A contribution to the embryogeny and developmental anatomy of the seedling in Quercus L.

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A CONTRIBUTION TO THE EMBRYOGENY AND DEVELOPIMENTAL
ANATOMY OF THE SEEDLING IN QUECUS L.

by

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INTRODUCTION

Although the anatomical investigations of the genus *Quercus* date back to the middle 1800's, most reports offer only fragments of information and do not begin to tell the complete developmental history. The area of study which has received the most attention is that of the mature wood in the red and white oak groups. Anatomical studies of the oak seedling are very few, and those of the embryo deal almost exclusively with the very early phases of development.

The objective of the present investigation was to follow the development of the embryo to dormancy, and then continue with the developmental anatomy of the seedling through the first season of growth. This report of the investigation provides basic information for further studies on the pathology, genetics, taxonomy and physiology of the oaks.
REVIEW OF PERTINENT LITERATURE

Very few reports are available in the literature on the anatomy of the oaks from a developmental standpoint. The present study is concerned principally with the developmental anatomy of Quercus, however, this review will bring together most of the known anatomical literature on the genus.

The Embryo and the Fruit

The earliest study of the embryo and fruit of Quercus was made by Hartig (1851). He studied the gross floral morphology of Q. rubra and Q. pedunculata, as well as the formation of the ovules and some early stages of embryo development.

Harz (1885), presented general descriptions of the mature acorns of a few species of oaks. He also described the internal structure of the mature pericarp of Q. pedunculata.

Stenzel (1890), discussed and illustrated the variation in size, number, and form of acorns from various oaks. However, his study was not anatomical.

Lubbock (1892), described the formation of the ovules in Q. pedunculata. He also followed the development of the fruit up to fertilization, and he stated that after fertilization "one ovule develops rapidly.... the other two cells of the ovary remain small and gradually become pushed to one side with their aborted ovules."

The development of the embryo sac in Quercus was studied again by Benson (1894). He described the presence of an extension of the embryo sac which he called the ceacum. He noted that this structure is also
present in Castanea. Benson also pointed out that although in some oaks it requires two seasons for the fruit to ripen, the pollen tubes do not actually reach the embryo sacs until the beginning of the second season.

In 1900, Conrad published the most complete study of embryo sac development in Quercus up to that time. Working with Q. velutina he described ovule development, megasporogenesis, and embryogeny up to the proembryo stage. Klebelsberg (1910), investigated the ovule and embryo sac development in Q. robur.

Vecchierello (1928), studied early embryonic stages in Q. prinus, but in the older stages he focused his attention entirely on the root histogens. Langdon (1939), studied the formation of the flower and cupule in Quercus and described the vascularization of these structures. She included a brief discussion of the enlarging fruit and embryo.

Bagda (1952), described embryo sac formation in Q. macrolepis. He also described and illustrated the development of an embryo (nearly to maturity) which he states is an apomictic embryo formed from an endosperm cell. Hjelmgqvist (1953), made a detailed study of the embryo sac development in Q. robur. He showed that the embryo sac is monosporic in origin rather than tetrasporic as was indicated by Conrad (1900). Hjelmgqvist stated that several megaspore mother cells may occur within one nucellus, a feature which Conrad (1900) also described. Hjelmgqvist pointed out that Casuarina also has this feature. He also described the presence of a caecum, like that described by Benson (1894).

The ontogeny of the staminate and pistilate flowers of Q. alba have been described by Turkel, et al. (1955). They followed the pistilate flower through the completion of megasporogenesis. Corti (1959), Scaramuzzi
(1960), and Bianco (1961), have studied the reproductive structures of *Q. ilex*, *Q. aeriflops*, and *Q. trojana* respectively. These investigators concentrated mainly on the development of the embryo sac, and described only a few phases of subsequent embryo development.

The most recent study of embryo development in *Quercus* is that by Stairs (1964), in which he described four stages of embryo development in *Q. coccinea*.

The Stem

The seedling seems to have received less attention than any other developmental phase of the oak. Sachs (1875), Englemann (1880), Lubbock (1892), and Fawcett and King (1917), described and illustrated the mechanism of acorn germination and subsequent seedling development, but without reference to internal anatomy. Bames (1910), studied the origin and development of the xylem rays in oak seedlings. Langdon (1927), has described the origin and course of the vascular bundles of *Quercus alba* in relation to the bud scales, leaves, and stipules.

Guignard (1885), studied the anatomical structure of twigs of *Quercus pedunculata*, *Q. sissileflora*, *Q. cerris*, and *Q. tosca* in order to determine the anatomical characters which could be used for taxonomic purposes. Those characters which he considered to be most significant for comparative purposes were: (1) the thickness and number of medullary rays, (2) the thickness and arrangement of the vessels in the annual rings, and (3) the relative number of lignified fibers in the wood. He concluded that anatomical characters of the wood are reliable for distinguishing closely related species.
Kuster (1900), gave a few short notes on the mechanical tissue, storage tissue and conducting tissue in Quercus. However, he gave very little detail and no illustrations were presented. Huberlandt (1914), and Nietoalfe and Chalk (1950), stated that the young twig of Quercus has a continuous bast fiber ring which later becomes interrupted by radial gaps resulting from growth stresses. Elliot (1914), in a study of four trees which were all designated as Quercus muehlenbergii (but were quite different from each other), described, along with several other characters, the structure of the wood and bark of current year twigs as well as that of older stems. Muslow (1915), made a detailed study of the 1st. year twigs of Quercus rubra, Q. schneckii, Q. coccinea, and Q. macrocarpa in a successful attempt to distinguish these four species histologically. In conjunction with the internal stem characteristics he also correlated gross leaf structure, internal leaf structure, stomata, and other characters.

Langdon (1918), studied the ray system in branches of Quercus alba from one to nineteen years of age. She categorized three types of rays: (1) uniseriate, (2) multiple, and (3) compound. The latter type consists of rays which are broader than the first two and have extensive masses of parenchyma. Her objective was to determine the effect of various conditions (suppression, vigorous growth, age, and position in the wood) on the ray system. Of these conditions, she found that the vigorous growth had more compound rays than the suppressed trees, and that the age or position in the wood did not modify the ray system.

Machado (1948), studied the origin and development of phloem fibers in the stems of Quercus suber. He found that the so-called "pericyclic" fibers have their origin in, and develop from, primary phloem tissue.
Machado (1949), also described and illustrated the origin and development of phellogen in the twigs of Quercus suber. He found that the phellogen originates in the subepidermis, that lenticels originate where stomata were previously, and that additional periderm segments are formed deeper in the cortex and even within the phloem of older branches. Bordina (1961) has recently studied the initiation and development of bud scales, axillary buds, and staminate and pistillate inflorescences in Quercus robur.

Several investigators have made critical studies of the structure of the secondary xylem in Quercus (Jeffery, 1917; Bailey, 1910a and 1920; Williams, 1939, 1942a, and 1942b; and Tillson and Muller, 1942). Other researchers have concentrated on the xylem rays of various species in the red and white oak groups (Boodle and Worsdall, 1894; Bailey, 1910b and 1911; Bannas, 1911; Jeffery, 1917; and Tippo, 1933).

The Root

Vecchierello (1923), studied the origin and development of the root histogens of Quercus prinus throughout their development in the embryo and in the germinating acorn. He found that the plerome-cylinder, periblem, and many of the cells that make up the indeterminate root-cap seem to arise from a common center of meristematic cells. He concludes that "the features of the method of origin of the primary histogens of Q. prinus indicates closer affinity to the Gymnospermous type of root development than to that of the typical Dicotyledons." This statement is based primarily on the fact that the periblem in Q. prinus (as in the Gymnosperms) is initiated by several layers of initial cells, at least eight in Q. prinus.

Holm (1910), investigated the primary and lateral roots of Quercus alba.
He found that the lateral roots have no pith and their xylem contains "very much thick-walled libriform." In the center of the primary root he found a "broad homogeneous pith with deposits of starch." Jeffery (1917), made reference to the broad rays present in oak roots. Stover (1951), in reference to cork formation in roots stated that the periderm "is formed in the cortex of Quercus agrifolia."

Ward (1892), has written a textbook-type review of the growth and development of the oak tree. In this, he presented various aspects of Quercus anatomy which were known up to that time.
COLLECTIONS FOR EMBRYO MATERIAL WERE MADE DURING THE SUMMERS OF 1963 AND 1964. THE MAJOR COLLECTIONS WERE TAKEN FROM A VIGOROUS TREE OF QUERCUS ALBA AND ONE OF Q. VELUTINA. OTHER COLLECTIONS WERE MADE FROM SEVERAL TREES OF BOTH SPECIES FOR CORROBORATION OF THE STAGE OF DEVELOPMENT IN THE MATURE EMBRYO.

DURING THE FIRST SUMMER, COLLECTIONS WERE TAKEN AT ONE WEEK INTERVALS. DURING THE SECOND SUMMER THEY WERE TAKEN AT THREE DAY INTERVALS. ACORNS WERE SELECTED FROM THE MIDDLE AND LOWER BRANCHES OF EACH TREE. EACH COLLECTION CONSISTED OF AT LEAST TEN ACORNS FROM EACH TREE AND AN ATTEMPT WAS MADE TO SELECT THE AVERAGE SIZED ACORNS AT EACH COLLECTION. THE ILLUSTRATIONS USED FOR ANY GIVEN DATE REPRESENT THE AVERAGE STAGE AS NEAR AS POSSIBLE, AS EACH COLLECTION USUALLY CONTAINED OVERLAPPING STAGES FROM THE PRECEDING AS WELL AS THE SUCCEEDING COLLECTIONS.

THE ACORNS WERE TRIMMED WITH A RAZOR BLADE AS CLOSE AS POSSIBLE TO THE EMBRYO TO ALLOW FOR PROPER PENETRATION DURING FIXATION AND EMBEDDING. ALL EMBRYO MATERIAL WAS FIXED IN GRAFT III AND DEHYDRATED IN A SERIES OF DIOXANE AND NORMAL-BUTANOL REAENTS (SASS, 1958), THEN EMBEDDED IN PARAFFIN. SECTIONS WERE CUT AT 10 TO 20 $\mu$ DEPENDING ON THE TOUGHNESS OF THE MATERIAL. SOME OF THE OLDER MATERIAL NECESSITATED PRE-SOAKING IN WATER BEFORE SECTIONING. SATISFACTORY RESULTS WERE OBTAINED BY STAINING ALL MATERIAL WITH A COMBINATION OF SAFRINGIN AND FAST GREEN.

FOR SEEDLING MATERIAL, MATURE ACORNS WERE STORED IN DRY SAND IN A PLASTIC CRISPER AND KEPT AT 35° F. THROUGH THE WINTER. ACORNS WERE GERMINATED ON PAPER IN MOIST PLASTIC CHAMBERS IN THE LABORATORY AT ROOM TEMPERA-
ture for the early stages. Other acorns were grown in 8" pots in the greenhouse for subsequent stages. The greenhouse plantings were made during early March, and collections were taken through mid September. Collections were made of the stem apex, developing epicotyl, and radicle during various phases of development, according to the length of the emerged radicle, the time of emergence of the plumule from the soil surface, or the number of visible nodes. The age of a seedling was reckoned from the time when the acorn was first placed in favorable growing conditions.

All material was fixed in Graf III or F.A.A. depending on maturity and toughness. The specimens were dehydrated in an ethyl alcohol series, gradually changed to xylene, and embedded in paraffin. Here also, the safranin and fast green staining combination proved very satisfactory.
Development of the Fruit of *Quercus alba* L.

**Embryogeny**

The ovary of *Quercus* has three locules, each of which contain two ovules. In *Quercus alba*, fertilization occurs during early and mid-June. This is approximately one month after pollination.

Eggs of all six ovules in a given ovary become fertilized at approximately the same time. In some cases the zygote has not yet divided by the 16th of June (Figure 1). Free-nucleate endosperm forms around the periphery of the embryo sac before the first division of the zygote.

The proembryo of all the ovules except one, apparently aborts very soon after fertilization, i.e. within a given ovary there was found to be only one normal proembryo. Within the embryo sacs of the other ovules the proembryo appears as a noncellular mass of protoplasm, about the size of a few-celled proembryo, in the process of disintegration.

All six ovules remain equal in size, even though they are enlarging, (Figure 2), until after the 20th of June when the ovule containing the normal embryo soon becomes much larger than the others (Figure 3). As the acorn enlarges, the abortive ovules are pushed toward its base.

By the 23rd of June, cell walls are formed between the endosperm nuclei near the periphery of the embryo sac. The embryo, which now consists of several cells, is encased in cellular endosperm. The embryo is nearly spherical in shape. Its cells are of approximately the same size except at the base, which consists of one or two larger cells (Figure 4).

By the 26th of June, the embryo has become perfectly spherical except
Figure 1. Longitudinal section through the ovule of white oak showing the zygote. June 16. 78X.

Figure 2. Transverse section through the ovary of white oak showing the slightly enlarged ovules. June 10. 47X.

Figure 3. Transverse section through the ovary of white oak showing the enlarged ovule and five aborted ovules. July 6. 19X.

Figure 4. Longitudinal section through the ovule of white oak showing the young embryo and cellular endosperm. June 23. 180X.

a - aborted ovule       o - outer integument
b - cotyledons         ov - ovule
e - endosperm          s - seed coat
em - embryo            z - zygote
i - inner integument
for its short suspensor. The outermost cells of the embryo are organized into a protoderm. The embryo still occupies a very small portion of the embryo sac (Figure 5).

By June 30th the upper portion of the embryo has begun to expand on either side, initiating the cotyledons. By the time the cotyledons have stretched outward a short distance, the cells in the central core of the embryo axis comprise a cylinder of procambium, which can be detected as darker staining cells extending from just below the shoot apex to a point just behind the root apex. By this time, the root histogens begin to take on their characteristic appearance (Figure 6).

Embryos of the July 6th collections have a distinct epidermis, especially on the cotyledons. The shoot apex is now more distinct. The endosperm has filled most of the volume of the embryo sac except immediately adjacent to the embryo, however, the latter condition may be shrinkage due to processing (Figures 7 and 15).

By July 12th, the embryo has filled nearly 2/3 of the embryo sac. The root histogens are well defined and the root cap is evident. The shoot apex is at this time a smooth, low arching dome with a uniseriate tunica. The procambium cylinder of the embryo axis is now distinct, and for the first time, procambium strands are visible within the cotyledons, however, no differentiation of vascular tissues has occurred (Figure 8).

By July 17th, the embryo nearly fills the entire volume within the seed coat except for a small amount of endosperm near the radicle, and some above and between the spreading cotyledons (Figure 16). The epidermis of the cotyledons consists of very small cells compared to the cells within. The epidermal cells of the embryo axis are about the same size as those
Figure 5. Longitudinal section showing a young white oak embryo. June 26. 78X.

Figure 6. Longitudinal section through a white oak embryo showing the beginning of cotyledon formation. July 2. 78X.

Figure 7. Longitudinal section showing the embryo of white oak. July 6. 78X.

- e - endosperm
- o - outer integument
- em - embryo
- c - cotyledons
- i - inner integument
Figure 8. Longitudinal section through a white oak embryo. 
July 12. 78X.

Figure 9. Longitudinal section through an embryo of white oak. 
July 18. 47X.

c - cotyledon lobe

ea - embryo axis

s - seed coat
within the axis, but are less elongated (Figure 9). Within the cotyledons, protoxylem cells with spiral wall thickenings have differentiated in some of the procambium strand. The procambium strands form a highly branched network throughout the cotyledons.

No significant changes occur up to the end of July, except that the embryo continues to increase in size, eventually becoming tightly appressed against the seed coat. Endosperm has essentially disappeared by the 21st of July. The lower lobes of the cotyledons soon grow down around the embryo axis (Figures 8 and 9), and eventually surround the radicle completely (Figure 10).

Soon after the middle of August, the stem apex initiates its first two leaf primordia. One leaf is initiated slightly before the other. The leaf primordia are initiated near the outer edge of the apex in a plane perpendicular to the plane of the attachment of the cotyledons. Thereafter the apex remains as a much smaller dome (Figure 11).

By the first week of September the first two leaf primordia have arched up over the stem apex, overlapping each other (Figures 12 and 13), and the stem apex has initiated two more leaf primordia 90° from the plane of the first two. The number of leaf primordia at maturity of the acorn was found to vary from three to five in different trees of white oak.

This is the state of the embryo at the time of maturity when the acorn falls from the parent tree, about the 2nd week in September.

Figure 20 shows the gross external features of developing acorns of white oak.
Figure 10. Longitudinal section through the embryo of white oak showing the lobes of the cotyledons around the embryo axis. August 3. 47X.

Figure 11. Longitudinal section through the stem apex of a white oak embryo showing the initiation of the first two leaf primordia. August 22. 78X.

Figure 12. Longitudinal section through the axis of a white oak embryo showing the first two leaf primordia after some growth has taken place. September 10. 15X.

Figure 13. Longitudinal section through the stem apex of a white oak embryo showing a closer view of the first two leaf primordia overlapping the stem apex. September 10. 78X.

c - cotyledon lobes
l - leaf primordia
sh - shoot apex
The fruit coat

At the time of fertilization the fruit coat of white oak consists mostly of parenchyma cells throughout, except for the upper portion near the stigma. Here there is a hard outer covering of very thick walled sclerenchyma cells. Inward from this there are broad areas of sclerenchyma cells which extend down from the base of the stigma nearly to the upper part of the locules (Figure 14).

By early July, the outer covering has become sclerified down over 3/4 of the fruit coat. The entire stigmatic area is highly sclerified and broad inner extensions of sclerenchyma extend down almost half the length of the fruit wall (Figure 15).

By mid or late July, additional scattered groups of thick walled sclerenchyma cells have developed within the parenchymatous center of the fruit coat (Figure 16).

By mid August, the outer sheath of sclerenchyma cells remains essentially as last described. But, the inner extensions of sclerenchyma of the enlarging fruit wall now occur near the pointed end of the acorn. Scattered throughout the major portion of the fruit coat there are now many isolated groups of thick walled sclerenchyma cells (Figures 16, 17, and 18).

The numerous hairs lining the inner walls of the locules in the young ovary soon disappear, and the inner wall of the mature fruit coat of white oak remains essentially glabrous (Figures 17 and 18).
Figure 14. Longitudinal section showing the young acorn of white oak about the time of fertilization. June 10. 17X.

Figure 15. Longitudinal section showing the developing acorn of white oak. July 6. 10X.

- cu - cup
- e - endosperm
- em - embryo
- f - fruit coat
- ov - ovule
- s - seed coat
Figure 16. Longitudinal section showing the developing acorn of white oak. July 17. 7X.

cu - cup

e - endosperm

Figure 17. Longitudinal section showing the nearly mature acorn of white oak. August 3. 5X.

f - fruit coat

s - seed coat

em - embryo
Figure 18. Longitudinal section showing the nearly mature fruit coat of white oak. August 22. 47X.

c - cotyledon tissue
s - seed coat
so - outer sclerenchyma covering

Figure 19. Longitudinal section showing the nearly mature seed coat of white oak. August 22. 47X.
Figure 20. External view of developing white oak acorns:

A. May 29.
B. June 11.
C. June 23.
D. July 6.
E. July 12.
F. July 18.
G. July 25.
H. July 30.
I. September 10.
The seed coat

At the time of fertilization, the outer integument consists of thin walled parenchyma cells about 10 to 12 rows thick. The outer row of cells is slightly darker staining and more cuboidal than the inner layers, many of which are already compressed. The inner integument consists of about 4 to 7 layers of thin walled parenchyma cells, all having a similar appearance (Figure 1).

Soon after enlargement of the embryo sac begins, in late June, the portion of the inner integument above the micropyle appears to degenerate, and only a thin layer of cell fragments remains on the border of the embryo sac. However, the portion of the inner integument which encloses the micropyle remains unchanged for some time (Figures 4, 5, 6, and 7).

Little change occurs through July except that the outer cells of the outer integument near the micropylar end of the young seed become very dark-staining and thicker walled. The portion of the inner integument which had previously been described as breaking down, has essentially disappeared (Figures 8 and 9).

Through the middle of August there is little or no change in the number of cells making up the width of the seed coat, however, the seed coat does increase in thickness. Vascular bundles with mature tracheal elements occur in a netted pattern throughout the seed coat.

The mature seed coat then, consists of only the outer integument, which is composed of 10-15 layers of parenchyma cells with slightly thickened walls and very densely-staining protoplasts; vascular bundles traverse throughout in a netted pattern (Figure 19).

Externally, the mature seed coat appears as a thin, light brown,
paper-like covering stretched tightly over the enclosed embryo.

**Development of the Fruit of *Quercus velutina* Lam.**

**Embryogeny**

The ovary of *Quercus velutina* contains three locules containing two ovules each (Figure 21). The embryo sac of all six ovules becomes matured by about the 10th of June. Fertilization occurs shortly after this, usually by the 16th of June. This is approximately 13 months after pollination.

By June 18th, the embryo is spherical in shape and consists of approximately 12 cells. By this time there is an abundant amount of free-nucleate endosperm (Figure 22). Only one of the six ovules in an ovary was found to contain a normal embryo. The embryos of the other five ovules had aborted very soon after fertilization. Possibly, some of the eggs abort even before fertilization. However, all the ovules continue to increase in size at the same rate (Figure 23) until about June 21st when the ovule with the normal embryo far outgrows the others. The aborted ovules soon stop growing and are forced into the pointed end of the developing acorn.

By June 23rd, the endosperm has become cellular around the periphery of the embryo sac. At the micropylar end of the embryo sac the endosperm surrounds the now somewhat larger embryo which consists of many more, but much smaller cells. The embryo is still essentially spherical except for its suspensor (Figures 24 and 32).

The upper flanks of the embryo enlarge, initiating the cotyledons. By the 26th of June the embryo is heart shaped due to the expansion of the cotyledons. The first beginnings of procambium formation can now be seen in the embryo axis (Figure 25).
Figure 21. Transverse section through the pistillate flower of black oak showing the young ovules before fertilization. May 17. 15X.

Figure 22. Longitudinal section through the embryo sac of black oak showing the young embryo. June 16. 180X.

Figure 23. Transverse section through the ovary of black oak showing the slightly enlarged ovules. June 16. 15X.

Figure 24. Longitudinal section through the ovule of black oak showing the young embryo. June 23. 180X.

- cu - cup
- o - outer integument
- em - embryo
- ov - ovule
- fe - free-nucleate endosperm
- ow - ovary wall
- i - inner integument
By July 2nd, procambium is distinct within the embryo axis and the root histogens are beginning to assume their characteristic appearance. The stem apex is a broad dome with a uniseriate tunica (Figure 26). Cellular endosperm fills the entire embryo sac by this time.

By July 6th, the cotyledons have grown to be more than twice the length of the embryo axis, and the embryo now fills about 2/3 of the embryo sac. Dense staining procambium strands are visible within the embryo axis and scattered throughout the cotyledons. A distinct epidermis of small, square cells covers the entire embryo (Figures 27 and 33).

By July 10th, the embryo nearly fills the embryo sac. Some endosperm remains at either end of the embryo sac and between the cotyledons. The root cap is now distinct and the cotyledonary lobes have begun growing down over the embryo axis (Figure 28). Spiral protoxylem vessels are present in the procambium of the cotyledons.

Usually by July 17th, all endosperm has disappeared and the embryo is tightly appressed against the inner portion of the seed coat. The lower lobes of the cotyledons have grown further down around the embryo axis (Figure 29).

By August 3rd, little change has taken place except that the entire embryo has increased in size and the cotyledonary lobes have increased in length (Figure 30). The embryo continues to increase in size and by August 22nd the lobes of the cotyledons surround the radicle (Figure 31).

The embryo is essentially morphologically mature by the time described in the last paragraph, and with the addition of some growth of the cotyledons, this is the state of the embryo when the acorn falls from the parent tree during the first two weeks of September.
Figure 25. Longitudinal section through the ovule of black oak showing the young embryo and the cotyledon primordia. June 26. 78X.

Figure 26. Longitudinal section through the embryo of black oak showing the embryo axis. July 2. 78X.

Figure 27. Longitudinal section through the developing seed of black oak. July 6. 18X.

c - cotyledons    i - inner integument

e - endosperm    o - outer integument

em - embryo    s - seed coat
Figure 28. Longitudinal section of the developing seed of black oak. July 10. 16X.

Figure 29. Longitudinal section through the embryo of black oak, cut perpendicular to the plane of the cotyledon attachment. July 17. 15X.

- c - cotyledon
- e - endosperm
- f - fruit coat
- s - seed coat
Figure 30. Longitudinal section through the axis of the black oak embryo, cut parallel to the plane of the cotyledon attachment. August 3. 15X.

Figure 31. Longitudinal section through the axis of the black oak embryo, cut perpendicular to the plane of the cotyledon attachment. August 22. 15X.

c - cotyledon lobe

em - embryo axis
The fruit coat

In early June, the fruit coat (the covering of the acorn) consists of thin walled, light-staining parenchyma cells, bordered on the outside by two to four tiers of very thick walled, elongate sclerenchyma cells which are positioned perpendicular to the surface of the young acorn. An epidermal layer with a thick cuticle occurs exterior to the sclerenchyma cells. Immediately underneath the sclerenchyma layer, are one to two rows of elongate parenchyma cells which later become sclerified and contribute to the thickness of the hard covering. Three to six layers of very dark-staining parenchyma cells border the inner portion of the fruit coat. Scattered throughout the width of the fruit coat are other parenchyma cells with dark-staining deposits. Several rows of cuboidal sclerenchyma cells extend down from just below the stigmas to the level of the necks of the young ovules, midway between the outer and inner surface of the fruit coat.

The outer sclerenchyma covering soon becomes much thicker, however, the inner extensions of sclerenchyma remain essentially the same for some time, as do the other tissues of the fruit coat except for a general enlargement of the entire acorn (Figure 32).

Through the month of July, the cells of the outer sclerenchyma covering become much thicker walled. The sclerenchyma cells extending down from the pointed end of the acorn become thicker walled, but as the fruit coat enlarges these cells comprise only a small group located in the pointed end of the acorn and do not contribute to the fruit coat proper. Occasionally, an isolated group of sclerenchyma cells occurs embedded within the parenchyma cells of the fruit coat. Parenchyma cells with dark-
Figure 32. Longitudinal section through a young black oak acorn. June 26. 8X.

Figure 33. Longitudinal section through the developing acorn of black oak. July 6. 6X.

cu - cup
f - fruit coat

e - endosperm
s - seed coat

em - embryo
staining deposits remain scattered throughout the parenchymatous portion of the fruit coat. Just underneath the outer sclerenchyma covering, several layers of dark-staining cells soon occur (Figures 33 and 34).

By late August, the fruit coat is morphologically mature and remains much the same as that last described. It consists of a very hard outer covering of sclerenchyma cells which is covered by a thin epidermal layer and a relatively thick cuticle; inward from this there is a zone of dark-staining parenchyma cells; from here inward there are dark staining cells scattered between other clear staining parenchyma cells. Several layers of the cells comprising the inner portion of the fruit coat are compressed together due to the stretching of the fruit and enlarging seed within (Figure 35).

The thick coating of hairs lining the locules within the young ovary of black oak remains as a thick mat attached to the inner surface of the fruit coat in the mature acorn.

Figure 37 shows the gross external features of the developing acorns of black oak.

The seed coat

At the time the eight nucleate stage of the embryo sac is complete, the outer integument has a thickness of 7 to 12 thin walled parenchyma cells. The outermost layer of cells is filled with dark-staining mucilaginous material. The inner integument is 7 to 10 cells thick, consisting of light staining, thin walled parenchyma cells throughout. No change takes place from the above until after fertilization. By the time the proembryo consists of a few cells, pigmented parenchyma cells are
Figure 34. Longitudinal section through the acorn of black oak.
July 21. 5X.

Figure 35. Longitudinal section through the nearly mature fruit coat of black oak. August 22. 69X.

c - cotyledon

f - fruit coat

cu - cup

s - seed coat

em - embryo axis

sc - outer sclerenchyma covering
Figure 36. Longitudinal section through the nearly mature seed coat of black oak. August 22. 78X.

Figure 37. External view of developing black oak acorns.

A. May 13.  
B. May 29.  
C. June 11.  
D. June 23.  
E. July 6.  
F. July 12.  
G. July 18.  
H. July 30.  
I. September 4.
scattered throughout the outer integument. The inner integument has become much reduced in thickness due to compression and breakdown of the cells comprising it. Only that part of the inner integument which surrounds the micropyle remains unchanged (Figure 22).

By the time the cell walls form between the endosperm nuclei (during the last of June), the inner integument has nearly broken down completely, except for the portion surrounding the micropyle (Figure 24).

Little change takes place during the development of the seed coat from the condition last described. The seed coat increases slightly in thickness, but remains about the same number of cells in width. The dark-staining deposits increase, and vascular bundles differentiate throughout in a netted pattern. All the cells remain thin walled. A small portion of the inner integument remains at the micropylar end of the mature seed, however, it contributes essentially nothing to the seed coat proper.

The mature seed coat of black oak then, consists of the outer integument only. In gross appearance the seed coat is a light brown, papery covering over the tightly enclosed embryo. Figure 36 shows a longitudinal section of the morphologically mature seed coat.
Development of the Seedling of *Quercus alba* L.

**Histogenesis of the stem**

**Primary tissues** The organization and structure of the shoot apex of the seedling is essentially the same as that of the shoot apex of the mature embryo, i.e. it consists of a tunica and corpus from which arise the primary tissues of the stem. The tunica consists of a single layer of cells maintained by anticlinal cell divisions. The corpus consists of an unstratified area of cells located immediately below the tunica. The corpus is maintained by cell divisions in random planes.

In the main axis of the stem of a young seedling the procambium first becomes distinct as an irregular cylinder of smaller dark-staining cells about .08 to .10 mm. below the stem apex. Individual bundles become evident within the procambium cylinder. The first differentiation within a given bundle is the formation of protoxylem on the innermost edge of the bundle. This occurs in the base of the next to the youngest leaf primordium, about .10 to .13 mm. below the stem apex. In some bundles the first-formed xylem cells are in a radial row toward the center of the bundle, and in other cases they are scattered on the inner edge of the bundle. The first protophloem cell becomes evident usually at least by the time when 1 to 3 primary xylem cells have differentiated (Figure 38). More primary phloem develops on either side and inward from the first protophloem cell, forming a small group across the outer periphery of the procambium strand. Approximately the outer 1/5 of the procambium strand cells differentiate into primary phloem, and on the
Figure 38. Projection drawing of a transverse section of a differentiating procambium strand, 350 μ below the stem apex of a two week old seedling which had an epicotyl 5 cm. in height. 550X.

Figure 39. Projection drawing of a transverse section of a vascular bundle, 5 mm. below the stem apex of the same seedling as described for Figure 38. 550X.

Figure 40. Projection drawing of a transverse section taken about 2 cm. below the stem apex of the same seedling as described for Figure 38. 550X.

p - protophloem
px - protoxylem
opposite side of the strand, rows of primary xylem differentiate almost to the center. Cells with dense staining cytoplasm (future xylem parenchyma) remain on either side of the rows of primary xylem. At this time, the cells in the center of the bundle form a dark band across its diameter parallel with the outer periphery of the stem. The cells immediately inward from the band of dark-staining cells begin periclinal divisions, initiating the fascicular cambium (this occurs about 3 to 7 mm. below the stem apex). By this time, the cells which will become phloem fibers have increased in diameter and become more vacuolate (Figure 39).

**Secondary tissues** After the initiation of fascicular cambium, the bundles increase in cross-sectional area rapidly. In many bundles the first formed secondary xylem elements are much larger in diameter than the primary xylem cells. The cytoplasm of the xylem parenchyma soon becomes less dense. Some of the cells in the dark-staining band immediately outside of fascicular cambium become vacuolate and differentiate into sieve tubes, the others become phloem parenchyma. The immature phloem fibers form distinct groups of vacuolate cells bordering the outer periphery of the vascular bundles.

By the time the first 2 or 3 layers of secondary xylem cells have enlarged to nearly their maximum diameter, interfascicular cambium has been initiated between some of the bundles (Figure 40). The cell walls of the phloem fibers become thick and lignified. At the same time, the xylem parenchyma and the parenchyma cells just inward from the interfascicular cambium become thicker walled. A continuous vascular cambium
forms around the circumference of the stem (Figure 41) and continues to produce secondary tissues throughout the growing season. The interfascicular cambium is initiated about 1 1/2 to 2 cm. below the stem apex and begins producing secondary tissue 3 to 4 cm. below the stem apex.

Shortly after the phase of development shown in Figure 41, periclinal divisions occur in the layer of cells immediately inward from the epidermis, thus initiating the phellogen (Figure 42) which soon produces several layers of cork (Figure 43) and eventually ruptures the epidermis (Figure 45). In white oak seedling stems the periderm is usually subepidermal, however, in the first internode above the cotyledonary node of some seedlings, phellogen is initiated inward from the zone of collenchyma cells in the cortex, just a few cells outward from the primary phloem fibers (Figure 44).

At the end of the first growing season the secondary xylem consists of large vessels in a somewhat ring-porous arrangement around the stem. Uniseriate and occasional biseriate xylem rays occur within a background of tracheids and scattered fiber-tracheids. Exterior to the vascular cambium the secondary phloem consists of small groups of sieve tubes and companion cells scattered among large phloem parenchyma cells. Frequent dark-staining uniseriate phloem rays occur throughout. By now the primary phloem fibers have become very thick walled and, in the older seedlings, very thick walled sclereids develop between the groups of primary phloem fibers (Figure 45). In the five and six month old seedlings, occasional groups of secondary phloem fibers occur.

Immediately outward from the primary phloem fibers, the cortex consists of rather loose-fitting parenchyma cells, some filled with dark-
Figure 41. Transverse section about 4 cm. below the stem apex of a white oak seedling which had an epicotyl 7 cm. in height, and the first foliage leaves just unfolding. 78X.

Figure 42. Transverse section from the base of a 7 cm. long epicotyl of a 20 day old white oak seedling. 180X.

Figure 43. Transverse section about 4 1/2 cm. below the stem apex of a 14 1/2 cm. epicotyl of a 4 month old white oak seedling. 78X.

Figure 44. Transverse section of the first internode above the cotyledonary node of a 4 month old white oak seedling, which had an epicotyl 14 1/2 cm. in height. 78X.

\textit{ph} - phellogen initiation

\textit{pe} - periderm
Figure 45. Transverse section of a 6 1/2 month old seedling stem of white oak taken from the 2nd internode above the cotyledonary node. 78X.

pe - periderm
staining deposits, others with large crystals. Just inward from the phellogen, a zone of collenchyma remains.

Histogenesis of the root

Primary tissues The development and composition of the root apex of *Quercus prinus* has been fully described by Vecchierello (1928). The results of the present study on *Quercus alba* and a previous study by Logensen (1963) on *Q. velutina* show no differences from those reported by Vecchierello.

Immediately behind the root meristem the future stele and cortex are easily distinguishable. They are distinctive mainly due to the presence of larger cells making up the periblem and the smaller cells of the plerome.

The plerome consists of a lighter staining center portion and a more darkly staining outer portion. Within this outer portion there are circular groups of cells evenly spaced around the entire circumference. It is near the center of these circular groups of cells that the first protophloem cell appears (this usually occurs about 1 mm. from the tip of the root). The protophloem is first distinguished by its slightly lighter staining cytoplasm, then as differentiation occurs, by its very clear interior and dark-staining cell wall (Figure 46). At first, one protophloem cell is formed in each of the aforementioned groups of cells, then two more protophloem cells differentiate on either side of the first (Figure 47). This occurs quite synchronously around the root.

The cells immediately surrounding the protophloem enlarge in diameter greatly and become lighter staining. The diameter of the center portion of the stele (future pith) increases as does the diameter of the root it-
Figure 46. Transverse section 1 mm. from the root tip of a 3 week old white oak seedling which had a radicle 14 cm. in length. 350X.

Figure 47. Transverse section 1.5 mm. from the root tip of the same seedling as described for Figure 44. 78X.

p - protophloem
Two to three cells outward from the outermost protophloem cells there is a distinct unicellular row of cells with dark-staining cytoplasm and more distinct nuclei. This layer later becomes thick walled and filled with dark-staining deposits (Figures 48 and 49). This possibly is the endodermis, however, no casparian strips were found. Slightly inward from the protophloem, metaphloem begins to differentiate. The areas of primary phloem become somewhat compressed as growth continues, and their volume increases more tangentially than radially. As the other cells of the root become lighter staining, the primary phloem strands are detectable only by the smaller size of these cells.

Next, the primary xylem begins differentiation (this occurs about 3/4 to 1 1/4 cm. up from the level where the first protophloem becomes evident). The first protoxylem cells are formed alternately between the primary phloem strands. At any given protoxylem pole the first two or three protoxylem cells seem to become thick walled almost simultaneously. About the time (or slightly before) the first protoxylem cells differentiate, the metaxylem cells can be detected as having a slightly larger diameter than the adjacent cells except where they merge into the larger cells of the pith (Figure 48).

The metaxylem cells gradually differentiate centripetally until the primary xylem strands consist of about 15 to 30 cells each. In all roots observed in this study, both in the radicle and lateral roots (except in the very small ones of the latter) there remained a permanent pith the whole length of the root (Figures 49, 50, and 51).

The number of primary xylem strands varies greatly between roots of different plants, between roots of the same plant, and even within the
Figure 48. Projection drawing of a transverse section about 1 1/2 cm. from the root tip of a 5 day old white oak seedling which had a radicle 3 cm. long. 820X.

en - endodermis
px - protoxylem
mx - metaxylem
Figure 49. Transverse section about 2 cm. from the root tip of a 5 day old seedling of white oak having a radicle 7 1/2 cm. long. 78X.

Figure 50. Transverse section about 8 cm. from the root tip of a 14 cm. radicle of a 20 day old white oak seedling. 78X.

Figure 51. Transverse section about 37 1/2 cm. from the root tip of a 50 cm. radicle of a 3 1/2 month old white oak seedling. 78X.

c - vascular cambium   ph - phellogen initiation
pe - periderm           pr - primary xylem
same root. The number in this study varied from 6 to 16 primary xylem strands. Within one root the number varied from 9 near the apex of the root to 16 near its base. In Quercus alba, it was found to be the usual case for the number of primary xylem strands to vary within the same root.

Secondary tissues About the time of the completion of primary growth, and usually before the initiation of vascular cambium, periclinal cell divisions occur in the layer of cells immediately inside of the "endo
dermis" (Figure 49). This is the initiation of phellogen which eventually becomes very distinct and produces cork cells to its exterior (Figures 50 and 51). Prior to the initiation of phellogen, the multilayered pericycle increases in width from about 3 to 5 or 6 cell layers.

The vascular cambium becomes initiated between the xylem and phloem nearly synchronously around the root at a given level. However, it seems to first be more distinct near the outer flanks of the primary xylem strands, then, just inside of the primary phloem, and finally outside of the protoxylem poles until a complete connection is made (Figure 50).

The vascular cambium produces secondary xylem continuous with the primary xylem, and as growth continues, the secondary xylem is laid down in broad sweeps radiating from the primary xylem poles. Uniseriate xylem rays occur frequently. In some cases a broad multiseriate ray is formed radiating from the primary xylem pole. Between the primary xylem poles the cambium produces broad multiseriate secondary rays of parenchyma and scattered fiber tracheids (Figure 51).

To the outside, the vascular cambium produces secondary phloem which
consists of a large amount of parenchyma, and in older roots (2 to 5 months) primary phloem fibers appear in small isolated strands near the position of primary phloem. Secondary phloem fibers are also produced, at first in scattered groups of one to five cells, then later in larger definite groups around the root. The older sieve tubes become isolated in small groups, and due to the enlarging parenchyma cells, many of them become crushed (Figure 51).
DISCUSSION

The Acorn

Several studies have been made on embryo sac development, and a few on early embryonic development in Quercus, however, none indicate the stage of development of the embryos in the abortive ovules at the time of abortion. Lubbock (1892) observed that after fertilization one ovule develops rapidly and the others soon abort and are pushed to one side. However, he mentions nothing of the embryo development within these ovules, nor whether fertilization even takes place. Ward (1892) states that "...each of the total of six eggs may be fertilized by the contents of so many pollen tubes.... but the rule is that five of the ovules with their contents perish at an early period, because one strong one takes the lead in development, and "starves the rest by taking all the available nourishment to itself." Ward gives no indication as to the developmental phase of the embryos at the time of abortion. Stairs (1964) offers evidence that ovule abortion is not due to failure of pollination or fertilization by stating that "several ovules within a single acorn contained developing endosperm prior to embryo development." However, he too, fails to mention how far the abortive embryos develop before they stop growing.

In the present study a normal embryo was not found in any of the abortive ovules. Usually free-nucleate endosperm is produced, and occasionally a normal zygote was found. However, a few days after fertilization and before the ovules had aborted completely, there was observed a spherical, noncellular mass of dark staining protoplasm the size of a few-celled pro-embryo. From the above information, the zygotes of the abortive ovules do
Several authors report the occurrence of multiple seeded acorns (Weehan, 1871; Coker, 1904; Smith, 1914; Buchholz, 1941; and Hosner, 1959). Harvey (1917), reported a multiple embryo condition in Quercus alba. In the present study none of the acorns observed had either several seeds or several embryos.

This study confirms that part of a classification used by Williams (1959), in which he states that the abortive ovules are located apically in mature acorns of the red oak group, and basally in those of the white oak group.

In the present study, no "caecum" was found on the embryo sac as has been reported by Benson (1894), and Hjelmqvist (1953).

The time of endosperm depletion has not been clearly described previously. It was found in this study that endosperm in Quercus alba has usually been absorbed by July 21st and certainly by August 3rd. In Q. velutina the endosperm is usually used up by July 17th or shortly thereafter.

Although pollination occurs approximately one year earlier in Q. velutina than in Q. alba, fertilization occurs at approximately the same time in both species. Subsequent embryo development is basically similar in the two species up to the last of July, except that in Q. velutina the acorns are slightly advanced both externally and internally over the acorns of Q. alba. However, after late July, Q. alba acorns develop very rapidly and soon overtake those of Q. velutina. This differs from Stairs' (1964) observations in that he reported that a particular stage in Q. alba was about 10 days behind that of Q. ilicifolia and Q. cocinina. This may be
true up to the last of July, but subsequently there was found to be a
great difference in differentiation and organogeny between Q. alba and
Q. velutina. The extent to which the lower lobes of the cotyledons extend
down around the radicle was found to be a relatively good indication of
the morphological maturity of a developing embryo. In Q. alba the extent-
ion of the cotyledonary lobes lags behind that of Q. velutina up to the
last of July, but by August 3rd the lobes in Q. alba have usually extended
down around the entire radicle. This does not occur in Q. velutina until
about the 22nd of August. More significantly, during mid or late August
in Q. alba the shoot apex initiates two leaf primordia which continue to
develop and overlap each other by early September. Meanwhile, there are
usually two more leaf primordia initiated 90° from the plane of the first
two. In Q. velutina the stem apex remains essentially devoid of leaf
primordia at dormancy (as does that of Q. coccinea, Stairs, 1964) and
does not reach that stage of development described for the mature embryo
of Q. alba until after germination of the acorn and the radicle has grown
approximately 2 cm. in length (Iovigensen, 1963). Only occasionally is
there found the very earliest initiation of leaf primordia in the mature
acorn of Q. velutina.

Although Stairs apparently worked on two members from the red oak
group (Q. ilicifolia and Q. coccinea) and one from the white oak group
(Q. alba) he reports only his observations on the embryogeny of Q. coccinea,
stating that the developmental stages of the embryo in all three cases
"are relatively uniform from a cytological or morphological viewpoint."
This was not found to be the case in the two species studied in the present
investigation.
The mature fruit coat of *Q. alba* is very similar to that of *Q. pedunculata* (Harz, 1885) and *Q. macrolepis* (Bagda, 1952) in that it consists of a thick outer covering of sclerenchyma and numerous groups of thick walled sclereids scattered throughout the parenchyma cells. However, the fruit coat of *Q. velutina* differs from that of *Q. alba* in that the outer sclerenchyma covering in *Q. velutina* is thicker, and only rarely are there found groups of thick walled sclereids within the parenchyma cells. The obviously tougher shell of the *Q. velutina* acorn then, is due to the outer stony layer and not to any support from the inner layers. A commonly used character for distinguishing members of the red oak group from those of the white oak group is that of the inner surface of the fruit coat being glabrous in the case of white oaks, and the inner surface of the fruit coat being hairy in the case of the red oaks. This was found to be true in the present investigation.

The seed coats of *Q. alba* and *Q. velutina* are essentially the same histologically. Their structure agrees with that figured by Harz (1885) for *Q. pedunculata*, and their origin, being from the outer integument, is in accordance with the findings of Bagda (1952) for *Q. macrolepis*.

The Stem

From a developmental standpoint, the seedling stem of *Q. alba* is basically the same as that reported by Mogensen (1963) for *Q. velutina*. They both possess the characteristic features of most dicot stems as reviewed by Esau (1943a, 1953, 1954): The stem apex is composed of a tunica (one layer in the case of *Quercus*) and corpus from which arise the primary tissues of the stem; the primary phloem fibers develop from pro-
cambium cells (this study corroborates the observations of Machado, 1948 on *Q. suber*); between the primary xylem and phloem there is formed a fascicular cambium, and subsequently an interfascicular cambium develops between the vascular bundles from the reactivation of interfascicular parenchyma. A continuous vascular cambium produces secondary xylem and phloem; and the first phellogen is generally initiated in the subepidermis.

Some features which differ from the usual, are (1) the formation of protoxylem before protophloem in many of the bundles (this has been reported by Sanio, 1865 in *Carpinus*, and was also indicated by Langdon, 1927 in *Quercus alba*), and (2) the occasional formation of the initial cork cambium deep in the cortex at the base of some seedling stems.

The anatomical structure of the seedling stem of *Q. alba* at the end of the first season of growth is also essentially the same as that reported for *Q. velutina* by Mogensen (1963). Using some of the criteria with whichMuslow (1915) helped to distinguish four species of oaks, it was found that: (1) the presence of separate bundles in the early vascular system is relatively distinct in the seedling stem of both *Q. velutina* and *Q. alba*. (2) In both species enough cork is produced in the first growing season to rupture the epidermis (3) the bast fibers in both species are in distinct strands. Late in the season there may be sclereids formed between the groups of bast fibers but the original groups can still be detected as distinctly separate, and (4) the xylem of both species is neither distinctly ring nor diffuse porous, however, that of *Q. alba* tends to be more ring porous in that the early wood vessels are usually larger in diameter than those formed in the late wood. Also, the commonly used character (in mature wood) of round and very thick walled late wood vessels in members
of the red oak group was not found in the seedlings of *Q. velutina*.

It seems that internal structure alone is not enough to distinguish between the seedling stems of *Q. alba* and *Q. velutina*.

### The Root

From an ontogenetic aspect, the root of *Quercus alba* differs from the root of *Q. velutina* studied by Kögensen (1963) in the following respects:

1. The protophloem in *Q. alba* roots first becomes arranged in several groups of 3 around the root, whereas in *Q. velutina* roots the protophloem is first arranged in localized groups of two.
2. In *Q. alba* roots there is only one strand of primary phloem between any two primary xylem poles. Ward (1892), described the root of an undesigned species of *Quercus* as having one strand of primary phloem between each two primary xylem poles, and (3) the number of primary xylem poles in *Q. alba* roots varied from 6 to 16 whereas this only varied from 6 to 7 in *Q. velutina* roots. Also, the number of primary xylem strands was found to vary within the same root of *Q. alba* (a feature also found in *Libocedrus decurrens* by Wilcox, 1962) and to remain constant within a given root of *Q. velutina*. Ward (1892), stated that there are five strands of primary xylem in the root of *Quercus*, and did not mention any variation from this number.

Some features which these two species have in common with each other and which can be correlated or contrasted with characteristics found in other roots are: (1) protophloem cells differentiate before protoxylem. This is a feature which according to Esau (1953) is common in angiosperm
roots (2) primary phloem and primary xylem differentiate centripetally. This also is known to be a common feature in angiosperm roots, and supports those observations by Ward (1892) in roots of Quercus (3) there is a permanent pith the whole length of the radicle. This is an uncommon feature in dicot roots, however, it has also been reported in Valencia Orange by Hayward and Long (1942), and judging from the illustrations of Cowes (1951) this is also the case in roots of Fagus sylvatica. Holm (1910), reported that the lateral roots in Q. alba have no pith, and Mogensen (1963) reported the same for Q. velutina. However, it was found in this study on Q. alba that only the smaller lateral roots lack a pith, and that in those cases where large lateral roots are produced they contain a pith. This probably is also the case in Q. velutina (4) phellogen is initiated at the same time or possibly slightly before the initiation of the vascular cambium. It is the usual case for phellogen to be initiated, somewhat after the initiation of the vascular cambium. Following the establishment of periderm, the primary cortex dies and becomes more or less sloughed off as is the usual case in woody dicot roots (5) Esau (1943b), states that in the pear root, it is the usual case for the first multiseriate xylem rays to be formed in a radial line with the primary xylem poles and the first uniseriate rays to be formed between the primary xylem poles. Barghoorn (1940), found this to be the case in most dicot roots. In both Q. velutina and Q. alba it was found that the multiseriate xylem rays are more commonly formed in a line between the primary xylem poles and less frequently radiating from the primary xylem poles.
SUMMARY

An investigation was made of the anatomical development of the acorns of Quercus alba L. and Q. velutina Lam. The developmental anatomy of the root and shoot of the seedling of Q. alba through the first season of growth was also studied.

Embryo development was followed from the very early stages to the mature embryo. It was found to be the usual case that five out of the six ovules in a given ovary abort very early, leaving only one normal seed per acorn. Fertilization takes place in the abortive ovules, but the zygote does not develop. The abortive ovules in Q. alba are located at the base of the mature acorn. In Q. velutina the abortive ovules are apical.

There were no cases of polyembryony or a multiseed condition found in the present study.

Endosperm, in Q. alba, was usually absorbed by July 21st and certainly by August 3rd. In Q. velutina the endosperm was usually depleted by July 17th or shortly thereafter.

Embryogeny in Q. alba and Q. velutina is similar in the early stages and up through late July, except that Q. alba lags behind Q. velutina. However, after the last of July the embryo of Q. alba develops very rapidly and surpasses that of Q. velutina in organogenesis. It was found that by late August, the shoot apex of Q. alba had initiated two leaf primordia which continue to grow and overlap each other by early September. Meanwhile, there are usually two more leaf primordia initiated 90° from the plane of the first two. In Q. velutina, the shoot apex of the mature
embryo is generally devoid of leaf primordia; only occasionally will there
be the very earliest initiation of leaf primordia before maturity of the
acorn is reached.

The seed coat in both species was found to be derived from the outer
integument only. The structure of the seed coat is essentially the same in
both species.

The structure of the mature fruit coat of *Q. alba* was found to consist
of a cuticle and epidermis covering a thick zone of thick-walled scleren-
chyma cells; the zone of sclerenchyma cells borders several inner layers
of parenchyma cells; the latter have scattered between them, several groups
of thick walled sclereids. The mature fruit coat of *Q. velutina* differs
from that of *Q. alba* in that the zone of thick walled sclerenchyma cells
is slightly thicker and only rarely are there found groups of sclereids
within the inner parenchyma layers. Also, the inner surface of the fruit
coat of *Q. alba* is glabrous, while that of *Q. velutina* is densely hairy.

The seedling stem of *Q. alba* was found to be essentially the same,
anatomically, as the seedling stem of *Q. velutina* which was previously
studied by Mogensen (1963). They both possess the characteristic features
of most woody dicot stems in that the stem apex is composed of a tunica
(one layer in the case of *Q. alba* and *Q. velutina*) and corpus from which
arise the primary tissues, the primary phloem develops centripetally
in reference to the exterior of the stem while primary xylem differentiates
centrifugally, the primary phloem fibers develop from procambium, a fas-
cicular and interfascicular cambium are formed and together produce
secondary xylem and phloem, and the first phellogen is generally iniated
in the subepidermis.
Some features which were found to differ from the usual are (1) the formation of protoxylem before protophloem, and (2) the occasional formation of the initial cork cambium deep in the cortex at the base of some seedling stems.

Ontogenetically, the root of *Q. alba* was found to differ from that of *Q. velutina*, studied by Mogensen (1963), in the following respects: (1) the protophloem in *Q. alba* roots first becomes arranged in several groups of 3 around the root, whereas in *Q. velutina* roots the protophloem is first arranged in localized groups of two (2) in at least one stage in the development of primary tissues in *Q. velutina* roots each primary xylem pole is associated with two distinct areas of primary phloem. This feature was not observed in roots of *Q. alba*, and (3) the number of primary xylem poles in *Q. alba* roots varied from 6 to 16 whereas they only varied from 6 to 7 in *Q. velutina* roots. Also, the number of primary xylem strands was found to vary within the same root of *Q. alba* and to remain constant within a given root of *Q. velutina*.

Anatomical features which were found to be consistent in roots of both *Q. alba* and *Q. velutina* are: (1) protophloem cells differentiate before protoxylem (2) primary phloem and primary xylem differentiate centripetally (3) there is permanent pith the whole length of the radicle, and also in the larger lateral roots (4) phellogen is initiated at the same time or slightly before the initiation of the vascular cambium, and (5) the broad multiseriate xylem rays are most commonly formed between the positions of the primary xylem poles rather than radiating directly outward from the primary xylem poles.
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