For working facilities at the Laboratory of Genetics and for valuable advice I wish to express my thanks to Professor, Dr. phil. C. A. JØRGENSEN, the Royal Veterinary and Agricultural College, Copenhagen.

Summary

Inhibition and resumption of meiosis in *L. decidua* due to low temperature is described. Irregularities of pollen mother cells and pollen grains were observed; the resulting mature pollen was sterile. The threshold temperature, at which inhibition of meiosis takes place was by refrigerator-experiments found to be about $+2-3^0$ C continuously applied, and it seems that the threshold is $1-2^0$ C lower at the stages late prophase-diakinesis than at the stages metaphase, — $anaphase_2$, and that there is some variation from tree to tree. — The mitotic poilen grain divisions were not synchronized, and they were not completed until about a week before the discharge of pollen. If this is a normal occurrence, it limits the period during which male buds can be forced for pollen extraction.

Zusammenfassung

Titel der Arbeit: *Ober den Effektvon niedriger Temperatur auf die Meiosis und die Pollen-Fertilität bei Larix decidua Mill.*

Die Unterbrechung und Wiederaufnahme der Reduktionsteilung bei *L. decidua* unter Einwirkung von niedriger Temperatur wird beschrieben. Es wurden Unregelmäßigkeiten wahrend der Meiosis und der Pollen-Mitose beobachtet; der entstandene reife Pollen erwies sich als steril — Die kritische Temperatur, bei welcher die Reduktionsteilung unterbrochen wird, wurde bei Kühlschrankversuchen mit konstanter Temperatur mit ca. +2 bis 3^0 C ermittelt Die kritische Temperatur scheint für die Stadien späte Prophase-Diakinese um 1 bis 2^0 *C* niedriger zu sein als für die Stadien Metaphase, — $Anaphase_2$, eine gewisse Variation zwischen den individuellen Bäumen ist wahrscheinlich. — Die mitotischen Teilungen der Pollenkörner waren nicht synchronisiert, und sie waren erst circa eine Woche vor dem Ausstäuben beendet. Wenn dies eine normale Erscheinung ist, bedeutet sie eine starke Begrenzung der Periode, während der männliche Blütenknospen für die Pollengewinnung angetrieben werden können.

Résumé

Titre de l'article: *Influence de températures basses sur la méïose et la fertilité du pollen de Larix decidua Mill.*

L'article décrit l'inhibition et la reprise de la meiose chez *Larix decidua* sous l'influence de basses temperatures. Des irrégularités ont été observées chez les cellules mères des grains de pollen et chez les grains de pollen; le pollen mûr était sterile. Le seuil de température qui déclenche l'inhibition de la meiose a ete determine par des experiences en refrigerateur: il correspond a une temperature continue de $+2^0$ a $+3^0$ C et il semble que ce seuil est inférieur de 1^0-2^0 C pour les stades finaux de la prophase — diakinèse que pour les stades de la metaphase 1 a anaphase 2; de plus, il existe certaines variations d'arbre a arbre. Les divisions mitotiques de grains de pollen n'étaient pas synchronisees et ne furent achevees qu'environ une semaine avant la dispersion du pollen. S'il s'agit d'un phenomene normal cela limite la période pendant laquelle les bourgeons mâles peuvent être forcés en vue de l'extraction du pollen.

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Pollen Dispersion of Slash Pine (Pinus elliottii Engelm.) with Special Reference to Seed Orchard Management

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(Received for publication February 13, 1960)

Introduction

The successful production of tree seed in a seed orchard depends on the effective control of pollen contamination. All extraneous pollen should be eliminated, and the free dispersion and ample supply of desired pollen should be maintained within the orchard to assure the quantity production of a crop with the desired genetic constitution.

In connection with the forest genetics research program of the University of Florida, 15 seed orchards of slash pine *(Pinus elliottii* ENGELM.*)* and loblolly pine *(Pinus taeda* L.) were established by cooperating wood-using industries in Alabama, Florida, Georgia, Mississippi and South Carolina. The management plans for these seed orchards provide for either wind pollination or hand pollination of the selected trees within the orchard. Provision must be made to pre-

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The authors wish to express their sincere thanks to CLAUD L. BROWN, RAY E. GODDARD, ROBERT MCELWEE, SCOTT S. PAULEY, PAUL O. RUDOLF, JONATHAN W. WRIGHT and BRUCE J. ZOBEL for their critical review of the manuscript.

vent lowering of the genetic quality of the seed by undesirable pollen blown from outside the orchard. Since pine pollen is wind-borne a pollen barrier or isolation strip will be required. The necessary width of the isolation strip and its effectiveness are dictated by the pollen dispersal distance of the tree species under consideration. Before the establishment of the above-mentioned seed orchards two series of observations on pollen dispersion of slash pine were made simultaneously in eastern and western Florida in the spring of 1956. To investigate the effectiveness of the isolation strips maintained at the seed orchards as pollen barriers, pollen samples were collected from the seed orchards in 1958. The results of these observations are presented here along with pertinent discussions on related problems.

Long Distance Pollen Dispersion

Pollen dispersion has been the subject of a series of investigations both from the theoretical point of view (Dyakowska 1936, Wright, S. 1940, 1943, 1946, Wolfenbarger 1946, Wright, J. W. 1955) and from the view of practical importance to tree seed orchard management (Wright, J. W. 1953, Andersson 1955, Schmitt 1955, Sarvas 1956, Strand 1957).

The total elimination of extraneous pollen by distance has been shown to be not feasible. Observations on pollen dispersal by Hesselman (1919), Malmström (1923), Erdtman (1938), Rempe (1937), Scamoni (1938), Dengler and Scamoni (1944), Andersson (1955), and others have shown that with the help of air movement tree pollen may be transported over considerable distances. For example, counts of 9 pollen grains (pine, spruce and birch) per month per square millimeter were found on light ships stationed 35 miles off the coast of the Baltic Sea. And the air of Atlantic Ocean 190 miles south of Nova Scotia was found to contain 3.5 pollen grains (*Carya, Juglans,* and *Fraxinus,* etc.) per 100 cubic meters.

The Effect of Long Distance Transport of Pollen on Seed Orchards

From the result of the above mentioned investigations, it is safe to infer that during the flowering season extraneous pollen is transported over considerable distances to the seed orchard even if the latter is protected by a wide isolation strip. Although there is no effective way to totally eliminate extraneous pollen, the effect of such pollen can be reduced to a negligible point by isolation barriers.

The relative long distance pollen migration as estimated from short distance dispersion data is so small for distances of more than 10 miles that it is concluded that pollen transport over greater distances is relatively ineffective in preventing the genetic differentiation of geographically separated populations (J. W. Wright 1955).

The quantity of pollen transported over long distances is so small in comparison with the quantity of pollen produced in a seed orchard under ordinary conditions that the chance of contamination by extraneous pollen dispersed over long distances is negligible indeed. The pollen output of Scotch pine (*Pinus sylvestris* L.) is calculated to be on an average of 152,000 — 162,000 grains per strobilus and 5,600,000 — 5,950,000 grains per cluster of strobili (Pohl 1937). In round figures the pollen output of an average 10-year-old Scotch pine is close to 346 million pollen grains. Although a part of the pollen undoubtedly will be transported to considerable distances, the bulk of the output will be dispersed within a relatively restricted range. The decrease in frequency of pollen incidence with increasing distances from the pollen source is a factor of greatest practical value in the planning and management of the seed orchard. The genetic quality of the seed produced by the seed orchard would be slightly affected if 99 per cent of the pollen came from superior trees within the orchard and 1 per cent of the pollen came as contamination by long distance transport.

J. W. Wright's study (1952) is the most comprehensive investigation of the pollen dispersion of American trees. This study revealed that most of the pollen falls within a few hundred feet of the source tree. Wright's data on one pinyon tree (*Pinus edulis* Engelm.) showed a rapid decrease in pollen deposition with increasing distances. The pollen frequency at 300 feet was but 1 per cent of the frequency at the pollen source. The standard deviation (σ_D) of pollen distribution from the source was 55 feet. The decrease in dispersion frequency as expressed by σ_D provides a measure of the effectiveness of an isolation strip as a pollen barrier, and a measure of the availability of pollen for cross pollination of trees within the seed orchard. The method of determination of the deviation from random mating is briefly described in the calculation section of this article.

Observation on the Dispersion of Slash Pine Pollen (Pinus elliottii Engelm.)

The time when southern pine species flower varies considerably from year to year (Dorman et al. 1956, Zobel et al. 1954). In the vicinity of Gainesville, Florida, flowering time of pines are generally within the following periods:

December 25 — January 25, Sand pine (*Pinus clausa* Vasey)

January 21 — February 15, Slash pine (*Pinus elliottii* Engelm.)

February 5 — March 1, Longleaf pine (*Pinus palustris* Mill.)

February 20 — March 16, Loblolly pine (*Pinus taeda* L.).

In normal years, such as the one in which this study was made, the time of peak pollen dispersal for each of these species is separated by a period of three weeks or more. Hence, dispersion in one species can be studied without contamination from other species.

The pollen dispersal of slash pine growing under the following conditions was observed: (1) isolated single pine tree in a large open area, (2) isolated natural groves of slash pine, and (3) slash pine plantations.

Ordinary microscope slides covered with a thin coat of petroleum jelly (vaseline) were used as pollen traps. The slides were fastened in a horizontal position on pedestals one meter above the ground. The slides were unprotected and were exposed in the open. The slides were set out between 4 and 5 p. m. and collected after a 24-hour interval. They were examined under the low power (51×) of a microscope, an area of 0.678 square centimeters being counted on each slide.

Pollen Dispersion from an Isolated Slash Pine

An ideal slash pine pollen source tree was found in the center of a large pasture of the Norris Cattle Company in Marion County, Florida, 35 miles southeast of Gainesville. This source tree is 35 feet tall, broad-crowned, and isolated

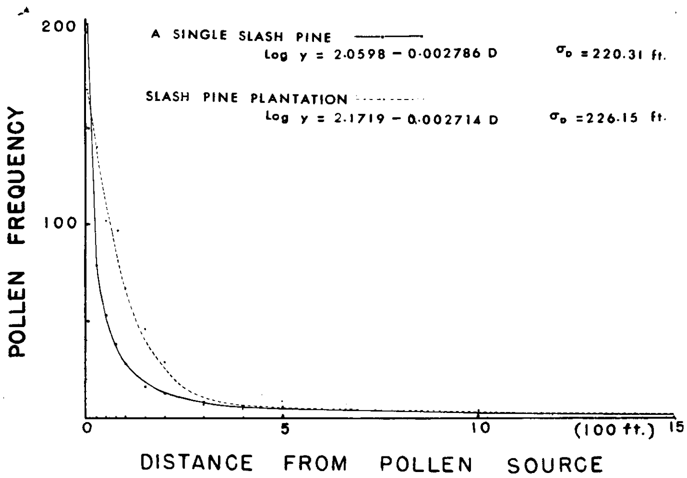

Figure 1. — Pollen frequency curve showing pollen collected at varying distances from an isolated slash pine (solid line) and an 80-acre slash pine plantation (dashed line). Standard deviation of the pollen dispersion distance (σ_D) was computed from the pollen data as a measure of pollen dispersion.

Table 1. — Pollen collected at varying distances from an isolated slash pine in 4 transects along 4 point of the compass.

Distance from source (feet)	Jan. 28	Jan. 29	Jan. 31 Feb. 2 Feb. 3
	Grains per 2.71 cm²		
0	78	204	45*)
25	28	79	23
50	30	53	7
75	17	38	20
100	7	28	0
150	9	16	0
200	1	13	2
300	0	8	0
400	4	4	0
500	0	6	0
1000	0	6	0
1500	3	1	0
2000	0	2	0
2500	0	2	0
2850	0	0	0
Total	177	460	97

*) Figures in this column are totalled grain counts of 3 days pollen samples. Area counted for each day is 2.71 cm².

from possible contaminants by more than a mile. Pollen samples were collected at the following distances from the pollen source tree on 4 transects along 4 points of the compass: 0, 25, 50, 75, 100, 150, 200, 300, 400, 500, 1000, 1500, 2000, 2500 and 2850 feet.

This open-grown, isolated tree was a relatively light pollinator, one of the earliest in the area to flower, preceding others by more than a week. The male catkins appeared to be mature on January 24, but a spell of cold weather delayed actual flowering until January 28. Pollen shedding continued until February 3. Nearly all the pollen fell within 200 feet of the source *(Table 1)*. The standard deviation (σ_D) of pollen dispersion as calculated from the grouped data for all days and all directions, was 220 feet.

Pollen Dispersion from Natural Groves of Slash Pine

A series of pollen samples was collected on Paine's Prairie along a transect of two miles between two natural groves of slash pine. The "Prairie" is a silted up lake bed utilized as a natural pasture for the most part of the year. It is treeless except for isolated cabbage palms *(Sabal palmetto* Todd.) and cypress *(Taxodium distichum* Rich.) near the border of the prairie, and shrubs and small broad-leaved trees along the causeway. The causeway is a 2-mile long elevated highway going across the prairie. The pollen samples were collected along a line that is parallel with and twenty feet west of this causeway.

Pollen samples were collected over a period of 10 days from January 30 to February 8. A series of 21 pollen slides was placed at 1/10-mile intervals beginning on the north border of the prairie. The pollen output during the first few days was low. The total number of pollen grains collected at the 21 stations was 114 for January 30 and 164 for February 3. With improving weather conditions pollen began to shed in quantity on February 6, when 430 grains were collected. The pollen output reached maximum of 2545 grains February 7 and dropped abruptly to 752 grains on the next day. The pollen data are given in *Table 2* and *Figure 2.*

Pollen Dispersion from Slash Pine Plantations

Observations on pollen dispersion from slash pine plantations were made on the holdings of the St. Regis Pulp and Paper Company, northeast of Pensacola, Florida. The

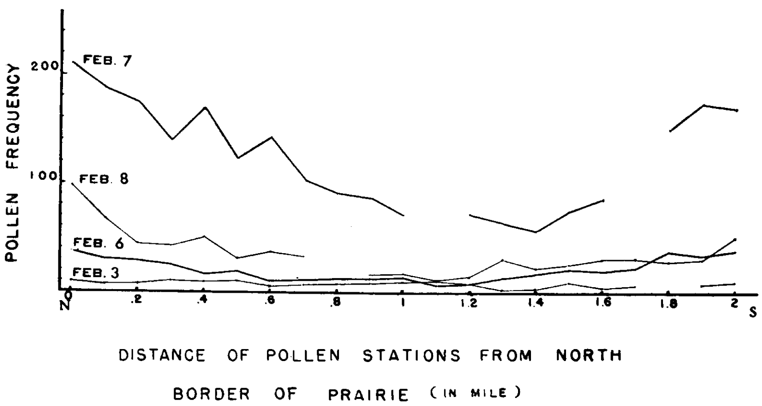

Figure 2. — Pollen collected along a 2-mile wide treeless prairie between two natural groves of slash pine. A series of 21 pollen collecting stations were arranged at 1/10 mile intervals beginning on the north border of the prairie.

Table 2. — Pollen collected along a 2-mile wide treeless prairie between two natural groves of slash pine.

Distance in miles from the N. end	*Grains per 0.678 cm²*			
	Feb. 3	Feb. 6	Feb. 7	Feb. 8
0	9	37	210	97
0.1	7	30	187	66
0.2	8	28	174	43
0.3	10	24	139	42
0.4	9	16	170	50
0.5	10	18	122	30
0.6	6	9	142	36
0.7	7	11	102	32
0.8	8	12	91	—
0.9	9	12	86	16
1.0	10	13	71	17
1.1	11	6	—	11
1.2	8	8	72	14
1.3	5	13	64	31
1.4	6	17	57	42
1.5	10	21	75	26
1.6	6	20	86	31
1.7	7	23	—	32
1.8	—	38	151	29
1.9	8	35	175	31
2.0	10	39	171	52
Total	164	430	2545	752

Table 3. — Pollen collected at varying distances inside*) and to leeward of a slash pine plantation.

Distance (in feet) from border of plantation	Transect D. Feb. 9	Transect D. Feb. 10	Transect E. Feb. 9	Transect E. Feb. 10
	Grains per 0.678 cm²			
150*)	16	182	26	35
100*)	27	145	17	49
50*	13	183	22	25
0	12	171	63	114
25	12	140	75	48
50	8	102	65	73
75	9	97	28	80
100	7	68	22	140
150	6	46	11	10
200	4	29	10	5
300	3	7	1	5
400	2	5	5	4
500	2	9	4	—
1000	2	3	6	—
1500	2	3	5	5
2000	6	1	4	22
Total	131	1191	364	615

*) Pollen collected inside of slash pine plantation. The figures indicate the distance from the border of the plantation.

plantations were established in 1940 and were over 45 feet tall at the time of study.

The three plantations are located conveniently for purposes of study of pollen dispersement. Two of the 80-acre plantings (plantations 1 and 3) are located ¼ mile apart and oriented east and west. The remaining plantation (2) extends east from plantation 1 for another ½ mile. The area between plantations 1 and 3 is covered by a young stand of longleaf pine 35 to 45 feet high and of varying stocking. The area to the north of plantations 1 and 2 is open pasture land used for dairy farming. The transects of pollen traps extend back into the plantations 150 feet. Several slash pine trees in the plantation were shedding pollen on February 4, but steady rain and cold weather held the pollen back until February 9, when pollen was first shed in quantity. Pollen was also trapped on February 10. The wind on February 9, was moderately strong, about 15 — 20 miles per hour from the north. The wind shifted about on February 10 and was about 20 — 25 miles per hour. A new storm front arrived on February 11 and forced the secession of observations. The pollen dispersion transects D. and E. *(Table 3)* extend from 150 feet inside the plantation out to the north for a distance of 2,000 feet. Pollen counts for February 9 and 10, from these transects, are recorded in *Table 3.* These counts were combined and averaged and fitted to a normal distribution curve *(Fig. 1).* As indicated in *Fig. 1,* there is good agreement between the pattern of decreasing pollen frequency with distance from an isolated tree.

Pollen dispersion transects A, B, and C, extending between plantations 1 and 3, give a picture of the pattern of pollen dispersal between two solid pollen sources over a scattered stand of longleaf pine *(Table 4, Fig. 3).* It is to be noted that the change in wind direction on Feb. 10 from north to south, to south to north did not materially alter the pattern of pollen dispersion.

In the establishment of slash pine seed orchards it was originally planned to have the seed orchards in blocks ¼ mile square. A ¼ mile square block with an isolation strip approximately 400 feet wide would leave about 6 acres of seed orchard in the middle of the 40 acres. The isolation strip would be planted with trees of another species that would not hybridize with the selected trees in the central plot. Data obtained from the three parallel transects A, B, and C indicate the degree of contamination that could be expected in such a seed orchard. Comparison of the results for transects A, B, and C as contrasted with transects D and E indicates that open land acts as a better pollen barrier than land covered with timber. The significance of this will be discussed in later sections.

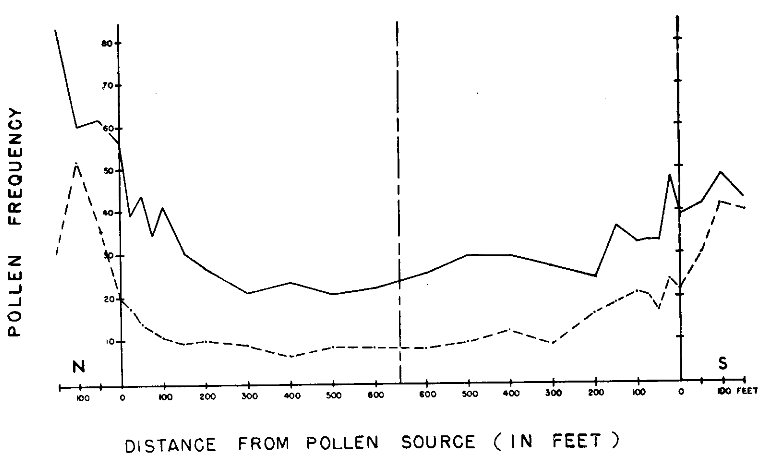

Figure 3. — Pollen collected at varying distances inside and between two 80-acre slash pine plantations. The distance between the two plantations is ¼ mile. The solid line represents the observations of February 9, the day of maximum pollen output, and dashed line February 10.

Mathematical Treatment of Dispersion Data

Standard Deviation σ_D as a Measure of Pollen Dispersion

The pollen dispersion distance is best expressed as the slope of a dispersion curve or as the standard deviation

Table 4. — Pollen collected at varying distances inside*) and between two slash pine plantations.

Distance in feet from border of plantations	(Average of Transects A, B, C) Feb. 9	Feb. 10
	Grains per 0.678 cm.²	
150*)	83.6	30.2
100*)	60.3	52.0
50*)	62.0	37.0
0	56.6	20.0
25	39.3	17.3
50	44.0	14.0
75	34.3	12.3
100	41.3	11.0
150	30.6	9.3
200	27.0	10.0
300	21.3	9.0
400	23.3	6.3
500	20.6	8.6
600	22.0	8.3
— — — (Space 120 feet) — — —		
600	25.3	8.0
500	29.6	9.3
400	29.3	12.0
300	26.6	9.0
200	24.3	16.0
150	36.6	18.6
100	33.0	20.6
75	33.3	20.0
50	33.3	16.3
25	48.3	24.0
0	39.3	21.3
50*)	42.0	30.0
100*)	48.6	41.3
150*)	43.0	40.3

*) Pollen collected inside of slash pine pantation. The figures indicate the distance from the border of the plantation.

of dispersion distance (σ_D). To obtain the σ_D the pollen data were fitted to the curve represented by the formula:

(1) $y = y_0 e^{-kD}$.

The logarithmic transformation of the curve is:

(2) $\text{Log } y = \text{Log } y_0 - (\text{Log }_{10}e)\ kD$.

y = frequency at a given distance D.

y_0 = frequency at sation 0 or the source frequency.

k = a constant relating to the decrease of dispersion rate with distance.

The variance (σ^2_D) is $2/k^2$, so that:

(3) $_D = \sqrt{2/k}$.

The procedures for calculating the standard deviation of pollen dispersion as outlined by SEWALL WRIGHT (1946) was demonstrated in a sample calculation with pinyon pine data by J. W. WRIGHT (1958, personal communication). The number of pollen grains at a station was used as the weight in the regression calculation with the ordinary regression formula. The weights are necessary because counts at the more distant stations are less reliable than the counts near the source.

The values of σ_D were calculated for the pollen dispersion from a single slash pine and for the dispersion from a slash pine plantation. The pollen counts for one day up to a distance of 1000 feet from the source were used. According to this formula the presence of a few pollen grains beyond 1000 feet which might be of extraneous origin distorted the value of σ_D considerably. The respective regression equations are:

Log y = 2.0598 — 0.002786 D (Pollen dispersion from a single pine),

Log y = 2.1719 — 0.002714 D (Pollen dispersion from a slash pine plantation).

The values of σ_D are 220 feet and 226 feet respectively for the single slash pine and the slash pine plantation.

Some Factors Affecting the Dispersion of Slash Pine Pollen

Wind and Pollen Dispersion

The pollen grain as a non-selfpropellent particle depends upon gravity, the movement of air, the other atmospheric conditions and natural agencies for its dispersion. According to the study of DYAKOWSKA (1936) the dispersion distance is mainly determined by wind velocity and the rate of fall of the pollen. SUTTON (1932) considered air eddies as more important than wind of a constant direction in influencing pollen dispersion distance.

It was found in a pollen dispersion study of several crop plants (JENSEN et al. 1941) that the dispersion distance was nearly as great on days of low average wind velocity (7 miles per hour), as on days of higher average wind velocity (12 miles per hour). In the dispersion of wheat spores ÖORST (1940) believed that weak winds were responsible for more distant dispersion than strong winds. In forest trees J. W. WRIGHT's study (1952) supported the view that average wind velocity is unimportant. The pollen traveled as far or slightly farther during relatively calm periods as during windy periods. But wind velocity did have profound influence on the shedding of pollen in Atlas cedar *(Cedrus atlantica* MANETTI) and *Pinus sylvestris* L. (SCAMONI 1938). The male strobili shed little pollen unless they are shaken by strong wind.

BUELL's study on shortleaf pine *(Pinus echinata* MILL.) pollen dispersion (1947) indicated that the highest percentage of pollen carried to a great distance was not in the period of heaviest pollen output. The highest percentage occurred on the day which was characterized by a prefrontal instability associated with a cold front. BUELL concluded that a great deal more pollen is lifted up and carried away from the forest when the atmosphere is relatively turbulent than when the atmospheric conditions are relatively stable. In the case of the shortleaf pine it amounted to doubling the proportion of pollen carried to a distance of a quarter of a mile from the forest.

The directional distribution of pollen as related to wind directions was observed in a number of plants. Similar phenomena were recorded in the extensive studies of spores. WOLFENBARGER's review (1946) on the dispersion of small organisms suggested that a tendency observed in many dispersion studies is for relatively short dispersions to be omnidirectional and for relatively long dispersion to be unidirectional.

In the studies of tree pollen dispersion, J. W. WRIGHT (1952) found that with Douglas fir, Atlas cedar, and pinyon pine the highest pollen counts were made to the leeward of the source tree.

BUELL (1947) found no correlation between wind direction and the distances to which a high percentage of pollen was carried in turbulent weather.

In the present pollen collection studies the prevailing wind direction and wind velocity according to the Beaufort scale were as follows: eastern Florida (Norris Ranch and Paine's Prairie): January 28, 29 and 30 south wind gentle (8 — 12 m. p. h.) to moderate (13 — 18). January 31 and February 1, east wind, moderate. February 2 to 7 south wind, gentle to moderate. Light showers of short duration on February 7. Western Florida, north of Pensacola: winds of 20 m. p. h. slightly affected the pattern of pollen dispersion between two slash pine plantations. It did show that more pollen was dispersed with the wind direction than against it. The pollen frequency of the transects are tabulated in *Table 5*.

Table 5. — Amounts of pollen caught at various directions from the pollen source.

Norris Ranch:	N	W	S	E
	Grains per .678 cm²			
January 28	30	26	24	19
January 29	67	70	58	61
January 31, February 2 and February 3	25	26	19	25
Paine's Prairie:				
January 30	77		43	—
February 3	83		72	—
February 6	197		220	—
February 7	1423		1051	—
February 8	436		299	—

Temperature and Pollen Dispersion

A distinct correlation was observed in the present study between the increase in the amount of pollen output from the tree and increasing temperature in the flowering period. This correlation was evidenced by the pollen dispersion from a single tree, from natural groves, and from plantations both in eastern and in western Florida.

The daily mean temperature of the two closest weather stations during the slash pine flowering season in Paine's Prairie are given in *Table 6* (U. S. Weather Bureau, 1956).

BUELL (1947) in his study on the mass dissemination of shortleaf pine pollen concluded that there is a noticeable correlation between the total pollen collected on the slides

Table 6. — Daily Mean Temperature and Evaporation at Gainesville and Ocala Weather Stations during the Slash Pine Flowering Period Jan. 28 — Feb. 9, Paine's Prairie, Florida.

Date	Temperature (°F) Gainesville	Ocala	Evaporation (inches)*) Gainesville
January 28	49	53	.10
January 29	51	51	.11
January 30	43.5	46.5	.13
January 31	47	49.5	.09
February 1	51.5	54	.11
February 2	56.5	61	.12
February 3	63.5	65.5	.09
February 4	61.5	61	.21
February 5	54	58.5	.10
February 6	64.5	69	.32
February 7	*71.5*	*70.5*	*.00 (light shower)*
February 8	60	60	.15
February 9	50.5	55	.13

*) Evaporation was measured in inches from a surface of 36 × 36 inches.

each day and the temperature and vapor pressure deficit. The Gainesville weather station recorded a trend of increasing evaporation in the period of increasing pollen dispersion. But this trend was disrupted by a light shower on the day of maximum pollen dispersion *(Table 6, Column 3).*

The slash pine flowering season of 1956 was abnormally cold. Both the daily maximums and the daily minimums were below the monthly average. However, the maximum pollen dispersion from a single tree (Jan. 28—29), from natural groves (Feb. 6—7), and from west Florida plantations (Feb. 9—10) was always coincident with the crests of rising temperatures.

The present study confirmed the result of Scamoni (1938) in his investigation of the influence of temperature on pollen dispersal of Scotch pine. He found that high temperature affects the time of the opening of the pollen sacs and of pollen shedding, and that high aerial humidity and low temperature delay the flowering time and prolong the flowering period.

The above generalization is applicable to slash pine and probably to a number of forest trees and plants. However, the optimum conditions for pollen dispersion are definite for each biological unit. Although warm days are needed to open the microsporangia of the autumn blooming *Cedrus atlantica* and *C. libani* Link., pollen shedding was found to be greatest on cold, windy days (J. W. Wright 1952).

Size of Slash Pine Pollen

Besides the effect of air movement and other external conditions the dispersion of pollen is influenced by its size, weight and buoyancy. Pine pollen differs from pollens of the non-gymnospermous plants and from some gymnosperms in the presence of two air sacs. These air sacs increase the size of the pollen, and affect its shape.

Erdtman (1943) doubted the effectiveness of the air sac on pollen dispersion. He observed that there is no proof of the idea which formerly was widely held that winged conifer pollen travels further than that of the angiospermous trees. On the contrary conclusive evidence has been produced which discounts the assumption that the winged conifer pollen is particularly liable to long distance wind transport. From the measurements of the rate of fall of the pollen grains, it appears that although the air sacs do have an effect, it is offset by the large size of the conifer grains, so that the conifers show somewhat higher rates of fall than angiospermous species such as birch and alder. Based on the rate of fall of pollen grains measured in still air by Dyakowska (1936), Sarvas (1952) pointed out that the rate of fall of European birches *(Betula verrucosa* Ehrh. and *B. pubescens* Ehrh.) pollen grains is 2.94 cm/sec. and of Scotch Pine 3.69 cm/sec. While the weight of the pollen grain of Scotch pine (18.4 g $\times$ 10^{-9}, Pohl 1937) is three times greater than a birch pollen grain (6.1 g $\times$ 10^{-9}, Pohl 1937), its fall is only about 1.3 times greater (Sarvas 1952). Pine pollen is large in size but low in specific gravity as compared to other pollens (Pohl 1937). The effect of gravity on the rate of fall of a pollen grain is easily offset by any air turbulence. A vertical air current of two meters per second was observed to reach an altitude of 1800 meters in fifteen minutes carrying Scotch pine pollen 1773 meters away from the pollen source.

The absolute weight of the pollen grain varies considerably with its moisture content. Pollen grains are generally very hygroscopic. The pollen grain size frequencies of a pine species are very consistent. Six species of southern pines were studied by Cain (1940). They are in the order of decreasing sizes: shortleaf pine, loblolly pine, pond pine *(Pinus serotina* Michx.), longleaf pine, sand pine and spruce pine *(P. glabra* Walt.). The southern pine species are characterized by a distinct size frequency which was successfully used for species identification.

In the present study the length, width, and depth of slash pine pollen grains were measured from two samples of slash pine pollen. For ready comparison the measurements were made according to the method used by Cain (1940). The mean values are based upon the measurement of ten different grains used for each measurement which was considered adequate for comparison. The size measurements of slash pine pollen of Alabama origin are: mean length 60 μ (extremes 54—65), mean depth 41 μ (37—44), mean breadth 45 μ (41—48). The size measurements for slash pine pollen of Florida origin are 61 μ (58—65), 41 μ (37—44), and 46 μ (44—48) respectively. The pollen of slash pine is smaller than longleaf pine and larger than sand pine and spruce pine. Rempe's study (1937) shows the height that pollen may attain is inversely correlated to the size of the pollen grains and air sacs. The southern pines have a slightly different pollen size range for each species, but the differences are not great. Hence, if the specific gravities of other pine species are comparable, the results of the present studies can be applied to the dispersion of pollen by other pine species.

Discussion

Pollen Dispersion and Geographic Races of Slash Pine

Knowledge of the means of pollen dispersion of a species is essential for estimation of the extent to which isolation is important in race formation. As it was pointed out by J. W. Wright (1952) "The further the pollen is dispersed and the more dense the population, the larger is the random breeding unit and the fewer are the chances for gene fixation within any given distance". Slash pine trees grow in the southeastern states in an almost continuous range without serious geographic barriers. However, one regional variety, South Florida slash pine (var. *densa* Little and Dorman) and other minor geographic differentiations are generally recognized. (Little et al., 1954, Dorman 1952).

The possibility of race formation in a population can be calculated from the formulas derived by S. Wright (1943, 1946). The size of the breeding population and the degree of isolation are estimated in terms of "neighborhood" size which is the largest population within which breeding takes place at random. The "neighborhood" size of slash pine is calculated from the following formula:

$$N = 2\pi\sigma_D^2 d$$

This formula is for a hermaphroditic population with a continuous range and only the pollen dispersed. The calculation of the number of breeding trees in a "neighborhood" (N) is based on the pollen dispersion data σ_D and the assumed population density (d) in terms of the number of flowering trees per linear foot of linearly continuous range or per square foot of areally continuous range. The dispersion of slash pine seed is very much less than the pollen dispersion. The seed dispersion is assumed to be 0 to facilitate the calculation.

Slash pine is a widespread and monoecious species, which may be regarded for the purposes of this discussion as meeting S. WRIGHT's requirements of a hermaphroditic population. It occurs in mixed stands with other pine species but mostly in pure stands of more or less even aged trees. Assuming areal continuity, σ_D of 225 ft., and 50 flowering trees per acre (corresponds to 30 × 30 foot spacing), the effective size of "neighborhood" from the following calculation is 365 trees.

$$N = 2\pi\sigma_D^2 d = \frac{6.28\ (225)^2\ (50)}{43560} = 365 \text{ trees.}$$

It is not unusual for a well stocked pure stand of slash pine to have more than 100 flowering trees per acre (corresponding to approximately 20 × 20 foot spacing). Assuming the population density as 100 flowering trees per acre, then the effective size of the "neighborhood" is doubled in size — 730 trees. In either case, with these sizes of "neighborhood", there should be little opportunity for racial differentiation within any continuous range of slash pine forest.

However, the range of slash pine is interrupted by many gaps which preclude effective pollination. The gaps exist in the form of swampland and open bodies of water and large tracts of deep sand barrens which support only sparse growth of longleaf pine, sand pine, scrubby oaks or lesser vegetation. A gap of two miles seems to be wide enough to reduce the pollen dispersion below the effective level. Furthermore, the gaps formed by swampland, open waters and deep sand ridges, in Florida at least, generally have a lineal continuity over considerable distances. Data from the present observations show that barriers as wide as these, under ordinary circumstances, greatly reduce the normal function of random pollination. Experiments with slash pine of different geographic seed source (University of Florida, unpublished data) confirmed the geographic differentiations of this widespread forest tree.

Pollen Dispersion and the Isolation of Seed Orchards

A tree seed orchard is an artificially created population for the production of tree seeds of a desired genetic constitution. The success of the orchard depends upon the effective isolation of the population from extraneous pollens and free access to an ample supply of pollen from all the clones of selected trees within the seed orchard so as to obtain the quantity production of a crop with the desired genetic constitution.

For Scotch pine seed orchards in Europe, isolation barriers of 3281 feet (1000 meters) were recommended by SCHMITT (1955). The present experiment shows that the pollen frequency at a distance of 400 to 500 feet is 2 to 5 per cent of the source frequency. But pollen frequency did not decrease by much more than 50% of the source frequency over a distance of 600 feet for transects A, B, and C *(Fig. 3)* where the scattered stands of timber may have effected a prolonged pollen flight by altering the turbulance patterns. The authors urge their industry cooperators to establish seed orchards with ¼ mile (1320 feet) of isolation strip. Isolation strips of 500 feet may be considered minimal for slash pine seed orchards. In the 15 slash pine and loblolly pine seed orchards established by industries cooperating with the University of Florida, pollen barriers used were 400 feet or more wide. The pollen barriers were either cut over areas or strips of standing timber free of the pine species planted in the seed orchard. This width of 400 feet corresponds to approximately two standard deviations (σ_D) of slash pine pollen dispersion.

In the spring of 1958 actual data were obtained on the effectiveness of isolation barriers in six seed orchards in Florida, Georgia, Alabama and Mississippi *(Table 7)*. Pollen samples were obtained from the borders and centers of the seed orchards at the height of the flowering season. The six seed orchards are between 2 and 4 acres in size and close to square in shape. Thus, the distance between the center and border of the seed orchards is between 104 feet, approximately 0.5 σ_D and 208 feet, approximately 1.0 σ_D Isolation strips extend outward from the plantation borders 400 feet or more.

Table 7. — Pollen Collected in the Isolated Seed Orchards.

Location of Seed orchard	Date (1958)	Border of Seed orchard	Center of Seed orchard
(1) Florida (Cantonment)	Feb. 4	3	1
(2) Alabama	Feb. 28	13	4
(Baldwin County)	Mar. 1	2	1
(3) Georgia (Egypt)	Mar. 4 and Mar. 5	5.75	11
(4) Georgia (Statesboro)	Mar. 11	0	1
(5) Mississippi	Feb. 25	0	1
(Greene County)	Mar. 10—12	7	4
(6) Florida*)	Feb. 28	29	12
(Yulee)	Mar. 1 (Rain)	3	5
	Mar. 3	96	29

*) Several pines have not yet been rogued out from the swamp hardwoods that form natural isolation strips on the eastern and western sides of the seed orchard. Hence the high pollen counts observed in this orchard.

According to theoretical considerations, in a seed orchard surrounded by isolation strips 2 σ_D in width, the percentage of extraneous pollen at distances of 0, 0.5, and 1.0 σ_D are 28%, 4.2% and 1.6% respectively (J. W. WRIGHT, 1953). These expected values were calculated on the assumption that the trees are equally spaced 0.1 σ_D apart, and that the trees produced equal amounts of pollen.

The six seed orchards examined were established in 1956 with grafted superior trees on 2 year old stock. Even at this early stage some of the grafted plants produced male and female flowers. The quantity of pollen produced by the grafted plants, however, is negligible in comparison with that of the surrounding trees.

The data in *Table 1* show that the pollen frequency at a distance of 400 to 500 feet is 2—5 per cent of the source frequency for slash pine. The amount of pollen observed in the first five seed orchards *(Table 7)* indicates that in general the source frequencies of extraneous pollen were well within the ordinary level of pollen output of slash pine plantations at the same distance. The percentage of extraneous pollen, therefore, would be negligible when the trees in the seed orchard begin to produce pollen in quantity as they reach seed production age. Turbulence and unusual weather, however, can make an isolation strip adequate one year and inadequate the next. The observations reported here show that most slash pine pollen strikes the ground within 400 feet of the source when bare land is used as an isolation barrier.

Summary

This paper reports on a series of observations made on pollen dispersion of slash pine (*Pinus elliottii* ENGELM.) during the years 1956 through 1958. These observations combined with a review of the literature provide the basis for a discussion of the significance of pollen dispersion patterns in the formation of tree races, and the establishment and management of seed orchards.

The pollen dispersal of slash pine growing under the following conditions was observed: (1) isolated single tree in a large open area, (2) isolated natural groves of slash pine, and (3) slash pine plantations. Pollen specimens were collected at the following distances from the pollen source tree: 0, 25, 50, 75, 100, 150, 200, 300, 400, 500, 1000, 1500, 2000, and 2500 feet.

The experiments showed that the pollen frequency at a distance of 400 to 500 feet is 2 to 5 per cent of the source frequency. Isolation strips of 500 feet may be considered minimal for slash pine seed orchards. Actual data were obtained on the effectiveness of isolation barriers in six slash pine seed orchards in Florida, Georgia, Alabama, and Mississippi. The width of the barrier is 400 feet, or approximately 2 σ_D in width. The amount of pollen observed in the seed orchards indicates that in general the source frequencies of extraneous pollen were well within the ordinary level of pollen output of slash pine plantations at the same distance. The percentage of extraneous pollen would be negligible when the trees in the seed orchard begin to produce pollen in quantity as they reach seed production age.

A distinct correlation was observed in the present study between the increase in slash pine pollen output and the rising of temperature in the flowering season. The effects of wind and pollen size on pollen dispersion were also discussed.

The standard deviation of the pollen dispersion distance (σ_D) was calculated from the pollen counts as a measure of pollen dispersion. It was calculated according to SEWALL WRIGHT's formula $y = y_0e^{-kD}$ (S. WRIGHT 1946).

The respective regression equations are:

$\text{Log } y = 2.05098 - 0.002786\, D$ (Pollen dispersion from a single tree),

$\text{Log } y = 2.1719 - 0.002714\, D$ (Pollen dispersion from a slash pine plantation).

The value of σ_D are 220 ft. and 226 ft. respectively for the single slash pine and the slash pine plantation

The possibility of race formation as expressed in the size of breeding population and the degree of isolation are estimated in terms of "neighborhood" size (N) according to the following formula for a hermaphroditic population with a continuous range and only the pollen dispersed:

$$N = 2\pi\sigma_D{}^2 d = 365 \text{ trees.}$$

With this size of N there should be little opportunity for racial differentiation within any continuous range of slash pine forest. However, the presence of barriers in the forms of sand barrens, swampland, and open waters greatly reduce the normal function of random pollination.

Zusammenfassung

Titel der Arbeit: *Pollenverteilung bei Pinus elliottii Engelm. unter besonderer Berücksichtigung der Samenplantagen-Bewirtschaftung.*

Diese Veröffentlichung beschreibt eine Reihe von Beobachtungen über den Pollenflug bei der „Slash Pine" (*Pinus elliottii* ENGELM.) von 1956 bis 1958. Die Beobachtungen bilden zusammen mit einer Literaturübersicht die Grundlage für eine Diskussion über die Bedeutung von Modellen der Pollenverteilung für die Rassenbildung und für die Anlage und Bewirtschaftung von Samenplantagen.

Unter folgenden Bedingungen wurde der Pollenflug bei *P. elliottii* beobachtet: 1. isolierter Einzelbaum auf freiem Feld, 2. isolierte natürliche *P. elliottii*-Gruppen und 3. „Slash-Pine"-Bestände. In folgenden Entfernungen von der Pollenquelle fing man den Pollen auf: 0,25, 50, 75, 100, 150, 200, 300, 400, 500, 1000, 1500, 2000 und 2500 feet.

Es stellte sich heraus, daß die Pollendichte in 400 bis 500 feet Entfernung 2 bis 5% der Dichte an der Pollenquelle entsprach. Isolierstreifen in 500 feet Entfernung müssen als Minimum für *P. elliottii*-Samenplantagen angesehen werden. Über die Wirksamkeit von Isolationsbarrieren liegen neuere Angaben aus sechs *P. elliottii*-Plantagen in Florida, Georgia, Alabama und Mississippi vor. Die Barriere ist 400 feet oder annähernd 2 σ_D breit. Die in den Samenplantagen festgestellte Menge fremden Pollens entspricht im allgemeinen dem gewöhnlichen Pollenangebot von *P. elliottii*-Beständen in gleicher Entfernung. Der Anteil von Fremdpollen wäre ohne Bedeutung, sobald die Pfropflinge in der Plantage mit dem Erreichen der Mannbarkeit größere Pollenmengen produzieren.

Zwischen der Zunahme des Stäubens und dem Anstieg der Temperatur während der Blütezeit wurden straffe Korrelationen festgestellt. Die Einwirkung von Wind und Pollengröße auf die Pollenverbreitung wird ebenfalls diskutiert.

Die Standard-Abweichung der Pollenverbreitungs-Entfernung (σ_D) wurde mit Hilfe der Pollenzählungen als Maß für die Pollenverbreitung in Anlehnung an SEWALL WRIGHTS Formel $y = y_0e^{-kD}$ berechnet (s. WRIGHT 1946).

Die entsprechenden Regressionsgleichungen lauten

$\log y = 2{,}05098 - 0{,}002786\, D$ (Pollenverbreitung, Einzelbaum),

$\log y = 2{,}1719 - 0{,}002714\, D$ (Pollenverbreitung *P. elliottii*-Bestand).

Die Werte für σ_D heißen 220 feet für den Einzelbaum und 226 feet für den Bestand.

Die Möglichkeit der Rassenbildung, die in der Größe der Mendelpopulation und dem Isolationsgrad Ausdruck findet, wird entsprechend der folgenden Formel für eine Fremdbefruchter-Population in einem zusammenhängenden Areal mit dem Begriff "neighborhoodsize" (N) bestimmt.

$$N = 2\pi\sigma_D{}^2 \cdot d = 365 \text{ Bäume.}$$

Mit diesem Wert für N sollte es nur eine geringe Möglichkeit zur rassialen Differenzierung innerhalb irgendwelcher zusammenhängenden Gebiete von *P. elliottii*-Beständen geben. Jedoch setzt das Vorhandensein von Barrieren in Gestalt von waldfreien Sandgebieten, von Sümpfen und offenem Wasser den normalen Ablauf der zufälligen (ungehinderten) Bestäubung weitgehend herab.

Résumé

Titre de l'article: *Dispersion du pollen de Pinus elliottii Engelm. avec application à l'établissement de vergers à graines.*

Cet article rend compte d'une série d'observations faites sur la dispersion du pollen de *Pinus elliottii* ENGELM. au cours des années 1956 à 1958.

Ces observations, appuyées par une revue de la littérature, fournissent une base de discussions sur le rôle des types de dispersion du pollen dans la formation des races d'arbres et dans l'établissement et la conduite des vergers à graines.

On a observé la dispersion du pollen de *P. elliottii* dans les conditions suivantes: — (1) Arbre isolé au milieu d'une large zone nue, — (2) Bouquet isolé d'arbres d'origine naturelle, — (3) Plantation de pins.

Des échantillons de pollen ont été récoltés aux distances suivantes de la source: 0 — 8 — 17 — 25 — 33 — 50 — 67 — 100 — 133 — 167 — 333 — 500 — 670 — 830 m.

Les expériences ont montré que la fréquence du pollen à une distance de 133 à 167 mètres est de 2 à 5% de la fréquence à la source. Une bande d'isolation de 167 mètres peut être considérée comme un minimum pour des vergers à graines de *P. elliottii.*

Des données concrètes ont été recueillies sur l'efficacité des barrières d'isolement dans 6 vergers à graines de *P. elliottii* en Floride, Géorgie, Alabama et Mississipi. La barrière a 133 mètres de large soit environ 2 σ_D. Les quantités de pollen recueillies dans les vergers à graines montrent que, en général, les fréquences à la source des pollens étrangers correspondaient bien à la production normale de pollen de plantations de *P. elliottii* situées à la même distance.

Le pourcentage de pollen étranger sera négligeable lorsque les arbres du verger commenceront à produire eux-mêmes du pollen en quantité.

Dans la présente étude on a observé une corrélation nette entre l'augmentation de la production du pollen et l'élévation de la température au moment de la floraison. Les effets du vent et de la dimension des grains de pollen sur la dispersion sont également étudiés.

L'écart-type de la distance de dispersion du pollen (σ_D) a été calculé à partir des comptages des pollens comme une mesure de la dispersion. Le calcul a été fait d'après la formule de SEWALL WRIGHT

$$y = y_0 e^{-kD}$$

Les équations de régression sont les suivantes:

Log y = 2.05098 — 0.002786 D (dispersion du pollen à partir d'un arbre isolé)

Log y = 2.1719 — 0.002714 D (dispersion du pollen à partir d'une plantation)

Pour les deux cas précédents, les valeurs de σ_D sont respectivement 73 et 75 m.

Les possibilités de différenciation raciale exprimée en fonction de la dimension de la population et du degré d'isolement sont estimées en termes de «dimensions du cercle de voisinage» (N) d'après la formule suivante valable pour une population hermaphrodite à aire continue avec dispersion de pollen seulement:

$$N = 2\pi\sigma_D^2 \cdot d = 365 \text{ arbres.}$$

Avec cette valeur de N il n'y aurait qu'une faible possibilité de différenciation raciale dans toutes forêts continues de *P. elliottii* cependant, la présence de barrières constituées par des sables nus, des marécages ou des plans d'eau réduit considérablement la portée de la fonction normale de pollinisation au hasard.

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