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Effect of years and origins into the seed production of Scots Pine (*Pinus sylvestris*) in Finland

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RESUMEN EN CASTELLANO

El 75% de la superficie de Finlandia está cubierta por bosque cuyas especies principales son: el pino silvestre (*Pinus sylvestris*), la pícea común (*Picea abies*), el abedul pubescente (*Betula pubescens)* y el abedul péndulo (*Betula pendula*). El pino silvestre es la especie dominante y ocupa un 65% de la superficie forestal del país. Se caracteriza por ser la especie más extendida del género *Pinus*, desde Portugal a Siberia y desde Noruega a España.

El objetivo de la política forestal finesa es garantizar la producción de madera de alta calidad al mismo tiempo que se conserva la biodiversidad y el uso múltiple de los bosques. Los bosques, los productos forestales y los servicios que proporcionan los ecosistemas son una parte importante de la economía nacional para mitigar el cambio climático y proporcionar servicios de bienestar a la sociedad.

El Instituto de Investigación Forestal Finés (METLA) es el principal centro de investigación de temática forestal de Finlandia y uno de los más grandes de Europa. El presente trabajo de investigación sobre la producción de semilla del pino silvestre en Finlandia y su posibilidad de adaptarse a futuras condiciones climáticas, se encuentra dentro de los estudios sobre cambio climático de METLA. Las preguntas que van ser respondidas son: (1) ¿Cuáles son los factores de variación más importantes en el ratio de flores que desarrollan conos y en el número de semillas por cono? (2) ¿Cuáles son las razones de dicha variación? (3) ¿Hay posibilidad de flujo genético? (4) ¿Podría el pino silvestre adaptarse al cambio climático?

Para ello, ocho áreas ocupadas de forma natural por *Pinus sylvestris* y localizadas a diferentes latitudes en Finlandia fueron seleccionadas y estudiadas desde 1997 hasta 2001. En cada una de ellas y de forma aleatoria, se seleccionaron tres rodales y entre 10 y 15 árboles por rodal. Desde 1997 a 2000, se realizó un seguimiento fenológico durante la estación de crecimiento de unas 27 flores masculinas y 27 femeninas por árbol, en el que se anotaba el comienzo y el final de la floración. Las piñas (que se obtuvieron de las flores femeninas medidas el año anterior) fueron recogidas al final de la estación de crecimiento y enviadas al Centro de Semillas entre los años 1998 y 2001.

Un análisis estadístico realizado con el programa SYSTAT 9 muestra el efecto de los años y las procedencias en la producción de semilla del pino silvestre. Las variables estudiadas son el ratio de flores que desarrollan cono y el número de semillas por cono. Se ha realizado un análisis de varianza de ambas variables y algunas correlaciones entre ellas y otras variables como el día de apertura de la flor femenina y el tiempo que permanece abierta.

Los resultados muestran que el 90.2% de los árboles cuyos de los brotes incluidos en el presente estudio desarrollan flores y el 78.7% llegan a convertirse en cono. El área 4 en 1997 posee el mayor ratio de flores que desarrollan cono (0.823; SD= 0.145) así como el mayor número de semillas por cono (22.828; SD= 6.110). El menor ratio de flores que desarrollan cono se encuentra en el área 8 en el año 2000 (0.145; SD= 0.244) y el menor número de semillas por cono se encuentra también en el área 8 pero en 1998 (5.633; SD= 6.043). Ambas variables tienen una

tendencia descendente con el paso de los años. En cuanto a la variación geográfica, los mayores ratios de flores que desarrollan cono se encuentran en las áreas situadas al norte y, en relación con el número de semillas por cono los mayores valores se encuentran en las áreas situadas en las zonas centrales del país. Se ha encontrado una correlación directa y positiva entre ambas variables de estudio: a mayor ratio de desarrollo, mayor cantidad de semillas por cono.

Debido a que era necesario que los pinos fueran capaces de producir flores (es decir, fueran árboles maduros) y de pequeño tamaño para poder realizar el seguimiento fenológico, las condiciones del emplazamiento de los rodales pueden ser diferentes entre el norte y el sur. Por lo general, los rodales situados en el norte se localizan en un sitio de mayor calidad que los rodales del sur (por ejemplo, los rodales del área 7 eran muy viejos y estaban en un terreno rocoso). Este factor se debe tener en cuenta y podría explicar en parte, los altos ratios de flores que desarrollan cono en las áreas del norte. Por otro lado, también son factores a tener en cuenta el tiempo de floración, la polinización y la posibilidad de flujo genético entre poblaciones. La floración del pino silvestre no está totalmente sincronizada, en otras palabras, las flores femeninas se encuentran receptivas antes que las masculinas empiecen a florecer y esta diferencia varía entre las distintas áreas. Además, la floración comienza antes en el sur que en el norte debido a las temperaturas. Este hecho y la posibilidad del polen del pino silvestre de viajar grandes distancias sin perder la capacidad para germinar hacen posible la existencia de flujo de genes entre poblaciones. Para esto puede haber dos interpretaciones: que las poblaciones del norte tengan más cantidad de polen y la polinización sea suficiente o que las diferencias genéticas entre el padre y la madre produzcan una baja productividad. En algunos casos del estudio, los mayores ratios y número de semillas aparecen cuando la floración masculina y femenina de la misma área coincide en el tiempo. Asimismo, existe una variación en función de los años. Las condiciones climáticas durante la iniciación del brote, la polinización y la fertilización afectan el desarrollo de la piña. Las primaveras de 1996 a 1998 fueron especialmente frías y esto puede justificar la disminución del ratio de flores que desarrollan conos y el número de semillas por cono descienda desde el año 1997 al 2000. El alto porcentaje de conos desarrollados en áreas en que la flor femenina está receptiva antes que la masculina apoya investigaciones previas sobre el movimiento de polen y la posibilidad de flujo genético.

Los años y las distintas procedencias afectan a la variación de producción de semilla del pino silvestre y muchos factores como las condiciones del lugar, el tiempo de floración, el flujo genético o las condiciones climáticas son responsables de esa variación. Además la existencia de dicho flujo genético a través del movimiento del polen puede favorecer a la adaptación del pino silvestre al cambio climático debido a que las poblaciones del norte reciben polen de las situadas al sur cuyo clima es más cálido. Sin embargo, sería necesario profundizar en esta investigación desarrollando estudios de mayor amplitud.

0. THESIS ABSTRACT

Eight areas of natural populations of Scots pine (*Pinus sylvestris L.)* located at different latitudes in Finland were selected and studied from 1997 to 2001 to analyse the differences in ratio of flowers which develop into cones and number of full seeds per cone.

Many factors as weather conditions, previous cone crops, site conditions and flowering time can affect the seed production. The results showed the possibility of gene flow from south to north due to the gap in flowering phenology and the pollen possibility to travel large distances without losing its viability. This fact can help Scots pine populations in their adaptation to future climate conditions.

Keywords: Scots pine (*Pinus sylvestris*), flowering, seeds, gene flow, adaptation.

1. INTRODUCTION

1.1. FORESTS IN FINLAND

Finland is one of the most heavily-forested countries in Europe and its forests cover 75 percent of Finland's area, 23 million hectares (Finnish Forest Association, n.d.; Finnish Forest Research Institute, 2011b). It is located in the northern coniferous area or the taiga (figure 1) that is characterized by a short growing season and a limited number of tree species (Finnish Forest Research Institute, 2011b). The most common species are Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), Downy birch (*Betula pubescens*) and Silver birch (*Betula pendula*) (Finnish Forest Association, n.d.; Finnish Forest Research Institute, 2011b). *Pinus sylvestris* is the dominant species on 65% of the forest land area (Finnish Forest Research Institute, 2011b).

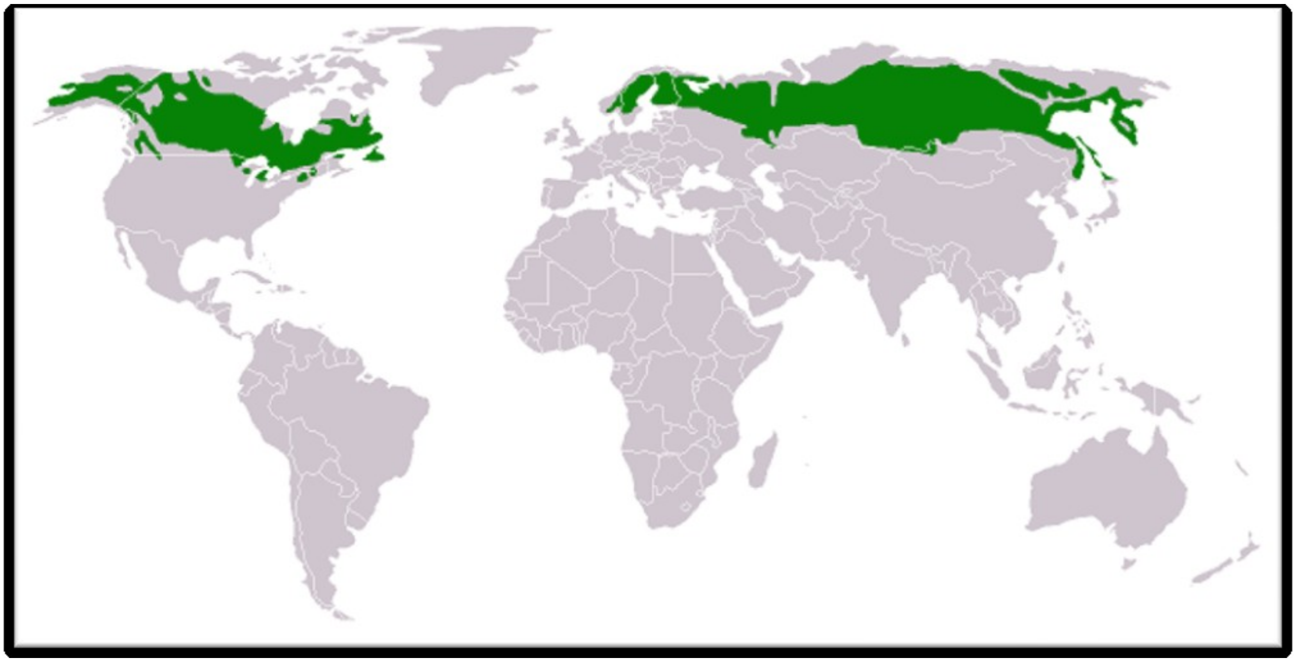

Figure 1. Distribution of the Taiga. Source: Wikipedia, 2009.

According with the last national forest inventory, the total growing stock volume is 2206 million m^3 over bark and the annual volume increment is about 100 million m^3 (Finnish Forest Research Institute, 2011c; Pulkkinen, pers.comm.). Nevertheless, the use of wood is far lower than that annual growth and its forests are also a carbon sink (removing carbon from the atmosphere equivalent to about half of the carbon dioxide emitted by Finland's industry per year) (Parviainen & Västilä, 2011).

The aim of Finnish forestry is to guarantee the production of high-quality timber and to preserve the forest biodiversity respecting the natural growth and cycle of boreal forest and the conditions of multiple use of forest (Finnish Forest Research Institute, 2011b).

Forests, forest products and ecosystem services are an important part of Finland's national economy to mitigate the impact of climate change to produce well-being services for citizens (Parviainen & Västilä, 2011).

1.1.1. Finnish Forest Research Institute

The Finnish Forest Research Institute (METLA) is the main forest research institution in Finland and one of the biggest forest research institutes in Europe. It was established in 1917 and it is an independent research organization working under the supervision of the Ministry of Agriculture and Forestry (Finnish Forest Research Institute, 2011a).

METLA carries out several activities within these areas: entrepreneurial and business activity based on forest, forest and the community, sustainable silvicultural chains and forest economy (and forest environment) based knowledge pool. Its mission is to promote the ecologically, economically and socially sustainable development of the forest and forestry through research (Finnish Forest Research Institute, 2011a).

1.2. SCOTS PINE

Scots pine (*Pinus sylvestris* L., family Pinaceae) is characterized by a very extensive range, the most extensive of all species of *Pinus* genus (Giertych & Mátyás, 1991). In Europe, it spreads from Portugal (8˚ W) to Siberia (140˚ E) and from Norway (70˚ N) to Spain (37˚ S) (Mirov, 1967) (figure 2). In the Northern Eurasia it grows from sea level up to 1000 m but in the southern regions it occurs only above 500 m in the mountainous areas (Finnish Forest Research Institute, 2010). It grows in dry and harsh habitats (Finnish Forest Research Institute, 2010).

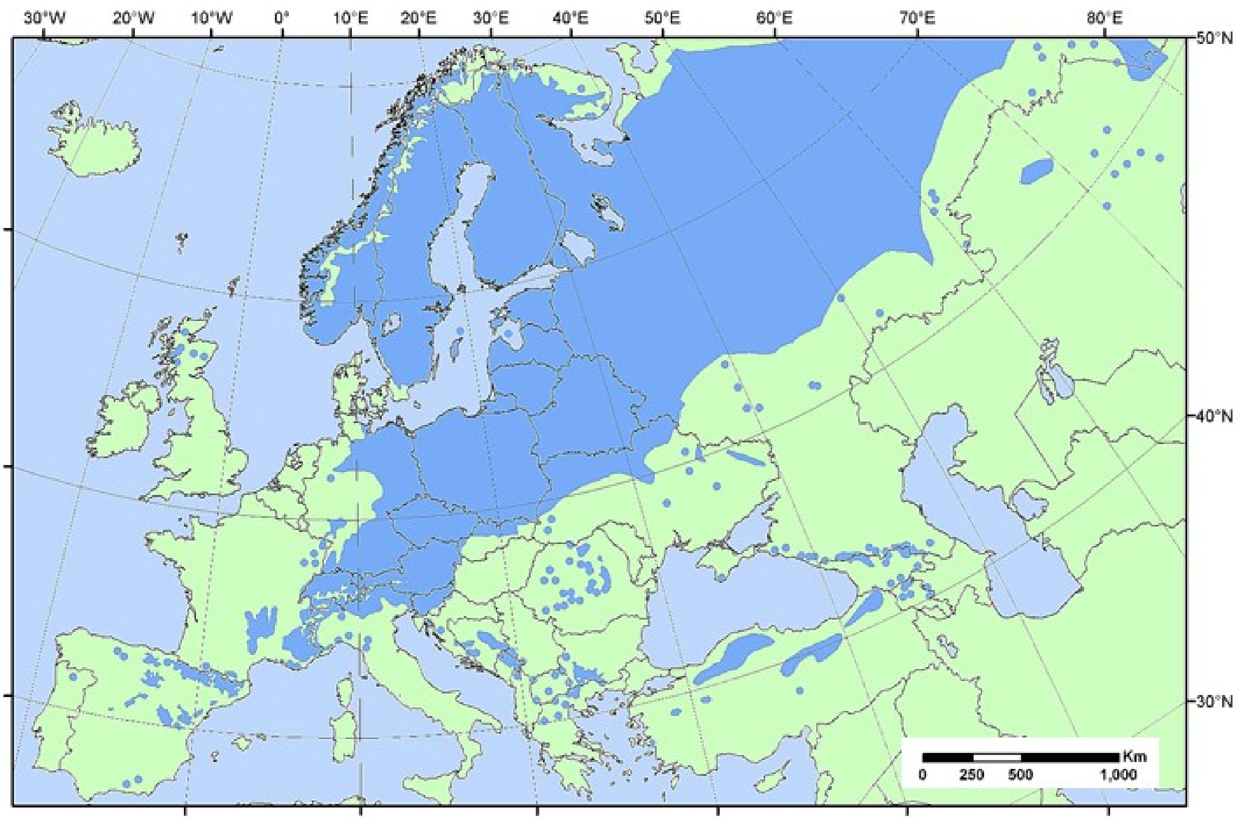

Figure 2. Distribution map of Scots pine (*Pinus sylvestris)* in Europe. Source: EUFORGEN, 2009.

This species evidently has an enormous capability of adapting to different climatic conditions and the marked genetic and vegetation variation within populations is an important factor that it contributes to its success (Parantainen & Pulkkinen, 2002).

1.2.1. Physical characteristics

Pinus sylvestris is an evergreen, light-demanding coniferous tree growing up to 25-40 m height and 50-120 cm at breast height (Finnish Forest Research Institute, 2010). The trunk is slim and straight with branches in the lower parts and the crown has variable shapes (Finnish Forest Research Institute, 2010). Its bark is thick, scarly dark grey-brown on the lower trunk, on the upper trunk and branches it is thin, flaky and orange. Until the pine stops its growth, the crown is conic and entire and then becomes flat-topped on long and bare (Mitchell, 1974).

The shoots are brown and often covered of sticky resin. Needles grow in pairs with a persistent grey 5-10 mm basal sheath, are glaucous blue-green and often darker green to dark yellowish green in winter. They are 2.5-5 cm long and 1-2 mm wide. Leaf persistence varies from two to four years in warmer climates and to nine years in subarctic regions (Trees for life, 1998).

Male and female flowers appear in May and they occur on the same tree (Trees for life, 1998). Female flowers are on the tips of the higher and more exposed branches and the male ones clustered together at the base of weaker new shoots on the branches below (Mitchell, 1974; Trees for life, 1998). Pollination is by wind and fertilised female flower need two years to become a full cone (Trees for life, 1998). The growth occurs during mid-May or early July and young trees can growth one metre per year (Mitchell, 1974). Life span is usually 150-300 years (Mitchell, 1974).

1.2.2. Seed development and maturation

Scots pine has a three-year reproductive cycle typical of most *Pinus* species. The first year of the cycle, the reproductive buds are initiated during the growing season. Male and female flowers appear in the spring of the second year. Male flowering is followed by the beginning of the development of the pollen tube. The development continues the following spring after the winter in a dormant condition. Approximately after 13 months the fertilization of the ovule takes place. Once pollinated the female flowers turn green and develop into mature cones (Nygren, 1987).

Seeds mature and cones ripen during the autumn and seed dispersal occurs from December to March (Nygren, 1987; Sullivan, 1993). In cool climate the time between the initiation of reproductive buds and the seed maturation is about 27 months (Nygren, 1987).

Cone production is variable; a mature tree with good seasons can produce 3000 cones, occurring every 3-5 years, while other tree will produce few cones or none at all. Seeds are carried as far as 50-100 metres from the parent tree but in some situations the seeds can travel several kilometres over the smooth, icy surface (Trees for life, 1998).

1.2.3. Gene flow and adaptation

Gene flow or gene migration is the transfer of alleles or genes from one population to another and it is possible in plants by the capacity of seed and pollen dispersal (Kremer et al., 2012). That dispersion can increase the genetic variation of local individuals and their effectiveness depends on several physical and biological processes that determine the amount of pollen and seeds like their movement, their viability before and during the movement or the probability of successful pollination (Kremer et al., 2012).

Local adaptation can be favoured by gene flow and his interaction with other evolutionary forces such as selection, phenotypic plasticity and inbreeding depression (Raymond et al., 2012). Gene flow is extensive enough to homogenize neutral variation among populations and increases the variance within populations (Raymond et al., 2012).

1.2.4. Utilization of Scots pine seeds in Finland

Scots pine is the most important species in forest regeneration in Finland (80% in the total artificial regeneration area). In the 80's it has been planted (70%) or direct-seeded (30%) on 100000 – 120000 ha annually. Natural regeneration has been practiced on a similar extension to direct seedling (Giertych & Mátyás, 1991).

The annual utilization of Scots pine seed has been around 3t in forest nurseries and 12t in direct seedlings. About 160 million plants per year are used for planting, but direct seedling predominates in the north (Giertych & Mátyás, 1991).

1.3. IMPACT OF CLIMATE CHANGE ON BOREAL FORESTS

Boreal forests are likely to be affected by climate change because of their sensitivity to warming and to respond to increasing external forcing in a non-linear way (i.e. warmer temperatures over the last decades have increased or decreased tree growing, depending on the species, site type and region) (Olsson, 2009).

The mean annual temperature is projected to increase from 2ºC to 6ºC and rainfall by 5% to 25% by the year 2100 as compared with the past 30 years (Parviainen & Västilä, 2011). Climate change may cause great impacts on growth (increase could be about 20% to 50%, depending on the tree species), health and biodiversity of boreal forest ecosystems (Finnish Forest Research Institute, 2011a; Parviainen & Västilä, 2011). Extreme weather phenomena like drought, forest fires, storms and snow damage can produce tree destruction or producing a massive proliferation of forest pests because of the accumulation of deadwood in healthy forest (Parviainen & Västilä, 2011). In addition, negative effects of climate change may be large because forests will be unable to adapt to altered environment conditions (Olsson, 2009).

The proportions of Scots pine and Norway spruce in Southern Finland will be reduced from the current 40-50% to less than 10-20%, with increased dominance of birches (Kellomäki et al., 2001). In Northern Finland, the proportion of these species will be balanced at a level of 40% (increase in spruce and reduction in pine) and the proportion of birches increased on the most fertile soils (Kellomäki et al., 2001).

Therefore, it is important to take actions to mitigate the climate change effects and to adapt the forests to the future changes on the international policies and the forest sector (Finnish Forest Research Institute, 2011a).

1.4. BACKGROUND

According to Sarvas (1962) there are several factors that affect the quantity of pine seed crop. Abundance of pollination, number of ovules developing in the spring at the time of flowering (abundance and size of female strobili that depend on environmental factors) and proper flowering (abortion of non pollinated ovules and dropping of falling down insufficiently pollinated female strobili after flowering) are the principal ones. In areas where pine grows abundantly, the cone crop of small mixed stands is high because the dropping of conelets is less frequent (Sarvas, 1962). Furthermore, damages by insects, fungi and weather can destroy the seed (Pukkala et al., 2010; Sarvas, 1962).

On the other hand, stand parameters like fertility, age, density, height and size of living crown influence the seed crop too (Pukkala et al., 2010; Sarvas 1962). There is a correlation between seed crop and site fertility (Sarvas, 1962). If we study the average annual seed crop of two stands in Southern and Northern Finland where the fertility is comparable, we will see that there are not significant differences (Sarvas, 1962). But, if we consider the differences in site fertility, the number of seeds in Northern Finland is smaller than in Southern Finland because the forest sites are much poorer by short and cool summers (Sarvas, 1962).

1.5. AIM OF THE STUDY

The purpose of this research is to analyse the seed production variation between Scots pine populations located at different latitudes in Finland and measured in several years, in order to study the variation depending on years and origins and to find the reason of that variation. In this study, we did not measure the cone production nor the flowering per tree because it is difficult and laborious to perform in large trees.

We are not able to talk about viable seed production per tree and population. We are going to study the ratio of flowers which develop into cones and the number of full seeds per cone. Female and male flowers were observed in wild fields and the cones were collected to store and treat.

The questions which are going to be answered are: (1) Which are the most important sources of variation in ratio of flowers which develop into cones and the number of seeds per cone? (2) Which are the reasons of this variation? (3) Is there any possibility of gene flow? (4) Could Scots pine adapt to climate change?

2. MATERIALS AND METHODS

2.1. STUDY AREAS

Eight areas located at different latitudes in Finland, from south to north (figure 3), were studied from 1997 to 2001 (during all the work we are referring to 1997-2000 when mentioning flowering years). The southernmost stand is located in Turku (latitude 60˚29'N) and the northernmost one in Kevo (latitude 69˚46'N) (figure 3).

In each area three natural stands were selected randomly. In some cases it was not possible to keep the same stands during the whole study. Between the years 1997 and 1998 stands 1 and 3 were replaced for stands 4 in Ivalo (area 3) and Läyliäinen (area 7) respectively (table 1).

Figure 3. Geographical location of the study areas. Source: Google Earth, 2013.

Table 1. Locations of the study stands (*Stand measured in 1997. **Stand measured from 1998 to 2000).

Names	Area	Stand	Latitude	Longitude
Kevo	1	1	69˚46'N	27˚01'E
		2	69˚46'N	27˚02'E
		3	69˚45'N	27˚01'E
Ivalo	2	1*	68˚37'N	27˚53'E
		2	68˚38'N	27˚50'E
		3	68˚09'N	27˚50'E
		4**	68˚02'N	28˚06'E
Sodankylä	3	1	67˚21'N	26˚33'E
		2	67˚00'N	26˚47'E
		3	67˚15'N	26˚19'E
Rovaniemi	4	1	66˚23'N	25˚17'E
		2	66˚23'N	25˚12'E
		3	66˚23'N	25˚11'E
Vuolijoki	5	1	64˚02'N	26˚55'E
		2	64˚02'N	26˚55'E
		3	64˚02'N	26˚55'E
Korpilahti	6	1	62˚03'N	25˚34'E
		2	62˚14'N	25˚32'E
		3	62˚15'N	25˚31'E
Läyliäinen	7	1	60˚36'N	24˚26'E
		2	60˚37'N	24˚22'E
		3*	60˚40'N	24˚21'E
		4**	60˚37'N	24˚25'E
Turku	8	1	60˚29'N	22˚19'E
		2	60˚29'N	22˚21'E
		3	60˚30'N	22˚18'E

2.2. DATA COLLECTION

The data were collected by Finnish Forest Research Institute (METLA) during the years 1997-2001. From ten to fifteen natural Scots pine trees per stand were selected and around twenty seven male and twenty seven female flowers per tree were measured each year.

A phenological monitoring was conducted during the growing season from 1997 to 2000 to observe over 20000 flowers each year (Jaatinen, pers.comm.). The growing season starts when daily mean temperatures exceed 5°C for at least 5 consecutive days in the spring, and ends when the 10 day running mean falls below 5°C (Venäläinen & Nordlund, 1988). The average temperatures and the growing season in each area and year with daily temperatures collected by

Finnish Meteorological Institute were calculated. Average temperatures increase from North to South of Finland and from the year 1995 to 2001 (figure 4). Growing season is longer in southern areas (figure 5) and starts earlier (figure 6) than in northern ones.

Female and male flowers were monitored daily for recording the onset and end of the flowering. Female flower's onset was considered when flower is receptive and its end when flowers are closed (it is unable to receive any pollen). Male flowering was considered when it was possible to shed pollen and its end when there was not any more shedding pollen (Pulkkinen, pers.comm).

Pine cones were collected from 1998 to 2001 at the end of the growing season from the female flowers measured the previous year and immediately sent to the Seed Centre. Cones were maintained at 4ºC until seeds were extracted to be counted and weighed (Jaatinen, pers.comm.).

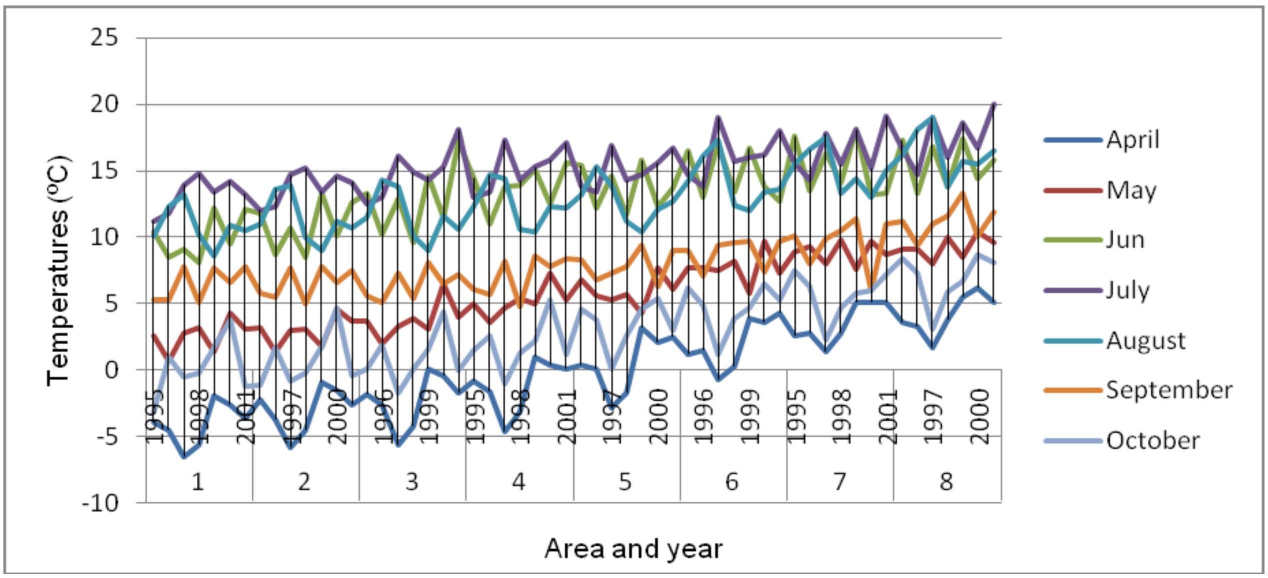

Figure 4. Average temperatures from April to October in the eight study areas from 1995 to 2001. Source: Finnish Meteorological Institute.

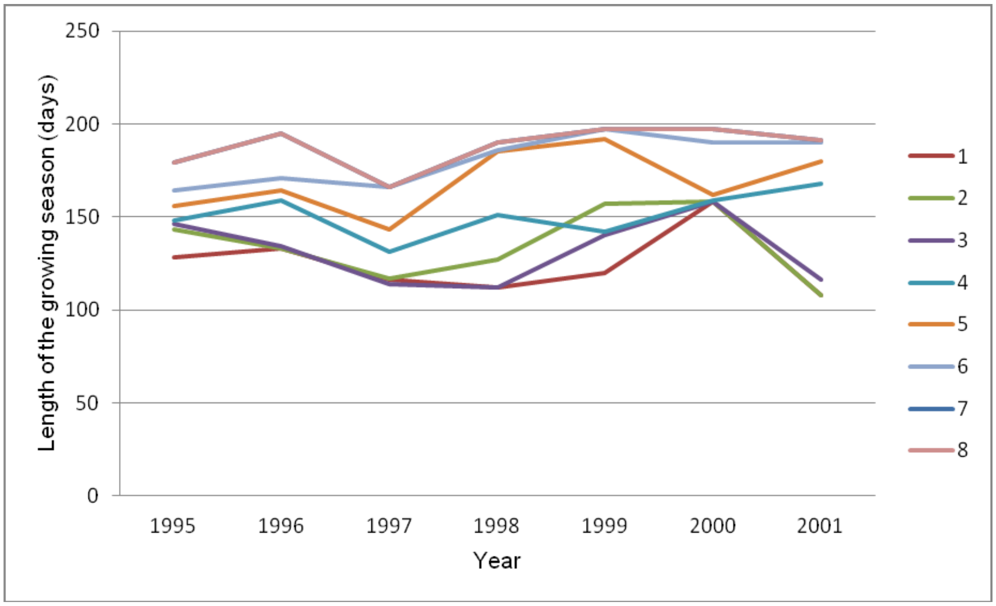

Figure 5. Length of the growing season (days) in the eight study areas from 1995 to 2001.

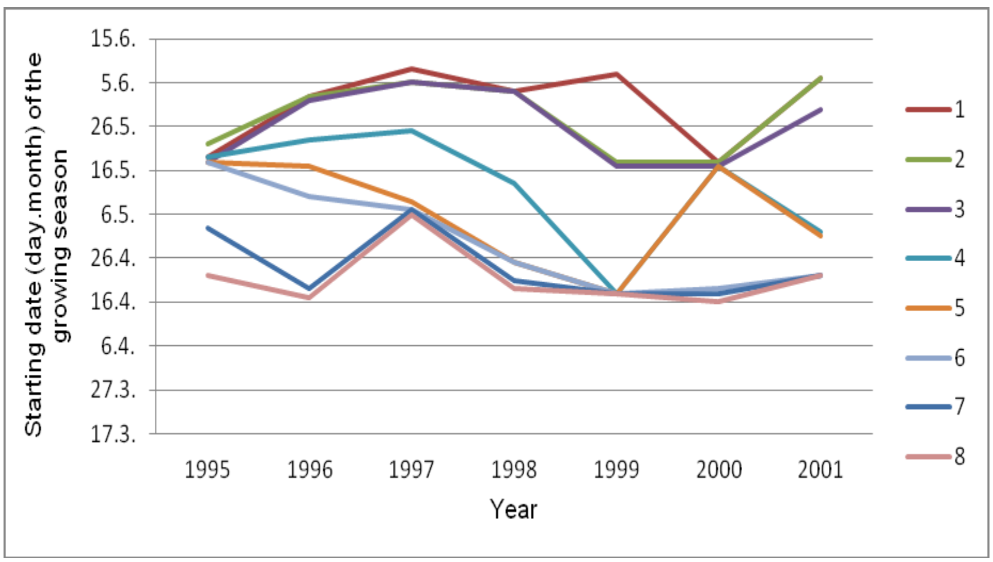

Figure 6. Starting date (day.month) of the growing season in the eight study areas from 1995 to 2001.

2.3. STATISTICAL ANALYSIS

The statistical analysis was carried out using the statistical programme SYSTAT 9, statistical and graphical software. The effect of years and origins in the studied variables were analysed using the analysis of variance (ANOVA).

The ratio of flowers which develop into cones and number of full seeds per cone were studied. The level of variation between years and areas was analysed. Our sources of variation are year, area and stand. Due to lack of data in the number of full seeds per cone (there is flowering data but not cones develop), it was necessary to delete the flowering year 1999 for running the ANOVA. Besides, the influence between flowering year and area on the two study variables was analysed.

In some cases there was not the number of full seeds per cone (only the weight was found) and it was necessary calculate it with a linear regression between the number of full seeds and their weight to get a completed data. To improve the regression, the random effect of flowering year and area were added into the model.

For checking if the data achieved the demands for the analysis of variance, normality (Shapiro-Wilk) and equality of variances (Levene), several randomly transformations of the variables were done. Squared, logarithmic and trigonometric transformations were done for seeds, cones, flowers, ratio of flowers which develop into cones and number of full seeds per cone. We selected those ones where P-value was not significant (P>0.05) in normality and equality. If P-value was always significant (P<0.05) we used the variables without transformations.

To present the results in that work, measures of variability using the mean with standard deviation (mean ± SD) were showed. In the bars graphs a standard deviation of 0.6825 was used as an error bar. In ANOVA's results, the squared multiple R was applied to see the efficiency of the model used and F-ratio to see the percentage of the variation that it is explained by the source.

In addition, some correlation analyses between the studies variables (ratio of flowers which develop into cones and number of full seeds per cone) and female flower opening day and length of the female flowering opening were done. Overlapping in female and male flowering time was studied to understand the different ratios depending on year and area.

3. RESULTS

3.1. CALCULATION OF NUMBER OF FULL SEEDS PER CONE

The following linear regression was used to calculate the number of full seeds per cone where only weight was provided. The variable "Newfullseednumber" is the number of full seeds; "weight" is the weight of the full seeds; "fyear" is flowering year and "area" is the study area.

Newfullseednumber = 6890.226 + 185.245*weight – 3.446*fyear – 0.647*area

The model explained 76.3% of the number of full seed variation. Weight, flowering year and area are significant factors (P<0.05) (table 2).

Table 2. Regression between number of full seeds and their weight.

N: 3259			**Multiple R: 0.874**		**Squared multiple R: 0.763**	
Adjusted squared multiple R: 0.763			**Standard error of estimate: 5.000**			
Effect	**Coefficient**	**Standard error**	**Standard Coefficients of Tolerance**		**t**	**P**
Constant	6890.226	165.441	0.000	0.000	41.648	0.000
Weight	185.245	1.970	0.803	0.998	94.052	0.000
Fyear	-3.446	0.083	-0.355	0.998	-41.617	0.000
Area	-0.647	0.059	-0.094	0.996	-10.961	0.000

Analysis of Variance

Source	**Sum-of- Squares**	**df**	**Mean-Square**	**F-ratio**	**P**
Regression	262022.983	3	87340.994	3493.773	0.000
Residual	81381.209	3255	25.002		

3.2. GENERAL RESULTS

The 90.2% of trees where female flowers buds were included in the study develop into the mature flowers and 78.7% produce cones. The result is 87.2%, in the ratio of flowers which develop into cones. Results are similar if these variables per tree depending on area and stand were studied, but northern areas have the highest percentages (table 3). Area 4 in 1997 has the highest ratio of flowers which develop into cones with a mean of 0.823 (SD= 0.145) and the area 8 in 2000 has the smallest one with a mean of 0.145 (SD= 0.244) (figure 7). Area 4 in 1997 has the maximum value of number of full seeds per cone with a mean of 22.828 (SD= 6.110) and the area 8 in 1998 has the minimum with a mean of 5.633 (SD= 6.043) (figure 8). In areas 5, 7 and 9 in 1999 the values are zero because there is a lack of data.

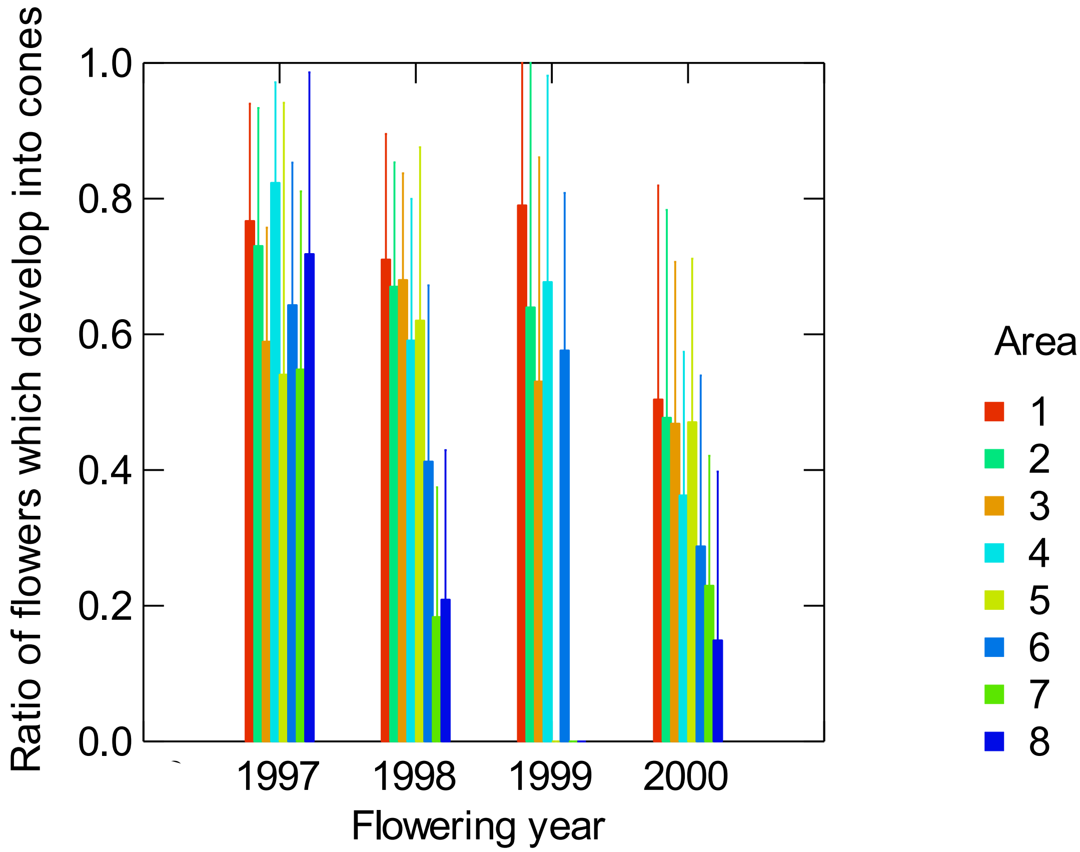

Figure 7. Ratio of flowers which develop into cones per flowering year and area. Standard deviation is included as an error bar (p=0.6825).

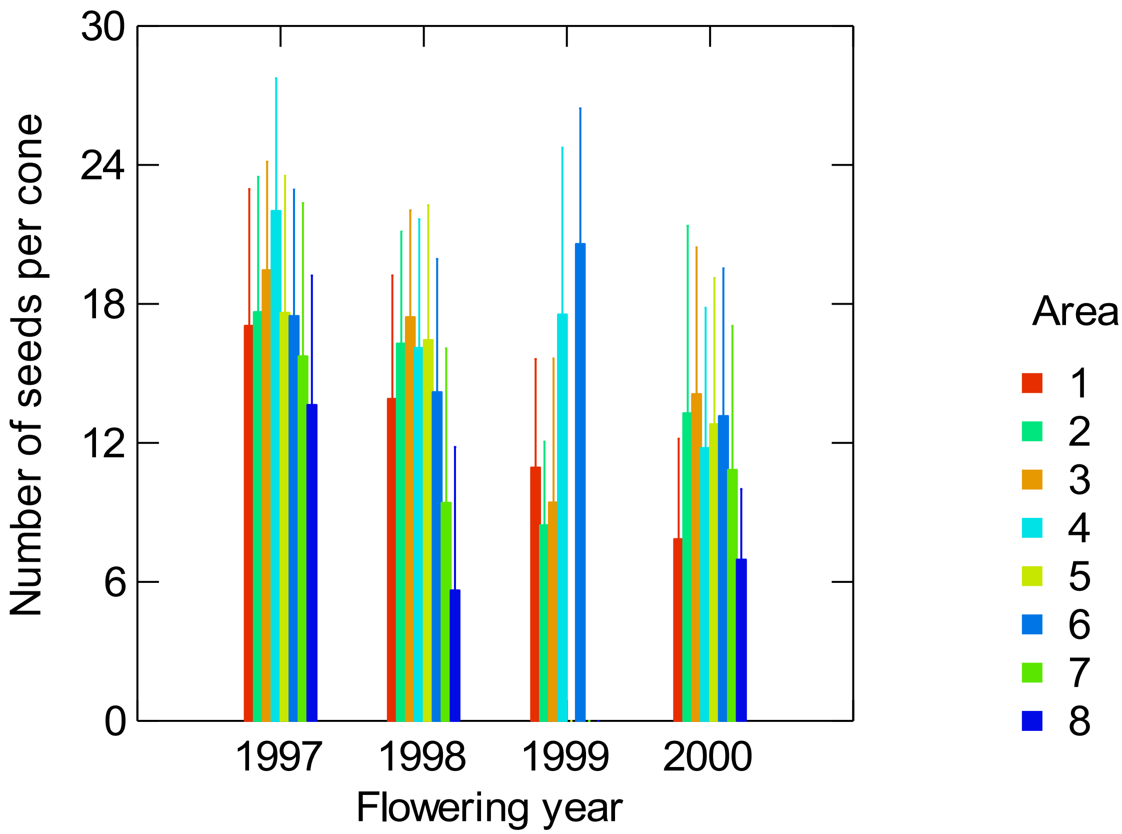

Figure 8. Number of full seeds per cone per flowering year and area. Standard deviation is included as an error bar (p=0.6825).

Table 3. Percentages of trees where the female flower bud develops into a mature flower, into a cone and trees where the female flower develops into a cone per area and stand.

Area	Stand	% Trees with flowers	% Trees with cones	%Trees where the flower develops into a cone
1	1	96.5	94.2	97.7
	2	99.1	97.1	98.0
	3	93.7	89.6	96.2
2	1	100.0	100.0	100.0
	2	85.9	78.6	92.8
	3	91.7	89.5	97.8
	4	93.5	92.0	98.56
3	1	93.9	90.9	97.0
	2	92.8	92.8	100.0
	3	94.4	94.4	100.0
4	1	89.7	88.3	98.7
	2	92.0	91.1	98.8
	3	86.1	86.1	100.0
5	1	82.3	64.4	82.2
	2	92.3	66.7	70.5
	3	80.3	59.9	82.3
6	1	97.9	95.1	97.2
	2	97.0	92.4	95.5
	3	100.0	88.2	88.2
7	1	100.0	73.0	73.0
	2	98.6	78.5	80.6
	3	100.0	100.0	100.0
	4	90.9	66.7	76.7
8	1	86.3	62.3	71.0
	2	92.1	56.9	62.5
	3	94.4	71.9	76.0

3.3. RATIO OF FLOWERS WHICH DEVELOP INTO CONES

ANOVA was used to analyse the effect of flowering year, area, interaction between flowering year and area and stand level within area in ratio of flowers which develop into cones. The model explains 52.8% of the variation and all sources of variation are significant factors ($P<0.05$). Flowering year is the most important source of variation ($F= 109.012$) (table 4).

Table 4. Analysis of variance for ratio of flowers which develop into cones.

N: 1286		Multiple R: 0.727		Squared multiple R: 0.528	
Analysis of Variance					
Source	**Sum-of- Squares**	**df**	**Mean-Square**	**F-ratio**	**P**
Fyear	15.990	3	5.330	109.012	0.000
Area	24.104	7	3.443	70.429	0.000
Area*Fyear	16.849	21	0.802	16.410	0.000
Stand (Area)	6.135	18	0.341	6.972	0.000
Error	60.431	1236	0.049		

How flowering year affects the ratio of flowers which develop into cones is shown in figure 9. The ratio decreases each year, from 0.671 (SD= 0.267) in 1997, 0.568 (SD= 0.266) in 1998, 0.452 (SD= 0.399) in 1999 to 0.394 (SD= 0.276) in 2000.

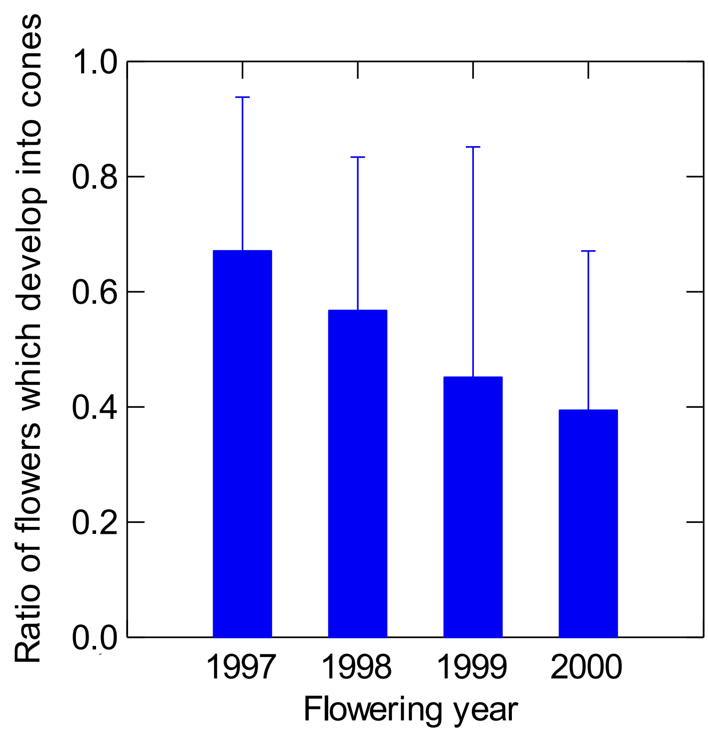

Figure 9. Influence of flowering year on ratio of flowers which develop into cones. Standard deviation is included as an error bar (p=0.6825).

On the other hand, area is the second important source of variation (F= 70.429). Northern areas have a higher ratio of development than southern areas (figure 10). Kevo (area 1) has the largest ratio, with a mean of 0.698 (SD= 0.253) and Läyliäinen (area 7) with 0.255 (SD= 0.272) has the smallest one (figure 10).

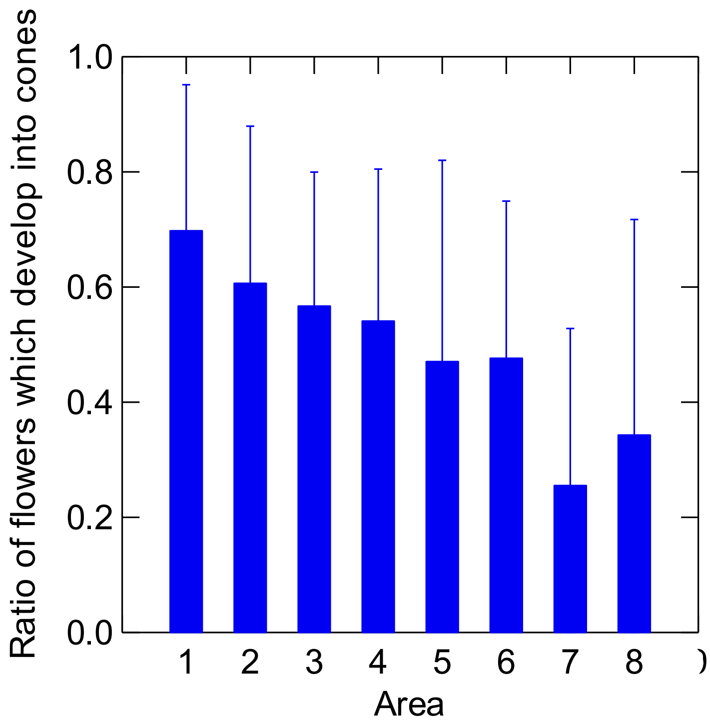

Figure 10. Influence of area on ratio of flowers which develop into cones. Standard deviation is included as an error bar (p=0.6825).

The ratio of flowers which develop into cones changes between years and areas (figure 11). As it was explained before, the flowering year 1997 has the highest ratio of development with a mean of 0.671 (SD= 0.267) and the ratio decreases from 1997 to 2000. In the different areas it is visible that there are not two productive consecutive years. For example, in area 4, in odd years the ratio increases and decreases in the even ones. The same result in areas 3, 5 or 6 can be seen. In areas 5, 7 and 8 in the flowering year 1999 the value is zero because there is a lack of data.

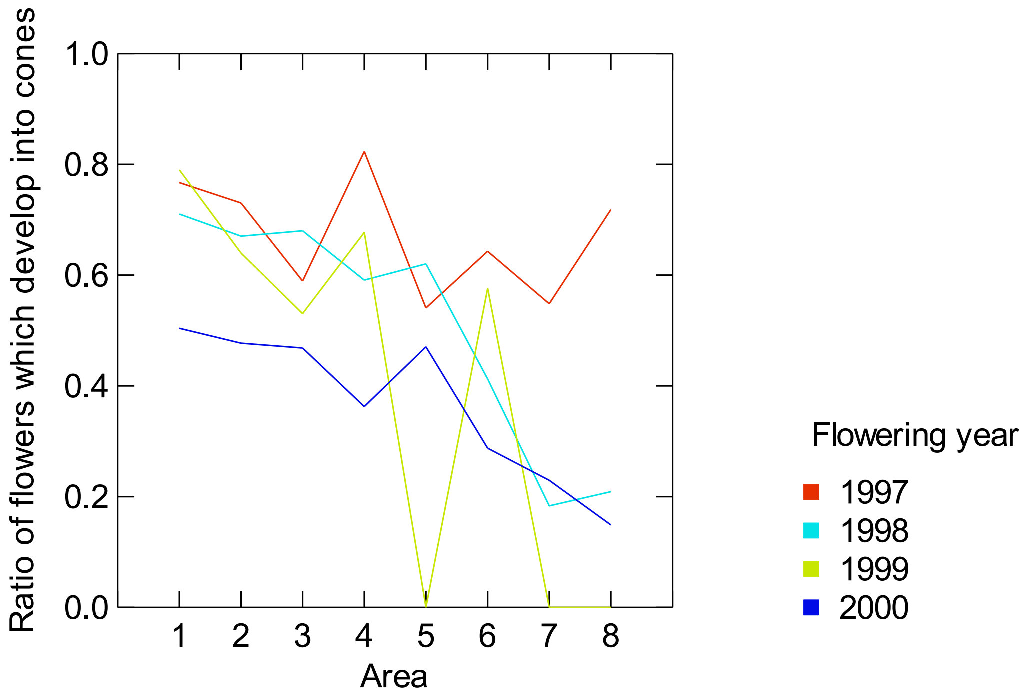

Figure 11. Influence of the interaction between flowering year and area on ratio of flowers which develop into cones.

In order to find variables which have a correlation with the ratio of flowers that develop into cones, the flower opening day and the length of the female flowering opening were analysed. There is a positive significant correlation (r>0 and P<0.05) in eight areas (from area 2 to area 8) between the ratio of flowers which develop into cones and the flower opening day (figure 12). If the flower opens later, it will be more possible its development into a cone. In seven areas, there is a negative (r<0) or non significant (P>0.05) correlation with the length of the female flowering opening day, only in area 5 there is a positive and significant correlation (figure 13). If the flower remains opened longer, there will be fewer possibilities of successfully developing into a cone.

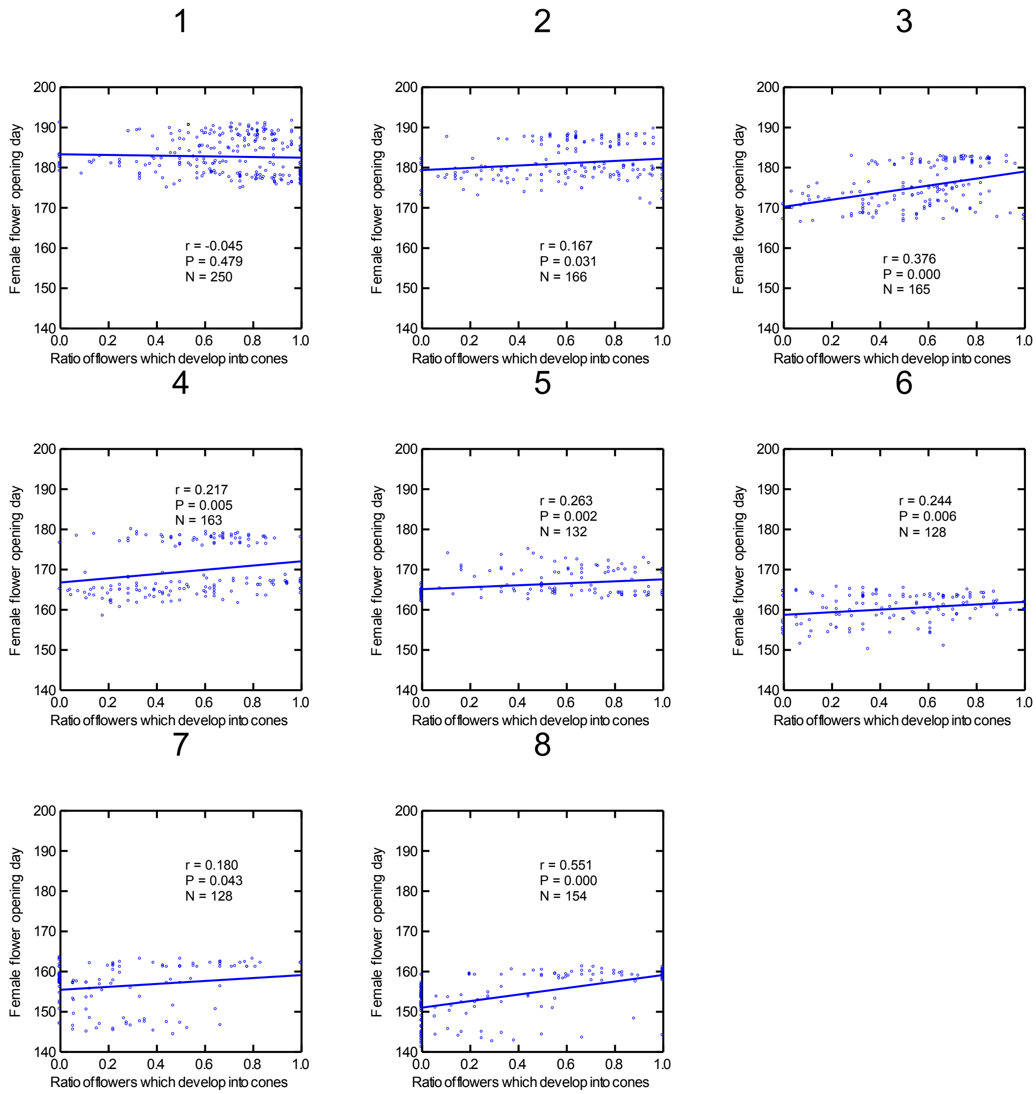

Figure 12. Correlations between the female flower opening day and the ratio of flowers which develop into cones in each study area.

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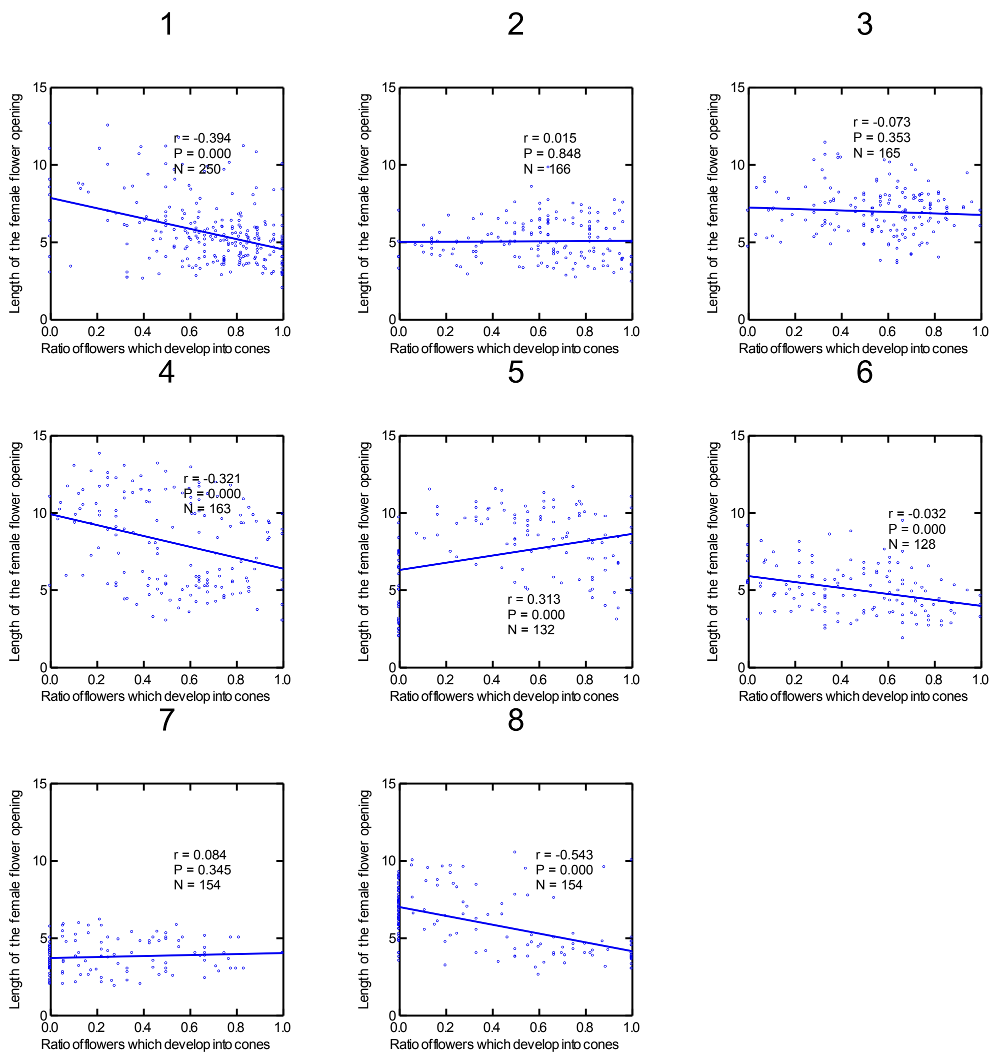

Figure 13. Correlations between the ratio of flowers which develop into cones and the length of the female flower opening in each study area.

Overlapping is another variable to understand the different ratios depending on year and area. In the flowering year 1997, the highest ratio occurs when overlapping is zero (when female and male flowering phenology starts at the same time) (figure 14). From 1998 to 2000, the largest development occurs when female flower opens before male flower. Similar results we have if we analyse it per areas (figure 15). From areas 1 to 6, the largest development occurs when female flower opens before male flower and close to zero in areas 7 and 8.

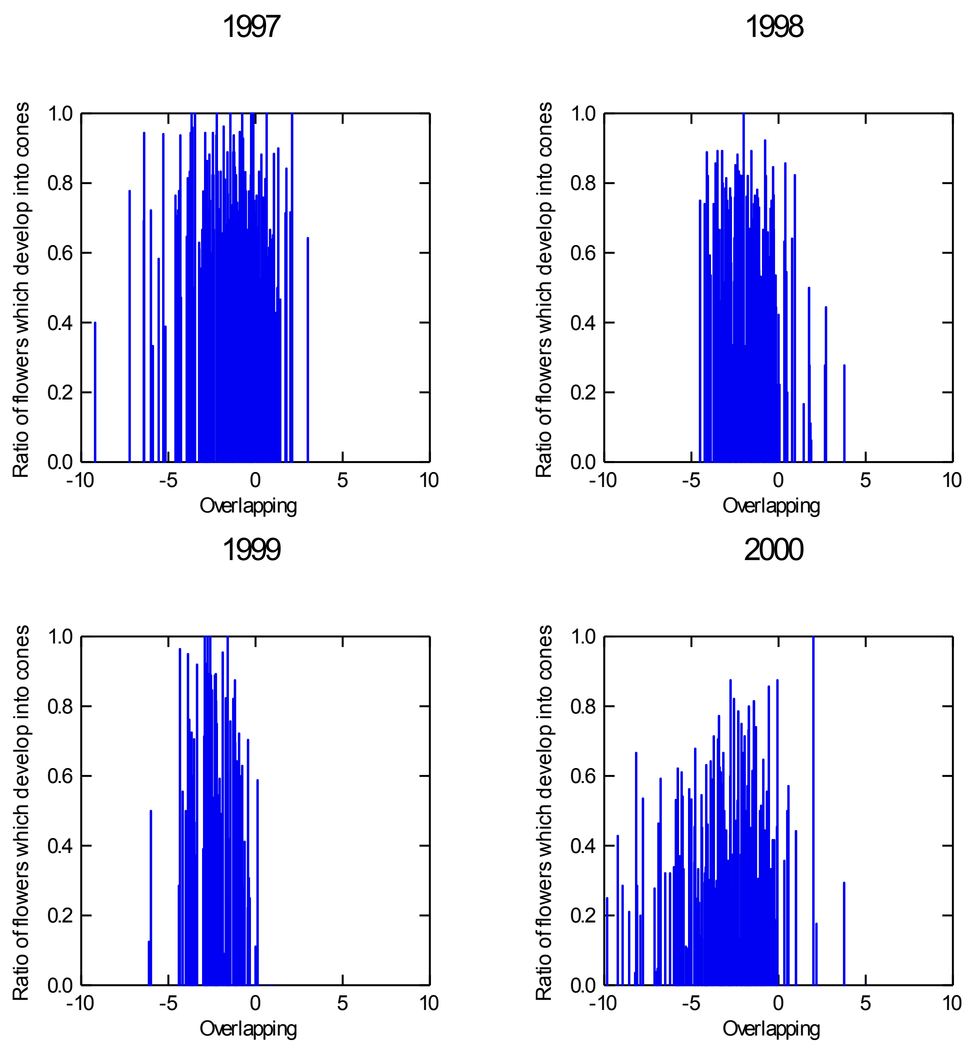

Figure 14. Influence of overlapping on the ratio of flowers which develop into cones in each flowering year (overlapping is zero when female and male phenology starts at the same time and it is negative or positive when female flowering starts earlier or later than male flowering respectively).

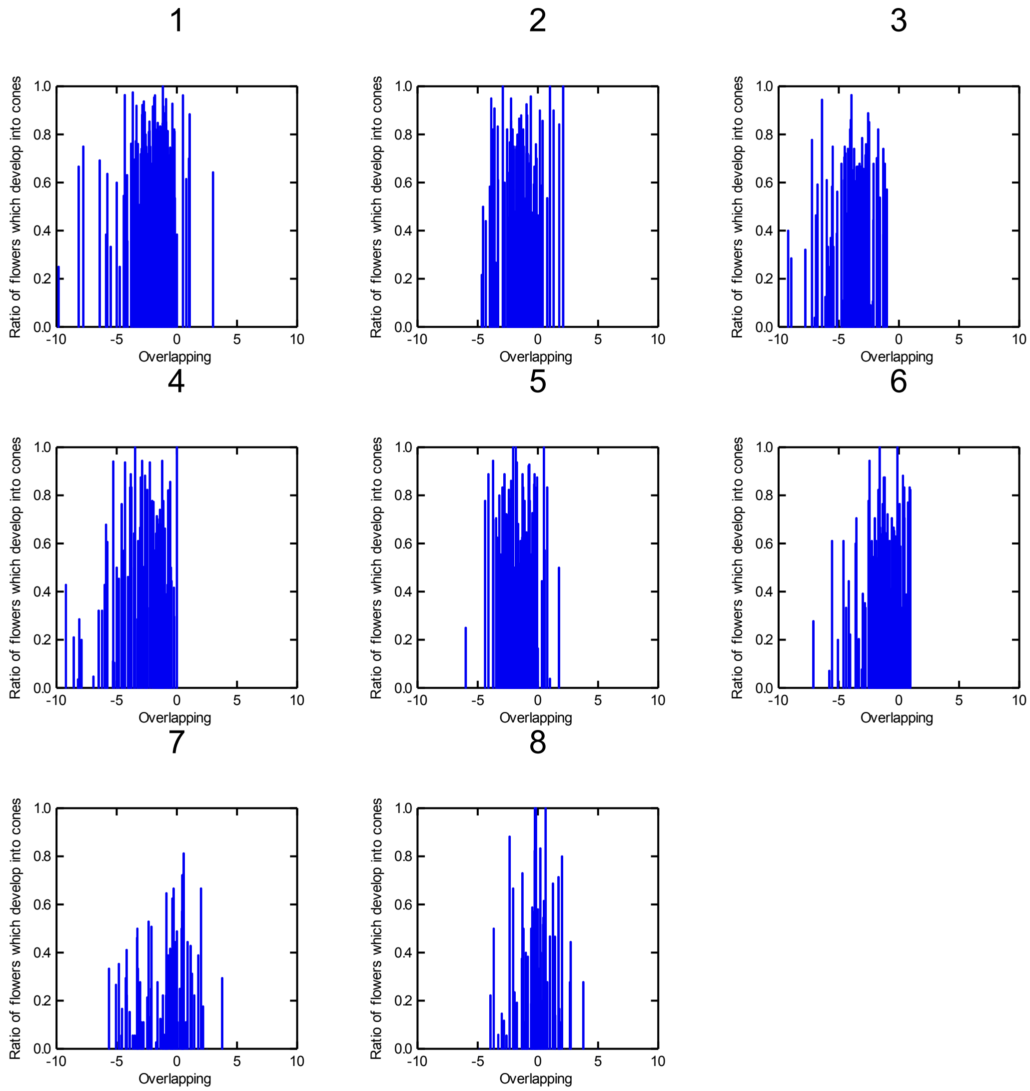

Figure 15. Influence of overlapping on the ratio of flowers which develop into cones in each study area (overlapping is zero when female and male phenology starts at the same time and it is negative or positive when female flowering starts earlier or later than male flowering respectively).

3.4. NUMBER OF FULL SEEDS PER CONE

ANOVA was used to analyse the effect of flowering year, area, interaction between flowering year and area and stand level within area in number of full seeds per cone. It was necessary to delete the flowering year 1999 for running the ANOVA due to a lack of data in that year. The model explained 34.5% of the variation and all sources of variation are significant factors ($P<0.05$). Flowering year is the most important source of variation (table 5).

Table 5. Analysis of variance for number of full seeds per cone.

N: 973			Multiple R: 0.587	Squared multiple R: 0.345	
Analysis of Variance					
Source	**Sum-of- Squares**	**df**	**Mean-Square**	**F-ratio**	**P**
Fyear	5872.438	2	2936.219	93.365	0.000
Area	4436.674	7	633.811	20.154	0.000
Area*Fyear	1201.279	14	85.804	2.728	0.000
Stand (Area)	3775.520	18	209.751	6.670	0.000
Error	29278.828	931	31.449		

How flowering year affects the number of full seeds per cone is shown in figure 16. The number of seeds per cone decreases each year, from 17.417 (SD= 6.575) in 1997, 14.845 (SD= 6.198) in 1998, 13.111 (SD= 6.793) in 1999 to 11.861 (SD= 6.535) in 2000.

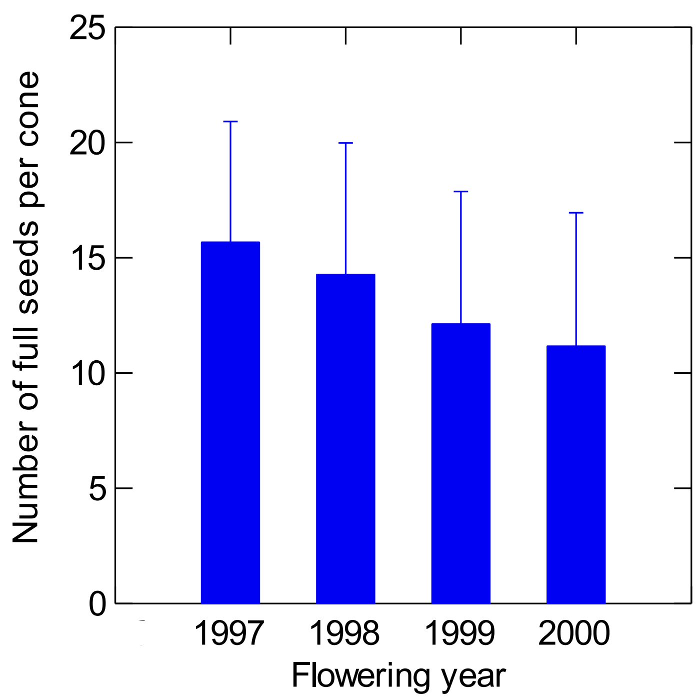

Figure 16. Influence of flowering year on number of full seeds per cone. Standard deviation is included as an error bar (p=0.6825).

Area is the second important source of variation (F= 20.154). Areas in Middle Finland (from area 2 to 6) have a higher number of seeds per cone than the other three areas (areas 1, 7 and 8) (figure 17). Korpilahti (area 6) has the largest number, with a mean of 16.718 (SD= 6.852) and Turku (area 8) with 10.855 (SD= 6.493) has the smallest one.

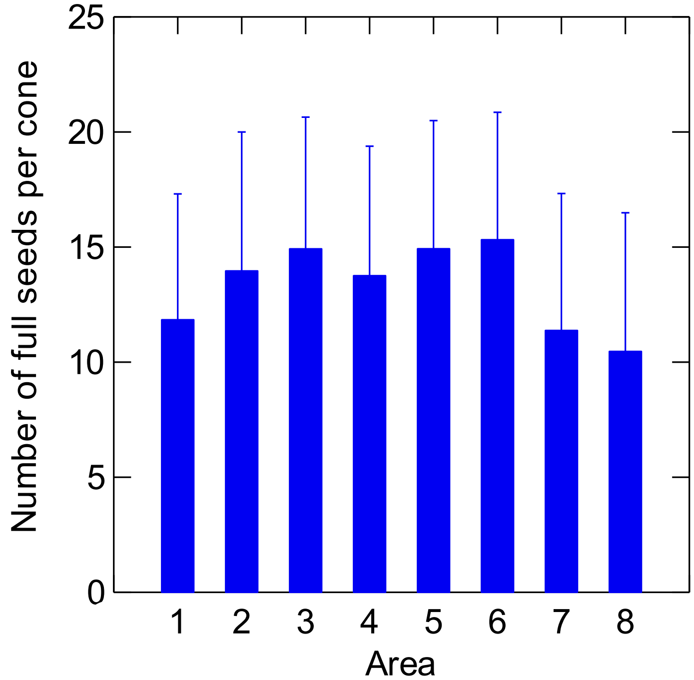

Figure 17. Influence of area on number of full seeds per cone. Standard deviation is included as an error bar (p=0.6825).

In the figure 18, the influence of the interaction between flowering year and area may be seen. As we explained before, the flowering year 1997 has the highest ratio number of seeds per cone (17.417; SD= 6.575). The flowering years 1997 and 2000 have a similar distribution, where the north and south areas have less number of seeds per cone than the ones in the middle. In 1999, the amount of seeds per cone is similar in North and Middle Finland but it is smaller in the South.

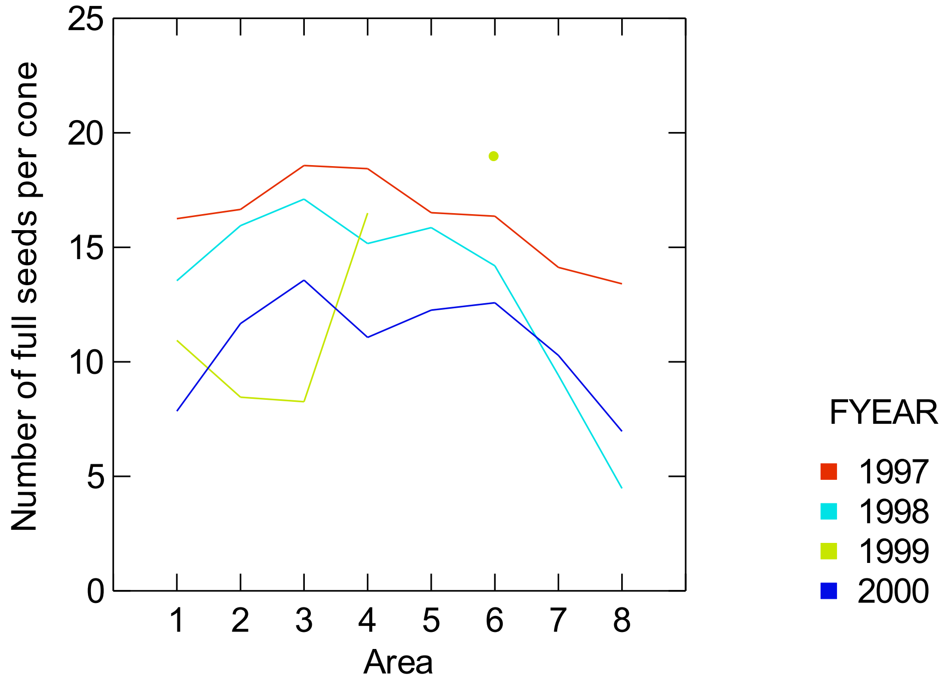

Figure 18. Influence of interaction between flowering year and area on number of full seeds per cone.

As it was previously done with the ratio of flowers which develop into cones, the flower opening day and the length of the female flowering opening were analysed to find a correlation with number of full seeds per cone. There is a positive and significant correlation (r>0 and P<0.05) between number of full seeds per cone and the flower opening day in four study areas (figure 19). In those cases, if the flower opens later, it will be more possible to have a higher number of full seeds per tree. There is a negative (r<0) and/or non significant correlation (P<0.05) with the length of the female flowering opening day in six of study areas (figure 20).

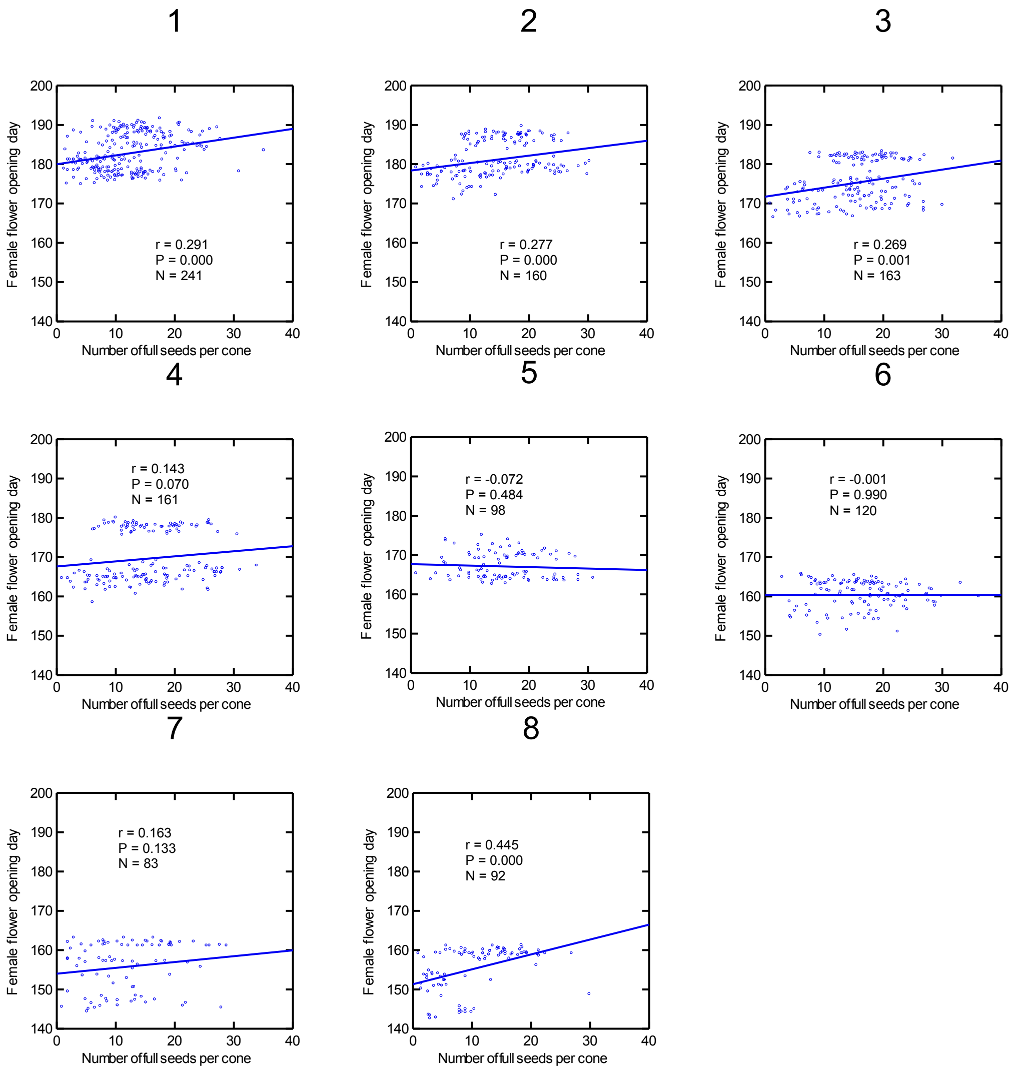

Figure 19. Correlations between the female flower opening day and the number of full seeds per cone in each study area.

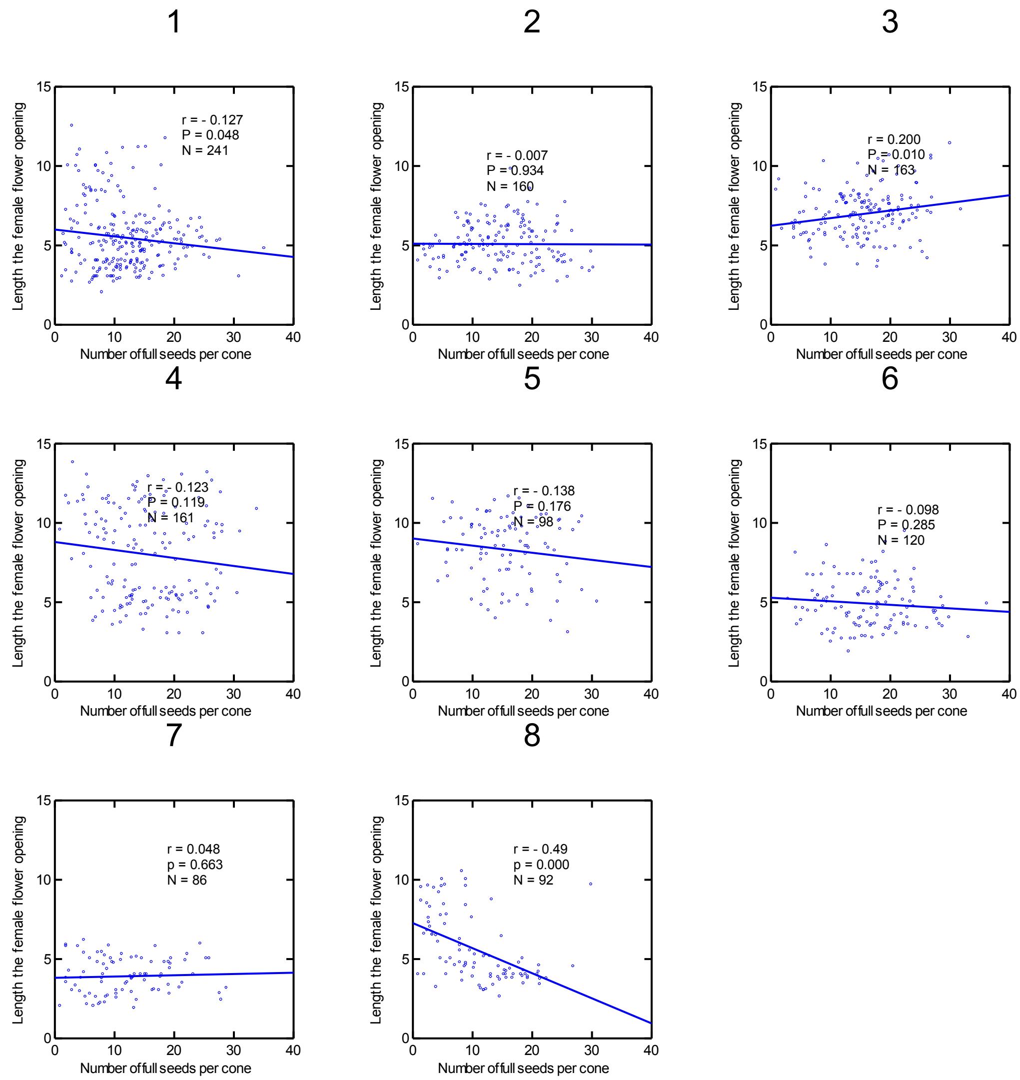

Figure 20. Correlations between the number of full seeds per cone and the length of the female flower opening in each study area.

3.5. CORRELATION BETWEEN THE VARIABLES OF THIS STUDY

The relation between the study variables was studied with a correlation. There is a positive and significant correlation ($r>0$ and $P<0.05$) between ratio of flowers which develop into cones and number of full seeds per cone in all the study areas (figure 21).

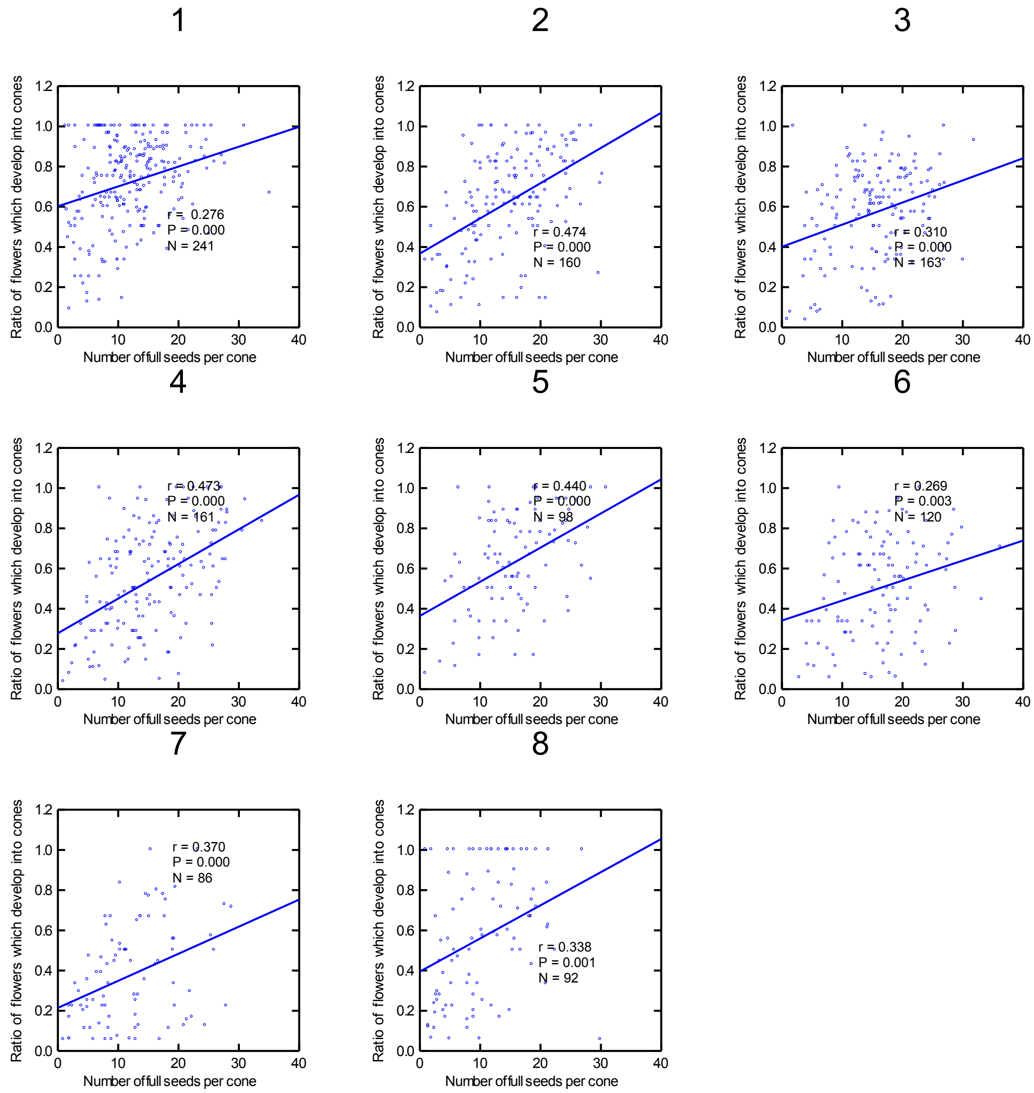

Figure 21. Correlations between the number of full seeds per cone and the ratio of flowers which develop into cones in each study area.

4. DISCUSSION

4.1. MONITORING TECHNIQUES

The study stands were selected to monitor the same trees during the experiment. The pines had to be able to flower (i.e. mature trees) and small enough for making the phenological monitoring. Due to that fact, the site conditions may differ from north to south (Pulkkinen, pers.comm). In some cases, it was impossible to keep the same stands every year. Another problem was the lack of data in 1999 in three of the eight study areas due to it was a rotten flowering year, this means there–were flowering data but no cones were developed (Pulkkinen, pers.comm).

The results show that 90.2% of trees where female flowers buds were included in the study develop into mature flowers, 78.7% produce cones and 87.2% of trees with mature flowers have cones. These high percentages can be the normal pine development.

4.2. GEOGRAPHICAL VARIATION

According to the results, area is the second important source of variation in ratio of flowers which develop into cones and number of full seeds per cone (tables 4 and 5). Northern areas have a higher ratio of flowers which develop into cones and in number of seeds per cone; areas in Middle Finland have the highest numbers (figure 10 and 17).

Pollen origin, site conditions and genetic characteristics affect the seed production in individual trees (Karlsson, 2000; Pulkkinen et al., 2003; Sarvas, 1962) and they are used to explain the results.

4.2.1. Flowering time, pollination and possibility of gene flow

In areas 1 and 2 the largest ratios of flowers which develop into cones occur when overlapping is zero, i.e. when pollen from the same tree or from a close one pollinates the female flower (figure 15). In addition, comparing with the other areas they have the highest ratios and number of seeds, this might be because mother and father material come from the same area, from the same genetic conditions and the pollination is sufficient.

One of the main reasons for the abortion of female conelets is the insufficient pollination, but even with abundant pollination the abortion of conelets can happen between 15% and 27% in natural southern areas (Pulkkinen at al., 2009; Sarvas, 1962).

As it can be seen in figure 15, flowering in Scots pine is not totally synchronized; female flowers are receptive before male flowers start to flower (Burczyk & Chalupka, 1997; Jonsson et al., 1976; Koski, 1970; Lindgren et al., 1995; Pulkkinen, 1994; Pulkkinen at al., 2009; Sarvas, 1962) and this gap is different between areas. In addition, it starts earlier in the south than in the north (Burczyk & Chalupka, 1997; Jonsson et al., 1976; Koski, 1970; Pulkkinen, 1994; Pulkkinen at al., 2009; Sarvas, 1962). According to Pulkkinen et al. (1995), when male flowers open later than female flowers, it is possible to have pollen contamination due to background pollination. A low survival rate can be expected because mother and father determinate in the same way the average hardiness of a progeny (Pulkkinen et al. 1995).

Scots pine produces pollen in enormous quantities that can travel long distances from south to north (due to southerly and south-westerly winds dominating in Finland during the pollen season) retaining its ability to germinate and arrive when local female strobili are receptive (Koski, 1980; Lindgren et al., 1995; Parantainen & Pulkkinen, 2003; Pessi & Pulkkinen, 1994; Pulkkinen at al., 2009; Varis, 2009). Because of that fact and the gap in flowering phenology, gene flow, which pollen movement is the main component (Koski, 1970; Parantainen & Pulkkinen, 2002), may be occurring within and among populations with overlapping flowering time (Koski, 1980; Parantainen & Pulkkinen, 2003; Pessi & Pulkkinen, 1994; Pulkkinen et al., 2009) and can be an important factor for adaptation of northern pine populations to a warmer climate because it creates connections from south to north (Varis, 2009). The finding that flowering in Scots pine is synchronized over a large area supports the possibility of long-range pollination (Pulkkinen & Rantio-Lehtimäki, 1995). The pollen season begins in South of Finland earlier than in the North and the pollen production is higher in the south than in the north (Pessi & Pulkkinen, 1994; Pulkkinen, 1994; Sarvas, 1962). Furthermore, there are years when northernmost pollen does not germinate at all and it increases the possibility of more southern gene flow (Pulkkinen, pers.comm). Moreover, some studies show that the temperature sum needed for the onset of the pollen season decreases from south to north (Pessi & Pulkkinen, 1994).

Due to gene flow and the fact that female strobili are receptive before local pollen shedding occurs, it is possible that the viable pollen is not from local origin and it is hundreds of kilometres to the south (Lindgren et al., 1995). Female structures are able to receive pollen during a short period of time, so the first pollen grain has an advantage and the pollen which arrives later may have a rather low chance of fertilizing receptive flowers (Lindgren et al., 1995). Maternal plants provide the environment of the developing embryos and may thus have more influence on developing seeds by aborting viable embryos than the paternal plant (Kärkkäinen et al., 1999).

4.2.2. Site conditions

Different site conditions can be one reason to explain differences between areas in ratio of flowers which develop into cones and the number of seeds per cone. In the first variable how the ratio decreases from north to south is evident and this result supports previous investigations about the correlation between seed crop and site fertility (Sarvas, 1962). In addition, Turku (area 7) has the smallest ratio and it belongs to an old and poor stand (Jaatinen, pers.comm). Environmental conditions such as soil fertility affect the seed crop (Delph et al., 1997; Sarvas, 1962) and Scots pine stands are usually in medium and poor sites (Sarvas, 1962). In this study, southern trees have grown in relatively poor sites compared to northern ones for following the experiment (Pulkkinen, pers.comm). Furthermore, adverse growing conditions can affect the pollen production, especially under conditions of pollen competition (Delph et al., 1997).

4.3. YEARLY VARIATION

The results show that flowering year is the most important source of variation in ratio of flowers which develop into cones and number of full seeds per cone (tables 5 and 6). The ratio of flowers which develop into cones and the number of full seeds per cone decrease each year from 1997 to 2000 (figure 9 and 16).

The number of seeds per cone fluctuates among years (Herrera et al., 1999; Sarvas, 1955) depends on yearly flowering variation, cone crops and weather conditions. In Sarvas' investigations (1955) the average number of seeds per cone varies from 16 to 25, from 1953 to 1954.

4.3.1. Flowering year variation

As explained above, flowering in *Pinus sylvestris* is not totally synchronized (Burczyk & Chalupka, 1997; Jonsson et al., 1976; Koski, 1970; Lindgren et al., 1995; Pulkkinen, 1994; Pulkkinen at al., 2009; Sarvas, 1962) and the time difference between female and male flowering may vary from year to year (Burczyk & Chalupka, 1997; Pulkkinen, 1994; Pulkkinen et al., 2009).

In 1997 the largest ratios of flowers which developed into cones occurred when overlapping is zero, when pollen from the same tree or from a close one pollinated the female flower (figure 14). In addition, comparing with the following years it has the highest ratio and number of seeds, maybe because mother and father material come from the same area, from the same genetic conditions.

The ratio of flowers which develop into cones can vary between years in the same area, like areas 3, 4, 5 and 6 (figure 11). In these areas, one productive year is followed by an unsuccessful one; there are not two consecutive productive years in these areas.

4.3.2. Cone crops

There is a positive correlation between cone production and seed development: seed abortion rate is lower among trees that produced many cones than among those that produce relatively few cones (Kärkkäinen et al., 1999). Huge cone crops in previous years may decrease the possibility to have large crops afterwards (Pulkkinen, pers.comm) and might be a reason to explain the results that show a decrease from 1997 to 200. In addition, abortion of developing seeds may be related with sex assignment of the tree: trees with higher female allocation produce many cones and abort few developing seeds whereas other trees allocate more to male functions such as production of pollen (Kärkkäinen et al., 1999). Some authors suggest that production of many cones with few seeds may evolve to reduce the reproductive loss due to cone predators (Kärkkäinen et al., 1999).

4.3.3. Weather conditions

The cold springs from 1996 to 1998 may explain that the ratio of flowers which developed into cones and the number of seeds per cone decreased each year from 1997 to 2000 and weather conditions affect directly pine cone development during flower bud initiation year, pollination year and fertilization year (Sarvas, 1955; Pulkkinen, pers.comm). In addition, weather conditions during pollination may have a large impact (Pulkkinen, pers.comm).

The climatic conditions of the spring (i.e. duration which depends on the temperature) affect many features in the seasonal cycle of flowering (Sarvas, 1955). In addition, Sarvas (1955) found great differences in the season cycle in different years and in the same stand, due to internal or external factors that affect the development of the buds and not to climatic conditions.

4.4. ADAPTATION TO CLIMATE CHANGE

Seed and pollen dispersal between populations transfers genes and increases genetic variation which is essential for evolution and an important factor for the success of the species (Davis & Shaw, 2001; Parantainen & Pulkkinen, 2002).

The fact that in every area a high percentage of development occurs when female flower opens before (negative overlapping) supports previous investigations about pollen movement and the possibility of gene flow. Pollen may travel from south to north and this can help in the adaptation to climate change.

Many authors have studied the role of gene flow in genetic structure and adaptation of Scots pine populations and have indicated the influence of southern tree characteristics in Northern Finland (Burczyk et al., 2004; Parantainen & Pulkkinen, 2002; Pessi & Pulkkinen, 1994), may be less adapted to the severe northern conditions than if gene flow by pollen do not occur (Lindgren et al., 1995). The highly plastic nature of pollen provides the potential for genotypes to respond differently to environmental variation (genotype-environment interactions), which would also promote the maintenance of genetic variation in pollen performance (Delph et al., 1997). In addition, mutation-drift balance and variable selection can affect the maintenance of variation in northern areas (Koski, 1970; Parantainen & Pulkkinen, 2002).

Gene flow has been a focus of evolutionary biology and nowadays it is an interesting subject because of issues surrounding genetically modified crops and predicting the consequences of climate change (Varis, 2009). Evolutionary and ecological effects of gene flow are quite different if we study the gene flow among nearby stands or between populations that are adapted to different environments (Burczyk et al., 2004). In Finland, due to northern populations receive pollen from southern populations adapted to a warmer climate; gene flow can be one adaptive mechanism because it may provide the alleles that help northern populations of Scots pine to adapt and tolerate a new and warmer climate (Burczyk et. al., 2004; Davis & Shaw, 2001; Parantainen & Pulkkinen, 2002; Pessi & Pulkkinen, 1994; Pulkkinen & Rantio-Lehtimäki, 1995; Varis, 2009).

Populations tend to inhabit areas colder than their future optimum; therefore gene flow and migration of pre-adapted genotypes may help to adapt to a warmer climate but it needs many generations (Rehfeldt et al., 2002; Varis 2009).

5. CONCLUSIONS

(1) The most important source of variation in ratio of flowers which develop into cones and number of full seeds per cone is flowering year and the second one is area. Several factors affect these variations.

(2) Geographic variation can be affected by site conditions and flowering time with the possibility of gene flow. Weather conditions, cone crops and flowering time affect yearly variation. It

can be concluded that seed production of Scots pine (*Pinus sylvestris*) in Finland is affected by the interaction of many elements and it is necessary to carry out more experiments.

(3) The results show that there is a possibility of gene flow from south to north. This is possible because flowering in Scots pine is not totally synchronized and the gap is different between areas. In addition, the fact that pollen can travel without losing its viability makes pollination possible among different populations.

(4) Adaptation of Scots pine populations may be favoured by gene flow because southern pollen may provide genotypes to adapt to a changing environment. In addition, some authors have previously found southern trees characteristics in northern trees within Finland.

6. REFERENCES

Burczyk J. & Chalupka W. 1997. Flowering and cone production variability and its effect on parental balance in a Scots pine clonal seed orchard. Annals of Forest Science 54: 129-144.

Burczyk J., DiFazio S.P. & Adams W.T. 2004. Gene flow in forest trees: how far do genes really travel? Forest Genetics 11 (2-3): 1-14.

Davis M.B. & Shaw R.G. 2001. Range shifts and adaptive responses to quaternary climate change. Science 292: 673-679.

Delph L.F., Johannsson M.H. & Stephenson A.G. 1997. How environmental factors affect pollen performance: ecological and evolutionary perspectives. Ecology 78(6): 1632-1639.

EUFORGEN. 2009. European Forest Genetic Resources Programme. http://www.euforgen.org/fileadmin/www.euforgen.org/Documents/Maps/JPG/Pinus_sylvestris.jpg. Search date: 30.01.2013.

Finnish Forest Association. N.d. Finnish forest resources increase. http://www.forest.fi/smyforest/foresteng.nsf/0/BE3C5576C911F822C2256F3100418AFD?Opendocument. Search date: 23.01.2013.

Finnish Forest Research Institute (METLA). 2010. Scots pine. http://www.metla.fi/metinfo/northernpine/manty-en.html. Search date 10.04.2013.

Finnish Forest Research Institute (METLA). 2011a. About the Institute. http://www.metla.fi/metla/index-en.html Search date: 23.01.2013.

Finnish Forest Research Institute (METLA). 2011b. General information. http://www.metla.fi/metla/finland/index-en.htm. Search date: 10.04.2013

Finnish Forest Research Institute (METLA). 2011c. Forest Finland in Brief. Vantaa, Finland. p4.

Finnish Meteorological Institute. They provided the weather data to Finnish Forest Research Institute (METLA).

Giertych M. & Mátyás Cs. 1991. Genetics of Scots Pine. Elsevier Science Publishers. Amsterdam.

Google Earth Version 6.2. 2013. Keyhole Inc.

Herrera C.M., Jordano P., Guitián J. & Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relatioship to pollination and seed dispersal. The American Society of Naturalists 152 (4): 576-594.

Jaatinen R. Personal Communication: 07.05.2013

Jonsson A., Ekberg I., & Eriksson G. 1976. Flowering in a seed orchard of *Pinus sylvestris* L. Studia Forestalia Suecica 135: 1-38.

Kärkkäinen K., Savolainen O. & Koski V. 1999. Why do plants abort so many developing seeds: bad offspring or bad maternal genotype? Evolutionary Ecology 13: 305-317.

Karlsson C. 2000. Seed production of *Pinus sylvestris* after release cutting. Canadian Journal of Forest Research 30: 982-989.

Kellomäki S., Rouvinen I., Peltola H., Strandman H. & Steinbrecher R. 2001. Impact of global warming on the tree species composition of boreal forest in Finland and effects on emissions of isoprenoids. Global Change Biology 7: 531-544.

Koski V. 1970. A study of pollen dispersal as a mechanism of gene flow in conifers. Communicationes Instituti Forestalis Fenniae 70(4): 1-77.

Koski V. 1980. On the variation of flowering and seed crop in mature stands of *Pinus sylvestris* L. Silva Fennica 14(1): 71-75.

Kremer A., Ronce O., Robledo-Arnuncio J.J., Guillaume F., Bohrer G., Nathan R., Bridle J.R., Gomulkiewicz R., Klein E.K., Ritland K., Kuparinen A., Geber S. & Schueler S. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecology Letters April 15(4): 378-392.

Lindgren D., Paule L., Xihuan S., Yazdani R., Segerström U., Wallin, J.-E. & Lejdebro M.L. 1995. Can viable pollen carry Scots pine genes over long distance? Grana 34: 64-69.

Mirov N.T. 1967. The Genus *Pinus.* The Ronald Press Company. New York.

Mitchell A. 1974. A field Guide to the Trees of Britain and Northern Europe. Collins, Grafton Street, London. p170

Nygren M. 1987. Germination characteristics of autumn collected *Pinus sylvestris* seeds. Acta Forestalia Fennica 201. Helsinki.

Olsson R. 2009. Boreal Forest and Climate Change. Air Pollution and Climate Series 23. Sweeden.

Parantainen A. & Pulkkinen, P. 2002. Pollen viability of Scots pine (*Pinus sylvestris*) in different temperature conditions: high levels of variation among and within latitudes. Forest Ecology and Management. 167: 149-160.

Parantainen A. & Pulkkinen P. 2003. Flowering and airborne pollen occurence in a *Pinus sylvestris* seed orchard consisting of northern clones. Scandinavian Journal of Forest Research 18(2): 111-117

Parviainen J. & Västilä, S. 2011. State of Finland's Forests 2011 Based on the Criteria and Indicators of Sustainable Forest Management. Ministry of Agriculture and Forestry and Finnish Forest Research Institute (METLA). pp6-20.

Pessi A-M. & Pulkkinen, P. 1994. Temporal and spatial variation of airborne Scots pine (*Pinus sylvestris*) pollen. Grana 33(3): 151-157.

Pukkala T., Hakkanen T. & Nikkanen T. 2010. Prediction models for the annual seed crop of Norway spruce and Scots pine in Finland. Silva Fennica 44(4): 629-642.

Pulkkinen, P. Personal Communication: 15.05.2013

Pulkkinen P. 1994. Aerobiology of pine pollen: dispersal of pollen from non-uniform sources and impact on Scots pine seed orchards. Reports from the Foundation for Forest Tree Breeding 8: 1-23.

Pulkkinen P., Haapanen, M. & Mikola J. 1995. Effect of southern pollination on the survival and growth of seed orchard progenies of northern Scots pine (*Pinus sylvestris*) clones. Forest Ecology and Management 73: 75-84.

Pulkkinen P., Parantainen A., Pakkanen, A. & Vakkari P. 2003. Southern pollen outcompetes northern pollen in seed siring success in transferred *Pinus sylvestris* seed orchards. The functionality of pollen and the effect of pollen source on seed maturation in *Pinus silvestrys* L.

Pulkkinen P. & Rantio-Lehtimäki A. 1995. Viability and seasonal distribution patterns of Scots pine pollen in Finland. Tree Physiology 15: 515-518.

Pulkkinen P., Varis S., Pakkanen A., Koivuranta L., Vakkari P. & Parantainen A. 2009. Southern pollen sired more seeds than northern pollen in southern seed orchards established with northern clones of *Pinus sylvestris*. Scandinavian Journal of Forest Research 24: 8-14.

Raymond J., Schnell R. J. & Priyadarshan P.M. 2012. Genomic of Tree Crops. Springer. http://books.google.es/books?id=9hg47qTc5BAC&pg=PA96&lpg=PA96&dq=gene+flow+and+local+adaptation+in+trees.&source=bl&ots=qnmY8QoxoV&sig=xm7Vald6R7ggC471EsLILyUux40&hl=es&sa=X&ei=hf_aUcTfD8SR7AaT5YDABw&sqi=2&ved=0CGAQ6AEwBg#v=onepage&q=gene%20flow%20and%20local%20adaptation%20in%20trees.&f=false. Search date: 08.07.2013. pp 96-97.

Rehfeldt G.E., Tchebakova N.M., Parfenova Y.I., Wykoff R.A., Kuzmina N.A. & Milyutin L.I. 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biology 8: 912-929.

Sarvas R. 1955. Investigations into the flowering and seed quality of forest trees. Communicationes Instituti Forestalis Fenniae 45(7): 31-32.

Sarvas R. 1962. Investigations on the flowering and seed crop of *Pinus silvestris*. Communicationes Instituti Forestalis Fenniae 53(4): 1-198.

Sullivan J. 1993. *Pinus sylvestris*. http://www.fs.fed.us/database/feis/plants/tree/pinsyl/all.html. Search date: 30.01.2013.

SYSTAT Version 9. 1988. SPSS Software Inc. for Windows. Chicago.

Trees for life. Restoring the Caledonian Forest. 1998. http://www.treesforlife.org.uk/tfl.scpine.html. Search date: 04.04.2013.

Varis S. 2009. The role of pollen in the changing environmental conditions of Scots pine. Dissertationes Forestales 105: 1-37.

Venäläinen A. & Nordlund A. 1988. Kasvukauden ilmastotiedotten sisältö ja käyttö. Report 1988:6, Finnish Meteorological Institute. Helsinki.

Wikipedia 2009. Taiga. http://en.wikipedia.org/wiki/File:Distribution_Taiga.png. Search date: 23.01.2013.

7. APPENDIX

Table 6. Average temperatures from April to October in the eight study areas from 1995 to 2001. Source: Finnish Meteorological Institute.

Area	Year	April	May	Jun	July	August	September	October
1	1995	-3.9	2.6	10.4	11.2	10.1	5.3	-3.1
	1996	-4.5	0.7	8.5	11.8	12.3	5.3	1.0
	1997	-6.5	2.8	9.1	13.9	13.2	7.8	-0.5
	1998	-5.6	3.2	8.1	14.8	10.2	5.1	-0.2
	1999	-1.9	1.4	12.2	13.4	8.6	7.7	1.7
	2000	-2.6	4.3	9.5	14.2	10.9	6.6	3.8
	2001	-3.6	3.1	12.1	13.2	10.5	7.8	-1.2
2	1995	-2.2	3.2	11.8	12.0	11.0	5.8	-1.1
	1996	-3.7	1.4	8.7	12.3	13.6	5.5	1.7
	1997	-5.8	3.0	10.7	14.7	13.9	7.7	-0.8
	1998	-4.5	3.1	8.5	15.2	10.0	5.0	-0.2
	1999	-0.9	1.8	13.3	13.4	9.0	7.8	1.8
	2000	-1.5	4.6	10.1	14.6	11.2	6.6	4.7
	2001	-2.6	3.7	12.6	14.1	10.7	7.5	-0.4
3	1995	-1.8	3.7	13.3	12.5	11.5	5.6	0.1
	1996	-2.6	2.0	10.2	13.0	14.3	5.1	1.9
	1997	-5.6	3.3	12.9	16.1	13.8	7.3	-1.7
	1998	-4.2	3.9	9.6	14.9	10.1	5.4	0.1
	1999	0.1	3.1	14.6	14.3	9.0	8.1	1.6
	2000	-0.4	6.5	11.5	15.3	11.6	6.5	4.4
	2001	-1.7	4.0	17.2	18.1	10.6	7.2	0.0
4	1995	-0.8	5.0	14.5	13.0	12.3	6.1	1.5
	1996	-1.6	3.6	11.0	13.4	14.7	5.7	2.6
	1997	-4.6	4.7	13.8	17.3	14.4	8.2	-1.0
	1998	-3.1	5.4	13.9	14.3	10.6	4.8	1.3
	1999	1.0	5.0	15.1	15.3	10.4	8.6	2.2
	2000	0.4	7.3	12.5	15.8	12.3	7.8	5.3
	2001	0.1	5.3	15.6	17.1	12.2	8.4	1.2
5	1995	0.4	6.8	15.4	13.8	13.2	8.3	4.6
	1996	0.1	5.6	12.2	13.4	15.3	6.8	3.8
	1997	-2.8	5.3	14.6	16.9	13.9	7.3	0.1

Table 6 (cont.). Average temperatures from April to October in the eight study areas from 1995 to 2001 Source: Finnish Meteorological Institute.

Area	Year	April	May	Jun	July	August	September	October
5	1998	-1.7	5.7	11.7	14.3	11.2	7.8	2.6
	1999	3.2	4.3	15.8	14.7	10.4	9.4	4.6
	2000	2.1	7.7	12.3	15.6	12.1	6.3	5.4
	2001	2.5	6.1	13.7	16.7	12.7	9.0	3.0
6	1995	1.2	7.7	16.5	14.7	14.2	9.0	6.2
	1996	1.5	7.7	13.0	13.8	16.1	7.1	4.9
	1997	-0.7	7.5	17.0	19.0	17.3	9.4	1.2
	1998	0.3	8.2	13.4	15.7	12.4	9.6	3.9
	1999	3.9	5.8	16.7	16.0	12.0	9.7	4.7
	2000	3.6	9.7	13.8	16.2	13.4	7.4	6.5
	2001	4.3	7.3	12.7	18.0	13.6	9.7	5.3
7	1995	2.6	8.9	17.6	15.6	15.5	10.1	7.5
	1996	2.8	9.3	13.5	14.3	16.6	8.0	6.3
	1997	1.4	8.0	16.3	17.8	17.5	9.9	2.3
	1998	2.8	9.8	14.1	15.5	13.3	10.5	4.7
	1999	5.1	7.6	18.1	18.1	14.4	11.4	5.8
	2000	5.1	9.7	13.2	15.2	13.0	6.0	6.0
	2001	5.1	8.7	13.3	19.1	15.0	11.0	7.2
8	1995	3.6	9.1	17.3	16.6	16.2	11.2	8.4
	1996	3.3	9.1	13.3	14.7	18.1	9.4	7.3
	1997	1.7	8.0	16.8	19.0	19.0	11.0	3.1
	1998	3.8	10.0	13.8	16.0	13.8	11.6	5.9
	1999	5.5	8.5	17.4	18.6	15.7	13.3	6.7
	2000	6.2	10.4	14.4	16.7	15.5	10.1	8.7
	2001	5.1	9.6	15.8	20.0	16.5	11.9	8.1

Table 7. Starting and ending date (day.month) of growing season and its length (days) in the eight study areas from 1995 to 2001.

Area		**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**
1	Start	19.05	2.06	8.06	3.06	7.06	18.05	6.06
	End	23.9	12.10	1.10	22.09	4.10	22.10	21.09
	Length	128	133	116	112	120	158	108
2	Start	22.5	2.06	5.06	3.06	18.05	18.05	6.06
	End	11.10	12.10	29.9	7.10	21.10	22.10	21.09
	Length	143	133	117	127	157	158	108
3	Start	18.05	1.06	5.06	3.06	18.05	18.05	30.05
	End	10.10	12.10	26.09	22.09	4.10	22.10	22.09
	Length	146	134	114	112	140	158	116
4	Start	19.05	23.05	25.05	13.05	17.05	17.05	02.05
	End	13.10	28.10	2.10	24.10	5.10	22.10	16.10
	Length	148	159	131	151	142	159	168
5	Start	18.05	17.05	9.05.	25.04	18.04	17.05	01.05
	End	20.10	27.10	28.10	26.10	26.10	25.10	27.10
	Length	156	164	143	185	192	162	180
6	Start	18.05	10.05	7.05	25.04	18.04	19.04	22.04
	End	28.10	26.10	19.10	27.10	31.10	25.10	28.10
	Length	164	171	166	186	197	190	190
7	Start	3.05	19.04	7.05	21.04	18.04	18.04	22.04
	End	27.10	30.10	19.10	27.10	31.10	31.10	29.10
	Length	179	195	166	190	197	197	191
8	Start	22.04	17.04	6.05	19.04	18.04	16.04	22.04
	End	28.10	30.10	18.10	27.10	31.10	31.10	29.10
	Length	179	195	166	190	197	197	191

Table 8. Ratio of flowers which develop into cones and standard deviation values per flowering year and area.

Flowering year	Area	Mean	Standard deviation
1997	1	0.767	0.171
	2	0.730	0.200
	3	0.589	0.164
	4	0.823	0.145
	5	0.541	0.396
	6	0.643	0.207
	7	0.548	0.259
	8	0.718	0.266
1998	1	0.710	0.184
	2	0.670	0.182
	3	0.680	0.156
	4	0.591	0.207
	5	0.620	0.252
	6	0.252	0.256
	7	0.183	0.188
	8	0.209	0.216
1999	1	0.790	0.221
	2	0.640	0.366
	3	0.531	0.321
	4	0.677	0.287
	5	0.000	0.000
	6	0.576	0.228
	7	0.000	0.000
	8	0.000	0.000
2000	1	0.504	0.313
	2	0.477	0.304
	3	0.468	0.237
	4	0.363	0.210
	5	0.470	0.237
	6	0.287	0.248
	7	0.230	0.189
	8	0.149	0.149

Table 9. Number of full seeds per cone and standard deviation values per flowering year and area.

Flowering year	Area	Mean	Standard deviation
1997	1	17.536	6.453
	2	18.077	6.092
	3	19.997	5.034
	4	22.828	6.110
	5	18.082	6.214
	6	18.564	6.721
	7	15.739	6.504
	8	13.641	5.533
1998	1	13.900	5.291
	2	16.292	4.792
	3	17.674	4.904
	4	16.349	5.772
	5	16.442	5.745
	6	14.194	5.650
	7	9.415	6.509
	8	5.633	6.043
1999	1	11.187	5.141
	2	8.455	3.441
	3	9.430	6.012
	4	17.546	6.799
	5		
	6	20.590	5.753
	7		
	8		
2000	1	7.847	4.291
	2	13.287	8.011
	3	14.111	6.288
	4	11.781	6.008
	5	12.815	6.185
	6	13.162	6.256
	7	10.836	6.118
	8	6.965	2.909

Table 10. Ratio of flowers which develop into cones and standard deviation values per flowering year.

Flowering year	Mean	Standard deviation
1997	0.671	0.267
1998	0.568	0.266
1999	0.452	0.399
2000	0.394	0.276

Table 11. Ratio of flowers that develop into cones and standard deviation values per area.

Area	Mean	Standard deviation
1	0.698	0.253
2	0.606	0.272
3	0.567	0.232
4	0.541	0.263
5	0.470	0.348
6	0.476	0.272
7	0.255	0.271
8	0.343	0.373

Table 12. Number of full seeds per cone and standard deviation values per flowering year.

Flowering year	Mean	Standard deviation
1997	17.417	6.585
1998	14.845	6.198
1999	13.111	6.793
2000	11.861	6.532

Table 13. Number of full seeds per cone cones and standard deviation values per area.

Area	Mean	Standard deviation
1	12.317	6.078
2	14.949	6.770
3	15.685	6.312
4	15.625	7.072
5	15.854	6.312
6	16.718	6.765
7	12.297	6.852
8	10.855	6.493