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A CONTRIBUTION TO THE ANATOMICAL DEVELOPMENT OF THE ACORN IN QUERCUS L.¹

H. Lloyd Mogensen²

ABSTRACT. An investigation was made of the anatomical development of the acorns in *Quercus alba* L. and *Q. velutina* Lam. Embryo and fruit development were followed from the very early stages to the mature acorn. It was found that usually five 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 zygotes do 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. Endosperm in *Q. alba* is usually absorbed by July 21 (about 77 days after pollination). In *Q. velutina*, the endosperm is usually depleted by July 17 (about one year and 73 days after pollination). Embryogeny in *Q. alba* and *Q. velutina* is essentially the same 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 (about 109 days after pollination) the shoot apex of *Q. alba* has initiated two leaf primordia which continue to grow and overlap each other by early September (about 128 days after pollination). 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 devoid of leaf primordia. The seed coat in both species was found to be derived from the outer integument. The structure of the seed coat is essentially the same in both species. The mature fruit coat of *Q. alba* was found to differ anatomically from that of *Q. velutina*. Also, the inner surface of the mature fruit coat of *Q. alba* is glabrous, while that of *Q. velutina* is very pubescent.

²The author wishes to thank Professor J.E. Sass for his guidance and encouragement during the planning and completion of this work. Thanks are also extended to Professor Harold S. McNabb, Jr. for his review of the manuscript.
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.

There have been a few studies on ovule and embryo sac development in Quercus; however, most of these studies end with the zygote, or go only to the first few-celled stages of the embryo. Even though some recent studies have been made on the later phases of acorn development, much information is still needed to complete the picture.

The objective of the present investigation was to follow the embryo and entire acorn from the very early phases of development to the mature condition. One species (Quercus alba L.) from the white oak group and one species (Q. velutina Lam.) from the red (or black) oak group were chosen for comparison.

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

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.

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

The variation in size, number, and form of acorns from various oaks was discussed by Stenzel (1890); however, his study was not anatomical.

The formation of the ovules in Q. pedunculata was described by Lub-bock (1892). 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."

Ward (1892) wrote a textbook-type review of the growth and reproduction of the oak tree. In this he presented what was known of the anatomy of the acorn up to that time.

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 caecum. He noted that this structure is also present in Castaneea. 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 early embryo stage. The ovule and embryo sac development in Q. robur was studied by Klebelsberg (1910).

The early embryonic stages in Q. prinus were studied by Vecchierello (1928). However, in his study of the later stages of embryo development he focused his attention entirely on the root histogens. The formation
ANATOMICAL DEVELOPMENT OF THE ACORN

of the flower and cupule in Quercus was investigated by Langdon (1939). She also described the vascularization of these structures and included a brief discussion of the enlarging fruit and embryo.

Embryo sac formation in Q. macrolepis was reported by Bagda (1952). He also described the development of an embryo (nearly to maturity) which he states is an apomictic embryo formed from an endosperm cell. Hjelmqvist (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). Hjelmqvist stated that several megaspore mother cells may occur within one nucellus, a feature which Conrad (1900) also described. Hjelmqvist 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 pistillate flowers of Q. alba have been described by Turkel et al. (1955). They followed the development of the pistillate flower through the completion of the mature embryo sac. Corti (1959), Scaramuzzi (1960), and Bianco (1961), have studied the reproductive structures of Q. ilex, Q. aegilops, 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.

MATERIALS AND METHODS

Collections of developing acorns were made during the summers of 1963 and 1964. The major collections were taken from a vigorous tree of Q. 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 1-week intervals. During the second summer, they were taken at 3-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 nearly as possible, since each collection usually contained overlapping stages from the preceding as well as the succeeding collections. The date of May 5 was selected as the time of pollination; however, pollination actually occurs over a 2 to 5 day period.

The acorns were trimmed with a razor blade as closely as possible to the embryo to allow for proper penetration during fixation and embedding. All material was fixed in Craf III and dehydrated in a series of dioxane and normal-butanol reagents (Sass, 1958), then embedded in paraffin. Sections were cut at 10 to 20 µ, 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 safranin and fast green.
Embryogeny

The ovary of *Quercus alba* has three locules, each of which contains two ovules. Fertilization occurs during early June. This is approximately 1 month after pollination (Figs. 1, 2).

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 (Fig. 4). Free-nucleate endosperm forms around the periphery of the embryo sac before the first division of the zygote.

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

All six ovules remain equal in size, even though they are enlarging, until after the 20th of June when the ovule containing the normal embryo soon becomes much larger than the others (Fig. 3). As the acorn enlarges, the abortive ovules are pushed toward the 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. Its cells are of approximately the same size except at the base, which consists of one or two larger cells (Fig. 5).

By the 26th of June, the embryo has become perfectly spherical except 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 (Fig. 6).

By June 30, the upper portion of the embryo has begun to expand on either side, initiating the cotyledons. By the time the cotyledons have grown 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 (Fig. 7).

Embryos of the July 6 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 because of shrinkage due to processing (Figs. 8, 9).

By July 12, 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 (Fig. 10).

By July 18, 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 (Fig. 11). The epidermis of
Figure 1. Longitudinal section of the young acorn of white oak about the time of fertilization. June 10. Approximately 36 days after pollination (17X).

Figure 2. Transverse section through the ovary of white oak showing the six ovules. June 10. Approximately 36 days after pollination (37X).

cu = cup. f = fruit coat. ov = ovule.
Figure 3. Transverse section through the ovary of white oak showing the enlarged ovule and five aborted ovules. July 6. Approximately 62 days after pollination (19X).

Figure 4. Longitudinal section through the ovule of white oak showing the zygote. June 16. Approximately 42 days after pollination (78X).

Figure 5. Longitudinal section through the ovule of white oak showing the young embryo and cellular endosperm. June 23. Approximately 49 days after pollination (180X).

Figure 6. Longitudinal section of a young white oak embryo. June 26. Approximately 52 days after pollination (78X).

Figure 7. Longitudinal section through a white oak embryo showing the beginning of cotyledon formation. July 2. Approximately 58 days after pollination (78X).

\[a = \text{aborted ovule} \quad i = \text{inner integument}\]
\[c = \text{cotyledons} \quad o = \text{outer integument}\]
\[e = \text{endosperm} \quad s = \text{seed coat}\]
\[em = \text{embryo} \quad z = \text{zygote}\]
Figure 8. Longitudinal section showing the embryo of white oak. July 6. Approximately 62 days after pollination (78X).

Figure 9. Longitudinal section of the developing acorn of white oak. July 6. Approximately 62 days after pollination (10X).

Figure 10. Longitudinal section through a white oak embryo. July 12. Approximately 68 days after pollination (78X).

\[
\begin{align*}
cu &= \text{cup} & f &= \text{fruit coat} \\
e &= \text{endosperm} & i &= \text{inner integument} \\
e_a &= \text{embryo axis} & o &= \text{outer integument} \\
em &= \text{embryo} & s &= \text{seed coat}
\end{align*}
\]
the cotyledons consists of very small cells compared with the cells within. The epidermal cells of the embryo axis are about the same size as those within the axis, but are less elongated (Fig. 12). Within the cotyledons, protoxylem cells with spiral wall thickenings have differentiated in some of the procambium strands. 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 pressed 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 (Figs. 10, 11, 12, 13) and eventually surround the radicle completely (Fig. 14).

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 (Fig. 15).

By the first week of September, the first two leaf primordia have arched up over the stem apex, overlapping each other (Figs. 15, 17), 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 varied 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.

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 (Fig. 1).

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 (Fig. 9).

By mid or late July, additional scattered groups of thick-walled sclerenchyma cells have differentiated within the parenchymatous center of the fruit coat (Fig. 11).

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 (Figs. 11, 13, 18).

The numerous hairs lining the 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 (Figs. 13, 18).
Figure 11. Longitudinal section of the developing acorn of white oak. July 17. Approximately 73 days after pollination (47X).

Figure 13. Longitudinal section through an embryo of white oak. July 18. Approximately 74 days after pollination (7X).

c = cotyledon lobe
cu = cup
e = endosperm
ea = embryo axis
em = embryo
f = fruit coat
s = seed coat
Figure 13. Longitudinal section showing the nearly mature acorn of white oak. August 3. Approximately 90 days after pollination (5X).

Figure 14. Longitudinal section through the embryo of white oak showing the lobes of the cotyledons around the embryo axis. August 3. Approximately 90 days after pollination (47X).

- c = cotyledon lobe
- cu = cup
- em = embryo
- f = fruit coat
- s = seed coat
- sh = shoot apex
Figure 15. Longitudinal section through the stem apex of a white oak embryo showing the initiation of the first two leaf primordia. August 22. Approximately 109 days after pollination (78X).

Figure 16. Longitudinal section through the axis of a white oak embryo showing the first two leaf primordia after some growth has taken place. September 10. Approximately 128 days after pollination (15X).

Figure 17. 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. Approximately 128 days after pollination (78X).

Figure 18. Longitudinal section of the nearly mature fruit coat of white oak. August 22. Approximately 109 days after pollination (47X).

Figure 19. Longitudinal section of the nearly mature seed coat of white oak. August 22. Approximately 109 days after pollination (47X).

t = cotyledon tissue sc = outer sclerenchyma
l = leaf primordia covering
s = seed coat sh = shoot apex
Figure 20. External view of developing white oak acorns:

A. May 29. 24 days after pollination.
B. June 11. 37 days after pollination.
C. June 23. 49 days after pollination.
D. July 6. 62 days after pollination.
E. " 12. 68 days after pollination.
F. " 18. 74 days after pollination.
G. " 25. 81 days after pollination.
H. " 30. 86 days after pollination.
I. September 10. 128 days after pollination.
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 (Fig. 4).

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 (Figs. 5, 6, 7, 8).

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 (Figs. 10, 12).

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. It 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 (Fig. 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 Q. velutina contains three locules containing two ovules each (Fig. 21). The embryo sac of all six ovules becomes mature 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 18, the embryo is spherical and consists of approximately 12 cells. By this time, there is an abundant amount of free-nucleate endosperm (Fig. 22). Only one of the six ovules in an ovary contains a normal embryo. The embryos of the other five ovules abort 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 (Fig. 23) until about June 21 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 23, 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 (Figs. 24, 25).

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 beginning of procambium formation can now be seen in the embryo axis (Fig. 26).

By July 2, 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 (Fig. 27). Cellular endosperm fills the entire embryo sac by this time.

By July 6, 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 (Figs. 27, 29).

By July 10, 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 (Fig. 30). Spiral protoxylem vessels are present in the procambium of the cotyledons.

Usually by July 17, 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 farther down around the embryo axis (Figs. 31, 32).

By August 3, little change has taken place except that the entire embryo has increased in size and the cotyledonary lobes have increased in length (Fig. 33). The embryo continues to increase in size, and by August 22 the lobes of the cotyledons surround the radicle (Fig. 34).

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.

The Fruit Coat

In early June, the fruit coat 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 (Fig. 25).

Through the month of July, the cells of the outer sclerenchyma covering become much thicker-walled. The sclerenchyma cells extending down
ANATOMICAL DEVELOPMENT OF THE ACORN

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-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 (Figs. 29, 32).

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 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 composing the inner portion of the fruit coat are compressed together due to the stretching of the fruit coat and enlarging seed (Fig. 35).

The thick coating of hairs lining the locules within the young ovary remains as a thick mat attached to the inner surface of the fruit coat in 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 until after fertilization. By the time the embryo consists of a few cells, pigmented parenchyma cells are scattered throughout the outer integument. The inner integument has become much reduced in thickness due to compression and breakdown of the cells composing it. Only that part of the inner integument which surrounds the micropyle remains unchanged (Fig. 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 (Fig. 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.
Figure 21. Transverse section through the pistillate flowers of black oak showing the young ovules before fertilization. May 17. Approximately 1 year and 12 days after pollination (15X).

Figure 22. Longitudinal section through the embryo sac of black oak showing the young embryo. June 18. Approximately 1 year and 44 days after pollination (180X).

Figure 23. Transverse section through the ovary of black oak showing the slightly enlarged ovules. June 16. Approximately 1 year and 42 days after pollination (15X).

cu = cup  
et o = outer integument
em = embryo  
fe = free-nucleate
   endosperm
i = inner integument
ov = ovule
ow = ovary wall
Figure 24. Longitudinal section through the ovule of black oak showing the young embryo. June 23. Approximately 1 year and 49 days after pollination. (180X).

Figure 25. Longitudinal section through a young black oak acorn. June 23. Approximately 1 year and 49 days after pollination (8X).

cu = cup
em = embryo
f = fruit coat
i = inner integument
o = outer integument
s = seed coat
ANATOMICAL DEVELOPMENT OF THE ACORN

Diagram 24:
- em
- o
- i

Diagram 25:
- s
- em
- f
- cu
Figure 26. Longitudinal section through the ovule of black oak showing the young embryo and the cotyledon primordia. June 26. Approximately 1 year and 52 days after pollination (78X).

Figure 27. Longitudinal section through the embryo of black oak showing the embryo axis. July 2. Approximately 1 year and 58 days after pollination (78X).

Figure 28. Longitudinal section through the developing seed of black oak. July 6. Approximately 1 year and 62 days after pollination (16X).

c = cotyledon

e = endosperm

ea = embryo axis

i = inner integument

o = outer integument

s = seed coat
ANATOMICAL DEVELOPMENT OF THE ACORN
Figure 29. Longitudinal section through the developing acorn of black oak. July 6. Approximately 1 year and 62 days after pollination (6X).

Figure 30. Longitudinal section of the developing seed of black oak. July 10. Approximately 1 year and 66 days after pollination (16X).

\[
\begin{align*}
\text{c} &= \text{cotyledon} & \text{em} &= \text{embryo} \\
\text{cu} &= \text{cup} & \text{f} &= \text{fruit coat} \\
\text{e} &= \text{endosperm} & \text{s} &= \text{seed coat} \\
\text{ea} &= \text{embryo axis}
\end{align*}
\]
Figure 31. Longitudinal section through the embryo of black oak, cut perpendicular to the plane of the cotyledon attachment. July 17. Approximately 1 year and 73 days after pollination (15X).

Figure 32. Longitudinal section through the acorn of black oak. July 21. Approximately 1 year and 77 days after pollination (5X).

c = cotyledon
cu = cup
ea = embryo axis
f = fruit coat
s = seed coat
Figure 33. Longitudinal section through the axis of the black oak embryo, cut parallel to the plane of the cotyledon attachment. August 3. Approximately 1 year and 90 days after pollination (15X).

Figure 34. Longitudinal section through the axis of the black oak embryo, cut perpendicular to the plane of the cotyledon attachment. August 22. Approximately 1 year and 109 days after pollination (15X).

Figure 35. Longitudinal section through the nearly mature fruit coat of black oak. August 22. Approximately 1 year and 109 days after pollination (69X).

Figure 36. Longitudinal section through the nearly mature seed coat of black oak. August 22. Approximately 1 year and 109 days after pollination (78X).

c = cotyledon lobes
ea = embryo axis
sc = outer sclerenchyma covering
Figure 37. External view of developing black oak acorns:

A. May 13. 1 year and 8 days after pollination.
B. May 29. 1 year and 24 days after pollination.
C. June 11. 1 year and 37 days after pollination.
D. June 23. 1 year and 37 days after pollination.
E. July 6. 1 year and 62 days after pollination.
F. " 12. 1 year and 68 days after pollination.
G. " 18. 1 year and 74 days after pollination.
H. " 30. 1 year and 86 days after pollination.
I. Sept. 4. 1 year and 122 days after pollination.
SUMMARY AND DISCUSSION

Several studies have been made on embryo sac development, and a few on early embryonic development in Quercus; however, none indicates the stage of development of the embryo 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 proembryo. From the above information, the zygotes of the abortive ovules do not appear to develop much, if any.

Several authors report the occurrence of multiple seeded acorns (Meehan, 1871; Coker, 1904; Smith, 1914; Buchholz, 1941; and Hosner, 1959). Harvey (1917) reported a multiple embryo condition in Q. 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 by Williams (1939), 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 Q. alba has usually been absorbed by July 21. In Q. velutina the endosperm is usually used up by July 17.

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 that a particular stage in Q. alba was about 10 days behind that of Q. ilicifolia and Q. coccina. This is true up to the last of July, but subsequently there was 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 is a relatively good indication of the morphological maturity of a developing embryo. In *Q. alba*, the extension of the cotyledonary lobes lags behind that of *Q. velutina* up to the last of July, but by August 3, 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 until the radicle has grown approximately 2 cm in length (Mogensen, 1963).

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 true with 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 well-known characteristics of the inner fruit coat being pubescent in members of the red oak group, and glabrous in members of the white oak group held true in the present study.

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*.

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MORPHOLOGICAL INVESTIGATIONS OF THE INTERNAL ANATOMY OF THE FIFTH LARVAL INSTAR OF THE EUROPEAN CORN BORER

H. G. Drecktrah, K. L. Knight, and T. A. Brindley

ABSTRACT. The gross internal morphology of the mature European corn borer [Ostrinia nubilalis (Hübner)] larva, reared on artificial diet in the laboratory, was investigated. Descriptions and illustrations are given for various organs or organ systems: alimentary canal; Malpighian tubules; mandibular, silk, and prothoracic glands; nervous system; reproductive systems; dorsal vessel; and wing buds. Respiratory system and musculature are not discussed. The basic pattern of internal structures conforms to the typical internal anatomy of lepidopterous larvae as presented by other researchers on this order of insects.

This investigation was undertaken to provide descriptions and illustrations of the gross internal anatomy of the mature larva of the European corn borer [Ostrinia nubilalis (Hübner)] for use in future research. Definitive studies of the internal anatomy of lepidopterous larvae probably began with the classical investigation of Lyonet (1762) who produced a monograph on larval structures of the goat moth caterpillar. The internal anatomy of the tomato hornworm [(Protoparce quinquemaculata (Haworth)] was studied in detail by Peterson (1912). El-Sawaf (1950) and Teotia and Pathak (1957) investigated the internal morphology of the greater wax moth (Galleria mellonella (L.)) and Laspeyresia tricentra Meyrick (as Enarmonia pseudonectis Meyrick), respectively. Very few studies have dealt with gross internal morphology of lepidopterous larvae but many authors have studied particular organs or organ systems of several different species of lepidopterous larvae.

Some aspects of the internal anatomy of the European corn borer have been studied. Larsson (1929) investigated the internal structures of the larva but some of his descriptions and illustrations seemed to be
inadequate and were somewhat diagrammatic. Crowell (1929) studied the structure of the respiratory system of the mature larva, and therefore, this system has been largely neglected in this study. McLeod and Beck (1963) reported on the neuroendocrine complex of the larva and its relation to diapause.

METHODS AND PROCEDURES

The European corn borer larvae were reared from egg masses obtained from caged, wild moths at the European Corn Borer Research Laboratory at Ankeny, Iowa. The procedure used for collecting the egg masses was described by Guthrie (1958). The egg masses were incubated in a rearing chamber having an almost constant temperature (85°F) and relative humidity (75%). All egg masses (3 days old) were heat treated to eliminate the possible infection of the microsporidian Perezia pyraustae Paillot by a slight modification of the technique used by Raun (1961). The egg masses were then placed in screw-top jars and returned to the rearing chamber.

Larvae less than 24 hours old were transferred from the screw-top jars to individual shell vials containing an artificial diet (Guthrie et al. 1965) which were placed in the rearing chamber. On the 12th day these larvae were removed from the vials and placed in 10% formalin for fixation and preservation.

Larvae, while submerged in water, were dissected in Petri dishes whose bottoms were covered with paraffin. In order to make internal structures more evident, Wright’s stain was applied to the specimen for approximately 30 seconds, rinsed with distilled water, and the specimen was then immersed in water. It was found that this particular stain gave good results in a short time, and the internal structures were much easier to distinguish. Wright’s stain could be removed from the tissue by flooding the specimen with 70% ethanol for a short period of time. This procedure also served as an easy method for preserving partially dissected larvae overnight or for several days.

DISCUSSION

Alimentary Canal

The alimentary canal and the fat body tissue (Fig. 1) are the most conspicuous structures encountered when a European corn borer larva is dissected. The alimentary canal is a relatively straight tube extending from the antero-ventral portion of the head to the last abdominal segment. In the thorax and abdomen it is usually surrounded by a discontinuous layer of fat body. The fat body, while allowing for expansion and contraction, helps to hold the gut in place.

Three distinct divisions of the alimentary tract occur: the stomadaeum, the mesenteron, and the proctodaeum (Figs; 2, 3). The stomadaeum, or fore-gut, extends from the preoral cavity between the mandibles to
FIGURE 1

Dorsal view of alimentary canal, fat body, and major tracheae of left side. (Fat body removed from posterior portion of mesenteron.)

(App. X7.6)
Dorsal view of alimentary canal. (App. X8)
Lateral view of alimentary canal, silk gland, mandibular gland, and Malpighian tubules (proximal and distal portions only). (App. X8)
the posterior region of the prothorax where it joins the much larger mesenteron (ventriculus or mid-gut). The mesenteron occupies much of the hemocoel of the larval body and connects with the proctodaeum, or hind-gut, in the posterior region of the 7th abdominal segment. The anterior portion of the proctodaeum is much smaller in size than the mesenteron, but its posterior portion is enlarged to the point of occupying almost the complete hemocoelic cavity of the 9th and 10th abdominal segments.

Since the alimentary canal does not have any major twists or coils, it is approximately the same length as the body. Certain regions of the gut may sometimes appear to be expanded beyond their normal size, a condition which can be attributed to the presence of a large amount of ingested food in the region of the expansion.

Stomodaeum (fore-gut)

The stomodaeum is located in the head and thorax (Figs. 2, 3, 4). It is connected to the mesenteron in the posterior region of the prothorax. The dilator muscles of the stomodaeum will be referred to by name and a number, the latter being used to designate the structure in Fig. 4.

The anterior portion of the stomodaeum is heavily muscled except for the walls of the short preoral cavity. A pair of dorsal dilator muscles, or cibarial muscles (1, 2), arising from the clypeus insert on the dorsal wall of the preoral cavity immediately anterior to the first ring of circular muscles of the buccal cavity.

The buccopharyngeal region is ringed by broad bands of circular muscles. The dorsal dilator muscles of this region are separated into two groups by the position of the frontal ganglion and define the buccal cavity and pharynx. The dorsal dilator muscles anterior to the frontal ganglion (3, 4) arise on the clypeus and define the buccal cavity. The dorsal dilator muscles posterior to the frontal ganglion (5, 6, 7, 8, 9) also arise on the clypeal region of the head and define the pharynx. Ventral dilator muscles of the pharynx (10, 11, 12) are present and extend to the posterior tentorial bridge (18).
The preoral and buccal cavities of the stomodaeum are typically flexed ventrad, but the following pharynx and esophagus assume a more horizontal position in the head. The esophagus narrows slightly as it extends to the crop. The esophagus is surrounded by strong circular muscles and is supplied with post-cerebral dilator muscles (13, 14, 15) which extend dorsad to the dorsal occipital region of the head capsule and ventral dilator muscles (16, 17) which extend ventrad to the ventro-posterior margin of the head capsule near the origin of the posterior tentorial arms.

The crop follows the esophagus which terminates approximately at the posterior margin of the head. The crop joins the mesenteron at the posterior margin of the prothoracic segment (Figs. 2, 3). It varies in size depending upon the presence or absence of food in its lumen but is invariably larger than the esophagus. When not expanded by food, it is "collapsed" in a series of longitudinal folds. The crop differs considerably from the anterior portion of the stomodaeum. Its musculature is much reduced but narrow bands of circular muscles appear near the connections to the esophagus and the mesenteron. There are also a few circular muscles around the midportion of the crop. The longitudinal muscles are less conspicuous. The walls of the crop are quite thin and almost transparent. It stains very lightly in Wright's stain.

The crop ends in a strong constriction, the cardiac or stomodaeal valve (Fig. 5), which extends into the lumen of the mesenteron for a short distance as a funnel-shaped, thin-walled structure. The tissue of the cardiac valve resembles that of the crop in being almost transparent and in not readily taking up Wright's stain. The junction between the stomodaeum and mesenteron is externally surrounded by circular muscles.
Mesenteron (ventriculus or mid-gut)

The mesenteron (Figs. 2, 3) is the largest portion of the alimentary canal, both in length and diameter. It joins the stomodaeum at the posterior margin of the first thoracic segment and terminates at the pylorus in the 7th abdominal segment.

The mesenteron is a long, thick-walled, undifferentiated, hollow tube which is well supplied with branches of the visceral tracheae which pass through the fat body surrounding the gut. The mesenteron has no musculature to hold it in place in the hemocoel as do the stomodaeum and proctodaeum. It is, however, supported by the large mass of fat body tissue which almost completely surrounds it on all sides (Fig. 1). The arrangement of muscle fibers of the mesenteron is the reverse of those of the stomodaeum and proctodaeum, since the principal longitudinal muscles are external to the circular muscles. The mesenteron almost always has circular folds or creases. No gastric diverticula, or caeca, were found.

Proctodaeum (hind-gut)

The proctodaeum is an invagination of the ectoderm, as is the stomodaeum. It follows the mesenteron, which ends in the 7th abdominal segment, and terminates as the rectum with its external opening in the last abdominal segment. The proctodaeum is divisible into the pylorus, the anterior intestine, and the posterior intestine or rectum (Figs. 2, 3).

The anterior division of the proctodaeum, the pylorus, is somewhat expanded and almost attains the size of the mesenteron at their junction. The anterior margin of the pylorus is defined by a conspicuous band of circular muscles (Figs. 6a, 6b). Widely spaced, branching, longitudinal muscles are anteriorly inserted beneath this circular muscle band and posteriorly attached beneath the sphincter muscles of the pyloric valve. Ventrad to these branched, longitudinal muscles inconspicuous circular muscles occur on the expanded portion of the pylorus (Figs. 6a, 6b, 7a).

The posterior region of the pylorus, which here may appear slightly bulbous, possesses strong circular sphincter muscles. Six small bundles of less conspicuous longitudinal muscles occur externally to the sphincter muscles (Figs. 6a, 6b, 7a). Internally, the walls of the posterior portion of the pylorus consist of conspicuously constricted longitudinal folds, which form the pyloric valve (Fig. 7b). This valve is capable of regulating the flow of food material between the mesenteron and the proctodaeum.

A pair of small Malpighian bladders, one on each side, lie next to the latero-ventral aspects of the pyloric region (Figs. 6b, 7a). From the posterior margin of each bladder, a small duct extends posteriad beneath the sphincter muscles of the pyloric valve and opens into the anterior intestine immediately posterior to the internal longitudinal folds of the pyloric valve (Fig. 7b).

The anterior intestine extends from the pylorus in the 7th abdominal segment into the 9th abdominal segment where it joins the rectum (Figs. 2, 3). In some insects the anterior intestine is divided into an ileum and a colon, but in the case of the European corn borer larva it is an undifferentiated tube connecting the pylorus to the rectum. Externally the anterior intestine is surrounded by conspicuous circular muscles which are attached to the intestine at six points (Fig. 6a). When the anterior
6a. Dorsal view of pylorus.

6b. Ventral view of pylorus
a. Lateral view of pylorus.
b. Sagittal section of alimentary canal through pylorus.
The intestine is devoid of food material it collapses into six longitudinal folds. The ridges (as opposed to the in-folded or collapsed portions) of the longitudinally folded intestine serve as the six points of attachment for these circular muscles. However, when the intestine is engorged with food the six longitudinal ridges are no longer evident and may appear as shallow surface furrows or grooves.

Paired suspensory, or dilator, muscles are attached to the anterior intestine (Fig. 3). The anterior pair originate on the lateral aspects of the intersegmental fold between the 7th and 8th abdominal segments and attach to the lateral aspects of the anterior intestine. They are fan-shaped at their attachment to the intestine. The posterior pair of muscles originate on the ventral aspect of the same intersegmental fold and extend dorsad to the intestine. However, the muscles from each side of the mid-ventral line criss-cross and attach to the latero-ventral aspect of the opposite sides of the intestine. The muscles are fan-shaped at their insertion on the intestine which would indicate they are dilator muscles.

The rectum, or posterior intestine, follows the anterior intestine approximately at the anterior margin of the 9th abdominal segment (Figs. 2, 3, 8). The internal opening between these two divisions of the proctodaeum is in the form of longitudinal folds resulting in an internal constriction, or rectal valve, similar to that of the pyloric valve. Externally, the rectum is rather bulbous and much larger than the anterior intestine, and it occupies most of the hemocoel of the 9th and 10th abdominal segments.

Dorsal view of posterior portion of proctodaeum.
The rectum receives the terminal portions of the three pairs of Malpighian tubules which penetrate the outer and inner membranous layers of the rectum and terminate between the inner membrane and the rectal epithelium. This situation will be discussed more thoroughly under the heading of Malpighian tubules.

The proctodaeum is also furnished with extrinsic muscles that originate on the body wall and insert on the six longitudinal ridges of the posterior portion of the anterior intestine immediately anteriad to the rectum (Fig. 8). Upon opening a larva, these muscles may appear to originate from the rectum; however, this is a result of tearing them from their origin on the intersegmental folds. There are two dorsal, two lateral, and two ventral groups of muscles, giving a total of six groups of extrinsic muscles. The two groups of ventral muscles originate on the intersegmental fold between the 8th and 9th abdominal segments, and each group typically consists of three or four distinct muscles. These muscles extend dorsad and attach to the latero-ventral longitudinal ridges of the anterior intestine. The most lateral muscle of each group assumes the anterior position of attachment on the intestine. The second most lateral muscle of each group is attached just posterior to the first lateral muscle and so on with the other muscles of these two groups. The other four groups of muscles originate on the intersegmental fold between the 9th and 10th abdominal segments. The two dorsal groups of muscles extend antero-ventrad across the dorsal portion of the rectum to the longitudinal ridges of the anterior intestine where they attach. The lateral muscle of each group again assumes the anterior position of attachment. Each of these groups consists of three or four (five have been seen) distinct muscles. This is also true for the remaining two lateral groups. These muscles originate on the lateral aspect of the previous intersegmental fold. The dorsal-most muscle of each group assumes the anterior attachment position on the anterior intestine.

Malpighian Tubules

The six Malpighian tubules, or excretory organs, lie along the alimentary canal beneath the fat body which surrounds the gut.

On each side of the alimentary canal a small bladder-like structure lies adjacent to the latero-ventral surface of the pylorus (Figs. 6b, 7a). From the posterior margin of the bladder, a small duct extends beneath the sphincter muscles of the pyloric valve and opens into the anterior intestine immediately posterior to the pyloric valve (Fig. 7b). A duct also arises from the anterior margin of the bladder, extends anteriad for a short distance, and then divides to form a pair of Malpighian tubules, one dorsal and one ventral. The dorsal tubule extends cephalo-dorsad and ultimately lies on the latero-dorsal surface of the mesenteron. The dorsal Malpighian tubule forks in the 5th abdominal segment, giving rise to a lateral and a mesal branch. The mesal branch extends cephalad until it reaches the middle of the 4th abdominal segment where its direction reverses. The mesal branch then extends posteriad and is parallel and mesad to its more proximal portion. The lateral branch of the dorsal Malpighian tubule extends cephalad and is parallel and ventrad to the mesal branch. The lateral branch also reverses its direction but in the
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3rd abdominal segment. The lateral branch then extends posteriad on the lateral surface of the mesenteron and is parallel and ventrad to its anterior-directed portion. The ventral Malpighian tubule extends cephalo-ventrad beneath the mesenteron and ultimately lies adjacent to the latero-ventral surface of the mesenteron. In the 4th abdominal segment, the ventral Malpighian tubule reverses its direction and then extends posteriad and is parallel and laterad to its anterior-directed portion. This arrangement of Malpighian tubules is repeated on the other side of the alimentary canal.

There is, then, a total of six Malpighian tubules (three on each side) lying adjacent to the alimentary canal. They appear as small, white tubes and proximally, are only slightly wavy. Distally, they are increasingly more wavy and convoluted and appear as thin, white tubes with a series of very close nodules or swellings.

When the posterior-extending portions of the Malpighian tubules reach the region of the anterior intestine they become greatly convoluted and intertwined with each other. The mandibular glands, which terminate in this region, also become intertwined with the tubules. The extensive fat body tissue holds the tubules and mandibular glands around the intestine. It is difficult to separate the tubules due to their highly convoluted state and the abundance of fat body tissue.

When the Malpighian tubules emerge from the fat body around the anterior intestine, their terminal portions penetrate the outer membranous layer of the rectum (Fig. 3). The two median dorsal Malpighian tubules penetrate the latero-dorsal aspects of the rectum near the union of the rectum and the anterior intestine. The two lateral dorsal tubules and the two ventral tubules penetrate the outer membranous layer of the rectum on the lateral and ventro-lateral aspects, respectively. Upon penetration the tubules become very thin and delicate and hard to trace. Caudally, they pass beneath the inner membranous layer which is composed of two layers of cells as opposed to the outer layer, which, according to Ishimori (1924) and Poll (1938), consists of a single layer of cells. In this area, where the tubules become easier to trace, they extend in a zig-zag manner, first cephalad and then caudad and finally terminate between the inner membrane and the rectal epithelium. Ishimori (1924) distinguishes six types of patterns formed by the terminal portions of the Malpighian tubules, but it was not determined to which type the tubules of the European corn borer belong.

Larsson (1929), in his studies of the internal anatomy of the European corn borer, did not recognize the fact that the terminal portions of the Malpighian tubules are situated beneath the rectal wall.

Mandibular Glands

Mandibular glands are found in some other orders of insects, but they attain their greatest development in many lepidopterous larvae. They are conspicuous in the European corn borer larva where they approach or slightly exceed the total length of the larva (Figs. 3, 9).

The orifices of the paired mandibular glands are located on the inner surface of the base of the mandibles. Each gland extends caudad from its orifice along the adductor muscle of the mandible. In the thorax it
becomes more dorsally located and parallels the alimentary canal in a lateral or dorso-lateral position. It is held next to or near the gut by the fat body tissue. Each gland extends posteriad as a simple, almost straight tube. They terminate in the region of the anterior intestine where they become convoluted and intertwined with Malpighian tubules and fat body tissue.

Silk Glands

Morphologically the silk glands of lepidopterous larvae are labial glands homologous with the true salivary glands of other insects. The hypopharynx and the prementum of lepidopterous larvae are united in a median lobe supported by the postmentum and the maxillary stipites, on the extremity of which the common duct of the silk glands open through a hollow spine, the spinneret. The common duct of the silk glands opens into the base of an organ known as the silk press which lies in the median lobe of the mouth parts formed by the united hypopharynx and prementum. Morphologically the silk press is a highly specialized development of the salivarium of more generalized insects.

The silk glands of the European corn borer larva arise from the base of the silk press as a short, median, common duct which bifurcates almost immediately to form the pair of silk gland ducts (Figs. 3, 10). These ducts extend caudad beneath the stomodaeum and each receives a very small duct from the small accessory acinous glands (glands of Lyonet or glands of Fillipi). These small accessory glands lie on the dorsal surface of the silk gland ducts just anterior to the region at which the ducts pass beneath the subesophageal ganglion.

The paired silk gland ducts extend posteriad from the head region beneath the stomodaeum and appear to be somewhat twisted in the thorax, depending upon the degree of elongation of the larva. Approximately at the posterior margin of the third thoracic segment they become enlarged to form the glandular portion of the silk glands which is about three times the size of their proximal portion. The silk glands continue posteriad beneath the mesenteron until the third abdominal segment where they reverse their direction and extend cephalad adjacent to their posterior-directed portion. In the anterior region of the second abdominal segment the silk glands again reverse their direction and extend caudad along the lateral aspects of the mesenteron in a somewhat more dorsal position than their proximal portions.

The silk glands are held in place beneath and on the sides of the mesenteron by the fat body tissue surrounding the alimentary canal. The tubes tend to decrease in size after they turn caudad. In the 7th abdominal segment they terminate rather abruptly in a thin, unattached terminal filament.

According to Larsson (1929), the accessory glands associated with the silk ducts are located in the prothorax. He also illustrated the common duct of the silk glands as extending into the prothorax. Neither of these conditions, however, were found in the larvae studied in this investigation.
Figure 9. Dorsal view of alimentary canal, silk glands, mandibular glands, and Malpighian tubules. (App. X6)

Figure 10. Dorsal view of silk glands. (App. X6)
The paired prothoracic glands of the European corn borer larva are located in the prothorax mesad to the prothoracic spiracle and its tracheal branches (Fig. 11). They resemble those described in other lepidopterous larvae (Lee 1948) in location, innervation, and structure. The glands appear as a band-like string of cells and are longitudinally situated. They are inconspicuous and may easily be overlooked unless special precautions are taken to find them. Larsson (1929) fails to mention them in his internal anatomical study of the European corn borer.

Lee (1948) described the branches which may arise from the main body of the prothoracic glands. According to her criteria, each prothoracic gland of the European corn borer larva has an anterior branch, a latero-dorsal branch, and a latero-ventral branch. The dorsal margin of the flared anterior branch is attached to the integument by a small

FIGURE 11

Internal view of left prothoracic gland and its relationship to the tracheae of the prothoracic spiracle.
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filament. The ventral margin of the anterior branch receives a subdi-
vision of the transverse nerve from the anterior median nerve of the
prothoracic ganglion. The two lateral branches are typically attached to
a small lateral muscle. The latero-ventral branch receives a subdi-
vision of the transverse nerve of the prothoracic ganglion.

Nervous System

Anatomically, the insect nervous system is divided into the central,
sympathetic or visceral, and peripheral nervous systems. These divi-
sions, including their ganglia and principal nerves, will be described
separately.

Central nervous system

The central nervous system includes the brain (or supraesophageal
ganglion), subesophageal ganglion, and ventral nerve cord, all of which
are united by paired connectives. The ganglia and nerves of the crani-
um will be referred to by name and a number, the latter being used to desig-
nate the structure in Figs. 12, 13.

Brain. The brain is located in the head dorsad to the esophagus.
Typically, the brain is divided into a protocerebrum, deutocerebrum and
tritocerebrum, but these divisions are not externally evident in the brain
of the European corn borer larva. Its brain is bilobed and tapers ante-
riorly. The tapered anterior portion of each hemicerebral lobe bifur-
cates, giving rise to the antennal nerve (9) and the labrofrontal nerve (4).
The latter then divides to give rise to the labral nerve (6) and the frontal
ganglion connective (5). All these nerves pass laterad to the dorsal
dilator muscles of the pharynx; however, the frontal ganglion connective
turns mesad as it passes these muscles and joins the frontal ganglion (7),
a part of the sympathetic nervous system. The antennal nerve (9) turns
latero-ventrad at these muscles, penetrates the mandibular muscles, and
extends to the antenna. The labral nerve (6), which receives a branch
(28) from the anterior frontal ganglion (26), continues anteriad to the
labral region where it gives rise to clypeal branches.

The paired circumesophageal connectives (3) arise from the latero-
ventral margins of the anterior portion of each hemicerebral lobe. Each
connective extends ventro-caudad to join the antero-dorsal margin of the
subesophageal ganglion (2). The subesophageal commissure (11) arises
as a branch from the dorsal portion of the circumesophageal connective.
The commissure completely encircles the esophagus uniting with the
circumesophageal connective of the opposite side. An anteriad-extending
branch (12) arises from the commissure directly beneath the esophagus
and innervates the ventral portion of the esophagus.

The optic nerve (10), arising slightly postero-dorsad to the circum-
esophageal connective origin, extends anteriad to the region of the dorsal
dilator muscles of the pharynx. Here, it turns latero-ventrad extending
through the mandibular muscles to the six simple eyes where it divides
and enters the six cup-shaped structures containing the internal mechan-
isms of the eyes.

Subesophageal ganglion. The oval subesophageal ganglion (2) is lo-
cated in the posterior part of the head, ventrad to the esophagus and
Lateral view of cranial nervous system

1, brain
2, subesophageal ganglion
3, circumesophageal connective
4, labrofrontal nerve
5, frontal ganglion connective
6, labral nerve
7, frontal ganglion
8, recurrent nerve
9, antennal nerve
10, optic nerve
11, subesophageal commissure
12, anterior branch of 11
13, anterior connective from corpus allatum-cardiacum complex to brain
14, anterior branch of 13
15, corpus allatum-cardiacum complex
16, posterior connective from corpus allatum-cardiacum complex to brain
17, connective to recurrent nerve and aorta
18, antero-ventral nerve of 15
19, posterior nerve of 15
20, mandibular nerve
21, maxillary nerve
22, labial nerve
23, lateral nerve of 2
24, interganglionic connective
25, frontal nerve
26, anterior frontal ganglion
27, branch of 13 to post-cerebral dilator muscles of esophagus
28, lateral nerve from 26
29, nerve from 15 to esophagus
30, nerve to clypeus
31, ventricular ganglion
32, lateral nerve of 31
33, lateral nerves of 8 to pharynx
34, lateral nerves of 8 to crop
35, ganglion of 18
36, nerve from 35 to 21
Diagrammatic illustration of stomadaeal sympathetic nervous system. (Outline of brain, esophagus, crop, and mesenteron shown as dashed lines.) Key: Refer to Fig. 12.
The paired circumesophageal connectives (3) from the brain join the antero-dorsal margins of the subesophageal ganglion.

The paired mandibular nerves (20), arising slightly mesad to the attachments of the circumesophageal connectives, extend anteriad from the subesophageal ganglion to the mandibular region where they innervate the mandibular muscles.

The paired maxillary nerves (21) arising slightly latero-ventrad to the origin of the mandibular nerves, extend antero-ventrad to innervate the maxillary region.

The paired labial nerves (22) arise slightly latero-ventrad to the origins of the maxillary nerves and also extend antero-ventrad towards the spinning apparatus, innervating the silk ducts, accessory glands, and spinning apparatus.

A pair of small lateral nerves (23), arising from the latero-dorsal margin of the subesophageal ganglion, extend latero-dorsad to the muscles of the cervical region.

A pair of separated interganglionic connectives (24), arising from the posterior margin of the subesophageal ganglion, extend to the prothoracic ganglion.

Ventral nerve cord. The ventral nerve cord (Figs. 14, 15), consisting of three thoracic and eight abdominal ganglia and their interganglionic connectives, lies on the mid-ventral line between the paired ventral longitudinal muscles. All the ganglia are oval-shaped, tapering slightly at their posterior margins to form the interganglionic connectives.

Thoracic ganglia. The thoracic ganglia are slightly more oval-shaped than the abdominal ganglia. The interganglionic connectives uniting the thoracic ganglia are widely separated.

Each thoracic ganglion has two pairs of lateral nerves. The anterior pair arise from the latero-dorsal margin of the ganglia adjacent to the attachment of the interganglionic connectives. These nerves extend laterad along the ventral aspects of the thoracic segments and then dorsad along the lateral walls to innervate the lateral and dorsal portions of the thorax. One of the several branches given off by the anterior lateral nerves of the mesothorax and metathorax extends to the transverse nerves of the preceding segments. The posterior pair of the lateral nerves arise from the ganglia in a more ventral position and extend laterad beneath the ventral muscles to innervate the structures in the ventral region.

Abdominal ganglia. The abdominal ganglia, located along the mid-ventral line, are somewhat oval-shaped. The anterior portions of the paired interganglionic connectives between the first seven ganglia are in such close proximity that they appear as a single connective. However, a short distance anteriad to the next ganglion they separate and two distinct connectives are evident. The 7th and 8th ganglia are fused and are located in the 7th abdominal segment. No interganglionic connectives are visible.

The lateral nerves of the first six abdominal ganglia are also paired. The anterior lateral nerves, arising from the antero-lateral margins of the ganglia, extend laterad. They pass over the first median internal longitudinal ventral muscle on either side of the mid-ventral line but ventrad to the remaining internal longitudinal ventral muscles. They
Dorsal view of brain, subesophageal ganglion, and ventral nerve cord and their principal nerves. (App. 7.5)

TG, thoracic ganglion
AG, abdominal ganglion
SG, subesophageal ganglion
Dorsal view of subesophageal ganglion, thoracic ganglia, abdominal ganglia 1, 2, and 7 + 8, and portions of the ventral sympathetic nervous system.
continue along the lateral and dorsal walls of the segment in which they are located and innervate the structures of these regions. The posterior pair of lateral nerves arise from the caudo-lateral margins of these ganglia. They extend caudo-ventrad and pass beneath the internal longitudinal ventral muscles, innervating the ventral structures of the segments in which they are located.

The lateral nerves of the anterior half of the fused 7th and 8th abdominal ganglia (i.e. the 7th abdominal ganglion) originate and extend outward in a pattern similar to the lateral nerves of the first six abdominal ganglia. However, the lateral nerves of the 8th abdominal ganglion arise in a different manner. The more anterior pair of lateral nerves arise from the lateral margins in the posterior portion of the ganglion and extend latero-caudad into the 8th abdominal segment where they give off several branches and innervate the latero-dorsal portion of the posterior segments. The posterior margins of the 8th abdominal ganglion taper to form two separated posterior nerves which extend almost parallel to each other into the posterior segments where they innervate the structures of the ventral regions of these segments. A pair of small nerves, arising antero-ventrad to the posterior nerves of the 8th abdominal ganglia, extend caudad into the 9th abdominal segment where they attach to the integument on either side of the mid-ventral line. These may be the caudal sympathetic nerves which are said to originate from the fused posterior abdominal ganglia. This was not verified, however.

Sympathetic or visceral nervous system

The sympathetic, or visceral, nervous system is set apart from the central nervous system functionally, though connected with it structurally. This system has been divided into the stomodaeal, the ventral, and the caudal sympathetic nervous systems.

Stomodaeal sympathetic nervous system. This division of the sympathetic nervous system has also been referred to as the esophageal, stomatogastric, and anterior sympathetic nervous system. It is directly connected to the brain and consists of several ganglia and nerves which will be referred to by name and a number, the latter being used to designate the structure in Figs. 12 and 13. This system innervates the stomodaeum, portions of the mesenteron, the heart, and certain other organs.

The most conspicuous anterior part of this system is the small, triangular frontal ganglion (7) located on the mid-dorsal surface of the buccopharyngeal region anteriad to the dorsal dilator muscles of the pharynx. The frontal ganglion is connected to the anterior portion of the brain by a pair of frontal ganglion connectives (5) arising from the lateral margins of the ganglion. A frontal nerve (25), arising from the anterior margin of the frontal ganglion extends anteriad for a short distance and then enlarges to form a smaller, inconspicuous ganglion (26), henceforth referred to as the anterior frontal ganglion. Arising from this ganglion, a pair of lateral nerves (28) extend laterad to join the labral nerves (6). From the anterior margin of this ganglion, a nerve extends anteriad, bifurcating almost immediately. The branches of this nerve extend to the clypeal region.
The recurrent nerve (8), arising from the posterior margin of the frontal ganglion, extends posteriad along the mid-dorsal surface of the pharynx. A pair of lateral nerves (33), arising from the recurrent nerve posterior to the two groups of dorsal dilator muscles of the pharynx, extend ventrad around the lateral surface of the pharynx. The recurrent nerve continues along the mid-dorsal surface of the stomodaeum ventrad to the aorta which passes beneath the brain. At this point and for a short distance posterior to the brain, the recurrent nerve and aorta are very closely associated and hard to differentiate. However, the aorta turns dorsad in the prothorax, but the recurrent nerve extends posteriad along the mid-dorsal surface of the crop, giving rise to several small lateral nerves (34). Near the posterior end of the crop, the recurrent nerve forms the small, triangular ventricular ganglion (31), a structure which is hard to differentiate from the recurrent nerve. This ganglion has also been called the caudal, stomachic, gastric, or vagus ganglion by other authors. Two lateral nerves (32), originating from the ventricular ganglion, extend caudo-ventrad along the lateral surface of the crop, there giving rise to branches which innervate the posterior crop and the anterior portion of the mesenteron.

Larsson (1929) reports finding a small, but distinct, hypocerebral ganglion along the recurrent nerve just behind the posterior margin of the brain. We have not been able to find this ganglion. If it is present it must be very minute.

A pair of small ganglionic complexes (15) are located latero-ventrad to the posterior portion of the brain. Each is termed the corpus allatum-cardiacum complex (McLeod and Beck 1963). There is no definite separation between the corpus cardiacum and corpus allatum as is found in some lepidopterous larvae, but the complex does appear to be slightly bilobed in some specimens of the European corn borer larvae. Each complex is connected to the brain by two nerves. A short connective (16) arises from the posterior portion of the complex and extends directly to the ventro-posterior portion of the brain. A second connective (13) originates from the anterior half of the complex, extends anteriad, giving off a branch (27) to the postcerebral dilator muscles of the esophagus, and joins the brain immediately posterior to the origin of the optic nerve (10). The anterior extension (14) of this nerve terminates on the inner surface of the head capsule. Another short nerve (29) originating on the mesal surface of the complex, extends directly to the esophagus. A nerve (18), originating from the anterior portion of the complex, extends antero-ventrad, and after a short distance forms what appears to be a small ganglion (35) which sends a branch (36) to the maxillary nerve (21) of the subesophageal ganglion. The main nerve continues antero-ventrad from this ganglion and terminates by joining the maxillary nerve (21) near the base of the maxilla. Another small nerve (19) extends postero-ventrad from the ventral side of the complex. McLeod and Beck (1963) state that this particular nerve was traced to an apodeme of the tentorial bridge. We cannot, however, verify this statement because we have been unable to trace it in its entirety. From the posterior margin of the complex a nerve (17) extends mesad giving off branches to the lateral wall of the aorta and to the recurrent nerve.
Ventral sympathetic nervous system. This division of the sympathetic nervous system typically consists of a single, unpaired median nerve (and its transverse branches) originating from the thoracic ganglia and the first six abdominal ganglia, but the prothoracic ganglion of the European corn borer larva has additional nerves belonging to this system.

The median nerve of the prothoracic ganglion (Figs. 14, 15) originates from the posterior margin of the ganglion between the widely separated interganglionic connectives. It extends posteriad for a short distance and then bifurcates into two lateral transverse nerves. The transverse nerves extend laterad and slightly caudal for a short distance and then each receives a branch from the anterior lateral nerves of the mesothoracic ganglion. The transverse nerves then continue in a slight latero-anteriad direction over the inner surface of the internal longitudinal ventral muscles. In the region of the prothoracic spiracle, branches are given off to the posterior portion of the prothoracic gland and the spiracle (Fig. 14). The branch to the prothoracic gland also receives another nerve branch from the anterior lateral nerve of the mesothoracic ganglion. The additional ventral sympathetic nerves of the prothoracic ganglion arise as a pair (or a single nerve has been seen) of short nerves from the anterior margin of this ganglion between the interganglionic connectives. These two short nerves join almost immediately. Two pairs of transverse nerves originate from this union. The anterior pair extends antero-laterad to muscles attached to the head capsule and then extends in a latero-dorsad direction towards the anterior portion of the prothoracic glands to which they connect. The posterior pair of the anterior sympathetic nerves extends from the aforementioned union in a latero-caudal direction to the tracheae of the prothoracic spiracle.

The median nerve of the mesothoracic ganglion arises from the posterior margin between the interganglionic connectives. It extends posteriad for a short distance and then bifurcates, giving rise to two lateral transverse nerves. These nerves proceed slightly latero-caudal, receive a nerve from the anterior lateral nerves of the metathoracic ganglion, and then extend in a more lateral direction, terminating in the lateral regions of the mesothorax.

The median nerve of the metathorax originates in a similar manner but bifurcates very near the anterior margin of the first abdominal ganglion. The transverse nerves lie very near the anterior lateral nerves of the first abdominal ganglion and are united to them by a pair of short nerves and a nerve plexus. The transverse nerves extend latero-caudal into the first abdominal segment and terminate in the region of the first abdominal spiracle.

The median nerves of the first six abdominal ganglia originate from the posterior margins but are obscured by the adjacent, paired interganglionic connectives. The median nerves of these ganglia extend posteriad into the following abdominal segments appearing at the point of separation of the interganglionic connectives. Only a short distance after becoming visible, each median nerve bifurcates into two transverse nerves. Each transverse nerve receives a branch from the anterior lateral nerves of the ganglia immediately posterior to them and then extends laterad over the inner surface of the internal longitudinal ventral muscles to the region of the spiracles. Therefore, the median nerves
of the metathoracic ganglion and the first six abdominal ganglia give rise to transverse nerves which innervate the spiracular region of the segment immediately posterior.

No median nerves were found originating from the fused 7th and 8th abdominal ganglia. However, a branch of the anterior lateral nerve of the 8th abdominal ganglion extends to the 8th abdominal spiracular region in a fashion similar to that of the transverse nerves and may serve to innervate this region in the absence of the median and transverse nerves.

**Caudal sympathetic nervous system.** This portion of the sympathetic nervous system is said to originate from the fused posterior abdominal ganglia and to innervate the posterior proctodaeum and the reproductive system. The pair of nerves (Figs. 14, 15) which arise in the most ventral position from the fused posterior abdominal ganglia may possibly belong to this division, but this was not verified.

**Peripheral nervous system**

The peripheral nervous system includes all the nerves extending from the ganglia of the central and sympathetic nervous systems. These nerves have been briefly described in the discussion of the other divisions of the nervous system.

**Reproductive System**

**Male reproductive organs**

The paired testes are located in the dorsal region of the fifth abdominal segment immediately laterad to the dorsal vessel and between the alary muscles of the dorsal vessel (Fig. 16). The testes are rather large, conspicuous, kidney-shaped structures, approximately one-half to three-quarters the length of the segment. They are bounded ventrally by the fat body surrounding the gut and are held in place by fat body tissue attached to their anterior and posterior ends. They are richly supplied with tracheal branches from the 5th abdominal spiracle.

Four internal chambers are faintly visible and seem to converge mesally. The chambers are much more evident if the outer testicular sheath is removed. A small duct, slightly expanded at its origin on the meso-ventral surface of each testis, extends postero-laterad along the internal longitudinal dorsal muscles. Each duct passes immediately dorsad to the visceral trachea of the 8th abdominal spiracle and here turns ventrad, extending parallel and in very close proximity to the tracheal tube leading to the genital pouch (Fig. 16). The ducts enter the antero-lateral margins of the genital pouch. The small, almost rectangular genital pouch is located in the 9th abdominal segment, ventrad to the rectum. It is attached to the ventral integument at its slightly tapered posterior margin. The pouch has two distinct internal chambers, but they have no visible external opening.

**Female reproductive organs**

The paired ovaries, located in the dorsal region of the 5th abdominal segment, are laterad to the dorsal vessel and between the alary muscles (Fig. 17). They are almost completely surrounded by fat body tissue lying ventrad to the internal longitudinal dorsal muscles. The oviducts,
Ventral view of male reproductive system. Anterior portion of alimentary canal removed. (App. X6)

Ventral view of female reproductive system. (App. X6)
when stained, are easily traced to the ovaries within the fat body tissue. The ovaries, whose shape varies from oval to slightly oblong, are considerably smaller than the testes, being about one-fifth the length of the 5th abdominal segment. Four internal tubules, converging posteriorly to open into a common duct, are evident when the ovaries are observed with a compound microscope.

A very thin oviduct arising from the posterior margin of each ovary extends postero-laterad along the dorsal musculature and passes dorsad to the visceral trachea of the 7th abdominal segment. Here it turns sharply ventrad following the ventral segmental trachea towards the mid-ventral line. Separating from this trachea, the oviduct passes beneath the ventral muscles and terminates by attaching very near the mid-ventral line of the integument, just opposite the oviduct from the other side of the body. In some specimens these ducts are connected by a thin strand of tissue at the point of their integumental attachments. No external openings are evident.

Dorsal Vessel

The dorsal vessel is located beneath the mid-dorsal line between the longitudinal dorsal muscles (Fig. 18). It is bounded on its ventral surface by the fat body surrounding the alimentary canal and viscera. The dorsal vessel extends from the head posteriad into the 8th abdominal segment. It is an inconspicuous, opaque, white tube as seen from a ventral view and is much easier to recognize after it has been stained.
The dorsal vessel is composed of a posterior pumping organ, or heart, and an anterior conducting vessel, the aorta, even though the structure is a continuous tube. The heart is found in abdominal segments one through eight. It is supplied with seven pairs of segmental alary muscles. The very fine alary muscles are broadly attached to the heart and converge to their intersegmental attachment points just posterior to the intersegmental folds. The heart is expanded in the 8th abdominal segment and appears to be closed. Only slight, if any, enlargements of the heart occur in each segment in the region of the alary muscle attachments.

The segmental ostia which are reported to occur on the heart of other insects were not recognized in the preserved European corn borer larvae even though the dorsal vessel was removed and examined under a compound microscope. No observations were made of living larvae.

The aorta is a continuation of the heart in the thorax and head. In the prothorax it turns ventrad and ultimately passes beneath the brain. At this point it reaches its smallest size. Anteriad to the brain, the aorta enlarges considerably and terminates as a funnel-shaped structure.

**Wing Buds**

Wing buds are present in the 5th instar of the European corn borer larva and are located in the latero-dorsal regions of the mesothorax and metathorax—not in the prothorax and mesothorax as reported by Larsson (1929).

The wing buds are concealed by the lateral musculature of the aforementioned segments. They are small, oval-shaped structures attached to the internal cuticular walls at their anterior margin. They are well supplied with tracheal branches from both the anterior and posterior aspects. If the buds are teased apart, an outer pouch, or epidermal invagination can be recognized within the two-layered wing bud.

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ABSTRACT. This paper reports 6-year results of a study of the survival and height growth of three Alpen and two Sudeten seed sources of European larch (Larix decidua Mill.) and one European x Japanese larch hybrid (L. eurolepis [L. decidua x L. leptolepis]) in northeast Iowa. Approximately 100 2-0 seedlings of each of the six seed origins were planted in a 6x6-foot spacing in each of two replications. Based on 6-year survival and height growth, seed sources from the Sudeten group and the Japanese x European hybrid appear to be superior to the Alpen group for planting on Fayette silt loams in northeast Iowa. However, because of the problems of larch canker infestations on larch planted beyond its natural range, extensive plantings in northeast Iowa of the more canker-resistant Sudeten group must be undertaken only at considerable risk until resistance of this group to the fungus is established in northeast Iowa.

Tree planting failures in Iowa are related to the lack of adequate information on the adaptability of introduced species and to the diversities of climate, soil and topography (Kepler and Gatherum 1964). To minimize tree planting failures, more accurate information is needed on the adaptability to specific sites of species and variants within species.

European larch (Larix decidua Mill.) has shown promise as a forest tree in species adaptation studies in Iowa. McComb (1955) cites European larch 80 to 95 feet tall on deep silt-loam soils of the Fayette series on exposed sites. These heights exceed by 5 to 15 feet the heights of adjacent native hardwoods. Strong valuable wood, rapid growth and high yields, adaptability to strongly calcareous (pH 7.8) and to quite strongly acid (pH 4.5) soils, resistance to winter kill, extreme wind firmness and great longevity make its use desirable on many sites and soil types in Iowa (McComb 1955).

However, within the geographical range of European larch, four separate major distributional groups are recognized: Alpen, Sudeten, Tatra and Polen plus several smaller outliers in Rumania. Major genetic differences are found between and within some of these groupings (McComb 1955). Consequently, field provenance tests have been established to aid in the selection of desirable variants within this species for planting in Iowa.

2 Professor, Department of Forestry, Iowa State University, Ames.
This paper reports 6-year results of a study of the survival and height growth of the seedlings of three Alpen and two Sudeten seed sources of European larch (Larix decidua Mill.) and one European x Japanese larch hybrid (L. eurolepis [L. decidua x L. leptolepis]) in northeast Iowa. Primary objectives of this study were (1) to determine the magnitude of the variation in survival and height growth among the six European larch variants and (2) to determine the relationships between survival and height growth and the altitude and latitude of the seed origins. This information should help to improve the selection of variants of European larch for planting in northeast Iowa, and aid in identifying satisfactory parent material for future breeding and hybridization studies.

MATERIALS AND METHODS

Origin of the six variants ranged from 44° to 56° N latitude and 0 to 2,000 meters altitude (Table 1). The study was conducted at the Paint Creek Unit of the Yellow River State Forest, Allamakee County. Geographic, physiographic, edaphic, climatic and vegetative descriptions of the experimental area are given by Jensen and Gatherum (1964).

This study was established as a randomized block design according to the design of Cochran and Cox (1957). Approximately 100 2-0 seedlings of each of six seed origins of European larch were planted in April 1959 at a 6x6-foot spacing in each of two replications. Six-year survival and height growth data were obtained in December 1964.

Table 1. Origin of European larch seed sources used in study.

<table>
<thead>
<tr>
<th>Provenance</th>
<th>Lat. °N</th>
<th>Long. °E</th>
<th>Altitude meters</th>
<th>Race or hybrid</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern alps, Austria (84)</td>
<td>48</td>
<td>14</td>
<td>600-1000</td>
<td>alpen</td>
<td>Alpen</td>
</tr>
<tr>
<td>Central alps, Austria (85)</td>
<td>47</td>
<td>12</td>
<td>1000-2000</td>
<td>alpen</td>
<td>Alpen</td>
</tr>
<tr>
<td>French alps, E. central France (96)</td>
<td>44</td>
<td>5</td>
<td>800-1400</td>
<td>alpen</td>
<td>Alpen</td>
</tr>
<tr>
<td>Breslau, Poland (97)</td>
<td>51</td>
<td>17</td>
<td>100-200</td>
<td>sudetica</td>
<td>Sudeten</td>
</tr>
<tr>
<td>Wroclaw, Poland (100)</td>
<td>52</td>
<td>20</td>
<td>400-700</td>
<td>sudetica</td>
<td>Sudeten</td>
</tr>
<tr>
<td>Jutland, Denmark (103)</td>
<td>56</td>
<td>8</td>
<td>0-500</td>
<td>x eurolepis</td>
<td>--</td>
</tr>
</tbody>
</table>
RESULTS

Six-year survival among the six seed origins varied from 37 to 96%, and 6-year height growth varied from 4.3 to 13.4 feet (Tables 2 and 3). Survival and height growth of seedlings of the European x Japanese larch hybrid and of the two Sudeten sources, in general, were greater than survival and height growth of seedlings of the three Alpen sources.

Six-year height growth of individual seedlings ranged from 1.0 feet for Alpen (96) to 19.0 feet for Sudeten (97) (Fig. 1). Regression of height growth on altitude of seed origin was significant, \( r = 0.805 \). A 1,000 meter increase in altitude of seed origin resulted in a 6.4-foot decrease in 6-year height growth.

![Image of European Larch in Northeast Iowa](image-url)
Table 2. Average 6-year provenance survival in percent, and height growth in feet.

<table>
<thead>
<tr>
<th>Group and provenance no.</th>
<th>Survival</th>
<th>Height growth</th>
</tr>
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<tbody>
<tr>
<td>x Eurolepis (103)</td>
<td>96%</td>
<td>13.4</td>
</tr>
<tr>
<td>Sudeten (97)</td>
<td>96%</td>
<td>8.9</td>
</tr>
<tr>
<td>Sudeten (100)</td>
<td>79% 5%</td>
<td>8.2</td>
</tr>
<tr>
<td>Alpen (96)</td>
<td>77% 1%</td>
<td>6.1</td>
</tr>
<tr>
<td>Alpen (85)</td>
<td>60%</td>
<td>5.6</td>
</tr>
<tr>
<td>Alpen (84)</td>
<td>37%</td>
<td>4.3</td>
</tr>
</tbody>
</table>

1 Means grouped by a line do not differ at the designated probability level (Duncan 1955).

Table 3. Analysis of variance of average 6-year provenance survival and height growth.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Total</th>
<th>Replication</th>
<th>Provenance</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height growth</td>
<td>11</td>
<td>117.71</td>
<td>6.20</td>
<td>107.12</td>
<td>4.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>21.42</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>24.40**</td>
<td></td>
</tr>
<tr>
<td>Survival</td>
<td>5</td>
<td>6706.00</td>
<td>65.33</td>
<td>6565.00</td>
<td>75.67</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>1313.00</td>
<td>15.13</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>86.76**</td>
<td></td>
</tr>
</tbody>
</table>

** Significant at 1% probability level.
The magnitude of the variation in survival and height growth among the six European larch seed origins indicates that care should be taken in the selection of European larch variants for planting in Iowa. Based on 6-year survival and height growth, seed sources from the Sudeten group and the Japanese x European hybrid appear to be superior to the Alpen group for planting on Fayette silt loams in northeast Iowa. For the seed sources sampled, the negative regression of height growth on altitude of seed origin supports the hypothesis of McComb (1955) that the European provenances from low elevations should prove more adaptable in eastern United States.

Although European larch is exceptionally pest-free and disease resistant in its natural range, larch canker caused by the fungus, Dasycypha willkomii (Hart) Rehm, often becomes a serious disease beyond its natural range (McComb 1955). Even though the Sudeten group appears to be much less susceptible to the fungus than the Alpen group (Munch 1936), extensive plantings of the Sudeten group in northeast Iowa must be undertaken only at considerable risk until resistance of this group to the fungus is established in northeast Iowa.

LITERATURE CITED


THE EFFECT OF ENVIRONMENTAL TEMPERATURE ON FORAGE DRY MATTER INTAKE AND MILK YIELD OF LACTATING COWS

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Iowa State University
of Science and Technology
Ames, Iowa

ABSTRACT. Environmental temperatures of 75°F or higher significantly lowered the intake of forage dry matter and yield of milk of high-producing mature Holstein cows in early to mid-lactation during an 84-day trial. Twelve cows were assigned to three treatment groups as dictated by another phase of the study. Forage consisted of alfalfa fed ad libitum as either hay, haylage, or green chop and differed among and within groups of cows during the trial. Concentrate feeding levels differed among groups but were held essentially constant within groups. The three groups of four cows each obtained about 48, 40 and 52%, respectively, of their total dry matter intakes from forages. Significant correlations between the variables studied were: -0.36 between daily mean temperature and forage dry matter intake, -0.42 between mean daily temperature and succeeding day's milk yield, and 0.60 between daily forage dry matter intake and the succeeding day's milk yield. Body weights were maintained throughout the trial.

Producers of all classes of livestock are generally aware of the close relationship between animal comfort and performance. Genetic and environmental adaptability factors conducive to efficient performance have received increasing attention in recent years in the efforts to improve livestock productivity in tropical areas.

The effects of extremes in environmental temperature on various physiological functions have been investigated in carefully controlled laboratory studies and to a limited degree under practical production conditions. Extensive data are not available on the effect of high environmental temperature on the feed intake and milk yield of dairy cows producing at high levels. Additionally, most earlier observations have been made with cows on grazed pasture, where the factors of declining amount and quality of forage, the annoyance of flies, and lack of shade and convenient water supply have affected the results.

Warwick (6) reviewed findings relating to the effect of high temperatures on growth and fattening in beef cattle, hogs, and sheep. The consensus of these findings was that high environmental temperature has a depressing effect on feed intake, rate of gain, and efficiency of gain. Hahn et al. (2) found in controlled temperature studies that lactating cows housed in an 85°F environment and breathing air of the same temperature consumed less feed and water and produced only 73% as much milk as their estimated yield in a 65°F environment. Johnston (5) studied environmental temperature effects on milk production and feed intake of Holstein and Jersey cows over a 120-day period. Under conditions varying from air conditioned to existing pasture environments, he found in one trial that Holstein cows exposed to maximum temperature of 70°F and 15 mm Hg maximum humidity averaged 25.4 lb of fat-corrected-milk yield per day as compared with 22.9 lb per day for cows in unshaded pasture exposed to maximum temperature of 93°F and maximum humidity of 12 mm Hg. Forage dry matter intake was recorded for the cows in the air-conditioned environment and amounted to an average of 24.9 lb per cow per day. It was concluded that lowered milk yield occurred only when depressed appetites reduced feed intake, rather than as a result of any direct effect of the hot environment. Achacoso et al. (1) found negative correlations of from -0.114 to -0.153 between mean daily temperature and milk production with different groups of cows. Jarrett and Fosgate (4) studied DHIA data for Holstein cows involving 2,799,792 cow-days. Approximately 43% of the total net energy intake of these cows came from concentrates. The study showed that fat-corrected-milk yield closely followed the net energy intake above maintenance requirements. At the highest levels of net energy intake, one therm of net energy produced 1.6 lb of fat-corrected-milk. The effect of month of the year on net energy intake and fat-corrected-milk yield was highly significant, with the highest intake and F.C.M. yield occurring in April and lower than average values in May through August. Hillman (3) studied the effect of grass silage versus hay, and combinations of the two, on milk production and found no significant differences. The correlation coefficient between forage dry matter intake and milk production was 0.572.

**EXPERIMENTAL PROCEDURE**

During the 12-wk period from May 27, 1963 to August 18, 1963, daily forage intake was recorded for three groups of four mature Holstein cows each in the Iowa State University herd. All the cows were in early to mid-lactation, and the groups were balanced on the basis of freshening date, production level, and body size. The average stage of lactation differed by less than 10 days among the three groups. The cows were housed in tie stalls in the main herd barn with good air circulation and were turned out daily for exercise after the sun went down.

Maximum and minimum air temperatures were obtained for each 24-hr period. The mean 24-hr temperature was computed by averaging the minimum and maximum values. Mean daily temperatures during the 12-wk period ranged from a low of 60°F on May 27 to a high of 84.5°F on August 2, and averaged 72.8°F for the 84 days. The days with mean
temperatures of 75°F or higher were well distributed throughout the experimental period, as follows:

<table>
<thead>
<tr>
<th></th>
<th>No. of days with</th>
<th>Mean temperature of 75°F or higher</th>
<th>Mean temperature of 80°F or higher</th>
</tr>
</thead>
<tbody>
<tr>
<td>First 4 weeks</td>
<td>10</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Second 4 weeks</td>
<td>16</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Third 4 weeks</td>
<td>12</td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>

The three groups of cows used for this experiment received different types of forage during the 12-wk period as dictated by another phase of the study. For the first two weeks, all three groups were fed alfalfa hay harvested in 1962. Subsequently, Group 1 received hay from the same source throughout the trial; Group 2 received alfalfa haylage stored in late May of 1963 for 9 wks, followed by hay for 1 wk; and Group 3 received green-chopped alfalfa for 5 wk, hay for 4 wk and alfalfa haylage for 1 wk. Dry matter determinations were made twice weekly for each forage from samples collected at the times it was fed during a 24-hr period. Forages were fed three times daily, and weighbacks of refused material were made once daily. Samples of the different forages and the concentrate mixture fed were taken periodically throughout the trial, and proximate analyses were obtained.

The same concentrate mixture was fed to all the cows during the trial. Concentrate feeding levels differed among cows but were held essentially constant for each cow throughout the experiment and at levels which resulted in negligible refusal. Daily dry matter intake from concentrates was held constant at 21.3 lb per cow for Group 1, ranged from 24.8 to 26.6 for Group 2, and was constant at 22.0 lb for Group 3. Comparisons of dry matter intakes from forages and concentrates showed that, over the 12-wk period, the approximate portions of total dry matter intake obtained from forage was 48% for Group 1, 40% for Group 2, and 52% for Group 3.

All cows were weighed at the same time of day on the first day of each week to record gross body weight changes.

Proximate analyses of the different feeds are presented in Table 1.

**RESULTS AND DISCUSSION**

The average forage dry matter intake per cow over the 12-wk trial was 19.8 lb. Cows in Group 3 consumed larger amounts of forage than those in Groups 1 and 2, regardless of type of forage or environmental temperature conditions. The temperature variations that occurred during the experiment were fortuitously favorable for observing their influence on forage intake since the variations were rather evenly distributed throughout the 12 weeks and were generally of short duration. Environmental temperature changes up to 75°F had no noticeable effect on forage intake. Average forage dry matter intake for the combined three groups of cows on days when the mean temperature was 75°F or higher was only 90% of that recorded on days when temperature was under 75°F.
### TABLE 1

Proximate analyses of feeds fed

<table>
<thead>
<tr>
<th></th>
<th>Percent Dry Matter (as fed)</th>
<th>Percent Crude Protein (air dry basis)</th>
<th>Percent Crude Fiber (air dry basis)</th>
<th>Percent Ether Extract (air dry basis)</th>
<th>Percent Ash (air dry basis)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Green chop</td>
<td>29.4-33.0</td>
<td>30.8</td>
<td>14.8-18.6</td>
<td>16.8</td>
<td>28.8-36.6</td>
</tr>
<tr>
<td></td>
<td>56.1-68.0</td>
<td>64.0</td>
<td>16.2-18.6</td>
<td>17.5</td>
<td>23.9-28.7</td>
</tr>
<tr>
<td>Hay</td>
<td>91.0</td>
<td>11.6</td>
<td>41.5</td>
<td>1.1</td>
<td>4.9</td>
</tr>
<tr>
<td>Concentrate mixture</td>
<td>92.0</td>
<td>16.6</td>
<td>5.7</td>
<td>1.8</td>
<td></td>
</tr>
</tbody>
</table>
The decline in forage intake was much sharper when mean daily temperatures reached 80°F and above. The average forage intake per cow on such days was 71% of that on days with temperatures under 75°F. Figure 1 shows the average daily forage dry matter intakes for the three groups combined and for each group separately during different environmental temperature ranges.

The relationships between mean daily temperature, forage dry matter intake, and milk yield are shown in Figures 2.1, 2.2 and 2.3. Increases in environmental temperature from 75°F and up were accompanied by concurrent decreases in forage dry matter intake. When the entire range of daily mean temperatures encountered during the 84-day period were considered, a significant (P<.01) negative correlation of -0.36 was found between daily mean temperature and forage dry matter intake. A lower, but significant (P<.01), negative correlation of -0.26 was found between maximum daily temperature and forage dry matter intake.

Milk production was, as expected, adversely affected by the high temperature and its accompanying drop in forage dry matter intake. Figures 2.1, 2.2 and 2.3 indicate that the drop in milk production lagged somewhat behind the drop in forage dry matter intake. This suggests that it is the lowered nutrient intake, rather than any direct effect of high environmental temperature, that exerts the main effect on milk production. A significant (P<.01) negative correlation of -0.42 was found between daily mean temperature and the succeeding day’s milk yield for the cows in all groups over the 84-day trial. A similar result was obtained for 12 regular herd cows of the same breed and at a similar stage of lactation and production level. Forage intakes were not recorded for these cows, and they were outdoors except at milking times, receiving free choice feeding of hay and green chop. For these cows, a significant (P<.01) negative correlation of -0.36 was found between daily mean temperature and the succeeding day’s milk yield.

The effect of forage dry matter intake on the succeeding day’s milk yield observed in Figures 2.1, 2.2 and 2.3 is substantiated by the significant (P<.01) correlation of 0.60 found between these two variables. Average daily milk yields for the three groups of cows are presented in Table 2, along with average milk output per pound of dry matter consumed from both forage and grain. The daily milk yields were remarkably consistent throughout the trial, with the exception of the temporary sharp declines associated with periods of high environmental temperature. Milk yield per pound of total dry matter intake also showed little variation during the 12-wk period, and the small differences among groups are in good agreement with what would be expected from the analyses of feeds and the proportions of total intake obtained from the different feed sources. Average body weight changes are shown in Figure 3. These were similar among groups and showed only minor fluctuations from week to week, with the exception of the weighing on July 1, which showed a sharp temporary drop apparently associated with the high temperature which occurred at that time. Essentially, body weight was just maintained by all three groups during the experiment.
Figure 1. Average daily forage dry matter intakes for three groups of Holstein cows during different environmental temperature ranges over a 12-week period.
Figure 2.1

Figure 2.2

EFFECT OF TEMPERATURE ON LACTATING COWS
Figures 2.1, 2.2 and 2.3. Mean daily environmental temperature, forage dry matter intake, and milk yield for 12 Holstein cows during three successive 4-week periods.
Table 2. Milk yield data for Holstein cows during 12-week feeding trial.

<table>
<thead>
<tr>
<th></th>
<th>Group 1</th>
<th>Group 2</th>
<th>Group 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average daily milk yield per cow (lbs):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Entire 12 weeks</td>
<td>57.0</td>
<td>63.9</td>
<td>63.5</td>
</tr>
<tr>
<td>1st week</td>
<td>67.2</td>
<td>70.3</td>
<td>68.3</td>
</tr>
<tr>
<td>12th week</td>
<td>51.7</td>
<td>59.9</td>
<td>57.4</td>
</tr>
<tr>
<td>12th week as % of 1st week</td>
<td>76.9%</td>
<td>85.2%</td>
<td>86.4%</td>
</tr>
</tbody>
</table>

Milk yield/lb of total dry matter intake (lbs)
1.40 1.56 1.39

REFERENCES
EFFECT OF HERBICIDES ON SEEDLING DEVELOPMENT IN AN IOWA CONIFER PLANTATION

Carl J. Goebel

ABSTRACT. Four preplanting herbicide treatments, amiben at 4 lb/A, diuron at 2 lb/A, 2,4-D at 4 lb/A, and simazine (wettable powder form) at 4 lb/A, were applied to control weeds in a conifer plantation on a silt loam soil. A machine cultivation and an untreated check treatment were also established, making a total of six preplanting treatments. Three 2 lb/A granular simazine postplanting treatments and a no follow up treatment were superimposed on each of the preplanting treatments. Cultivation gave the best control of weeds, but it was more costly than the other treatments. The preplanting herbicides and several granular simazine postplanting applications controlled weeds without injuring eastern white pine, Scotch pine, Austrian pine, Virginia pine, and Norway spruce seedlings.

INTRODUCTION

The establishment of desirable forest vegetation in areas capable of producing valuable forest stands is an important but often difficult responsibility of foresters. Areas well suited to trees also, too often, are suitable for prolific growth of undesirable vegetation. Invading vegetation thus competes intensively with tree seedlings. Such competition for light, soil moisture, and nutrients can be critical until the young trees have established themselves.

In recent years, the use of chemical sprays has been of considerable aid in controlling undesirable vegetation. Unfortunately, difficulties have arisen from a lack of basic knowledge concerning the chemical action within the plants as well as the mechanics of application. For example, spotty accumulations due to drifting foliage sprays have often proved to be uneconomical and sometimes hazardous to more desirable forms of life. Often the species to be encouraged may be injured or killed, particularly if the sprays are applied during its growing period.

Because of the prospect that granular herbicides might alleviate some of the complications and problems associated with foliage sprays, the introduction of these granular forms has received much attention in fields

2 Plant Ecologist, Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S.D.A., Portland, Oregon. Formerly Assistant Professor of Forestry, Iowa State University, Ames, Iowa.
other than forestry. The reduced drifting of granular herbicides, because of the weight of the individual particles, together with the possibility of applying the granular herbicides during the growing season without injury to the desirable tree species, has prompted investigation of their usefulness in the field of forestry. The purpose of this study was to test techniques which may aid in establishing conifer species upon soils of Iowa having adverse environmental conditions, including abundant herbaceous competition. Of primary consideration was the desirability and effectiveness of using a granular herbicide in combination with or as a complete substitute for foliage sprays in controlling weeds.

REVIEW OF LITERATURE

A plethora of information has been published upon the use of herbicides, their mode of action, and their limitations in forestry and allied fields. Practically all of this literature, however, has been concerned with the applications of herbicides in a liquid form; few studies have considered application of the granular form. Observers have reported that expanded demand and commercial use of granular carriers have forged ahead of investigational work on these formulations (Danielson 1959; Krausche 1961; Switzer and Fernandez 1963). As a consequence, it has been difficult to find specific recommendations on the use of granular herbicides and their particular limitations.

In forestry, investigation of the use of granular herbicides in the field has barely begun. Clarke and Grover (1963) have reported upon the application of granular herbicides for weed control in newly planted shelterbelts. Pruett and Gatherum (1961), while working with granular chloro IPC on forest plantings, found that the granular herbicide was as effective as several of the sprayed treatments and sometimes resulted in better weed control.

The successful use of granular herbicides in allied fields suggests that their use may be increased in future forestry work. Some of the advantages that have been listed by investigators are: (1) It may be possible to apply granular herbicides directly over the tree seedlings during their growth period (Burnside and Behrens 1961); (2) water does not have to be hauled for application purposes, so less weight per application is involved and no mixing is necessary (Knake 1963); (3) the granular formulations are easy and convenient to apply and chemical irritation to the operator is reduced (Staniforth et al. 1960; Knake, 1963).

The residual, or carryover, effect of granular herbicides reported by investigators (Burnside and Behrens 1961; Burnside et al. 1963) may be an advantage or disadvantage in forestry work. If the residue is sufficient to carry over a 1-year period but limited to the surface area, this may alleviate the necessity of treating the area each year. However, if the residual material is durable and of sufficient intensity to leach down to the root zone of the tree seedlings, then the accumulation may be disadvantageous to seedling survival and growth.

Disadvantages of using granular herbicides in forestry are:

1. They require some form of moisture to activate and get them into the soil.
EFFECT OF HERBICIDES ON CONIFER SEEDLINGS

2. Because of the special application equipment and calibration required (Staniforth et al. 1960; Krausche 1961; Clarke and Grover 1963), granular herbicides are generally more expensive to apply than the wettable powder form. The bulkiness of the material also contributes to the higher shipping and storage costs than the wettable powder forms (Ragsdale 1962; Staniforth et al. 1960).

3. Some investigators report that granular forms are not as effective as the wettable powder forms (Giordano and De France 1960; Switzer and Fernandez 1963); however, others have found granular formulations to be equal in effectiveness to wettable powder herbicides if employed as soil applications (Staniforth et al. 1960; Pruett and Gatherum 1961).

One of the most promising of the granular herbicides for use in forest plantation and shelterbelt establishment is 2-chloro-4,6-bis(ethylamino)-s-triazine (simazine). Although comparatively new in the chemical herbicide field (Burnside and Behrens 1961), it has already gained much recognition as a selective herbicide (Burnside and Behrens 1961; Warren 1965; Kay and McKell 1963), partly because of its limited penetration into the soil. Although this herbicide has been largely used as a pre-planting treatment (Burnside and Behrens 1961; Poulsen 1964), it shows promise for postplanting application in forestry work.

STUDY AREA

The study was begun in the fall of 1960 and was located on the Albia Pasture Farm in south-central Iowa. The average annual precipitation for the area is 32.5 inches, computed from 30 years of records (U.S. Weather Bureau 1931-1961). Annual averages ranged from 16.3 inches in 1910 to 51.4 inches in 1905, with approximately 30% falling during the May to July period. In 1961, however, only 7% of the total 45 inches of precipitation was received during this critical period.

Determination of evaporation losses in the area from a free-water surface shows that approximately 78% are incurred during the May through July period (U.S. Weather Bureau 1957). Temperature means since 1891 are 24.9°F for January and 77.4°F for July.

Pershing silt loam is the predominant soil type found in the relatively level study area. This soil type is characteristically dry at the summer and exceptionally wet during the spring.

The competing vegetation consisted of mixtures of annual grasses and forbs. Dominating species were yellow bristlegrass (Setaria lutescens), green bristlegrass (Setaria viridis), tall ragweed (Ambrosia trifida), little ragweed (A. artemisifolia) and lambsquarters (Chenopodium album). Other herbaceous competition found in the area consisted of teal lovegrass (Eragrostis hypnoides), witchgrass (Panicum capillare), annual bluegrass (Poa annua), smooth crabgrass (Digitaria ischaemum), barnyardgrass (Echinochloa crusgalli), wild dock (Rumex crispus), redroot amaranth (Amaranthus retroflexus), chicory (Cichorium intybus), Russian thistle (Salsola kali var. tenuifolia), rough buttonweed (Diodia teres), and knotweed (Polygonum spp.). The reference used for grasses was the second edition of A.S. Hitchcock's "Manual of the Grasses of the United States." The scientific plant names for broad-
METHODS AND PROCEDURE

During the fall of 1960, the 3-acre study area was disked to remove all herbaceous and woody plants. Early in the following April, 2,200 conifer seedlings were hand-planted. Five coniferous species, which from previous plantings in the vicinity had appeared promising for establishment, were equally represented in the experiment. They were eastern white pine (Pinus strobus), Scotch pine (P. sylvestris), Virginia pine (P. virginiana), Austrian pine (P. nigra), and Norway spruce (Picea abies). The seedlings were obtained from the State Conservation Commission Nursery near Ames, Iowa. Scotch and Virginia pine were 2-0 stock; white pine was 2-1. The other two species were 3-0 seedlings.

Treatment for the study consisted of several herbicidal sprays followed, in most instances, with a granular herbicide. The design used in the application of the various herbicides was a split-plot pattern.

Preplanting Treatments

To test pre- and postplanting treatments of herbicides in controlling weed competition, the study area was designed to include six randomly assigned treatments applied within each of three blocks. Four preplanting herbicides were randomly applied as ground sprays 3 weeks before planting (Fig. 1) at the following rates: amiben at 4 lb/A, diuron at 2 lb/A, 2,4-D at 4 lb/A, and simazine at 4 lb/A. A fifth plot, randomly located within each block, was machine and hand-cultivated throughout the growing season. The sixth plot served as a check.

Postplanting Treatments

After the preplanting chemicals were applied and the seedlings were planted, a granular form of simazine was applied randomly on one-half of the plots three times during the growing season, resulting in the split-plot experimental design previously mentioned. Division was the long axis of each plot. The granular herbicide was applied at the rate of 2 lb/A during each application. The amount and distribution of the granular herbicide was controlled by an adapted 5-foot-wide Gandy grass seeder designed by Mr. W. G. Lovely of the Agricultural Engineering Research Division, Agricultural Research Service, Ames, Iowa (Fig. 2). The herbicide was applied directly over the conifer seedlings, and no attempt was made to shake the granular material out of the few fascicles of needles where some particles may have lodged. Time of application was determined by the appearance of weed seedlings in the plots. Minimum number of tree seedlings which were then subjected to each sub-treatment was 12 of each species.

Measurements

Responses of the five species to herbicide treatments were evaluated in terms of (1) seedling survival and (2) height growth at the end of the first growing season after planting. Survival was measured in percent of original seedlings alive in October. Height growth was determined
Figure 1. Application of preplanting herbicides on the Albia Experimental Farm study area. Sprayer is 11 feet wide and approximately 15 inches above the ground surface. Note the moist soil conditions within this heavy soil type.

Figure 2. Even distribution of granular herbicide directly over tree seedlings was obtained by means of a broadcast applicator equipped with controls for rate of application. The model used had 18-inch clearance above the ground and covered about a 5-foot swath. The applicator was pulled at an approximate speed of 4 miles per hour.
by measuring the height of each seedling at planting time and again at the end of the growing season (live seedlings only).

RESULTS

Survival

Although the first year survival of all species was reasonably high (average 89%), the difference in survival rates among the species was statistically significant. White pine survival was exceptionally good and averaged 90% for all treatments. Norway spruce also had a vigorous appearance in the field, and a high survival. Austrian pine’s 80% was the lowest average survival of the five species tested (Table 1).

Statistical tests of significance were conducted on appropriate transformations of the percentage data. The white pine data were deleted in the analysis of variance because the uniformly successful establishment of this species resulted in a survival variance which was not compatible with that of the other species, even after being transformed.

These results indicated that the effect of granular simazine depends upon which preplanting herbicide or treatment was applied. The interaction between preplanting and postplanting treatments was highly significant. This interaction evidently concealed any difference between preplanting treatments alone or postplanting treatments alone in the formal analysis of variance.

However, the survival percentages indicated that the granular simazine postplanting treatment with no preplanting treatment was as effective as any of the other treatments (Table 1).

Height growth

The various herbicide treatments resulted in significant differences in the one-year height growth of the tree seedlings. The lowest height growth occurred in the check plot which received no postplanting granular herbicide—in this plot the growth was .25 feet. The highest average growth for all species combined was .38 feet which occurred in the plot which received an amiben preplanting application with granular simazine applied after planting. The average height growth of all species which received only the postplanting granular herbicide (no preplanting herbicide) was .37 feet as compared to the .25 feet for no herbicide at all.

The effect of the treatments on different species was highly significant also. Scotch pine had the greatest growth, an average of .45 feet, as compared with Virginia pine which averaged only .29 feet for all treatments. The average for all species combined was .34 feet. (Table 2)

Weed Competition

The check plots with no herbicides contained almost twice as many weeds per square foot as any that received herbicide treatment (Fig. 3). It was quite apparent that the 2,4-D and amiben treatments without granular herbicide followup applications gave less control of weeds than the other herbicide treatments.

Granular herbicide application did control numbers of weeds quite well, although not as effectively as treatments in which a preplanting herbicide had been used. Treatments which most effectively controlled
Figure 3. Composite of representative results of six major pre- and postplanting herbicides of which one-half of each plot received additional applications of granular herbicide during the growing season.
Table 1. **Percentage of tree seedlings surviving at the end of first growing season**

<table>
<thead>
<tr>
<th>Species</th>
<th>Simazine&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Diuron&lt;sup&gt;a&lt;/sup&gt;</th>
<th>2,4-D&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Amiben&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Cultivation&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Check&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>s n s n s n s n s n s n s n</td>
<td>s n s n s n s n s n s n s n</td>
<td>s n s n s n s n s n s n s n</td>
<td>s n s n s n s n s n s n s n</td>
<td>s n s n s n s n s n s n s n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White pine</td>
<td>100 100 97 100 100 100 100 97 100 100 86 98</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Austrian pine</td>
<td>85 83 75 73 86 82 91 77 81 83 84 55 80</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Scotch pine</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Virginia pine</td>
<td>85 96 73 96 97 100 92 95 78 100 92 67 89</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Norway spruce</td>
<td>97 97 83 97 100 85 94 86 97 92 94 95 93</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>92 93 84 81 93 94 94 92 88 94 93 67 89</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Preplanting treatments are shown above the line; postplanting treatments are shown below the line—either a granular simazine followup (s) or no followup (n).
Table 2. *Average height growth (feet) of surviving tree seedlings during the 1961 growing season*

<table>
<thead>
<tr>
<th>Species</th>
<th>Simazine&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Diuron&lt;sup&gt;a&lt;/sup&gt;</th>
<th>2,4-D&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Amiben&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Cultivation&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Check&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Average</th>
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<tr>
<td></td>
<td>s</td>
<td>n</td>
<td>s</td>
<td>n</td>
<td>s</td>
<td>n</td>
<td>s</td>
</tr>
<tr>
<td>White pine</td>
<td>0.33</td>
<td>0.30</td>
<td>0.38</td>
<td>0.31</td>
<td>0.31</td>
<td>0.23</td>
<td>0.35</td>
</tr>
<tr>
<td>Austrian pine</td>
<td>.28</td>
<td>.34</td>
<td>.30</td>
<td>.33</td>
<td>.32</td>
<td>.31</td>
<td>.34</td>
</tr>
<tr>
<td>Scotch pine</td>
<td>.45</td>
<td>.41</td>
<td>.47</td>
<td>.46</td>
<td>.42</td>
<td>.39</td>
<td>.51</td>
</tr>
<tr>
<td>Virginia pine</td>
<td>.33</td>
<td>.29</td>
<td>.39</td>
<td>.19</td>
<td>.25</td>
<td>.22</td>
<td>.35</td>
</tr>
<tr>
<td>Norway spruce</td>
<td>.33</td>
<td>.33</td>
<td>.35</td>
<td>.36</td>
<td>.34</td>
<td>.25</td>
<td>.36</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>.34</td>
<td>.33</td>
<td>.38</td>
<td>.33</td>
<td>.33</td>
<td>.28</td>
<td>.38</td>
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<sup>a</sup> Preplanting treatments are shown above the line; postplanting treatments are shown below the line—either a granular simazine followup (s) or no followup (n).
weeds were diuron, amiben, and simazine preplanting applications with granular followup. The average density of weeds for these three treatments were 0.04, 0.04, and 0.21 plants per square foot, respectively. Thorough mechanical and hand cultivation completely controlled the weeds in the cultivated plots, but required considerable investment of time and supervision.

Total numbers of weeds varied not only with the type of treatment, but also with the phenological stage of the plants. In the beginning of the growing season, there were as many as 60 weed seedlings per square foot in the check plots with no granular followup. During the peak of the growing season, however, when such weeds as lambsquarters and tall ragweed were 48 to 60 inches tall, the highest density per plot had dropped to 5.0 weeds per square foot.

Forbs, such as lambsquarters and ragweeds, made up a large portion of the competing weeds on untreated plots. The most prevalent grass competitors were the bristlegrasses.

DISCUSSION

Of the 12 treatments tested in the experiment, there were several which show promise for establishing forest plantations in southeastern Iowa.

Cultivation gave the best control of weeds and success in seedling survival, although labor and machinery requirements were much greater than the other treatments.

 Practically equivalent to the cultivation treatments in control of weeds were the diuron, amiben, and simazine preplanting herbicide treatments, followed by additional applications of granular herbicide during the growing season. Although these treatments insured almost complete control of the competing weeds and allowed from 88 to 96% of total sunlight to reach the seedlings, this may not always be desirable. Such complete control exposes the site to the danger of soil erosion. In addition, these more effective methods of control are expensive.

For survival and height growth of the tree seedlings, this limited study would indicate that either the preplanting herbicides alone or the granular herbicide applications during the growing season may be entirely adequate to control weeds competing with conifer seedlings. The added effect of combining the two types of application may not be justified unless maximum control of competing vegetation is necessary.

In these one-year tests, the granular form of the simazine was as effective as the preplanting liquid herbicides in controlling undesirable weed competition. No apparent damage to the tree seedlings in the first season could be attributed to the granular herbicide, at the rates applied, even though the simazine was added directly over the tree seedlings during the growing season. Because of the added advantages of uniform distribution and minimum drift, granular herbicides show promise of usefulness in forestry in areas where sufficient rainfall is present to make them effective shortly after their application.
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