seed orchard is also affected in such a manner that the question is when, which and how much of the pollen first reaches the female strobili of the seed orchard as soon as they become receptive. Therefore, if the effective amount of pollen originated from the seed orchard itself has reached the receptive female strobili, the outside pollen reaching the orchard after that time will be ineffective in pollinating the female strobili that have already been pollinated to the upper limit of open pollination and the amount of pollen contamination will be minimal. However, if outside pollen reaches the receptive female strobili of the seed orchard before the effective amount of pollen from the seed orchard itself has reached the receptive strobili, the amount of pollen contamination will be increased in proportion to the increasing rate of the outside pollen until the upper limit of open pollination is achieved. In this respect, the difference in time and the quantity of male flowering between the seed orchard and the surrounding stands of the same species is an important factor determining the rate of pollen contamination as well as the time of female flowering.

Evidences from the observations on Scots pine flowering indicate that the proportion of pollen contamination can be eliminated to an acceptable level by the transfers of northern clones to warmer regions. If the transfer is made in combination with other isolating mechanisms and also with the elimination of the deviants in flowering, the proportion of pollen contamination will be considerably reduced. In clonal or provenance transfer for the establishment of seed orchards, special

attention should also be given to the extent of transfer in order not to cause risks such as abnormal flowering, the delay of floral development or frost damage by late spring frost and the synchronization of flowering of transferred trees with other tree species. In this study, the delay of floral development in northern clones by low-temperature stress due to long-distance transfer evidently hamper the physiological reporductive isolation between the transferred northern clones and the southern local populations. The calculated proportion of pollen contamination of northern clones in the south was 17 % in 1977 when the pollen migration rate was 60 % from outside of an imaginary seed orchard. Theoritically, if the floral development of the northern clones was not delayed in that year, the proportion of pollen contamination would have been 1 %. SARVAS (1970 a) reported that the pollination of northern Scots pine clones can be hampered by plugging the micropyle tubes of the Scots pine by the pollen of Norway spruce in southern Finland. Actually, the pollen shedding of neighbouring Norway spruce was partially overlapped with the receptive period of early flowering northern Scots pine clones in the observation area in 1976.

The seed development of northern clones in the south was clearly favored as mentioned at the beginning of this part of discussion. However, the efficiency of seed development of early flowering northern clones appeared to be much lower than that of the intermediate or late flowering central and southern clones in the south. Even though the early flowering northern clones had a larger number of fertile ovules (Tab. 13) the number of seeds produced per cone was not greater than for the other clones (Tab. 14) and they had lower percentages of filled seeds to fertile ovules or of filled to total seeds per cone than the other clones (Tab. 15). This fact can be interpreted as such that the pollination and seed setting in the early flowering northern clones was not in proportion to the number of fertile ovules while that of the central and southern clones was. The lower percentage of filled to total number of seeds per cone in the early flowering northern clones also indicates that there are some other factors that affect the seed development of northern clones after pollination and fertilization in the south. Genetic barriers may affect the seed development after cross-pollination between distantly related populations or species but no report concerning this matter is available for this study. (The female strobili of young northern clones in the observation area were usually pollinated by the pollen of the local population because the northern clones did not produce enough pollen to ensure good pollination within the clone bank by the time of flowering observation and seed collection).

Generally the seed development in 1977 was better than that of 1976 in spite of the fact that the quantity of male and female flowering was smaller in 1977 than in 1976. This fact also indicates that the weather conditions during the male and female flowering period is important for a good seed development. In 1976 the temperature was rather cool and there was frequent rainfall while in 1977, the weather was warm and fine during the major parts of the flowering periods. There are also indications that pollination is favored for the intermediate flowering clones (Tab. 15) whose female flowering usually best synchronizes with the peak of pollen shedding within the population as a whole. This fact indicates that synchronization of male and female flowering within a seed orchard is very important for good pollination and seed development even though the receptive periods of most female strobili last until the maximum pollen shedding within the population is reached, with the exception of the late flowering trees. Therefore, effective pollen shedding with high pollen density at the time of maximum receptivity of female strobili appears to be a prerequisit for a good pollination of the receptive ovules.

Conelet drop and the abortion of ovules due mainly to insufficient pollination (SARVAS 1962) and nutritional competition between the developing conelets and growing shoots (SWEET 1975, SWEET and BOLLMANN 1970) appears to account for the majority of the loss of seed productivity. SARVAS (1962) reported 20–30 % conelet drop in mature Scots pine stands. According to him the conelet drop in younger trees was 8–12 % less than that of mature ones. BHUMIBHAMON (1978) found that the percentages of female flower abscission decreased with tree age, which is contradictory to Sarvas' observation,

being 6.5 and 6.2 % for flowering in 1975 and 1976 respectively at a graft-age about 18 years in southern Finland. The corresponding female flower abscission values in younger trees were 25.8, 38.6 and 37.9 % for northern, central and southern clones respectively, in a clone bank located in southern Finland at a graft-age of about 8 years (BHUMIBHAMON 1978).

In this study during which the observation was made for 1978 flowering in the same clone bank used by BHUMIBHAMON (1978) the tendency of conelet abscission was reversed from that of BHUMIBHAMON'S observation being 33.2 %, 16.4 % and 17.1 % for early flowering northern clones, intermediate flowering central and southern clones and late flowering southern clones respectively. Here again, this fact clearly indicates that the synchronization of male and female flowering is very important for good pollination which can be followed by normal seed and conelet development. In 1978, the female strobili of early flowering northern clones reached receptivity approximately five days earlier than the peak day of pollen shedding in the observation area. Therefore, many of the northern clones' strobili are expected to be pollinated improperly or else might be pollinated at the end of the receptive period. In this respect, clone mixtures in a seed orchard originating from distinctly different climatic regimes may lead to a considerable reduction of potential seed yield due to improper pollination by the differences in flowering time. The great differences in flowering time between the clones within a seed orchard may form a low pollen density spreading over a relatively long, period, and thus cause a low probability of pollination of the receptive female strobili within the seed orchard. This may also cause a pollen contamination problem of the seed orchard.

5. SUMMARY

The flowering time and characteristics of cones and seed development of Scots pine plus tree clones originating from various parts of Finland and planted (grafts) in southern Finland (61° 48′ N, 29° 19′ E) were studied during 1976–1978.

The new year's floral development of the Scots pine clones appears to begin from late April to early May and reaches flowering in early to middle June, depending on the meteorological conditions before and during the new year's floral development. Temperature factor appears to paly a major role in the initiation of new year's floral development as well as the floral development itself. However, some other factors seem to be involved in the initiation of new year's floral development.

The development of female strobili from initiation to the flowering of the south-Finnish plus tree clones in the spring appeared to follow almost exactly the period unit scale (SARVAS 1972) under southern Finnish climatic conditions. However, the development of female strobili of northern and central clones seems to be disturbed by low-temperature stresses at the flushing stage in late May or early June in the years of late spring frost in south-Finnish climatic conditions and showed delayed flowering with larger p.u. sums for flowering than usual.

The flowering time (or p.u. sums for flowering) of those plus tree clones showed a wide range of variation between and within populations at the observation area (61° 48′ N, 29° 19′ E, 80 m a.s.l.) according to the origin of localities, where the selections were made. Generally the tree populations are adapted to the specific local climates (particularly to local temperature factor) in that the clones from colder regions with lower local temperature sums flower earlier or at lower p.u. sums than those from warmer regions with higher local temperature sums, in the observation area.

The estimated p.u. sums required from the initiation of new year's floral development through flowering of female strobili ranged approximately from 4900 to 5300. However, in some cases, the p.u. sum for flowering from the starting point increased from 4900 up to 5500 most probably due to the delay of floral development caused by low-temperature stresses at the time of strobili's most low-temperature sensitive developmental stages. The most low-temperature sensitive stage appeared to be around female flower developmental stage 2–1; the time of flower flushing out of its flower bud scales, when the estimated p.u. sum for floral development from the starting point reaches 3900–4200.

A long distance transfer from a colder to a warmer region may cause a delay of floral development in the years of late spring frost. Consequently, the effective physiological reproductive isolation of a provenance transfer from a colder to a warmer region may be hampered to a certain extent, if the transfer distance is too long to induce low-temperature stresses of the developing floral organs. This is because the delay of floral development caused by late spring frost will increase the risk of greater pollen contamination by the local pollen in the south.

The mechamism of physiological reproductive isolation by the north-south transfers of Scots pine clones does not appear to be merely by the absolute difference in female flowering time of the transferred and the male flowering time of the southern local populations but by the differences in pollination time within and between the populations. The receptive period of the northern clones' female strobili except for very early flowering northern clones usually last until the maximum male flowering of the southern clones but, in most cases, the strobili can be pollinated by the northern clones' pollen before the pollen of southerrn clones reach the receptive female strobili of the northern clones. When we consider that 10 % of pollen contamination is permissible, effective physiological reproductive isolation can be achieved within Finland if a transfer is made with increasing local temperature sums greater than 20 % of the temperature sums of the clonal origin, provided that the transfer does not cause a delay of floral development by late spring frost.

The northern clones had a larger number of total and potentially fertile ovuliferous scales per cone but did not produce a greater number of seeds than those of central or southern clones in southern Finland. However, the seed development of northern clones in the south was clearly more favored than in the north by the warmer weather conditions in the south.

The significance of tree's growth rhythm which is closely related to and attained through the adaptation and natural selection in the local climatic conditions was also discussed in connection with tree improvement and provenance transfers.

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SELOSTE:

MÄNNYN (PINUS SYLVESTRIS L.) KUKKIMISOMINAISUUKSISTA, ERITYISESTI KUKKIMISEN SOPEUTUMISESTA PAIKALLISEEN LÄMPÖ-ILMASTOON

Suomen eri osista peräisin olevien kantapuiden varteklooniен kukintaa seurattiin Metsäsntutkimuslaitoksen Punkaharjun (61°48′ N, 29°19′ E) kloonikokoelmassa kolmena eri kasvukautena.

Osoitettiin populaatioiden välisiä eroja kukinta-ajassa mitattuna p.u.-summana. Erot johtuivat etupäässä alkuperäpaikan lämpösummasta. Kukintojen, käpyjen ja siementen kehittyminen kevään ja kesän aikana osoittivat selvää riippuvuutta koepaikan lämpötilaan. Kehittyminen oli nopeaa ja tasaista korkean lämpötilan vallitessa.

Pohjois-Suomen siemenviljelysten perustaminen Keski- tai Etelä-Suomeen on pidettävä oikeutettuna paremman lämpö-ilmaston takia. Näin aikaansaadaan optimaalinen kukkiminen, hyvä siemenen kehitys sekä mahdollisimman täydellinen kukkimisfysiologiasta johtuva suvullinen eristys ympäröivistä männyn populaatioista.

Metsänjalostuksen tuloksellisuuden kannalta tarkastellaan eräitä kasvurytmihäiriöitä jotka johtuvat siemenviljelysten siirrosta pohjois-etelä suunnassa.

CHUNG, MIN-SUP O.D.C. 161.6+232.311.3
Pinus sylvestris

1981. Flowering characteristics of *Pinus sylvestris* L. with special emphasis on the reproductive adaptation to local temperature factor. – ACTA FORESTALIA Vol. 169:1–68. Helsinki.

The flowering time, characteristics of cones and seed development of Scots pine plus tree clones originating from various parts of Finland and planted in southern Finland (61° 48' N, 29° 19' E) were studied. The flowering time (in terms of period unit (p.u.) sums for flowering) of the Scots pine plus tree clones showed characteristics specific to each population and the characteristics appear mainly adapted to the local temperature factor within Finland. Generally, the development of floral organs, cones and seed in the spring and summer seasons also showed a temperature dependence in that the reproductive organs are developed rapidly and/or favorably under higher temperature conditions within its optimum range.
In this respect, establishment of northern Scots pine seed orchards in central or southern Finland for an optimum flowering, and a favorable seed development with an optimum physiological reproductive isolation from surrounding Scots pine populations can be justified. Problems arising from the north-south transfer of seed orchards and the significance of trees' growth rhythm are discussed in connection with tree improvement.

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