ACTA FORESTALIA FENNICA

201

GERMINATION CHARACTERISTICS OF AUTUMN COLLECTED PINUS SYLVESTRIS SEEDS

MÄNNYN SIEMENTEN ITÄMISTUNNUKSET SYYSKERÄYKSISSÄ

Markku Nygren

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Markku Nygren

Seloste

MÄNNYN SIEMENTEN ITÄMISTUNNUKSET SYYSKERÄYKSISSÄ

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XII of the University, Aleksanterinkatu 5, Helsinki, on 25 March 1988, at 12 noon

HELSINKI 1987

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Germination tests in varying photoperiod- and temperature-regimes showed that for early autumn collections, germination of Scots pine (*Pinus sylvestris* L.) seeds is delayed, especially at low incubation temperature (+10 °C) and in darkness. The presence of light during germination (8– or 24-hour photoperiod) or high incubation temperature (+20 °C) enhanced germination. As autumn proceeded, a greater proportion of seeds were able to germinate in darkness and also in low temperature regime. This result was consistent in both populations studied – in seeds from the natural stand (Hyytiälä, southern Finland) and in seeds from the Hyytiälä clone archive trees, growing in the same site.

An attempt was made to relate the development of germinability during autumn to previously accumulated chilling unit (optimum temperature +3.5 °C) sum. Germination percent variation in subsequent cone-collections could not, however, be explained with accumulated chilling.

Tutkimuksessa tarkastellaan syksyllä kerättyjen männyn (*Pinus sylvestris* L.) siementen itämistunnuksia. Erilaisissa lämpötila-päivänpituus-yhdistelmissä tehtyjen idätyskokeiden perusteella osoitetaan, että aikaisin syksyllä kerätyt siemenet itävät hitaasti sekä matalassa lämpötilassa (+10°C) että pimeässä. Korkeassa lämpötilassa (+20°C) ja pitkän päivän (8 ja 24 h) olosuhteissa itäminen sitävastoin on nopeata ja itämisprosentti korkea. Myöhemmin syksyllä siemenet itivät enenevässä määrin myös matalassa lämpötilassa ja pimeässä. Molemmissa tutkituissa populaatioissa (luonnonmetsikkö ja kloonikokoelma samalla paikalla) tulokset olivat tässä suhteessa samanlaisia.

Itäneiden siementen osuuden muutoksia syksyn aikana tarkasteltiin suhteessa kylmäkäsittelyindeksiin (optimilämpötila +3,5 °C); vaihteluita ei kuitenkaan onnistuttu kuvaamaan yksiselitteisesti em. tunnuksen avulla.

Key words: *Pinus sylvestris,* seed germination, seed maturation, seed dormancy, chilling requirement
ODC 174.7 *Pinus sylvestris* + 181.524 + 181.525

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PREFACE

This study was initiated in 1982, while the author was holding a grant from the Foundation for Research in Natural Resources in Finland for a research project on the autumn dormancy of Scots pine seeds. The present investigations were carried out in 1984–1986 in the Department of Silviculture and at the Forest Field Station of the University of Helsinki.

I am grateful to many who have contributed to the completion of the present study. The positive attitudes of Professor Matti Leikola and Dr. Pentti K. Räsänen, Associate Professor, towards my studies have been of great importance. I am indebted to acting Prof. Pertti Hari, Dr. Markku Kanninen, Prof. Seppo Kellomäki, Dr. Veikko Koski, Mr. Ahti Kotisaari, Lic. For., Dr. Juha Lappi, Prof. Olavi Luukkanen, Dr. Pauline Oker-Blom, Dr. Pasi Puttonen and Dr. Heikki Smolander, as well, for their support and assistance during various stages of the study.

I wish to thank the staff at the Department of Silviculture and at the Forest Field Station of the University of Helsinki and at the tree-breeding stations at Ruotsinkylä and Punkaharju in the Finnish Forest Research Institute for many kinds of assistance. Most of all, I would like to thank Ms. Pirkko Heimo for skilful technical assistance throughout the study.

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Finally, I would like to thank my wife Leena, and children Tuomas, Matti, Maija and Minna, for being so patient and understanding.

Helsinki, December 1987

Markku Nygren

1. INTRODUCTION

1.1. Scots pine seed development and maturation

Scots pine (*Pinus sylvestris* L.) possesses a three-year reproductive cycle typical of most species of *Pinus*. During the growing season of the first year of the cycle, the reproductive buds are initiated. Anthesis occurs in the spring of the second year. Following anthesis, the pollen tube development is initiated, but it stops and the ovule overwinters in a dormant condition. After overwintering, the development resumes the following spring, when the growth of the pollen tube continues, and the fertilization takes place approximately 13 months after pollination. In southern Finland, for example, the time for syngamy is usually in the beginning of July (Sarvas 1962).

Development of the fertilized ovule is rapid. Typically, the megagametophyte usually has reached its ultimate size at the time of syngamy (Sarvas 1962). Within two weeks from fertilization, a corrosion cavity is formed by a breakdown of cells in the central portion of the megagametophyte and the growing embryo is pushed into this cavity by elongating suspensor cells (Sarvas 1962). This increase in embryo-size is accompanied by accumulation of reserve material – mainly proteins and lipids – both in the embryo and in the megagametophyte. Seeds mature during autumn, approximately ten weeks after fertilization, overwinter in cones and are shed the following spring. Thus, in cool and temperate climate the time from the initiation of reproductive buds to seed maturation is approximately 27 months.

Seed anatomy in all conifers is rather uniform as the relationship between embryo and megagametophyte is more or less constant in a well developed seed (Simak 1980). Accordingly, the size of the embryo in relation to the size of the embryo cavity is used as an expression of seeds' *anatomical maturity*.

The dominant role of temperature regime in determining the anatomical maturation of Scots pine seeds has been well documented in a number of studies since early 1900s. Hagem (1917) and Eide (1932) in Norway, Wibeck (1928) in Sweden and Heikinheimo (1921) and Kujala (1927) in Finland were all able to demonstrate that seeds matured during warm summers had well developed embryos and thus, were anatomically mature. On the contrary, seeds from harsh climatic conditions, for example, in northern Scandinavia were frequently anatomically immature with poorly developed embryos.

Temperature requirements for anatomical seed maturation have been expressed using monthly mean temperatures of June-August or June-September, i.e. the approximate time from fertilization to seed maturation. Kohh (1968), for example, suggested that in Scandinavian conditions a mean temperature of 11.8 °C in June-August or 10.8 °C in June-September is required for anatomical seed maturation. In addition, the timing of anatomical maturation has been related to previously accumulated day-degrees above a threshold temperature (thermal time) during the year of maturation (Mork 1957, Bergman 1960, 1976, Sarvas 1970, Simak 1973, Alfjorden and Remröd 1975, Henttonen et al. 1986).

Sarvas (1967, 1970) suggested that over the main part of the natural range of Scots pine, the temperature sum required for anatomical seed maturation (half of the seeds of a given population having an embryo occupying at least 3/4 of the length of the embryo cavity) is 77 % of the local average annual value. He emphasized, however, that this holds true only for subpopulations that have adapted to the local climate, and that many marginal stands, such as those near the polar timber line, do not meet this condition.

Besides anatomical maturation, conifer seeds exhibit *biochemical* (Rediske 1961) or *physiological* (Edwards 1980) maturation. These are general terms referring to biochemical changes in the reserves of both embryo and megagametophyte during late embryogeny, the most important being the change from mobile to storage forms of reserves (Rediske 1961, Ching and Ching 1962, Jensen et al. 1967, Kardell et al. 1973, Skre and Gjels-

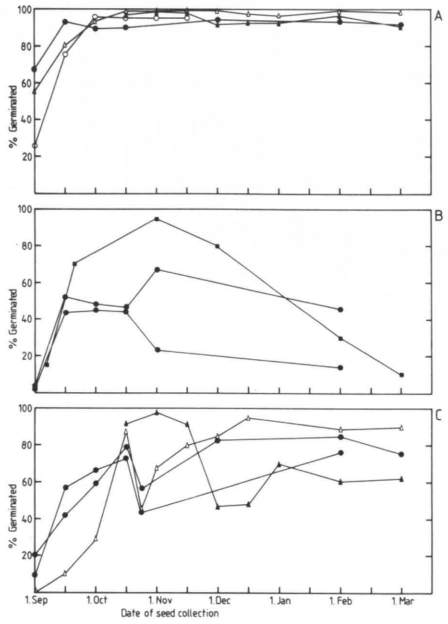

Figure 1. Three types of germination development patterns of Scots pine seeds during autumn and winter. Data from Blomqvist 1972 (▲), Remröd and Alfjorden 1973 (○), Kardell 1973a, b and 1976 (●), Blomqvist 1975 (△) and Alfjorden 1976 (■). See text.

vik 1980). Other processes generally related to physiological maturation are seed dehydration and the decline in respiratory activity (Ching and Ching 1962), as well as changes in the levels of endogenous hormones in maturing seeds (Krugman 1967).

Physiological and biochemical activity within the seed continues after the organic accumulation is complete and the embryo is fully elongated. Håkansson (1956), for example, found mitotic activity and formation of starch in Scots pine embryos in late October in seed samples collected from southern Sweden. In this case the seeds were anatomically fully mature in the middle of August.

A seed's ability to germinate is determined largely by its degree of maturity. Anatomically or physiologically immature seeds germinate slowly even in favourable conditions. Thus, effective forest tree seed procurement requires cone collections at the time of seed maturation.

Contradictory results have been obtained when Scots pine seed germinability has been studied during the late stages of maturation in autumn and winter (Figure 1). A strong year-to-year variation exists in this respect, and at least three patterns of germination can be distinguished:

Type A: Germination percentage reaches the maximum level early in the autumn and remains about the same until the time of seed dispersal the following spring.

Type B: Germination percentage is poor in general, the highest values being attained during late autumn. A decline in germinability then occurs, and very low values are found at the time of seed dispersal.

Type C: Germination percentage increases steadily during autumn. This phase is followed by a temporary decline, and then a relatively high level of germinability is again attained which is maintained until the time of seed dispersal.

For interpretation of these results, an aspect as important as the degree of maturity is the seeds' germination process *per se* and the possible role of seed dormancy.

1.2. Seed germination and dormancy

Kermode et al. (1986) point out that the major metabolic events associated with seed development are distinctly different from those of seed germination. The former is characterized by reserve deposition and reduced metabolism as the seed matures and desiccates. In the latter process the reverse occurs – renewed metabolism and reserve breakdown.

Germination *sensu stricto* refers to a series of processes which begin with water uptake in the dry seed and terminate with the emergence of the radicle or the hypocotyl through the seed coverings (Bewley and Black 1986, Come and Thevenot 1982) . Accordingly, events subsequent to this phase are associated with seedling growth. Thus, mobilization of food reserves from the

megagametophyte or from the cotyledons is not strictly a component of germination. It is worth noting that at the time of the emergence of a radicle from a germinating Scots pine seed the bulk of the reserves in the megagametophyte is still non-hydrolysed; cells in the megagametophyte do not begin to supply nutrients for the growing embryo until it has used up the bulk of its own protein reserves (Simola 1974a, b).

For each individual seed, germination is an all-or-nothing event: the seed either germinates or does not. The rate of the germination process for each individual seed is the reciprocal of the time required from sowing to radicle emergence. The rate can also be defined for a seed population as the number of seeds germinating per unit of time. To distinguish between these two rate-concepts, the *rate of germination process* is applied to the individual seed, and the *rate of germination* to the seed population. Other germination characteristics for a seed population are the cumulative distribution function of rate of germination, referred to as *cumulative germination* and visualized by *germination curve* in this study, and the *germination percentage*, a point chosen from the germination curve at a specific time (21 days for Scots pine seeds, International Rules for . . .1985) after the initiation of a germination test (Figure 2).

The rate of germination process varies between individual seeds within a population; seeds germinate at different times. This variation may be due either to genetic differences between individual seeds or to differences in other seed inherent properties such as degree of maturity or of dormancy.

Seed dormancy is a state of inhibited and/or suspended growth, that is, the failure of seeds to germinate even when placed under favourable conditions (Amen 1968). Ross (1984) considers seed dormancy as a time of suspended growth during which physiological development and differentiation can still occur. Dormant seeds must be distinguished from *quiescent* ones; the latter term refers to a phase of arrest or retardation of metabolism and growth due to unfavorable environmental conditions such as lack of water, of oxygen supply or of suitable temperature.

The factors causing seed dormancy and the conditions which break it are extremely diverse (Nikolaeva 1969). In general, the

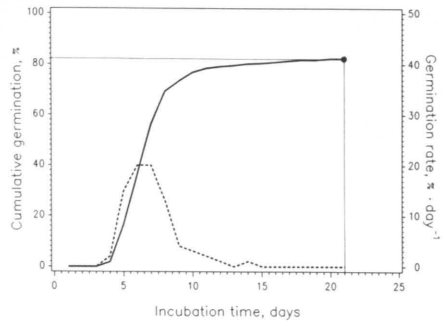

Figure 2. Curves of cumulative germination (solid line) and rate of germination (dotted line) for hypothetical seed population as function of incubation time. Germination percentage (●) measured after 21 days of incubation. See text.

causes of seed dormancy fall into five classes (Amen 1968):

(1) anatomical immaturity (rudimentary embryos)
(2) physiological immaturity (inactive enzyme systems)
(3) mechanically resistant seed coats
(4) impermeable seed coats
(5) presence of germination inhibitors

Nikolaeva (1969) distinguished between two main seed dormancy types: (1) *exogenous dormancy*, in which the properties of the outer coverings of the embryos (pericarp or seed coat) cause dormancy, and (2) *endogenous dormancy*, in which properties of the embryo or endosperm (megagametophyte) cause the dormant condition. In this classification the anatomical immaturity is referred to as morphological dormancy and is included in the endogenous dormancy type. Another type of endogenous dormancy is the physiological dormancy, which may be shallow, intermediate or deep (Nikolaeva 1969).

Following the classification of Nikolaeva (1969) described above, it may be stated that anatomically immature Scots pine seeds are morphologically dormant. Evidence also exists that anatomically mature Scots pine seeds collected in the autumn, prior to natural seed fall, sometimes exhibit physiological immaturity or dormancy with a low rate of germination process (Håkansson 1956, Simak

1966, Kardell 1973a,b, Remröd and Alfjorden 1973).

In order to break morphological dormancy, certain conditions for the completion of anatomical embryo development are needed. According to Nikolaeva (1969) the embryos of most plants of moderate climates complete their development most successfully at the relatively high temperature of +15–30 °C under moist conditions.

A number of studies have been made with Scots pine seeds, especially from northern latitudes, in which embryo development was enhanced by storage of cones at temperatures above +10 °C (Nordström 1950, 1955, Edlund 1959, Simak and Gustafsson 1959, Asplund et al. 1973). Results from these studies indicate that embryos may develop anatomically after harvest at high temperature; Simak and Gustafsson (1959), however, pointed out that storage of early harvested cones is not always beneficial to seeds. In their study, one month's storage of cones at +24 °C suppressed embryo development, while another storage treatment at +4 °C had no such effect.

Physiological dormancy, in turn, is broken by prolonged exposure of hydrated seeds to low (0 – +10 °C) temperature (chilling or stratification), storage of dry seeds in cold (after-ripening), or the presence of light during germination (Bewley and Black 1980). Accordingly, the storage of Scots pine seeds at the latter temperatures has also been studied (Stefansson 1951, Edlund 1959, Simak 1966, Blomqvist 1972, 1975, Kardell 1973, 1974, Remröd and Alfjorden 1973, Alfjorden 1976, Nygren 1986a, b). Generally, storage of cones at low temperatures has been more beneficial than storage at high temperature. Both anatomical embryo development and an increase in germinability have been observed (see Kardell 1974, for example).

Sarvas (1964) suggested that autumn-collacted Scots pine seeds require low temperature treatment for rapid and complete germination. In his simulation model for the entire annual cycle of development for cool- and temperate-zone tree-species he quantified the chilling requirement for the breakage of autumn dormancy (Sarvas 1974). In his model, the effective chilling temperatures range from –3.5 °C to +10.5 °C, and the dependence of the rate of development is modelled by a

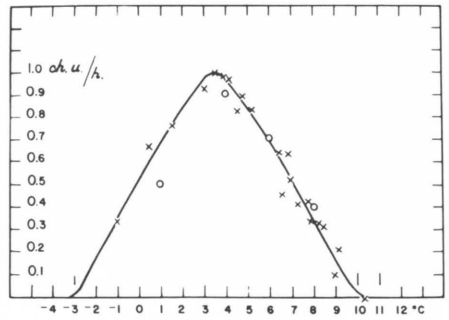

Figure 3. Regression of the rate of progress (chilling unit/h) of autumn dormancy on temperature (Sarvas 1974). Crosses refer to experiments with *Betula pubescens* Ehrh. 'seeds' (catkins) and circles to seedlings of the same species.

convex function, with a maximum value at +3.5 °C. (Figure 3). A same kind of seed stratification requirement model for a number of deciduous fruit-tree species was presented by Seeley and Damavandy (1985). In Sarvas' model the physiological time is measured by the integrated chilling unit sum – one hour at +3.5 °C equals one chilling unit. Each genotype has a specific value for the chilling unit sum at which its dormancy is broken. For Scots pine seeds of Rovaniemi origin (approximately 66°12' N, 26°00' S) Sarvas (1973) reported the chilling requirement to be approximately 60 chilling units.

The concept of the chilling requirement for seeds is complicated considerably by the fact that the requirement for chilling or stratification can be replaced by a long photoperiod during germination (Black and Wareing 1955, Asakawa 1959, Toole, 1973). Usually, with an increased period of chilling or stratification, germination in darkness increases. This has been documented for a number of conifers (Stearns and Olson 1958, Toole et al. 1961, 1962, Hatano and Asakawa 1964, Edwards and Olsen 1973, Farmer et al. 1984, Adkins et al. 1984), including Scots pine (Eliason and Heit 1941, Nordström 1955, Nyman 1963). According to Nordström (1955) prematurely collected Scots pine seeds are particularly light-dependent in their germination; Blomqvist (1972) has stated that

"germination tests in darkness have given a more dependable measurement of the degree of ripeness than testing the seed in light."

1.3. The approach and aim of the study

The features described above underline those factors which affect germination, not all of which are of immediate environmental origin. Some of them, such as the maturation process, are of historic significance, i.e. the ontogenetic processes leading up to the present state of the seed.

In the present study, it is hypothesized, that (1) as Scots pine seeds mature during autumn their physiological condition changes, and (2) this change is reflected in their ability to germinate in different environments. A third hypothesis is that the main variable responsible for this change is the seeds' exposure to chilling temperatures during the autumn, while still in cones.

Accordingly, the aim of this study is to analyse the germination characteristics of autumn-collected Scots pine seeds under different light and temperature regimes, and to monitor the changes that occur in germination characteristics during seed maturation. In addition, the effect of pre-harvest chilling temperatures on germinability is evaluated and an attempt is made to develop a method to predict germination percentage for autumn-collected seeds with integrated chilling unit sum.

2. MATERIAL AND METHODS

Three separate experiments were carried out during the study, one in 1984 and two in 1986. Scots pine seeds were collected from a natural stand and a clone archive, both adjacent to the Forestry Field Station of the University of Helsinki in Hyytiälä, southern Finland. Cone-collections were made at various intervals during autumn and early winter, and germinability was measured under varying photoperiod- and temperature-regimes. During seed development and maturation, temperature data were recorded at the Hyytiälä weather station. The three germination experiments will be described first.

2.1. Germination experiments

Experiment 1

For the analysis of the effects of the date of cone collection and of germination conditions on germination characteristics, Scots pine seeds were collected during the period September-December 1984 from a natural, 25-year-old stand near the Forestry Field Station of the University of Helsinki in southern Finland (61°51 N, 24°20 E, 170 m a.s.l.). This experimental stand is located on a low fertility soil of *Vaccinium*-site type (Cajander 1949). The density of the stand was approximately 2200 stems/ha and the average height 9.7±0.3 m (±s.e. mean). The collection dates were: September 2, 17, October 5, 26, November 15, and December 13.

A total of 100 trees were chosen from the stand and numbered. Among these, eight sample trees were chosen on each collection, and a total of 144 cones, 18 from each sample tree, were collected on each date. An attempt was made to choose the sample trees randomly, but due to a sparse cone crop on most of the trees, this was not possible.

On each collection, the sample material was divided into 6 sublots of 24 cones. The seeds were extracted immediately in a ventilated oven at 35°C for 72 hours. Seed-extraction, hand-dewinging, seed-count, and seed-weighing (accuracy of 10^{-4} g) were done on an individual-cone basis. Due to varying numbers of seeds per cone the number of full seeds (excluding empty and damaged seeds) in each sublot varied from 363 to 588.

Each sublot was randomly allocated for germination test in six cabinets. These were placed in a cold room (+4.5±1 °C), and the temperature inside each cabinet was thermostatically controlled at an accuracy of ±1 °C. The experimental design included six permutations of temperature regimes (+10±1 °C and +20±1 °C) and photoperiods (24/0 h, 8/16 h, and 0/24 h light regimes). A cool-white 8-W fluorescent tube was placed inside each cabinet; this provided an illumination of approximately 3000 lx (approximately 47 μE m^{-2} s^{-1}) at seed level. According to the manufacturer, the spectral energy distribution of the light-source equals that of direct sunlight.

Seeds from each individual tree were kept separate in the test. They were germinated in covered Petri dishes on filter paper disks which were kept wet by wicks carrying water from a reservoir below. The temperature inside each cabinet was monitored by a multipoint recorder throughout the germination tests. Due to limited space in cabinets, the incubation time was 21 days.

Experiment 2

In the fall of 1986, in order to analyse the effect of increased chilling on the development of germination percentage, I initiated an experiment somewhat similar to that described above.

Due to the very sparse cone crop in natural stand in 1986, pine seeds were collected from open-pollinated 15-year old grafts at the clone archive of the Forestry Field Station. This clone collection is located on an abandoned field (150 m a.s.l.) and includes a total of 54 grafts representing clones from both northern and southern Finland (Table 1).

Table 1. The grafts and their origin in the Hyytiälä clone archive (Plus tree data from Oskarsson, 1972).

Plus tree no.	Commune	Location Latitude	Location Longitude	Number of grafts
P 244	Pello,	67° 00′ N,	24° 10′ E	12
P 4905	Pelkosenniemi,	67° 12′ N,	27° 52′ S	4
P 5860	Sodankylä,	67° 21′ N,	27° 03′ S	4
P 5864	Kittilä,	67° 17′ N,	24° 55′ S	4
P 5880	Kittilä,	67° 17′ N,	24° 55′ S	4
K 386	Saarijärvi,	62° 35′ N,	25° 20′ S	4
K 917	Jäppilä,	62° 26′ N,	27° 32′ S	4
K 1580	Lohtaja,	64° 01′ N,	23° 29′ S	3
K 1613	Kärsämäki,	63° 55′ N,	25° 40′ S	4
E 88	Sysmä,	61° 20′ N,	25° 47′ S	3
E 2561	Lammi,	61° 15′ N,	25° 00′ S	4
E 2565	Lammi,	61° 15′ N,	25° 00′ S	4

Cone collections were made at three- to four-day intervals during August and September 1986, the first collection date being 29 August. Two cones were picked from each graft on each date. Prior to seed-extraction, a sample of 5 × 50 seeds was taken by the cutting of fresh cones in order to determine seed water-content. This was done on a fresh weight basis by weighing the samples before and after drying for 16 hours at +85 °C.

Seed extraction conditions were similar to those in experiment 1 except that seeds from individual clones or grafts were not kept separate. In each collection, after the extraction and hand de-winging, the total amount of seeds was divided into four sub-lots of 200 seeds using a 'soil-divider' for complete randomization. Germination conditions for these sublots were: at +20±1 °C both in dark and in continuous light; incubation time, 21 days.

Experiment 3

An extended incubation time of 50 days was used in this experiment in order to analyse the rate of germination beyond the routinely applied 21 days for Scots pine seeds (International Rules for Seed . . . 1985).
A sample of fifteen cones from ten trees was picked from the same stand as in experiment 1 on 16 October 1986. Seed extraction and de-winging were done in a manner similar to that in experiment 2; seeds from individual trees were not kept apart in the analysis. Four sub-lots of 200 seeds were randomly partitioned, and the following treatments were used in the germination tests:

- +10 ±1 °C, continuous light, incubated for 50 days
- +10 ±1 °C, darkness, "
- +20 ±1 °C, continuous light, incubated for 50 days
- +20 ±1 °C, darkness, "

In all three experiments, the germination was counted for each day after imbibition began, and the seeds were recorded as germinants if the primary root and hypocotyl together exceeded 5 mm in length. For seeds germinated in the dark, germination counts were carried out under a green safe light generally known not to affect germination (Mayer and Poljakoff-Mayber 1982, Adkins et al. 1984). After 21 test days (50 days in experiment 3), the percentage of empty and viable seeds among those ungerminated was determined by a cutting test. The germination characteristics studied are based on the number of full seeds in the germination test.

Further, in each experiment a sample of 100 or 200 seeds was taken from each sample representing different collection dates, for measuring anatomical maturity. This was done by X-raying the samples in the Ruotsinkylä and Punkaharju experiment stations of the Finnish Forest Research Institute and determining the number of seeds in a sample representing particular embryo-class. The classification of the seeds (cf. Ryynänen 1973) was as follows:

I Endosperm and embryo cavity developed but no embryo observed.
II Embryo occupying less than 10 % of the length of the embryo cavity.
III Embryo occupying 10 . . . 65 % of the length of the embryo cavity.
IV Embryo occupying more than 65 % of the length of the embryo cavity.

2.2. Temperature regime during seed development and maturation

The temperature regime during the 1984 and 1986 experiments was monitored by means of temperature data from the Hyytiälä weather station. This station is located ap-

proximately 100 meters south of the experimental stand and approximately 400 meters east of the Hyytiälä clone archive. The altitude of the weather station is 170 m a.s.l.; it is thus located approximately 20 meters higher than is the clone archive.

Air temperatures at the height of three meters are automatically recorded at two-minute intervals at the weather station. From these values, mean day temperature and mean hourly temperatures were calculated using the programs available at the Forest Field Station. The mean day temperatures were used in estimating the cumulative degree-day values (thermal time) from 1 January to the date of each cone collection. This was calculated as:

$$\text{Degree days} = \sum_{m=1}^{n} (t_m - 5) \quad (1)$$

where base temperature is +5 °C, n is the total number of days with a mean temperature greater than +5 °C, and t_m is the daily mean temperature on those days, taken as an arithmetic mean of hourly mean temperatures.

In addition, the cumulative chilling unit sum was calculated from temperature data utilizing a procedure similar to that of Sarvas (1973, 1974). Chilling unit sum integration was begun when the degree day value reached 950 degree-days. This value corresponds to the point in time when approximately 50 % of the Scots pine seeds are anatomically mature (embryo occupying at least 3/4 of the length of the embryo cavity) (Henttonen et al. 1986).

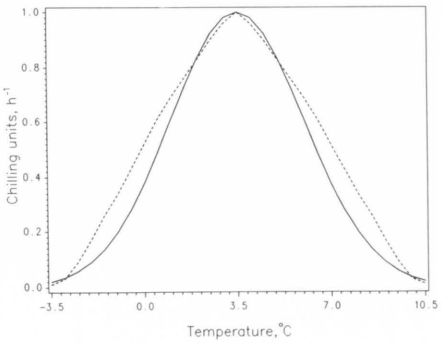

Figure 4. Function for integrating chilling unit sum (solid line) and that used by Sarvas (1974) (dotted line).

The type of convex function applied was the same as that used by Sarvas (1974) (Figure 4):

$$\text{Chilling units} = \sum_{i=1}^{j} \exp\{-0.5\,[(t_i - 3.5)/2.5066]^2\} \quad (2)$$

where +3.5 °C is the base temperature at which the function is at its maximum, j is the total number of hours from the beginning of the integration to the time of last cone collection and t_i is the hourly mean temperature.

In addition, in both years daily minimum temperatures (Figure 5) were examined during embryogeny in order to examine the possible effects of summer and autumn frosts on seed development (cf. Kardell 1976, Simak 1972).

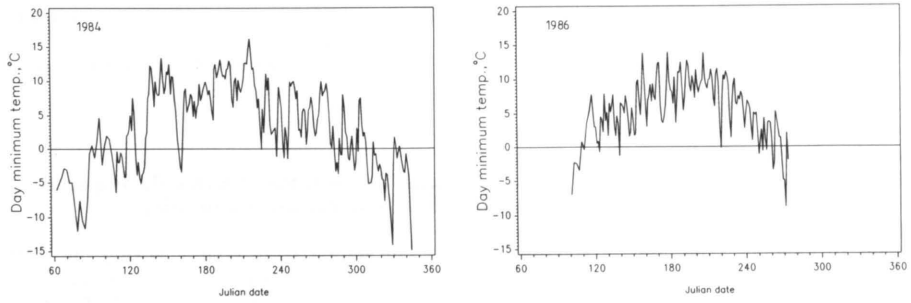

Figure 5. Daily minimum temperatures in Hyytiälä in 1984 and 1986 during this study.

Mean monthly temperature data from May to October during 1984 and 1986 are given in Table 2. Summarized data for the three experiments are given in Table 3.

Table 2. Mean monthly temperature in Hyytiälä, May – October 1984 and 1986. Average values for 1931–1980 are estimated by the method of Ojansuu and Henttonen (1983).

	Monthly mean temperature, °C					
	May	Jun	Jul	Aug	Sep	Oct
Year 1984	12.4	11.9	14.2	12.6	7.8	4.9
Year 1986	9.7	15.1	14.8	11.1	4.8	4.4
Average 1931–80	9.0	13.7	16.8	14.7	9.4	3.8

2.3. Analyses of germination data

Cumulative germination

Cumulative germination was analysed by plotting the cumulative frequency distribution of germinated seeds (in relation to all viable seeds) against incubation time. These germination curves for different treatment combinations were then visually inspected.

Germination percentage

Germination percentage was measured as the frequency of seeds that germinated of all viable (excluding empty and damaged seeds) seeds under given test conditions in 21 days (50 days in experiment 3.).

The effect of cone-collection date and of germination conditions on germination percentage was analysed utilizing log-linear

Table 3. Data from germination experiments.

Experiment no.	Cone collection date	Julian days	Temperature sum, degree days	Chilling unit sum	Seed weight, mg	Germination conditions
Experiment 1.	Sep. 2.	246	995.1	73.9	4.3	+10 °C and
Year 1984,	Sep.17.	261	1055.5	164.8	3.9	+20 °C with
Hyytiälä,	Oct. 5.	279	1109.1	356.8	4.0	0, 8 and 24
natural	Oct.26.	300	1116.7	614.9	4.3	hour photoperiod,
stand	Nov.15.	320	1124.9	838.0	4.1	incubation
	Dec.13.	348	1124.9	988.7	3.9	time 21 days
Experiment 2.	Aug. 29.	241	953.8	10.2	6.9	+20 °C
Year 1986	Sep. 2.	245	960.0	57.2	7.3	with 0 and
Hyytiälä	Sep. 5.	248	968.9	66.9	6.4	24 hour
clone	Sep. 9.	252	972.5	112.1	6.4	photoperiod,
archive	Sep.12.	255	975.6	150.4	6.9	incubation
	Sep.16.	259	978.5	219.4	6.5	time 21 days
	Sep.19.	262	978.5	261.5	6.0	
	Sep.23.	266	980.8	328.6	7.0	
	Sep.26.	269	980.8	373.3	6.8	
	Sep.30.	273	981.9	428.1	6.8	
Experiment 3. Year 1986 Hyytiälä natural stand	Oct.16.	289	992.9	634.4	..[1]	+10 °C and +20 °C with 0 and 24 hour photoperiod, incubation time 50 days

[1] Not measured.

model (Sokal and Rohlf 1981, Dobson 1983, Fienberg 1985). Only the material from experiment 1 was used in this analysis. Since there were large differences in germination percentage between individual trees, the analyses were based on separate seed material from three sample trees. Two of these sample trees (No. 9 and No. 26) were represented in all but first and last collections in 1984. The third one, tree No. 100 was represented in the last three collections in 1984.

The frequencies of germinated and non-germinated but viable seeds after incubation produced a multiway frequency table according to following categorical variables:

Explanatory variable *1;* Cone collection date

(*i* = *1*)	Sep. 17.	Trees No. 9 and 26
(*i* = *2*)	Oct. 5.	
(*i* = *3*)	Oct. 26.	
(*i* = *4*)	Nov. 15.	
(*i* = *5*)	Dec. 13.	Tree No 100

Explanatory variable *2;* Photoperiod during germination test

(*j* = *1*) 0 hour photoperiod
(*j* = *2*) 8 hours photoperiod
(*j* = *3*) 24 hours photoperiod

Explanatory variable *3;* Temperature during germination test

(*k* = *1*) 10 ± 1°C
(*k* = *2*) 20 ± 1°C

Response variable *4;* State of a seed after incubation

(*l* = *1*) germinated
(*l* = *2*) ungerminated

The log-linear model represents the logarithm of the expected cell frequency in a table as a linear combination of either the main effects or the interactions in a manner similar to the analysis of variance model.

For a four-way contingency table we may write the simplest model corresponding to the complete independence of all four variables as the logarithm of the expected cell frequencies:

$$\ln \hat{f}_{ijkl} = u + u_{1(i)} + u_{2(j)} + u_{3(k)} + u_{4(l)} \quad (3)$$

where $\hat{f}_{ijkl}$ is the expected frequency for the (i,j,k,l) cell in the table, u is the mean of the logarithms of the expected frequencies, and $u_{1(i)} + u_{2(j)} + u_{3(k)} + u_{4(l)}$ are the effects of categories i,j,k and l of factors *1,2,3* and *4*.

Since it is likely that there is an association between the four variables in the table, one has to analyse log-linear models that include two-factor and higher-order interaction terms.

The association between the explanatory variables and the response variable is analysed as follows: a hierarchy of models is tested, starting with a model that includes all possible interaction terms. For a four-way table this is:

$$\ln \hat{f}_{ijkl} = u + u_{1(i)} + u_{2(j)} + u_{3(k)} + u_{4(l)} + u_{12(ij)} + u_{13(ik)} + u_{23(jk)} + u_{14(il)} + u_{24(jl)} + u_{34(kl)} + u_{123(ijk)} + u_{124(ijl)} + u_{134(ikl)} + u_{234(jkl)} + u_{1234(ijkl)} \quad (4)$$

The model above is referred to as saturated, since it contains all possible effects. By setting certain effect to zero, a different model is formed. Thus, when comparing two different log-linear models, one model is a special case of the second.

The goodness-of-fit of a model is checked using either of the following statistics (Fienberg 1985):

$$X^2 = \Sigma \frac{(\text{Observed frequency} - \text{Expected frequency})^2}{\text{Expected frequency}} \quad (5)$$

or

$$G^2 = 2 \Sigma \text{ Obs. freq. } \ln \left(\frac{\text{Obs. freq.}}{\text{Exp. freq.}} \right) \quad (6)$$

where the summation in both cases is over all cells in the table. If the model fitted is correct and the total sample size is large, both X^2 and G^2 have approximate χ^2 distributions with degrees of freedom given by the formula:

$$\text{d.f.} = \text{no. of cells in the table} - \text{no. of parameters fitted} \quad (7)$$

When comparing the goodness-of-fit between two models and choosing the appropriate one, the likelihood ratio G^2-statistic for goodness of fit is computed for both models, and the difference between the G^2-values is used to test whether the difference between the expected values for the two models is simply due to random variation. The difference between the G^2-values also has an asymptotic chi-square distribution, with degrees of freedom equal to the difference in the degrees of freedom for the two models (Fienberg 1985), and it is used as a test statistic in model selection.

Three points should be noted here. First, the structure of the model is hierarchical, i.e. whenever an interaction term is included in the model, all lower order interaction terms involving variables in the higher order term are included (cf. Fienberg 1985). For example, if $u_{234(jkl)}$ is included in a model, the terms $u_{23(jk)}$, $u_{24(jl)}$ and $u_{34(kl)}$ are also included.

Secondly, in a factorial experiment like this, only factor *4* (germinated, not germinated) is random; other factors are fixed by the design of the experiment. In this case, we can only test the presence of those terms in the model which include factor $u_{4(l)}$. The effect of $u_{24(jk)}$, for example, cannot be tested, because it is under the investigator's control (Sokal and Rohlf 1981) and is included automatically in the model. Thirdly, when the response variable has only two levels, as in this study, we actually analyse one probability, (germinated, $l = 1$) in the table.

The G^2-value indicates an overall goodness-of-fit of a model. In addition, departures from the model may be detected by inspecting the residuals. Standardized residuals for each cell are calculated as:

$$r = \frac{(\text{Observed frequency} - \text{Expected frequency})}{\sqrt{\text{Expected frequency}}} \quad (8)$$

The values of standardized residuals which are too far from zero in either direction (approximately $|r| > 3$) correspond roughly to the 1 % probability of the standard normal distribution (Dobson 1983).

The association between the effects of explanatory variables and the response variable may be either negative or positive. This feature of the frequency table was analysed by examining the values of individual parameter estimates at different category levels in a model that fit the data; a negative estimated parameter value indicates that the effect decreases the expected cell frequency and vice versa. The estimation method used was maximum likelihood with the program CATMOD (SAS . . . 1985). Because CATMOD treats observed zero frequencies as structural zeros, these were changed to 0.5 in the analyses.

In an attempt to analyse the development of germination percentage in relation to accumulated chilling units another type of generalized linear model – logistic regression – was used.

For the linear logistic model the proportion of germinated seeds at +20 °C in darkness after 21 days incubation was taken as:

$$p_i = \frac{e^{b_1 + b_2 x_i}}{1 + e^{b_1 + b_2 x_i}} \quad (9)$$

i.e.

$$\ln \left(\frac{p_i}{1 - p_i} \right) = b_1 + b_2 x_i \quad (10)$$

where p_i is the proportion of seeds germinated, x_i is the accumulated chilling unit sum at the time of cone collection and b_1 and b_2 are parameters estimated from the data. The analysis was carried out using the program CATMOD (SAS . . . 1985) with maximum likelihood parameter estimation.

3. RESULTS

3.1. Anatomical seed maturity

There was a clear difference between the two populations studied in seeds' anatomical maturity. At the same thermal time (degree days, +5 °C threshold) value, the seeds collected from the natural stand included a greater proportion of anatomically poorly developed seeds than did those collected from Hyytiälä clone archive (Table 4).

3.2. Seed weight, seed water content and empty seed percentage

In the natural stand, the average seed weight was 4.3 ± 0.03 mg (± s.e. mean, n = 288) and in the clone archive material 6.9 ± 0.18 mg (± s.e. mean, n = 34), respectively. The seed water content was measured only for the clone archive material. In 1986, it remained constant, at approximately 30 % (fresh weight basis), throughout the whole collection period.

When measured by cutting test after germination analysis, the empty seed percentage was 14.4 ± 0.3 % (± s.d., n = 15161) in the natural stand, and when measured in X-rayed samples, 8.2 ± 0.9 % (± s.d., n = 1000). In the clone archive material these values were 13.1 ± 0.5 % (± s.d., n = 3998) and 16.4 ± 1.1 % (± s.d., n = 1049), respectively.

Table 4. Embryo-class distribution of seeds representing different experiments. Values based on X-raying random samples of either 200 (Exp. 1.) or 100 (Exp. 2. and 3.) seeds, empty seeds excluded.

Experiment no.	Cone collection date	Seeds in embryo class, %[1]			
		I	II	III	IV
Experiment 1. Year 1984, Hyytiälä, natural stand	Sep. 2.	7.0	10.6	8.8	73.6
	Sep.17.	8.2	14.0	11.0	66.8
	Oct. 5.	15.2	17.5	6.4	60.9
	Oct.26.	8.5	11.9	8.5	71.1
	Nov.15.	4.1	18.1	5.7	72.1
	Dec.13.	..[2]	..[2]	..[2]	..[2]
Experiment 2. Year 1986, Hyytiälä clone archiv	Aug.29.	0.0	0.0	2.6	97.4
	Sep. 2.	0.0	1.2	3.5	95.3
	Sep. 5.	1.3	1.3	2.5	94.9
	Sep. 9.	1.4	1.4	1.4	95.8
	Sep.12.	1.1	1.1	17.9	79.9
	Sep.16.	0.0	4.5	9.1	86.4
	Sep.19.	..[2]	..[2]	..[2]	..[2]
	Sep.23.	0.0	0.0	7.7	92.3
	Sep.26.	2.4	1.2	13.1	83.3
	Sep.30.	..[2]	..[2]	..[2]	..[2]
Experiment 3. Year 1986, Hyytiälä, natural stand	Oct.16.	0.0	0.0	30.8	69.2

[1] Embryo classes:
I Endosperm and embryo cavity developed but no embryo observed.
II Embryo occupying less than 10 % of the length of the embryo cavity.
III Embryo occupying 10 . . .65 % of the length of the embryo cavity.
IV Embryo occupying more than 65 % of the length of the embryo cavity.

[2] No data available because of small amount of seeds in total sample.

3.3. Cumulative germination

Cumulative germination curves of seeds from the natural stand under different treatments are visualized in Figure 6. First, the effect of incubation temperature was obvious; seeds germinated more slowly at +10 °C than at +20 °C. Secondly, the rate of germination was low in darkness, but was enhanced at both 8-hour and 24-hour photoperiods. Thirdly, these effects were not consistent with respect to cone-collection date. Instead, subsequent cone-collections showed an increasing proportion of seeds which began to germinate even at a low incubation temperature and in darkness.

A somewhat similar trend with respect to the cone-collection date was found in the clone archive material (Figure 7). The rate of germination was enhanced by continuous light during incubation, when compared to samples germinated in the dark; this was found especially in the first cone-collections. In later collections, however, differences in cumulative germination between the two treatments tend to decrease, suggesting a gradual loss of germination light requirement. In addition, there were declines in the rate of germination and also in cumulative germination at both light regimes, but these were not observed at the same collection date in light- and dark-germinated seeds.

Extended incubation time

The germination curves in extended incubation conditions are seen in Figure 8. As expected, both light and temperature regime affected cumulative germination similarly to earlier observations. When incubated for 50 days, however, even the seeds at +10 °C and in darkness did germinate, although sluggishly.

Tree-to-tree variation

Germination curves of seeds from individual trees in the natural stand material collected on 26 October and 13 December are shown in Figures 9a and 9b. Tree-by-tree cumulative germination figures for the other cone-collection dates in this material appear in Appendices 1–4.

Generally, cumulative germination varied considerably between trees, but this was true only if the seeds were germinated in the dark. When either 8-hour or 24-hour photoperiods were applied during the incubation, the germination curves were almost equal, and differences between trees in this respect could not be detected. This effect was found irrespective of germination temperature in all cone-collections except the last (cf. Figure 9b). In that material the germination curves varied between individual trees even if light was present during incubation.

3.4. Germination percentage

Interactions between cone collection date and incubation conditions

As indicated by the cumulative germination curves described above, germination percentage was also greatly affected by date of cone collection and germination conditions, and this was true of both populations studied in both years.

For the natural stand material, the germination percentage for each sub-lot is given in Table 5 (p 22). The seeds collected in September and october germinated poorly in darkness at both temperatures. For 8-h and 24-h photoperiods, germination percentage values ranged from 0 to approximately 98 %, depending on temperature regime. In the November and December collections, germination percentage was between 82 and 97 % in all treatment combinations except at +10 °C/darkness: in this treatment germination per-

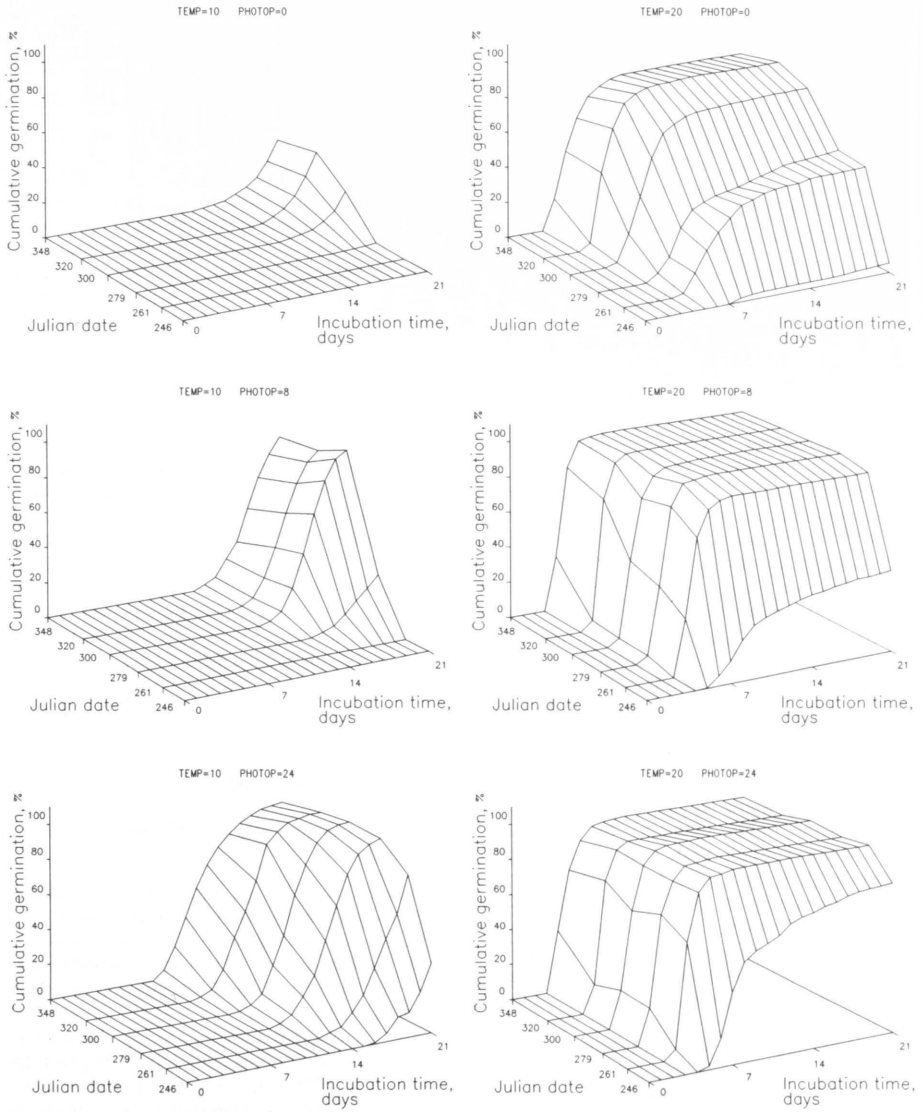

Figure 6. Cumulative germination measured on six occasions, 2 September – 13 December, 1984. Two temperature regimes (10 and 20 °C) and three photoperiods (0, 8 and 24 hour light) combined as six treatments. Each treatment – collection date combination represented by a sub-lot of 363 – 588 full seeds.

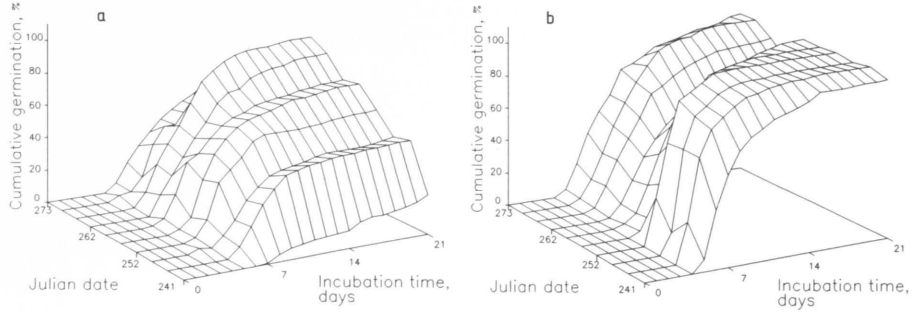

Figure 7. Cumulative germination measured on ten occasions, 29 August – 30 September, 1986. Incubation of 21 days in darkness (a) and continuous light (b), both at 20 °C. Each curve based on a sample of 151 – 191 full seeds.

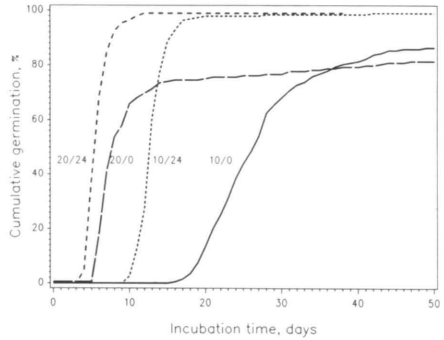

Figure 8. Cumulative germination as a function of incubation time in extended incubation conditions. Germination conditions: 10 °C/0 hour photoperiod, 10 °C/24 hour photoperiod, 20 °C/0 hour photoperiod and 20 °C/24 hour photoperiod. Each curve represents a sample of 153 – 195 full seeds. Seeds collected 16 October 1986.

centages were approximately 36 and 32 %, respectively.

Analysis of the frequencies of germinated and non-germinated seeds showed interaction effects between collection date and germination conditions for all three sample trees studied. For both trees No. 9 and 26, the frequency data could be adequately described with log-linear model including all second-order interactions and all third-order interaction terms:

$$\ln \hat{f}_{ijkl} = u + u_{1(i)} + u_{2(j)} + u_{3(k)} + u_{4(l)} + u_{12(ij)} + u_{13(ik)} + u_{23(jk)} + u_{14(il)} + u_{24(jl)} + u_{34(kl)} + u_{123(ijk)} + u_{134(ikl)} + u_{124(ijl)} + u_{234(jkl)}. \quad (11)$$

The likelihood ratio statistics for this model was $X^2 = 13.37$ for tree No. 9 and $X^2 = 13.28$ for tree No. 26, respectively. Both values exceed $\chi^2_{.05[6]} = 12.59$ indicating that the model (11) does not fit particularly well; although it provides an adequate description of the data as indicated by small residual values. The analysis of variance table as well as the expected frequencies and standardized residuals under the model (11) are given in Appendix 5a for tree No. 9 and 5b for tree No. 26, respectively.

For tree No. 100, a more parsimonious model than (11) fitted the data adequately:

$$\ln \hat{f}_{ijkl} = u + u_{1(i)} + u_{2(j)} + u_{3(k)} + u_{4(l)} + u_{12(ij)} + u_{13(ik)} + u_{23(jk)} + u_{24(jl)} + u_{34(kl)} + u_{123(ijk)} + u_{124(ijl)} + u_{134(ikl)}. \quad (12)$$

The likelihood ratio statistics for model (12) was $X^2 = 7.39 < \chi^2_{.05[8]} = 15.51$ indicating a good fit to the data. Thus, both cone-collection date x germinability ($u_{14(il)}$) and cone-collection date x germination temperature x germinability ($u_{134(ikl)}$) interaction terms were not needed in order to describe

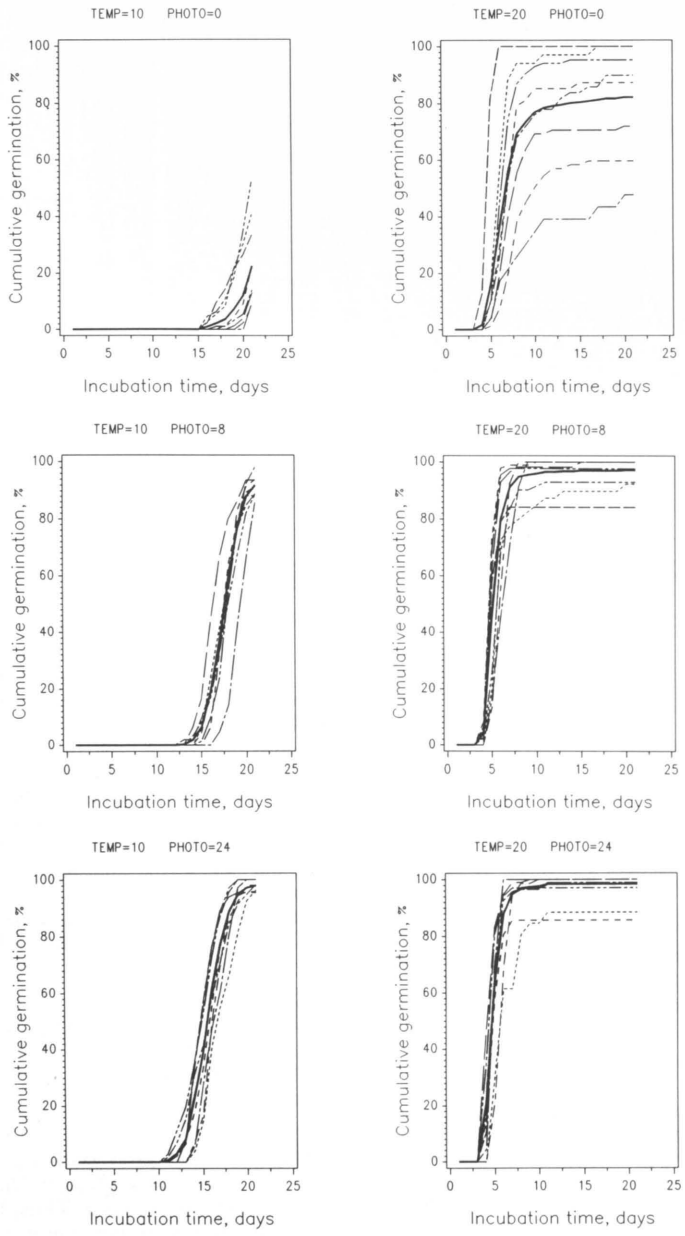

Figure 9a. Germination curves for seed samples from individual trees (dotted lines). Sample size 17 – 96 full seeds. The solid line denotes cumulative germination when samples were combined in one sub-lot. Seeds collected 26.10.1984.

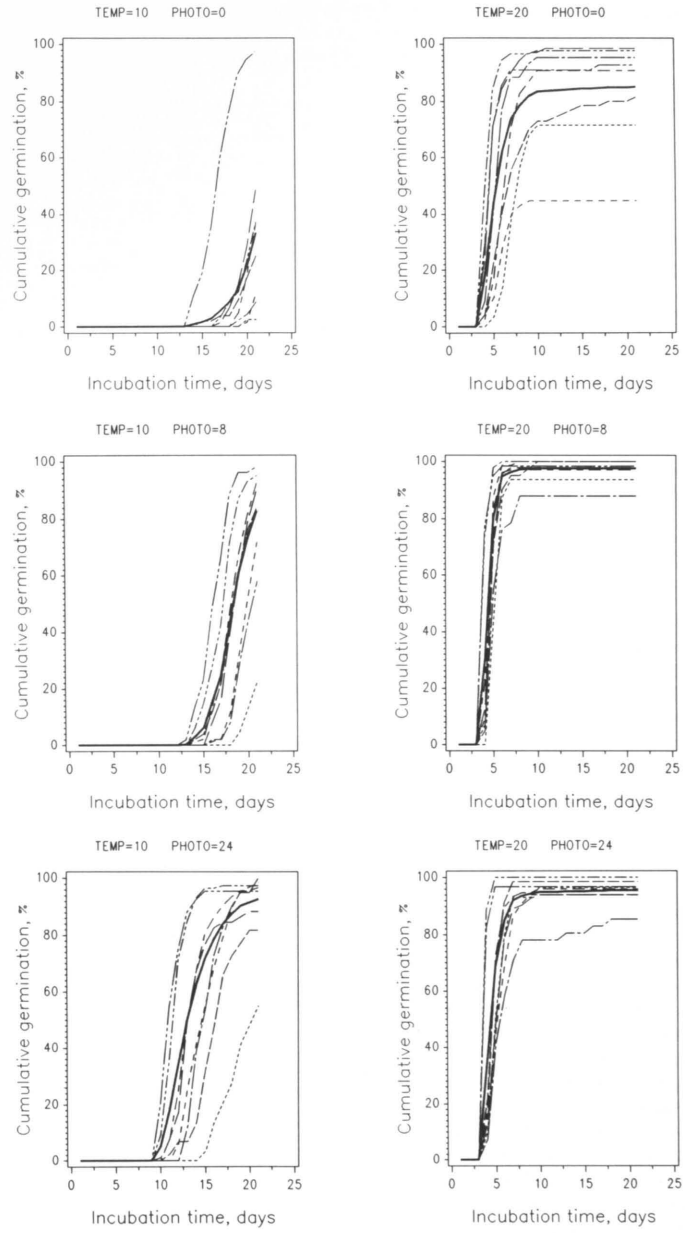

Figure 9b. As in Figure 9a. but seeds collected 13. 12. 1984. Sample size 22 – 118 full seeds.

Table 5. Germination percentage (incubation time 21 days) of seeds collected 2 September – 13 December, 1984 and incubated at six different combinations of temperature and photoperiod. Size of sample in each combination varied from 363 to 588 full seeds.

Cone-collection date	Germination temperature, °C					
	10 ± 1			20 ± 1		
	Photoperiod, h					
	0	8	24	0	8	24
	Germination percentage (21 days), %					
Sep. 2.	0.0	0.0	38.4	4.9	44.7	82.9
Sep.17.	0.0	0.0	81.9	52.2	93.6	98.1
Oct. 5	1.5	28.9	95.8	54.7	97.4	96.4
Oct.26.	22.3	91.9	97.9	82.3	97.3	98.4
Nov.15.	36.8	84.5	96.3	89.8	97.8	94.5
Dec.13.	32.2	82.8	92.8	85.1	97.6	95.6

the data. Summary of the likelihood ratio statistics and the expected frequencies and standardized residuals under the model (12) is given in Appendix 5c.

In the next step the estimated parameters and their standard errors were examined in order to determine whether there was a negative or positive association between the different categories of the variables studied (Table 6).

As regards cone collection date, germinability of seeds from trees No. 9 and No. 26 was suppressed in the first two (17. Sep. and 5. Oct.) collections, (with parameter estimate $u_{14(il)}$ being negative when $i = 1$ and 2), but enhanced in the two later collections (26 Oct. and 15 Nov., $i = 3$ and 4, respectively). The estimated standard error of the parameter estimate $u_{14(il)}$ is very high for both trees when $i = 4$. This indicates low level of significance for this parameter estimate in the last cone-collection date examined. For tree No. 100 there was no evidence of association between the cone-collection date and germinability.

The values of the parameter estimate $u_{24(jl)}$ indicate that, in general, 24 hour photoperiod during germination ($j = 3$) enhanced germination percentage compared to germination under 8 hour photoperiod and in darkness.

Table 6. Estimated parameters and their standard errors under the model (11), trees No. 9 and 26, and model (12), tree No.100, interpreting the effects of collection date ($i = 1 \ldots 5$), photoperiod ($j = 1 \ldots 3$) and temperature ($k = 1 \ldots 2$) on frequency of germinated seeds ($l = 1$).

Tree No.	Parameter	Parameter estimate	Estimated standard error
	$u_{14(il)}$		
9	$i = 1$	–0.736	0.208
	$i = 2$	–0.357	0.164
	$i = 3$	0.703	0.176
	$i = 4$	0.390	0.549
	$i = 5$	not measured	
26	$i = 1$	–0.789	0.255
	$i = 2$	–0.254	0.127
	$i = 3$	0.684	0.165
	$i = 4$	0.358	0.547
	$i = 5$	not measured	
100	$i = 1$	not measured	
	$i = 2$	not measured	
	$i = 3$	non-significant	
	$i = 4$	non-significant	
	$i = 5$	non-significant	
	$u_{24(jl)}$		
9	$j = 1$	–1.082	0.144
	$j = 2$	–0.237	0.109
	$j = 3$	1.319	0.252
26	$j = 1$	–1.661	0.252
	$j = 2$	–0.027	0.174
	$j = 3$	1.688	0.426
100	$j = 1$	–1.068	0.072
	$j = 2$	0.547	0.107
	$j = 3$	0.522	0.179
	$u_{34(kl)}$		
9	$k = 1$	–0.597	0.079
	$k = 2$	0.597	0.079
26	$k = 1$	–1.184	0.238
	$k = 2$	1.184	0.238
100	$k = 1$	–0.314	0.064
	$k = 2$	0.314	0.064

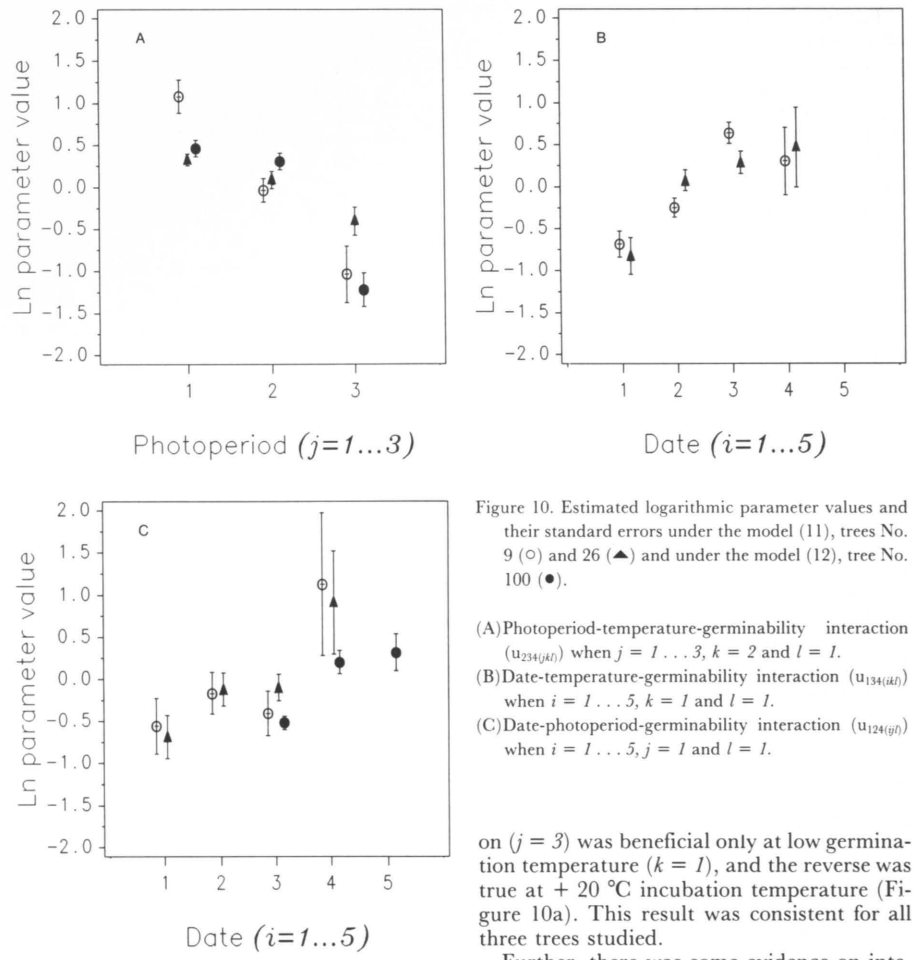

Figure 10. Estimated logarithmic parameter values and their standard errors under the model (11), trees No. 9 (○) and 26 (▲) and under the model (12), tree No. 100 (●).

(A) Photoperiod-temperature-germinability interaction ($u_{234(jkl)}$) when $j = 1 \ldots 3$, $k = 2$ and $l = 1$.
(B) Date-temperature-germinability interaction ($u_{134(ikl)}$) when $i = 1 \ldots 5$, $k = 1$ and $l = 1$.
(C) Date-photoperiod-germinability interaction ($u_{124(ijl)}$) when $i = 1 \ldots 5$, $j = 1$ and $l = 1$.

All trees included in the analyses showed similar pattern in this respect.

All three trees reacted in a similar way also to temperature regime; at higher germination temperature (20 °C) the probability of seeds germinating within 21 test days was higher than at +10 °C with parameter $u_{34(kl)}$ estimates being positive when $k = 1$ and negative when $k = 2$, respectively).

The estimated parameter values for higher order interactions in the frequency table were as follows: continuous light during germination ($j = 3$) was beneficial only at low germination temperature ($k = 1$), and the reverse was true at + 20 °C incubation temperature (Figure 10a). This result was consistent for all three trees studied.

Further, there was some evidence on interaction effect between date of cone-collection and germination temperature. For trees No. 9 and 26, a germination temperature of 10 °C decreased the frequency of seed germination in first seed samples collected on 17 September – 5 October (parameter estimate $u_{134(ikl)}$ being negative when $i = 1 \ldots 2$), but in later collections the reverse was true (Figure 10b). Estimated parameters for last collection date had, however,large standard errors; this suggests that the inclusion of the parameter $u_{134(ikl)}$ in the model (11) is mainly due to variation in germinability between the first three cone-collection dates.

For tree No. 100, there was no interaction effect between cone-collection date and temperature on germinability.

Of additional interest is the interaction of collection date and photoperiod with frequency of germinated seeds. Generally, the fit of both models (11) and (12) was improved when the effect of cone-collection date – photoperiod interaction was included in the model (cf. Appendix 5). The individual parameter estimates ($u_{124(ijl)}$, $j = 1$) (Figure 10c), however, have large standard error when $i = 4$ for trees No. 9 and 26. This indicates that the improvement of the overall fit of model (11) is mainly due to the differences in the germination response between first three cone collections.

3.5. Chilling requirement for germination

For clone archive material, germination percentages are given in Table 7. These results indicate a rise in germination percentage during September 1986 similar to that noticed two years earlier in the natural stand. In addition, the germination percentage was enhanced by continuous light during the germination test, and there was also a gradual decrease in the light requirement as autumn proceeded. This was manifested as an increase in germination percentage in darkness.

Table 7. Germination percentage of Scots pine seeds collected on ten occasions, 29 August – 30 September, 1986. Incubation time 21 days at +20 °C in both continuous light and darkness. Size of sample in each occasion varied from 151 to 191 full seeds.

Cone collection date	Photoperiod, h	
	0	24
	Germination percentage (21 days), %	
Aug.29.	24.3	95.4
Sep. 2.	51.5	98.9
Sep. 5.	49.1	97.2
Sep. 9.	61.1	98.8
Sep.12.	73.1	98.1
Sep.16.	71.5	98.9
Sep.19.	83.6	86.8
Sep.23.	89.8	91.4
Sep.26.	66.3	98.9
Sep.30.	70.7	98.9

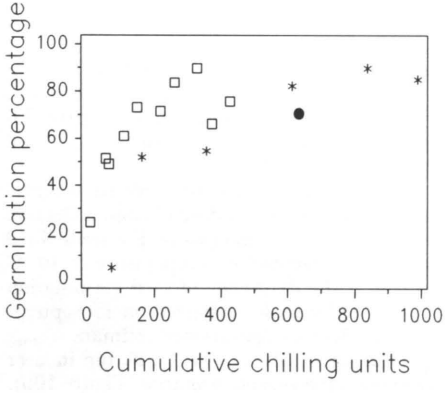

Figure 11. Germination percentage of Scots pine seeds in relation to accumulated chilling unit sum. Germination conditions: +20 °C, darkness, incubation 21 days. (*) Natural stand 2 Sep. – 13 Dec. 1984, (●) natural stand 16 October 1986, (□) clone archive 29 August – 30 September 1986.

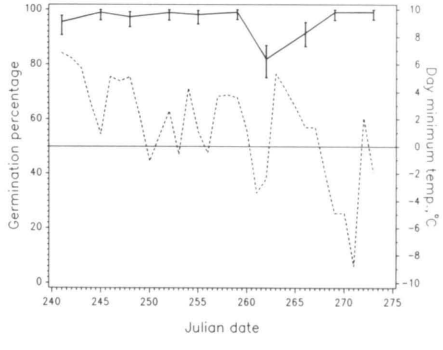

Figure 12. Daily minimum temperature (dotted line), 29 August – 30 September 1986, and germination percentage (solid line) of Scots pine seeds germinated at 20 °C and in darkness. Bars show 95 % confidence limits for the estimate.

Figure 11 illustrates the development of the germination percentage at +20 °C/dark in relation to accumulated chilling units in natural-stand and in clone-archive material. In the logistic regression analysis of this material, the logistic model (9) with accumulated chilling unit sum as an explanatory variable, did not fit the data. The likelihood ratio statistic was $X^2 = 404.12$ which far exceeds the critical value of $\chi^2_{.05[14]} = 23.68$.

In the clone archive material, there were declines of germination percentage in both light regimes at subsequent collections. First, this was found among the samples germinated in continuous light, where the germination percentage fell from almost 99 % to approximately 86 % in two subsequent collections. A same kind of decline was also apparent in dark-germinated seeds later in the autumn. These declines, however, were temporary, so that after a 'recovery period' the former germination percentage value was again achieved. The temporary decline in germination percentage is illustrated in Figure 12 together with the daily minimum temperatures during the cone collection period.

4. DISCUSSION

4.1. Anatomical seed maturation

In this study, Scots pine seeds were anatomically mature (embryos occupying more than 65 % of the length of the embryo cavity) at the beginning of September. The degree-day value for this phase (990 d.d.in 1984 and 950 d.d. in 1986, respectively) is well in accordance with the results for this species as published by Sarvas (1970), Ryynänen (1976), and by Henttonen et al. (1986). There was, however, variation in the anatomical development between the seed-material from the two populations. Seeds collected from the 25-year-old natural stand had greater variation in their anatomical development than did those collected from the Hyytiälä clone archive. This result may be due to differences in microclimatic conditions between the two sites. The density of the natural stand is approximately 2200 stems/ha, whereas in the clone archive it is approximately 400/ha. Thus, there is less competition for light and nutrients between individual trees in the clone archive, and this will also favour the development of the seed (Sarvas 1970). In addition, the attainment of anatomical maturity has been shown to vary considerably between individual trees in Scots pine (Matyas 1973, Remröd and Alfjorden 1973, Ryynänen 1982).

Bergman (1976), in northern Sweden, emphasized the effects of microclimatic conditions on the maturation of Scots pine seeds. He discovered that seeds collected from south side of the crown of a single tree possessed better anatomical development and better germinability than did those collected from north side of the crown. Similar results by Ilstedt and Eriksson (1982) indicate the impact of microclimate - good sun exposure, for example, on seed maturation. Thus, variables other than temperature, such as radiation regime, should also be studied when quantitatively relating the effects of maturation environment to the anatomical seed development (Edwards 1980, Winston and Haddon 1981).

Another obvious reason for differences in anatomical maturity between the two populations is the different origin of the seed material. Most of the cone-bearing grafts in Hyytiälä clone archive were of northern origin. According to Sarvas (1967, 1970), when compared with seeds of southern populations, they require less thermal time (degree days) to reach the same stage of anatomical maturity; this holds true even if the clones are transferred to the south in order to enhance seed development, and the female flowers are pollinated by pollen from southern populations (Ryynänen 1976). In the present study, there was some evidence that seeds from northern grafts also have higher germination percentages (when germinated in darkness) at the same thermal time (chilling units) value when compared with seeds from the local, southern population. It must be emphasized, however, that temperature recordings in this study were not made in experimental stands; especially, temperature data from Hyytiälä weather station may not describe the temperature regime accurately enough in the clone archive area.

Bhumibhamon (1978) did not find any differences in germinability (energetic index of germination) between open-pollinated seeds from northern grafts and local seeds, both of which were collected at Punkaharju tree bank in southern Finland. In his study, however, seeds belonging to anatomical embryo-class IV were used in germination tests, and seeds were germinated under continuous light.

Late frosts at the beginning of June, 1984, might be one reason for the occurrence of poorly developed seeds in that year's seed material. Simak (1972), studying the effects of low temperatures (−2 . . . −4 °C) on Scots pine embryogeny *in vivo*, demonstrated that both embryo and megagametophyte development were often retarded or arrested after the cold treatment. In the present study, frosts in June 1984 occurred before fertilization, which normally takes place in southern Finland at approximately 400 degree-days (Sarvas 1967). The main effect of frost might thus

have been in delaying the date of fertilization and as a consequence, also the date when anatomical maturity was reached.

Seeds collected from the clone archive were heavier than those collected from the natural stand. Seed-weight does not, however, affect germination *sensu stricto*. Instead, it implies the amount of reserves in the megagametophyte, and is probably correlated with post-germination events such as growth of the embryo and seedling establishment. Bergsten (1985), for example, found that seeds from young Scots pine trees were heavier than those from old ones; there was, however, no difference in germinability under laboratory conditions between the seeds of different weight.

The percentages of empty seed measured in this study were near to those reported for Scots pine by Sarvas (1962, 13.7 %) and Koski (1972, 12.7 %). This indicates an average level of self-fertilization, and thus normal embryo development in this respect in both stands studied.

4.2. Germination characteristics

4.2.1. Autumn dormancy

Dormant seeds do not germinate under conditions which would be favourable for normal growth. In most cases, seed dormancy is a physiological adaptation which delays germination until favourable conditions occur. Dormancy can thus be regarded as a selective adaptation of plants of temperate regions which prevents seeds from germinating in the fall because the seedlings would probably be severely damaged during winter Sarvas (1964).

In the present study, autumn-collected Scots pine seeds were dormant: their germination rate was slow both in darkness and at +10 °C germination temperature. The rate of germination was, however, gradually enhanced during autumn so that seeds collected in November and December were able to germinate readily even at +10 °C.

The result is in accord with the model of dormancy by Vegis (1964) who proposed that as buds and seeds enter dormancy the range of environmental conditions (temperature) over which they are capable of developing becomes progressively narrower. As dormancy is released the range again becomes wider until the seeds or buds are non-dormant. True dormancy prevents germination under any external conditions; relative dormancy prevents germination except within a certain more or less limited range of conditions.

It was not possible to characterize precisely what type of dormancy was involved in the germination of autumn-collected Scots pine seeds because the seed-coat effects were not studied, and thus the possibility of exogenous dormancy (Nikolaeva 1969) cannot be ruled out. The gradual enhancement of germination percentage during autumn, and the rapid and uniform germination when light was present during incubation suggest, however, that autumn-collected Scots pine seeds show endogenous embryo dormancy.

There were large differences between individual trees in their dormancy and germination characteristics. Typically, seeds from some of the sample trees were able to germinate in the darkness, while others were positively photoblastic, requiring an 8– or 24-hour photoperiod for germination. This phenomenon, known as polymorphism or heteroblasty (Bewley and Black 1982) with respect to the germination light requirement, has been reported earlier for Scots pine seeds (Eliason and Heit 1941). These results can be related to the fact that nutrition, microsite, or other edaphic features in the environment of different female trees influence seed development, or to genetic influence on germination characteristics. As suggested by Bramlett et al. (1983) these two effects could be separated in clonal seed orchards if diallel crosses were replicated on individual ramets of a given clone.

4.2.2. Light and temperature requirements for germination

Light during germination decreased variation in both germination rate and germination percentage between individual trees. Similarly, Adkins et al. (1984) found that in the germination of *Abies fraseri* (Pursh) Poir. seeds, the presence of light during incubation was more important than seed stratification in broadening the range of temperatures for

optimum germination and increasing total germination at low temperatures.

The light dependence of Scots pine seed-germination has been documented in a number of studies (Eliason and Heit 1941, Sarvas 1950, Nordström 1955, Huss 1961, Nyman 1961, 1963). Nyman (1963) demonstrated that Scots pine seed-germination depends upon the photostationary state of phytochrome within the seed, the 'active' form of phytochrome – P_{fr} – being needed for the germination process to proceed.

When interpreting the results of the present study, it may be hypothesized that the photoperiod effects observed are, at the biochemical level, also phytochrome mediated. Light dependence of germination in seeds of some of the sample trees suggests that these seeds probably lacked sufficient germination promoting phytochrome. The spectral energy distribution of the light source used in this study was, however, similar to direct sunlight, which establish a high ratio of P_{fr}/P_{total} in seeds and allow them to germinate. In the present study the seeds received some light during the seed processing, de-winging, etc. that might have affected their photostationary state. It is worth noting that in some pine species photoconversion of phytochrome takes place even in 'dry' (6 . . . 9 % water content, fresh weight basis) seeds (Nyman 1963 for *Pinus sylvestris*, Tobin and Briggs 1969 for *Pinus palustris* Mill., Orlandini and Malcoste 1972 for *Pinus nigra* Arn.).

There was some evidence also of the negative effects on germination percentage of a continuous light-regime during incubation. In natural stand material a 24-hour photoperiod during incubation enhanced germinability at the +10 °C germination temperature, but it decreased the germination percentage at +20 °C. The inhibitory effect of prolonged light exposure in seed germination has been documented for a number of tree species (Toole, 1973), including *Betula pendula* Roth (Vaartaja 1956) and *Tsuga heterophylla* (Raf.) Sarg. (Edwards and Olsen 1973). For the above named species the inhibiting effect of continuous light was also noticed at a high temperature-regime (+20 . . . 30 °C) but not at a lower temperature (<+20 °C).

Generally, the temperature effects on germinability found in this study are in agreement with those reported earlier for forest tree species (Hatano and Asakawa 1964). The interaction effect between cone-collection date and temperature regime during incubation has not, however, been reported earlier for Scots pine seeds. The widening of the temperature range for germination during autumn suggests that the relationship between the rate of germination and temperature is not constant throughout the autumn; instead, it may be lower following chilling. This has been documented also for CO_2 uptake in Scots pine at the end of the annual photosynthetic period (Pelkonen 1981).

Light requirement for germination also interacted with cone-collection date. As autumn proceeded, a greater proportion of seeds were able to germinate in darkness. This finding is in agreement with earlier observations of Scots pine seed light requirement (Nordström 1955, Blomqvist 1972).

The generalization drawn from the present results naturally depends on the adequacy of the assumptions involved. It must be noted that germination data on only three of the sample trees was included in the statistical analysis. Since distributional results depend on having a large sample, the estimated parameters and their standard errors provide informal rather than exact guides to the reliability and interdependence of the effects.

In addition, analysis of germination percentage, i.e. frequency of germinated seeds at a single pre-specified time, does not fully recognise the dynamic nature of the problem. For example, when germination characteristics are compared for seeds incubated at +10 °C and at +20 °C in continuous light (Figure 8), it is evident that germination percentage after 21 incubation days is practically the same for both temperature regimes; germination curves, however, are not similar. Thus, some information is lost when only germination percentage is considered. This suggests that incubation time should also be included in the analysis as an explanatory variable. The binary dependent variable (germinated, not germinated) could then be related by a logistic regression model to a vector of explanatory variables.

4.2.3. Chilling requirement

The approximate chilling requirements for 50 % germination in the present study were 70 chilling units for the clone archive material and 200 units for the natural stand material. As regards the clone archive seeds, this result agrees with the data reported by Sarvas (1973) for Scots pine seeds of Rovaniemi origin.

In some tree species the promotive effects of chilling can be partly replaced by long photoperiods; the longer the period of chilling the less the effect of long photoperiods (Cannel and Smith 1983). This has also been demonstrated with Scots pine seedlings (Jensen and Gatherum 1965, Aronsson 1980). In the present study, this effect of chilling was obvious with Scots pine seeds, and was manifested as a greater proportion of seeds germinating in darkness as autumn proceeded.

In laboratory conditions, where temperature, light, and moisture conditions are easily adjusted, the effect of chilling (stratification) on germinability is often linear with germination percentage and rate, gradually increasing with increased chilling time (McLemore and Czabator 1961, Kardell 1974, Sorensen 1983). Thus, the amount of chilling needed for 50 % germination, for example, can be quite easily determined.

Chilling conditions in natural environments are, however, quite different from those in the laboratory. The integration of the chilling unit sum raises several questions. First of all, one has to consider the optimum temperature for chilling because it is commonly recognized that chilling temperatures are not all equally effective (Sarvas 1974, Seeley and Damavandy 1985). In the present study, an optimum chilling temperature was chosen on the basis of Sarvas' (1974) data on dormancy release of *Betula pendula* catkins and seedlings. Generally, temperatures between +1 . . . +10 °C are regarded as effective chilling temperatures (Bewley and Black 1986). Nikolaeva (1969) pointed out, however, that the biochemical changes such as increase in enzyme activity and in hydrolytic processes of food reserves are observed in seeds during low-temperature treatment, and these processes also proceed at higher temperatures. Thus, the changes cannot be shown to be uniquely characteristic of low-temperature dormancy-breaking.

In addition, chilling temperatures alternating with warm temperatures can be less effective than chilling temperatures alone (interrupted chilling, cf. Hänninen 1987). Seeley and Damavandy (1985), for example, suggested that temperatures above +16 °C counteract previous chilling. Thus, the temporary declines in germinability observed in this study might be a result of the nullifying effect of high temperatures on previous chilling. Hänninen and Pelkonen (1987) found that in Scots pine seedlings intermittent warm periods, when occurring in a late phase of the chilling stage, nullified much of the effects of previous chilling. In seed-germination studies, similar observations have been made for Norway spruce (*Picea abies* L.) seeds from individual trees; Jensen et al. (1967) suggested that the temporary declines in germination percentage could be due to occasional mild weather conditions that would bring seeds back to a state of maturation approximating that in early autumn.

On the other hand, some authors consider temporary changes in germinability to be a result of freezing temperatures and resultant possible damage to the embryo (Kardell 1974, 1976, Blomqvist 1975). Kardell (1974), in material collected from northern Sweden, demonstrated that in natural environments the percentage of seeds with damaged embryos increased considerably during winter. He also reported reduced germinability and embryo damage as a result of different cone-freezing treatments in autumn-collected material. Simak (1972) noticed that the early stages of embryogenesis were more sensitive to cold treatment than were later ones. Anatomically mature seeds were, however, also damaged by freezing treatment. According to Tanaka (1982) the effect of sub-zero temperatures on noble fir (*Abies procera* Rehd.) seeds was highly dependent on seed and cone moisture content ; seeds with a low moisture content were less damaged during freezing than those with a high moisture content. Similar results with Scots pine seeds have been obtained by Keefe and Moore (1982); surface-dry, although fully imbibed Scots pine seeds could stand sub-zero temperatures better than those embedded in a moist substrate.

There are, however, reports suggesting

that sub-zero temperatures might also have positive effects on Scots pine seed maturation and germination percentage. Messer (1958) suggested that Scots pine cones should not be harvested before the occurrence of early frosts because of the effect of sub-zero temperatures in promoting germinability. Kardell (1976) got similar results when studying the effects of sub-zero temperatures on Scots pine cones and seeds under laboratory conditions.

Temporary germination-percentage declines observed in this study in subsequent cone collections may result either from changes in the seeds' physiological stage or, more probably, from the fact that the clone archive population was, in fact, a mixture of different populations. Because seeds from individual trees differ considerably in germination characteristics, results of a germination test naturally depend on the proportion of seeds of different trees in a sample.

Difficulties arise from the 'timing' of chilling unit sum integration, i.e. the choice of the starting point of the integration. Sarvas (1974) suggested that integration should be started when the mean daily temperature falls below +10 °C. In the present study the integration of the chilling unit sum was started when thermal time value was 950 degree days. The main argument for choosing this starting point was the hypothesis that the embryo should be nearly fully differentiated before the chilling temperature could be effective in breaking its dormancy. However, in order to clarify this particular question, more information is needed on the physiological processes occurring in seeds during the late stages of maturation.

In the present study, the water-content of the seeds was rather constant (approximately 30 % on a fresh weight basis) throughout the cone-collection period in September, 1986. This has implications when considering the effects of chilling temperatures on seeds; Sarvas (1974), for example, pointed out that in the removal of autumn dormancy from seeds by chilling, the moisture content of the seeds is of particular significance. When stratified under laboratory conditions between moist filter papers, Scots pine seeds have a water-content between 30–40 % (fresh weight basis) (Nygren 1986c). In this respect, the water-content of the seeds on trees, in this particular year, was near to that in laboratory stratification conditions.

Some authors consider chilling of seeds in hydrated condition to be a low-temperature germination (Daniel 1967). Nikolaeva (1969) for example points out that during the period of stratification, gradual hydrolysis of proteins takes place in the seeds. This view is supported by the fact that seeds of many temperate-zone conifers start to germinate during the chilling treatment, i.e. they are capable of germinating even at the low temperatures (0 . . .+5 °C) generally used for stratification (Tanaka 1976, Danielson and Tanaka 1978, Blazich and Hinesley 1984). This was also apparent in the present study when the seeds collected in October, 1986 did germinate at the low temperature (+10 °C) in darkness when incubated for 50 days. It may thus be hypothesized that low incubation-temperature has some chilling effect on seeds which is manifested as a high germination percentage at the end of test-period. The germination rate in turn, is low because of the slow rate of physiological processes at the +10 °C required for germination.

In summary, this study suggests that more than one combination of incubation temperature and photoperiod should be used for the germination test when autumn cone collections are scheduled. In addition, special attention should be given to the fact than forest tree seed lots usually are mixtures of different populations. When differences between individual trees in germination characteristics are taken into account, the use of chilling unit sum as a method to predict germination percentage for autumn collected seeds is more feasible. Clearly, germination studies oriented to individual trees, with emphasis on the ecophysiology of seed maturation, dormancy, and germination processes, are an area in which further investigation is needed.

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SELOSTE

Männyn siementen itämistunnukset syyskeräyksissä

Useiden viileän vyöhykkeen metsäpuiden siemenet eivät idä syksyllä välittömästi tuleentumisen jälkeen, vaikka olosuhteet olisivat itämiselle suotuisat. Tämä ns. syyshorros esiintyy etenkin sellaisessa lauhkean tai viileän ilmastovyöhykkeen puiden siemenessä, joka varisee syksyllä, mutta itää pääasiassa vasta seuraavana keväänä.

Siementen syyshorros purkautuu syksyn kostean ja viileän sääjakson aikana. Sarvas (1974) mittasi syyshorroksen (dormansi I) purkautumisnopeuden lämpötilariippuvuuden hieskoivun siemenissä ja silmuissa ja totesi horroksen purkautuvan tehokkaimmin +3,5°C:n lämpötilassa.

Myös männyn siementen syyshorros purkautuu ja itävyys paranee, kun siemenet altistuvat tuleentumisen loppuvaiheessa ± 0 – +10°C lämpötiloille joko luonnonolosuhteissa tai esimerkiksi käpyjä varastoitaessa ja siemeniä stratifioitaessa (Sarvas 1964, Simak 1966, Asplund ym. 1973, Kardell 1973a,b, Kardell ym. 1973).

Itämistunnusten muutokset kylmäkäsittelyn seurauksena eivät kuitenkaan ole yksiselitteisiä. On kiinnitetty huomiota siihen, että itämiseen tarvittava kylmäkäsittely voidaan koeolosuhteissa suurelta osin korvata idättämällä siemenet valossa, erityisesti pitkän päivän olosuhteissa (Nordström 1955, Blomqvist 1972).

Tässä työssä tutkittiin syys-joulukuussa kerättyjen männyn siementen itämistunnuksia – kumulatiivista itävyyttä ja itävyysprosenttia 21 vrk:n kuluttua idätystestin aloittamisesta – erilaisissa idätysolosuhteissa. Päämääränä oli selvittää toisaalta idätyslämpötilan ja -päivänpituuden vaikutukset siementen itämiseen ja toisaalta tarkastella vaikutusten pysyvyyttä suhteessa siementen keräysajankohtaan. Niinikään asetettiin tavoitteeksi siementen kylmäkäsittelytarpeen määrittäminen kylmäkäsittelyindeksin avulla.

Mittaukset tehtiin kahdessa populaatiossa. Vuonna 1984 mitattiin itämistunnukset 25-vuotiaasta kylvömänniköstä, Helsingin yliopiston metsäaseman metsämeteorologisen mittausaseman (61°51'N, 24°20'E, 170 m m.p.y.) välittömästä läheisyydestä syys-joulukuussa kuutena ajankohtana. Vuonna 1986 mitattiin vastaavat tunnukset metsäaseman vartekokoelmasta elo-syyskuussa 3-4 päivän väliajoin; lisäksi mitattiin lokakuussa näyte em. kylvömänniköstä.

Idätystesteissä käytettiin kuutta lämpötila-päivänpituusyhdistelmää: lämpötilat olivat 10 ± 1.0°C ja 20 ± 1.0°C ja päivänpituudet kummassakin 0, 8 ja 24 tuntia.

Syksyllä kerättyjen männyn siementen itäminen osoittautui ennen kaikkea idätysolosuhteiden – päivänpituuden ja lämpötilan säätelemäksi. Em. tekijöiden vaikutus itävyyteen ei ollut kuitenkaan riippumaton siementen keräysajankohdasta; myös idätysolosuhteiden ja siementen keräysajankohdan välinen yhdysvaikutus osoittautui tilastollisesti merkitseväksi itämisprosentin selittäjäksi.

Niinikään todettiin, että itävyydessä on suurta puukohtaista vaihtelua; joidenkin puiden itämistunnukset olivat lähestulkoon riippumattomia esimerkiksi päivänpituudesta, kun taas joidenkin puuyksilöiden siemenet vaativat ehdottomasti valoa itääkseen.

Vartepopulaatiossa (jonka puista suurin osa oli Pohjois-Suomesta) siemenet kehittyivät nopeammin kuin paikallista alkuperää edustavat kylvömännikön siemenet. Tätä tulosta on kuitenkin pidettävä vain suuntaa antavana, koska (1) mittaukset tehtiin eri vuosina eri populaatioista ja (2) yhdessä havaintopisteessä tehdyt lämpötilamittaukset eivät todennäköisesti kuvaa riittävän tarkasti lämpööloja tutkituissa populaatiossa.

Sarvaksen (1973) mukaan Rovaniemen alkuperää olevan männyn siemenen kylmäkäsittelytarve on 60 chilling unit-yksikköä, jotta siemenhorros purkautuisi. Tässä työssä saatiin samaa suuruusluokkaa oleva tulos vartepopulaation siemenille.

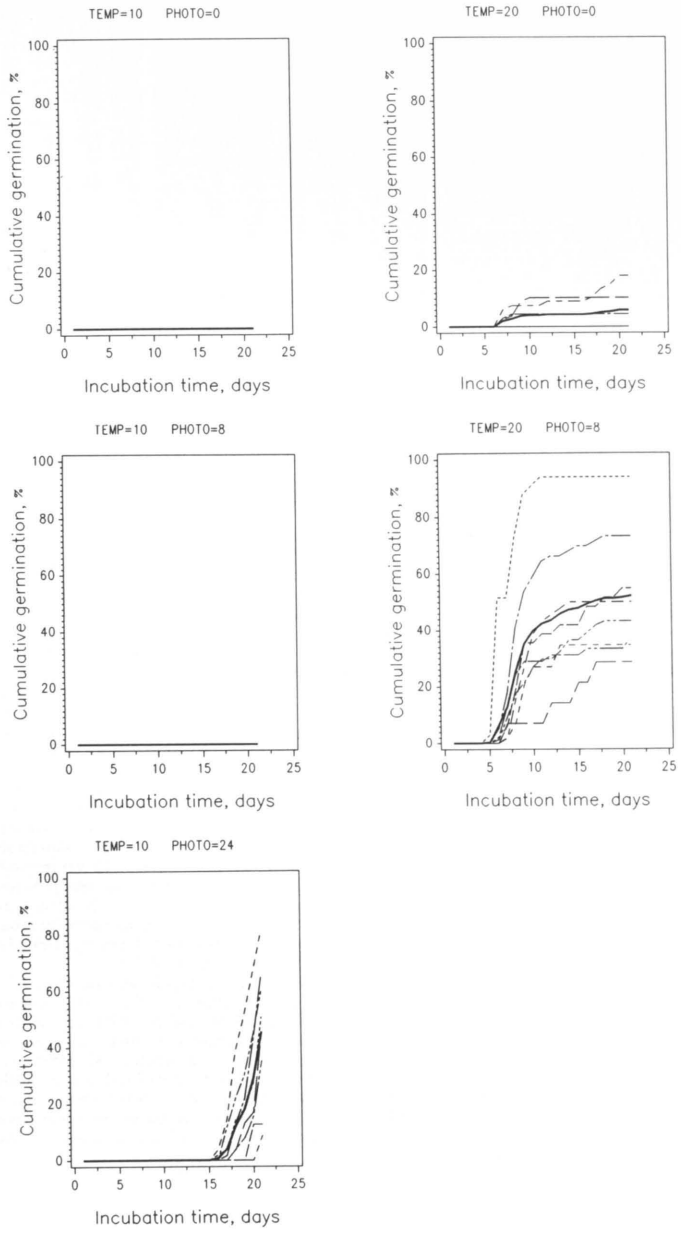
Siementen ja pähkylähedelmien kylmäkäsittelyn aiheuttamat muutokset itämisen valo-ja lämpötilariippuvuudessa tunnetaan myös muilla viileän vyöhykkeen metsäpuilla (Black ja Wareing 1955, Stearns ja Olson 1958, Asakawa 1959, Winston ja Haddon 1981, Adkins ym. 1984, Farmer ym. 1984). Kokoavasti voidaan todeta, että kylmäkäsittelyn jälkeen itämiselle suotuisa lämpötila-alue laajenee ja itämisen valoriippuvuus vähenee (ks. myös Hatano ja Asakawa 1964).

Saatujen tulosten perusteella männyn siementen itävyyden 'vuosirytmi' näyttää pääpiirteissään samanlaiselta kuin useiden viileän vyöhykkeen metsäpuiden silmujen dormansin synkronointi vuodenaikojen vaihtelun kanssa (vrt. Vegis 1964, Sarvas 1974). Sarvas (m.t.) korostaakin vegetatiivisten silmujen ja siementen horroksen yhtäläisiä piirteitä. Hän totesi hieskoivun silmujen ja siementen syyshorroksen purkautumisen kylmäkäsittelyn tuloksena olevan likimain samanlainen.

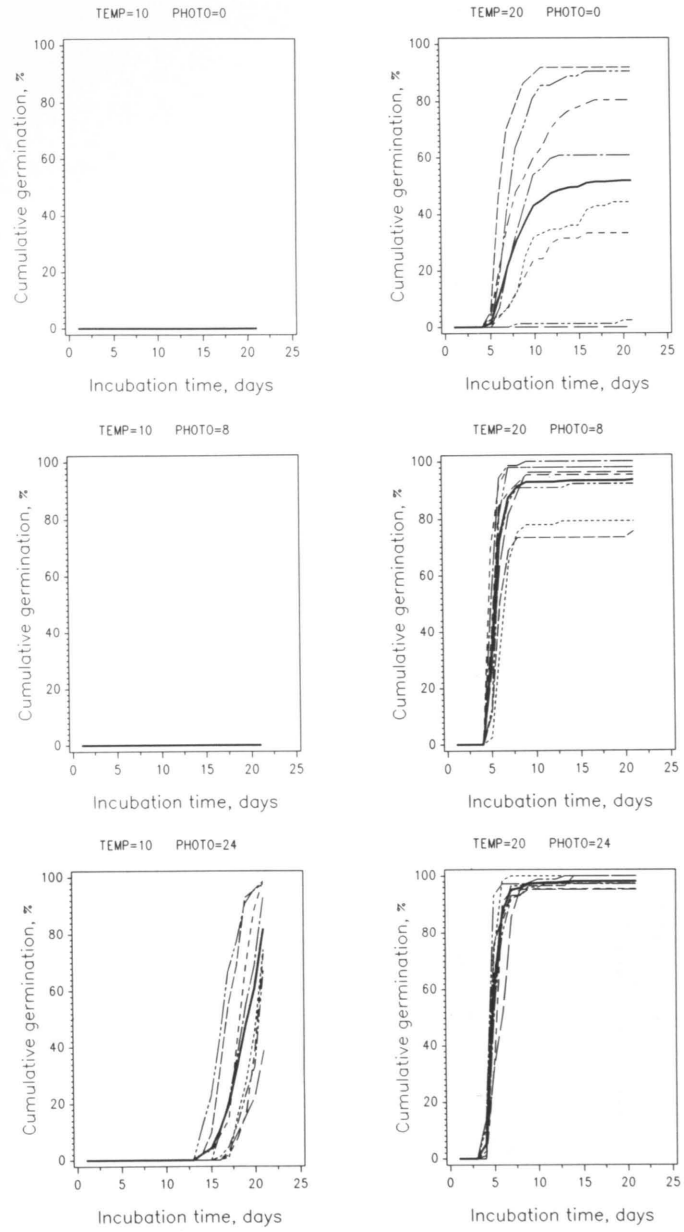
Tässä työssä saadut tulokset osoittavat, että männyn siementen kylmäkäsittely voidaan ainakin osittain korvata idättämällä siemenet pitkän päivän olosuhteissa. Myös männyn vegetatiivisten silmujen horrosta tutkittaessa on havaittu, että silmujen kylmäkäsittelytarve voidaan korvata pitkän päivän kasvatusolosuhteilla (Jensen ja Gatherum 1965, Aronsson 1980). Männyn siementen kylmäkäsittelyn ja idätysolosuhteiden, erityisesti päivänpituuden välisen yhteisvaikutuksen itämisessä ovat aikaisemmin todenneet mm. Eliason ja Heit (1941), Vaartaja (1956) sekä Nyman (1963).

Mitattaessa syksyllä kerätyn männyn siemenen itävyyttä on ratkaiseva merkitys sillä, minkälaisissa olosuhteissa idätykset tehdään. Idätyslämpötilan ja päivänpituuden aiheuttamat vaihtelut idätystuloksissa tulisikin ottaa huomioon arvioitaessa siemensadon keräyskelpoisuutta männyn siemenviljelyksillä. Niinikään on otettava huomioon puiden välinen vaihtelu itämistunnuksissa; pienten osapopulaatioiden tunnukset eivät ole sellaisinaan yleistettävissä laajempaa perusjoukkoa koskeviksi.

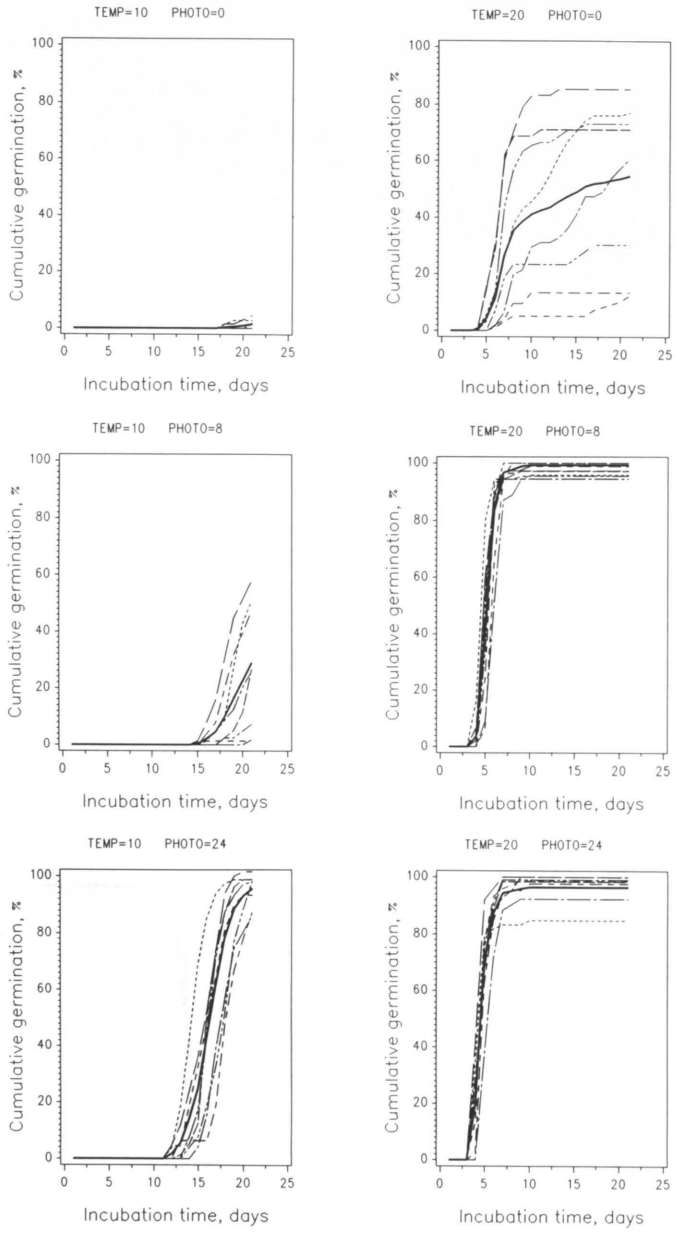
Appendix 1. Germination curves for seed samples from individual trees (dotted lines). Sample size 35 – 60 full seeds. The solid line denotes cumulative germination when samples were combined in one sub-lot. Seeds collected 2.9.1984. Data in 20 °C – 24 h photoperiod combination was, unfortunately, lost during processing.



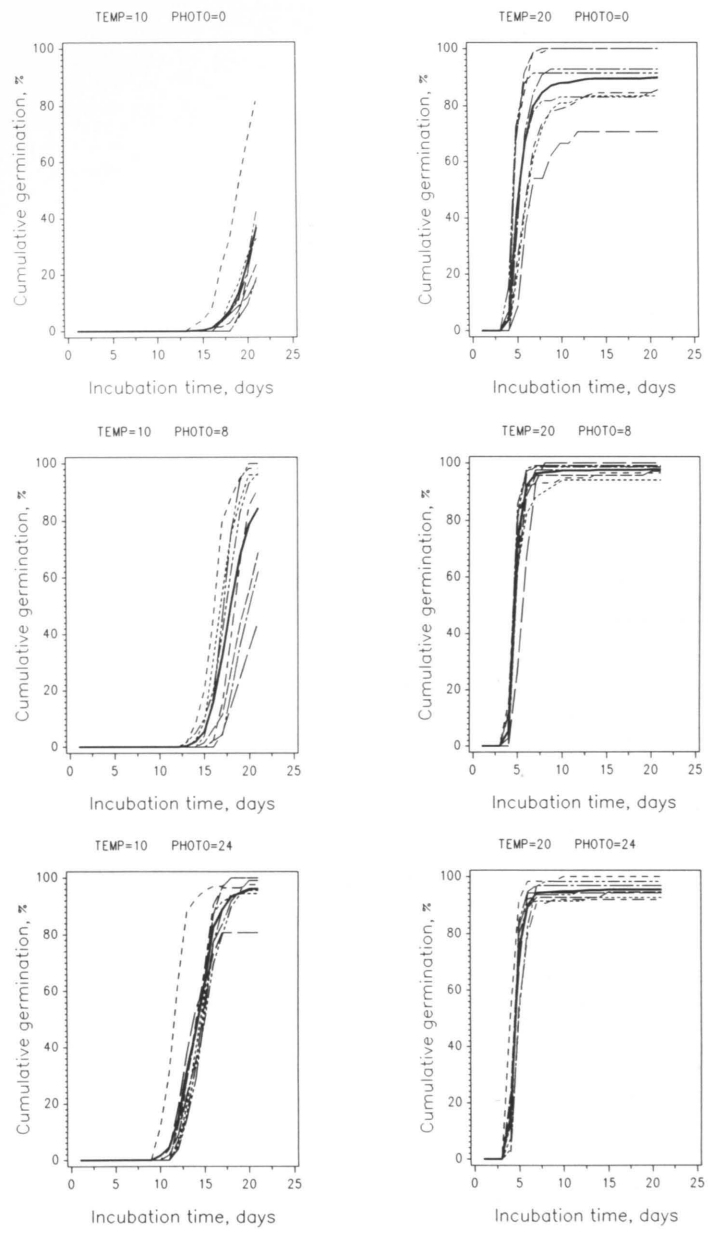
Appendix 2. Germination curves for seed samples from individual trees (dotted lines). Sample size 20 – 94 full seeds. The solid line denotes cumulative germination when samples were combined in one sub-lot. Seeds collected 17.9.1984.



Appendix 3. Germination curves for seed samples from individual trees (dotted lines). Sample size 38 – 109 full seeds. The solid line denotes cumulative germination when samples were combined in one sub-lot. Seeds collected 5.10.1984.



Appendix 4. Germination curves for seed samples from individual trees (dotted lines). Sample size 15 – 105 full seeds. The solid line denotes cumulative germination when samples were combined in one sub-lot. Seeds collected 15.11.1984.



Appendix 5a. Analysis of variance table for the model (11), tree No. 9.

SOURCE		DF	CHI-SQUARE	PROB
GERM	$u_{4(l)}$	1	181.02	0.0001
DATE	$u_{1(i)}$	3	12.89	0.0049
TEMP	$u_{3(k)}$	1	0.22	0.6382
PHOTO	$u_{2(j)}$	2	23.67	0.0001
DATE*TEMP	$u_{13(ik)}$	3	1.95	0.5818
DATE*PHOTO	$u_{12(ij)}$	6	98.85	0.0001
TEMP*PHOTO	$u_{23(jk)}$	2	21.06	0.0001
DATE*TEMP*PHOTO	$u_{123(ijk)}$	6	75.37	0.0001
GERM*PHOTO	$u_{24(jl)}$	2	80.46	0.0001
GERM*TEMP	$u_{34(kl)}$	1	56.82	0.0001
GERM*DATE	$u_{14(il)}$	3	44.82	0.0001
GERM*DATE*TEMP	$u_{134(ikl)}$	3	37.45	0.0001
GERM*TEMP*PHOTO	$u_{234(jkl)}$	2	72.57	0.0001
GERM*DATE*PHOTO	$u_{124(ijl)}$	6	11.82	0.0660
LIKELIHOOD RATIO		6	13.37	0.0375

Observed and predicted frequencies, and standardized residuals:

GERM (l)	DATE (i)	TEMP (k)	PHOTO (j)	OBS. FREQ.	PRED. FREQ.	RESIDUAL r	GERM (l)	DATE (i)	TEMP (k)	PHOTO (j)	OBS. FREQ.	PRED. FREQ.	RESIDUAL r
1	1	1	1	0.5	0.01	0.69	2	1	1	1	45	45.37	–0.61
1	1	1	2	0.5	2.20	–1.30	2	1	1	2	49	47.29	1.31
1	1	1	3	41	39.66	1.15	2	1	1	3	1	2.33	–1.15
1	1	2	1	34	35.35	–1.16	2	1	2	1	3	1.65	1.16
1	1	2	2	34	33.15	0.91	2	1	2	2	1	1.84	–0.92
1	1	2	3	29	28.49	0.71	2	1	2	3	0.5	1.01	–0.71
1	2	1	1	0.5	1.01	–0.71	2	2	1	1	49	48.49	0.71
1	2	1	2	21	20.12	0.93	2	2	1	2	58	58.87	–0.94
1	2	1	3	79	79.36	–0.60	2	2	1	3	1	0.64	0.60
1	2	2	1	35	36.66	–1.29	2	2	2	1	3	1.33	1.29
1	2	2	2	70	69.01	0.99	2	2	2	2	2	2.98	–0.99
1	2	2	3	62	61.31	0.87	2	2	2	3	1	1.69	–0.83
1	3	1	1	14	16.84	–1.68	2	3	1	1	28	25.15	1.69
1	3	1	2	51	47.66	1.82	2	3	1	2	1	4.34	–1.83
1	3	1	3	46	46.48	–0.69	2	3	1	3	0.5	0.01	0.69
1	3	2	1	54	52.46	1.23	2	3	2	1	0.5	2.03	–1.24
1	3	2	2	16	18.16	–1.47	2	3	2	2	3	0.84	1.47
1	3	2	3	56	55.37	0.79	2	3	2	3	1	1.63	–0.79
1	4	1	1	16	13.01	1.72	2	4	1	1	52	54.99	–1.73
1	4	1	2	46	48.50	–1.58	2	4	1	2	15	12.49	1.58
1	4	1	3	31	31.47	–0.69	2	4	1	3	0.5	0.02	0.69
1	4	2	1	70	68.51	1.21	2	4	2	1	0.5	1.98	–1.22
1	4	2	2	68	67.66	0.57	2	4	2	2	2	2.33	–0.58
1	4	2	3	52	53.81	–1.34	2	4	2	3	3	1.18	1.35

Appendix 5b. Analysis of variance table for the model (11), tree No. 26.

SOURCE		DF	CHI-SQUARE	PROB
GERM	$u_{4(l)}$	1	153.50	0.0001
DATE	$u_{1(i)}$	3	14.63	0.0022
TEMP	$u_{3(k)}$	1	0.16	0.6924
PHOTO	$u_{2(j)}$	2	14.15	0.0008
DATE*TEMP	$u_{13(ik)}$	3	14.53	0.0023
DATE*PHOTO	$u_{12(ij)}$	6	34.67	0.0001
TEMP*PHOTO	$u_{23(jk)}$	2	41.86	0.0001
DATE*TEMP*PHOTO	$u_{123(ijk)}$	6	44.50	0.0001
GERM*PHOTO	$u_{24(jl)}$	2	170.70	0.0001
GERM*TEMP	$u_{34(kl)}$	1	94.09	0.0001
GERM*DATE	$u_{14(il)}$	3	50.15	0.0001
GERM*DATE*TEMP	$u_{134(ikl)}$	3	21.02	0.0001
GERM*TEMP*PHOTO	$u_{234(jkl)}$	2	36.24	0.0001
GERM*DATE*PHOTO	$u_{124(ijl)}$	6	36.81	0.0001
LIKELIHOOD RATIO		6	13.28	0.0389

Observed and predicted frequencies, and standardized residuals:

GERM (l)	DATE (i)	TEMP (k)	PHOTO (j)	OBS. FREQ.	PRED. FREQ.	RESIDUAL r	GERM (l)	DATE (i)	TEMP (k)	PHOTO (j)	OBS. FREQ.	PRED. FREQ.	RESIDUAL r
1	1	1	1	0.5	0.02	0.69	2	1	1	1	86	86.47	–0.69
1	1	1	2	0.5	1.33	–0.91	2	1	1	2	86	85.16	0.91
1	1	1	3	66	65.64	0.59	2	1	1	3	5	5.35	–0.59
1	1	2	1	53	53.47	–0.69	2	1	2	1	34	33.52	0.69
1	1	2	2	72	71.16	0.91	2	1	2	2	0.5	1.33	–0.91
1	1	2	3	86	86.35	–0.59	2	1	2	3	0.5	0.14	0.59
1	2	1	1	0.5	1.36	–0.93	2	2	1	1	94	93.13	0.93
1	2	1	2	27	25.84	1.07	2	2	1	2	77	78.15	–1.07
1	2	1	3	102	102.28	–0.53	2	2	1	3	2	1.71	0.53
1	2	2	1	68	67.13	0.93	2	2	2	1	25	25.86	–0.93
1	2	2	2	86	87.15	–1.07	2	2	2	2	4	2.84	1.10
1	2	2	3	101	100.71	0.53	2	2	2	3	1	1.28	–0.53
1	3	1	1	13	14.61	–1.27	2	3	1	1	80	78.38	1.27
1	3	1	2	64	62.35	1.28	2	3	1	2	8	9.64	–1.28
1	3	1	3	74	74.03	–0.18	2	3	1	3	0.5	0.46	0.18
1	3	2	1	81	79.38	1.27	2	3	2	1	4	5.61	–1.27
1	3	2	2	89	90.64	–1.28	2	3	2	2	2	0.35	1.28
1	3	2	3	93	92.96	0.18	2	3	2	3	1	1.03	–0.18
1	4	1	1	33	30.99	1.41	2	4	1	1	59	61.00	–1.41
1	4	1	2	56	57.96	–1.40	2	4	1	2	34	32.03	1.40
1	4	1	3	109	109.03	–0.19	2	4	1	3	1	0.96	0.19
1	4	2	1	90	92.00	–1.41	2	4	2	1	7	4.99	1.41
1	4	2	2	104	102.03	1.40	2	4	2	2	1	2.96	–1.40
1	4	2	3	93	92.96	0.19	2	4	2	3	3	3.03	–0.19

Appendix 5c. Analysis of variance table for the model (12), tree No. 100.

SOURCE		DF	CHI-SQUARE	PROB
GERM	$u_{4(l)}$	1	327.19	0.0001
DATE	$u_{1(i)}$	2	26.28	0.0001
TEMP	$u_{3(k)}$	1	3.02	0.0821
PHOTO	$u_{2(j)}$	2	56.63	0.0001
DATE*TEMP	$u_{13(ik)}$	2	8.30	0.0157
DATE*PHOTO	$u_{12(ij)}$	4	11.50	0.0215
TEMP*PHOTO	$u_{23(jk)}$	2	5.67	0.0586
DATE*TEMP*PHOTO	$u_{123(ijk)}$	4	9.85	0.0429
GERM*PHOTO	$u_{24(jl)}$	2	225.03	0.0001
GERM*TEMP	$u_{34(kl)}$	1	23.00	0.0001
GERM*TEMP*PHOTO	$u_{234(jkl)}$	4	41.18	0.0001
GERM*DATE*PHOTO	$u_{124(ijl)}$	2	30.87	0.0001
LIKELIHOOD RATIO		8	7.39	0.4954

Observed and predicted frequencies, and standardized residuals:

GERM *(l)*	DATE *(i)*	TEMP *(k)*	PHOTO *(j)*	OBS. FREQ.	PRED. FREQ.	RESIDUAL r	GERM *(l)*	DATE *(i)*	TEMP *(k)*	PHOTO *(j)*	OBS. FREQ.	PRED. FREQ.	RESIDUAL r
1	3	1	1	7	7.90	–0.95	2	3	1	1	67	66.09	0.95
1	3	1	2	76	77.07	–1.03	2	3	1	2	5	3.92	1.04
1	3	1	3	68	69.92	–1.38	2	3	1	3	3	1.07	1.39
1	3	2	1	46	45.78	0.46	2	3	2	1	31	31.21	–0.47
1	3	2	2	82	81.61	0.62	2	3	2	2	0.5	0.89	–0.62
1	3	2	3	74	72.76	1.11	2	3	2	3	0.5	1.73	–1.11
1	4	1	1	33	31.09	1.38	2	4	1	1	57	58.90	–1.38
1	4	1	2	75	75.57	–0.76	2	4	1	2	7	6.42	0.76
1	4	1	3	84	82.63	1.17	2	4	1	3	2	3.36	–1.17
1	4	2	1	88	90.08	–1.44	2	4	2	1	16	13.91	1.44
1	4	2	2	77	76.60	0.62	2	4	2	2	1	1.39	–0.63
1	4	2	3	69	70.54	–1.24	2	4	2	3	6	4.45	1.24
1	5	1	1	30	31.00	–1.00	2	5	1	1	52	50.99	1.00
1	5	1	2	86	84.34	1.29	2	5	1	2	7	8.65	–1.29
1	5	1	3	92	91.44	0.74	2	5	1	3	3	3.55	–0.74
1	5	2	1	68	66.13	1.37	2	5	2	1	7	8.86	1.37
1	5	2	2	100	100.78	–0.89	2	5	2	2	3	2.21	0.89
1	5	2	3	72	71.68	0.56	2	5	2	3	4	4.31	–0.56

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