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Pollen production of *Alnus incana* at its south Norwegian altitudinal ecotone

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Pollen production of *Alnus incana* at its south Norwegian altitudinal ecotone.

Preliminary observations

DAGFINN MOE

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The pollen production (number of pollen grains per catkin) of *Alnus incana* is studied along two vertical transects across the altitudinal limit of the species. Annual variation in pollen quantity, and a considerable reduction in the number of pollen are found with increasing altitude. Normal pollen is virtually not produced at the ecotone. It is suggested that parameters such as the temperature of the preceding summer, length of the growing season, and soil factors are limiting factors. A test study shows no germination of seed from the ecotone, and reduced fertility is suggested.

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general, knowledge of pollen production, pollination and local seed production and germination for most species in marginal, ecotonal areas is limited (Pohl 1937, for *Quercus* and *Fagus* see comments Markgraf 1980). Reduced flowering is known for *Carex curvula* ssp. *curvula* and *C. curvula* ssp. *soae*, towards the alpine ecotone. Numerous dead abortive flowers were found, and any expansion of the species was by vegetative shoots (Erschbamer & Winkler 1995).

Surface pollen studies from North Norway (Alm et al. 1996) show low influx values of *Alnus incana* close to high altitudinal arctic- or alpine stands. In a test count on some *A. incana* catkins from a site close to the altitudinal limit of the species in south Norway (loc. 1, Fig. 1), a value of 329 *Alnus*-pollen per catkin was registered (Moe & Odland 1992). This was small compared with known values for *A. glutinosa* 4–4 million found by Pohl (1937). In the same study, the “Mean maximum July Temperature” was suggested as being the critical parameter for the altitudinal distribution of the growth of *A. incana*.

In Norway the altitudinal limits of the different vegetation zones, including the treeline and the ecotone of *A. incana*, decrease towards the north and the coastal areas in the west (Moen 1987).

Two transects in South Norway (Figure 1) were selected for studying the pollen production of *A. incana* towards its altitudinal limit. The quantity of pollen in catkins collected during the period from the beginning of December to early February is used as an indicator of local pollen production.

SITE DESCRIPTIONS

Two areas in the west of Norway, with known high altitude sites (Herbarium BG) of *Alnus incana* were selected: the eastern one Skurdalen (Buskerud county), includes the uppermost locality, loc. 1 at 995 m a.s.l. with the highest known

A. incana station in Norway, and a western one, Fana/Os (Hordaland county) lies in a more oceanic climate region.

The exposure in the eastern area is south-eastern, the habitat is mostly a wet minerogenic one, the ground is slightly sloping, and the local vegetation in the upper part of the area is dominated by *Betula pubescens*. The eastern area includes 9 stands at 8 different altitudinal levels, from 995 m (potential local treeline around 1100 m) to 800 m a.s.l. (Fig. 1, Table I.).

The western area includes 4 sites, and covers altitudes from 403 m to 95 m a.s.l. (the potential treeline is thought to be between 450 m and 500 m). A small stand, 3 individuals, at 403 m a.s.l. on the mountain Lyshornet, Os, was included, where *A. incana* is thought to grow very close to its altitudinal ecotone. The exposure is southern, and the habitat and local vegetation are the same as in the eastern.

METHODS

Fieldwork

In the south-west coastal area of Norway, *A. incana* normally flowers in March–April (Krzywinski 1976); at higher altitudes presumably a little later (Frenguelli et al. 1991). Almost fully developed pollen and catkins are produced during the previous growing season (Strasburger et al. 1978) as in the case with many Betulaceae species (Dunbar & Rowley 1984, Blackmore & Knox 1990).

In the present study catkins were collected during the period from the end of December to early February (see text Table II), that is well before the start of flowering. For bushes carrying catkins of different sizes, all sizes were collected. Some of the fieldwork was limited by weather conditions.

From localities 1, 2, 4, 5b and 9 in Skurdalen soil/moss surface samples were collected for pollen analysis (29.9.1993) (Table I and II). For each locality, within a radius of 1 meter from the specimen used for the catkin studies, three to four subsamples were collected and combined into a general sample.

Tree-ring studies were carried out on one of the oldest stems from the studied stand at loc. 1. Half a metre above the ground the

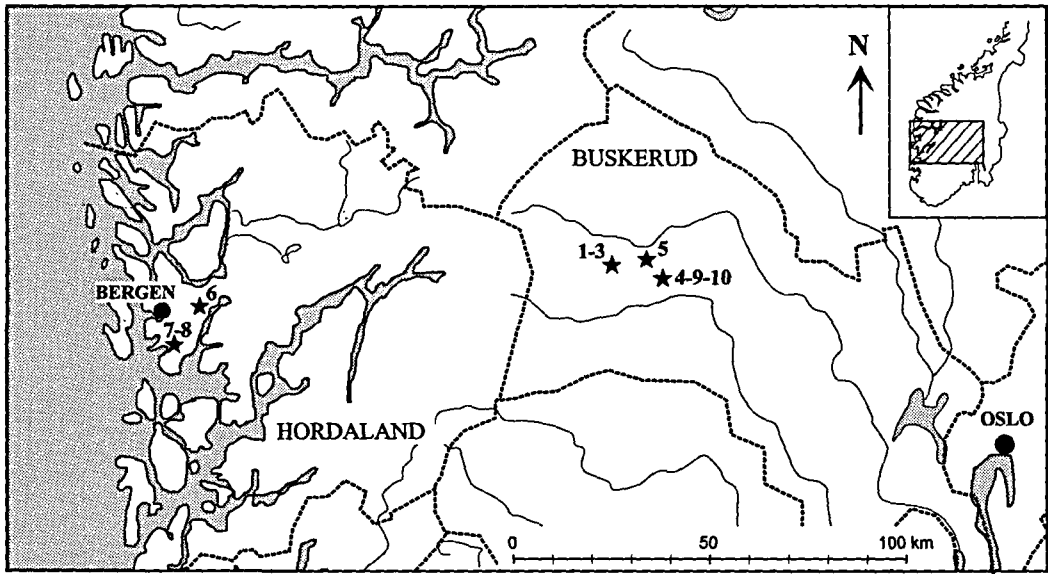


Fig. 1. Survey map of the central part of south Norway showing the two areas studied.

Table I. Localities studied

No	Locality	Coordinates	Remarks on sites	
1.	Skurdalen, Hol, Buskerud, 995 m a.s.l.	UTM MN 547046	Shrubby individual/stand, about 2-metres high on mire, ca 5–15 mN of the road to Tuva	One of three stands was used
2a,b.	Skurdalen, Hol, Buskerud, 993 m a.s.l.	UTM MN 547046	Several individual trees, 5–7 m high on some drier soil	Two trees were used.
3.	Skurdalen, Hol, Buskerud, 970 m a.s.l.	UTM MN 547047	Shrubs, on a wet mire, like loc. 1	Two-three stands.
4.	Skurdalen, Hol, Buskerud, 835 m a.s.l.	UTM MN 558047.	Trees/stands close to the road and the gate for the Tuva-road	
		Several trees, 5–7 m, on mixed soil		
5a.	Skurdalen, Hol, Buskerud, 942 m a.s.l.	UTM MN 613059	Shrubs (two small stands), 2–4 m, on some wet soil, close to a brook private road and c. 60 m SW from Moestugu	One stand was used
5b.	Skurdalen, Hol, Buskerud, 950 m a.s.l.	UTM MN 613060	Shrubs (two stands), 2–4 m, on some wet soil, 20 m NW from the Moestugu cottage	One stand was used
6.	Samdalen, Fana, Hordaland, 95 m a.s.l.	UTM LM 088938	Trees, 5–8 m, near the road	
7.	Lyshornet, Os, Hordaland, 403 m a.s.l.	UTM LM 012838	Trees/shrub 2–3,5 m, (two-three stands) near to the summit and the trigonometric mapping point	
8a.	Lyshornet, Os, Hordaland, 280 m a.s.l.	–	Stands of shrubs, 2–4 m, close to the path to Lyshornet, on a mire	
8b.	Lyshornet, Os, Hordaland, 250 m a.s.l.	–	Stands of shrubs, 2–4 m, close to the path to Lyshornet, on a mire	
9.	Skurdalen, Hol, Buskerud, Lia, 800 m a.s.l.	UTM MN 645033	Trees, 5–7 m on mixed soil close to the main road	
10.	Skurdalen, Hol, Buskerud, Kleiva, 810 m a.s.l.	UTM MN 588052	Trees, 5–7 m, on mixed soil close to the main road	

diameter of the stem was 9 cm including bark, and 45 year-rings were counted. Mean year-ring width was measured and found to be between 0.3 mm and 1.0 mm year⁻¹. At 1 metre, the diameter was 7 cm and the age 43 years. Above the snowcover the oldest stems were mostly decayed, and only younger branches from below existed. Snow protection during winter is assumed to be important for the winter survival, preventing damage caused by wind erosion and

snow crystals. Snow-break, however, may cause damage during the winter and spring.

The cones produced in the season 1992 were numerous in the eastern area, at all localities from 995 m downhill. Seeds from loc. 1 were tested at the Botanical garden, UiB, but none of them germinated. Flowering took place on the next to last year shoots. The maximum age for alder at the altitudinal limit is not known,

Table II. Number of *Alnus*-pollen per catkin per year

Sampling took place in December or the following January/February. (Abbr.: 1=measurements on small catkins, pollen badly developed if any; 2=small and normal catkins; 3- normal catkins; --=no sample.).

a. Skurdalen, Buskerud.

Loc.	Level	1989	1990	1991	1992	1995	1996
1.	995 m	329 ¹	0 ¹	40 ¹	0	–	0 ¹
2a.	993 m	–	33 ¹	160 ¹	9486 ³	–	–
2b.	993 m	–	698 ²	–	14,161 ³	–	–
3.	970 m	–	0 ¹	14	0 ¹	–	–
5b.	950 m	–	–	–	0 ¹	–	0 ¹
5a.	942 m	–	–	41	0 ¹	–	–
4.	835 m	–	18,430	143,370	124,177 ³	–	–
10.	810 m	–	–	391,500	–	–	–
9.	800 m	–	–	–	–	–	1.63 × 10 ⁶

b. From Fana/Os, Hordaland

Loc.	Level	1989	1990	1991	1992	1995	1996
7.	403 m	–	–	55 ¹	1 ¹	–	0 ¹
8a.	280 m	–	–	–	0 ¹	636,401	0 ¹
8b.	250 m	–	–	–	666,700 ³	899,056	0 ¹
9.	95 m	–	1.24 × 10 ⁶	–	54	–	637,397
					1772		

and vegetative formation prolonging its local existence should not be excluded.

Laboratory work

For the pollen production study, 3 catkins from the same tree were used. Pollen quantities were counted relative to an added exotic as follows: 1–3 *Lycopodium* tablets, Stockmarr 1971 for the years 1989–1992, and 1/2–1 ml *Impatiens walleriana* in liquid suspension (Siegfried Tatzreiter unpubl.) for 1995–1996. The added amount varied depending on the presumed pollen content.

The chemical treatment of the catkins and surface samples followed the guidelines for fossil pollen preparation in Faegri & Iversen (1989). In addition, HF-treatment was used for soil surface samples.

RESULTS AND DISCUSSION

Some field observations

At loc. 1 (Fig. 1, Table I) three shrubby individuals/ stands of *A. incana* (between 2.70 m and 3.20 m tall) were growing on a soligenic mire, 10 m apart. The local *Parmelia olivacea*-limit was 1.65–1.75 m. Snowcover was 1.55 m deep (2.1.1991). The shrub on the mire had several female cones (all above the snowcover) produced in 1990, but no catkins were found that year. During the following winter visits, no “normal” catkins were found at loc. 1, 5b and 7, only very small, abortive, initiating stages, only 1–3 mm in length were found (Figs. 2 and 3).

At localities 2, 5a and 8a, on shrubs growing partly on drier ground (see Table I), more normal intermediate catkins, around 3/4 cm long and 2–3 mm wide in size, were found

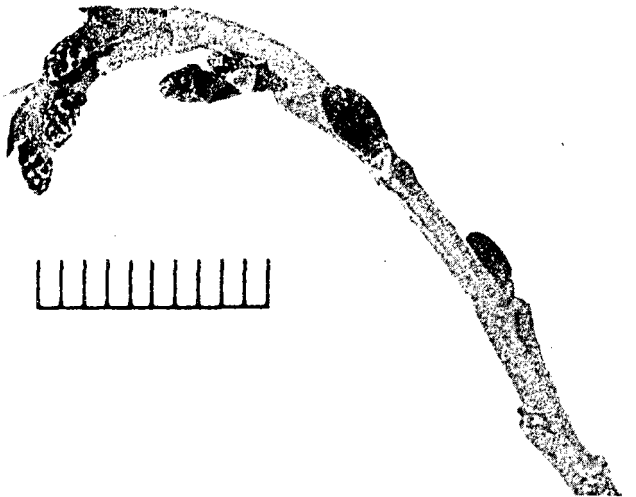


Fig. 2. Abortive *Alnus incana* catkin from an individual close to its altitudinal limit at Lyshornet (403 m a.s.l., loc. 7 in Fig. 1), Os, Hordaland, see text, collected 3.1.1997. Scale – Total 10 mm. (Photo: Stephan Medgyesy).

partly on the same branch as the small ones. The number of such catkins varied from year to year. The small abortive catkins, however, predominated. In the eastern area, at loc. 4, 150 m lower, only normal catkins were found, except following the 1992 season. In the west, loc. 6 has always had large catkins (Fig. 3). No material was collected in 1993 and 1994.

At the western localities 7, 8a, and 8b no large catkins were observed in December 1996, after a growing season which was relatively cold, the mean temperature for December was about 2°C cooler than 1961–90 average. (Table IV). It is suggested that climate conditions such as temperature and length of the growing season etc. must be important for the development of the catkins.

Pollen analyses

The following stages of pollen development could be recognized. The morphological stage of development of the pollen varied a lot, from very thin-walled, undefined bodies, which it was hardly possible to identify, to “normal” *Alnus* pollen.

Thin-walled juvenile/abortive pollen, which was possibly *Alnus* pollen, was not included in the counting, while some intermediate types may have been counted together with *A. incana* pollen. It was difficult to make clear indisputable definition between the different stages of ripe and unripe pollen.

There was a tendency for more unripe pollen to be found in the catkins towards the altitudinal limit both in the eastern and in the western areas. In some of the results both types were included (see Table II).

Pollen production

The results clearly demonstrate variation in the yearly production of *A. incana* pollen per catkin at localities at and close to the ecotone. At lower altitudinal levels the relative



Fig. 3. *Alnus incana* catkins collected from different altitudes in January 1997 (3.1.1997). From left to right: loc. 7 (403 m); loc. 9 (800 m); and loc. 6 (95 m). Scale bars – 1 cm. (Photo: Stephan Medgyesy).

variations decrease. The highest pollen production was found in both areas at the lowermost localities studied, loc. 9 and loc. 6 with values of 1.63×10^6 and 1.24×10^6 pollen respectively. These values can be compared with *Alnus* pollen production of 2.16×10^6 pollen per catkin found in a case study from the Oslo region, south-east Norway (ref. ca. 4.4×10^6 pollen per catkin for *A. glutinosa*, Pohl 1937).

High pollen values were found at site 8a in 1995. Precipitation or water supply was unlikely to have been the limiting factor for the species in this region, but the differences in temperature between 1995 and 1996 are striking (Table IVb) (Mamen 1997). During June–October mean temperatures in Bergen were above the long-term mean value, especially in the two last months. This may have affected the length of the growing season and most probably also pollen development at critical altitudes. Such yearly local variation in pollen production will affect the following year airborne pollen values recorded close to arctic-alpine areas (e.g. Norway and Finland: Ramfjord 1985–1995, Hicks 1994, Hicks et al. 1994, Alm et al. 1996).

The generally very low pollen production values noted in this study correspond to the values found in the soil surface

(Table III), despite the fact that these values may also reflect the abundance of trees. The production values, however, coincide with the low *Alnus* (*A. incana*) pollen influx values from north Norway (Alm et al. 1996). That study was made in Tromsø, North Norway, at the arctic-alpine limit of the species. The study suggests “an influx rate of 100 pollen, or less, to be indicative of grey alder stands in the immediate surroundings ...”, and may be comparable with the present study.

Further studies are planned on the relationship between the local pollen influx and pollen production.

CONCLUSION

This study covers the pollen production of only a few years, and greater variations than those observed are likely to occur.

Despite the short period, however, the results show considerable altitudinal differences, from no pollen at the ecotone in some years, to more than 1×10^6 pollen per catkin at lower levels. It is suggested that variations in yearly pollen production correspond to such climate factors as local summer temperature, frost injury and/or length of the grow-

Table III. Number of pollen in soil surface samples from the Skurdalen area (Hol), Buskerud (see Fig. 1).

For sites, loc., see Table I. (Abbr.: %Ap/%TOT = %-values of *Alnus* pollen on AP/TOT, ot = other trees, AP = arboreal pollen, Sh = shrub, Hb = herbs, TOT = total pollen, SPO = Total fern spores.) Vegetation: loc. 1, 2 and 5b – mires with local birch predominate; Loc. 4 and 9 – mixed *Pinus-Betula* forest with stands of *Picea*).

Loc.	Altitude	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Alnus</i>	%Ap	%TOT	ot	AP	Sh	Hb	TOT	SPO
1.	995 m	12	109	333	4	0.9	0.8	2	460	3	59	522	12
2.	993 m	13	99	321	4	0.9	0.8	4	443	5	146	594	6
5b.	950 m	18	141	221	0	0.0	0.0	0	380	1	75	456	3
4.	835 m	6	27	531	38	6.3	6.1	2	604	5	14	623	12
9.	800 m	1	99	110	45	17.1	14.0	8	263	8	50	321	13

Table IV. Meteorological data for Bergen meteorological station (Florida).

Mean monthly precipitation (a) and temperature (b) values for: the period 1961–90; 1995; and 1996.
a. Precipitation in mm

Year	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Average Sum
1961–90	190	152	170	114	106	132	148	190	283	271	259	235	2250
1995	246	324	277	172	96	81	248	100	158	543	256	143	2644
1996	30	167	51	73	64	146	164	91	75	408	226	196	1691

b. Temperature in C°

Year	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Average Sum
1961–90	1.5	1.6	3.3	5.9	10.5	13.5	14.5	14.4	11.5	8.7	4.7	2.6	7.7
1995	2.5	2.5	3.4	5.2	8.9	13.6	14.7	14.8	12.7	10.3	4.1	−0.9	7.7
1996	0.8	0.1	2.3	6.8	8.6	12.2	12.8	17.5	11.6	9.6	1.5	0.8	7.1

ing season, as is the case for successful seed development (Wagner & Tengg 1993, Lardon & Triboi-Blondel 1994). Obviously, to maintain a yearly pollen production, the climate parameter suggested for the arctic-alpine distribution of *Alnus incana* (a mean-maximum-July temperature of at least 17.2°C) is not sufficient (Moe & Odland 1992).

On the basis of different local habitat conditions and observed results, it is presumed that the pollen production of *A. incana*, at and close to its altitudinal limit, is also dependent on soil/wetness conditions.

The low yearly influx values of *Alnus*-pollen in air/trap studies found at high altitudes/ latitudes (Hicks 1994, Hicks et al. 1997, Alm et al. 1996), probably reflect rather a general long distance transport than very low local production, as seen at localities 1 and 7. On the other hand marked annual peaks in such values may reflect changes in local climate and therefore pollen production, primarily from the previous year.

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