

The Extent of South-North Pollen Transfer in Finnish Scots Pine

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In order to evaluate the possibility of long distance gene flow in Scots pine (*Pinus sylvestris* L.), we measured the amount and germinability of airborne pollen and flowering phenology in central, northern, and northernmost Finland during 1997–2000. Totally 2.3% of the detected germinable pollen grains were in the air prior to local pollen shedding. The mean number of germinable pollen grains m^{-3} air per day was lower prior to local pollen shedding, but in the year 2000 there were more germinable pollen grains in the air of central study site prior to local pollen shedding. Prior to the onset of pollen shedding, 7.5% of female strobili which we observed were receptive. On average female strobili became receptive three days earlier than local pollen shedding started. During the period of pollen shedding in the central study site, we detected germinable airborne pollen in the northern site in years 1997, 1999 and 2000. At the northernmost site, we detected germinable airborne pollen during the pollen-shedding period of the northern site in 2000. Our detection of germinable airborne pollen and synchrony of strobili maturation from south to north suggest that populations of Scots pine in central and northern Finland may provide genetic material to populations in northern and northernmost Finland, respectively.

Keywords coniferous phenology, gene flow, adaptation, *Pinus sylvestris*, plant population biology, boreal forest dynamics

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1 Introduction

Gene flow among populations is believed to be one of the key elements in adaptation of forest tree species to climate change. Garcia-Ramos and Kirkpatrick (1997) showed how models in which genes flowed from central to peripheral populations prevent local adaptation at the distributional limits. Scots pine (*Pinus sylvestris* L.) is at the edge of its natural range in northern Finland where the production of female and male strobili is lower than in central Finland, possibly due to the maladaptation to harsher environment caused by constant gene flow from south (Sarvas 1962, Pessi and Pulkkinen 1994, Parantainen and Pulkkinen 2002, Savolainen et al. 2007). In a warming world, gene flow from southern to northern populations may provide alleles that are (pre)adapted to a future climate (Davis and Shaw 2001).

Climatologists predict that climate change will affect the entire distribution of Scots pine within 100 years. In Finland, future climate models predict an increase in annual mean temperature of 4 °C (Ruosteenoja et al. 2005), and in the far north the mean temperature sum will increase from 500–700 d.d. to 900–1100 d.d. (Kellomäki et al. 2005, Ruosteenoja et al. 2005). These conditions are currently typical of central Finland (Kellomäki et al. 2005).

Adaptation to this kind of rapid change requires, among other things, long distance gene flow mediated by pollen transport (Davis and Shaw 2001). In observation studies pollen grains of wind pollinated trees species have been reported to rise high above the trees and travel long distances, usually tens of kilometers (Koski 1970). Earliest reports are from Gulf of Bothnia where Hesselman (1919) observed pollen of spruce, pine and birch even 55 km from the coast (rev. Koski 1970). Recent aerobiological studies have shown that pollen grains can rise to over a kilometer in altitude and travel over 1000 km per day (Checci et al. 2003, Sofiev et al. 2006, Skjoth et al. 2007, Siljamo et al. 2008a). During the reproduction period of Scots pine air currents coming from more southern areas brings warm air mass to the north. It enables the maturing of female and male strobili, and may bring pollen grains from areas where pollen shedding has already started.

Pollen grain germinability after long distance

transport is of critical importance to gene flow. The mean germination percentage of Scots pine pollen after exposure to air for 24 h was as high as 75.7% (Lindgren and Lindgren 1996). Lindgren et al. (1995) collected airborne pollen of Scots pine in central Sweden and pointed out that the early pollen likely came from distant trees, and its germinability remained high enough to fertilize egg cells in most of their samples.

Even if pollen can remain germinable over long distances, receptive female strobili must receive them upon their arrival. Scots pine flowering starts from south and the female strobili of individual trees and nearby stands usually mature and become receptive before male strobili begin shedding pollen (Sarvas 1962, Chung 1981). Pulkkinen and Rantio-Lehtimäki (1995) conducted a one year study about the amount and germinability of airborne Scots pine pollen in relation to male flowering, but as far as we know there is no studies combining the data from airborne pollen collections, germinability testing and observations of both male and female flowering.

Our aim was to evaluate long distance (several hundreds of kilometers) gene flow in Scots pine by investigating the amount and germinability of airborne pollen grains during the reproductive season in central, northern and northernmost Finland. To evaluate the origin of pollen we made observations of the synchrony in the occurrence of airborne pollen, receptive female strobili and pollen shedding male strobili across the country. Our hypothesis is that in areas where female strobili are receptive but male strobili have not yet begun shedding pollen, airborne pollen may originate from southern populations that may be a considerable distance away.

2 Materials and Methods

Between 1997 and 2000, flowering phenology of Scots pine and the occurrence and germinability of airborne pollen was studied at sites in central (Korpilahti, 62°15'N), northern (Rovaniemi, 66°23'N), and northernmost (Kevo, 69°45'N) Finland (Fig. 1). The northernmost site (Kevo) is an isolated forest approximately 50 km north from the Scots pine tree line. Each of the three

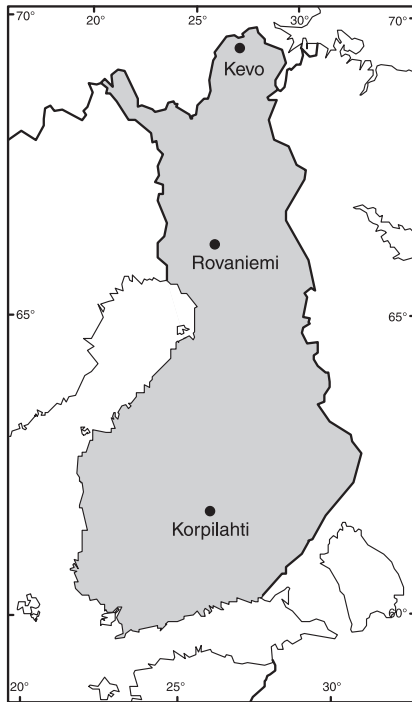


Fig. 1. Locations of the study sites.

natural forest sites contained three sample locations where flowering phenology and airborne pollen were measured. Pollen was collected in an open area near the forest location for germinability testing (see below). All study sites were between 100 and 150 m above sea level and the mean annual temperature sum was approximately 1150 d.d. in the central, 900 d.d. in the northern, and 590 d.d. in the northernmost site.

We recorded the developmental stage of approximately 20 strobili of both sexes on each of approximately 45 trees per site (total of 10765 female and 6786 male strobili; Table 1); when possible, we sampled the same trees each year. Strobili were chosen equally from south- and north-facing branches located between 1.5 and 3 m above the ground. The female strobilus was classified as receptive when upper scales had opened and finished when scale thickness prevented pollen from entering the micropylar tube (Jonsson et al. 1976, Parantainen and Pulkkinen 2003). Male strobili were classified as mature if pollen was released by gently snapping the flower

Table 1. Numbers of trees, female strobili and male strobili according to year and site.

Year	Location	Trees	Female strobili	Male strobili
1997	Central	32	529	525
1997	North	26	448	468
1997	Northernmost	38	795	584
1998	Central	33	554	576
1998	North	61	1675	557
1998	Northernmost	74	2091	537
1999	Central	30	421	499
1999	North	10	122	558
1999	Northernmost	81	1146	696
2000	Central	33	549	586
2000	North	65	1625	612
2000	Northernmost	57	810	588

(Jonsson et al. 1976, Parantainen and Pulkkinen 2003).

The number of pollen grains per cubic meter of air was measured using Rotorod samplers (Perkins and Leighton 1957), which consist of two metallic rods that rotate around a fixed circumference at constant speed and with petroleum-jelly-covered tape attached to their leading edges. Two samplers were used in each site and employed for a 5-minute period between 1200 and 1500 hrs each day. During those hours the air humidity is at the lowest and the probability of pollen movements at the highest. Tapes were removed and pollen grains were identified with the aid of microscope and counted to estimate pollen per cubic meter on the basis of tape area and the volume of air the rod had passed through during its 5-minute rotation.

Pollen grain germinability was determined from one sample location per site. Pollen collection and germinability testing were as described in Pulkkinen and Rantio-Lehtimäki (1995), except we used B&K medium (Brewbaker and Kwack 1963) to wash particles from the air-sampler filters (20.3 × 25.4 cm) onto the germination filter (4.7 cm diameter). Collection filters were changed at 0800 and 2000 hrs to test the germinability of airborne pollen at night and day. Air samplers were placed at the same height as the treetops.

In 1997, 215 female strobili were receptive in the northern site in the first day of observations

indicating that the flowering had started before observation. Similarly, pollen collection started when there was already a considerable amount of pollen in the air in 1997 (northern site) and 2000 (central site).

Pollination and flowering time was divided into three periods based on the stage of female and male flowering: 1=females not receptive and local males not shedding pollen, 2=females receptive but local males not shedding pollen, and 3=females receptive and local males shedding pollen. The airborne pollen prior to local pollen shedding was predicted to be nonlocal.

The daily mean germination percentage is the mean of night and day samples. A new variable, "germinable pollen grains m^{-3} air", was created by dividing the daily amount of pollen grains (m^{-3} air) by the daily mean germination percentage.

One-way ANOVA and Tukeys HSD post hoc test was used to test the significance of differences in the amount of pollen grains per cubic meter of air, the proportions of receptive female strobili and pollen shedding male strobili between periods and sites. The number of pollen grains m^{-3} air were natural log (ln) transformed to equalize the variances between the groups. The Kruskal-Wallis test was applied when population variances were not normalized by transformation. Differences were considered significant at the 5% risk level

($p < 0.05$) and all statistical analyses were carried out using SPSS (version 15).

3 Results

Germinable pollen grains were detected in the air before local pollen shedding had started, except in northernmost study site in year 1999 (Table 2). The situation when there was germinable non-local pollen in the air lasted from one to four days depending on the year and study site. In total, the germinable nonlocal airborne pollen was detected on 26 days, which was 17.8% of days on which germinable airborne pollen grains were detected.

Totally 2.3% of the detected germinable pollen grains were in the air prior to local pollen shedding. The mean number of germinable pollen grains m^{-3} air per day was lower prior to local pollen shedding ($F = 37.91$, $p < 0.005$), but in the year 2000 there were more germinable pollen grains in the air of central study site prior to local pollen shedding (Table 2). The mean number of germinable nonlocal pollen in m^{-3} air per day was 12.0 ± 21.0 in 1997, 0.1 ± 0.2 in 1998, 1.0 ± 2.1 in 1999, and 12.2 ± 28.1 in 2000 (NS). At the central site, the mean number of germinable nonlocal

Table 2. The mean number of germinable pollen grains in m^{-3} air, receptive female strobili, and pollen shedding strobili per day in different years and locations. Situation 1 = females not receptive and local males not shedding pollen, 2 = females receptive but local males not shedding pollen, and 3 = females receptive and local males shedding pollen.

Year	Location	Mean number of germinable pollen grains m^{-3} per day			Mean number of receptive female strobili per day		Mean number of pollen shedding strobili per day
		1	2	3	2	3	3
1997	Central	0.72		181.01		187.08	178.75
1997	North	35.62		171.75		363.58	159.92
1997	Northernmost	0.13	0.08	48.97	6.00	341.93	159.79
1998	Central		0.22	18.68	1.00	284.54	157.85
1998	North		0.05	244.34	4.25	1012.00	161.60
1998	Northernmost		0.02	134.46	91.00	1225.91	205.64
1999	Central	0.06	1.69	13.15	32.67	237.30	166.80
1999	North		0.04	7.72	29.00	74.00	207.14
1999	Northernmost		0.00	3.86	65.50	484.55	272.82
2000	Central	90.93	7.17	38.47	7.40	232.50	162.81
2000	North		0.46	37.05	59.00	982.00	164.63
2000	Northernmost	1.19	0.20	7.28	61.25	443.47	253.12

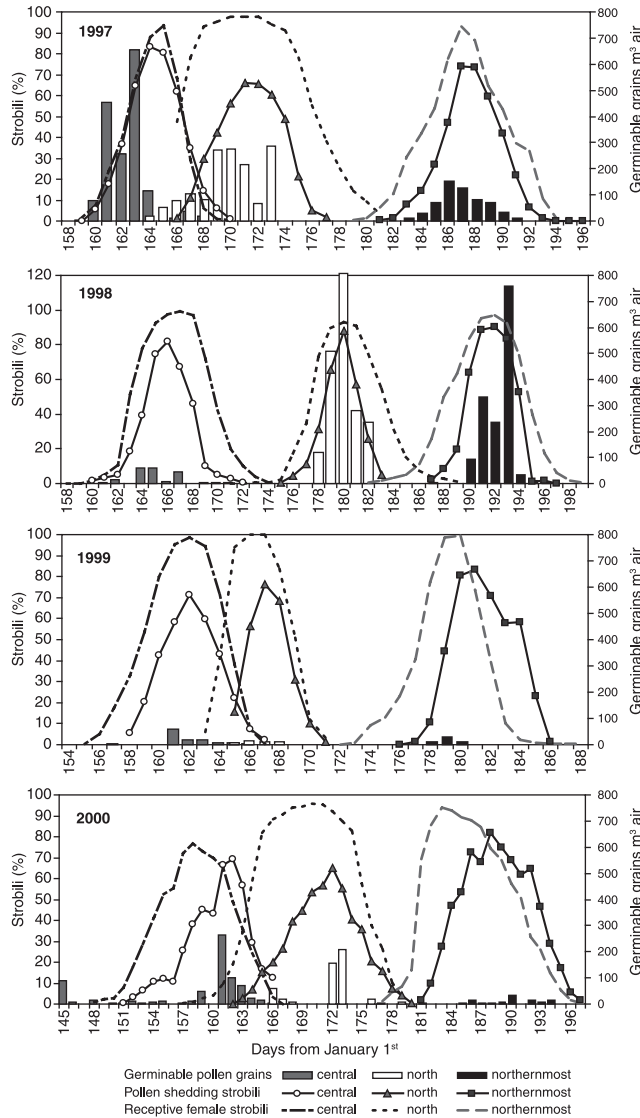


Fig. 2. Temporal occurrence of germinable airborne pollen, receptive female strobili and pollen shedding male strobili in central, northern and northernmost Finland.

pollen grains in m⁻³ air per day was 10.5 ± 25.8, in the north 12.0 ± 21.1, and in the far north 0.3 ± 0.4 m⁻³ (NS).

From all studied female strobili 809 (7.5%) became receptive prior to the start of local pollen shedding. Female strobili became receptive from two to five days earlier than local pollen shedding started. In 1997, female and male strobili in the

central and northern locations matured simultaneously (Table 2). The mean number of receptive female strobili per day was lower before local pollen shedding started ($\chi^2 = 49.03$, $p < 0.005$).

In 1997, 1999, and 2000, germinable pollen grains were detected in the air of the northern site when male strobili in the central site were actively shedding pollen (Fig. 2). In northern

site 4.9% of the detected germinable pollen was in the air prior to local pollen shedding in 1997, 0.1% in 1998, and 0.1% in 2000. In 2000, germinable pollen grains were detected in the air at the northernmost site when male strobili in the northern site were actively shedding pollen. In 2000 in the northernmost site, 3.8% of detected germinable pollen grains m^{-3} air were in the air prior to local pollen shedding.

4 Discussion

Our observations of pollen shedding, germinable airborne pollen grains and receptive female strobili suggest that pollen-mediated gene flow over several hundred kilometers in a south-north direction is possible for Finnish Scots pine. Germinable pollen grains were detected in the air when local female strobili were receptive but male strobili were immature. The occurrence of airborne pollen in northern and northernmost sites overlapped with male flowering in more southern locations, especially in 2000.

The amount of pollen flow from outside the study site have been 21 to 76% in seed orchards in Sweden and Finland (El-Kassaby et al. 1989, Harju and Muona 1989, Pakkanen et al. 1991, Wang et al. 1991). In our study the amount of nonlocal pollen in the air varied from almost zero to relatively high, depending on the year and study site. The number of receptive female strobili also varied between years and study sites, in a way that the simultaneous abundance of nonlocal pollen and receptive strobili was a rare phenomena. However, theoretical models (Gregorius 1983) and experimental studies (Sorensen and Webber 1997) show that pollination success is a rapidly saturating positive function of pollen capture, where even small pollen capture rates facilitate maximum pollination (Sorensen and Webber 1997). Furthermore, pollen from nonlocal sources most likely continues to arrive after local male strobili begin shedding pollen. In that situation the possibility of pollen competition arises.

Pollen competition exists when female strobili are receptive and pollen is being shed by male flowers both locally and distant populations. Pollen competition is well studied in angiosperm

species (rev. Skogsmyr and Lankinen 2002; Bernasconi 2003), but only few experiments have been done with coniferous species (Owens and Simpson 1982, Webber and Yeh 1987, Parantainen and Pasonen 2004, Varis et al. 2008, Pulkkinen et al. 2009, Varis et al. 2009). Artificial crosses with Scots pine pollen mixtures has either identified a competitive advantage for pollen from southern Finland (Pulkkinen et al. 2009) or no difference among pollen strains (Varis et al. 2008). In our earlier studies (Varis et al. 2008), we also found that the early arrival of southern pollen in the female strobili did not translate to a sexual advantage. Sarvas (1962) claimed that the pollen grain entering first to the nucellus tissue of Scots pine have an advantage in pollen competition. Owens and Simpson (1982) found the pollen grains of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) applied in the first two days of pollination period to be entangled in the stigmatic hairs more close to the micropyle than grains applied later. Our results from sequential artificial pollinations do not unconditionally support those hypothesis and results (Varis et al. 2008), and Webber and Yeh (1987) found similar differences in seeds siring success of first coming pollen in Douglas-fir. Comparing to Scots pine Douglas-fir has stigmatic hairs directing pollen grains to the pollen chamber instead of pollination drop (Owens et al. 1981), and in Scots pine the secretion and reabsorption of pollination drop may affect the outcome of pollen competition. It is also important to bear in mind that these studies were done under current climatic conditions and future changes may influence pollen competition and sexual selection in other directions.

While our study exposed the possibility of long-distance pollination in Scots pine, its design could not confirm the transfer of genetic material between distant populations. Parentage studies provide precise and detailed information but only from small populations or portions of larger populations (Burczyk et al. 2004). In most cases, such studies have found pollen dispersal to be on the meter rather than kilometer scale (e.g. Burczyk et al. 2004, Robledo-Arnuncio and Gil 2005, O'Connel et al. 2007). Although there is high genetic variation in adaptive traits in Scots pine (Kylmänen 1980, Pulkkinen et al. 1995, Hurme et al. 1997, Savolainen et al. 2004), differentiation

in molecular markers among populations is low (Karhu et al. 1996, Dvornyk et al. 2002, García-Gil et al. 2003, Savolainen et al. 2004), which makes molecular diagnostics of long distance gene flow impossible. Instead of that, phenotypic differences in the offspring of northern populations may be an indicator of gene flow from southern populations. For example, comparison of easily measured traits such as frost hardiness development during autumn (Andersson 1992) could provide additional information on pollen-mediated long distance gene flow. Lately, modelers have estimated emissions and long-distance pollen transport of various plant species on a European scale (e.g., Sofiev et al. 2006, Siljamo et al. 2008a,b, Vogel et al. 2008). Incorporating meteorological, phenology and germinability-with-distance data could enhance existing models and provide more information concerning long distance gene flow in plants.

In a review examining post-glacial plant response, Huntley (1991) concluded that migration rates of trees were at best equal to but more likely lagging behind periods of rapid deglacial warming. Traditionally, the growth and survival of trees have been considered to be well adapted to the areas in which they are found (e.g. Kylmänen 1980, Pulkkinen et al. 1995, Hurme et al. 1997), but evidence is now accumulating to suggest that local populations of wind-pollinated trees are less-than-maximally adapted to their growing sites (Matyas 2002, Rehfeldt et al. 2002). Populations tend to inhabit areas colder than their optima and this is explained by the high within-population variation caused by gene flow (Rehfeldt et al. 2002). Thus the ability of forest trees to adapt to a rapidly changing climate in northern parts of the boreal forest zone will depend on the availability of additive genetic variation within those populations (Hamrick et al. 1992). There is high genetic variation in adaptive traits like bud set date and frost hardiness between Scots pine populations in southern and northern Finland (Savolainen et al. 2004). This variation is also seen in northern progeny test areas, where background pollinated Scots pine seedlings from southwards-transferred seed orchards of northern Scots pine have lower survival rate than seedlings from local seed orchards (Kylmänen 1980, Nikkanen 1982, Rousi 1983, Mikola 1993, Pulkkinen et al. 1995).

This study established the possibility of long distance pollen transport in natural populations of Scots pine in Finland. Forest tree pollination is a dynamic process operating over a variety of spatial and temporal scales arising from the interaction of inherited phenology and stochastic environmental factors, e.g., weather and climate. Whether forest trees can adapt to a rapid change in climate, either by natural processes or forestry practice, is an important socio-economical and ecological question. Pollen-mediated gene flow is fundamental information to biologists evaluating the escape risk of genetic material from transgenic or non-native plants, conservation managers working to protect or reconnect fragmented populations, and foresters dealing with background gene-flow in seed orchards and plantations.

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