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Needed: a New Approach to the Study of Pollen Dispersion

By RONALD M. LANNER[1])

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As genetics assumes more importance in forestry, the need for accurate information on pollen dispersion becomes critical. In recent years forest geneticists have made many studies of pollen dispersal. And their results have been used to determine safe isolation distances around seed orchards and to estimate distances across which populations may interbreed.

The usual approach to the study of pollen dispersal is to measure the pollen density of the air a Eew feet above the ground, at various distances from a known source, usually the edge of a forest or isolated trees.[2]) Typically these counts describe a gradient in which the frequency of airborne pollen declines rapidly as the distance from the source increases (figure 1). This rapid decline has led to the belief that relatively narrow isolation strips (0.25 to 0.7 miles) are satisfactory barriers to pollen contamination in seed orchards (STRAND 1957; WANG et al. 1960). WANG et al. (1960) admit that under certain conditions (e. g. atmospheric turbulence and strong winds) foreign pollen may penetrate the barrier, but it is expected that such pollen will be greatly outnumbered by pollen produced within the seed orchard.

WRIGHT (1953) has extrapolated short-distance dispersion data in estimating long-distance migration rates of pollen. He concluded that pollen transported more than 10 miles is ineffective in preventing genetic differentiation, largely because of the very small number of viable grains that he estimates would be present.

Departures from tha Model

Because of the reliance that has been placed on the results of short-distance dispersion studies, it is important to explain departures from the model depicted in figure *1*. The magnitude of such departures is evidenced by the following:

(a) SILEN (1962) monitored Douglas-fir (Pseudotsuga *menziesii* [MIRB.] FRANCO) pollen in the center of a 3 X 14.5-mile treeless area in the Willamette Valley, Oregon. He recorded up to 246 pollen grains per inch^2 per 24 hours during a 5-day period. The count would probably have been higher if counts had been made daily, thus showing peakc in the capture pattern. This view is based on the assumption that, as SARVAS' data (1955, 1962) show, peaks lasted only a few hours.

(b) MESHKOV (1950) observed a deposit of pine pollen sufficiently heavy to color the soil of the main street in a village on the steppes of the USSR after a rainstorm. The nearest pine stands were 6—7 miles distant.

(c) FLORENCE (1958) monitored slash pine (Pinus elliottii ENGELM.) pollen in a seed orchard that was 2.5 miles from the pollen source and surrounded by a 2-mile wide screen of hardwoods 100 feet tall. In a period of calm weather, and a fairly heavy pollen crop, he found pollen density was more than 6 percent of the density at the source. In the

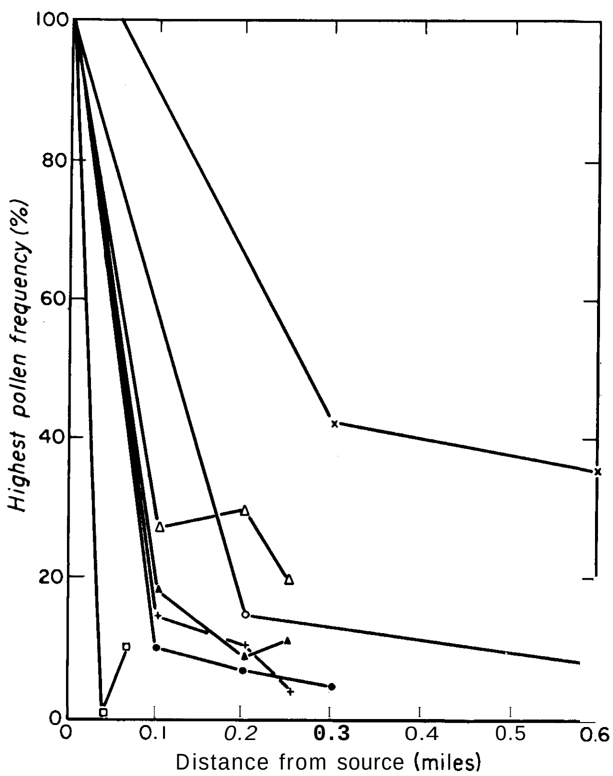

Figure 1. — Typical pollen dispersion curves derived from studies of short-distance transport, from several sources cited in *footnote* 2.

[1]) Formerly Forester, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Hilo, Hawaii; now with the School of Forestry, University of Minnesota. St. Paul.

[2]) BUELL 1947, COLWELL 1951, FLORENCE 1958, SILEN 1962, STRAND 1957, WANG et al. 1960, WRIGHT 1953, etc.

previous year the pollen crop was heavier, and dry winds favored transport of pollen from source to seed orchard. Yet, density at the orchard was only 0.4 percent of that at the source. FLORENCE's results for 3 years at the same location indicate great variation in pollen dispersion for different flowering seasons.

(d) SARVAS (1955) monitored the pollen rain on a lightship 12 miles off the Finnish coast and in forests along the shore. For three of the four species he studied, more pollen was collected at sea than in the forest. The highest 24-hour count for *Betula pubescens* was 997 grains per mm^2, equivalent to over 600,000 per $inch^2$. This count was about nine times that made in the forest during the same period.

(e) ILLY and SOPENA (1963) monitored pollen of maritime pine *(Pinus pinaster* AIT.) outside the vast pineries of the Landes of Gascony. At Lavit, about 36 miles from the forest, they collected a maximum of 147 grains per cm^2 per 24 hours. This was 29 percent of the corresponding catch at Hermitage, a station within the forest, and 38 percent of the catch at Castillon, a site within a zone scattered maritime pine stands.

(f) ANDERSSON (1955) collected pollen along a series of transects both for Scots pine and Norway spruce *(Picea abies* [L.] KARST.) in Sweden. At Yfre he collected 47 percent as much spruce pollen at 1.5 miles as at the edge of the forest. At Kumla he found the density of pine pollen to be at 2.5 miles 57 percent of the density at the forest edge.[3])

Some later observations made by ANDERSSON (1963) are even more striking. In 1954 the pollen crop in Sweden was so heavy that clouds of pollen were mistaken for forest fires. Some high rocky islands in Lake Vänern (Lurö Archipelago) which were 2.5 to 5 miles from the nearest forest were covered with a layer of spruce pollen almost 1 cm deep. The following year Scots pine pollen was blown in from Germany to the south coast of Skåne about 45 miles over open water at the rate of 22 miles per day. The pollen concentration averaged 368 grains per cm^2 per hour, and viability was 75 percent.

Such densities so far from source are obviously not the attenuated tails of gradient like those in *figure 1.* They cannot be accommodated by any of the theories on dispersal of small particles discussed by STRAND (1957). Yet these theories describe fairly well the short-distance gradients determined empirically by several investigators. This seems paradoxical until it is noted that all theories alluded to were designed to cope with the dispersal of small particles being displaced by wind exerting a horizontal force. For whatever fraction of pollen is subject to such force, the model in *figure 1* is relevant. But how much of the pollen produced in a stand is blown outward? And how much is lofted upward and deposited out of reach of the typical short-distance transect? Apparently the only published data that bear on this question are the observations of SARVAS (1960). In several stands of Scots pine *(P. sylvestris* L.) he found an average of only 17 percent of the pollen produced fell within the stand. This amount leaves 83 percent to account for the gradient outside the stand, for pollen intercepted by the trees, and pollen lofted upwards and away.

Mechanism for Mass Movement of Pollen

By what mechanism can masses of pollen be lifted and transported, finally to be deposited *en masse?* As a means of uplift and transport one especially likely mechanism (and the only one suggested here) is the thermal shell or vortex shell recently described by CONE (1961, 1962). This is not a continuous rising current or column of air; rather it is a discrete air mass with a complex internal circulation system. Forming at ground or canopy level, it is comprised of heated or moistened air that rushes inwards, forms a bulge, and breaks away as an independently moving air mass, like a free balloon. And like a balloon, it may be carried by winds aloft for at least 15 to 20 miles — the distance depending on wind speed and lapse rate of the air.[4]) Pollen trapped within a thermal shell would not be released until the shell dissipated.

Weather conditions favoring anthesis promote the formation of strong thermal shells, but shells can also form at other times. The thermal shell seems admirably adapted to the task of collecting and transporting masses of pollen without heavy losses so long as the shell retains its internal circulation. The thermal shell is not uncommon but is, rather, the normal mechanism by which warmed or moistened air rises. It is a natural and ubiquitous phenomenon that can provide a means for uplift and transfer of pollen, *en masse,* over moderate distances.[5]) [6])

By what mechanism can such masses of pollen be deposited to earth? Again, only one such mechanism will be suggested here, though there are undoubtedly others. MESHKOV's report (1950) of deposition, apparently during a rainstorm, provides an observed instance of the efficiency of raindrops in capturing small particles. Other instances are the "rains of mud" recorded in France and elsewhere in which prodigious quantities of windblown dust were brought down by raindrops (TALLON 1960). Theoretical models (MCDONALD 1962) indicate very high collection efficiencies for raindrops passing through clouds of pollen. For example, a drizzle yielding 1 mm of rain composed of raindrops 2 mm in diameter removes from the air 99 percent of *Picea excelsa* LINK and *Juniperus communis* L. pollen. Though MCDONALD (1962) pointed out the possible role of such capture in washing pollen from the air and thereby lowering seed sets, raindrop washout may also be a means of bringing pollen to receptive ovules. SARVAS' (1960) observation that the pollination drop of Scots pine is expressed from the nucellus tip to the micropyle during rain shows that at such times this species is receptive to pollen. ALLEN and SZIKLAI (1962) have succeeded in pollinating Douglas-fir with suspensions of pollen in water, applied as a spray, thereby showing that viability is not necessarily impaired by immersion in water.

During rainy weather, local pollen shedding is at a minimum. Possibly on occasion rain-scavenged pollen deposited on receptive ovules might have an advantage over pollen produced in the stand. This is purely speculation as there are apparently no data on rain-borne pollen in natural

[3]) STRAND (1957) used some of ANDERSSON's data in fitting observed pollen-density values to a theoretical model. He omitted the Kumla data, however, giving this explanation: "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.*" (Italics added.)

[4]) Correspondence with C. D. CONE, Jr., February 13, 1963.

[5]) I wish to tank Drs. S. M. A. HAQUE and M. A. ESTOQUE of the Dept. of Meteorology and Oceanography, University of Hawaii, Honolulu, for assistance with the literature on thermal shells.

[6]) The possibilities of other small particles (seeds, spores, insects spray droplets, etc.) being transported in the same way should also be considered.

conditions. The possible importance of pollen captured by raindrops has been overlooked in the studies referred to earlier. The pollen traps used were not capable of collecting it. Thus, in several studies impending rain forced closing of pollen collection activities (BUELL 1947; SILEN 1962; WANG *et al.* 1960).

The possibility that masses of pollen can be picked up and let down, still in concentrated form, affects forestry in two ways. First, it makes the practical isolation of open-pollinated seed orchards seem even riskier than presently thought and subject to erratic and perhaps unpredictable meteorological forces. And secondly, it suggests that under the right circumstances the random breeding unit can swell to an indeterminate size; and that hybridization between distant populations may be controlled less by distance *per se* than by phenological differences and meteorological patterns at the time of pollination.

Admittedly the foregoing analysis is based on the conjunction of fragments of evidence, but the purpose of this note is heuristic, not dogmatic. The intent has been to raise questions, rather than to provide answers, and to suggest that these questions cannot be answered by pollen dispersal studies that follow the established pattern.

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Newsletter

Proceedings: **Ninth Meeting of the Committee on Forest Tree Breeding in Canada,** Petawawa Forest Experiment Station, Chalk River, Ont. Part II, Reports and Papers. Dept. of Forestry of Canada, Ottawa, pp. VI + 201 (1964).

A general report of this meeting was published in Silvae Genetica **13**: 187 (1964). The following brief notes refer to the main subject matters dealt with by the authors in their reports to the Committee, or in special papers. For a similar report on the previous meeting see HATTEMER, Silvae Genetica **13**: 86 (1964).

Members' Progress Reports

BOYER, M. G.: Heritability of resistance to blister rust infection of white pine seedlings and the incidence of recovery of infected seedlings.

CARMICHAEL, A. J.: Wood quality studies in black spruce conducted by the Ontario Research Foundation. Correlations found between characteristics of foliage and of stem. Techniques developed for testing pulping properties of small wood samples.

CAISSON, L. P.: Interspecific hybrids of *Abies* in Nova Scotia.

CRAM, W. H.: Breeding of *Caragana arborescens* for shelterbelts in the prairie provinces. Self- and cross-compatibility tests demonstrate genetic differences; clones progeny tested for combining ability; genetic markers used to estimate natural self- and cross-pollination in *Caragana*. Spruce *(Picea pungens),* elm *(Ulmus pumila)* and poplar *(Populus* spp.) breeding, selection and testing also reported. Cooperative provenance tests established in Scots pine *(Pinus sylvestris),* Norway spruce *(Picea abies)* and white spruce *(Picea glauca).*

DYER, W. G.: Seed orchards and seed production areas in Ontario. Hard pines and spruces; vegetative propagation.

EBELL, L. F.: Biochemical analyses of Douglas fir tissues in relation to flowering and seasonal growth.

FARRAR, J. L.: See: "Introgressive hybridisation in red spruce and black spruce" by E. K. MORGENSTERN and J. L. FARRAR, Univ. Toronto, Faculty of Forestry Tech. Rep. No. 4, 46 pp.

FOWLER, D. P.: Breeding studies in hard pines, particularly red pine and jack pine. A number of inter-specific hybrids made for testing shoot moth resistance.

FRASER, D. A.: Physiological and biochemical studies of white and black spruce in relation to seasonal development.

GRIFFITH, B. G.: Intra-specific variation in Douglas fir growing at the University (B. C.) Research Forest.

HADDOCK, P. G., and WALTERS, J.: Provenance research in Douglas fir from the interior of British Columbia.

HEAMAN, J. C.: Douglas fir breeding by the B. C. Forest Service: plus tree selection; seed orchards; wood properties; provenance research; grafting.

HEIMBURGER, C.: Breeding of white pine for resistance to blister rust and weevil, combined with satisfactory growth and form. Reports acquisition of scions and seed; extensive hybridisation program. Selection and breeding of aspen like hybrids *(Populus* spp.) suitable for growing in southern Ontario.

HOLST, M. J.: Genetics and breeding of spruce and hard pines in eastern Canada. Provenance research, species hybridisation, vegetative propagation, flower induction, wood properties. A full account given of breeding objectives and biological problems involved.

MACGILLIVRAY, H. G.: Breeding studies in the Maritime provinces, including provenance and species trials in *Pinus, Picea, Abies,* and *Larix.*

MOORE, R. J.: Cytogenetic studies in *Caragana*. Descriptions given of the growth and morphology of sexually propagated tetraploid plants.