Pollen Dispersal

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1. Introduction

An understanding of pollen dispersal is of importance, both for forest tree breeding and for provenance research. Full clarity regarding these problems cannot be achieved before extended experiments are undertaken out in the field. While a series of experiments has been carried out regarding the dispersal of pollen for various agricultural growths, there is little literature dealing with the dispersal of tree-pollen.

SUTTON (1932, 1934, 1947 a and b) has evolved theoretical models for the dispersal of light particles. An examination of these formulae is of interest, because they have given good results in many instances (dispersal of smoke particles, spores and pollen). In the following pages, the main emphasis is laid on a checking-up of SUTTON's formulae, at the same time reporting on the results of the author's own investigations into pollen dispersal.

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2. Theoretical models for dispersal of pollen

According to the dimensions of the source of dispersal, a distinction can be made between three types: — (1) point, (2) line and (3) plane sources of dispersal. — In practice, an individual flower can be regarded as a point source of dispersal (if the distances are not too small), while a stand must be regarded as a plane source of dispersal.

21. Point source of dispersal

SCHMIDT (1918 and 1925) seems to be one of the first who has attempted to make calculations regarding the dispersal of light particles, using as a basis the theory of turbulent wind. Calling the density of the particles τ, he sets out the "diffusion equation"

$$\frac{\partial \tau}{\partial t} = \frac{A}{\varrho} \frac{\partial^2 \tau}{\partial z^2} \qquad (1)$$

where **A** is a coefficient which is called the "Austauschkoeffizient" and ϱ represents the density of the air.

The solution of the differential equation (1) is

$$\tau = \frac{1}{\left(\pi \frac{4}{\varrho} At\right)^{1/2}} \cdot e^{-\frac{z^2}{\frac{4}{\varrho} At}} \qquad (2)$$

This formula assumes that the velocity of fall of the particles is 0. In the case of investigations into the dispersal of pollen over long distances, therefore, corrections must be made. Where dispersal in the immediate neighbourhood of the source is concerned, however, it is not necessary to take this into account. The velocity of fall will as a rule represent only small percentage of the wind velocity. If, for example, the velocity of fall is 5 cm/sec, and the wind velocity 5 m/sec, this will mean that after 20 seconds the particles will have moved 100 metres in a horizontal direction, but only one metre in a vertical direction. With a distance of 100 metres from the source of dispersal, the particles will be so widely spread that a vertical displacement of one metre is of no consequence.

While SCHMIDT begins with an equation from the kinetic gas theory, SUTTON attacks the problem from a statistical point of view (1932, 1934 and 1947 a). The line of argument is as follows: —

For a particle which follows the movements of the air, there will, according to experience, be a certain correlation between the movements of the particle at a given moment, and the movements ζ seconds afterwards. Generally, the correlation will depend upon the moment at which the observations are taken, t, and the interval of time between the observations. The correlation function can therefore be expressed R (ζ, t). Experiments show that the function R (ζ, t) may be written

$$R(\zeta, t) \propto (\zeta \sigma_w^2)^{-n} \qquad (3)$$

where σ^2_w is the variance of the wind component in a certain direction and n is a constant which expresses the turbulence of the wind. (*a* is used as **a** symbol meaning "proportional to".)

In the following, the co-ordinate system is presumed to be orientated in such a manner that the x-axis coincides with the direction of the wind, the y-axis is positioned vertically on the x-axis and lies in the horizontal plane, while the z-axis is positioned vertically.

Using a formula given by TAYLOR (1922), the density for an instantaneous source at the point (x, y, z) is found to be

$$\tau(x, y, z; t) \propto \frac{1}{\pi^{3/2} C_x C_y C_z (ut)^{3m/2}} \exp\left[-\frac{1}{(ut)^m}\left\{\frac{x^2}{C_x^2} + \frac{y^2}{C_y^2} + \frac{z^2}{C_z^2}\right\}\right] \qquad (4a)$$

where m = 2 — n, and u represents the average wind velocity. **As** a rule, m will be approximately equal to 1.75, and will always be in the interval between 1 and 2.

In formula *(4a)*, the co-ordinate system is presumed to be moving in the wind direction with velocity u. Keeping the co-ordinate system fixed, the density for a continuous source at the point (x, y, z) is

$$\tau(x, y, z) \propto \frac{1}{\pi C_y C_z x^m} \exp\left[-\frac{1}{x^m}\left\{\frac{y^2}{C_y^2} + \frac{z^2}{C_z^2}\right\}\right] \qquad (4b)$$

The coefficients C_x, C_y and C_z are proportional to $(U)^{-n/2}$. But as n is of magnitude 0,25, the poillen will be distributed in more or less the same way wether the wind is weak or strong.

A fact which is particularly important to notice is that *for* points which lie on the *same level* as the *source* of dispersal, *and* in the direction of the wind, the density (T) *decreases with the distance (x), in accordance with the formula.*

$$\tau \propto x^{-m} \tag{5}$$

22. Line source of dispersal

The dispersal of pollen from a line source which extends from (0, $-y_0$, 0) to (0, $+y_0$, 0) can be found by integrating the formula for a point source of dispersal.

$$\tau(x, y, z) \propto \frac{\exp\left(-\frac{z^2}{C_z^2 \cdot x^m}\right)}{C_z \cdot x^{m/2}} \left[\varnothing\left(\frac{y_0 + y}{C_y^2 \cdot x^m}\right) + \varnothing\left(\frac{y_0 - y}{C_y^2 \cdot x^m}\right) \right] \tag{6}$$

$$\text{where } \varnothing\left(\frac{y}{\sigma}\right) = \frac{2}{\sqrt{\pi}} \int_0^{y_0} e^{-t^2} \cdot dt$$

If y_0 tends towards infinity, formula *(6)* becomes

$$\tau(x, y, z) \propto \frac{1}{x^{m/2}} \exp\left[-\frac{1}{x^m} \frac{z^2}{C_z^2}\right] \tag{7}$$

For points on the same level as the source of dispersal, the density decreases much more slowly in relation to the distance than in the case of a point source:

$$\tau \propto x^{-m/2} \tag{8}$$

23. Plane source of dispersal

For a plane source of dispersal (a source of dispersal with extension also in the direction of the wind) the dispersal can be computed in the following manner: The density in distance x from a line source of dispersal is given by formula *(7)*. It is assumed that the number of particles released per unit of area from the source is constant over the whole area. If the source of dispersal is infinitely long, the density of the particles which are released from a narrow strip of the source of dispersal, with the longitudinal direction across the direction of the wind and the depth Δ x, will be proportional to

$$\tau \propto \frac{1}{x^{m/2}} \exp\left\{-\frac{z^2}{C_z^2 \cdot x^m}\right\} \Delta x$$

If the depth of the source of dispersal is B, the density at distance x from the leeside is proportional to

$$\int_x^{B+x} \frac{1}{x^{m/2}} \exp\left\{-\frac{z^2}{C_z^2 \cdot x^m}\right\} dx$$

This expression can be written

$$\int_x^{B+x} \frac{1}{x^{m/2}} \left\{1 - \frac{z^2}{C_z^2\, x^m} + \frac{z^4}{2!\, C_z^4 \cdot x^{2m}} - \ldots\right\} dx$$

When x is larger than, for example, one metre, the density will be approximately proportional to

$$\int_x^{B+x} \frac{1}{x^{m/2}}\, dx \propto \left[(B + x)^{1-\frac{m}{2}} - x^{1-\frac{m}{2}}\right] \tag{9}$$

For a plane source of dispersal, the density decreases even more slowly with the distance than for a linear source of dispersal.

24. Effect of an absorbing wall

Particles which are dispersed from a low height will, because of turbulence, have a tendency to be driven against the ground and held there. This will occur even if the velocity of fall is 0. The total number of particles in motion will therefore gradually decrease. For dispersal over greater distances, this will be a factor of considerable importance.

In the following it is assumed that the surface of the ground acts as a fully effective absorbing wall, so that particles which have once come into contact with it are not released again.

The problem with an absorbing wall is solved in connection with "random-walk" models. For a particle which moves in jumps of length l along a line, the probability that after N jumps it will be found in the interval z, z+Δ z is approximately expressed by

$$\tau(z, N)\, \Delta z = \frac{1}{(2\pi N l^2)^{1/2}} \exp\left\{-\frac{z^2}{2 N l^2}\right\} \Delta z$$

(CHANDRASEKHAR 1943). If the particle starts at point 0, and absorbing wall is found at $-z_1$, the probability that the particle at the moment t will be in the interval z, z + Δ z is expressed by

$$\tau(z, N; -z_1) = \frac{1}{(2\pi N l^2)^{1/2}} \left\{\exp\left(-\frac{z^2}{2 N l^2}\right) - \exp\left(-\frac{(z-2z)^2}{2 N l^2}\right)\right\} \tag{10}$$

Putting Nl = (ut) and l = $\frac{C_z^2}{2}$ $(ut)^{m-1}$, formula *(10)* becomes

$$\tau(z, t; -z_1) = \frac{1}{(\pi\, C_z^2\, (ut)^m)^{1/2}} \left\{\exp\left(-\frac{z^2}{C_z^2 (ut)^m}\right) - \exp\left(-\frac{(z - 2z_1)^2}{C_z^2\, (ut)^m}\right)\right\} \tag{11}$$

A transition such as suggested from formula *(10)* to formula *(11)* should be permissible. That is to say, the assumption is made that the jumps become longer and longer, or, in this case where one is dealing with vertical dispersal, that the jumps become more and more directed upwards and downwards.

3. Investigations regarding pollen dispersal

Some minor investigations regarding pollen dispersal were undertaken during the flowering periods 1949—1952. These can be placed in the following groups: —

A. Artificial dispersal of pollen from a point source.
B. Pollen dispersal from an isolated Norway spruce.
C. Pollen dispersal on steep hillsides.
D. Pollen dispersal from the edge of a forest over an open space.

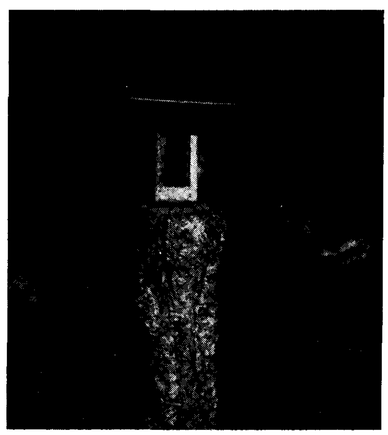

Fig. 1. — Holder for microscope slide, used for the interception of pollen.

The same technique was used in all these investigations. Microscope slides were placed at varying distances from the source of dispersal. The slides were coated with glycerine gelatine, and secured in rigid tin holders *(fig. 1)*. The coated side of the glass faced towards the prevailing wind direction. At the time for collection, a covering glass was placed over the slide. The covering glass was found to attach itself better after being slightly warmed. This technique proved to be satisfactory, especially because the transportation of the slides could be so easily arranged.

The counting was done by means of a microscope with a mechanical stage. A fixed number of counting lines were laid over the covering glass. All pollen grains which lay more than half inside the field of vision were included in the count. In some cases the counting was made difficult by the presence of a clump of pollen, consisting of many grains. In these cases, the grains could cover one another so that it was difficult to isolate the individual grains.

31. Artificial pollen dispersal

In the spring of 1952, experiments in the dispersal of pollen by artificial means were undertaken. The microscope slides were placed along two lines which formed an angle of approximately 30° with each other. The pollen was shaken carefully out of a test tube at the intersection point between the two lines. The results of the experiments appear in *fig. 2*. The wind force varied somewhat from one experiment to another, between 1 and 7 m./sec.

The decrease in the pollen density corresponds very well with what can be expected from a point source of dispersal. Neither is there any distinct variation between experiments undertaken at different wind forces. The experiments support, therefore, the theoretical results which are given in previous sections.

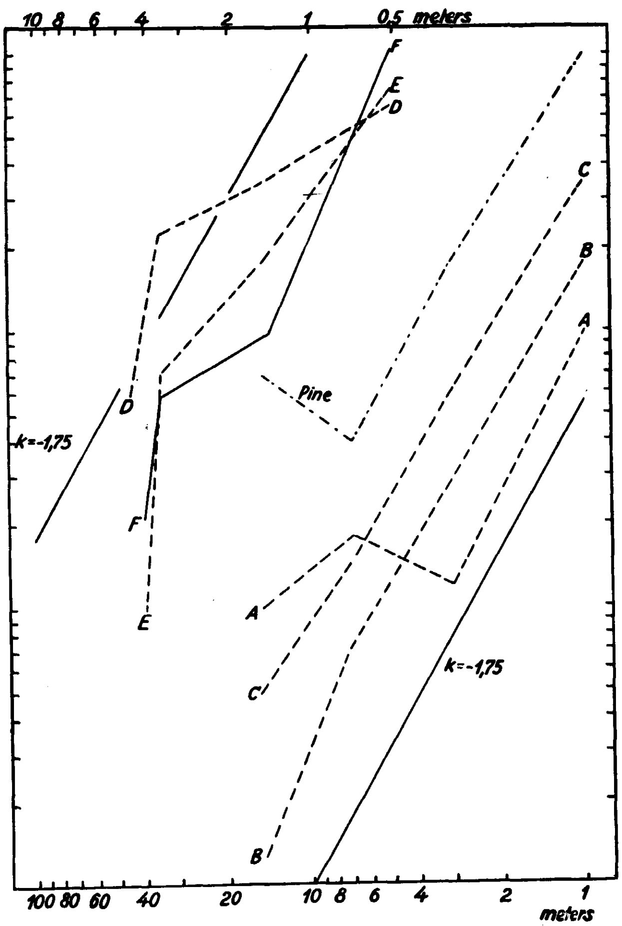

Fig. 2. — Pollen density at varying distances from an artificial point source of dispersal. Note that the scale for the density is logarithmic.

32. Pollen dispersal from an isolated Norway spruce

Investigations regarding the dispersal of Norway spruce pollen can with advantage be undertaken in West Norway. In many places here can be found solitary spruces, separated by great distances from others of their kind, due to the fact that this species does not occur naturally, apart from purely local examples.

In the spring of 1952, investigations were made into the dispersal from an isolated Norway spruce on a pasture in Sogn. The height of the tree was 10 metres, and the crown diameter approximately 7 metres. Flowers were found from a height of about 6 metres and upwards.. Microscope slides were laid out in three directions. The weather during the observation period was fine and dry.

The number of pollen grains per square centimetre for the individual days is shown in *table 1*.

Table 1. — *Number of pollen grains per sq. cm. at various distances from an isolated Norway spruce*

Date	Side									
	North					East				
	Distance in metres									
	0.5	3.5	6.5	12.5	18.5	0.5	3.5	6.5	12.5	18.5
16/5	185	111	37	0	37	444	296	37	37	0
17/5	3920	296	0	0	0	1000	296	111	37	37
18/5	1590	518	407	148	148	1590	148	74	185	148
19/5	222	222	0	37	37	296	37	111	0	37
20/5	74	74	0	0	0	964	74	74	37	0
21/5	37	37	0	37	0	222	148	0	0	0
Total	6028	1258	444	222	222	4516	999	407	296	222

The total number of pollen grains is set out in *fig. 3*. The curves concerned are marked "Norway spruce 1952".

A similar investigation was undertaken in the spring of 1949. Here it proved that the pollen grains showed a strong tendency to appear in clumps on one particular day. The counting for this day, therefore, offered difficulties. The total number of pollen grains for the other days is set out in *fig. 3*. The curves are marked "Norway spruce 1949".

On comparing the two observation columns, it appears that the decrease in pollen density with the distance is more marked in 1949 than in 1952. This is reasonable, because the microscope slides were placed at greater distances in 1949 than in 1952. For a source of dispersal with the dimensions of a tree, the distribution in the vicinity of the tree will correspond approximately to that from a linear source, while at greater distances it resembles more the distribution from a point source of dispersal.

An interesting phenomenon was observed at the counting of the pollen during 1952. The flowering of the pine appeared to begin on the 20th May, as quite large quantities of pollen were then observed on the slides. In *table 2* are given the figures for the 20th and 21st May.

Table 2. — *Number of pine pollen grains per sq. cm., 1952*

Date	Side									
	North					East				
	Distance in metres									
	0.5	3.5	6.5	12.5	18.5	0.5	3.5	6.5	12.5	18.5
20/5	444	260	702	633	964	964	518	2520	3780	5140
21/5	592	480	555	555	480	148	296	185	1335	222

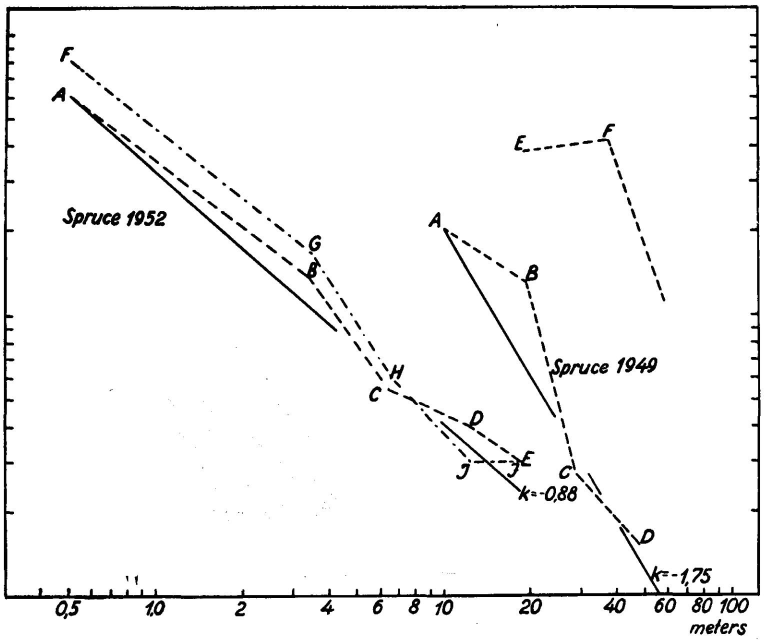

Fig. 3. — Pollen density at varying distances from an isolated Norway spruce. Note that the scale for the density is logarithmic.

The direction of the wind throughout these two days was from the west, which explains the large quantities of pollen for the series on the east side compared with the north side. It is clear that the number of pine pollen grains is much lower on the slides which were in the immediate neighbourhood of the tree than it is on those further away. The Norway spruce tree has acted as a kind of filter which has held back some of the pine pollen. A similar happening is recorded by von DELLINGSHAUSEN (1954), DENGLER (1955) and PERSSON (1955).

33. Pollen dispersal on steep hillsides

Pollen dispersal on steep hillsides clad with pine forest was investigated in 1949 in Sogn. The microscope slides were placed at various heights above sea level along three different lines. The positioning appears in *fig. 4.*

Table 3. — Total number of pine pollen grains for a series of three-day periods

Place	Height above sea l. *meters*	Date					
		2/6—4/6	5/6—7/6	8/6—10/6	11/6—13/6	14/6—16/6	17/6—19/6
A	100	36	1734	1213	2554	662	274
B	200	4	137	93	1456	255	213
C	320	24	77	37	937	2672	4314
D	400	10	15	21	926	227	524
E	470	23	157	68	731	346	512
F	580	3	39	50	212	156	131
G	660	45	147	81	544	384	766
H	100	76	2248	3994	1284	1412	954
I	200	63	1373	3685	2217	1755	397
K	300	20	227	646	449	1044	1732
L	400	11	370	612	437	2666	538
M	500	5	136	39	61	71	287
N	100	6	65	84	669	237	236
O	200	10	232	220	5689	552	624
P	300	3	200	679	1858	4419	1881
R	400	4	80	116	300	985	1518

The weather was mainly fine during the period of observation, with little rain. The temperature, however, was comparatively low. A summary of the counting results for a series of three-day periods is given in *table 3.*

The gradual displacement of the maximal numbers of pollen grains higher and higher up the hillside is shown by the table. It appears that this displacement takes place somewhat more slowly than the displacement in the flowering time, as is shown by the following observations: At each place where the microscope slides were set out, five trees were chosen, in good time before flowering began. When the slides were changed, a note was taken of the development undergone by the flowers. These observations showed that the flowering time was retarded from 2 to 5 days for every 100 metres ascended, the average being 3 days.

34. Pollen dispersal from the edge of a forest

In 1950, slides were set out for the interception of pollen on an open piece of ground. The

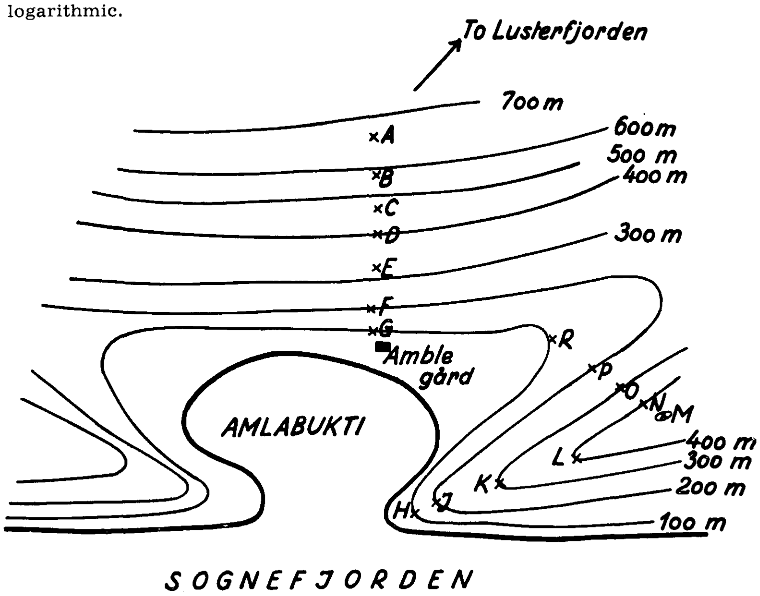

Fig. 4. — Sketch of positioning of microscopic slides for the investigation of pollen dispersal on steep hillsides.

intention was that this ground should be used later on for the establishment of a pine seed orchard. Towards the west and north-west the ground faced open country. Otherwise, it was surrounded by Norway spruce forest in such a way that the shape of the ground was approximately a half-circle with a diameter of about 600 metres. Ten slides were placed at equal distances along the diameter of the half-circle, in a north/south direction. The slides A and K were inside the forest, the others at a greater or less distance from its nearest edge. The coated side of the slide was always turned towards the nearest edge of the forest (in the case of A—E southwards, and for F—K northwards). The results for the individual days are noted in *fig. 5.* There was very little pollen movement on the days which are omitted.

The maximum pollen density on most of the days was shown on the slides which were closest to the edge of the forest (but not actually inside the forest), while the pollen

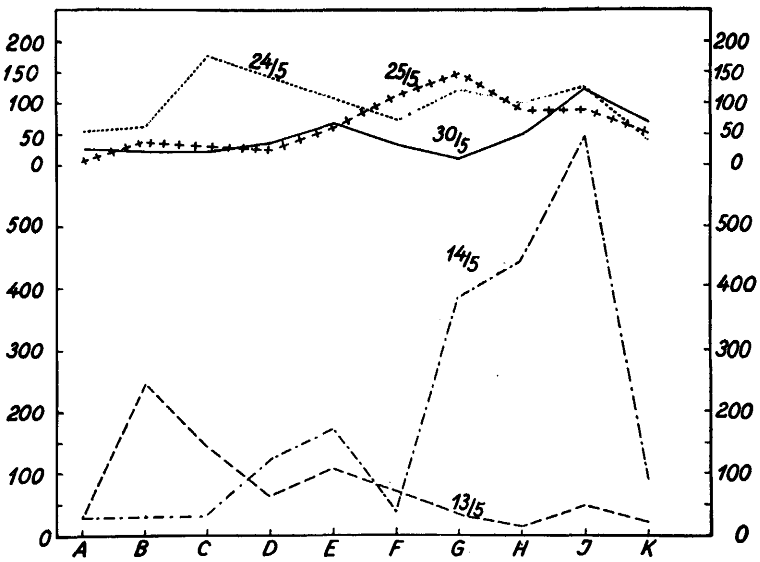

Fig. 5. — Pollen density (162 sq. mm.) for the individual positions in the investigation into pollen dispersal over open ground.

density decreased gradually outwards towards the opposite side of the field. This must be because the wind has been fairly stable these days, though it has varied somewhat in direction from day to day. This has led to the lowest total number of pollen grains being in the centre of the field, a gradual increase being shown as the edges are approached. The difference between the pollen density at the edges of the forest and in the centre of the field is quite clear.

4. Discussion

The formulae *(5)*, *(8)* and *(9)* have been tested by experiments published by STEPANOV (1935), WILSON and BAKER (1946), BONDE and SCHULTZ (1943), OORT (1940), POHL (1933), REMPE (1938), WRIGHT (1952), JENSEN and BÖGH (1942), JONES and NEWELL (1946), BATEMAN (1947 a), SUNDELIN (1934), ROEMER (1932), WIT (1952), GRIFFITHS (1950) and ANDERSSON (1955). Space does not permit the publication of all the comparisons between the observed and the estimated values here. As an example of such a comparison, the theoretical and observed values for pollen density from a series of experiments (ANDERSSON 1955) are noted in *fig. 6*.

The experiment at Kumla has been deleted, as there seems to be much "long-distance" pollen. The main impression given by the comparisons is that the formulae express well the decrease in pollen density in relation to the distance, as long as the distance does not become too great. Unfortunately, there is no appropriate material available to test formula *(11)*, which also takes into account the thinning-out effect.

There seem to be no experiments which deal with the dispersal of pollen inside forest stands, apart from some observations mentioned on p. 131. It is probable that in this case one must assume some pollen is intercepted by branches and leaves. Otherwise, one must expect that the pollen density decreases with increasing distance in approximately the same way as over open ground.

In practice, there will be many factors affecting pollen dispersal. Although one cannot expect that pollen will be dispersed in exactly the same manner as the theoretical models indicate, these can still give a range of valuable information in many ways. The most important are: —

1. — The dimensions of the source of dispersal are of great significance in the relation between pollen density and distance. *In experiments with pollen dispersal, therefore, the dimensions of the source of dispersal ought to be stated.*
2. — Because there is a radical difference between the dispersal from a point source and a plane source, the results obtained for the relationship between pollen density and distance, on the basis of the dispersal from one tree, cannot be applied th the dispersal from a stand.
3. — In investigations regarding the connection between pollen density and distance, the results for the shortest distances will often be subject to large errors, because a minor change in the distance has a great effect on the results. In practice, it is often difficult to decide the average distance to the nearest flowers.

The central query in connection with pollen dispersal is how the distance affects the crossing between two particular trees. The opinion on the whole seems to have been that the pollen is carried so far that trees must be expected to cross with one another to a great extent, even over long distances (cf. HOLTEN 1952, DENGLER and SCAMONI 1944 and HESSELMAN 1919).

What is decisive is not in itself that the pollen is very light, and that it can therefore be carried over great distances by the wind. The degree of crossing by long-distance pollen is decided by the relation between the quantity of pollen which comes from the neighbouring trees and that which comes from trees at greater distances. As mentioned previously, the pollen density decreases very rapidly with increasing distance from the source of dispersal. In many cases, the direction of the wind will vary during the course of a flowering period, so that at certain

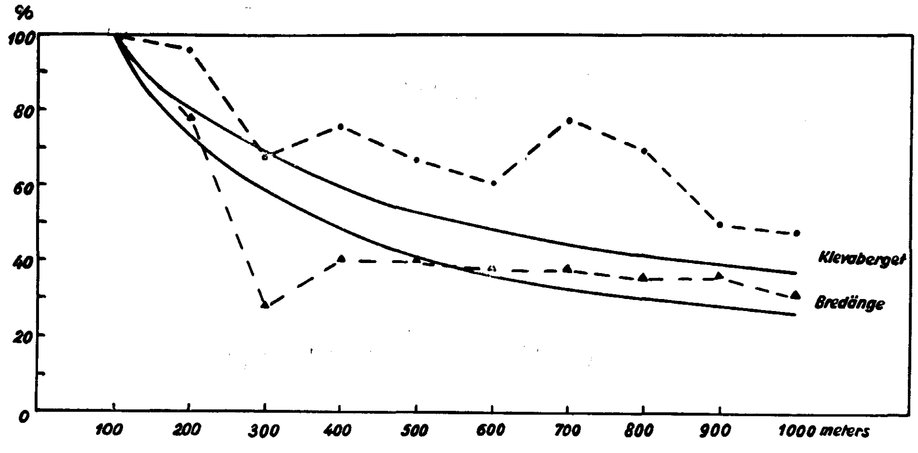

Fig. 6. — Example of comparison between theoretical (————) and observed (— — — —) values for pollen density (after ANDERSSON 1955).

times there may be no long-distance pollen conveyed at all. This will result in the pollen density decreasing still more rapidly with the distance. For agricultural growths, JENSEN and BÖGH (l. c.) have calculated that if the wind blows equally in all directions, this means a reduction in the probability of crossing between two particular fields to 15—20% of what it is in the wind direction. The reduction is greatest for long distances. *All these conditions will tend to bring about that a particular individual in general will cross with its nearest neighbours.* This is confirmed also by investigations made by LANGNER (1953a).

Another factor which must be taken into account, and which applies particularly in uneven country, is that the mass of pollen will have a different composition at different times. In the discussion regarding the investigation into the dispersal of pollen on steep hillsides, it was mentioned that the male flowering was retarded from 2 to 5 days for every 100 metres climbed. A similar staggering also takes place in the case of the female flowers. In areas with somewhat greater variations in height, this factor can minimize to a considerable degree the possibilities for crossing between trees at different altitudes.

SCAMONI (1949) has undertaken investigations at Riesengebirge which in many ways resemble those undertaken at Sogn. In this case, the flowering on an average was retarded somewhat more than four days for every 100 metres. One must therefore be able to say that it appears to be quite a general trait for height above sea level to have a great significance for the time of flowering, and it is not very likely that there will be any considerable crossing upwards and downwards over steep hillsides during the course of a flowering period.

In districts without great differences in height, the flowering time will, in all probability, not vary to such a great extent. Several micro-climatic investigations (GODSKE et. al. 1945, MORK 1933 and GEIGER 1950) show, however, that even within quite limited areas there can be fairly wide variations in temperature. If, for this reason, individual groups of trees show somewhat irregular flowering times, this can be a factor which contributes to strengthen the effect of the isolation afforded by the distance.

WRIGHT (1952) has carried out a number of calculations regarding the "effective population size". This is so defined that if the probability of self-fertilization is p, the "effective population size" is expressed as $N = 1/p$ (cf. WRIGHT 1943). On the basis of such calculations, WRIGHT found fairly large variations from one tree species to another. In some cases, the population size was so small that the possibility of local differentiation could be taken into account. It is previously pointed out that there seems to be little difference between the species where the dispersal of pollen over open ground is concerned. When, in spite of this, one finds large variations in the calculated population size, this must be due to other things than the way the pollen is dispersed. Factors of importance here can be, for example, the filtering effect which the trees have on the pollen.

In connection with the establishment of seed orchards, several queries which are directly concerned with the dispersal of pollen raise themselves. Contamination in seed orchards by pollen which is conveyed from outside will depend particularly on the following factors: —

1\. — The distance from the seed orchard to the surrounding stands from which the contamination originates. The size of the seed orchard and the size of the stands are also of significance. A single small stand will have no influence worth mentioning on the contamination in a large seed orchard, if the distance is some hundred metres. It can be otherwise if the seed orchard is encircled by larger tracts of forest. The results from the experiments referred to in section 34 are of interest here. In this case, the forest around the open ground extended for many kilometres. In spite of this, the pollen density is not abnormally high. In addition, there is a noticeable decrease in the density from the edges and in towards the centre. The comparatively low pollen density must be due to the thinning-out effect. Of the total quantity of pollen which is released, a very considerable amount is absorbed.

2\. — The relation between the flowering time for the trees in the seed orchard and in the districts around is of great importance. This factor can play an important part where northerly provenances are transferred to the south in order to obtain a better seed production.

3\. — In many cases, the planting of hedges, etc., to minimize the danger of contamination, can be of actual interest. Observations made by JENSEN and BÖGH (1942) and JONES and BROOKS (1952) show how effective a hedge can be in this way.

In the laying out of seed orchards, the positioning of the sorts which make up the orchard is very important. It is indicated that the pollen density declines very quickly with the distance from the source of dispersal. If the seed orchard is to be built up of trees which belong to different clones, one should try to avoid that trees from the same clone come in the neighbourhood of each other ,unless, of course, self-pollination is aimed at. The ideal composition is obtained if the clones are spread in such a manner that there is the maximal average distance between individuals from the same clone, as pointed out by LANGNER (1953 b).

In the cases where contamination is expected by pollen coming from outside, seed should not be gathered from the outermost rows of the seed orchard. There is a great difference between the degree of contaminating pollen in the outermost row and that in the one next to it. An experiment by GRIFFITHS (1950) shows this clearly (see *table 4).*

Table 4. — Contaminating pollen in the individual rows, within groups at varying distances from the source of dispersal. The experiment concerns rye-grass (After GRIFFITHS 1950)

Row	Group I 25 yds. %	Group II 50 yds. %	Group III 100 yds. %	Group IV 200 yds. %	Group V 400 yds. %
1	42.63	12.09	5.60	1.81	0.81
2	32.01	7.99	4.83	0.99	0.41
3	27.15	6.86	4.00	0.75	0.34
4	24.92	6.44	4.01	0.83	0.66
5	19.34	5.07	2.26	0.62	0.30
6	17.86	4.97	1.65	0.70	0.59

The marked decrease in the percentage of contaminating pollen from the first to the sixth row must be due principally to the fact that the density of the pollen which comes from the plants in the groups concerned increases very noticeably from the first to the sixth row. Over such short distances, there will be no essential reduction in pollen density for the pollen which comes from the contaminant.

From what is mentioned, it appears clear that there are a series of different factors which are responsible for the crossing conditions between single trees or groups of trees. At the moment, the knowledge of these factors is very limited, and it is to be hoped that these problems, which are of fundamental importance for work concerning forest tree breeding and provenance research, will be given closer investigation.

Summary

1. The theory of the dispersal of light particles from point, line, and plane sources of dispersal is discussed.

2. The theoretical calculations regarding the reduction in pollen density with the distance from the source of dispersal, agree quite well with experiments in the field, as long as the distances are short.

3. There are great differences in the way the pollen is dispersed from sources of varying dimensions.

4. The results of both experiments and calculations indicate that a given tree will on the whole cross with its nearest neighbours.

5. Investigations into the dispersal of pollen on steep hillsides show that the isolation afforded by distance, and the variation in the time of flowering, prevent crossing upwards and downwards on the hillside.

6. In a appraisal of the dangers of contamination in seed orchards, there are a number of factors which are of significance. The most important are the distance to the source of dispersal which provides the contaminating pollen, and the size of this source. The part of the seed orchard from which the seed is gathered also has considerable influence.

Zusammenfassung

Titel: *Pollenverbreitung.* —

1. Die Theorie für die Verbreitung leichter Partikel von einem Punkt, einer Linie und einer Fläche aus wird diskutiert.

2. Die theoretischen Überlegungen hinsichtlich der Verminderung der Pollendichte mit wachsendem Abstand von der Verbreitungsquelle stimmen für kurze Abstände gut mit den Ergebnissen der Untersuchungen im Freiland überein.

3. Große Unterschiede bestehen hinsichtlich der Pollenverbreitung je nach dem Umfang der Verbreitungsquellen.

4. Die Ergebnisse sowohl der Experimente wie der Berechnungen zeigen, daß ein gegebener Baum sich im allgemeinen nur mit seinen unmittelbaren Nachbarn kreuzt.

5. Untersuchungen über Ausbreitung des Pollens an Steilhängen zeigen, daß die durch den Abstand verursachte Isolierung und die Unterschiede in der Blütezeit Kreuzungen bergauf und bergab entgegenwirken.

6. Für die Abschätzung der Gefahr unbeabsichtigter Kreuzungen in Samenplantagen sind mehrere Faktoren bedeutungsvoll. Die wichtigsten sind der Abstand von der Pollenquelle, welche den unerwünschten Pollen verbreitet und die Größe dieser Quelle. Auch ist die Beerntungsstelle auf der Plantage von beträchtlichem Einfluß.

Résumé

Titre de l'article: *Dispersion du pollen.* —

1. — L'auteur discute la théorie de la dispersion de particules légères à partir de sources d'émission représentées par un point, une ligne ou une surface.

2. — Les calculs théoriques sur la diminution de la densité du pollen en fonction de l'éloignement de la source concordent assez bien avec les expériences sur le terrain, tout au moins pour les courtes distances.

3. — Il y a de grandes différences dans la façon dont le pollen se disperse à partir de sources de dimensions variables.

4. — Les résultats des expériences aussi bien que des calculs montrent qu'un arbre donné se croisera pratiquement avec ses voisins immédiats.

5. — Des recherches sur la dispersion du pollen sur les pentes raides montrent que l'isolation assurée par la distance et la variation dans les dates de floraison empêchent les croisements vers le haut et vers le bas des pentes.

6. — En estimant les dangers de contamination dans les vergers à graines, on peut mettre en évidence un certain nombre de facteurs dont les plus importants sont la distance à la source qui fournit le pollen contaminateur, et les dimensions de cette source. La partie du verger à graines où sont récoltées les graines a aussi une grande importance.

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Altersphasenentwicklung der Waldbäume und Forstpflanzenzüchtung

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Bei vielen Waldbäumen wurde seit langer Zeit beobachtet und nachgewiesen, daß die Blattorgane junger und alter Bäume morphologisch und anatomisch verschieden sind. Es sei auf die in Forstkreisen wenig bekannten Arbeiten von Goebel (6), Nordhausen (10) und Schramm (20) verwiesen. Während man früher die Verschiedengestaltigkeit der Blätter bei jungen und alten Bäumen ausschließlich auf Licht- und Ernährungseinflüsse zurückführte und demgemäß die Begriffe Licht- und Schattenblätter prägte, ist durch die genannten Arbeiten erwiesen, daß das Licht zwar wesentlich, aber nicht ausschließlich Bau und Gestalt der Blätter formt; es modifiziert die Gestalt bei gleichalten Pflanzen; aber nicht alle Unterschiede in Bau und Gestalt der Blätter, die zwischen jungen und alten Bäumen auftreten, können durch den Lichtfaktor oder andere Umwelteinflüsse allein erklärt werden. Der Beweis dafür ließ sich dadurch erbringen, daß bei Baumsämlingen, die nicht im Waldesschatten, sondern im vollen Freilandlicht angezogen werden, die Primärblätter deutlich die Eigentümlichkeit der sog. Schattenblätter aufweisen. Diese Eigentümlichkeit sind unter anderem geringere Blattdicke und schwächere Ausbildung des Palisadengewebes. Die Primärblätter des Baumsämlings, die in ihrer Gestalt und in ihrer anatomischen Struktur erheblich von den „normalen“ Blättern des erwachsenen Baumes abweichen, stellen erblich fixierte Jugendformen dar. Das Blatt des älteren Baumes dagegen, das man gemeinhin als Sonnenblatt bezeichnet, ist das Ergebnis einer längeren Entwicklungszeit; es ist die Folge- oder Altersform. Zwischen Jugend- und Altersform reihen sich Übergangsstufen aneinander. Bei der Buche dauert es etwa 20 Jahre, bis der Baum die typischen Alters- oder sog. Sonnenblätter bildet. Freistand und Besonnung können die Entwicklung von der Jugend- zu der Altersform fördern, Lichtmangel und Beschattung erheblich hemmen und verzögern. Das Durchlaufen der einzelnen Altersphasen ist außerdem individuell verschieden. Einzelne Pflanzen verlassen das Jugendstadium rascher als andere.

Das bekannteste Beispiel für die Heterophyllie junger und alter Pflanzen ist der Efeu. *Hedera helix* bildet in der Jugend kriechende Triebe mit dünnen, fünfteilig gelappten Blättern. Im Verlauf der Entwicklung werden die Blatteinbuchtungen weniger ausgeprägt, und im Alter trägt die Pflanze senkrecht aufstrebende Triebe mit ungelappten, eiförmigen und zugespitzten Blättern (Abb. 1).

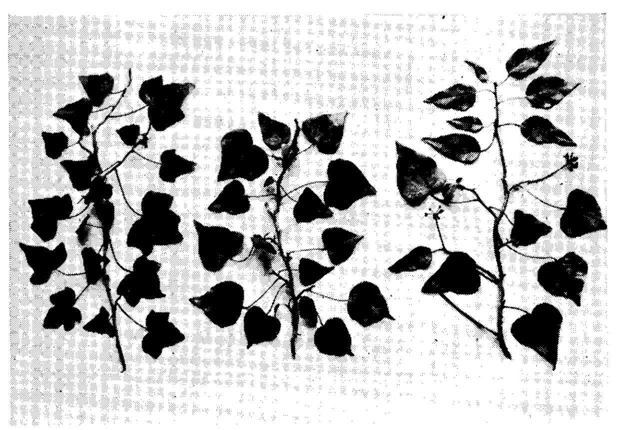

Abb. 1. — Efeublätter einer Pflanze. — *Links:* Jugendform vom unteren Teil mit fünfteilig gelappten Blättern; — *in der Mitte:* Übergangsform; — *rechts:* Altersform vom oberen Teil mit ungelappten, eiförmigen und zugespitzten Blättern und mit Fruchtständen. (Foto: R. Dimpflmeier)

Die Jugendphase trägt keine Blüten und Früchte, die Altersphase ist fertil. Beide Entwicklungsstadien lassen