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A THESIS

Presented to the Graduate School of Michigan State College of Agriculture and Applied Science in Partial Fulfillment of Requirements for the Degree of Doctor of Philosophy

Horticulture Department
East Lansing, Michigan
1930

STUDIES OF THE STAMINATE INFLORESCENCE AND POLLEN OF HICORIA PECAN[1]

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INTRODUCTION

From the producer's standpoint one of the most important limiting factors to profits in pecan culture is low yields. These may be due to any one or to a combination of several factors, such as the failure of the trees to differentiate flowers, more especially pistillate flowers, poor pollen, unfavorable weather during the flowering season, or insect or disease attack upon flowers or developing fruits. Considerable study has been devoted to some of these questions. Little, however, has been recorded regarding the development of pollen in the pecan, though pollen deficiencies are known to be responsible for unsatisfactory fruit setting in certain varieties of apples, pears, plums, grapes, and many other fruits. It therefore appeared to the writer that a study of the morphology of the staminate inflorescence and physiology of the pollen would throw some light on practical questions of pollination.

REVIEW OF LITERATURE

Unfruitfulness of the pecan (*Hicoria pecan* Brit.) is associated more closely with the initiation and development of pistillate than of staminate flowers, and it is therefore logical that the pistillate flowers should have been studied first. Studies of the morphology of pistillate flowers of pecans have been made by Woodroof (*27*, *28*),[3] Shuhart (*21*), and Isbell (*12*), and the results have shown close agreement as to the time and manner of development. Staminate flowers have received secondary attention, but fragmentary descriptions have appeared in a few reports (*23*, *26*, *12*, *27*, *28*).

Stuckey (*23*) studied the development of staminate flowers of 33 varieties of pecans. He divided the varieties into two groups on the basis of the length and size of the catkins, length of bracts, and time of shedding pollen. Woodroof (*26*, *27*) found that catkins were differentiated in lateral buds throughout the growing season of

[1] Received for publication Sept. 19, 1929; issued June, 1930. Presented to the faculty of Michigan State College of Agriculture and Applied Science, in partial fulfillment of the requirements for the degree of doctor of philosophy and published with the approval of the director of the Georgia Agricultural Experiment Station as paper No. 31, Journal Series.

[2] In the investigations here reported Naomi C. Woodroof, of the Department of Botany, and J. E. Bailey, of the Department of Horticulture, of the Georgia Agricultural Experiment Station, aided in collecting field data and in preparing material for laboratory studies. Otis Woodard, of the Georgia Coastal Plain Experiment Station, furnished a part of the data for Table 5; C. F. Williams, of the North Carolina Agricultural Experiment Station, and R. M. Middleton, of the Georgia station, furnished a part of the data for the same table. Members of the Department of Horticulture of Michigan State College offered suggestions in the planning of the work and criticized the manuscript; and W. C. Dutton aided in making photomicrographs.

[3] Reference is made by number (italic) to "Literature cited," p. 1103.

the year prior to the shedding of pollen. He reported measurements of catkins of the two groups of varieties during the winter stage and described the method of shedding bud scales the following spring. Isbell (*12*) published 13 photomicrographs illustrating progressive stages of catkin development during the summer.

Higgins (*10*) described a disease (*Microstroma juglandis* (Bereng.) Sacc., var. *robustum*, n. var.) of pecan catkins that appeared on all of the varieties observed and sometimes destroyed one-third of the pollen. The tissues of the catkin were not killed outright, but the pollen grains degenerated, often leaving collapsed walls. This disease is common in the orchard in which the present studies were made, but care was taken to avoid using diseased material.

Schuster (*18*) stated that the amount of pollen produced by filberts in Oregon varies from season to season and is influenced by many factors. Many varieties produce a heavy crop of staminate and pistillate flowers one year, and a light crop of both the following year.

Valleau (*24*), working with strawberries, Dorsey (*8*) with plums, Knowlton (*15*) with the J. H. Hale peach, and Asami (*3*) with Shanghai peach, report that the first abnormal development in pollen was seen at the time of liberation from the tetrad wall; thereafter microspores were found in various stages of abortion. Shoemaker (*19, 20*) found lagging chromosomes in the heterotypic division, giving rise to abnormal pollen in the apple and cherry.

The germination of pollen on artificial media has been unsatisfactorily accomplished with pollen of many plants. Wood [4] found that almond and walnut pollen did not germinate well on sugar-agar media, and concluded that there was no satisfactory laboratory method of ascertaining the viability of pollen of various varieties. Anthony and Harlan (*2*) attempted to duplicate natural conditions for germinating barley pollen by placing a piece of mesophyll from the leaf of the garden pea in the cell to supply water. The cell was covered with a cover glass and placed in the open to allow the condensation of moisture on the pollen grains. Germination was accomplished with both mesophyll and drops of water for humidifiers. Beaumont and Knight (*5*) and Knowlton (*15*) attempted to approach natural conditions for germinating apple pollen by adding stigmas of the same or different varieties to a hanging drop at the same time the pollen was added. They concluded that further improvement of the method of germination was necessary to produce pollen-tube length equal to that produced under natural conditions. Lidforss (*17*) reported that artificial media for germinating pollen must contain not only the essential nutritive substances but that it must not contain substances which prevent growth, especially mineral salts, as calcium.

The most satisfactory results, from pollen-germination tests in general, have been obtained by using from 1 to 2 per cent agar or gelatin and 5 to 20 per cent sucrose in the media. Howlett (*11*) used 10 per cent sucrose and 2 per cent agar; Beaumont and Knight (*5*) used 5 per cent sucrose and 1 per cent gelatin for germinating apple pollen; Booth (*6*) used 15 per cent sucrose and 1½ per cent gelatin for germinating plum pollen and 10 per cent sucrose and 5 per cent gelatin for germinating cherry pollen; Schuster (*18*) obtained best germination of filbert pollen in 12 to 15 per cent sucrose but observed bursting of

[4] WOOD, M. N. POLLEN STUDIES OF ALMOND AND WALNUT. 1917. (Master's thesis. University of California.)

pollen grains and tubes; Auchter (*4*) germinated apple pollen in distilled water; and Knight (*14*) increased apple-pollen germination by adding a trace of asparagine to the medium.

Valleau (*24*) determined the percentage of defective grains in strawberry pollen and reported that—

> lactic acid has the advantage over water or alcohol for this purpose as it is not volatile and seldom, if ever, breaks the pollen grains through osmotic pressure. It readily enters and expands the normal grains, while it leaves the aborted grains collapsed.

Dorsey (*8*) studied plum pollen and reported that the extent of pollen abortion in selected forms was determined partly from mounts in lactic acid and partly from stained sections. In Shoemaker's (*19*) work with apples lactic acid was employed to afford a liquid medium which would prevent bursting and germination of the pollen grains. Beaumont and Knight (*5*) hand-pollinated apple blossoms, and after the pollen had germinated and penetrated the stigmas the latter were flattened on a cover glass and mounted in lactic acid which killed and fixed the pollen tube. Snow (*22*) used lactic acid in a similar manner in studying the pollen of stocks. Florin's (*9*) germination tests closely checked with the lactic acid examinations of apple and pear pollen.

METHODS

Material for morphological studies was taken from an orchard of 28 varieties at the Georgia Experiment Station. The location is about 150 miles north of the center of pecan production in Georgia. Most of the trees are 20 years old and have had uniform culture. Data on pollen dissemination were taken in commercial orahards near Barnesville, Ga.

In general, the methods of collecting, killing, fixing, embedding, sectioning, and staining material for microscopical studies were the same as those described in previous reports (*27*, *28*, *31*).

The Alley and Frotscher varieties were chosen as typical of Groups 1 and 2, respectively, according to Stuckey's classification (*23*). Other varieties were repeatedly used to verify results. Juel's fixative [5] and picro-sulphurous acid [6] were used as killing and fixing agents, the latter giving the better results. Material was taken at 15-day intervals throughout the year from each variety, alternating the fixatives. Normal buds were selected from representative shoots, and normal flowers were taken from catkins typical of the variety. From the mother-cell stage until pollen shedding, catkins of the Stuart variety were collected daily; and during the reduction division, material of the Frotscher and Stuart varieties was collected at 3-hour intervals. Buds collected during the actively growing season were sectioned 5 microns in thickness. The hairy nature of winter buds rendered it difficult to section them sufficiently thin for cellular studies.

A modification of the smear method, as described by Kaufmann (*13*), was used to determine the number of tetrads per anther and the number of pollen grains per pollen sac. An anther in the tetrad stage was placed in a drop of water on a slide and thoroughly macerated with a needle. The tetrads separated from the anther wall and floated independently in the medium. After the fragments of the anther

[5] Juel's fixative: $ZnCl_2$, 2 gm.; acetic acid, 2 c. c.; alcohol, 95 per cent, 50 c. c.; distilled H_2O, 50 c. c.

[6] Picro-sulphurous acid: Sulphurous acid, 6 per cent, 10 c. c.; picric acid, 1½ gm.; alcohol, 75 per cent, 90 c. c.

wall were removed the tetrads were stained with eosin, covered with a cover glass, and examined under the high power of the microscope.

Dissemination of pollen was studied by catching pollen from the air on slides greased with vaseline, a method similar to that used by Waugh (*25*) for catching plum, pear, and apple pollen. Two yardsticks wrapped with cheesecloth and loosely bolted together made a convenient holder for 12 slides. About two-thirds of the length of each slide was exposed, the remainder being held firmly between the yardsticks. Three series of slides were mounted on a slender pole,

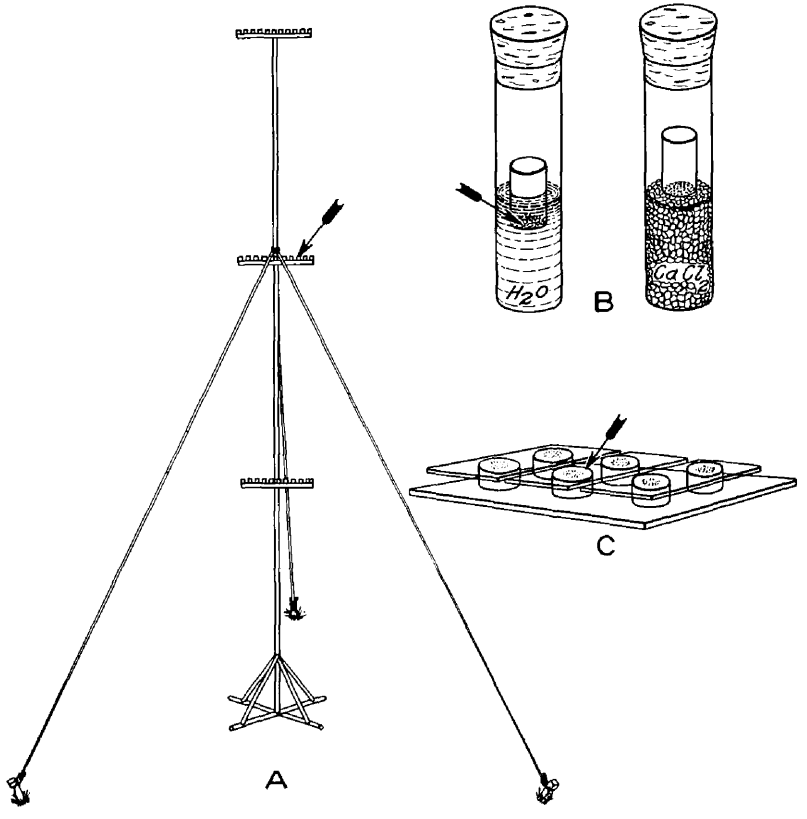

FIGURE 1.—A, Pole 30 feet high supported by guy wires to which were attached three series of greased slides for catching pollen from the air; B, vials containing water and calcium chloride, in which were placed smaller vials containing pecan pollen which was kept "moist" and "dry" respectively; C, cells for germinating pollen. Arrows in each case indicate position of the pollen

one series each 10, 20, and 30 feet above the ground. The slides were set on the leeward side of the trees, at a 45° angle with the ground, the greased face of the slide being turned toward the pollen-shedding trees. The slides were changed by lowering and raising the pole with three guy wires. (Fig. 1, A.)

Pecan pollen grains on the greased slides were identified and counted under the low-power objective of the microscope. After the area of the microscopical field was calculated, the number of grains in 200 fields were counted, averaged, and calculated to the number of grains per square centimeter.

The wind velocity was determined by the use of a Robinson cup anemometer with electric connections and a buzzer which indicated the number of miles per hour. The relative humidity was determined by the use of a stationary hygrometer placed in the orchard.

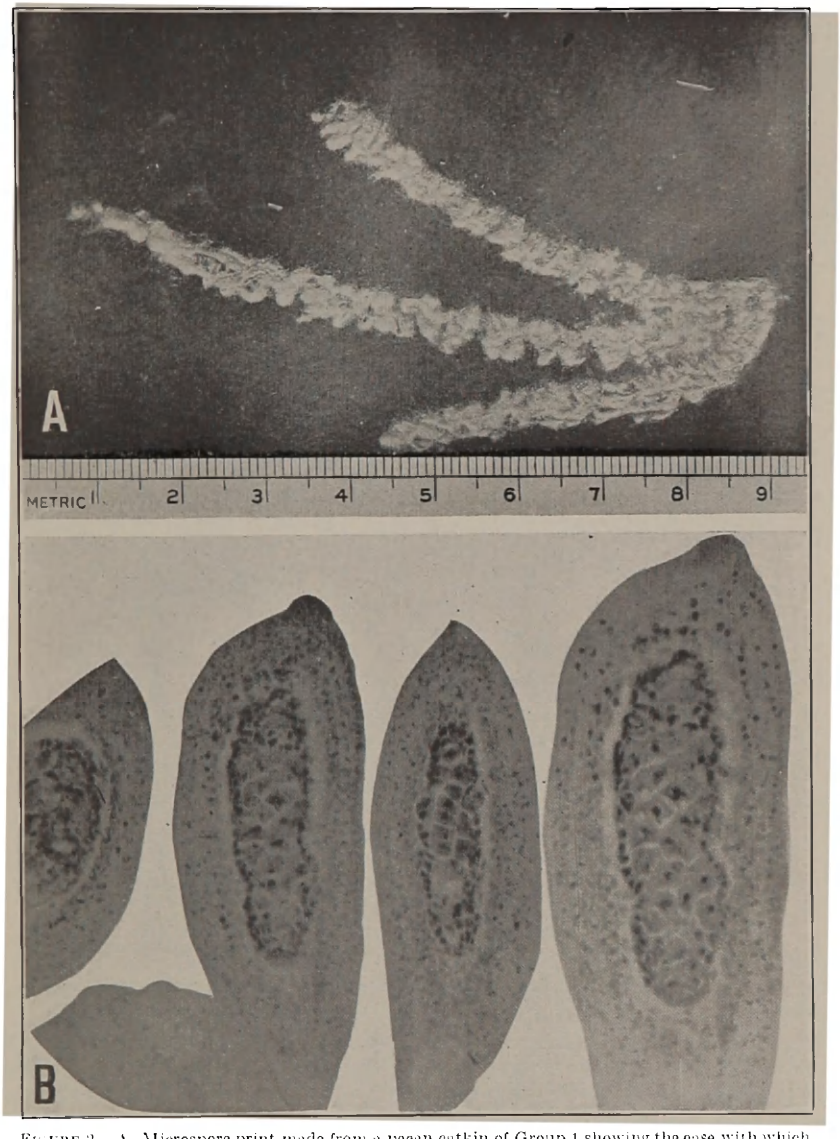

FIGURE 2.—A, Microspore print made from a pecan catkin of Group 1 showing the ease with which pecan pollen may be collected in quantity; B, photo micrograph of longitudinal section of Alley variety anther while in the mother-cell stage on April 1; in some cases there seem to be rows of mother cells

Pollen for germination tests was obtained from ripe anthers which were allowed to dehisce in the laboratory. (Fig. 2.) In this way the time of dehiscence could be determined to within two hours. Cells for germinating pollen were made by shellacking six hard

rubber rings, 15 mm. in diameter and 10 mm. high, to glass slides 2 inches wide and 3 inches long. Water to supply moisture for germination was placed in the bottom of each cell. A drop of sterile germinating medium was placed on a cover glass while hot and allowed to solidify. The pollen was dusted on the medium and the cover glass was inverted and sealed on the cell with vaseline. Examinations were made at intervals under low power without disturbing the cell. (Fig. 1, C.)

Dry and moist storage conditions were provided by placing calcium chloride and water, respectively, in two 50 c. c. vials. A 10 c. c. vial containing pollen was placed in each 50 c. c. vial and the latter was corked. (Fig. 1, B.) A duplicate series was set up for each variety and temperature. Electric ovens provided tempera-

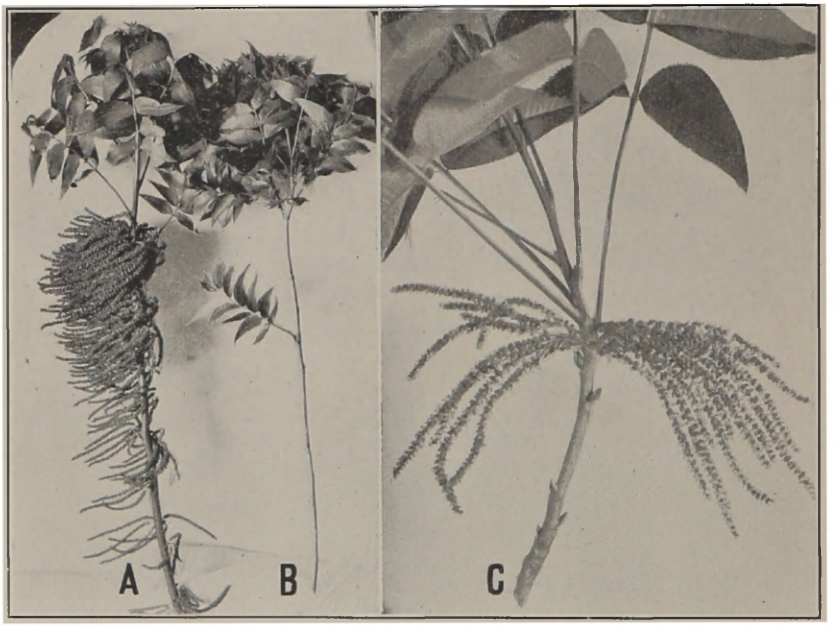

FIGURE 3.—A, Twig from Stuart pecan tree which bore 3 pounds of nuts last year; B, twig from Mobile tree which bore 29 pounds of nuts last year. This tree and that in A are both 12 years old and have received the same fertilizer and cultural treatments since being set in the orchard. C, Twig from McAlister variety, a supposed hybrid between *Hicoria pecan* and *Carya alba*, which has a catkin producing habit like *C. alba*, i. e., only the terminal bud produces catkins

tures constant at 32°, 25°, 23°, and 22° C.; and a refrigerator provided a temperature of 5° C.

Mounting pollen in lactic acid for microscopical determination of the percentage of defective grains seems a more reliable method than germinating it on artificial media. Two drops of 90 per cent lactic acid placed on a slide with a small amount of pollen and covered with a cover glass render the grains containing a normal amount of protoplasm distinct from those containing less than the normal amount. About three minutes are required for complete penetration; after three hours the grains become bleached and differentiation of defective and normal grains is uncertain. Fresh mounts and high magnification are necessary for one to make reliable counts by this method.

PRESENTATION OF EXPERIMENTAL DATA

The lateral buds of a growing shoot on a bearing pecan tree differentiate catkin primordia by the time the subtending leaf is one-tenth grown (*26*, *27*). Differentiation begins about two weeks after active growth starts in the spring (April 15) and continues throughout the growing season. In the pecan, catkins are always produced in lateral, axillary buds (figs. 3, 4), and the number of catkin primordia formed is in proportion to the number of leaves produced on that shoot. Normally there are two groups of three catkins each produced at each node. In other native hickories (*Carya alba*, *C. ovalis*, *C. glabra*) the catkins are produced in the terminal bud. (Fig. 3, C.)

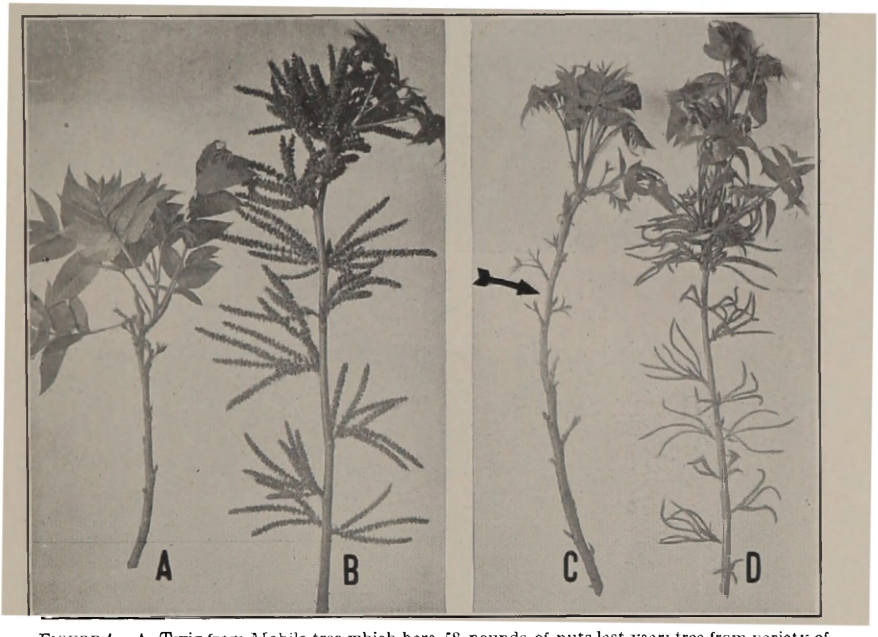

FIGURE 4.—A, Twig from Mobile tree which bore 58 pounds of nuts last year; tree from variety of Group 1; B, twig from Alley tree which bore 34 pounds of nuts last year; tree from variety of Group 1; C, twig from Frotscher variety which bore 100 pounds of nuts last year; tree from variety of Group 2; D, twig from Stuart tree which bore no nuts last year; tree from variety of Group 2. All of these trees are 20 years old and have received the same fertilizer and cultural treatments since being set. Arrow indicates point of abscission of the catkin buds on April 9

The characteristics of the buds and inclosed catkin primordia have been previously described by the writer (*26*). The central catkin is formed and develops somewhat in advance of the catkins borne on either side, and ultimately reaches a greater length at maturity. (Figs. 5, 6, 4.)

THE TWO GROUPS OF VARIETIES

Stuckey's (*23*) description of the two groups of varieties was based on characteristics of the catkins at the time of pollen shedding. The writer (*26*) found that the catkin primordia of Group 1 have a greater diameter and lesser length than those of Group 2 in both October and January (*26*). Such measurements aid in differentiating the

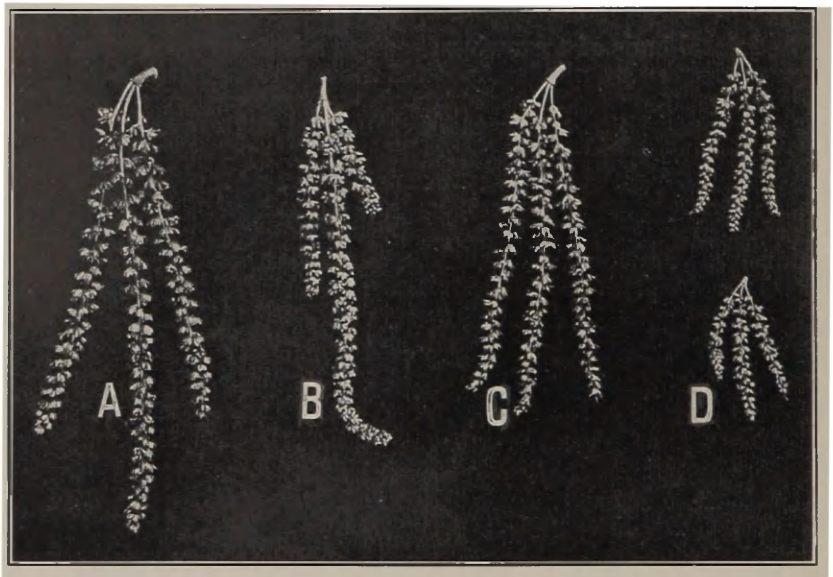

FIGURE 5.—Catkins of pecan varieties in Group 1: A, Alley; B, Jerome; C, Mobile; D, Mobile from nonvigorous bud (0.57 natural size)

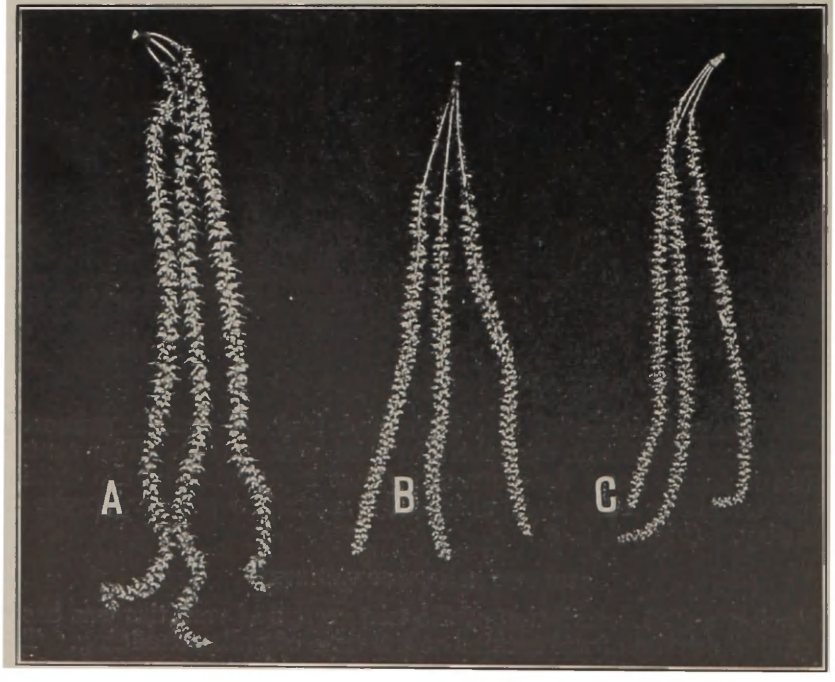

FIGURE 6.—Catkins of pecan varieties in Group 2: A, Van Deman; B, Frotscher; C, Teche. The Frotscher and Teche varieties have a large number of aborted flowers near the base of the cluster (0.57 natural size)

two groups, but as diameter and length vary with the vigor of the tree, they can not be depended upon solely.

There seems to be no difference between the mode of differentiation and type of growth of the catkins of the two groups of varieties during the spring and summer, but a marked difference is evident by early fall.

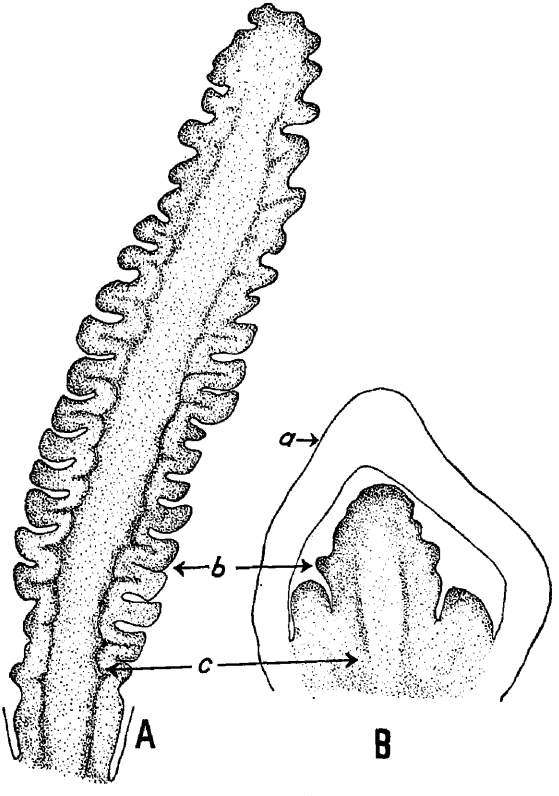

FIGURE 7.—Primordia of staminate inflorescence: B, Initial formation of a group of three catkins within a single bud scale, May 15; A, single inflorescence six weeks later: *a*, bud scale; *b*, primordium of an individual flower; *c*, initial formation of vascular bundles. Frotscher variety. × 181

Individual flower primordia develop as lateral "bumps" on the axis of the catkin primordium, beginning at the base and progressing toward the terminus. (Fig. 7.) In Group 1 flower primordia continue to form at the terminus, while the older ones near the base differentiate anthers by early fall. By the time growth practically ceases in the fall anthers are distinguishable along the entire length of the axis. (Figs. 8 and 9 and Table 1.) Thus the winter stage of Group 1 shows complete differentiation of anthers and bracts.

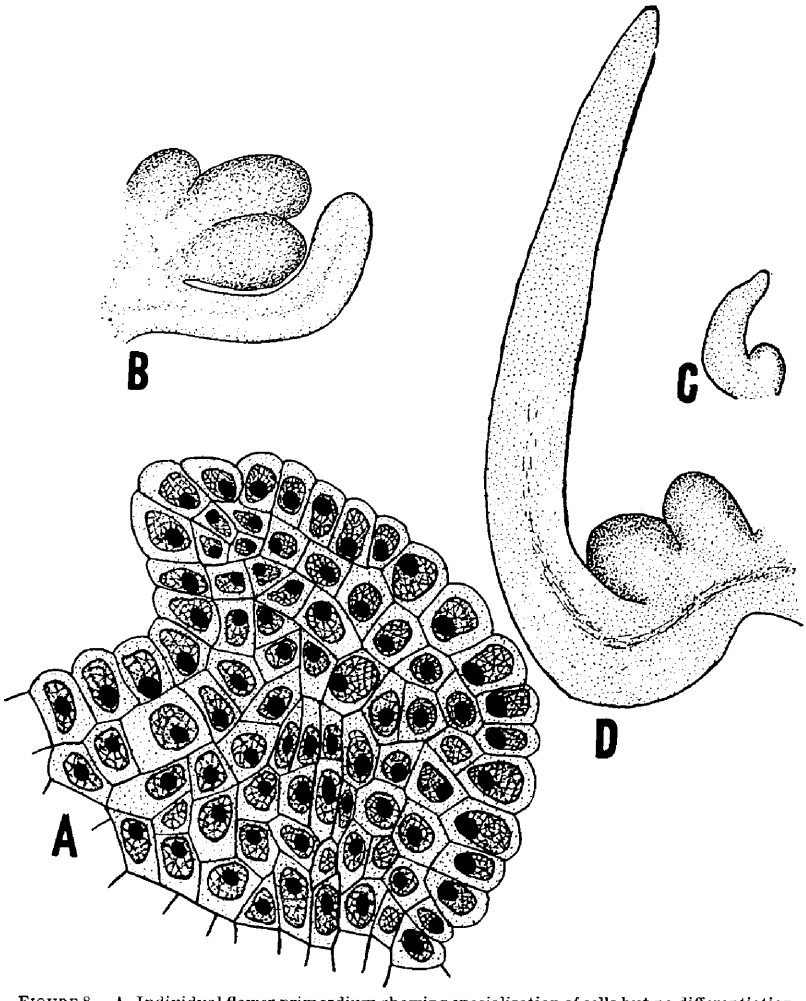

FIGURE 8.—A, Individual flower primordium showing specialization of cells but no differentiation of floral organs; enlargement of Figure 7, × 1040; B, Alley variety on March 15 showing floral organs well differentiated; × 114; C, Frotscher variety on March 15 showing very early stage in differentiation of floral organs; × 114; D, Frotscher variety on April 1 showing floral organs in same stage as Alley on March 15; × 114

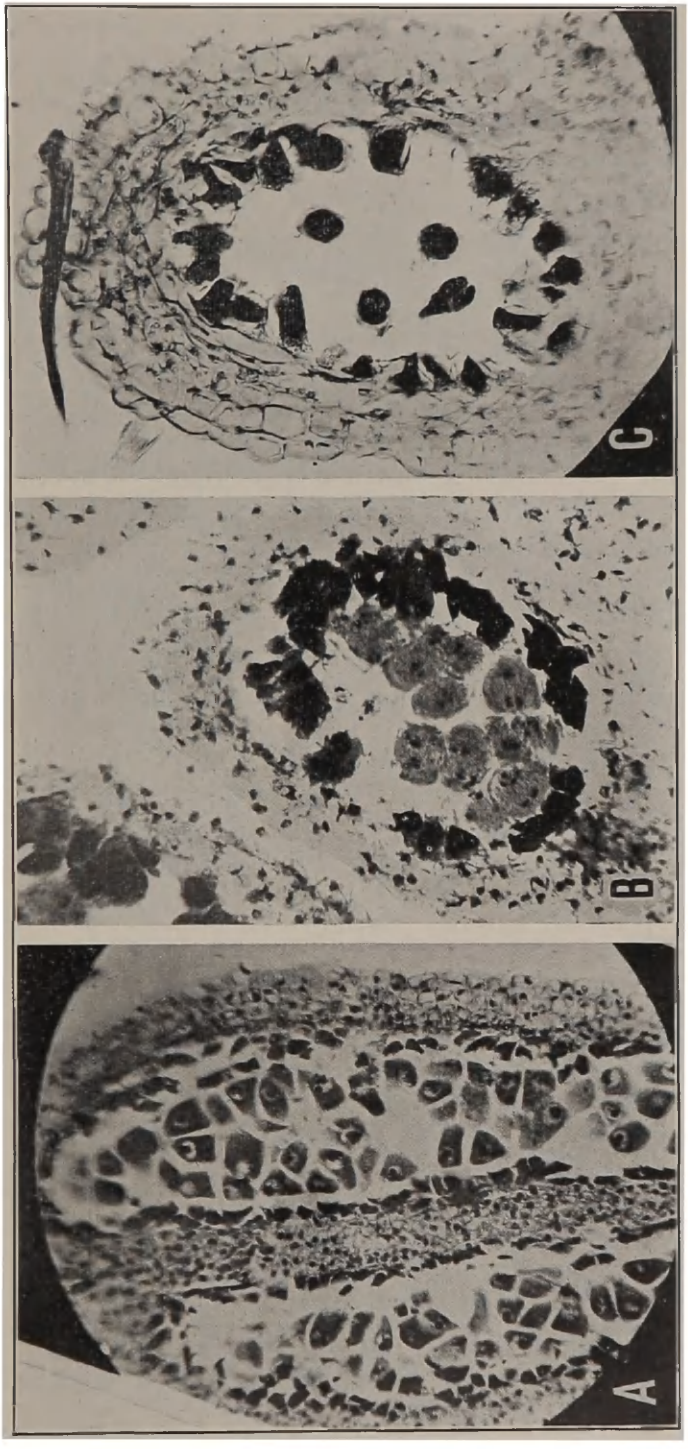

FIGURE 9.—A, Photomicrograph of longitudinal section of two lobes of an anther showing mother cells just before rounding up; B, photomicrograph cross section of one lobe of an anther showing mother cells undergoing reduction division; C, photomicrograph cross section of one lobe of anther showing tapetum cells disintegrating, and tetrads within the mother cell walls; one tetrad is elongated, indicating abnormality

TABLE 1.—*Stages of development of pollen of pecan varities in Groups 1 and 2*

Stage of development	Groups at stage of development mentioned at time indicated																	
	April	May	June	July	August	September	October	February	March			April			May			
									1	10	20	1	10	20	1	10		
Differentiation of inflorescence	1, 2	1, 2	1, 2	1, 2	1, 2	1, 2												
Differentiation of anthers						1	1	2	2	2								
Formation of anther lobes										1	1, 2	2						
Archesporial cells										1	1, 2	2						
Mother cells											1	1, 2	2					
Rounding-up of mother cells											1	1, 2	2					
Reduction division											1	1, 2	2					
Tetrads												1	1, 2	2				
Microspore liberation												1	1, 2	2				
Anther dehiscence														1	1, 2		2	

In Group 2 the flower primordia continue to form as long as growth continues in the fall, but no differentiation of anthers occurs

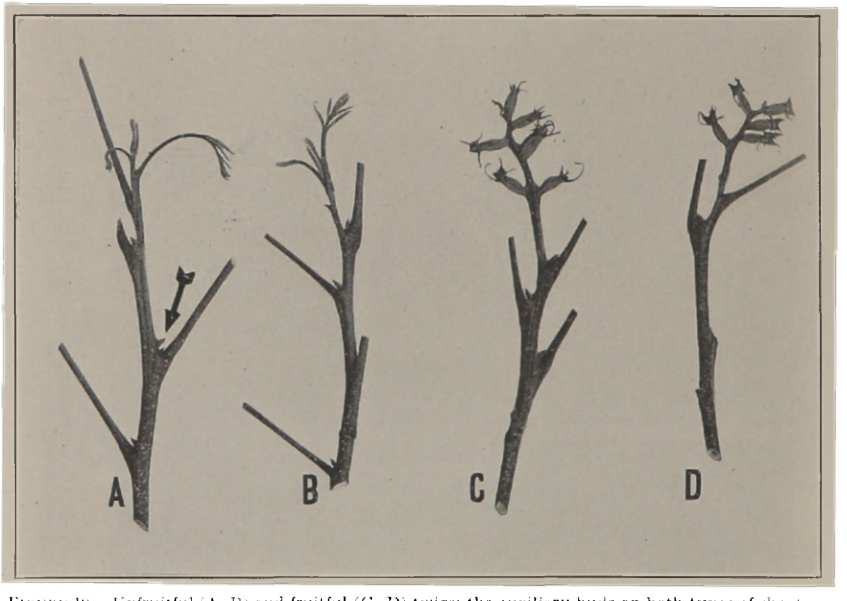

FIGURE 10.—Unfruitful (A, B) and fruitful (C, D) twigs; the auxiliary buds on both types of shoots produce staminate flowers the following spring (0.48 natural size)

until the following spring. Thus the individual flower primordia reach an inactive stage soon after formation and remain so for from four to nine months, while additional flower primordia continue formation toward the actively growing terminus. (Fig. 7.) Thus catkins of varieties of Group 2 are longer than those of Group 1. The period of inactivity varies with the time of formation—the basal and first-formed ones remain inactive longer than the newly formed terminal ones; also those formed in buds near the base of the new shoot early in the season are inactive for a longer time than those toward the terminus of the shoot. (Fig. 10.)

From early fall until the anthers are mature the following spring the development of the catkin primordia and the catkins of Group 1 is considerably in advance of that of Group 2. In the fall the difference is from 2 to 3 weeks; in winter when growth is almost at a standstill the maximum difference of 3 or 4 months occurs; while in spring when growth is most rapid the difference is from 10 to 15 days (figs. 4, 5, 6, and 11), and under some seasonal conditions the shedding of pollen of the two groups may be nearly coincident. (Table 5.)

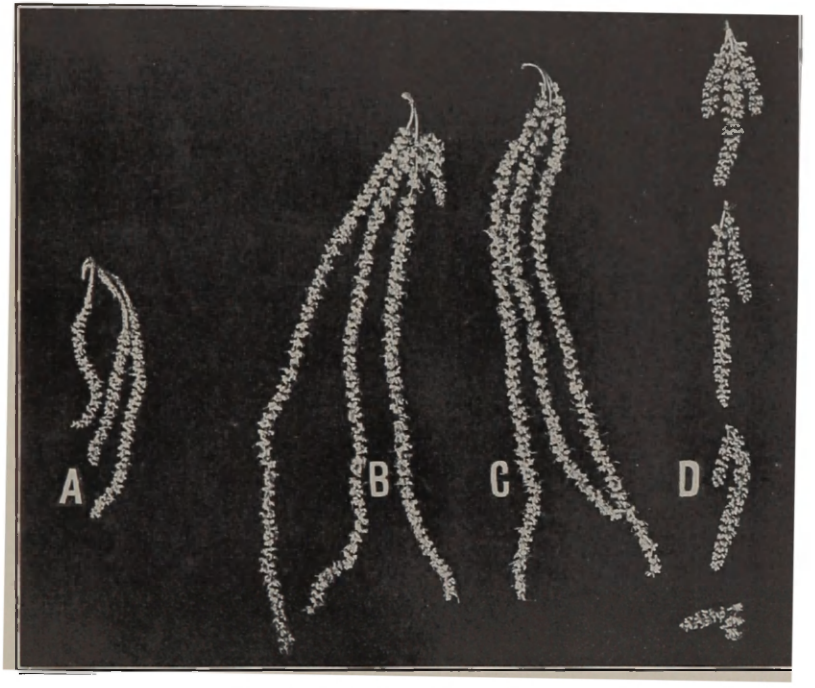

FIGURE 11.—A, Weak catkins with aborted flowers at base; B, vigorous catkins branched at base; C, normal catkin; D, aborted flowers from weak shoots. Indiana variety. (0.55 natural size)

The varieties of pecans can be separated into two groups in winter on the basis of the internal appearance of the lateral buds. Carefully cut and stained free-hand sections are sufficient to enable one to make the distinction. Practical use has been made of this fact in determining in advance the approximate date on which pollen of a new or unknown variety should shed.

The practical significance of the time of pollen shedding of the two groups will be discussed later. Anthers of varieties of Group 1 are differentiated several months before pollen shedding and differentiation occurs during the previous growing season, while differentiation of anthers of varieties of Group 2 occurs about two months before pollen shedding and takes place during the current growing season, as is the case with pistillate flowers (*28, 21, 12*). A closer relation thus exists in respect to time of differentiation between staminate and pistillate flowers of Group 2 than between staminate and pistillate flowers of Group 1.

INFLORESCENCE

A catkin primordium consists of three regions.

(1) The interior region occupies, as seen in longitudinal section, almost one-half of the diameter of the primordium. It consists entirely of large, slightly elongated, parenchyma cells, extending longitudinally with the axis. These remain parenchyma cells throughout the life of the catkin and are analogous to pith cells in a young shoot. The diameter of the spherical nuclei is about one-third the smallest diameter of the cell. The nuclei and cytoplasm do not stain as heavily as in the parenchyma cells of the primordia of individual flowers.

(2) Surrounding the interior region is a cylinder of small, narrow cells, with elongated nuclei which more than half fill the cells. The outline of this region is slightly irregular in both cross and longitudinal sections. In longitudinal section the cells vary greatly in size and shape and lie very close together. As growth continues these cells become sclerenchyma cells of the vascular bundles which connect each flower with the vascular system of the catkin.

(3) The third region of the catkin primordium consists of individual flower primordia which are made up entirely of parenchyma cells from the time of differentiation until September. (Fig. 8, A.)

In longitudinal section the epidermal cells of the flower primordium are rounded, uniform in size, but somewhat elongated. They lie close to one another and form a complete layer one cell thick over the surface. Directly beneath the epidermal layer are closely appressed 3-sided to 6-sided meristematic cells which vary widely in size. Sections made from material collected August 1 show that some of these cells are several times larger than others and are in a state of division. In the center of a flower primordium are several layers of elongated cells with oblong nucleii. These become sclerenchyma cells of a vascular system connecting each bract and anther with the vascular system of the catkin.

Bracts are differentiated about 10 days before the anthers. The first appearance of the bracts is shown by a turning of the terminus of the flower primordia toward the terminus of the catkin primordium, forming an angle of about 45°. As growth continues the bend becomes less abrupt and a protrusion appears in the axil. This protrusion divides immediately into four or five smaller ones, and each of these becomes an anther. (Figs. 8, 7.)

The development of bracts in spring is very rapid. Three branches soon form, the middle one being broader and longer than those on either side. The three almost envelop the developing anthers. (Figs. 6, 12.) The bracts contain chlorophyll, have numerous hairs on their surfaces and small veins, and presumably function as true leaves.

ANTHER

The anthers of the Frotscher variety on March 5 (40 days before shedding pollen) were a homogeneous mass of parenchyma cells covered by an epidermis. (Fig. 13, B.) Very early the anther appeared 4-lobed in cross section (fig. 14, B); and the differentiation of the vascular strand of the connective tissue outlined the general plan of structure. Almost simultaneously with the formation of lobes, a plate of hypodermal (archesporial) cells became differentiated in each lobe,

faintly distinguished from the adjacent cells by their large size, numerous sides, large nucleii, and less dense staining.

Subsequent divisions up to the mother-cell stage follow one another very rapidly. The archesporial cells divide by periclinal walls, form-

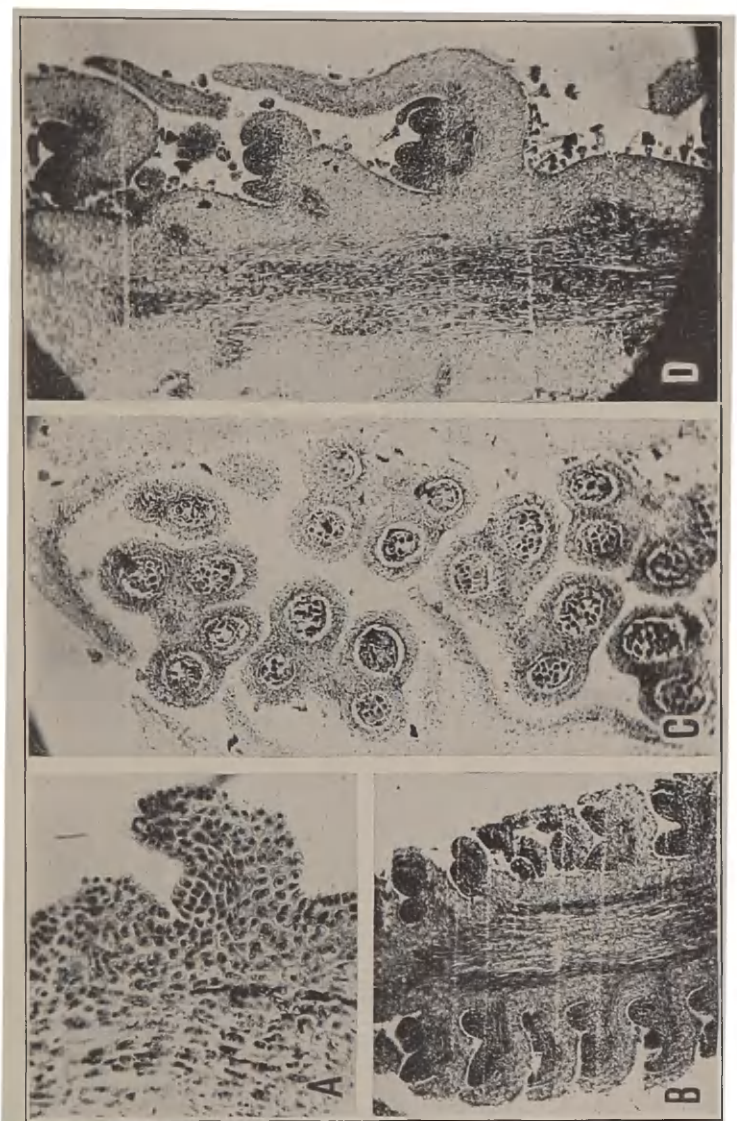

FIGURE 12.—Photomicrographs showing condition of flowers of Groups 1 and 2 on two different dates: A, Individual flower primordium just before differentiation of anthers, Group 2, Frotscher variety, December 1; B, longitudinal section of a catkin showing anthers formed in the Alley variety on December 1 as is typical of varieties in Group 1; C, cross section of several anthers showing tapetum cells broken down and mother cells separating, Alley variety, Group 1, April 1; D, longitudinal section of flowers of Frotscher variety, Group 2, on April 1, showing the anthers not yet differentiated into lobes

ing an outer layer of primary parietal (primary tapetum) cells, and an inner layer of primary sporogenous cells; the former producing the wall of the embedded sporangium and the latter the sporogenous tissue. The primary tapetum cells successively divide by periclinal walls until six or seven layers are formed. The inner layer is known

as the endothecium or tapetum, the outer layer as the exothecium or epidermis, the three or four remaining layers as "middle layers." The exothecium cells are thin walled, large and cubical, with large vacuoles and small oval nuclei which adhere to the sides of the cells toward the center of the anther. The cells of the middle layer are much smaller, somewhat compressed, many-sided, thin-walled, contain no vacuoles, have nuclei centrally located, are elongated, and

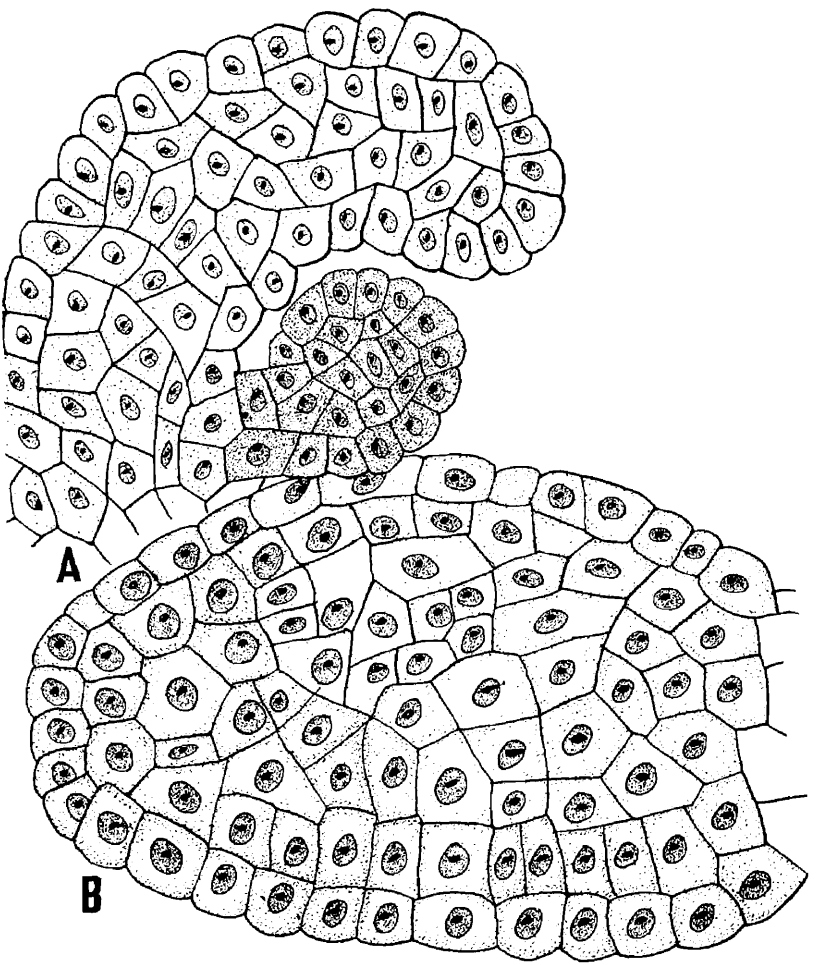

FIGURE 13.—Enlargements of Figure 8: A, Figure 8, C × 1,000; B, Figure 8, B × 1,000

stain lightly. The thick-walled, deeply staining, 6-sided, closely pressed, small nucleate tapetum cells form a jacket about the sporogenous cells, one or two cells in thickness.

Simultaneously with the division of the primary tapetum cells the primary sporogenous cells multiply without definite order to form mother cells. Division apparently occurs in every direction with occasional formation of layers but no definite massulae. Longitudi-

nally, the mass of closely compressed, many-sided, large nucleate mother cells extends almost the length of the anther, and about three cells wide. (Fig. 15, B.) They stain about as deeply as the middle layers but much lighter than the surrounding tapetum cells.

Further development is accompanied by separation, disorganization and disintegration of tapetum cells; and separation, increase in

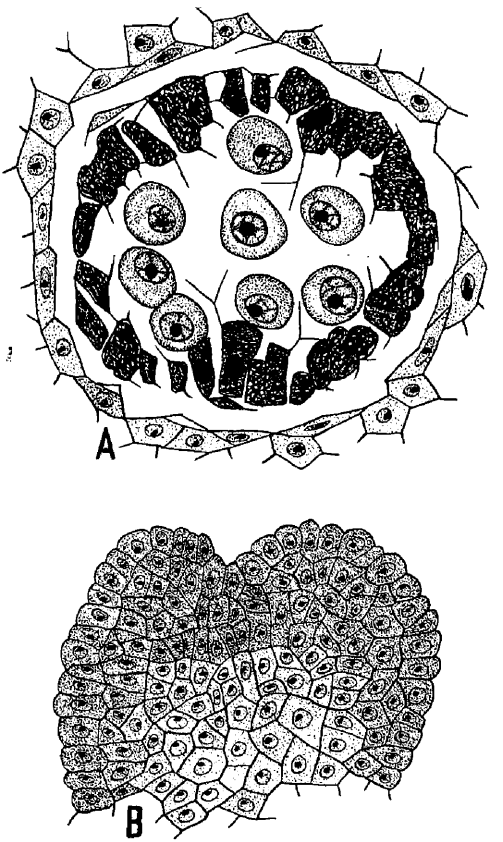

FIGURE 14.—A, Camera lucida drawing of cross section of an anther of Alley variety on April 5, showing rounding-up stage of the mother cells and continued disintegration of the tapetum cells; × 410: B, cross section of an anther of Frotscher variety on April 5, showing lack of differentiation of the interior into typical tapetum and mother cells; × 410

size, increase in thickness of walls, and rounding-up of the mother cells. (Figs. 14 and 16.)

The first evidence of disintegration of the tapetum cells occurs about 35 days before pollen shedding. (Fig. 15, B.) The layer of cells adjacent to the mother cells undergoes nuclear division once or twice, withdraws from the mother cells, shrinks in size, and clusters around the mother cells in a deeply staining irregular mass. Disintegration of the tapetum layer is increasingly rapid for 15 days, after which disintegration is almost complete and the fragments form an

incomplete layer around the mother cells. The layers of cells adjacent to the tapetum undergo similar but less rapid disintegration. These cells lose their contents and the walls collect around the periphery of the pollen sac. (Fig. 17.) The epidermis and the layer

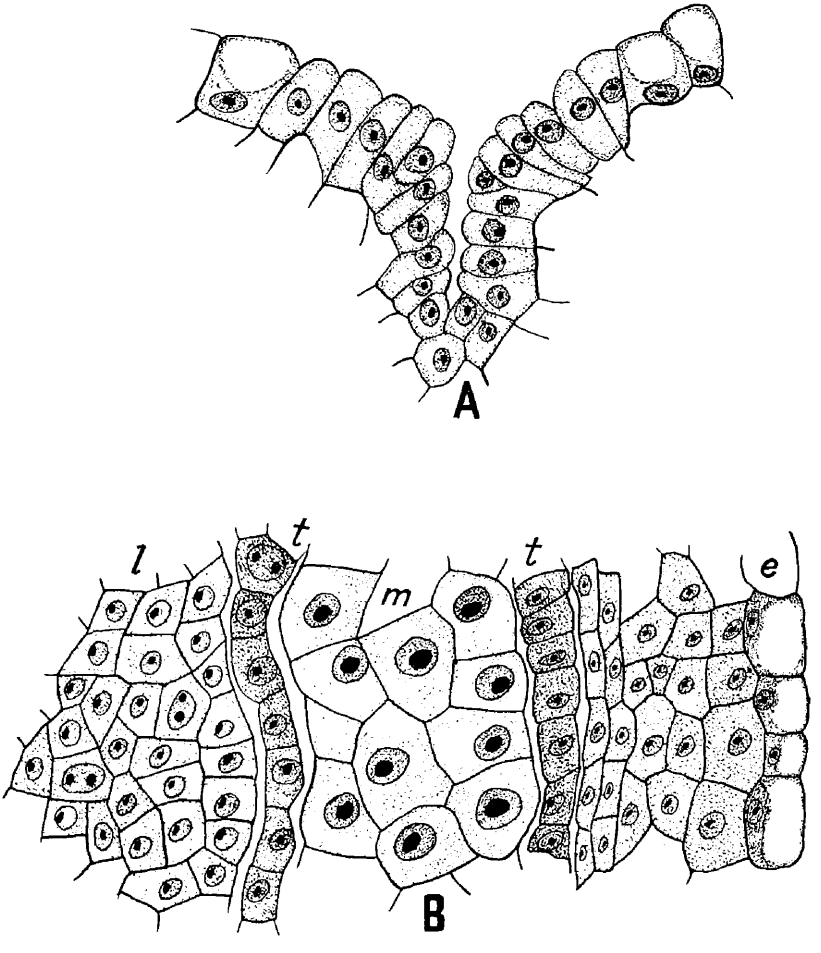

FIGURE 15.—A, Camera lucida drawing of cross section of a stomium of a mature anther; B, longitudinal section of a microsporangium showing the mature mother cells, *m*, just before rounding up; the tapetum cells, *t*, showing the first signs of disintegration; the cells between the loculi, *l*, and the epidermis, *e*

of cells next to it do not disintegrate, but increase in radial diameter. The cells of the middle layers continue to disintegrate until the pollen is mature and the wasting away of the wall separating two loculi on either side of the anther allows them to fuse into one, and is a part of the process of dehiscence.

The mother cells do not increase in number after the tapetum cells reach full size (35 to 40 days before pollen shedding). As the tapetum cells disintegrate, the mother cells become separated and loosely fill

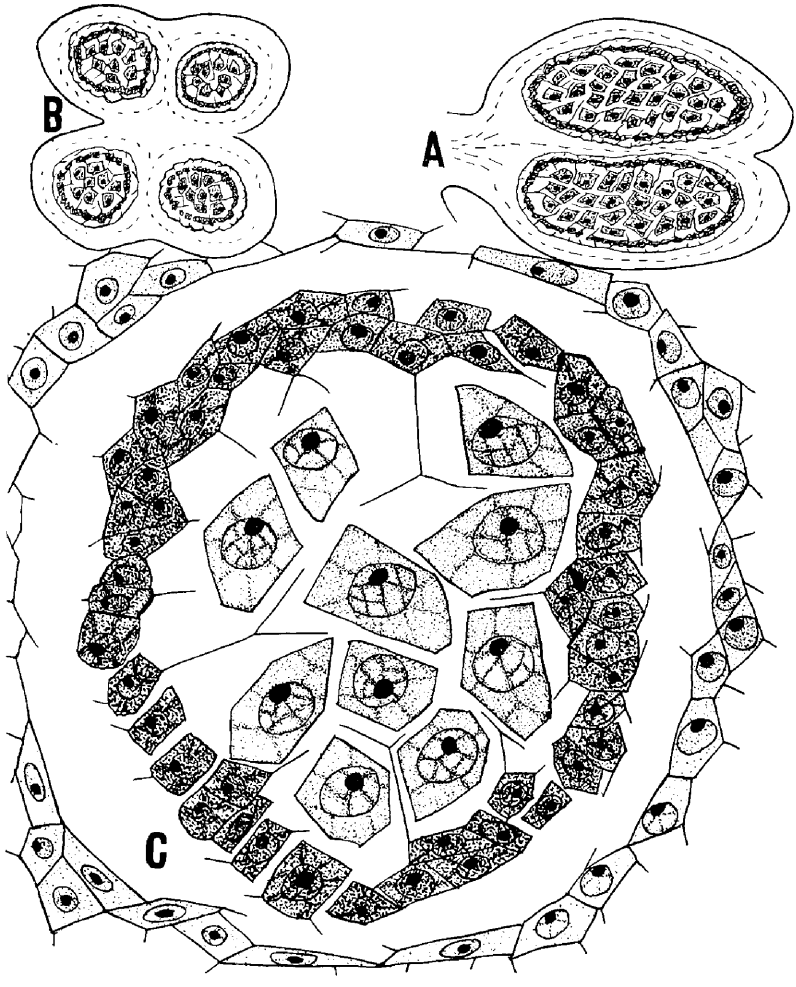

FIGURE 16.—A, Camera lucida drawing of longitudinal section of an anther of the Alley variety on April 1 showing the mother cells breaking apart and the tapetum cells rapidly disintegrating, × 110; B, A shown in cross section; × 110; C, enlargement of A; × 1003. The Frotscher variety reached this same stage on April 15

the sporangium. Rounding up occurs about 21 days before pollen shedding and reduction division follows immediately.

Division of the mother cells and formation of tetrads apparently require only a few hours and the entire process seems to go to completion in an anther at a specific time on a single day. (Fig. 18.)

TETRAD

It is during the heterotypic and homotypic divisions that the first abnormal behavior has been observed. The appearance of all of the mother cells is normal, and they seem very uniform in cell contents, staining reaction, and size and shape. (Figs. 2, 14, and 19.) In the process of division various types of abnormalities occur. Dividing cells were found in the Frotscher variety April 26 at 9 a. m. Practically all steps in the process of heterotypic and homotypic divisions were present in a single anther. In the formation of new nuclei the organization of the chromatin results in nuclei of various sizes and

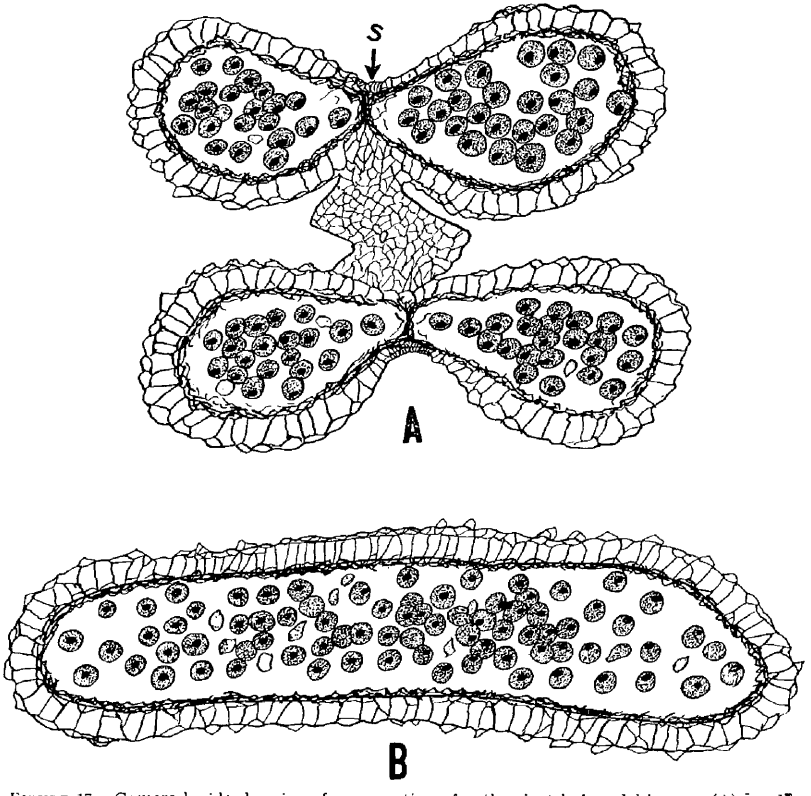

FIGURE 17.—Camera lucida drawing of cross section of anther just before dehiscence (A), and a tangential longitudinal section of the same (B); stomium at *s*. Stuart variety, May 13. × 110

density as determined by the intensity of staining. Because of the minuteness of the chromosomes the number has not been definitely determined. In most cases the haploid number was found to be 12, in others only 10. In some cases where the nucleus was in the anaphase stage of the first division, one or two chromosomes were lagging slightly, but in some of the more advanced stages they had completely caught up with the other chromosomes.

Both the successive and simultaneous methods of division of the mother cells are common in pecans, producing bilateral and tetrahedral arrangements, respectively, of the microspores. (Figs. 20, and 21.) In the bilateral arrangement the spindles lie in the same or

in perpendicular planes, and no wall is formed between the successive divisions. The two arrangements are about equally common. No case has been observed where the four microspores were in a row within the tetrad wall, nor has a failure of four microspores to form been found. Small supernumerary microspores are often seen which, according to Shoemaker (*19*), may be the result of small nuclei formed from lagging chromosomes, or, according to Coulter and Chamberlain (*7*), from division of one or more members of the tetrad. Small microspores are especially numerous in lots of pollen containing a

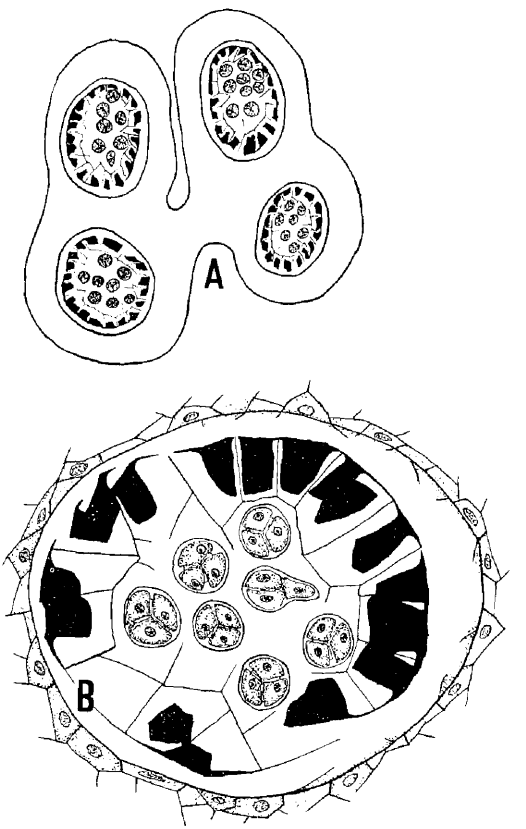

FIGURE 18.—A, Camera lucida drawing of cross section of an anther of the Frotscher variety on April 26 showing the tetrad stage with fragments of the tapetum cells; × 82; B, enlargement of A; × 400. Alley reached this stage on April 10

high percentage of defective grains and are almost always partially or totally void of cell contents. A few oversized grains were found, and the cell contents of most of them appeared normal. The normal number of pores is three, and variance is very rare with normal or undersized microspores; however, oversized microspores often have five or six pores.

At maturity some of the microspores are without nuclei and others without either nuclei or cytoplasm. The lack of protoplasmic contents is the basis of the lactic acid method of determining the percent-

age of defective pollen. By the use of this method defective grains were found in all lots examined, the number ranging from 0.3 to 81.7 per cent.

Flowers of the Beverage variety were found in the tetrad stage on April 24, and counts were made as follows: Four anthers taken from the base of a catkin contained 294, 373, 331, and 357 tetrads, respectively; and four anthers taken from the middle of the catkin contained 380, 380, 317, and 488 tetrads. Since each anther contains four pollen sacs, and each tetrad contains four microspores, the above figures also

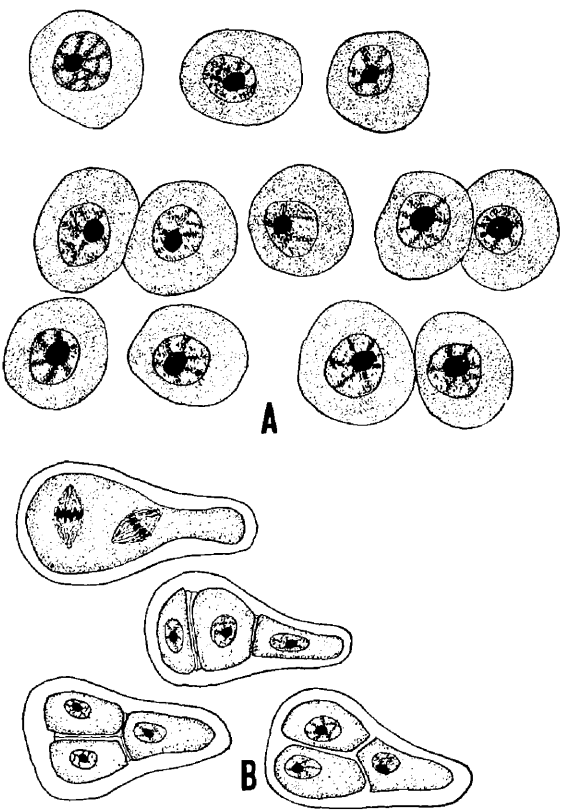

FIGURE 19.—A, Camera lucida drawing of mature mother cells that appear normal; B, mother cells with abnormal microspores. × 850

represent the average number of pollen grains per pollen sac in the respective anthers, the general average being 365.

Liberation of the microspores (pollen grains) occurs from 15 to 20 days before the pollen is shed. Because of the disintegration of the tapetum and surrounding cells, the pollen sac is only partially filled with pollen. Upon liberation from the tetrad wall the grains wander independently within the pollen sac and rapidly enlarge in size, but as the cavity continues to enlarge, owing to the continued disintegration of the surrounding sterile cells, the pollen sac remains only partially filled.

DEHISCENCE OF ANTHERS

The fusion of the four pollen sacs into two loculi by the dissolution of the separating wall occurs only a few days before the opening of

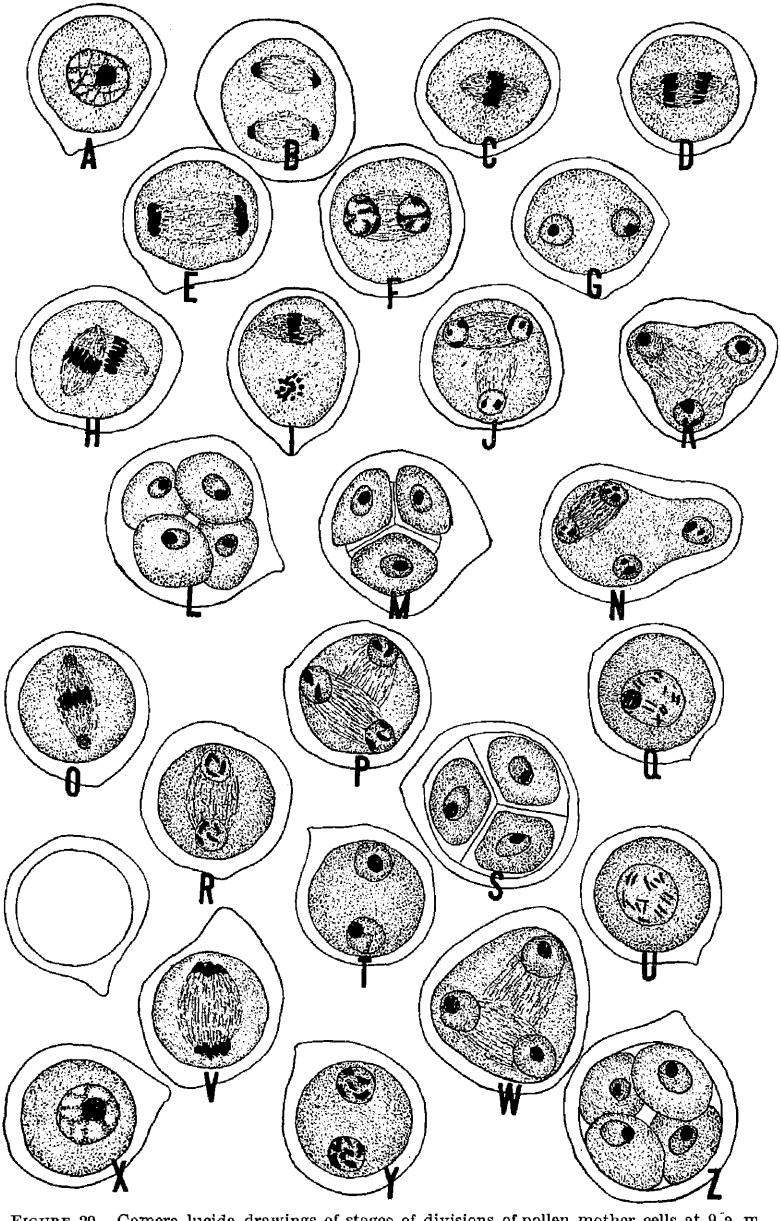

FIGURE 20.—Camera lucida drawings of stages of divisions of pollen mother cells at 9 a. m., April 26; Frotscher variety. Note formation of both bilateral and tetrahedral arrangements of microspores; all had reached the tetrad stage the following day. × 850

the anther on either side by means of a stomium, with consequent liberation of pollen grains at maturity. (Figs. 15 and 17.) The anther wall is two cells thick, with fragments of one or more additional

layers. The opening of the anther is due to drying of the exterior or epidermal cells and consequent contraction of the outer in proportion to the inner surface. Reclosing of anthers occurs when moisture is

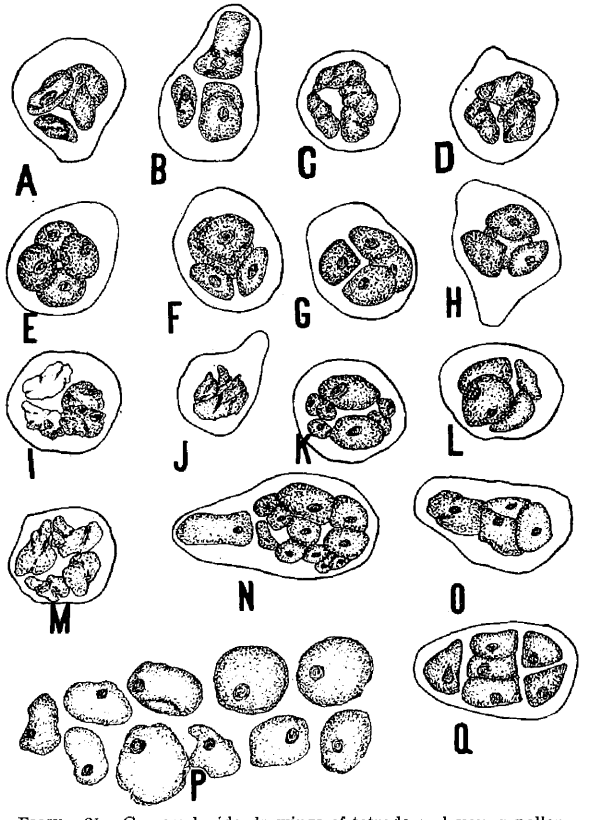

FIGURE 21.—Camera lucida drawings of tetrads and young pollen grains: E, F, G, and H appear normal; K, N, and Q contain more than four microspores; at P are shown pollen grains two days after liberation from the mother cell wall, some of the grains being defective. × 450

restored. No opening takes place in an atmosphere more than about 85 per cent saturated. (Tables 2 and 3.)

TABLE 2.—*Data on dehiscence of ripe anthers when placed in moist and dry air at different temperatures*

Temperature	Humidity	Condition of anthers
3° C	Moist	Failed to dehisce.
	Dry	Dehisced in 5 days.
22° C	Moist	Failed to dehisce.
	Dry	Dehisced in 2 days.
23° C	Moist	Failed to dehisce.
	Dry	Dehisced in 18 hours.
32° C	Moist	Failed to dehisce.
	Dry	Dehisced in 6 hours.

TABLE 3.—*Summary of data or pollen dissemination at various times of day in 26 varieties of pecans in the Georgia Experiment Station orchard*

Date	6. p. m. to 6 a. m.				6 a. m. to 9 a. m.				9 a. m. to 12 m.				12 m. to 3 p. m.				3 p. m. to 6 p. m.			
	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter
1929	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*
Apr. 18																	66	68	1	39
Apr. 19	68	66	1	11	75	67	12	24	65	72	8	17	57	77	4	18	86	60	3	1
Apr. 20	60	86	3	32	65	74	6	24	61	77	11	54	61	77	7	71	51	70	10	10
Apr. 21	70	51	10	7	87	69	15	6	71	77	4	6	65	81	3	50	67	75	2	7
Apr. 22	75	67	2	4	70	72	14	31	65	74	15	84	69	72	11	69	78	65	3	74
Apr. 23	65	78	3	65	67	64	12	30	60	67	7	61	58	72	5	38	72	64	4	37
Apr. 24	64	72	4	63	81	64	4	27	70	72	6	128	66	77	7	248	76	70	1	129
Apr. 25	70	76	1	26	97	64	6	0	94	73	11	10	60	80	14	67	73	77	8	81
Apr. 26	77	63	8	5	81	62	9	18	76	64	8	0	75	63	8	0	80	59	4	28
Apr. 27	59	80	4	10	81	60	5	63	78	64	4	2	76	68	5	17	86	62	4	6
Apr. 28	62	86	4	13	83	72	12	0	81	74	13	37	90	72	8	13	98	61		0
Apr. 29	61	98		0	90	68	3	0	70	75	3	13	59	77	6	8	50	78	3	4
Apr. 30	78	50	3	10	74	63	7	16	83	70	2	24	83	80	4	10	90	64	4	1
May 1	64	90	4	0	90	72	6	0	81	77	9	2	83	76	7	16	81	70	3	0
May 2	70	81	3	0	78	74	11	4	90	67	12	9	77	58	12	1	90	49	10	0
May 3	49	90	10	0	72	55		0	69	62		2	68	62	10	1	75	58	2	0
May 4	58	75	2	0	75	62	5	0	65	70	7	1	86	62	2	2	65	64	4	0
May 5	64	65	4	0	60	77	6	1	75	73	9	1	75	75	4	1	78	72	3	6
May 6	72	78	3	0	85	73	8	0	82	76	9	1	71	80	9	5	69	79	3	2
May 7	79	69	3	0	90	72	9	0	87	75	10	2	84	73	11	4	87	69	10	5
May 8	69	86	3	2	80	68	10	17	72	74	3	4	93	64	6	0	93	64	2	0
May 9	64	93	2	0	95	62	8	0	90	66	6	0								
Average	66.6	76.2	3.9	11.9	79.8	67.3	8.4	12.4	75.5	71.4	7.9	21.8	72.8	72.3	7.2	32.0	76.7	66.6	4.2	20.2
1928																				
May 2					36	70	1	0	33	76	5	34	45	80	3	41	55	66	2	43
May 3	58	77	1	7	42	77	4	52	42	82	5	49	41	85	4	9	50	74	2	4
May 4	60	73	2	2	39	78	5	12	36	82	5	22	31	86	2	35	56	77	2	13
May 5	66	61	2	3	59	76	10	196	69	82	6	50	45	81	2	81	59	76	4	125
May 6	57	88	3	136	79	62	12	16												
May 7	49	86			85	52			93	50			93	49	9					
May 8													77	57	4	3	87	52	4	4
May 9	44	93	6	2	72	59	8	1	38	72	4	50	40	75	6	88	44	66	2	21
May 10	53	75	3	6	52	71	3	9	38	81	2	16	26	84	6	28	59	69	0	17
May 11	60	68	2	10	39	78	6	7	32	84	7	4	30	88	7	6	39	78	1	6

TABLE 3.—*Summary of data or pollen dissemination at various times of day in 26 varieties of pecans in the Georgia Experiment Station orchard*—Continued

Date	6 p. m. to 6 a. m.				6 a. m. to 9 a. m.				9 a. m. to 12 m.				12 m. to 3 p. m.				3 p. m. to 6 p. m.			
	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter	Relative humidity	Temperature	Wind velocity	Pollen per square centimeter
1928	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*	*Per cent*	*° C.*	*Miles per hour*	*Grains*
May 12	60	78	8	10	71	67	1	8	62	67	12	10	55	69	7	19	48	70	4	38
May 13	58	61	7	14	74	62	10	10	60	71	11	8	53	72	8	4	64	62	5	2
May 14	53	81	6	2	45	67	8	4	42	73	10	5	48	77	8	6	59	68	6	2
May 15	58	88	6	4	68	66	8	1	41	76	7	6	47	77	7	10	56	68	4	9
May 16	60	81	1	6	72	70	5	20	65	73	8	14	69	72	7	151	72	69	2	48
May 17	64	90	4	9	81	70	2	90	67	78	1	122	91	74	2	3	51	69	1	6
May 18	68	90	2	1	74	75	6	32	64	80	6	486	81	86	7	381	59	77	2	57
May 19	69	90	1	4	78	76	4	7	73	81	7	121	98	72	3	90	------	------	------	10
May 20	67	90	4	------	82	73	7	1	71	78	8	4	67	78	6	16	78	73	4	8
May 21	65	95	4	1	83	69	6	0	67	77	6	1	68	76	6	5	70	75	3	1
May 22	65	95	2	0	85	66	1	0	77	71	4	0	------	------	------	0	------	------	------	------
Average	59.7	82.1	3.6	12.8	65.8	69.2	5.6	24.5	56.3	75.5	6.3	55.7	58.2	75.6	5.5	51.4	59.2	69.9	2.5	23.0
1927																				
Apr. 22	------	------	------	------	------	------	------	6	------	------	------	7	------	------	------	3	------	------	------	6
Apr. 23	------	------	------	1	------	------	------	1	------	------	------	------	------	------	------	2	------	------	------	1
Apr. 24	------	------	------	0	------	------	------	0	------	------	------	1	------	------	------	2	------	------	------	5
Apr. 25	------	------	------	1	------	------	------	------	------	------	------	3	------	------	------	0	------	------	------	0
Apr. 26	------	------	------	0	------	------	------	1	------	------	------	0	------	------	------	1	------	------	------	4
Apr. 27	------	------	------	2	------	------	------	0	------	------	------	1	------	------	------	5	------	------	------	13
Apr. 28	------	------	------	6	------	------	------	3	------	------	------	2	------	------	------	18	------	------	------	55
Apr. 29	------	------	------	------	------	------	------	51	------	------	------	------	------	------	------	------	------	------	------	------
May 4	------	------	------	------	------	------	------	17	------	------	------	82	------	------	------	62	------	------	------	16
May 5	------	------	------	3	------	------	------	1	------	------	------	15	------	------	------	10	------	------	------	------
May 6	------	------	------	------	------	------	------	3	------	------	------	------	------	------	------	26	------	------	------	14
Apr. 7	------	------	------	19	------	------	------	12	------	------	------	1	------	------	------	------	------	------	------	------
Average	------	------	------	4	------	------	------	8.5	------	------	------	12.4	------	------	------	14.3	------	------	------	12.7

An idea of the maturity of pollen can be had from the stiffness of the catkin. A catkin that would not shed pollen within 48 hours is relatively stiff; one that would normally shed within 12 hours in warm, sunny weather is limber. Within two days after pollen is shed the catkin becomes dry, very stiff, and falls to the ground.

The stage of maturity of pollen can best be determined by the color of the anthers. From the time of emerging from the bud scales until 48 hours before pollen would normally shed under suitable conditions, the anthers are the same color as the bracts and leaves. After this time, however, the green color gradually disappears and the anthers take on more and more of the orange-yellow color of the pollen. When fully ripe the anther is pale greenish yellow. If conditions are suitable, dehiscence will occur immediately, but if the temperature is too low, or the humidity above about 85 per cent, the catkin may remain for five days or more without falling to the ground.

The rapidity of opening of ripe anthers depends somewhat on temperature but largely on the relative humidity of the air. On a warm, sunny day a single anther will completely shed its contents in an hour after opening begins. Due to variations in catkins, twigs, trees, and varieties under the same conditions, a single catkin will shed pollen for 2 days, a single tree will shed pollen for 5 or 6 days, a single variety will furnish pollen for 10 or 12 days, and a collection of three or more varieties of each group will furnish pollen for about 3 weeks.

If wilting was produced very rapidly by the high temperatures immediately after the catkins were removed from the tree, opening did not occur. Likewise, if the relative humidity was above 82 per cent the anthers remained closed. Partly or completely open anthers closed in a few minutes when subjected to a relative humidity of more than 90 per cent. Catkins that had fallen from the tree and become dry reabsorbed moisture and the anthers closed in the presence of high humidity.

Records taken in the orchard at 3-hour intervals showed that the time of most rapid shedding of pollen varied from day to day, depending on the temperature and the relative humidity of the air. No shedding occurred when the relative humidity was above 85 per cent. On some days the peak was reached before 9 a. m. On other days it was delayed until after 3 p. m., but it never occurred between 6 p. m. and 6 a. m. The temperature, relative humidity, and wind-velocity data in Table 3 were taken at the end of the time of exposure of the slides, and in some cases do not accurately indicate the conditions that prevailed during the period of exposure. The apparatus for catching pollen (fig. 1, A) remained in the same place throughout the pollen-shedding season for three years.

In 1928, in the midst of the pollen-shedding season, a period of 64 hours elapsed with no shedding because of rain. Three 24-hour periods occurred during the same season when no pollen was shed. As a result of low temperatures and high humidity in 1929, not more than 5 days out of 21 covered in the pollen-shedding season were really favorable for pollen dissemination. The relative humidity and temperature reached during clear nights with a gentle breeze were not sufficient to cause anthers already open to close, but they did prevent the further opening of anthers. A dew or rain which caused

the relative humidity to rise above 90 per cent caused all anthers to close and delayed shedding until several hours after sunrise on the following morning.

Since very high or very low temperatures do not occur at the time that pecans shed their pollen, the influence of temperature and wind velocity is chiefly indirect in regulating the relative humidity of the air. Though there is no opening of anthers during damp, rainy weather, immature anthers continue to reach the stage of maturity, therefore a period of high relative humidity followed by a prolonged period of low relative humidity is accompanied by the shedding of a very large quantity of pollen for several hours.

Close observation and careful records kept for a number of years (*30*) show that the length of the receptive period of the pistillate flowers is as responsive to conditions of temperature and humidity as that of staminate flowers. The same conditions which delay the shedding of pollen also prolong the receptive period of the stigmas. Trees on which the stigmas became receptive at a time unfavorable for pollen shedding and favorable for pollen germination did not have a heavy May "drop."

The effect of high humidity is mainly that of retardation. Instances have been observed in which stigmatic surfaces dried as much in 24 hours under dry, windy conditions as they did in two weeks of damp, cloudy weather. During a prolonged drought the susceptibility of the stigmatic surfaces to rapid drying increases as the receptive stage is approached, and on the second day after becoming receptive the roughened surface darkens, shrinks, and dies.

In rainy weather the receptive stage is reached very gradually, and after about 10 days the stigmatic surfaces show symptoms of drying. If cloudy weather continues the stigmas do not become completely dry for about 15 days. The normal period of receptivity of a single flower is about five days.

Observations of about 25 varieties for seven years show that during rainy seasons there are usually enough sunny days to effect pollination; and that dry weather, though optimum for pollen dissemination often precedes a heavy May drop. Data in this paper indicate that the degree of humidity optimum for pollen shedding is not sufficient to cause germination of pollen; also a low relative humidity markedly reduces the viability of the pollen.

Table 4 shows the amount of pollen caught on greased slides at various distances from pollen-shedding trees. The apparatus was always kept on the leeward side of the trees. The difference between the amount of pollen caught at a height of 10, 20, or 30 feet is insignificant. The amount of pollen that will be blown by the wind depends on the humidity, temperature, and velocity of the circulating air. The path of the pollen from a small group of trees is narrow at a given time, but the horizontal direction of air currents is likely to vary greatly during the 10 or 12 days of pollen shedding of a single variety. Throughout the southeastern part of the United States winds from the east and south are somewhat moist and are not as conducive to pollen shedding as winds from the west and northwest.

TABLE 4.—*Amount of pollen blown by a 2 to 5 mile-per-hour wind from a 20-year-old pecan orchard of Mobile, Stuart, and Teche varieties, 1927 and 1928*

Distance from orchard	Height from ground	Year and time of day	Pollen per square centimeter	Day after pollen shedding began
		1927		
	Feet		*Grains*	
500 feet	10	2 p. m. to 5 p. m.	70.7	First.
Do	20	do	80.7	Do.
Do	30	do	92.6	Do
Do	10	6 p. m. to 7 a. m.	0.8	Do.
Do	20	do	3.7	Do.
Do	30	do	4.5	Do.
800 feet	10	8 a. m. to 11 a. m.	137.8	Second.
Do	20	do	162.5	Do.
Do	30	do	156.5	Do.
Do	10	do	3.8	Fourth.
Do	20	do	5.2	Do.
Do	30	do	5.6	Do.
1,000 feet	10	11 a. m. to 2 p. m.	19.3	Do.
Do	20	do	28.0	Do.
Do	30	do	28.3	Do.
Do	10	2 p. m. to 5 p. m.	8.3	Do.
Do	20	do	16.6	Do.
Do	30	do	15.5	Do.
Do	10	5 p. m. to 7 a. m.	13.1	Do.
Do	20	do	21.4	Do.
Do	30	do	19.1	Do.
Do	10	7 a. m. to 11 a. m.	11.1	Fifth.
Do	20	do	13.2	Do.
Do	30	do	13.5	Do.
Do	10	11 a. m. to 2 p. m.	64.9	Do.
Do	20	do	107.1	Do.
Do	30	do	134.7	Do.
Do	10	2 p. m. to 5 p. m.	28.6	Do.
Do	20	do	44.8	Do.
Do	30	do	39.7	Do.
		1928		
3,000 feet	20	2 p. m. to 2 p. m.[a]	10.6	First.
Do	30	do	8.4	Second.
Do	10	do	10.6	Third.
Do	20	do	13.3	Fourth.
Do	30	do	13.6	Fifth.

[a] 24 hours.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*

1926

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
Tifton, Ga.:						
Alley	Apr 27		Apr. 30		1	Yes.
Big Z	Apr. 29		Apr. 28		2	Yes.
Bradley	do		Apr. 26		2	Yes.
Curtis	Apr. 28		Apr. 28		2	Yes.
Delmas	May 1		Apr. 27		2	Yes.
Frotscher	May 4		Apr. 29		2	Yes.
Mobile	Apr. 26		Apr. 28		1	Yes.
Moneymaker	May 1		Apr. 27		2	Yes.
Moore	Apr. 26		Apr. 26		1	Yes.
Nelson	do		Apr. 27		1	Yes.
Pabst	do		Apr. 28		1	Yes.
President	Apr. 28		Apr. 30		2	Yes.
Schley	Apr. 29		Apr. 28		2	Yes.
Stuart	Apr. 30		Apr. 29		2	Yes.
Summers	Apr. 26		Apr. 28		1	Yes.
Teche	Apr. 30		do		2	Yes.
Van Deman	Apr. 28		Apr. 25		2	Yes.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*—Continued

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
1927						
Tifton, Ga.:						
Alley	Apr. 21		Apr. 29		1	No.
Big Z	Apr. 29		May 7		2	No.
Bradley	Apr. 21		Apr. 28		2	No.
Curtis	Apr. 22		May 3		2	No.
Delmas	Apr. 26		Apr. 29		2	Yes.
Frotscher	Apr. 12		Apr. 18		2	Yes.
Mobile	Apr. 29		May 6		1	No.
Moneymaker	Apr. 18		Apr. 21		2	Yes.
Moore	Apr. 21		Apr. 26		1	Yes.
Nelson	Apr. 9		Apr. 22		1	No.
Pabst	Apr. 18		Apr. 29		1	No.
President	Apr. 21		Apr. 26		2	Yes
Schley	do		Apr. 29		2	No.
Success	do		do		1	No.
Teche	do		do		2	No.
Van Deman	Apr. 26		do		2	Yes.
1928						
Tifton, Ga.:						
Alley	Apr. 30		May 5		1	Yes.
Big Z	Apr. 28		May 7		2	No.
Bradley	do		May 5		2	No.
Mobile	Apr. 30		May 3		1	Yes.
Moneymaker	do		May 5		2	Yes.
Moore	Apr. 28		May 2		1	Yes.
Nelson	Apr. 21		Apr. 28		1	No.
Pabst	Apr. 30		May 2		1	Yes.
President	do		May 5		2	Yes.
Schley	Apr. 28		May 2		2	Yes.
Success	do		May 5		1	No.
Teche	Apr. 30		do		2	Yes.
1929						
Tifton, Ga.:						
Alley		Apr. 20	Apr. 22		1	No.
Big Z	Apr. 22			Apr. 20	2	No.
Bradley	do				2	No.
Curtis	Apr. 24			Apr. 21	2	No.
Delmas		Apr. 18		Apr. 20	2	Yes.
Frotscher	Apr. 23			Apr. 21	2	No.
Mobile		Apr. 19	Apr. 22		1	No.
Moneymaker	Apr. 21		Apr. 21		2	Yes.
Moore		Apr. 18	Apr. 20		1	No.
Nelson		Apr. 22	Apr. 25		1	No.
Pabst		Apr. 21	Apr. 24		1	No.
President	Apr. 20			Apr. 20	2	Yes.
Rome		Apr. 18	Apr. 22		1	No.
Schley	Apr. 21		Apr. 21		2	Yes.
Stuart	Apr. 24			Apr. 21	2	No.
Success		Apr. 18	Apr. 22		1	No.
Summers		Apr. 19	Apr. 21		1	No.
Teche	Apr. 23			Apr. 20	2	No.
Van Deman	do		Apr. 22		2	Yes.
Williams	do		Apr. 23		2	Yes.
Cordele, Ga.:						
Frotscher	Apr. 20		Apr. 20		2	Yes.
Mobile	Apr. 20			Apr. 29	1	No.
Moore	Apr. 18		Apr. 20		1	Yes.
Nelson		Apr. 18	Apr. 21		1	No.
Schley	Apr. 20		Apr. 20		2	Yes.
Stuart	do		do		2	Yes.
Van Deman	Apr. 23			Apr. 19	2	No.
Albany, Ga.:						
Schley	Apr. 22			Apr. 25	2	Yes.
Stuart	do			Apr. 26	2	Yes.
Van Deman	do			Apr. 25	2	Yes.

TABLE 5.—*Dates on which pollen was shed and on which pistillate flowers were receptive of commercial varieties of pecans in leading pecan-growing centers of southeastern United States*—Continued

1929

Location and variety of pecan	Pollen shedding		Pistils receptive		Group	Self-pollinated
	Began	Ended	Began	Ended		
Monticello, Fla.:						
Curtis	Apr. 21		Apr. 19	Apr. 25	2	Yes.
Frotscher	Apr. 24			Apr. 22	2	No.
Mahan	Apr. 21			Apr. 23	2	Yes.
Moore		Apr. 18	Apr. 21		1	No.
Russell	Apr. 20			Apr. 22	2	Yes.
Schley	Apr. 22		Apr. 22		2	Yes.
Stuart	Apr. 24		Apr. 23		2	Yes.
Teche	Apr. 22		Apr. 21		2	Yes.
Experiment, Ga.:						
Alley	Apr. 18	Apr. 24	Apr. 28	May 8	1	No.
Appomattox	Apr. 28	May 3	Apr. 22	May 1	2	Yes.
Beverage	Apr. 18	Apr. 24	do	May 6	1	Yes.
Bradley	Apr. 29	May 7	do	Apr. 26	2	No.
Centennial	Apr. 18	Apr. 25	Apr. 25	May 3	1	No.
Curtis	Apr. 30	May 12	Apr. 23	May 2	2	Yes.
Delmas	do	May 7	Apr. 21	do	2	Yes.
Indiana	May 6	May 12	Apr. 30	May 8	2	Yes.
Jerome	Apr. 21	Apr. 30	Apr. 24	May 9	1	Yes.
Mantura	Apr. 18	Apr. 23	Apr. 22	May 1	1	Yes.
Mobile	do	Apr. 24			1	No.
Moore	do	Apr. 23	Apr. 22	Apr. 30	1	Yes.
Nelson	do	Apr. 24	do	do	1	Yes.
Pabst	Apr. 20	do			1	No.
Randal	Apr. 18	Apr. 27				No.
Robson	do	Apr. 24	Apr. 23	May 3	1	Yes.
Rome	Apr. 20	Apr. 30	Apr. 24	May 9	1	Yes.
San Saba	Apr. 21	Apr. 26	do	May 8	1	Yes.
Schley	Apr. 29	May 7	Apr. 22	May 3	2	Yes.
Stuart	do	May 8	do	May 7	2	Yes.
Success	Apr. 22	Apr. 26	Apr. 25	May 9	1	Yes.
Teche	Apr. 29	May 7	Apr. 20	Apr. 24	2	No.
Van Deman	May 1	May 8	Apr. 21	Apr. 28	2	No.
Thomasville, Ga.:						
Frotscher	Apr. 22			Apr. 21	2	No.
Mobile		Apr. 18	Apr. 22		2	No.
Stuart	Apr. 22			Apr. 24	2	Yes.
Schley	do			do	2	Yes.
Athens, Ga.:						
Alley		May 3	May 6	May 13	1	No.
Delmas	May 6	May 15	May 3	May 11	2	Yes.
Frotscher	Apr. 31	May 6	May 1	May 9	2	Yes.
Jerome		do	May 5	May 13	1	Yes.
Mobile		do			1	No.
Nelson		May 3			1	No.
Pabst	May 1	May 9	May 6	May 13	1	Yes.
Success	May 7	May 13			1	Yes.
Schley	May 6	do	May 2	May 10	2	Yes.
Stuart	do	May 14	May 3	May 12	2	Yes.
Teche	May 7	do	May 2	May 11	2	Yes.
Van Deman	May 6	May 15	Apr. 30	May 9	2	Yes.
Raleigh, N. C.:						
Appomattox	May 3	do	Apr. 29	May 10	2	No.
Bradley	May 6	do		May 1	2	Yes.
Curtis	May 10	May 23	May 1	May 19	2	Yes.
Delmas	May 9	May 19	May 3	May 11	2	Yes.
Frotscher	May 7	May 21		May 3	2	No.
Georgia		May 6	May 5	May 23	1	Yes.
Krakezy		May 1	do	May 21	1	No.
Louisiana	May 6	May 15		May 8	2	Yes.
Manture		May 5	May 5	May 18	1	No.
Mobile		May 1	May 1	May 23	1	No.
Moneymaker	May 5	May 16		May 3	2	No.
Pabst	May 1	May 15	May 3	May 23	1	Yes.
President	May 10	May 23	May 1	May 11	2	Yes.
Russel	May 9	May 19	May 3	May 10	2	Yes.
Schley	May 10	May 23	May 1	May 17	2	Yes.
Sovereign		May 3	May 3	May 24	1	No.
Stuart	May 5	May 21	May 1	May 13	2	Yes.
Success	do	May 18	May 3	May 24	1	Yes.
Teche	May 7	May 22	May 1	May 15	2	Yes.
Van Deman	May 10	May 21	do	May 10	2	No.

Table 5 contains incomplete data on dates of beginning and ending of pollen shedding and beginning and ending of receptivity of stigmas of 142 varieties from eight pecan-producing sections in these States.

In varieties of Group 1 there were 31 instances of homogamy and 25 instances of complete dichogamy, all of the latter being protandrous. In varieties of Group 2 there were 57 instances of homogamy and 29 instances of dichogamy—11 instances of protandry and 18 instances of protogyny.

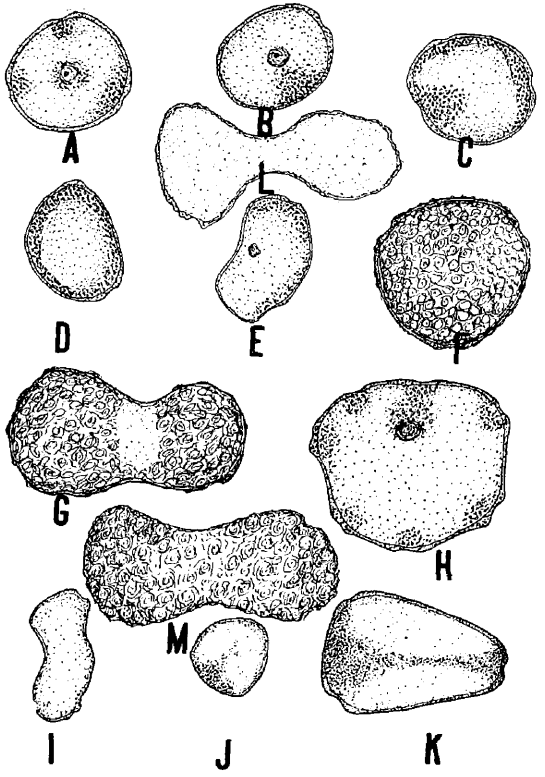

FIGURE 22.—Camera lucida drawings of pollen grains in lactic acid mounts: A, B, C, D, E, H, I, J, and K contain a small amount of finely granular cytoplasm; G and M are elongated grains; H, a grain with seven pores; F, a normal grain. × 850

EXAMINATION OF POLLEN

The writer has confirmed Stuckey's (*23*) observation that "in size, shape and general character, the pollen of the two groups of varieties of pecans differ almost none." However, the grains are not "rather flattened," as he described them.

Dry pollen grains from a single variety vary slightly in size and shape, are sculptured, and uniformly pale yellow. They are spherical but become shrunken immediately after shedding, and when exposed to very dry air the shrinking increases. Fresh pollen taken from an atmosphere 80 per cent saturated at 21° C. and placed in an oven at 32° lost 5.5 per cent moisture; when placed in an oven at 60° it lost 10 per cent. Dry grains containing no protoplasm can not be distinguished from those with protoplasm. Though the increased amount of shrinkage which accompanies the absence of protoplasm

may serve as a means of identifying certain defective grains, many abnormal grains appear normal when dry.

Normal pollen grains mounted in distilled water swell immediately and turn dark. Grains without protoplasm fail to swell, and grains containing protoplasm in less than the normal amount swell so that they are indistinguishable from normal grains.

When mounted in lactic acid, normal grains become light cream in color and spherical in outline, and assume in one minute an appearance distinct from defective grains. The latter either fail to swell and remain opaque, or swell and become almost transparent. The

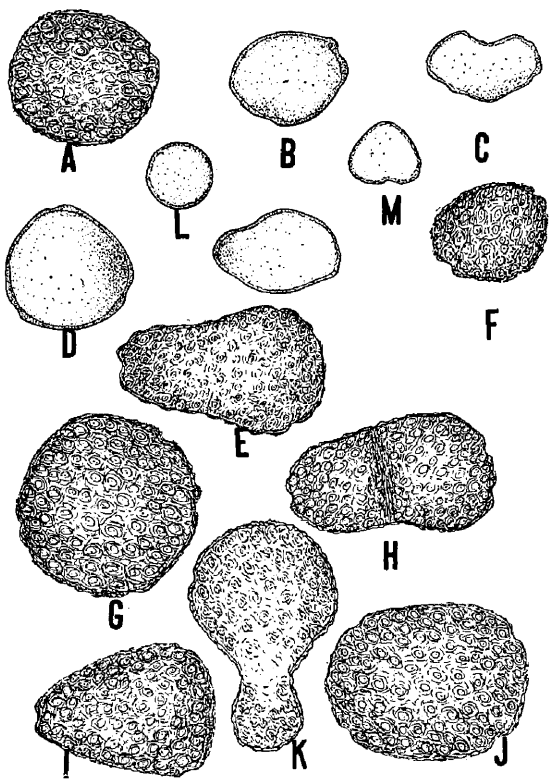

FIGURE 23.—Camera lucida drawings of pollen grains in lactic acid mounts: A, Normal grain with coarsely granular cytoplasm (Jerome); B, C, D, L, and M contain no cytoplasm (Jerome); F, a grain of less than normal size (Jerome); E, G, H (Jerome), I, K (Beverage), grains enlarged, abnormally shaped. × 800

lack of normal protoplasmic content in certain grains is clearly evident. Some grains are without either protoplasm or pores, indicating that abnormality began early in the development; others contain a small amount of protoplasm and one or more pores; still others have the normal number of pores and swell normally, but the protoplasm granules are very fine and sufficiently different from normal grains to be termed defective.

A single pollen grain observed in lactic acid amount is spherical with a roughened surface. When the percentage of normal grains is high they are extremely uniform in size, but if the percentage of

defective grains is high there are numerous large, small, and odd-shaped grains. (Figs. 22 and 23.) A normal grain is about 50 microns in diameter (*23*) with a wall about 2 microns in thickness. There is no appreciable difference in the size of pollen of any of the varieties studied except variations due to a large amount of defective pollen.

PERCENTAGE OF DEFECTIVE POLLEN

Table 6 contains data on the amount of defective pollen found when 169 lots were examined by the lactic acid method. The total number of grains examined was 169,000.

TABLE 6.—*Percentage of defective pollen as found by counting 1,000 grains in lactic acid mounts, 1928 and 1929* [a]

1928

Pecan variety and vigor	Average defective grains	Percentage of defective grains found at position indicated			Pecan variety and vigor	Average defective grains	Percentage of defective grains found at position indicated		
		Apex	Middle	Base			Apex	Middle	Base
Alley	19.5				Pabst:				
Atlanta	3.0	3.7	2.5	2.9	Vigorous	4.5	6.7	2.9	4.0
Beverage	6.7				Nonvigourous	4.4			
Bradley	8.3	10.2	8.9	6.3	Randal	5.9			
Centennial	35.1	33.5	34.5	37.1	Robson	7.1			
Curtis	6.3	8.6	6.7	4.1	Rome	29.6			
Delmas	5.4	4.4	7.6	4.1	San Saba:				
Frotscher	7.9	9.2	8.1	6.3	Vigorous	10.3	14.7	5.4	11.3
Indiana	6.4	6.0	7.3	6.0	Nonvigorous	13.4			
Jerome:					Schley	14.3	12.8	16.0	14.0
Vigorous	27.2	32.4	37.1	42.2	Stuart	46.6	81.7	27.6	20.6
Nonvigorous	35.2	31.6	33.5	40.5	Teche	7.5	8.0	5.1	9.4
Mantura	71.2				Unknown	13.1	12.2	9.4	17.6
Moneymaker	23.8	10.5	44.8	16.3	Van Deman	29.2	35.6	44.5	37.5
Moore	20.2				Wauchenah	5.8	5.7	6.3	5.3
Nelson	20.2								

1929

Pecan variety	Location	Vigor	Average defective grains	Percentage of defective grains found at position indicated		
				Apex	Middle	Base
Alley	Experiment, Ga	Medium	10.2			
Appomattox	do	do	.3			
Beverage	do	do	.9	1.4	1.4	0
Bradley	do	do	6.9	7.7	4.4	8.5
Centennial	do	do	31.7			
Curtis	do	do	4.6			
Delmas	do	Vigorous	7.0			
Ga. Giant	Tifton, Ga	do	10.4			
Indiana	Experiment, Ga	Medium	3.3	4.3	2.3	4.4
Jerome	do	do	3.3			
Mahan	Monticello, Fla	Vigorous	12.0			
Mantura	Experiment, Ga	Medium	20.0			
McAlister	do	do	8.2			
Mobile	do	do	1.1	.8		1.4
Do	Cordele, Ga	do	8.4			
Do	Milner, Ga	Vigorous	1.7			
Do	Barnsville, Ga	do	3.7			
Do	do	do	2.6			
Do	do	do	8.0			
Do	do	Medium	5.4			
Do	do	do	3.6			
Do	do	Not vigorous	3.0			
Do	do	do	2.3			

[a] Pollen from various pecan varieties when examined in 1929, 13 years after collection, showed the following percentages of defective grains: Frotscher, 4.5; Moneymaker, 6.2; Pan American, 9.8; President, 4.1; Teche, 30.6; Van Deman, 3.

TABLE 6.—*Percentage of defective pollen as found by counting 1,000 grains in lactic acid mounts, 1928 and 1929*—Continued

1929

Pecan variety	Location	Vigor	Average defective grains	Percentage of defective grains found at position indicated		
				Apex	Middle	Base
Moore	Experiment, Ga.	Medium	6.3	9.8	2.5	6.7
Nelson	do	do	5.6	5.4	4.6	6.8
Do	Barnsville, Ga.	do	12.3			
Pabst	Experiment, Ga.	do	1.0	1.1	.9	.9
President	Tifton, Ga.	do	6.5			
Robson	Experiment, Ga.	do	2.7	2.2		3.2
San Saba	do	do	5.2	2.9	3.7	7.8
Schley	do	do	5.9	6.5	5.6	5.7
Do	Baconton, Ga.	Vigorous	6.0			
Do	Griffin Ga.	Not vigorous	37.5			
Do	Tifton, Ga.	Vigorous	6.0			
Summers	do	do	16.4			
Stuart	Experiment, Ga.	do	7.2			
Success	do	do	3.7			
Teche	do	do	1.2			
Van Deman	do	do	41.0	36.6	46.0	41.5
Do	do	Not vigorous	32.1			
Do	Tifton, Ga.	Vigorous	46.0			
Do	Cordele, Ga.	do	9.6			
Do	Baconton, Ga.	Medium	26.0			
Wauchenah	Experiment, Ga.	Not vigorous	11.2			
Williams	Tifton, Ga.	Vigorous	10.4			
		Fertilizer				
Stuart	Experiment, Ga.	None	5.4			
Do	do	Complete	3.0			
Do	do	High P	5.6			
Do	do	High N	8.6			
Do	do	High K	7.2			
Do	do	Stable manure	6.5			

In 1928 pollen was much more plentiful in the orchards than in 1929, and the percentage of defective grains was about twice as high. The differences between the percentages of defective pollen shed from the apex, middle, and base of the same catkins is negligible. The Centennial and Mantura were the only varieties that produced pollen more than 19 per cent of which was defective in 1928 and 1929, and the Pabst was the only variety that produced pollen less than 5 per cent of which was defective in both years. The variation in percentages of defective pollen of the Mobile variety, taken from four localities and from trees of unequal vigor in 1929, is very small; also the variation in percentages of defective pollen taken from Stuart trees which received different kinds of fertilizers is insignificant. On the other hand, Schley pollen from nonvigorous trees at Griffin had about six times as high a percentage of defective pollen as that gathered at Experiment, Baconton, or Tifton, and Van Deman pollen from vigorous trees at Cordele had about one-third as high a percentage of defective pollen as that from trees of medium vigor at Baconton and about one-fourth as high as that from vigorous trees at Experiment or Tifton.

Table 7 shows the magnitude of variation of defective grains in successive lots of 100, that is, the percentage of defective grains in successive lots. The table includes 6 varieties and 12 lots of 1,000 grains each which were shown in Table 6. In general, it may be said that in counting 1,000 grains in lots of 100 grains each, the

lowest percentage of defective grains is about half that of the highest percentage.

TABLE 7.—*Magnitude of the variation (per cent) of defective grains as counted in successive lots of 100*

Percentage of defective grains at position mentioned in pollen from—									Percentage of defective grains in pollen from—		
Centennial			Jerome			Schley			Alley	Mantura	Curtis
Apex	Middle	Base	Apex	Middle	Base	Apex	Middle	Base			
34	32	30	33	33	44	11	20	13	30	57	54
30	34	32	19	35	38	13	14	21	16	72	51
35	30	33	36	47	42	9	16	15	16	80	52
35	34	44	24	37	40	15	15	12	13	57	53
32	38	41	40	33	45	10	22	9	17	74	54
33	40	44	30	35	43	16	17	8	19	74	77
43	29	42	36	46	47	10	13	16	25	68	60
34	36	34	31	34	54	15	17	13	21	77	56
45	34	33	40	39	39	17	14	18	17	28	56
19	38	38	35	30	30	12	12	14	21	81	48
33.5	34.5	37.1	32.4	37.1	42.2	12.8	16	14	19.5	71.2	56.1

The data recorded in Table 8 were obtained when the rubber-ring cells were used, as previously described.

TABLE 8.—*Pollen germination under varying conditions*

SERIES 1 [a]

Sugar used	Strength	Germination	Tube length	Grains bursting
	Per cent			
Maltose	20	0.5	Short	Few.
Do	15	.5	do	Do.
Do	10	1.0	do	Do.
Do	5	1.0	do	Do.
Sucrose	20	25.0	Long	None.
Do	15	30.0	do	Do.
Do	10	50.0	do	Do.
Do	5	40.0	do	Do.
Lactose	20	50.0	do	Do.
Do	15	40.0	do	Do.
Do	10	30.0	do	Do.
Do	5	30.0	do	Do.
Glucose	20	15.0	Short	Few.
Do	15	10.0	do	Do.
Do	10	5.0	do	Do.
Do	5	2.0	do	Do.
Fructose	20	0	do	Do.
Do	15	.5	do	Do.
Do	10	1.0	do	Do.
Do	5	1.0	do	Do.
Galactose	20	20.0	do	Do.
Do	15	15.0	do	Many.
Do	10	10.0	do	Do.
Do	5	5.0	do	Do.

[a] Using 2 per cent agar, pollen stored in laboratory for 24 hours, germination at 25° C., 4 drops of water in bottom of cell.

TABLE 8.—*Pollen germination under varying conditions*—Continued

SERIES 2[b]

Reagent added	Amount used	Germination	Tube length	Grains bursting	Remarks
	Per cent	*Per cent*		*Per cent*	
Asparagine	1.0	75	Long	10	
Do	.5	80	do	10	
Do	.1	85	do	10	
Tannic acid	1.0	0		0	
Do	.5	0		0	
Do	.1	0		0	
Peptone	1.0	20	Long	10	
Do	.5	50	do	15	
Do	.1	75	do	20	
Sodium hydroxide	1.0	0		0	Stained brown.
Do	.5	0		0	Do.
Do	.1	0		0	Do.
Do	.05	20	Long	20	
Do	.025	30	do	20	
Check		75	do	10	

SERIES 3[c]

Storage conditions	Storage period	Germination	Tube length	Grains bursting
	Hours	*Per cent*		
Fresh		70.0	Very long	None.
Laboratory	48	25.0	Medium	Do.
Desiccator	48	0		Do.
Moist chamber	48	30.0	Medium	Do.
25° C., dry	48	20.0	do	Do.
On ice	48	40.0	Short	Few.
Laboratory	72	15.0	do	Many.
Moist chamber	72	20.0	do	Do.
25° C., dry	72	0		None.
On ice	72	30.0	Short	Many.
Laboratory	96	.2	do	Few.
Moist chamber	96	10.0	do	Do.
On ice	96	20.0	do	Many.
Laboratory	120	0		None.
Moist chamber	120	5.0	Short	Do.
On ice	120	10.0	do	Many.
Moist chamber	144	0		None.
On ice	144	2.0	Short	Many.
In mail, moist	48	25.0	do	Do.
In mail, semimoist	48	20.0	do	Do.
In mail, dry	48	5.0	do	Do.
In mail, moist	192	5.0	do	Do.
In mail, semimoist	192	2.0	do	Do.
In mail, dry	192	0		Few.

[b] Using 10 per cent sucrose, 1½ per cent agar, Success pollen stored in laboratory for 24 hours, germination at 22° C., cell half filled with water.

[c] Using 20 per cent sucrose, 2 per cent agar, germination at 25° C., 4 drops of water in cell.

TABLE 8.—*Pollen germination under varying conditions*—Continued

SERIES 4 [d]

Pecan variety	Period of storage	Percentage germination under storage conditions indicated									
		32° C.		23° C.		22° C.		In orchard		5° C.	
		Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist
	Hours										
Schley	24	0	0	0	65	0	65	30	64	50	65
Stuart	24	0	0	0	80	0	80	45	80	65	80
Van Deman	24	0	0	0	50	0	50	25	45	45	50
Schley	48	0	0	0	50	0	55	0	60	25	60
Stuart	48	0	0	0	65	0	70	0	75	35	75
Van Deman	48	0	0	0	30	0	40	0	45	20	45
Schley	72	------	------	------	0	------	20	------	30	0	55
Stuart	72	------	------	------	0	------	25	------	45	0	65
Van Deman	72	------	------	------	0	------	10	------	20	0	40
Schley	96	------	------	------	------	------	0	------	15	------	30
Stuart	96	------	------	------	------	------	0	------	25	------	40
Van Deman	96	------	------	------	------	------	0	------	10	------	25
Schley	120	------	------	------	------	------	------	------	0	------	3
Stuart	120	------	------	------	------	------	------	------	0	------	5
Van Deman	120	------	------	------	------	------	------	------	0	------	0
Beverage	120	0	0	0	0	0	0	0	0	0	0
Nelson	120	0	0	0	0	0	0	0	0	0	3
Robson	120	0	0	0	0	0	0	0	0	0	2
Centennial	120	0	0	0	0	0	0	0	0	0	0
Alley	120	0	0	0	0	0	0	0	0	0	1

SERIES 5 [e]

Germinating temperature	Percentage germination of—			Germinating temperature	Percentage germination of—		
	Schley	Stuart	Van Deman		Schley	Stuart	Van Deman
3° C	0	0	0	23° C	65	80	50
22° C	60	75	50	32° C	0	0	0

[d] Using 20 per cent sucrose, 1½ per cent agar, germination at 23° C., cells half filled with water (percentage germination).

[e] Using 10 per cent sucrose, 1½ per cent agar, cell half filled with water, fresh pollen.

Media containing 10 per cent sucrose, 1½ per cent agar, plus either one of the following formed a precipitate, failed to solidify at 20° C., and was not used: United States Pharmacopoeia citric acid, 1, 0.5, and 0.1 per cent; 91 per cent lactic acid, 0.5 and 0.1 per cent; United States Pharmacopoeia tannic acid, 1 per cent.

Under suitable conditions pollen began to germinate in 1½ hours and completed germination in 12 hours, but 14 to 18 hours were required for pollen tubes to reach full length before bursting. If allowed to remain longer than about 18 hours the tubes burst and emptied their contents into the surrounding medium. (Fig. 24.)

Bursting of pollen tubes is distinct from "pseudo germination" or bursting of ungerminated grains as described by Andronescu (*1*) and as used in Table 8. If the conditions remain favorable for growth all of the pollen tubes will burst in about 30 hours.

No tubes in artificial media have been found to branch, as occurs in the tube growth in the pistils (*31*); nor has any of the germination percentages equaled the percentage of normal pollen as shown by counts in lactic acid.

Pollen failed to germinate in pure water, or in any concentration of agar which did not solidify at 25° C. Satisfactory results were obtained with 1½ or 2 per cent agar when sugar was added. No germination was obtained when no water was placed in the cell to provide moisture for the pollen. From four to eight drops of water were found best for this; less than this amount did not keep the pollen sufficiently moist for germination, and much more than this caused excessive bursting of grains.

Data in Table 8 show that of the six sugars used in the media for germinating pollen, lactose and sucrose gave highest percentage

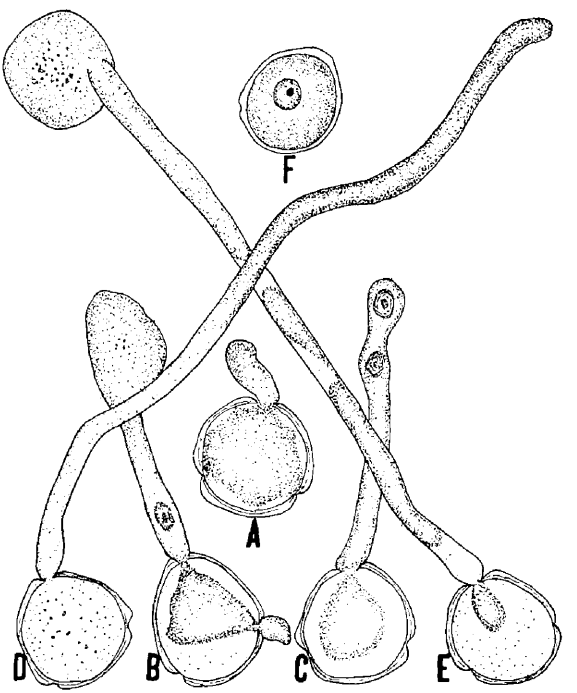

FIGURE 24.—Camera lucida drawing of stages in the germination of pollen grains on sugar-agar medium: A, Normal germination; B, formation of two tubes from a single pollen grain; B and E, swelling at end of tube which may later burst; C, two nuclei in the pollen tube; D, a normal tube; F, section of a pollen grain 10 days before shedding. × 750

germination and least bursting of the grains; galactose and glucose produced fair germination; and fructose and maltose caused an extremely low percentage germination and a high percentage of bursting.

One-tenth of 1 or one-half of 1 per cent asparagine when added to the medium produced a slight increase in percentage of germination; 1 per cent neither increased nor decreased the percentage of germination. More than 0.1 per cent of peptone caused a decrease in percentage of germination. Tannic acid prevented germination when 1, 0.5, or 0.1 per cent was added to the medium. Sodium hydroxide decreased germination when as low as 0.025 per cent was added to the medium, and more than 0.1 per cent prevented germination.

Pollen was stored under ten temperature and humidity conditions. That stored under both moist and dry atmospheric conditions at 32° C. lost its vitality in 24 hours. That stored at either 23° or 22° in a dry atmosphere did not germinate after 24 hours, but other lots germinated after being stored for 48 and 72 hours, respectively, under moist conditions. That stored dry at 5° germinated after 48 hours, and that stored moist germinated after 96 hours. No temperature and humidity condition was found under which pollen could be stored for longer than 96 hours with certainty of germination. The optimum temperature for germination was found to be about 23° C.

RELATION OF SIZE OF CROP PRODUCED IN ONE YEAR TO NUMBER OF FLOWERS PRODUCED THE FOLLOWING YEAR

In Table 9 is shown the relation between the size of crop of nuts of one year and the size of crop of staminate and pistillate flowers of the next year. In order that the data from trees of different varieties and ages might be comparable, each tree was rated and placed in one of six groups. The summary of all varieties shows that a large or very large crop of nuts is followed by a somewhat reduced crop of both staminate and pistillate flowers the following season; and no crop or a fair, poor, or very poor crop of nuts is followed by a large crop of both staminate and pistillate flowers.

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*

[A=very large crop; B=large crop; C=fair crop; D=poor crop; E=very poor crop; F=no crop]

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Alley	7	0.6 pound	D	C	B
Do	7	0.1 pound	D	C	B
Do	7	do	D	C	B
Do	18	34 pounds	C	A	D
Do	20	44 pounds	C	A	D
Appomattox	18	37 pounds	B	F	B
Atlanta	20	57 pounds	A	F	F
Beverage	20	21 pounds	D	A	A
Bradley	20	58 pounds	B	C	A
Centennial	20	3 pounds	E	B	C
Curtis	18	29 pounds	B	F	E
Delmas	12	10 pounds	D	A	A
Do	18		D	B	A
Do	18		D	B	A
Do	18		D	B	A
Do	20		E	A	A
Do	20		E	A	A
Do	20		E	A	A
Frotscher	20	110 pounds	A	F	F
Do	20	100 pounds	A	F	F
Do	16	3,259 nuts	A	E	A
Do	16	4,895 nuts	A	E	A
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Do	20		B	C	B
Indiana	12	5 pounds	E	A	B
Do	12	6 pounds	E	A	B
Jerome	20	44 pounds	C	A	A
Mantura	20	34 pounds	C	A	F

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Mobile	18	63 pounds	A	E	F
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18		F	A	A
Do	18	3,202 nuts [a]	F	A	A
Do	18	2,938 nuts [a]	A	A	D
Do	18	4,704 nuts [a]	A	A	C
Do	18	856 nuts	D	A	A
Do	25	22,735 nuts [a]	A	F	F
Do	22	15 pounds	D	B	B
Do	11	41 pounds	A	F	F
Do	11	54 pounds	A	F	F
Do	11	28 pounds	A	F	F
Do	11	29 pounds	A	F	F
Do	11	25 pounds	A	F	F
Do	11	33 pounds	A	F	F
Do	11	43 pounds	A	F	F
Moneymaker	20	46 pounds	C	F	F
Moore	12	21 pounds	B	A	A
Do	12	6 pounds	E	A	A
Nelson	20	110 pounds [a]	A	B	F
Do	18	66 pounds [a]	A	B	F
Do	19		A	E	B
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	F
Do	19		A	E	B
Do	16	1,504 nuts [a]	A	A	B
Do	16	1,354 nuts [a]	A	A	C
Do	16	1,779 nuts [a]	A	A	B
Pabst	20	91 pounds	A	B	F
Randal	20	96 pounds	A	F	F
Robson	20	48 pounds	C	B	D
Rome	12	11 pounds	C	B	B
Do	20	40 pounds	C	B	B
San Saba	18	25 pounds	C	B	B
Schley	12	55 pounds	A	E	E
Do	18		A	C	A
Do	18		A	C	A
Do	18		A	C	A
Do	8	17 pounds	B	C	C
Do	9	22 pounds	B	D	E
Do	18		A	C	A
Do	18		A	C	A
Do	18		A	B	A
Do	18		A	B	B
Do	18		A	B	B
Do	22		D	B	B
Do	22		D	B	B
Do	22		D	B	B
Do	22		D	C	B
Do	22		E	C	B
Do	16	615 nuts	B	D	B
Do	18	689 nuts	C	D	B
Stuart	20	2 pounds	E	A	B
Do	18	2,161 nuts	C	B	B
Do	18	1,961 nuts	C	B	B
Do	18	999 nuts	D	B	B
Do	18	2,136 nuts	C	B	B
Do	18	1,273 nuts	C	B	B
Do	18	992 nuts	D	B	B
Do	18	1,533 nuts	C	B	B
Do	16	852 nuts	C	C	B

[a] Nuts poorly filled.

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1928 crop of nuts	1928 crop rating	Rating of 1929 crop of—	
				Catkins	Pistillate flowers
	Years				
Stuart	16	717 nuts	C	A	B
Do	16	1o4 nuts	D	A	A
Do	18	763 nuts	D	A	A
Do	18	607 nuts	D	A	A
Do	18	625 nuts	D	A	A
Do	18	663 nuts	D	B	A
Do	11	3 pounds	E	A	B
Do	11	2 pounds	E	A	B
Do	11	7 pounds	E	A	B
Do	11	1 pound	E	A	B
Do	11	4 pounds	E	A	B
Do	11	17 pounds	C	A	B
Do	11	1 pound	E	A	B
Do	11	4 pounds	E	A	B
Do	11	3 pounds	E	A	B
Do	11	7 pounds	E	A	B
Do	11	16 pounds	C	A	B
Do	11	3 pounds	E	A	B
Do	11	13 pounds	D	A	B
Do	11	9 pounds	D	A	B
Do	11	12 pounds	D	A	B
Do	11	17 pounds	C	A	B
Do	11	17 pounds	C	A	B
Do	11	6 pounds	E	A	B
Do	11	9 pounds	D	A	B
Do	11	1 pound	E	A	B
Do	11	16 pounds	C	A	B
Do	11	9 pounds	D	A	B
Do	11	9 pounds	D	A	B
Do	11	6 pounds	E	A	B
Do	11	6 pounds	E	A	B
Do	11	17 pounds	C	A	B
Do	11	6 pounds	E	A	B
Do	11	8 pounds	D	A	B
Do	11	11 pounds	D	A	B
Do	11	16 pounds	C	A	B
Do	11	8 pounds	D	A	B
Do	11	2 pounds	E	A	B
Success	12	4 pounds	E	A	A
Teche	20	55 pounds	B	D	D
Do	20	81 pounds	A	F	F
Do	20	61 pounds	B	D	F
Do	20	71 pounds	A	F	F
Do	18	258 nuts	E	B	A
Do	18	1,083 nuts	C	B	A
Do	18	1,167 nuts	C	C	A
Do	18	434 nuts	D	B	A
Do	11	24 pounds	B	F	C
Do	11	21 pounds	B	D	C
Do	11	18 pounds	B	E	C
Do	11	8 pounds	C	D	D
Do	11	18 pounds	B	E	F
Do	11	15 pounds	C	D	F
Do	11	7 pounds	B	B	F
Do	11	24 pounds	C	C	F
Do	11	20 pounds	A	A	F
Van Deman	20	19 pounds	C	A	F
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		C	A	C
Do	19		E	A	A
Do	19		E	A	A
Wilson	12		C	A	C
Do	12		C	A	C

TABLE 9.—*Relation between the size of crop of nuts of one year and the production of catkins and pistillate flowers the following year*—Continued

Pecan variety	Age of tree	1926 crop rating	Rating of 1927 crop of—		Pecan variety	Age of tree	1926 crop rating	Rating of 1927 crop of—	
			Catkins	Pistillate flowers				Catkins	Pistillate flowers
	Years					*Years*			
Mobile	9	A	F	F	Stuart	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Do	9	A	F	F	Do	9	C	A	A
Stuart	9	C	A	A	Do	9	C	A	A
Do	9	C	A	A	Teche	9	C	A	F
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	C	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	F
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	B
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	C
Do	9	C	A	A	Do	9	C	A	F

SUMMARY OF ALL VARIETIES

Previous year's crop of nuts	Current year's crop of—											
	Catkins						Pistillate flowers					
	A	B	C	D	E	F	A	B	C	D	E	F
56 A's	5	6	7	0	14	24	10	7	1	1	2	35
27 B's	2	0	15	5	2	3	2	14	4	1	2	4
71 C's	52	13	2	3	0	1	24	23	11	5	0	8
31 D's	16	14	1	0	0	0	12	19	0	0	0	0
29 E's	26	2	1	0	0	0	9	19	1	0	0	0
6 F's	6	0	0	0	0	0	6	0	0	0	0	0

DISCUSSION

The general course of development of the pollen of the pecan is the same as that of other fruits. The fact that floral differentiation occurs a year before the pollen sheds shows that either the quantity or the quality of pollen may be influenced by the condition of the trees during the summer, fall, or winter previous to the shedding of pollen. On the other hand, pistillate flower differentiation occurs only about four months before the flowers become receptive. Therefore it would be expected that the condition of the tree during the previous year would influence staminate flower development much more than it would pistillate flower development.

Irregularities and abnormalities were found in the development of pollen in both groups of varieties. In a few cases there were rather high percentages of defective pollen. However, in view of the rather universal abundance of catkin formation, and therefore of pollen, it seems unlikely that pollen defects or impotence are factors of im-

portance in limiting the setting of fruit, except in cases of an isolated tree or variety, and then only when conditions are such as to cause a failure of staminate flowers to develop.

On the other hand, the more or less complete dichogamy that characterizes the pecan may occasion pollination difficulties. This is accentuated by the fact that pollen shedding is practically inhibited when the humidity remains above a certain point for any considerable period. It is still further accentuated by the fact that the period of receptivity of the stigmas is greatly reduced if the weather is very dry. In selecting varieties, therefore, the question of securing proper pollination should be considered. For practical purposes it seems that at least two varieties of each group should be included in a commercial planting. This would provide for at least one variety to shed pollen early in the season and at least one variety to shed late.

It also seems that the number of trees of either of these two varieties could be reduced to one-twentieth of the total number of trees.

SUMMARY AND CONCLUSION

Catkin primordia are differentiated in lateral buds on new shoots throughout the growing season. In varieties of Group 1, anthers are differentiated in the fall of the year in which the catkin primordia are formed; in varieties of Group 2 anthers are differentiated early the following spring.

No abnormal behavior was observed in the development of catkin primordia, individual flower primordia, archesporial-cell stage or the mother-cell stage, but abnormalities occurred in all varieties studied during the reduction-division stage.

The smear method for counting the number of tetrads per anther, and the lactic acid method for determining the percentage of defective grains of pollen, have been successfully applied to pecan pollen studies. A method for quantitatively catching pollen from the air at various distances from pollen-shedding trees and at various heights from the ground was developed.

Though an entirely satisfactory method for germinating pecan pollen has not been developed, much was learned about the temperature, humidity, and nutritional requirements for germination on artificial media. The longevity of pollen was found to be about equal to or less than the period of receptivity of the stigmas, which indicates that there must be a continuous shedding of pollen throughout the period of receptivity of the stigmas.

When 1,000 grains from each of 169 lots of pollen were examined by the lactic acid method, the defective grains were found to range from 0 to 81.7 per cent. Pollen produced on trees of low vigor or on trees which bore very heavy crops of catkins had a slightly higher percentage of defective grains than pollen produced on trees of high vigor or on trees which had a light crop of catkins.

Records of blooming dates showed that either homogamy, protandry, or protogyny may occur in pecans.

It was found that pollen sheds only when the relative humidity of the air is below about 85 per cent and that practically all shedding occurs between 9 a. m. and sundown.

Conditions which were optimum for pollen shedding were destructive to the vitality of pollen. Optimum conditions for shedding of pollen are those which exist in the orchard on a warm, sunny day;

and optimum conditions for germination are found in an orchard on a warm, dewy night.

From the data contained herein it seems that all of the methods of studying pecans which involve hand pollination, used by the writer and others, have been somewhat at fault in that account was not taken of the fact that during times of low humidity there may be an enormous amount of pollen in the air even at great distances from pollen-shedding trees.

The size of the crop of nuts of one year was found to influence the size of crop of both staminate and pistillate flowers of the following year. A very heavy crop of nuts usually follows and is followed by a lighter crop. Certain varieties of pecan produce a medium-size crop of staminate flowers, pistillate flowers, and nuts each year.

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U. S. GOVERNMENT PRINTING OFFICE: 1930