My original intent in this paper was to present a chronology of events for the reproductive biology of northern red oak (*Quercus rubra* L.) based on a review of the literature. However, because there is so little information available about northern red oak, results from studies of other species of *Quercus* will be included to provide some continuity. This may lead some readers into a false sense of security about what we really know of the pathway from flowers to seed maturation in northern red oak.

There are two major subgeneric groups of North American oaks: Section *Quercus* (formerly *Lepidobalanus*) or the white oaks, and *Lobatae* (*Erythrobalanus*) or the red oaks. These two groups differ structurally and chemically. However, we will concern ourselves only with differences in the reproductive cycle. Simply put, the white oaks require only one growing season from the time of pollination to acorn maturation. The red oaks, however, require two growing seasons. [Editor's note: There are a few exceptions to this rule, such as *Quercus agrifolia*, *Q. hypoleucoides*; the third major North American subgeneric group, Section *Protobalanus* or golden oaks, also requires two growing seasons.] Pollination occurs in the first season, and the ovule primordia remain as placentae or rudimentary bulges until the following growing season, when the ovules develop, fertilization is accomplished, and the acorns mature. These structures and processes will be the primary focus of this paper.

**Pistillate Flowers**

Acorns develop from fertilized pistillate (female) flowers. Because there has been little demand for oak breeding programs, there has been little desire to understand and manipulate the reproductive cycle. Our knowledge has been provided almost exclusively by botanists with an academic interest in studying a structure or process, and not by foresters with an interest in managing trees. Thus, the descriptions of the flower must use specific botanical terminology. The developmental morphology of the unfertilized pistillate flower of *Q. rubra* was described by Langdon (1939) and Sattler (1973); their interpretations are combined in this part of the paper.

The pistillate flower originates as a stalk or inflorescence in the axil of a developing leaf primordium during the summer before pollination, and contains several bracts arranged spirally on its axis. After the inflorescence and bracts overwinter, floral apices differentiate in the axils of each of the lower, opposite bracts of the inflorescence, and then flatten and assume a three-cornered appearance as a result of growth occurring at their periphery. The individual flower, partially enclosed by a cupular involucre of inbricating scales, consists of a cup-shaped perianth tube, non-diverged from the walls of a three-celled ovary that bears three
stigmatic styles. The involucre is first formed as a few separate primordia in the axils of the bracts located at the based of the floral apex. Three inner perianth members are initiated simultaneously between the outer perianth members, and all then are raised up on a common base as three gynoecial (carpel) primordia arise on the broad flat apex opposite the outer perianth members. The carpel primordia differentiate into the three stigmas.

In the first growing season, further ovary maturation occurs about one month after pollination. The young ovary becomes closed as a result of the appression of the three gynoecial primordia as they are carried up with the extending ovary wall. Concurrently, growth between and at the base of the gynoecial primordia initiates the three septa, which eventually become appressed at only their upper inner margins. Two placenta form initially as slight protrusions along the base and on each side of a septum. In each of the three locules or chambers of the ovary, there are two placenta—one from each septum (figure 1). The ovules will develop from these placental bulges in the second growing season (Sattler 1973). Botanically speaking, an ovule is a megasporangium; i.e., a structure that bears the megaspore mother cell (MMC) (Davis 1966).

![Figure 1. A Q. rubra pistillate flower at the time of pollination. 1A. Cross section of an ovary, showing three septa that divide the ovary into three locules or chambers. A locule contains two placenta or primordial bulges, each of which will differentiate into an ovule. Only one of the six ovules will mature into an acorn. 1B. Longitudinal section of a flower at the time of pollination, with two of the three locules shown.](image-url)
Between late July of the first season and early April of the second, only the cupule (the future acorn cup) develops further, enclosing the flower during the winter, with only lignified vestiges of the styles and perianth above its rim. By early May of the second season, the ovary wall has expanded, the placental axis has elongated, and the ovules bear the rudiments of the inner and outer integuments (Langdon 1939). By mid-May the nucellus is now covered by the inner and outer integuments, which have elongated over the end of the nucellus and have formed a "hole" called the micropyle. At the time of fertilization, the margins of the outer integument, toward the open end, greatly increase in height and form a lip (Sattler 1973). This is the route through which the pollen tube approaches the embryo sac (Benson 1894). Major food reserves of starch and lipid are located almost exclusively within the outer integument, while the inner integument is virtually void of food reserves (Mogensen 1973). The MMC undergoes meiosis or reduction-division, producing four haploid cells, only one of which survives to become the functional megaspore. By a series of mitotic divisions, the megaspore gives rise to the megagametophyte or embryo sac, an eight-nucleate structure at the tip of the nucellus (figure 2). A feature of the Q. rubra nucellus during growth of the megagametophyte is the appearance of a central strand of procambial elements that extend through the base of the nucellus and are continuous with the vascular tissues of the raphe and funiculus (Langdon 1939).
Once the embryo sac is formed, fertilization of its egg and central cell via germinating pollen must occur for seed development to continue. During fertilization, the pollen tube discharges two haploid gametes into the embryo sac. One fuses with the egg to produce a diploid zygote; the other gamete fuses with the 2N central cell (formed by the earlier fusion of the two polar nuclei) to produce the 3N (triploid) endosperm. Following fertilization, a free-nuclear endosperm grows before the first division of the zygote occurs (Hjelmqvist 1953, 1957; Brown and Mogensen 1972). In general, as the endosperm becomes cellular, the embryo begins to differentiate (Singh and Mogensen 1976), moving quickly through the heart-shaped stage (figure 3).

![Diagram](image)

**Figure 3** Some embryological stages of *Q. rubra*. A. The free nuclear endosperms. Nuclei are triploid (3N) and exist in a common cytoplasm; i.e., there are no cell walls separating the nuclei. B. As the endosperm begins to form cell walls centripedally between the free nuclei, the diploid zygote begins to grows into a proembryo. C. The embryo is at the heart-shape stage when the endosperm becomes completely cellular. The "wings" of the embryo are the cotyledons that will grow and eventually fill most of the acorn.

Information about later embryo and cotyledon growth of acorns is very limited. Mogensen (1965) provided the most detailed picture in his comparative study of *Q. alba* and *Q. velutina*. One major difference he noted between the two species was that the epicotyl apex of *Q. alba* produced from three to five leaf primordia before acorn maturity, but *Q. velutina* produced none. Stairs (1964) also found no leaf primordia in mature embryos of *Q. coccinea*. 

*Journal of the International Oak Society* ISSUE 7 13
Staminate Flowers

When we mention flowers, we tend to think only of the pistillate flower that gives rise to the acorn. But there is another flower on the tree: the staminate or male flower that is the source of pollen.

The origin of the staminate flowers is similar to that of the pistillate flowers, except that the inflorescence or catkin on which they are assembled differentiates from a meristem in the axil of a bud scale, not a leaf. The first sign of differentiation of the staminate inflorescence primordium in those white oak species studied appeared from late May to July. The inflorescence is without appendages until late June or early July, when meristematic areas appear on the axis (Merkle et al. 1980). These floral apex primordia appear before or coincident with the subtending bract primordia (Turkel et al. 1955). However, Sattler (1973) found that the ovate-shaped floral apex of the staminate flower in *Q. rubra* was initiated in the axil of a small ridge-shaped bract close to the apex of the inflorescence, just the opposite of where the female apex forms on its inflorescence. The perianth members arise on the flanks of the floral apex in a spiral sequence; however, the sequence of stamen initiation is quite regular. The stamen primordia appear on the apex opposite the perianth members from mid-July to late July. By fall, these stamen primordia grow into immature anthers and filaments. The overwintering condition of the slightly lobed anther is that of a homogeneous parenchymatous mass.

Anther development resumes in early March to late April, varying by species and location. In higher plants, the parenchymatous mass differentiates into the sporogenous mass, its cell numbers increase mitotically, and eventually they undergo meiosis to become microspores and, finally, pollen grains. For oaks, there is only a pictorial account of meiotic stages *per se* as provided by Stairs (1964). Thus, there is a need for research on the entire topic of oak pollen development.

Dehiscence of pollen grains occurs about six weeks after differentiation of the anther tissues begins (Turkel et al. 1955). Before leaf flush, the staminate inflorescence of *Q. rubra*, bearing numerous staminate flowers, elongates and emerges from the bud scales as the familiar catkin (Vogt 1969). At first the catkins are erect and clustered, but they soon elongate further and droop (figure 4). During maturation of the male flowers, the female flowers continue to develop in the axils of expanding leaves of the new shoot.

One to two weeks after the catkins appear, the small anther sacs split open to expose the pollen grains (figure 5). Pollen shedding is usually complete in 3 to 4 days. The time of pollen shed is probably the best local index of the beginning of the visible portion of the seed production cycle. If relative humidity is high at time of pollen maturity, the pollen sacs may not split open. Wolgast (1972), using growth chambers, demonstrated that relative humidity at the time of pollen shed and stigma receptivity can limit the size of an acorn crop. No pistillate flowers survived when relative humidity exceeded 61 percent because the anther sacs did
**Figure 4.** Catkins (inflorescences) (A) emerge from the axils of bud scales. Staminate flowers (B), bearing the pollen grains, are assembled along the length of the catkin.

**Figure 5.** Pollen grains are released from the pollen sacs when suitable temperature and relative humidity conditions have been met.

**Figure 6.** The stigma of a flower receives the pollen grains during pollination. After the pollen grains germinate, the pollen tubes grow partially through the transmitting tissue of the stigmas and cease growth after several weeks (arrow). In the second growing season, pollen growth resumes and the tubes enter the compitum, a free space between the three styles, where they proceed into the locule to fertilize the egg.
not open; but about half the flowers matured into acorns when relative humidity was lower. Continued cool, rainy weather may cause overripe male flowers to fall from the trees without shedding, resulting in a poor seed crop. Variation in date of flowering within a crown and among trees within a stand may offset some of the pollen loss related to weather conditions.

There have been conflicting observations about the dynamics of pollen tube growth after the pollen grain lands on the stigmatic surface. For instance, Benson (1894) did not find pollen tubes in *Q. robur*, a white oak, until just before fertilization. Jovanovic and Tukovic (1975) observed that pollen germination in *Q. robur* was completed within 24 hours, but fertilization occurred 6 to 7 weeks later, suggesting that pollen tube growth did not proceed until the ovule had completed development. In contrast, Allard (1932) observed that, "When pollen reaches the stigma of members of the white oak group, the growth of the pollen tube containing the male cells follows an uninterrupted advance into the tissues of the style until the ovules are fertilized." These conflicting observations of pollen tube behavior for members of the same section and species suggested that an investigation of this anomaly was required. Cecich (unpublished data) observed pollen tube growth in *Q. rubra*, *Q. velutina* and *Q. alba* with fluorescence microscopy. All three species had the same pattern of pollen tube growth soon after the pollen grains landed on the stigmas of the pistillate flowers. Within 24 hours, the pollen tube germinates from the pollen grain and penetrates the epidermis of the stigma. A callose plug is synthesized to seal off the contents of the tube from the pollen grain and the pollen grain falls off the stigma. The pollen tubes grow through the transmitting tissue of the stigma for about three weeks, when they cease growth just above the juncture of the three stigmas (figure 6). The white oak pollen tubes resume growth toward the ovules in early June and enter the locules. Fertilization is accomplished by about June 15. In the two red oak species, *Q. rubra* and *Q. velutina*, the pollen tubes ceased growth, as noted, until the following growing season when pollen tube growth resumed and fertilization occurred in late May (*Q. rubra*) and late June (*Q. velutina*). Allard (1932) also found that, in the red oak group, the pollen tubes ceased growth at the base of the style until the following spring when the ovules were fertilized.

**Factors Affecting Reproductive Success**

Acorn crops are the product of a long, arduous journey from the initiation of the flower primordium to the mature acorn. The differentiation of reproductive structures extends from the primordium stage in late May (year one), through pollen shed and female receptivity (year two), and finally fertilization, embryogenesis, and maturation (year three). Over that length of time, what causes an acorn crop to succeed or fail?

Except for deep freezes in late spring (Sharp 1958, Sharp and Sprague 1967, Goodrum *et al.* 1971, Wol gast and Trout 1979), does the weather affect differentiation? Probably the most important factor controlling the emergence of pistillate flowers in the spring and their receptivity is temperature, which directly or
indirectly influences flower emergence through branch and leaf elongation. Emergence of the staminate inflorescence and shedding of pollen are known to increase or hasten with rising temperatures and to slow with decreasing temperatures (Romashov 1957). Rainy weather, associated with decreased temperature, also decreased pollen dispersal. Mature pollen is more resistant to frost than anthers or the filaments of the catkins (Sharp 1958, Sharp and Sprague 1967). Pollen tube growth also may be affected by temperature, thus influencing the northern boundaries for the species range (Jicinska and Koncalava 1978). Sork et al. (1993) studied flower and acorn production in the same population of Q. rubra, Q. velutina, and Q. alba for eight years. They suggested that these three species have inherent cycles of reproduction that are modified by weather conditions—Q. velutina with a two-year cycle, Q. alba with a three-year cycle and Q. rubra with a four-year cycle. However, they concluded that the patterns of acorn production were not simply responses to weather events, but were also a function of prior reproduction history.

Genetic control over seed production in oaks has been demonstrated by a number of investigators. During six year of observation, Grizez (1975) found no Q. rubra seed crops that were better than poor. He did not observe flower crops because pistillate flowers were difficult to see from the ground. Grizez stated that his observations confirmed other reports that seed-producing capacity is, to a large extent, genetically controlled by the female parent. Farmer (1981) found that in a given year, seed production among clones of Q. rubra was most highly correlated with the percentage of pistillate flowers that were fertilized; while year-to-year differences were associated with variation in the number of flowers. He believed that fecundity could be increased by selecting high-yielding clones in a grafted orchard. Grafting of oak scions selected from mature, flowering individuals can be readily accomplished and, thus, flowers can be made quickly available (Irgens-Moller 1955). Ledig et al. (1971) and Wright (1953) also found much tree-to-tree variation in reproductive ability.

Schlarbaum and Rhea (unpublished data) evaluated flowering in a 17-year-old Q. rubra seedling seed orchard in Tennessee. They selected light-, medium-, and heavy-flowering trees and counted all pistillate flowers. The majority of flowers were located in the upper one-third of the crown of each tree, and flower numbers did not differ among the four quadrants in a crown. Sharp and Chisman (1961) found that pollen catkins were evenly distributed across the crown of mature Q. alba. I also have observed the latter in Q. alba, Q. rubra, and Q. velutina.

Insects can have a big impact on acorn crops. Most accounts are about weevils (Curculio spp. and Conotrachelus spp.) as they destroy acorn crops (Gibson, 1964, Kearby et al. 1986). However, weevils do not oviposit until midsummer, when the embryo's cotyledons are enlarging. Most of the potential seed crop has been lost through flower abortion before then (Cecich 1993; Cecich et al. 1991), suggesting that weevils are not the major insect cause of poor acorn crops. Treehoppers (Membracidae) are another group of insects that deserve attention. These sucking insects can spend their entire life cycle in the crown of an oak tree (Kopp
Several authors have concluded that the size of an acorn crop is not related to the size of a flower crop; i.e., the appearance of numerous pistillate flowers in the spring does not guarantee numerous acorns (Sharp 1958, Sharp and Chisman 1961, Wright 1953, Gysel 1956, Cecich et al. 1991, Sork and Bramble 1993). Factors that inhibit or enhance flower development, pollination, fertilization, and embryogenesis appear to be more important in determining the success of a seed crop.

Little information is available about the reproductive biology of *Q. rubra*. In fact, no complete detailed life history for any species of oak has been written. Therefore, our knowledge of oak flowering biology is based on a few reports about selected events in only a few species. These references are often combined to tell

---

**Figure 7.** A typical survival curve of oak pistillate flowers. White oak takes one growing season to produce its acorn crop; red oak requires two. Most of the flower loss occurs in May and early June, when treehoppers are actively feeding. Inadequate pollination may also contribute to the early abortion. Weevils oviposit after most of the potential seed crop has aborted. In either species of oak, less than 5 percent of the flowers usually survive to become acorns.
a developmental "story" about a hypothetical oak--an oak that probably does not exist. Before we try to interpret how various factors influence the production of flowers and acorns, we must develop a solid understanding of the reproductive cycle of individual species. The fragmented information about oak flowering does not give us an accurate picture of the flowering process, but it does indicate where the shortcomings and opportunities exist. We then can ask meaningful questions and do the appropriate research. We must study the biology of *Q. rubra* if we are truly interested in managing *Q. rubra* acorn crops.

*This article was adapted from Biology and Silviculture of Northern Red Oak in the North Central Region: A Synopsis, published by the United States Department of Agriculture, Forest Service, North Central Forest Experiment Station, General Technical Report NC-173.*

Robert Cecich is a Research Plant Physiologist with the North Central Forest Experiment Station, Forestry Sciences Laboratory, Columbia, Missouri, USA.

**LITERATURE CITED**


