

T H E S I S

on

A STUDY OF POLLINATION AND  
FERTILIZATION IN THE FILBERT.  
      (Corylus Avellana)      

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A STUDY OF POLLINATION AND FERTILIZATION  
IN THE FILBERT.

Frank J. Rimoldi.

INTRODUCTION.

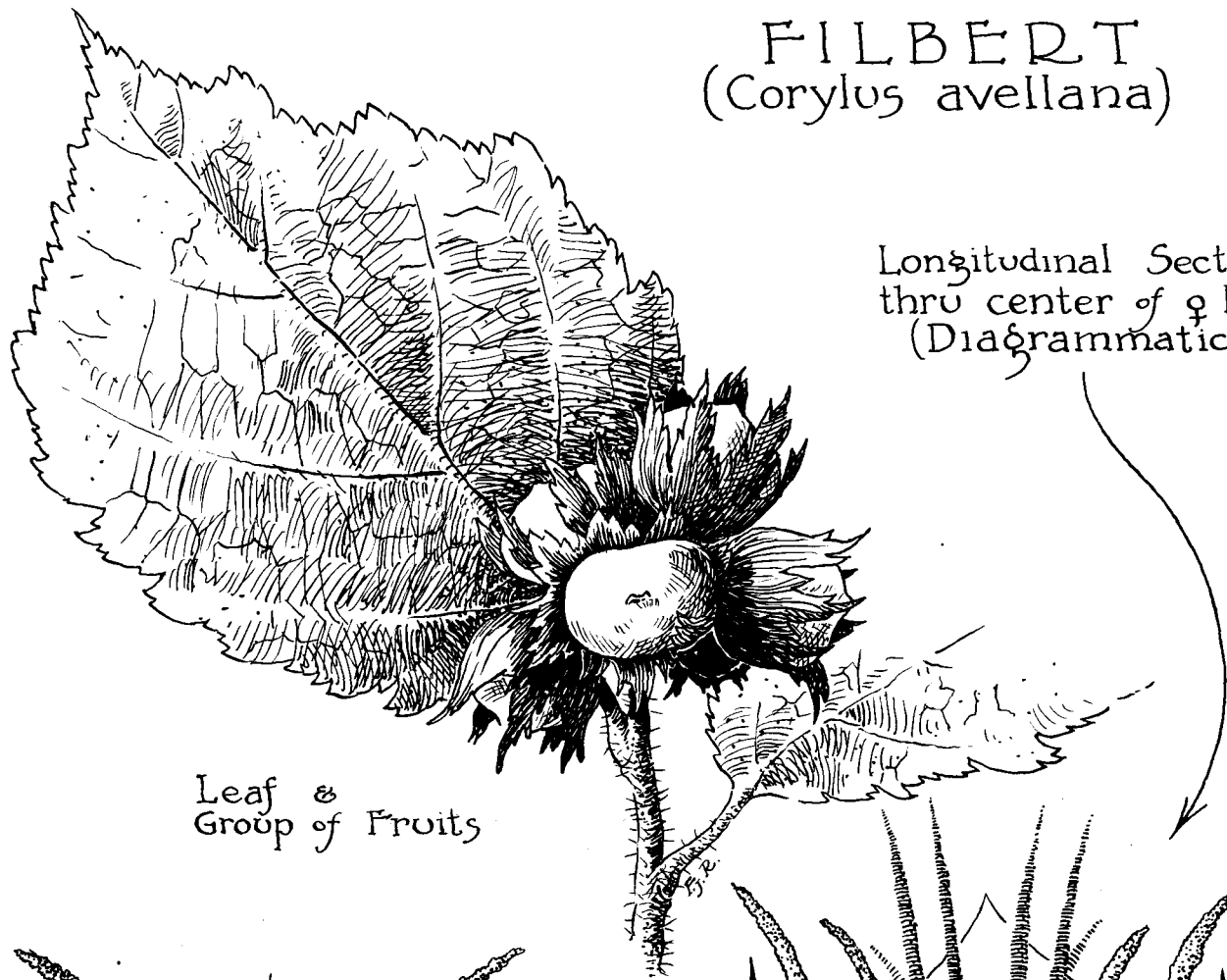
Throughout Southern Europe and the British Isles the filbert (*Corylus*) has been grown from the very earliest times. Methods of its culture has been handed down to the present generation from prehistoric times. The filbert industry has since assumed considerable proportions in that region and the nuts are now exported from there to all parts of the globe.

Examination of the history of the filbert in America indicates that many unsuccessful attempts have been made to introduce the European species into the Atlantic States. These essays were frustrated by the attacks of a fungus (*Cryptosporella anomala*, Sacc.) which was native on the wild hazel (*C. americana*) causing what later became known as "Filbert Blight".

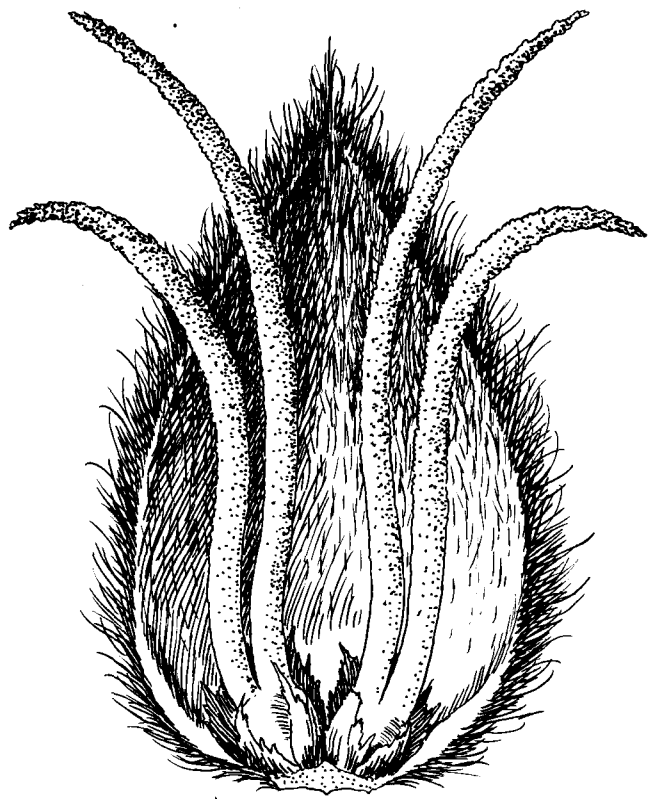
As a result of various trials made during the past twenty-five years, however, we are led to believe that the filbert deserves consideration among the horticultural products worthy of further development and study for the Pacific Northwest. A brief survey of conditions prevailing in the State of Oregon, shows that a large amount of interest has developed in the possibilities of this crop. There are already many bearing filbert orchards in the Willamette Valley,

# FILBERT (*Corylus avellana*)

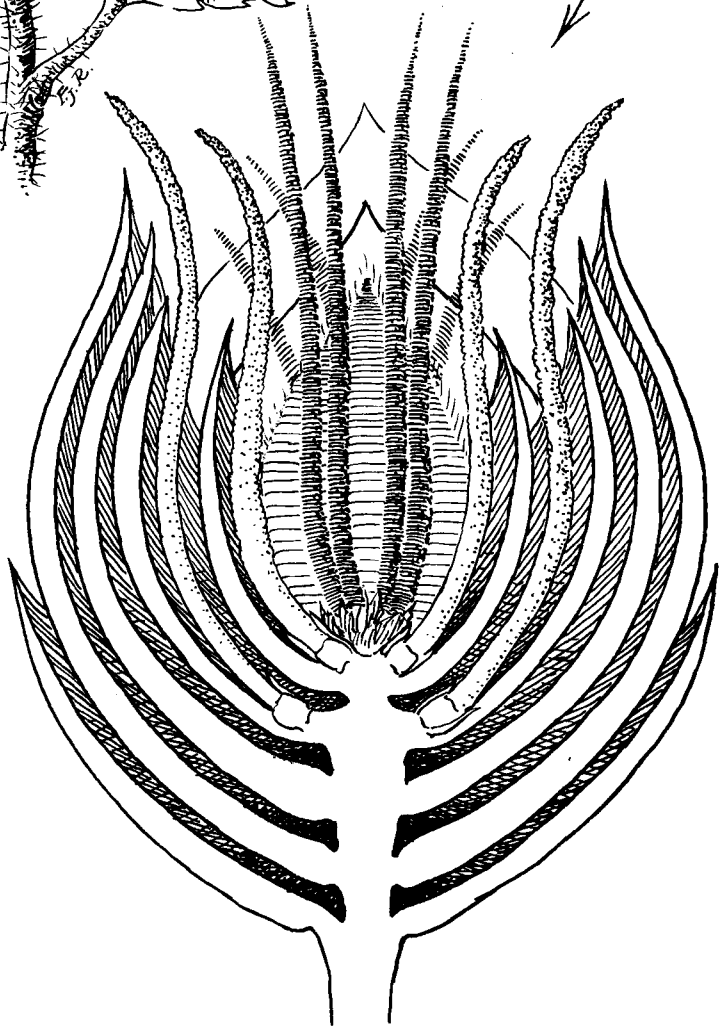
Longitudinal Section  
thru center of ♀ bud  
(Diagrammatic)



Leaf &  
Group of Fruits



Bract with 2 ♀ flowers



and many more are being set out. Many varieties\* which have been selected during these recent years of experimentation, seem to thrive in our soil and climate and quite satisfactorily survive the vicissitudes of our wet winters and dry summers. The problems of heavy and regular bearing, however, still seem to limit the more general planting and cultivation of filberts. The fact that the native hazel (*C. californica*) thrives in this region, together with the knowledge that our climate so nearly approximates that of England, where great quantities of filberts (and cobnuts) are grown, would seem to justify the belief that with the problems of fruitfulness and regularity of bearing solved, this should become an important crop for Oregon.

From the usual experience with the development and adaptation of other fruit crops to new regions, the first phase of the problem we naturally turn to in a case of this kind is that of a study of the mechanism of pollination and fertilization for the genus. Preliminary to the study of this question a brief general questionnaire on the status of filbert growing was sent to many representative filbert growers in Oregon in October 1920. Out of twenty-four replies to this questionnaire, (representing about 100 acres of filberts) eighteen growers believe that pollination and fertilization are the phases of filbert growing upon which more experimental work and study

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\*Practically all European varieties which have been introduced into this country came from *C. avellana* and *C. tubulosa*, the species domesticated from the wild, in Southern Europe.



need to be done at this time. Some growers report a large percentage of empty nuts on certain varieties. More report irregular and shy-bearing as characteristic of others, etc. These data tended to emphasize the necessity for more knowledge on the causes of the phenomenon of sterility or partial sterility, together with the establishment of certain general facts necessary to an intelligent study of the fertilization process in *Corylus* and especially for *C. avellana*. If the work of this first year establishes these working data, it will be well worth while.

A relatively small amount of time was devoted to studying varietal inter-fertility in this project because of:

(1) The greater importance attached to the development of accurate knowledge on the more fundamental mechanism and factors which enter into pollination and fertilization.

(2) The limited number of varieties available at the station orchard for this purpose.

(3) This being a separate problem upon which another member of the staff is now carrying on extensive experiments in various orchards of the state, results of these inter-fertility studies will soon be published. The field crosses made in this project then, are simply to bring out any significant differences in pollinating ability of the ten varieties tested, and possibly correlate these differences with any accompanying characteristics which may manifest in the pollen and stigma studies.

An attempt will be made, as a result of this study,

to answer such questions as:

(A) Relative to Pollen and of Stigmas.

1. What influence has sunlight on pollen germination?
2. Does pollen viability vary at different parts of shedding period?
3. What is the longevity of filbert pollens?
4. What effect has low temperatures (freezing) on both pollen and stigma?
5. What effect has high temperatures (varying humidity) on the pollen?

(B) As a Result of the Histological Study.

6. What is the normal mechanism of fertilization?
  - (a) What becomes of the pollen tube during pre-fertilization period?
  - (b) Are there any varietal differences?

(C) As Result of Varietal Field-Crosses and Observations.

7. What varieties overlap to best advantage for successful pollination? Has this any significance as to inter-fertility?
8. Which varieties seem to be the best pollenizers for Barcelona and DuChilly? Any correlation?
9. Which factors capable of augmenting fruit setting are within control of orchardist?

## REVIEW OF LITERATURE

A complete history of the work on pollination and fertilization would constitute a sizeable book in itself. Only a very brief outline of some of the more important work will here be outlined, by way of general setting: Literature on the

filbert proper, is extremely scant to say the most, and with the exception of the brief, but admirable work of Benson (1) on the Embryology of the Amentiferae (1893, 1905) little of any scientific value has as yet been published on this subject.

Although the phenomenon was doubtless noticed before, it was not generally known until 1793, when Sprengel (2) published his observations, that cross pollination took place in certain plants, and the role played by insects in the crosses. Another investigator, Knight (3) in 1799 came to believe that cross pollination between plants of the same species was nature's normal method, and that, "in no plant does self-fertilization take place for indefinite generations."

Perhaps the first man who really understood the importance of cross pollination was Chas. Darwin. (4) He mentions it in his "Origin of Species (1856)" and considerable popular interest developed subsequent to the publication in 1862 of his "Various Contrivances by which British and Foreign Orchids are Fertilized by Insects". Here he pointed out how "nature abhors perpetual self fertilization", and how in many cases, "it is injurious and results in inferior offspring". Quoting further he observes through the process of evolution, "that plants are endlessly modified to insure cross fertilization". From his observations, Darwin perceived the following laws:

1. Nature abhors perpetual self-fertilization.
2. Continued self-fertilization is injurious and results in inferior and less fertile offspring.
3. Cross fertilization is necessary for the production of healthy seedlings.

4. Plants are endlessly modified to secure this end. Nature, working through almost unlimited time periods, has developed and evolved a nice set of means for bringing about cross fertilization, e.g.

1. By the separation of the sexes (dioecious plants).
2. By special mechanical contrivances which prevent pollen of a flower from getting on its own stigma.
3. By contrivances which favor pollen carrying by insects.
4. By plants producing on distinct individuals, two and sometimes three forms of flowers, with different pistil and stamen lengths, or different kinds of pollen, etc.
5. By difference in the time of maturing of pollen and of stigma in the same flower.
6. By more or less complete sterility of flowers to their own pollen, and a corresponding affinity for pollen of another individual.

Although it has been generally known for many years that orchard fruits are more prolific when varieties are "mixed", that the real cause of barrenness or shy bearing was due to self pollination was not known until Waite's (5) experiments with pear flowers, (1894) when he showed that many varieties of pears require cross pollination to set fruit, while others were capable of complete self fertilization. In concluding he states that although there were slight differences between the crosses, he found the finest specimens of either self-sterile or self-fertile varieties to be the results of crosses.

Beach (6) corroborated these results at about the same time while working on the grape. Waugh (7) showed in 1896, that *Prunus domestica* is more free from defective

pistils than any other plum species. The following year, he showed in a table a strong correlation between defective pistils and reduced size of fruit crop in American plums. Fletcher (8) in 1900 while working extensively on pollination and sterility of the wild Goose Plum sums up his findings thus, "cross-pollination probably gives better results than self-pollination with nearly all varieties". Likewise the work of Powell (9) in 1902 and that of Green, same year, on pears and apples respectively, each add their quota of evidence to the importance of cross-pollination and fertilization.

Later investigations endeavored to get at causes. Cummings (11) in 1904 attributed abnormal fertilization to:

1. Incomplete development of the pollen tubes

- (a) because of impotent pollen or poisonous stigmatic fluid.

- (b) lack of nourishment of pollen tube.

2. Non fusion of nuclei.

In 1909 this Station published the work of Lewis and Vincent on cross-pollination of apples. Out of eighty-seven varieties tested, fifty-nine were found to be self-sterile, while but fifteen were self-fertile. Even these gave better results when crossed. In 1911 Backhouse (13) working with European plums, found that only nine of the twenty-one varieties tested, were self-fertile. He says, "if in one of these self-sterile varieties, the flowers were not pollinated at all, they would fall off from three to four days after opening; while if they are self-pollinated, the fruit may swell until it reaches the size of a pea, but sooner or later drops, usually within a few weeks."

Hooper (14) in 1912 found out of sixty-seven varieties of apples, eleven were self-sterile. Gardner (15) of this Station, recently found that most varieties of sweet cherries are self-sterile, and also that some of the best economic varieties are inter-sterile. On the other hand, Whitten (16) in 1914 confirmed the observations of others on peach pollination. He says, "all the leading varieties of peaches grown on the horticultural grounds, proved to be self-fertile.

In spite of these few exceptions, it is now generally established that not only pollination but cross-pollination and fertilization are essential for any reasonable set in most fruits. Therefore anything which interferes with the normal functioning of either of these processes has a direct and substantial influence on the subsequent crop. In our enthusiasm over the recent revelations on these two of nature's processes, we must not ignore the many other factors which periodically play their parts in various combinations, to successful fruit setting, & not attribute all success or failure to self-pollination or inter-sterile varieties. Brief reference here to some of the many other factors which according to the vagaries of nature may influence fruitfulness, will be timely. Some of these are:

1. It is characteristic and desirable that some varieties naturally drop or "thin" some of the excessive fruits. Otherwise overbearing and breaking of limbs, etc. would result.
2. If previous season was dry, fruit buds are less numerous and weaker than if developed under normal conditions.

3. Extreme winter freezes often kill winter fruit buds.
4. Late spring frosts often occur after blooming time and kill pistils.
5. Scarcity of plant food may limit fruitfulness.
6. Too much food may induce excessive vegetative growth at the expense of fruit bud formation. This and the preceeding situation might be due to unfavorable relations of carbohydrates and nitrogen.
7. Cold rains or low temperatures throughout major portion of blooming and pollination season may reduce crop by:
  - (a) preventing germination of pollen.
  - (b) diluting stigmatic juices.
  - (c) inhibiting bee flights and reducing cross-fertilization.
8. Attacks of fungi; e. g. pedicel infections of Apple Scab fungus. (*Venturia inaequalis*)
9. etc. etc.

Leaving the literature of the general subject of fruit pollination and fertilization, we may now proceed to the more specific; that of pollination and fertilization in the filbert (*Corylus*). Here, as has already been intimated, we meet with a great scarcity of information. In the bibliography (page 55) are enumerated a few books and articles which refer mainly to the classification and cultivation practices of this but, both in this country and abroad. Probably the best systematic treatment which takes up its botany is that of F. Goeschke, "Die Haselnuss".

With the exception of Benson (1) practically everything published on this fruit consists of mere gross observations, or work of an empirical nature on various phases of cultivation. A few quotations and conclusions from some of

these works bearing on sterility may be pertinent here.

W. P. Corsa (18) of U. S. D. A. speaking of European hazels and filberts in 1896 says, "The pistillate blossoms sometimes bloom later in the spring than the staminate ones on the same bush, and in such cases it is necessary to supply pollen from other sources at the proper time to secure a crop of nuts. This the European growers accomplish by hanging twigs of staminate flowers, collected from the wild hazel, on the upper branches of the trees in their hazel orchards". The importance of pollination was early recognized, as here indicated.

E. A. Bunyard (19), an English authority on filberts writing in 1920, says, "Dry frosty weather does no harm, but a constant succession of wet days (during pollination) is a potent cause of crop failure. Judging from large orchards one would assume that the commonly grown varieties are quite self-fertile."

George Dorris (20) a pioneer filbert grower in Oregon, writing in the American Nut Journal (March 1919) devotes considerable space to the question of pollinization. He says, "Whatever variety (filbert) is selected it must be borne in mind that none of the varieties I have mentioned are self-fertile to any but a limited extent. Therefore the different varieties must be so assembled as to assure pollination".

From "Contributions to the "Embryology of the Amniferæ" Part I (1894) and, same, Part II "Carpinus Betulus" (1905) by Benson we find our only real valuable basis and insight into the probable mechanism of the phenomena peculiar to this family. (Betulaceae) Miss Benson's first paper in addi-



tion to summing up the work of such predecessors as Goebel, Schacht, Trent and others, develops considerable data on the maturation, fertilization and embryology of various typical Amentiferae. Her second paper, published in 1905, (in Transactions of Linnean Society of London) deals especially with the course of the pollen tube and double fertilization in *Carpinus Betula*. In these papers she establishes the following characteristics of this group in respect to the pollen tube:

1. Resting Stage.
2. Chalazogamic Route.
3. Branching Tube.

Interesting and suggestive similarities will subsequently be shown to exist in *Corylus avellana*; hence no further elaboration of these points will be undertaken here.

#### LOCATION AND GENERAL METHODS.

The material used in this study was secured from the college filbert orchard. This orchard is in a heavy clay soil, on a rather flat and exposed site of about 250 feet elevation above sea level. Twelve Barcelona, and three DuChilly trees of five to seven years of age were used as the female, or host plants in the crosses. Pollen was used generally from some fifty other trees for the ten varietal pollination tests. The trees chosen were all in fairly good physical condition and vigor, although they still showed effects of the severe freeze of the winter of 1919-20. The orchard is clean cultivated. Tables I and II (accompanying) show range of weather during January and February, or throughout the pollen shedding

T A B L E I.Weather Conditions - Jan. 1 - Feb. 1 - 1921. Corvallis, Ore.

DATE	MAX. TEMP. °F	MIN.	RAIN INCHES	CHARACTER of DAY
Jan. 1	48	43	.22	Cloudy
2	49	48	.82	Part Cloudy
3	49	40	.28	Cloudy
4	54	51	.51	Cloudy
5	54	34	1.32	Trace snow Cloudy
6	36	31	0	Part Cloudy
7	43	32	.57	Trace " Clear
8	43	35	.07	Cloudy
9	37	31	.10	Clear
10	39	26	0	Clear
11	39	25	0	Cloudy
12	43	33	.53	Cloudy
13	48	40	.22	Cloudy
14	51	54	.03	Cloudy
15	50	32	.50	1.75 snow Cloudy
16	40	33	.10	Cloudy
17	40	36	.26	Cloudy
18	40	34	.07	Cloudy
19	43	35	.15	Cloudy
20	44	27	0	Clear
21	40	27	0	Clear
22	34	28	0	Cloudy
23	34	28	0	Cloudy
24	49	33	.17	Part Cloudy
25	47	32	.04	Part Cloudy
26	49	38	0	Clear
27	49	38	.51	Cloudy
28	47	35	0	Part Cloudy
29	50	39	.47	Cloudy
30	47	33	.03	Cloudy
31	50	39	.18	Cloudy
Sum	1386	1070	7.15	1.75
Mean	46.2	35.7		

T A B L E II.Weather Conditions - Jan. 1 - Feb. 1 - 1921, Corvallis, Ore

DATE	MAX. TEMP. °F	MIN.	RAIN INCHES	CHARACTER of DAY
Feb. 1	52	37	.08	Clear
2	32	39	.27	Part Cloudy
3	49	40	.49	Cloudy
4	48	39	.37	Cloudy
5	46	36	.10	Clear
6	49	35	0	Clear
7	48	41	.25	Cloudy
8	52	44	.45	Cloudy
9	56	44	.10	Cloudy
10	56	52	.13	Cloudy
11	57	51	0	Part Cloudy
12	54	38	.32	Cloudy
13	40	35	.45	Cloudy
14	41	33	.11	Trace snow Clear
15	43	31	.09	Trace snow Clear
16	45	35	0	Clear
17	45	26	0	Clear
18	44	28	0	Part Cloudy
19	47	38	.40	Part Cloudy
20	54	38	1.41	Cloudy
21	53	39	0	Clear
22	53	33	0	Part Cloudy
23	60	41	0	Clear
24	64	36	0	Clear
25	61	35	0	Clear
26	64	41	0	Clear
27	63	43	.35	Cloudy
28	55	40	.01	Cloudy
Sum	1449	1068	5.38	
Mean	51.7	38.1		

period. As will readily be seen, cool, wet, cloudy weather is the rule, and sunshine the exception during this period.

The work was divided into three main parts, viz.:

- I. (a) Germination studies of pollen throughout shedding period as to viability, longevity, hardiness.  
(b) Hardiness of stigmas and period of receptivity.
- II. Histological study of pistils, to understand exact mechanism of fertilization, from specimens brought in at regular intervals from pollination period to fruit setting period.
- III. Field studies in cross pollination, sterility and inter-fertility. Record of periods of shedding, receptivity and fertilization. (Parthancarpy)?

#### DETAILED PROCEDURE AND RESULTS.\*

##### I. (a) STUDY OF POLLEN (Viability, Longevity, Hardiness).

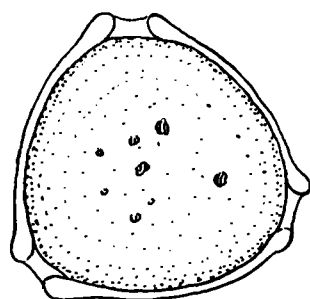
Weekly collections of male catkins were made throughout the period of pollen shedding (Jan. 1 - Feb. 15). Twigs bearing the catkins were kept in the greenhouse with the cut ends in damp sand. The tops were covered with thin paper sacks to prevent the pollen from mixing. The greenhouse used was not heated, and thus except for eliminating the rain, conditions were practically normal. This "forced pollen" was used in the studies below. The supply for field crosses was also treated

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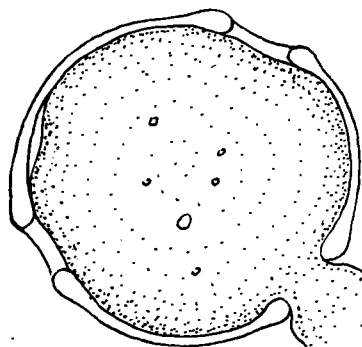
\* The terms "viability" and germinability" are used synonymously in this discourse. Pollen viability was based on the actual percentage which sent out a tube, after resting in or on the medium, which was suspended on a cover glass in a Van Tiegham cell; Kraus method. All germinations were made at room temperature (21° C) and very little rupturing of the grains or tubes occurred.

# FILBERT POLLEN (*Corylus avellana*)

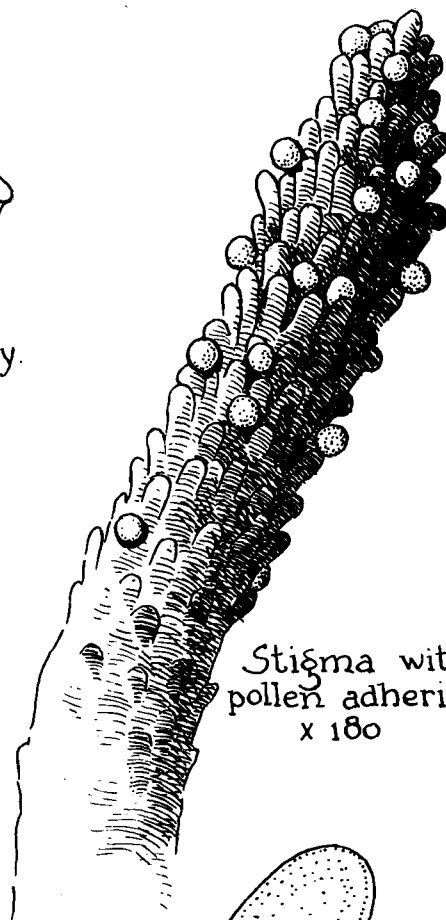
PLATE -III-



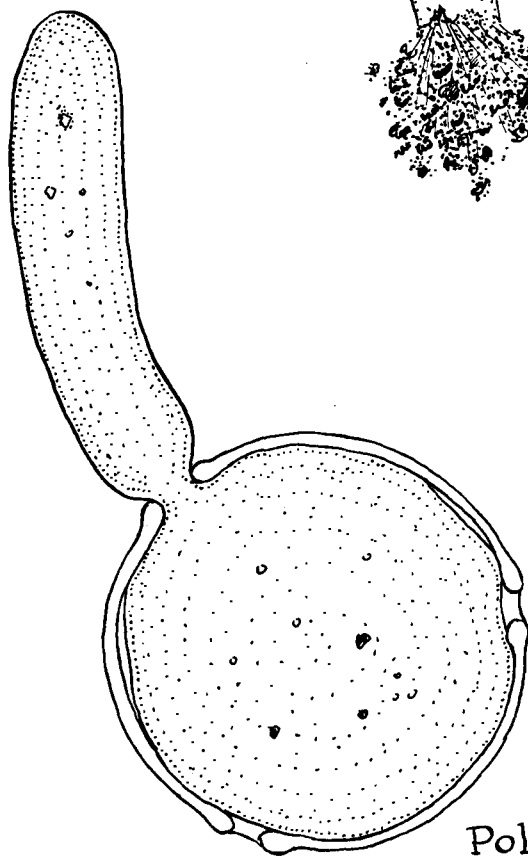
Pollen grain, dry.  
x 2000



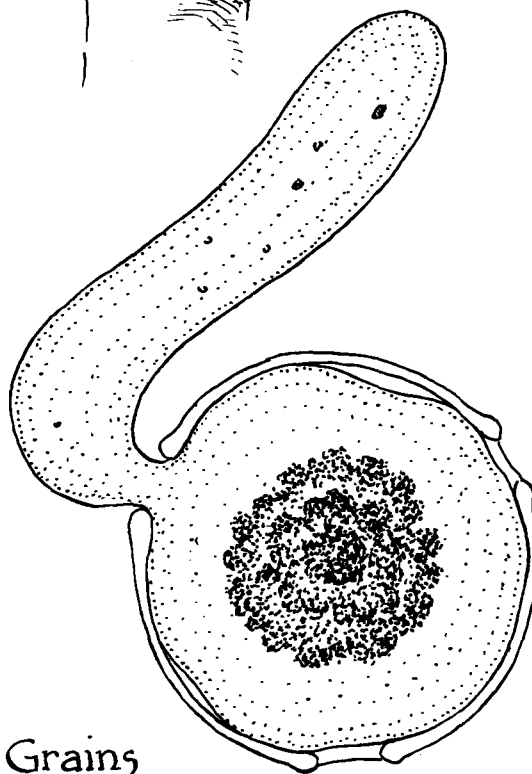
Germ. tube  
ruptured  
x 2000



Stigma with  
pollen adhering  
x 180



Pollen Grains  
germinating  
x 2000



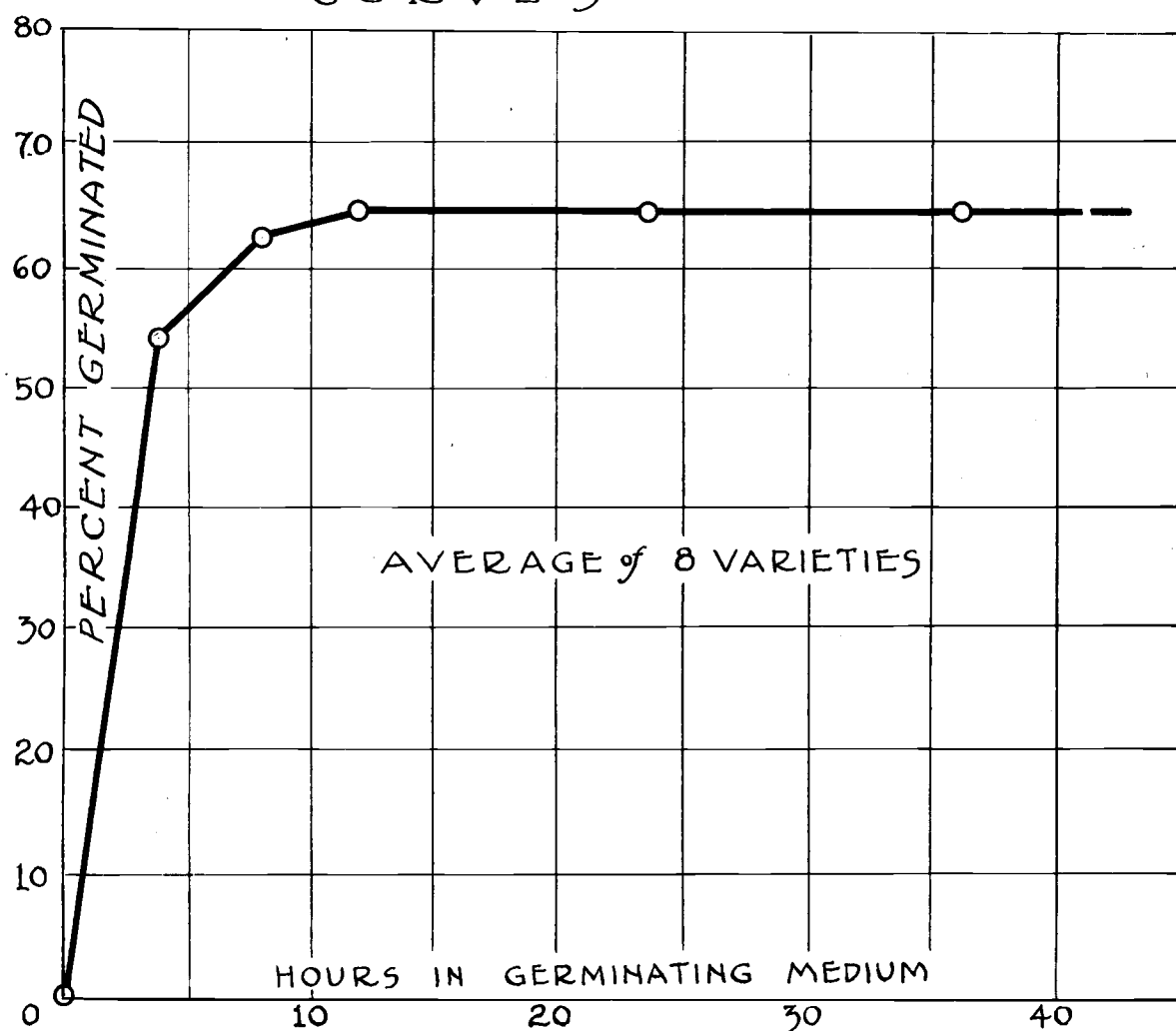
# FILBERT POLLEN

## TEST TO DETERMINE MINIMUM GERMINATING TIME

TABLE-3-

VARIETY	PERCENT GERMINATED					
	4 hrs.	8 hrs.	12 hrs.	24 hrs.	36 hrs.	48 hrs.
Barcelona	80	85	85	85	85	85
Cosford	85	85	85	85	85	85
Daviana	90	95	95	95	95	95
D'Alger	40	80	82	82	82	82
Du Chilly	80	85	85	85	85	85
Fertile de Coulard	30	50	53	53	53	53
Nottingham	60	70	75	75	75	75
White Aveline	75	75	80	80	80	80
Average	54	62.5	64	64	64	64

CURVE-3-



this way. After reserving a small sample of each of these collections for histological examination, the following tests were made:

1. To determine the minimum time for maximum germination. (Table 3) This really belongs to preparatory work or that of development of methods. It is included here to show the reason for making subsequent germination records on the basis of eight hours in the medium rather than to allow the surmise that it was arbitrarily chosen. As seen in Table 3 and accompanying curve, filbert pollen germinates very rapidly. After being in the medium (8 % sucrose and 2 % gelatin solution; this being previously found to be the best of twelve different media tested) for eight hours practically all the grains destined to germinate had done so. After twelve hours a maximum was reached. With the exception of the pollen that was frozen,— in which case a longer time seemed necessary for complete germination,—the interval for all viability or germination determinations, was eight hours.

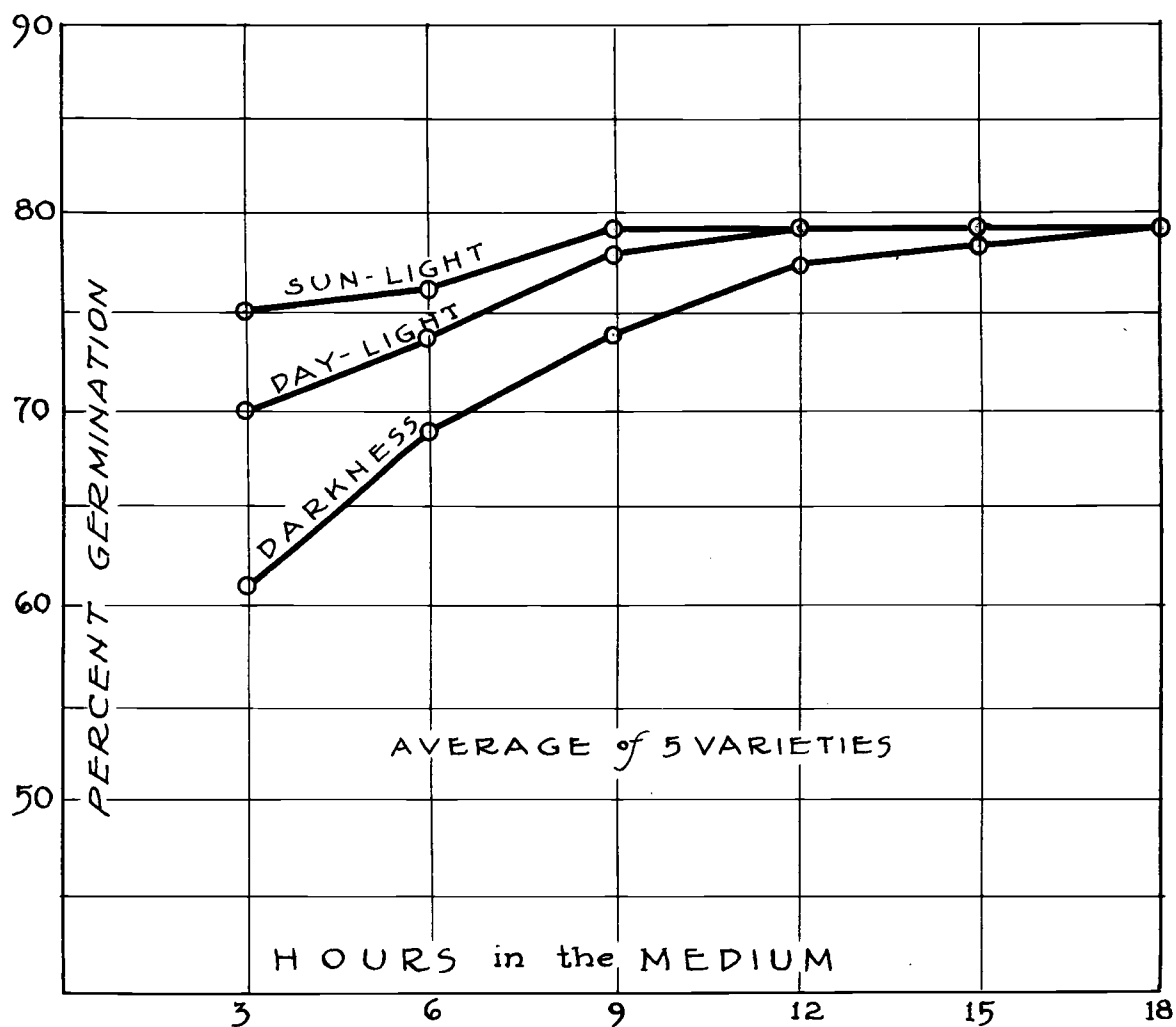
2. To determine influence of Sunlight on Germination.

The results obtained by Sandsten (21) with tomato pollen, and the fact that much dark, cloudy weather ordinarily accompanies pollination<sup>season</sup> in this region, suggested the possible interest in this test. Although Curve No. 3<sup>a</sup> shows a slightly more rapid initial germination in favor of sunshine over daylight and darkness, at the end of eighteen hours, they reach the same percentage of germination. It is quite likely that the accompanying temperature factor was more influential here than that of sunlight itself.

# FILBERT POLLEN

## INFLUENCE of LIGHT on GERMINATION

CURVE -3<sup>a</sup>-





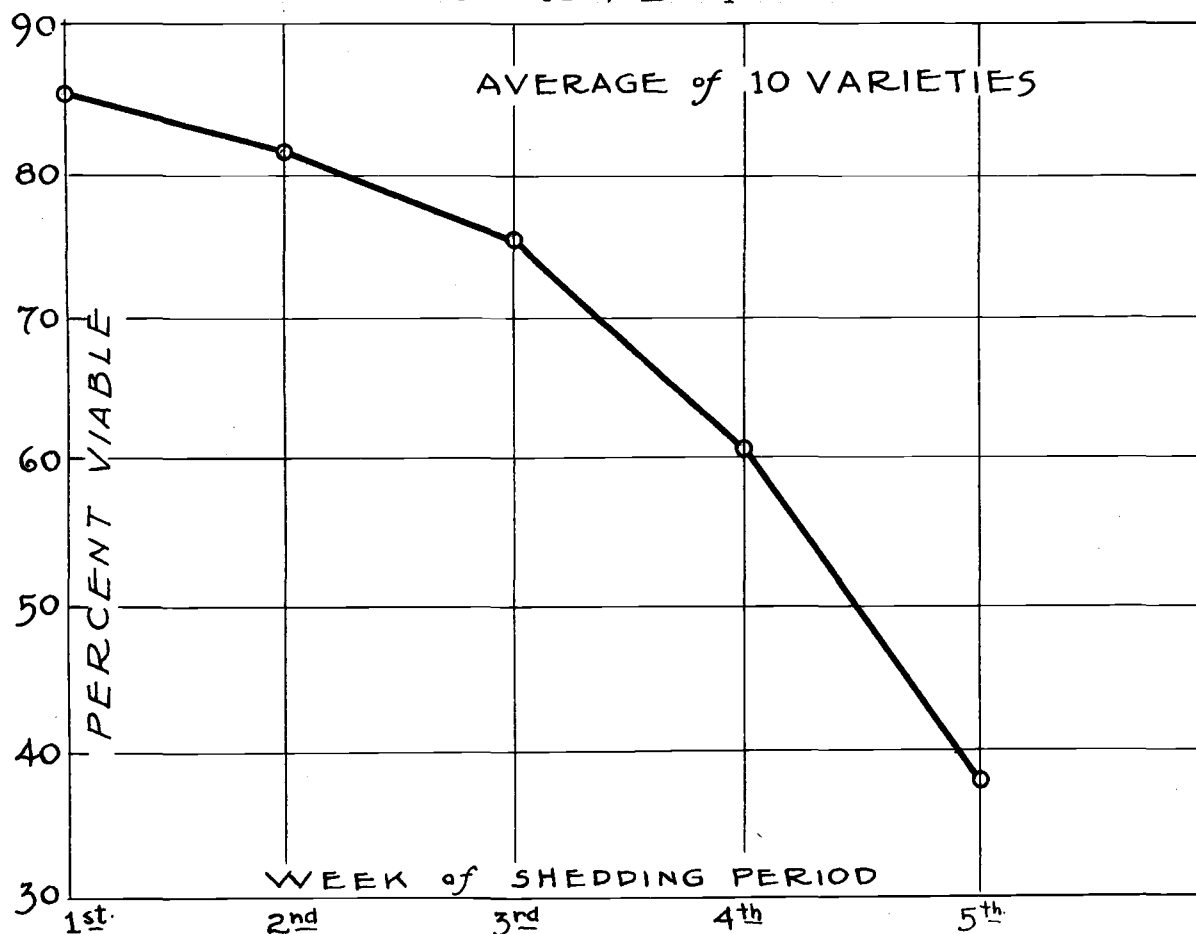
# FILBERT POLLEN

## VIABILITY at DIFFERENT PARTS of SHEDDING PERIOD

TABLE - 4 -

VARIETY	PERCENT VIABLE				
	1 <sup>st</sup> Week	2 <sup>nd</sup> Week	3 <sup>rd</sup> Week	4 <sup>th</sup> Week	5 <sup>th</sup> Week
Barcelona	90	90	80	70	50
Cosford	85	80	70	50	35
Daviana	90	80	80	80	60
D'Alger	85	85	80	70	35
Du Chilly	98	95	85	80	55
Fertile de Coulard	60	65	60	30	20
Nottingham	80	85	80	50	30
Macrocarpa	98	90	80	60	40
Merveille de Bollwiller	85	80	80	65	30
White Aveline	80	65	65	50	30
Average	85	81.5	76	60.5	38.5

CURVE - 4 -



### 3. To determine Pollen Viability at Different Parts of Shedding Period for each variety.

Table 4 presents the results of this experiment. Pollen was collected from the same set of trees of the ten varieties listed at weekly intervals. The curve clearly indicates the tendency for the earliest maturing pollen to be more viable than that of any subsequent time. If this is a constant characteristic of the filbert it would suggest the wisdom and importance in not only choosing varieties which have their respective stigmatic-receptivity and pollen-shedding periods coincident, but rather those which have the beginning or first part of shedding period coincide with period of greatest receptivity for best results in cross pollination.

### 4. To determine Longevity of Filbert Pollens.

At the beginning of the shedding period of each variety, representative samples of pollen were collected. These samples were kept in envelopes outdoors, and tested for germination at five day intervals until each sample showed no visible viability. Table 5 and curve accompanying give the results. Although there were some small fluctuations in individual varieties, (probably due to experimental error), the average for the ten varieties shows a steady and uniform loss of viability which varies almost directly with the time. Two months seems to be the limit of germination longevity.

### 5. To determine effect of how Temperatures on Pollen Viability.

Twigs with catkins attached, were used in this experiment, and the representative samples of pollen were taken

# POLLEN-LONGEVITY-TEST

Each variety collected at beginning of its shedding time & kept out-doors.  
Germinated in 8% sucrose 2% gelatin sol. for 8 hrs. at 21° C (70° F)

CURVE-5-

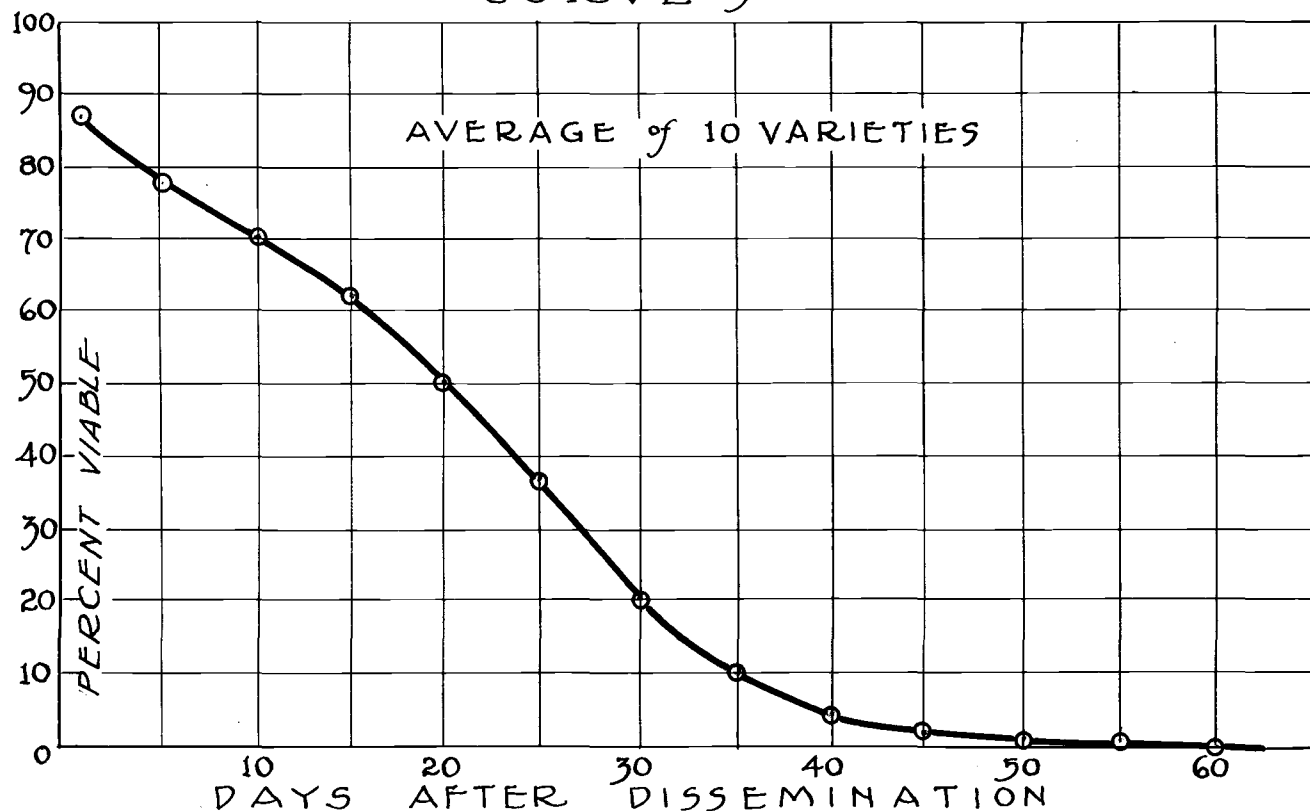


TABLE-5-

VARIETY	PERCENT GERMINATED													
	JANUARY							FEBRUARY					MAR.	
	1 <sup>st</sup>	5 <sup>th</sup>	10 <sup>th</sup>	15 <sup>th</sup>	20 <sup>th</sup>	25 <sup>th</sup>	30 <sup>th</sup>	5 <sup>th</sup>	10 <sup>th</sup>	15 <sup>th</sup>	20 <sup>th</sup>	25 <sup>th</sup>	1 <sup>st</sup>	5 <sup>th</sup>
Barcelona		90	75	75	70	50	30	10	0	0	0			
Cosford		85	85	70	70	50	35	20	0	1	0	0		
Daviana			90	80	80	70	50	30	10	3	0	0		
D'Alger			85	80	70	70	55	45	25	2	2	0	1	0
Du Chilly			95	98	80	75	60	60	40	20	0	0		
Fertile de Coulard	60	60	60	55	60	60	55	50	35	15	5	2	1	0
Nottingham			80	75	60	65	70	65	30	10	1	0	0	
Macrocarpa					98	95	85	75	40	3	1	0	0	
Merveille de Bollwiller					85	70	65	30	10	0	0	0		
White Aveline			80	65	65	55	60	40	20	2	1	1	0	
Average		85	78	71	63	50	37	20	9	4	2	1	0	0

# FILBERT POLLEN

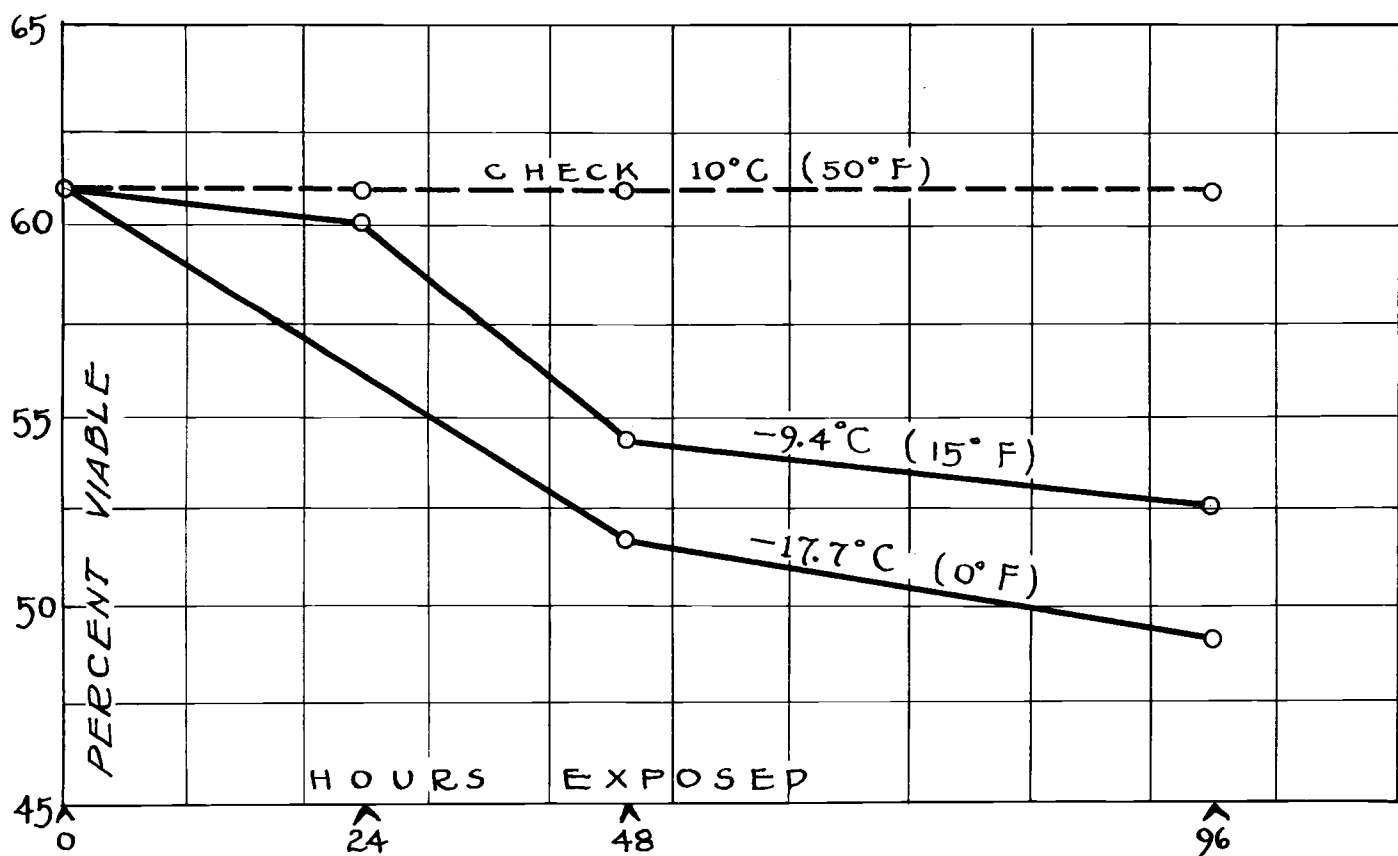
## EFFECT of LOW TEMPERATURES on VIABILITY

Germinating medium = 8% sucrose 2% gelatin for 16-hrs at 21°C (70°F)

TABLE -6-

VARIETY	PERCENT GERMINATED					
	CHECK	15°F-24hrs	15°F-48hrs	15°F-96hrs	0°F-48hrs	0°F-96hrs
Barcelona	30	25	30	30	30	30
Cosford	60	60	50	45	45	40
Daviana	75	75	75	75	75	70
D'Alger	60	60	50	50	55	50
Du Chilly	70	70	65	60	60	60
Fertile de Goulard	45	45	40	40	40	40
Nottingham	80	80	65	60	45	45
Macrocarpa	50	50	45	45	45	45
Merveille de Bollwiller	85	80	75	70	75	70
White Aveline	55	55	50	50	50	50
Average	61	60	54.5	52.5	52	49

CURVE -6-



after shaking many male catkins in a paper bag. This was to avoid error due to individual catkin differences. The twig ends were wrapped with damp cloths to prevent drying out, and any consequent abnormal conditions in the anthers. Pollen was frozen both in and out of the anther. As will be seen by referring to Table 6, very little deleterious results followed. The abscissa of this curve is drawn to enlarged scale to make the small effect more evident. From 61 percent viability in the check, or untreated samples, freezing for 96 hours at  $0^{\circ}$  F reduces the average viability of ten varieties but 12 percent. It is to be remembered that only on extremely rare occasions does the winter temperature go as low as this in Oregon\*. On page 34 an interesting comparison is made of stigma versus pollen hardness to cold. Here the pollen curve is drawn in red and to same abscissa scale as that for the stigmas.

6. To determine the effect on Pollen of High Temperatures in Dry Atmosphere.

Samples of each of ten varieties of pollen were put in envelopes and placed in electric oven. These were exposed for forty-eight hours intervals at  $90^{\circ}$  F ( $26.6^{\circ}$  C),  $100^{\circ}$  F ( $32.2^{\circ}$  C), and  $110^{\circ}$  F ( $37.6^{\circ}$  C). At the end of each heating, germination tests were made and the results are tabulated and plotted in Table and Curve No. 7. It will be seen that viability rapidly decreases under high temperatures. Fortunately orchard conditions never seem to offer any such high temperatures during period of pollination. Reference again to Tables

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\* See weather record Pages 18, 19

## FILBERT POLLEN

TABLE -7-

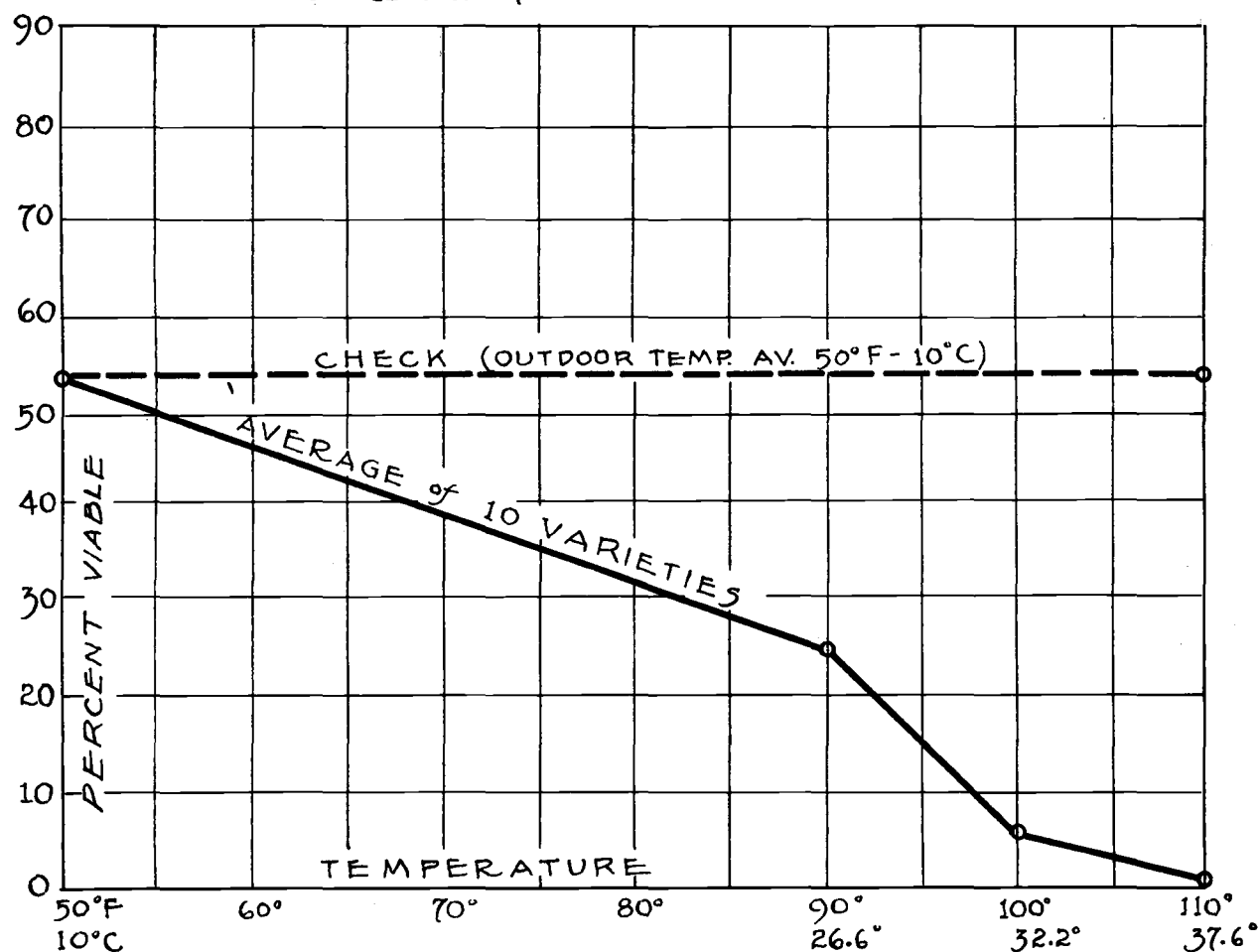
## EFFECT of HIGH TEMPERATURE in DRY AIR.

Each exposure, 48 hrs. in oven.

Germinated in 8% sucrose, 2% gelatin, for 16 hrs. at 21°C.

VARIETY	PERCENT VIABLE			
	CHECK	90°F-26.6°C	100°F-32.2°C	110°F-37.6°C
Barcelona	30	10	8	0
Cosford	55	35	5	0
Daviana	75	40	10	2
D'Alger	60	25	2	0
Du Chilly	70	30	10	0
Fertile de Coulard	35	15	5	0
Nottingham	80	40	5	1
Macrocarpa	35	15	3	0
Merveille de Bollwiller	30	10	5	0
White Aveline	60	25	10	1
AVERAGE	53.	24.5	6.3	0.4

CURVE -7-



## FILBERT POLLEN

TABLE-8-

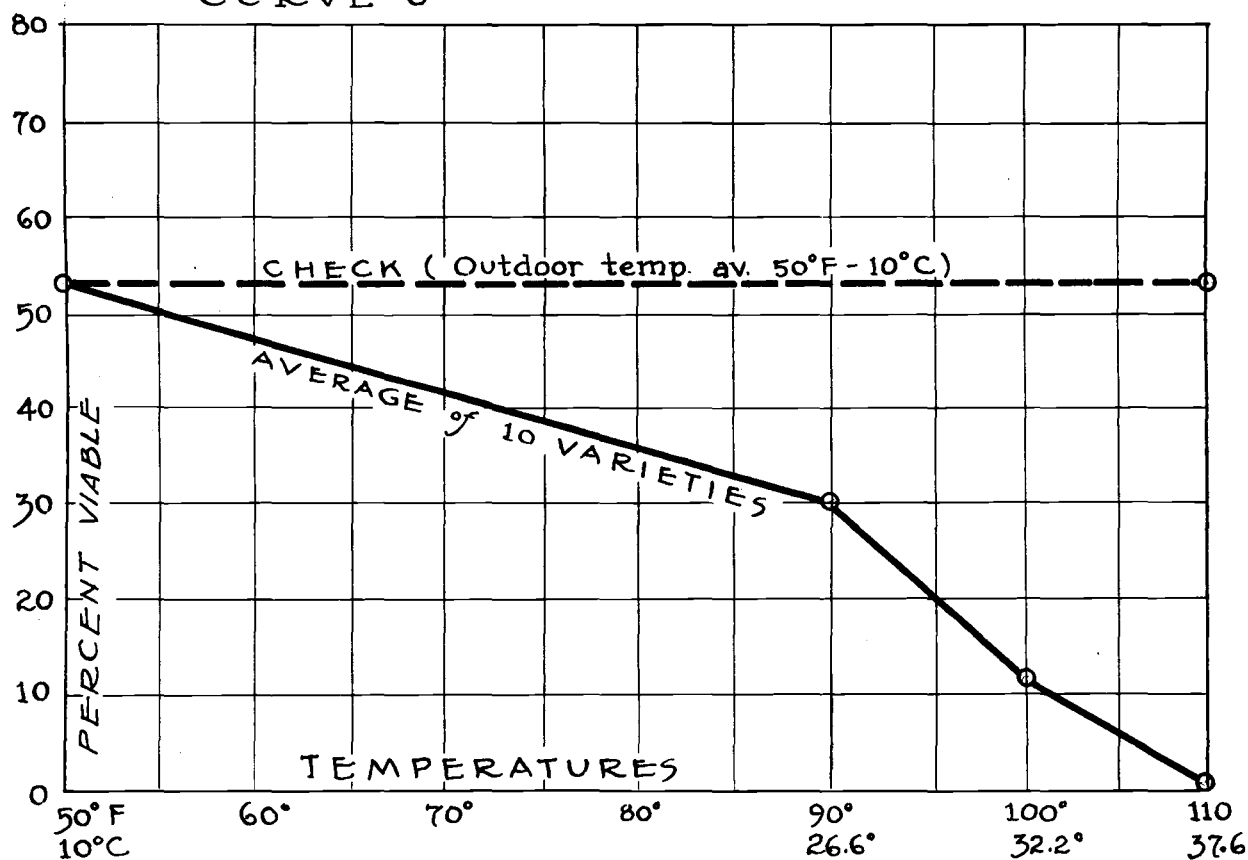
## EFFECT of HIGH TEMPERATURES in SATURATED AIR

Each exposure, 48 hrs. in oven

Germinated in 8% sucrose, 2% gelatin, for 16 hrs. at 21°C.

VARIETY	CHECK	PERCENT VIABLE		
		90°F-26.6°C	100°F-32.2°C	110°F-37.6°C
Barcelona	30	20	10	0
Cosford	55	30	8	1
Daviana	75	50	12	1
D'Alger	60	25	5	0
Du Chilly	70	50	15	2
Fertile de Coulard	35	20	10	0
Nottingham	80	50	20	3
Macrocarpa	35	20	10	0
Merveille de Bollwiller	30	10	8	1
White Aveline	60	20	20	0
Average	53	29.5	11.8	0.8

CURVE-8-



1 and 2 will show that the

Mean Maximum for Jan. 1921 was  $46.2^{\circ}$  F.

" Minimum " " " "  $35.7^{\circ}$  F.

" Maximum " Feb. " "  $51.7^{\circ}$  F.

" Minimum " " " "  $38.1^{\circ}$  F.

7. To determine effect on Pollen of High Temperatures in Saturated Atmosphere.

This test was conducted exactly the same as No. 6 above, except that the envelopes containing the pollen were suspended over a water surface in a tightly stoppered jar and this placed in the oven. A similar inhibitory effect upon germination or devitalization of the pollen results. Table and Curve No. 8.

I (b) GROSS STUDIES WITH STIGMAS:

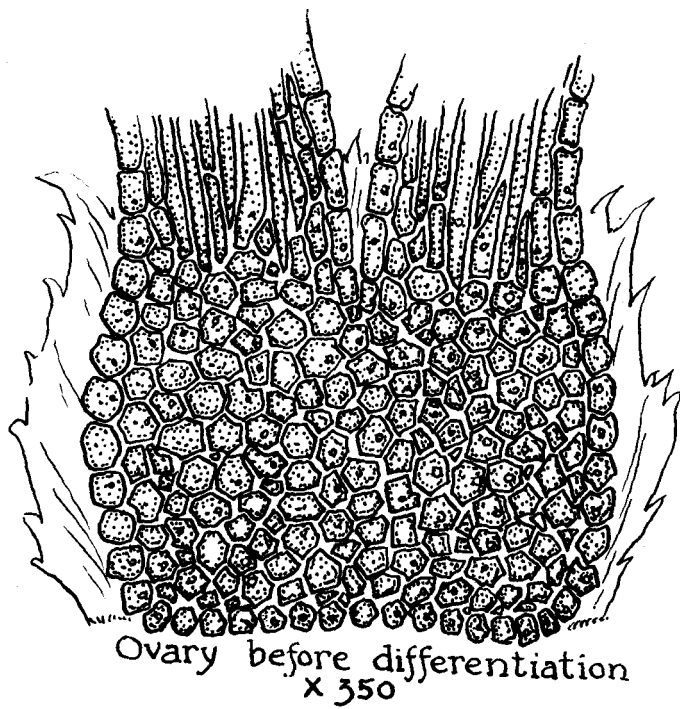
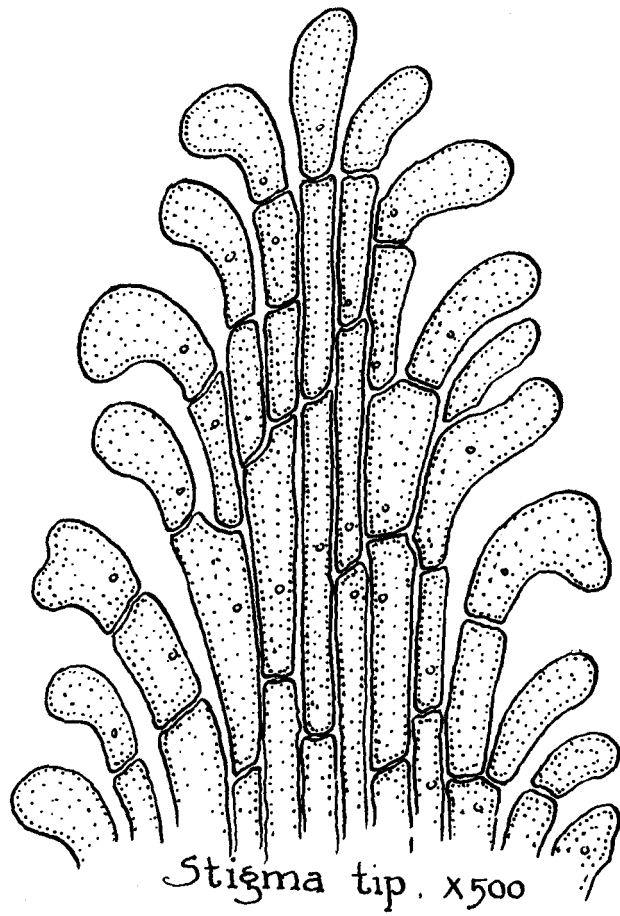
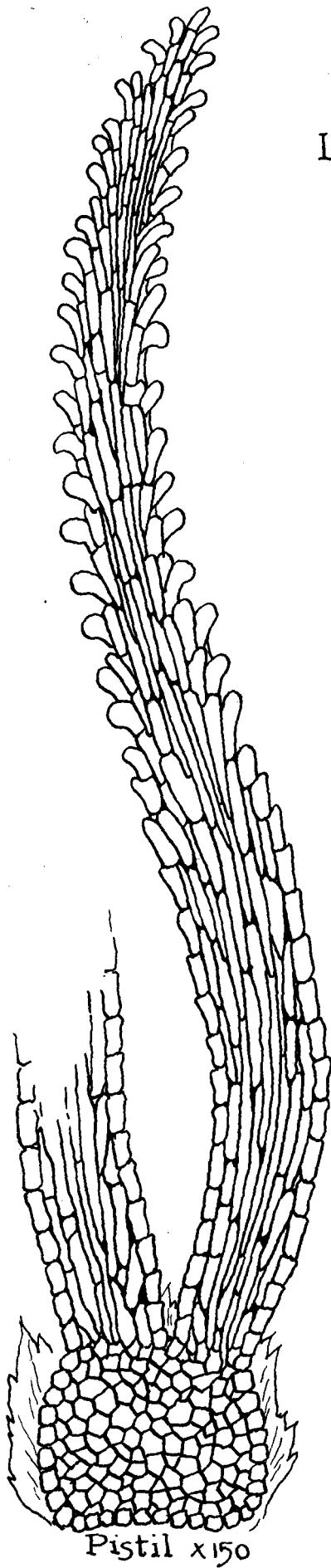
8. To determine effect of Low Temperature on Stigmas (in bloom)

Twigs with female catkins of ten varieties were taken during blooming season, and cut ends wrapped with damp cloths to prevent drying. These were placed in cold storage, as was done with pollen. A glance at Curves No. 9 will reveal the extreme susceptibility of the stigmas when in this condition, to injury from freezing. Exposure to temperatures of  $15^{\circ}$  F ( $-9.4^{\circ}$  C) and  $0^{\circ}$  F ( $-17.7^{\circ}$  C) eventually seem to kill the cells especially in the region of the stigma tip where the structure is loose and spongy. Later when ~~taken~~ allowed to thaw, a blackened and withered appearance presents itself and all of the stigmatic parts which protruded beyond bud scales



# FILBERT

Longitudinal Sections of Pistil



# FILBERT STIGMAS

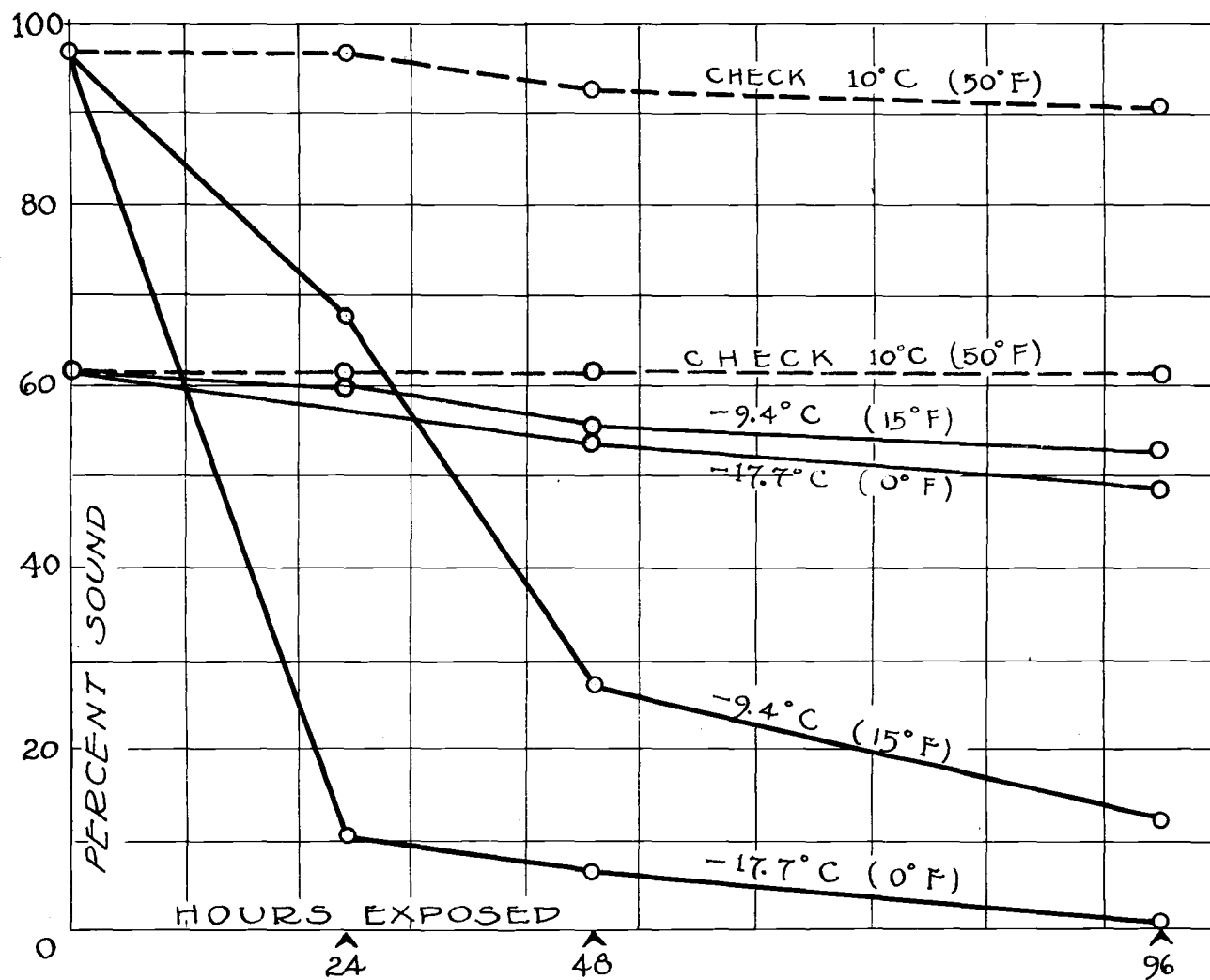
CURVE-9-

## EFFECT of LOW TEMPERATURES :

Twig-ends wrapped to prevent drying-out, & placed in Cold Storage for various intervals.

Only parts of Stigmas considered here were those with protruded thru bud ( $\frac{1}{2}$ - $\frac{3}{4}$  of whole)

Curves in Red show relative ability of POLLEN to withstand Low temperature. % = % germinated.



or bracts <sup>were</sup> ~~is~~ dead for all practical purposes of pollination. Revelation of this character suggests the possibility of a severe weakness in varieties which bloom early and subject their tender stigmas to the hazards of low temperatures during or before pollination.

#### 9. Observations to determine Normal Period of Stigma Receptivity for each Variety.

This, of course, must be carried on over a period of several years to be of value. No deductions or recommendations would be warranted on the basis of but one season's record. Table 10 summarizes these observations for 1921 and presents a graphic comparison of varietal receptivity period, as well as shedding periods for the ten varieties studied. After more data accumulates on this point we shall be in a better position to select the most efficient varieties for inter-fertilization purposes.

#### II. HISTOLOGICAL STUDY OF POLLINATION AND FERTILIZATION PROCESSES.

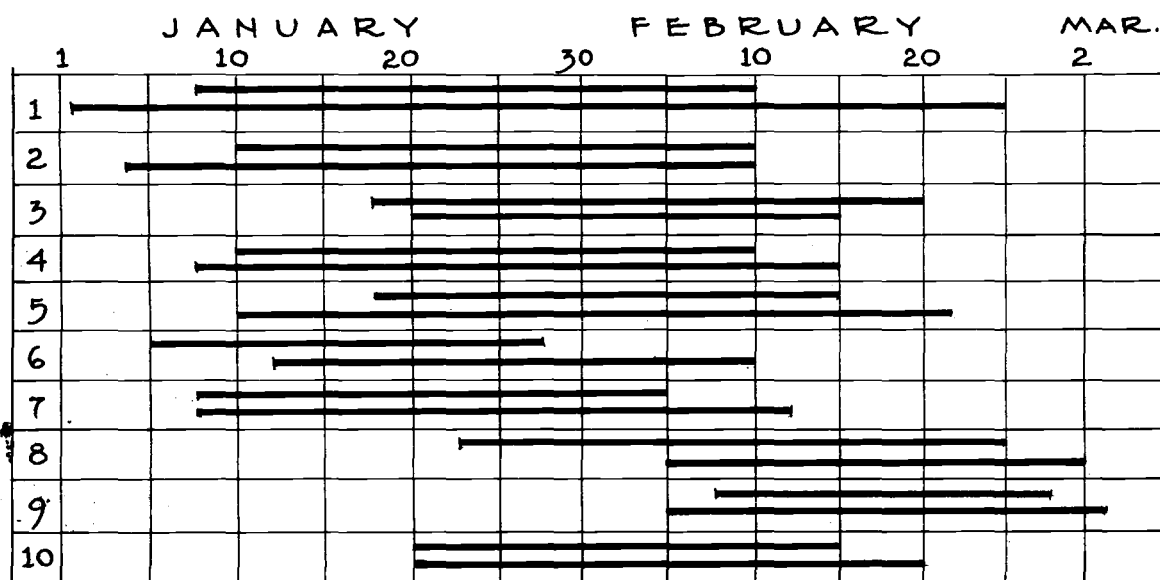
In a short time, experimentation with the gross factors of sterility and fertility in the filbert will cease to yield valuable results. Further progress will then depend upon the acquirement of more exact data concerning the minute factors and characteristics in the mechanism of pollination and fertilization. This part of the study, then, should furnish a basic contribution to further studies and field applications with the filbert.

Collections of 50 female blossoms of Barcelona x wind.

DATA on:  
FIELD CROSSES, SHEDDING & RECEPTIVITY  
TABLE 10-

VARIETY of POLLEN USED	PERIOD of		% POLLEN VIABLE				NUMBER BARCELONA FLOWERS		# % SET
	POLLEN SHEDDING	STIGMA RECEPTIVE	1 <sup>st</sup> CROSS	2 <sup>nd</sup> CROSS	3 <sup>rd</sup> CROSS	4 <sup>th</sup> CROSS	POLLINATED ★	SET #	
1 Barcelona	1/8-2/10	1/1-2/25	85	85	80	72	200	8	4
2 Cosford	1/10-2/10	1/4-2/10	85	80	75	60	"	37	18.5
3 Daviana	1/18-2/20	1/20-2/15	70	75	75	70	"	50	25
4 D'Alger	1/10-2/10	1/8-2/15	80	80	75	55	"	41	20.5
5 Du Chilly	1/18-2/15	1/10-2/22	85	85	85	60	"	62	31
6 Fertile de Coulard	1/5-1/28	1/12-2/10	40	50	50	50	"	27	13.5
7 Nottingham	1/8-2/5	1/8-2/12	55	60	75	75	"	50	25
8 Macrocarpa	1/23-2/25	2/5-3/2	70	70	70	60	"	36	18
9 Merveille de Bollwiller	2/8-2/28	2/5-3/3	70	70	65	65	"	26	13
10 White Aveline	1/20-2/15	1/20-2/20	75	75	70	55	"		
<u>RECIPROCAL CROSSES</u>									
Barcelona X Du Chilly			80	82	72	75	1000	310	31
Du Chilly X Barcelona			84	80	78	76	"	90	9

CURVE-10-



————— = shedding period      ————— = stigmas apparently receptive  
 ★ each ♀ catkin averages 10 flowers.  
 # see page 60

Collections of 50 female blossoms of Barcelona X Du Chilly

" 50 " " " Du Chilly X wind

" 50 " " " " X Barcelona.

were made from the orchard bi-weekly from January 1st until May 24th\*. The following materials were tried for killing and fixing; absolute alcohol, Carnoy's fluid, Gilsons mixture, formalin alcohol, chromo-acetic acid, (as per Chamberlain "Methods in Plant Histology"). Of these Carnoy's fluid and absolute alcohol were chosen as the best agents. After going through the regular xylol series, the catkins were imbedded in 52° paraffin.

The extreme hairiness of the bracts and other parts of the female catkins made microtome sectioning of the whole catkin, impossible. The material persisted in tearing out of the paraffin. Celloidin imbedding was next tried but with no greater success. To work out methods for handling such unusual material would probably constitute a problem in itself. It was finally found necessary to dissect out the pistils and remove all adhering bractlets, under the binocular microscope. These dissected pistils were then treated and mounted individually in paraffin. Although considerable tearing out still occurred (due to pubescence of ovarian region) it was possible by making a large number of sections, to secure some fairly good slides. Microtome sections were cut of .09 mm. thick and stained with Erlich's haematoxylin for study. About 300 slides were pre-

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\* It was originally hoped that this period of collections would include fertilization, no information being available on the possible date of this event for this region. It is accordingly unfortunate that it will be impossible to include more date on the embryology at this writing, as this thesis must be concluded by June 1st.

pared in this way.

The mechanism of pollination and fertilization as far as it could be worked out was as follows:

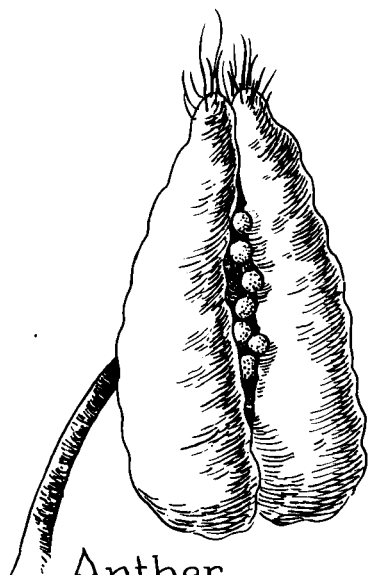
A. The Microspore: (Pollen grain)

The male floral bracts number about 150 per catkin. There are eight anthers per bract and it was estimated that each anther averages some 1000 pollen grains. This would make  $(150 \times 8 \times 1000)$  about 1,200,000 microspores per catkin. From the large number of catkins borne on each plant (see Plate II) a conception is easily developed of the enormous pollen prolificacy in this genus. The dry pollen grain measures about .024 mm. in diameter.

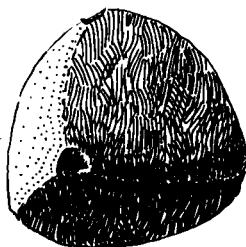
The male catkin is formed in the late summer, the pollen mother cell stage probably being in August during which time it is thought reduction-division takes place. The uninucleate stage is passed by January as collections taken then show binucleate pollen grains. The compact catkins pass the winter in a naked condition. (See Plate VIII.) In January and February the catkin elongates, male flowers mature and the anthers freely shed their pollen grains during dry windy days. The pollen floats in the air and lights upon the receptive stigma tips, which in most varieties protrude their spongy ends beyond the female catkin soon after pollen shedding begins. Reference to graphic representation of the periods of shedding and of receptivity for each variety (Table 10), shows three varieties out of ten to be proterandrous; five

# FILBERT

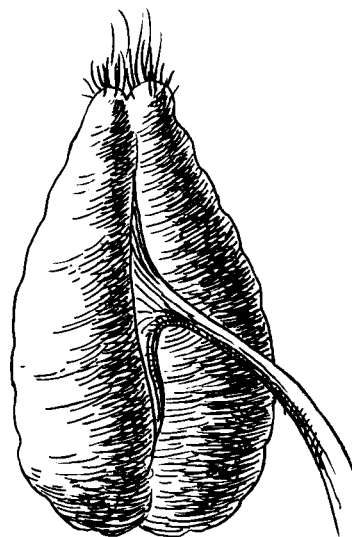
## PLATE II



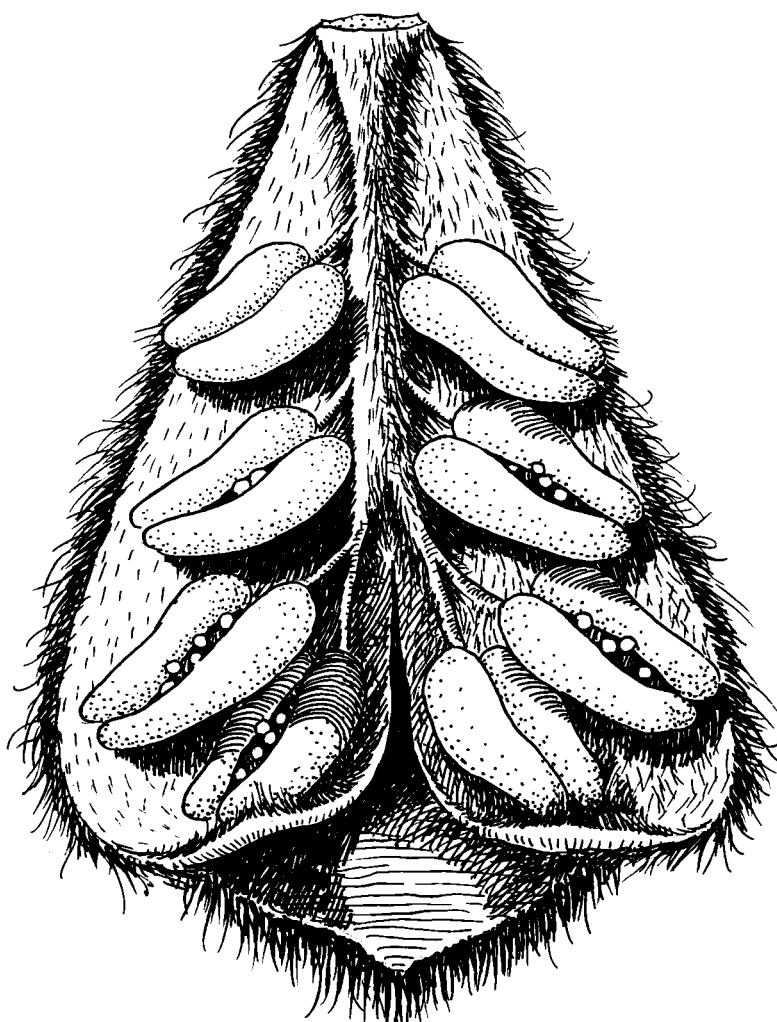
Anther  
(Suture opening)  
X 40



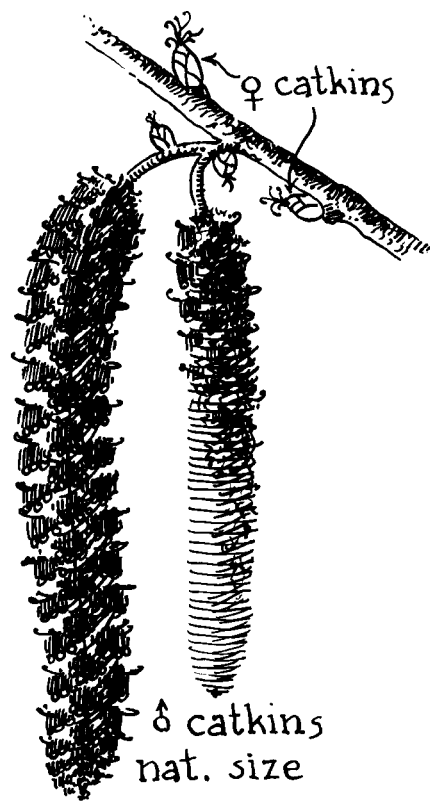
Pollen Grain  
X 1600



Anther (dorsal view)  
X 40



Male flower  
X 20



varieties out of ten to be protogynous, and two varieties wherein shedding and receptivity develop simultaneously. Further examination of the graphs will show that in all varieties (of the ten tested) except one, receptivity ante-dates termination of shedding period. The microspores find lodgment in the inter-papillate spaces toward the apical end of the stigma. Germination occurs within a few days, depending of course, on environmental conditions (temperature, humidity, etc.) The germ tube penetrates the loose styler tissue to the basal region of the stigma; the nuclei following down with the growth of the tube. These nuclei with a small amount of cytoplasm contract into a small solid sphere or cyst of .012 mm. diameter (Plate VI), the connecting tube rapidly breaks down, and the RESTING STAGE commences. From the work of Benson (1) and our work to date we may say that this resting stage continues for about four months in *Corylus*, while the megaspore is developing, previous to fertilization.

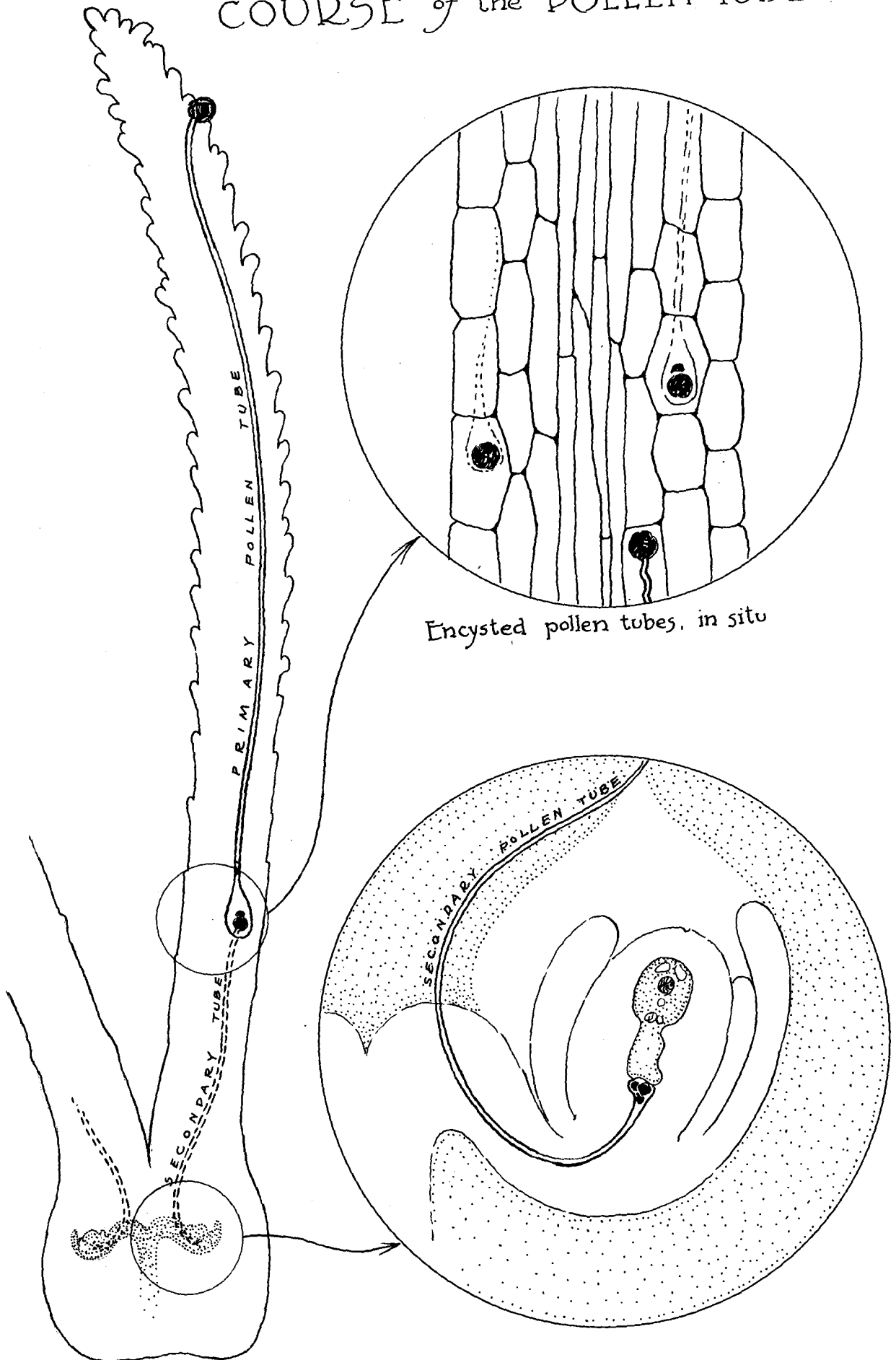
As will be subsequently explained, development of the megaspore is considerably retarded. Maturation of the female gametophytes occurs not before June or sometimes July. This necessitates the male gametophyte remaining in a dormant or resting condition over a period of three to four months before fertilization. Many of the encysted spheres were seen in the styler tissues in sections of material taken during this

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\* This adaptation seems to be characteristic of a group including *Betula*, *Carpinus*, *Alnus*, (Benson) and some species of *Quercus* (Conrad) where 1, 2, 3, 11 and 13 months respectively, are passed in this encysted condition between pollination and actual fertilization. In this respect we see a striking resemblance to the phenomenon so characteristic of gymnosperms, and showing how primitive this genus is among angiosperms.



# COURSE of the POLLEN TUBE



resting period. (Feb. - June) (See Plate VI).

When the megaspore completes maturation this encysted pollen tube sends out a secondary tube which penetrates the stylar and ovarian tissue and enters the embryo sac via the chalazal route. (Plate VI lower right figure). This secondary germination and growth must take place within a very short time after reduction division and maturation of female gametophyte. It is unfortunate that this process occurs too late in the season to permit of a detailed description at this writing. The studies will be continued, however, and the results annexed as a Supplement.

In 1891 Treub announced the phenomenon of chalazogamy in *Casuarina*. Two years later Newashin observed it in *Betula*, and in 1894 Benson noted that it was characteristic of *Alnus*, *Carpinus* and *Corylus* as well. It would be interesting to corroborate this phenomenon in our case with *C. avellana* as well as that of the branching pollen tube, (so uncommon in angiosperms). The retardedness of these phenomena, however, will make it necessary to leave any observations found thereon as well as fertilization itself to the Supplement. In the meantime a few extracts from Benson's conclusions (1905) will be suggestive of what might be expected:

"The pollen-tube (secondary) does indeed in some instances tunnel the cell-layers which cover the apex of the embryo-sac, but it has, in such cases, reached these cell-layers by a route wholly as abnormal as Trent has pointed out in the case of *Casuarina*. It descends from the tissue at the base of the stylar rudiments and, running parallel with the

vascular bundle of the raphe, turns abruptly up into the nucellus on reaching its chalazal region. The base of the nucellus will be observed to lie in such a direction that the pollen-tube following the trend of the cells in the neighborhood of the vascular bundle of the raphe cannot fail to find its way into the nucellus. This position of the base is gradually acquired by unequal growth of the two halves of the ovule which cause the very characteristic curvature of the ovules in *Alnus*, *Betula*, *Corylus* and *Carpinus*. From the difference in the one case and the agreement in the other, we are, I think entitled to regard this feature as a special adaptation for chalazogamy.

I have given two figures of pollen-tubes in contact with the base of the embryo-sac caeca (*Corylus* and *Carpinus*). In the case illustrated we find the tube abutting on the comparatively short caecum of *Corylus*. In figs. 44 and 45 which also exhibit the tube ascending the nucellus the lower part of the tube alone is represented. The pollen-tube enters the base of the fertile embryo-sac in *Corylus* and *Carpinus*, and, continuing its course up the whole length of the caecum, eventually reaches and fertilizes the oosphere by direct contact... The inconspicuous development of the synergidae and their early dissolution are now explained. They are not required to assist in any way in the act of fertilization, for the pollen-tube reaches the oosphere from below, having previously entered the embryo-sac in its basal region.

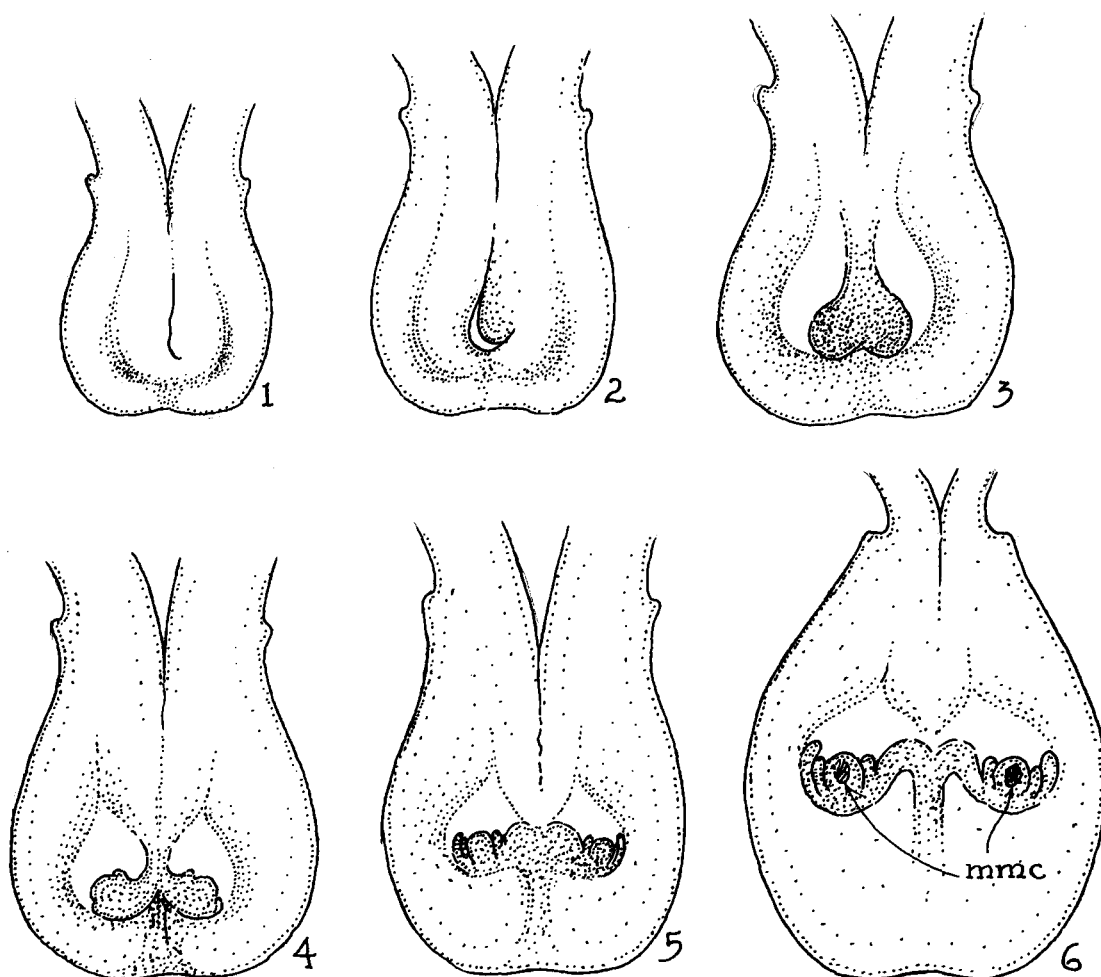
The pollen tube presents another point of likeness with that of *Casuarina*, inasmuch as it sends out a short re-

curved branch on entering the nucellus. This branching of the pollen-tube is a very general feature in the amentiferae. Even in those genera in which we do not find the chalazal course of the tube, we find a process of bifurcation still very widely present. In the case of chalazogamic Amenticerae the recurved branches found are simply caeca and probably contain no portion of the fertilizing element."

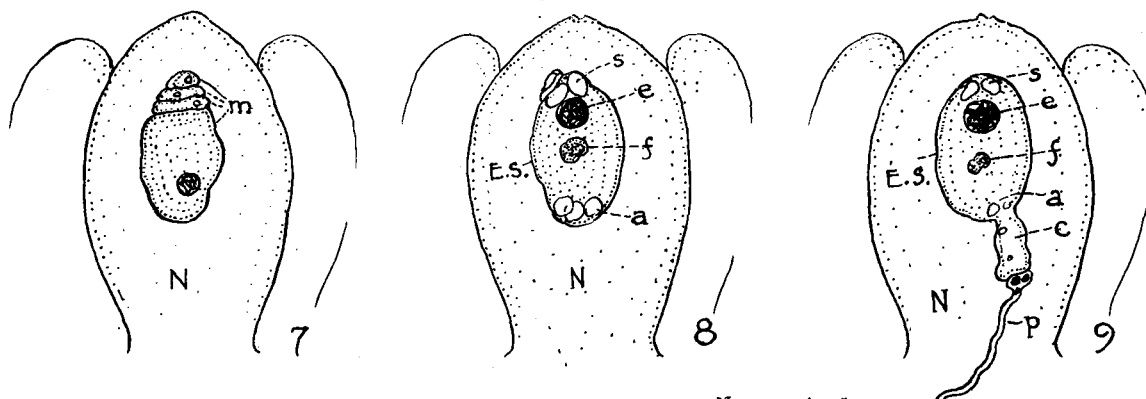
B. The Megaspore. (and female gametophyte).

The first evidences of ovarian tissue differentiation into ovules was from collections made April 2nd. An attempt is made by means of illustrations (Plate V) to trace out the subsequent steps in ovule development up to the production of the female gametophyte. The variety used was Barcelona. The process seems to be identical with other varieties except that some are relatively retarded. Distinct anatropous ovules were first recognizable from female catkins May 20. The primary sporogenous cell is the megaspore mother cell. From Benson's work we may expect the following development: This divides twice by reduction division (maturation) and a row of four megaspores is produced. The innermost one, or the one furthest from the micropyle matures into the true megaspore (Plate V). The remaining three are later absorbed by the embryo. The megaspore nucleus goes through three successive free nuclear divisions resulting in the completion of the female gametophyte with its egg, fusion nucleus (endosperm nucleus) synergids and antipodals. As in the case of the microspore, it was not possible to trace development further than this because of the necessity of concluding this paper

## DEVELOPMENT of FILBERT OVULE



## MATURATION of ♀ GAMETOPHYTE



m - megaspores  
 mmc - megaspore mother cell  
 N - nucellus  
 e - egg  
 f - fusion nucleus

p - pollen tube  
 a - antipodals  
 s - synergids  
 E.S. - Embryo-sac  
 c - caecum.

by June 1. Fertilization will be studied, however, and it is hoped that this together with some of the early embryology may be included in a supplement.

### III. FIELD STUDIES.

These studies accompanied the pollen and pistil studies which were carried on in the laboratory, and partially supplied material for the latter. On December 13th and 14th (1920) before any pollen shedding took place, 3000 female Barcelona flowers, and 1000 female DuChilly flowers\* were bagged with paraffin-dipped paper sacks, to exclude foreign pollen. These later formed the hosts for the following crosses.

1000 Barcelona X Du Chilly

1000 Du Chilly X Barcelona.

This was to test inter-fertility of these two commercial varieties, and to provide material for histological study. The remaining 2000 female Barcelona flowers were pollinated as follows:

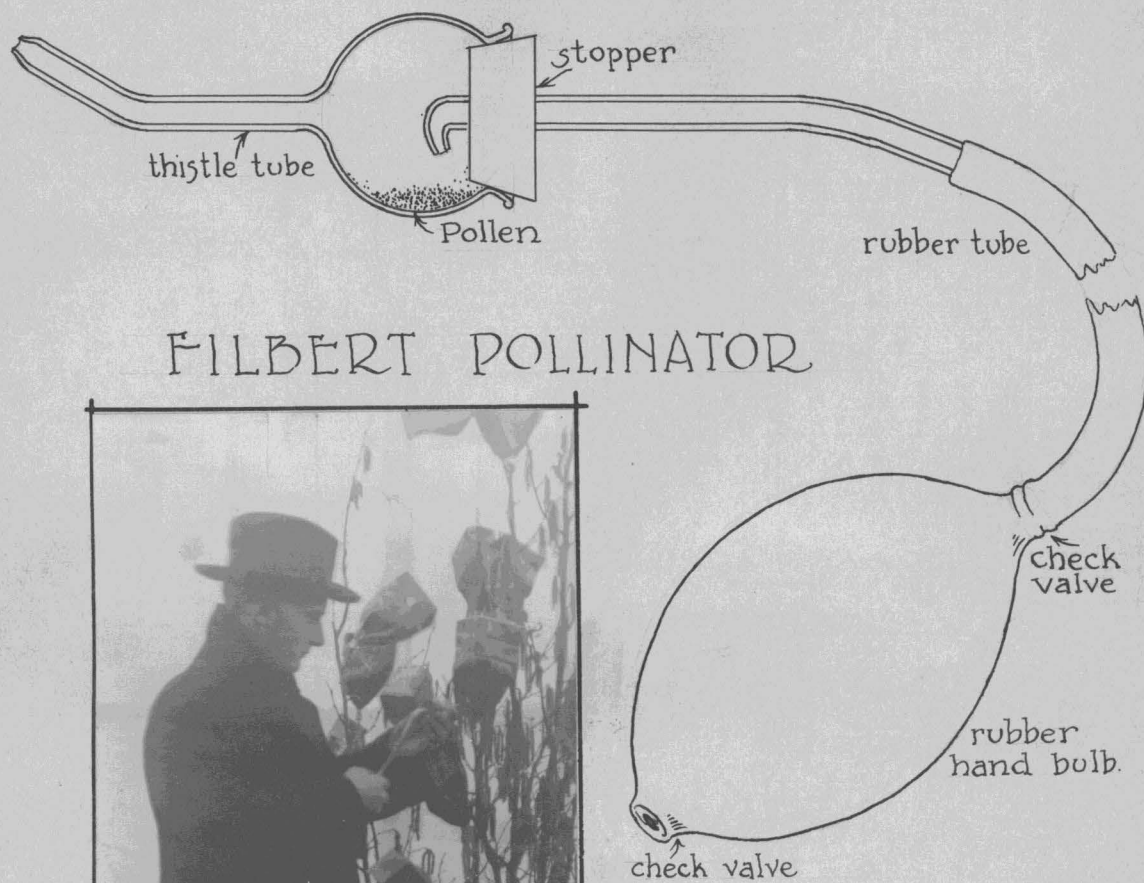
200	Barcelona	x	Barcelona	(self)
200	"	x	Cosford	
200	"	x	Daviana	
200	"	x	D'Alger	
200	"	x	Du Chilly	
200	"	x	Fertile de Coulard	
200	"	x	Nottingham	
200	"	x	Macrocarpa	
200	"	x	Merveille de Bollwiller	
200	"	x	White Aveline	

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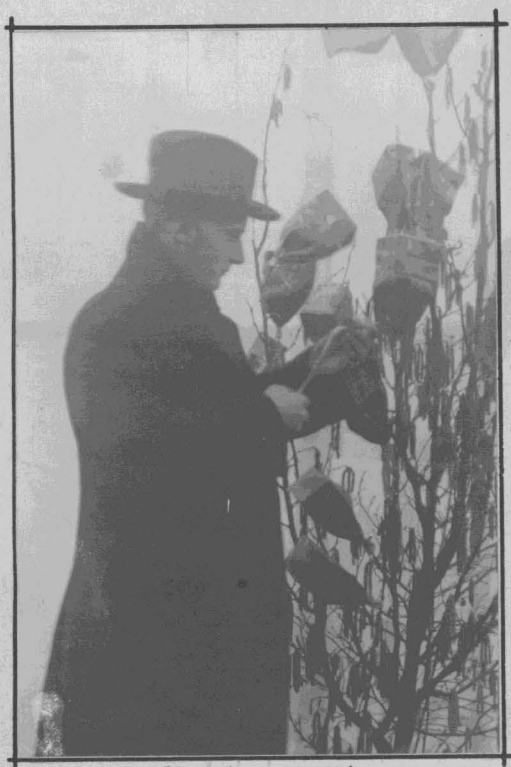
\* Each female catkin contains average of ten flowers. These varieties were suspected of value among those available at Corvallis.

This was to test in a gross way the relative value of these as pollinizers for Barcelona and for Du Chilly. Results are included in Table No. 10. All pollinations were repeated four times, being made on January 10, 15, 22 and 30th. Instead of removing the paper sacks (which become rather brittle after lengthy exposure) and applying pollen to each female catkin separately, an improved form of the M. C. Coulter Pollinator (described in Bot. Gazette 68, p. 63, 1919) was used. This pollination (improved) is illustrated on the accompanying page. Pollen is placed in the thistle chamber, a slit is cut in the side of the bag and pollinator end is inserted. A few compressions of hand bulb blows in a cloud of pollen some of which settles on the stigmas. The slit is then closed and a paper fastener applied to keep it shut until the time for the next application. This proved a very rapid and efficient method for this work. The viability of all pollen used in these crosses was tested in 8 percent sugar (sucrose) and 2 percent gelatin solution before each application. Table No. 10 gives these data, and summarizes the field crosses. It will be noticed that the columns on "No. of flowers set" and "percent set" are still left blank. Although rough estimates might be made at this time, it was thought best to wait until after fertilization had taken place before these figures are concluded. This will not be possible to accomplish until sometime late in June. It will then be possible to develop a correlation between varietal range of shedding period, and stigma receptive period, with the efficacy of the different pollens in fruit setting. Due to the

## PLATE - VII -



## FILBERT POLLINATOR



Pollinator, in Use.



retardedness of growth all data on parthenocarpy (which is suspected of being a frequent phenomenon in this genus) will have to be waived for the present and included in a supplementary paper. See (

### SUMMARY OF RESULTS.

Although a single year's investigation would hardly warrant drawing many too rigid conclusions the following results and observations may be significant, and will sum up the progress of the investigation thus far:

1. The best germinating medium for filbert pollen seemed to be 8 percent sugar and 2 percent gelatin solution.
2. Practically all varieties tested are vigorous in germination and reach a maximum percentage of viability in twelve hours. (Table 3).
3. Sunlight probably has no appreciable influence on pollen germination. (Table 3a)
4. Highest viability was recorded at the beginning of the shedding period for each variety and a gradual decrease from that time to the end of shedding period. (Table 4).
5. Under field conditions, the pollen remains viable for about two months. Deterioration varies almost directly with time after shedding. (Table 5).
6. Temperatures as low as 0° F have no apparent deleterious effect on pollen either in anther or

after shedding. (Table 6).

7. Temperatures of 90° or higher in dry or saturated atmosphere rapidly deteriorate viability of pollen. (Tables 7 and 8). These temperatures rarely occur in Oregon, however, during pollination time.
8. Contrast to hardness of pollen, when filberts are in bloom, stigmas of female flowers are rather sensitive to low temperatures, 15° F. killed a large percentage of expanded stigmas. (Table 9)
9. The period of apparent stigma receptivity varies with each variety; in some it precedes while in others it succeeds period of pollen shedding. Barcelona and Du Chilly have the longest periods of receptivity of the ten varieties recorded, thus suggesting a correlation between this character and their economic value. (Table No. 10-Curve No. 10).
10. Although pollination takes place in January and February, fertilization does not occur until June. The pollen tube remaining in a resting stage in the stylar tissues as an encysted spore during this three or four months interval. (Plate VI)
11. Differentiation of ovular tissue commenced about beginning of April, while maturation of the female gametophyte is not accomplished until June. (Plate V)

12. Fertilization is probably accomplished by the rapid growth of secondary pollen tube from encysted pollen-tube-spore, via the chalazal route and nuclei often enter embryo sac at a caecum.

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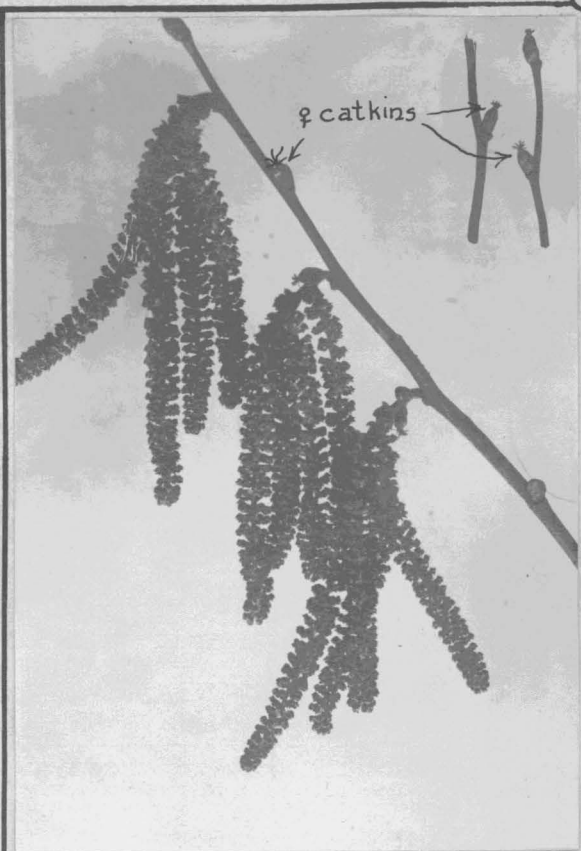
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### III. IN PERIODICALS.

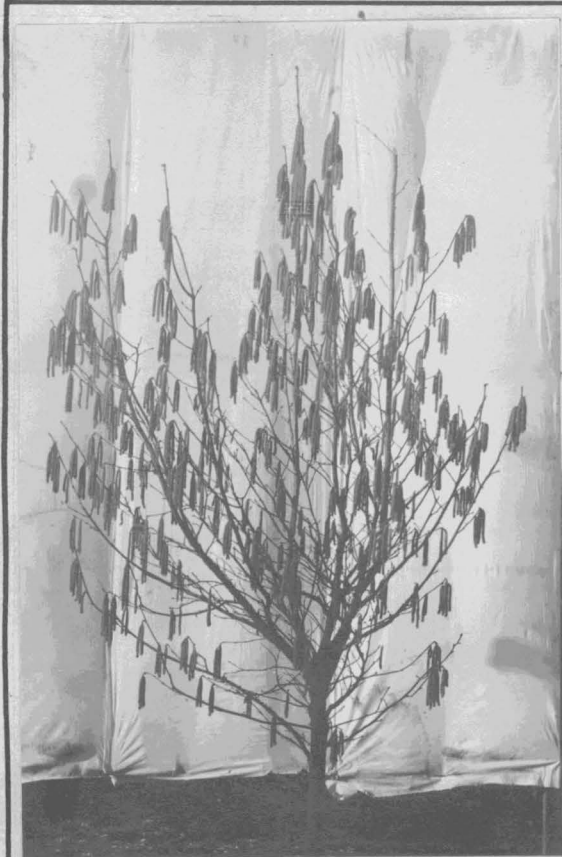
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MALE CATKINS in WINTER



MALE CATKINS (after shedding)

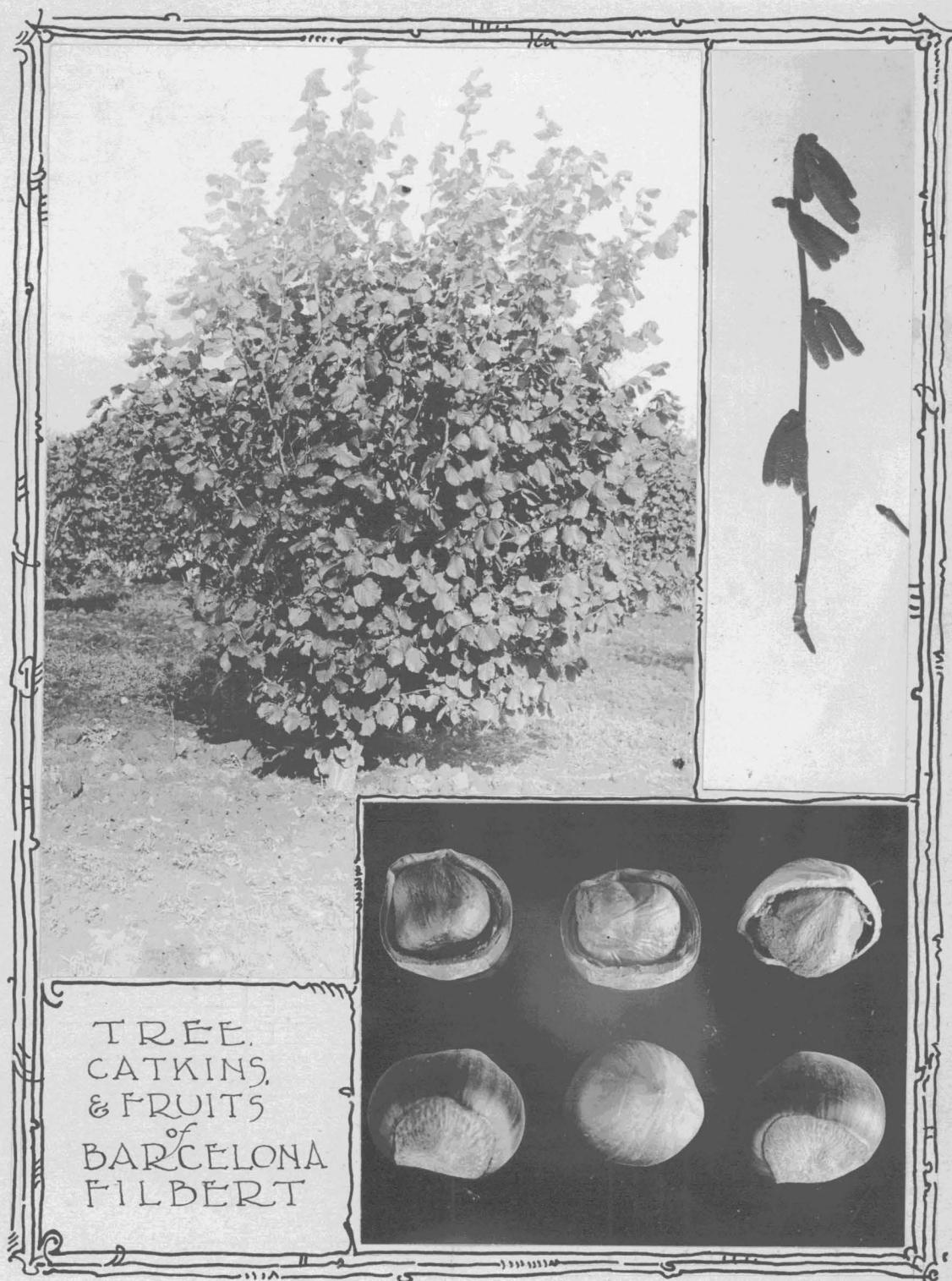


6-Year FILBERT TREE in BLOOM



FEMALE CATKINS BAGGED





S U P P L E M E N T.  
(July 10, 1921)

The work was continued throughout the month of June and into early July until fertilization had taken place and the embryos had reached 1 mm. in size. At this stage the two cotyledons and the plumule are already quite distinct. Fertilization, as suggested in Plates V and VI, took place for most of the ten varieties studied, during the first week of July. For a few days the endosperm (resulting from the fertilization of the fusion nucleus) develops quite rapidly, but is later absorbed by the continuously growing dictyledonous embryo, which eventually ruminates throughout the whole pericarp or nut. See Plate X.

During the past month (June) the pericarps grew very rapidly and from all external appearances, one might think that they were ready for harvesting. (Full size is reached early in July). Upon breaking these open, however, one is surprised to find that the ovary is almost entirely filled with parenchymous tissue or pith, with nothing but a small central placenta, (raphe) attached to the top of which is the relatively small and inconspicuous anatropous ovule. This pith is gradually absorbed by the developing embryo; the pellicle being made up of compressed remnants of this tissue together with the remains of the integuments. Plate X shows the relative sizes of these parts before and after fertilization.

Field observations show that after the pollination season, only 10 - 30% of the ovaries enlarge into potential

filbert nuts. It seems that the presence of the encysted pollen tube may be accountable for subsequent enlargement of the ovary. It is now obvious that the actual percentage of fruits set is not determinable before harvest time, when the number of "blanks" or empty nuts can be counted. It will also be interesting at that time to work out a correlation between the present "apparent set" and the "actual set".

The last two columns of Table 10 were completed on the basis of "apparent set" rather than from the "actual set". This was necessitated in order to conclude this paper at this time. In fact, it is doubted if sufficiently accurate data could be recorded in the fall, because of the large amount of pilfering which occurs in the orchard subsequent to the opening of college at that time.

The following conclusions may be drawn from this year's field work:

13. From estimates based on the apparent set of the fruits, soon after fertilization has taken place (July 8) it seems:

- (a) Barcelona is practically self sterile.
- (b) that Du Chilly is a good pollenizer for Barcelona.
- (c) but Barcelona does not satisfactorily pollenize Du Chilly.
- (d) The relative value of the ten varieties tried as pollenizers for Barcelona is as follows:

(from Table 10)

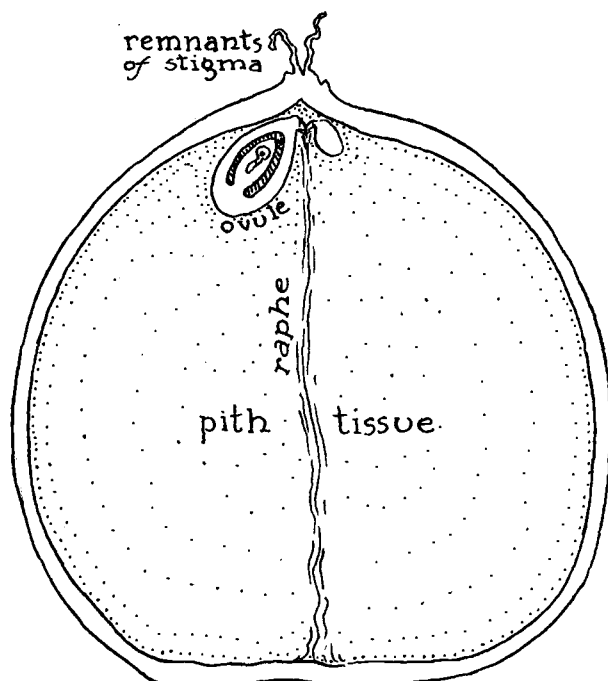
<u>Var. Pollen</u>	<u>% Set.</u>
Cosford	18.5
Daviana	25.
D'Alger	20.5
Du Chilly	31.
Fertile de Coulard	13.5
Nottingham	25.
Macrocarpa	18.
Merveille de Bolliwiller	13.
*White Aveline	—

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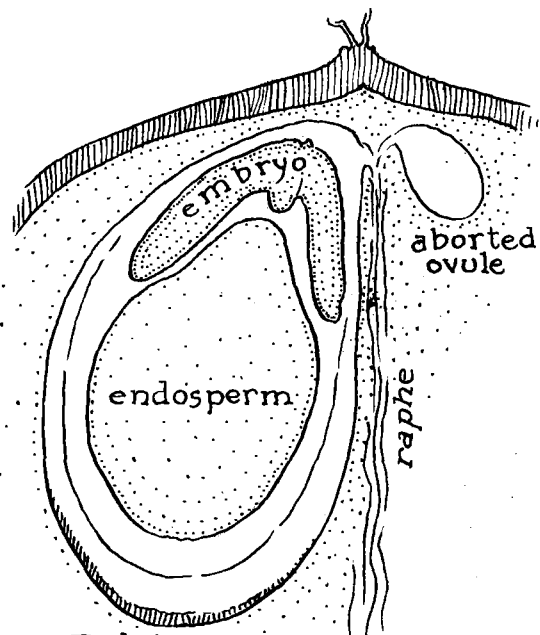
\*The branch containing sacks was broken soon after the fourth pollination and hence this variety had to be omitted in the record.

The whole subject of parthanocarpy will have to be taken up another year.

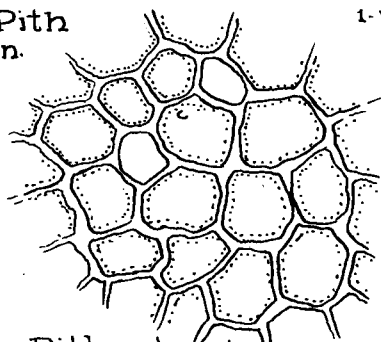
## DEVELOPMENT of FILBERT EMBRYO



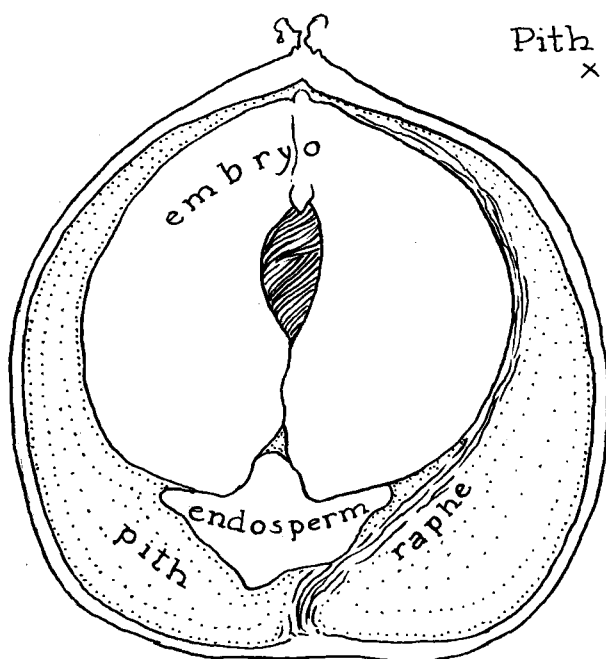
Rel. size of Ovule & Pith  
just before fertilization.  
June 20-30. x4



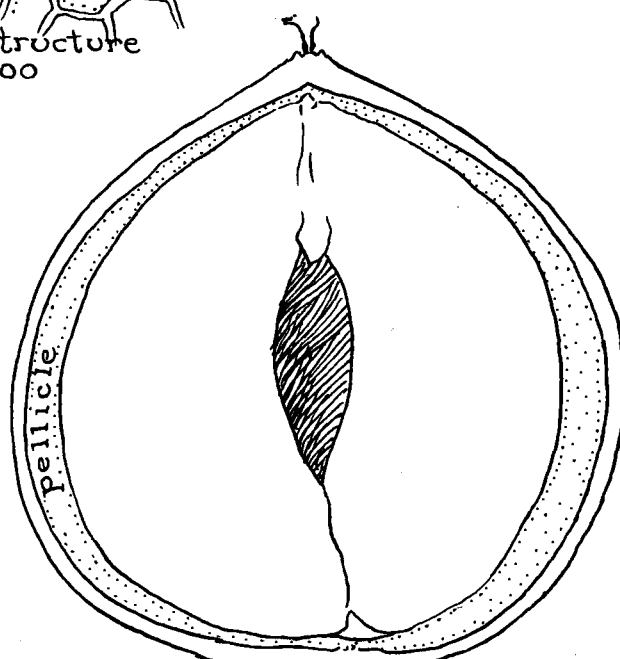
Relative size of  
Embryo & Endosperm  
1-week after fertilization  
July 1-10



Pith structure  
x 200



Embryo absorbing Endosperm  
July-Aug. x4.



Position of Embryo at  
maturity. (Sept.) x4.