

USDA United States
Department of
Agriculture

Forest Service

**Northeastern
Research Station**

General Technical
Report NE-295



Biotic and Abiotic Mechanisms in the Establishment of Northern Red Oak Seedlings: a Review

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Abstract

The sustained presence of northern red oak (*Quercus rubra*) in forests throughout the eastern and central hardwood regions of the United States often depends on seed-origin reproduction. However, in some hardwood forests, small northern red oak seedlings may be sparse for extended periods. This is particularly the case in the central Appalachians, where seedlings apparently become established in single-cohorts during anomalous years when acorn production is above average. A better understanding of the mechanisms that drive the establishment of seedlings could increase the potential for sustaining the species within these regions. This report summarizes the literature on acorn production, predation by insects and vertebrates, infection of acorns by microorganisms, and environmental factors that affect germination. Recommendations for future research are presented.

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Manuscript received for publication 1 February 2002

Cover Photo

Mature red oak acorns in second year of development and current-year acorns visible in leaf axils of new growth (photo by Paul S. Johnson)

Published by:
USDA FOREST SERVICE
11 CAMPUS BLVD SUITE 200
NEWTOWN SQUARE PA 19073-3294

For additional copies:
USDA Forest Service
Publications Distribution
359 Main Road
Delaware, OH 43015-8640
Fax: (740)368-0152

May 2002

Introduction

The sustained presence of northern red oak (*Quercus rubra*) in forested ecosystems often depends on seed-origin reproduction (Ward 1966; Arend and Scholz 1969; Sander and others 1976; Watt 1979; Crow 1988), particularly on highly productive sites. There are concerns about the ability of oaks and northern red oak in particular to regenerate from seed (Minckler and Jensen 1959; Loftis 1988; George and Fischer 1991). Most research has focused on the inability of small oak seedlings to grow from the herb to the shrub layer, i.e., to become well-established advanced regeneration. Forest managers often ignore the mechanisms involved in the initial establishment of seedlings because, in many reported cases, small seedlings (less than 15 cm tall) are present, but larger ones are not. It is generally believed that the stock of oak seedlings builds up slowly as small numbers of acorns escape vertebrate predation and insect infestation during years of heavy seed production. When abundant oak seedlings or saplings are present, the timing of silvicultural treatment is not critical because there are adequate numbers of seedlings or saplings for release.

However, in parts of the eastern and central hardwood regions of the United States — about 235,000 square miles — small northern red oak seedlings may be sparse or absent for extended periods. This is particularly common in the central Appalachians where, rather than slowly increasing in number, seedlings apparently become established in single cohorts during anomalous years of abundant acorn production and favorable weather (McGee 1967; Gribko 1995a; Schuler and Fajvan 1999). Silvicultural treatments that favor the release of oak seedlings must be timed carefully to take advantage of each regeneration wave. However, there are few opportunities to release abundant oak seedlings in most forests. A better understanding of the mechanisms that drive the establishment of northern red oak seedlings could increase the potential for sustaining this species within these regions.

In the eastern and central hardwood regions it is expected that many forests with a significant northern red oak component eventually will be dominated by species such as red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and American beech (*Fagus grandifolia*). The specific consequences of such conversions are not known, though none of these species has the ecological or economic value of northern red oak. The loss of oak from forest overstories will lead to reductions in availability of acorns as a winter food source for numerous wildlife species, including white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and black bear (*Euarctos americanus*). Densities of these

species as well as those of many small mammals and nongame birds are closely tied to oak masting (Bendell 1959; Gilbert and Krebs 1981; Wentworth and others 1992; McShea and Schwede 1993; Wolff 1996; McCracken and others 1999; McShea 2000). In addition, red oak lumber and veneer have high monetary value. The limited availability of oak in these regions would have a substantial adverse impact on the economic viability of many value-added forest enterprises, including the furniture, hardwood flooring, and cabinetry industries.

Specific factors affecting the initial establishment of northern red oak seedlings include the lack of: 1) seed production, 2) viable seed due to insect and vertebrate predation or infection by microorganisms, and 3) acorn germination due to environmental factors. Each of these is discussed with reference to pertinent literature. Much of the research cited pertains directly to northern red oak regeneration; examples are drawn from investigations of other oak and hickory (*Carya* spp.) species.

Background

Seed Production

There are several methods for assessing seed production in oaks. The most common entails the use of seed traps of various size and construction. The simplest trap is a bushel basket affixed to a stake and placed under a tree crown (Liscinsky 1984). Downs and McQuilken (1944) first reported the use of rectangular wood-frame traps with hardware cloth bottoms and sides to collect acorns. These traps were about 1.0 m² and covered with 3-cm-mesh poultry netting to prevent predation by mammals. Variations on this trap design were used by Burns and others (1954), Christisen and Korschgen (1955), and Goodrum and others (1971). Also used were funnel-shaped traps of various size and construction material; some featured a hardware cloth collection bin at the apex and a poultry cloth cover (Easley and Chaiken 1951; Gysel 1957; Tryon and Carvell 1958; Klawitter and Stubbs 1961; Ovington and Murray 1964; Beck and Olson 1968; Shaw 1968a; Christisen and Kearby 1984). Marquis and others (1976) designed a variation of the funnel trap in which a large rectangular sheet of plastic was affixed to wire supports; one end of the sheet was elevated, allowing acorns to roll into a collection bin at the opposite end. Thomson and McGinnes (1963) and Gysel (1956) compared the efficacy of various rectangular and funnel traps.

Another common method of assessing acorn production entails the use of open ground quadrats (Wood 1934; Kautz and Liming 1939; Allen and McGinley 1947; Cypert and Webster 1948; Dalke 1953). Open plots can

be used with seed traps to assess predation rates (Downs and McQuilken 1944; Shaw 1968a; Goodrum and others 1971). Other researchers have attempted direct counts of acorns still on the tree (Verme 1953; Sharik and others 1983). In some cases, individual branches are marked and inventoried annually (Petrides and others 1953). A modified ground method in which binoculars are used is favored by many state wildlife agencies to quickly assess relative annual production over a wide area (Sharp 1958; Koenig and others 1994). Indirect observation of crop size by counts of shed acorn caps was reported by Wood (1934), Shaw (1968a, 1974), and Auchmoody and others (1993). Because vertebrate predators tend to ignore the caps while foraging, this method can provide a more accurate estimate of the entire crop size than others cited.

Regardless of the method used, sampling design and intensity affect how estimates can be used and the conclusions that can be drawn. Estimates for individual trees have been made by locating traps and ground plots under the crowns of mature acorn-producing stems. By assessing individual-tree production, particularly over a number of years, one can observe variability within a single species or among several species (Greenberg 2000). This method also is the basis for studies of the effects of tree age, size, and other characteristics on acorn production. Area wide production estimates have been made by locating ground plots and traps randomly or systematically through forest stands. Such evaluations are most useful when wildlife food crops are being studied (McShea and Schwede 1993), when correlations between acorn production and silvicultural treatments are of interest (Beck and Olson 1968), or when estimating the proportion of acorns in total litterfall (Nielson 1977).

Production usually is reported as number or weight of acorns per tree or unit ground area. Estimates of zero to more than 600,000 acorns per hectare have been reported (Down and McQuilken 1944; Gysel 1956; Gysel 1957; Tryon and Carvell 1962a; Marquis and others 1976; Beck 1977; Christisen and Kearby 1984; Liscinsky 1984; Auchmoody and others 1993). Care must be taken when comparing study results because sampling techniques and intensities differ and standard errors sometimes are not provided. Generally, estimates based on cap counts are higher than those based on samples from seed traps, that in turn are higher than estimates from ground-plot samples. Estimates from samples from under the crown of individual trees are higher than those obtained on randomly or systematically located plots. Placement of traps and plots under more or less productive portions of the crown also can affect results (Gysel 1956; Christisen and Kearby 1984).

Relative crop size often is reported using terms such as bumper (76 to 100 percent of the maximum crop), good (51 to 75 percent), fair (26 to 50 percent), poor (10 to 25 percent), trace (less than 10 percent), and none (Sharp 1958), and there are numerous variations (Snow 1940; Allen 1952; Uhlig and Wilson 1952; Wright 1953;

Thompson and Lemke 1954; Christisen and Kearby 1984). Wildlife agencies in several southern states use a scale of 1 to 10 to rate acorn abundance across regularly surveyed routes within defined areas (Carlock and others 1983). In attempting to standardize the rating systems, Auchmoody and others (1993) developed a crop guide that converts subjective rankings to estimates of acorns produced per unit ground area and vice versa.

Observers of northern red oak and other acorn crops have concluded that production variability is considerable among individual trees and years. Acorn crops have been characterized as sporadic, infrequent, and unpredictable (Sharp and Chisman 1961; Watt 1979; McQuilken 1983; Auchmoody and others 1993). Northern red oak and other oaks of the subgenus *Erythrobalanus* generally are more consistent producers of acorns than are oaks of the subgenus *Leucobalanus*, which may fail to produce any acorns for several consecutive years (Gysel 1956, 1957; Tryon and Carvell 1962a; Christisen and Kearby 1984; Liscinsky 1984). In most years, northern red oaks produce at least a moderate acorn crop; Liscinsky (1984) reported germination failure in northern red oak, black oak (*Q. velutina*), and scarlet oak (*Q. coccinea*) in only 2 years of an 11-year study.

Some researchers have tried to determine periodicity in the production of bumper crops of northern red oak acorns. Christisen and Kearby (1984) reported bumper crops of northern red oak acorns to be less cyclic than those of white oak acorns. However, other observers have noted trends toward heavy crops at 3-, 4-, or 5-year intervals (Sharp 1958; Tryon and Carvell 1962a; Beck 1977; Sork and others 1993).

Annual variations in the size of acorn crops are not completely understood but are thought to be driven primarily by environmental factors that affect the survival and pollination of the flower crop (Cecich 1993, 1994, 1997; Cecich and Sullivan 1999). Studies of oak flowering revealed little yearly variation in initial flower crop sizes, suggesting that physiology and heredity have negligible roles in the annual variability acorn crops (Sharp and Chisman 1961; Sharp and Sprague 1967; Olson and Boyce 1971; Farmer 1981; Cecich and others 1991; Sork and others 1993). Temperature, wind, late frost, prolonged rain, and relative humidity can affect flower development, the opening and closing of anthers, and pollen dissemination (Sharp and Chisman 1961). Fertilization rates are higher when pollen shed and the receptivity of pistillate flowers are closely aligned. Sharp and Sprague (1967) observed that acorn crops usually were large when warm weather in late April, which stimulated early catkin emergence, was followed by cool temperatures in May. This delayed pollen dispersal until pistillate flowers matured. Consistently low temperatures in late April, strong, dry winds in early May, or warm weather throughout April and May can cause pollen development and dispersal to be out of synchrony with

the receptivity of pistillate flowers (Sharp and Sprague 1967; Cecich 1997). High relative humidity, especially when associated with prolonged rainy periods, may delay pollen dispersal (Wolgast and Stout 1977a; Jovanovich and Tucovic 1975), though no significant effects have been observed under field conditions (Sharp and Sprague 1967; Cecich 1997).

Even in years of generally favorable spring weather, flowers can be damaged or destroyed by a late freeze (Reid and Goodrum 1957; Beck 1977; Wolgast and Trout 1979; Sork and Bramble 1993), hail (Cecich 1997), or insects, particularly treehoppers (Membracidae) (Kopp and Yonke 1973a, b, c, 1974; Cecich and others 1991). Dormant flower buds also can be damaged or destroyed when winter temperatures are extremely low (Kramer and Kozlowski 1979). By early July, virtually all of the flower crop can be lost due to a combination of pollination failure and physical damage (Cecich 1993).

The proportion of flowers that actually produce acorns is reduced further by premature abscission. Although the abscission of immature fruits is greatest between pollination and fertilization (Turkel and others 1955), acorns continue to be aborted throughout summer and into early fall (Christisen and Kearby 1984). As many as 95 percent of all white oak abscissions were premature in a 2-year Kentucky study (Williamson 1966). Possible causes of premature abscission include gypsy moth (*Lymantria dispar*) defoliations (Gottschalk 1988), infestations of seed insects (Galford and others 1988), and early fall frosts (Kramer and Kozlowski 1979). Drought was cited as a factor by Christisen and Kearby (1984) and Sork and others (1993), but not by Sharp and Sprague (1967) or Goodrum and others (1971). Drought effects might be confounded by timing, soil type, and tree species (Kramer and Kozlowski 1979). Generally, any substantial stress during the 2-year maturation cycle can reduce crops of northern red oak acorns. Moreover, it has been hypothesized that different factors may be responsible for early abscissions from different branches on the same tree (Stephenson 1981). Thus, it is not yet possible to predict acorn production for individual trees more than several weeks in advance (Gysel 1957; Koenig and others 1994; Cecich 1993). However, Greenberg and Parrosel (2000) analyzed the characteristics of southern Appalachian oaks and developed a statistical method to predict within-year acorn production for a specified area based on the proportion of trees with acorns and the basal area of each species present. Larsen and Cecich (1997) presented a probabilistic model that can be used to explore the many factors that may cause annual variations in the production of white oak acorns.

Acorn production by individual trees has been linked most consistently to inherent genetic capacity (Irgens-Moller 1955; Sharp and Sprague 1967; Grisez 1975). Variation also may be related to tree age (Reid and

Goodrum 1957; Harper and White 1974; Wolgast and Stout 1977b), size and relative position of the crown (Downs and McQuilken 1944; Burns and others 1954; Tryon and Carvell 1962a), size of the bole (Downs 1944; Goodrum and others 1971; McQuilken and Musbach 1977; Hashizume 1979; Kanazawa 1982; Greenberg 2000), and/or overall tree vigor measured as radial growth rate (Wood 1938; Burns and others 1954; Goodrum and others 1971). Investigations of individual-tree characteristics and their impact on acorn production often have produced conflicting results due to confounding by shading or the inherent production capacity of the study trees (Goodrum and others 1971). However, it is generally thought that 40 to 99-year-old northern red oaks (40 to 50 cm in d.b.h.) with large, healthy, unshaded crowns and an innate ability to set flowers produce the largest acorn crops (Toumey and Korstian 1937; Downs 1944; Verme 1953; Sharp 1958; Goodrum and others 1971).

The amount of light reaching the crown also is critical as reduced light affects acorn crops by inhibiting floral initiation, fruit set, and fruit development (Lassoie and others 1980). Because both seed number and size can be reduced by inadequate direct sunlight, oaks in suppressed and intermediate crown positions usually produce negligible seed crops (Kittredge and Chittendon 1929; Moody 1953; Gysel 1956). In dominant and codominant trees, acorn production is greatest in the upper crown, particularly the south- and west-facing sides which receive more direct sunlight (Verme 1953; Sharp and Sprague 1967). The death or loss of large limbs in the upper crown of large older trees also can cause acorn production to drop sharply (Sharp 1958; Goodrum and others 1971).

Site productivity and physical characteristics of growing site also have been investigated as possible sources of tree-to-tree or local variation in acorn production (Gysel 1957; Tryon and Carvell 1962a). The results of these studies have been inconclusive except Gysel's (1957) finding that the weight (not number) of acorns produced by several oak species in the Great Lakes region was positively correlated with site quality. It generally has been concluded that most local variation, particularly in mountainous terrain, is due to frost pockets and other local weather effects that limit the percentage of pistillate flowers that are fertilized (Gysel 1956; Farmer 1981).

The lack of acorn production has not been reported as directly responsible for sparse seedling establishment (Walters 1990). In fact, Tryon and Carvell (1962b) found that density of oak seedlings was independent of acorn production on a site in the central Appalachians. However, selective harvest of large dominant and codominant northern red oaks and increasing mortality of mature oaks due to drought and attacks by opportunistic organisms will significantly impede future seed production (Healy and others 1997).

Insects, Vertebrates, and Microorganisms

Insects

Three important insect pests have been identified in autumn collections of northern red oak acorns: *Curculio* weevils (Coleoptera: Curculionidae), larvae of an acorn moth, *Melissopus latiferreanus* (Lepidoptera: Oleuthreutidae), and gall-forming wasps of the genus *Callirhytis* (Hymenoptera: Cynipidae) (Gibson 1969, 1982; Oak 1992). These insects can breed in otherwise sound acorns that are developing on the tree (Gibson 1982). Although never implicated in complete germination failures, high *Curculio* infestation rates were reported by Brezner (1960), Marquis and others (1976), Gibson (1982), Galford and others (1991a), Gribko and Jones (1995), and Steiner (1995). A much lower incidence of *Melissopus latiferreanus* (Brezner 1960; Dorsey and others 1962; Galford and others 1991a; Gribko and Jones 1995) and wasp-forming galls, especially *Callirhytis fructosa*, (Dorsey and others 1962; Gibson 1982; Gribko and Jones 1995) was reported, though populations of these species may be locally high in some years (Myers 1978; Gibson 1972, 1982).

It is generally assumed that most “weeviled acorns” do not produce viable seedlings. Insecticidal and mechanical treatments have been suggested to control infestations (Dorsey 1967; Stockton and Morgan 1979; Crocker and Morgan 1983; Crocker and others 1987, 1988; Galford and others 1988). However, several authors found small numbers of *Curculio*-damaged acorns that produced seedlings. These usually were acorns with an undamaged embryo and most of the endosperm intact (Downs and McQuilken 1944; Oliver and Chapin 1984; Weckerly and others 1989b). It is thought that infested acorns that remain viable are vulnerable to infestation by secondary insects, fungi, bacteria, and other microorganisms, though data from the Allegheny Plateau in West Virginia suggest that large numbers of weevil-infested northern red oak acorns can produce viable, healthy seedlings (Gribko 1995a).

Other insects present in northern red oak acorns often are ignored due to their low numbers or to the erroneous perception that they act primarily as scavengers of the frass and detritus left in acorns vacated by *Curculio* weevil and acorn moth larvae. These insects cannot breach the acorn shell and must use damaged, previously infested, or germinating acorns for oviposition sites. The most important of these secondary insects are weevils of the genus *Conotrachelus* (Coleoptera: Curculionidae), an acorn moth, *Valentinia glandulella* (Lepidoptera: Blastobasidae), and a nitidulid sap beetle, *Stelidota octomaculata* (Coleoptera: Nitidulidae). Each has been observed in small numbers of damaged northern red oak acorns in autumn and in greater numbers of germinating acorns in spring (Brezner 1960; Dorsey and others 1962; Gibson 1964; Gibson 1982; Galford 1986a; Galford and others 1988, 1991b; Gribko 1995b).

Widespread infestations of germinating northern red oak acorns by these insects can result in germination failure (Galford and others 1991a), severely reduced germination rates (Krajicek 1960; Galford 1986a; Galford and others 1988; Auchmoody and others 1994), or reduced vigor of seedlings (Gribko 1995b). *Valentinia glandulella* was observed feeding primarily on the surface of the cotyledons; its most serious impact on germinating acorns may be the attraction of more destructive *Conotrachelus* weevils and nitidulid sap beetles (Galford 1986a). Cool wet springs and late freezes may limit damage from these insects (Gribko 1995b).

Other secondary insect pests of northern red oak acorns are dipterous larvae of the families Drosophilidae (pomace flies), Cecidomyiidae (gall gnats), Mycetophilidae (fungus gnats), Psychodidae (moth flies), and Anthomyiidae (anthomyiid flies) (Winston 1956; Dorsey and others 1962). All are found in acorns that have been vacated by weevil or lepidopterous larvae or in the cotyledons of badly diseased or decomposed acorns. These insects act primarily as scavengers or fungus feeders (Winston 1956; Dorsey and others 1962; Borrer and White 1970).

Although they do not infest the cotyledons of acorns, two nonnative weevils, *Cyrtopistomus castaneus* (Asiatic oak weevil) and *Barypeithes pellucidus*, cause extensive damage to germinating northern red oak acorns and seedlings by feeding on emerging radicles, roots, and shoots (Galford 1986b; Ferguson and others 1992). A millipede, *Ptyoiulus impressus*, was observed feeding heavily on emerging radicles (Galford and others 1992).

Vertebrates

Acorns are low in crude protein, fiber, calcium, and phosphorus, but high in digestible cell contents and nitrogen-free extract (Waino and Forbes 1941; Reid and Goodrum 1957; Short 1976; Lassoie and others 1980). Digestible cell contents include lipids (or fats), starches, soluble protein, nonprotein nitrogenous compounds, sugars, and pectins (Short 1976). Nitrogen-free extract, the substance that remains after crude fat, protein, ash, and crude fiber are subtracted from the dry matter, contains soluble carbohydrates and vitamins B and C (Reid and Goodrum 1957; Short 1976). Acorns are a high-energy, easily digested food for squirrel (*Sciurus* spp. and *Glaucomys* spp.), white-tailed deer, wild turkey, black bear, deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*), blue jay (*Cyanocitta cristata*), and many other species of wildlife (Van Dersal 1940; Hamilton 1941; Mosby and Handley 1943; Cypert and Webster 1948; Martin and others 1951; Reid and Goodrum 1957; Duvendeck 1962; Korschgen 1962; Nixon and others 1968; Beeman and Pelton 1980; Lassoie and others 1980; Pekins and Mautz 1987). It has been demonstrated that the density of seed predators may be set by the size, frequency, and quality of mast crops. The reproductive success and condition of white-

tailed deer (Wentworth and others 1992), gray and fox squirrel (Allen 1943; Christisen and Korschgen 1955; Uhlig 1955), small mammals (Jameson 1955; Gore 1988), and black bear (Eiler 1981) can be linked to the previous year's mast crop.

Mammalian and avian acorn predators generally can be divided into species that consume acorns before they drop from the tree (predispersal) and those that eat them when they reach the ground (postdispersal). Squirrel, chipmunk, mice, several species of birds, and even white-tailed deer have been observed eating acorns as they ripen on the tree. The predispersal loss of acorns to vertebrate predation can have a significant impact on germination (Sharp 1958; Goodrum and others 1971). Removal/consumption rates have ranged from 18 to 27 percent (Cypert and Webster 1948; Tryon and Carvell 1962a). Damage rates of approximately 25 percent were reported by Downs (1944, 1949) and Cypert and Webster (1948).

Open plots or a combination of open and screened plots have been used to assess the impact of vertebrates once acorns reach the forest floor. Most investigators reported high levels of acorn predation for a variety of oak species (Table 1). Small mammals and squirrel were assumed responsible for the depredations or were observed removing acorns from the study plots. Screening devices and barriers have been used to segregate the effects of different wildlife species (Table 2). The results of these studies confirmed that small mammals such as mice and chipmunks remove a large proportion of acorns from the forest floor. In Pennsylvania, white-tailed deer also have a substantial impact on acorn removal (Marquis and others 1976).

Vertebrates that feed on seeds such as acorns may act as seed predators or seed dispersers or both. White-tailed deer, turkey, and bobwhite quail (*Colinus virginianus*) are acorn predators because they destroy the seeds that they consume. Dispersal agents are vertebrates that enhance plant reproduction and distribution by transporting seeds from the parent plant (Janzen 1971; Sork 1983). Dispersal occurs when a proportion of the acorn crop is cached by small mammals and birds. Species that scatterhoard acorns at shallow depths in the forest floor, e.g., squirrel, blue jay, and mice, usually are given credit for some dispersal even though they eat large numbers of acorns and other nuts (Darley-Hill and Johnson 1981; Sork 1983, 1984; Miyaki and Kikuzawa 1988; Thorn and Tzilkowski 1991). Species such as chipmunks that larder- or nest- hoard are not considered effective as dispersal agents (Smith and Reichman 1984).

Despite their propensity to scatterhoard, the role of squirrel and mice in the dispersal of significant numbers of acorns is questionable. Squirrel may successfully recover virtually every buried nut by spring (Cahalane 1942) and their habit of biting off the tips of acorns (notching), destroys the viability of large numbers of

cached nuts (Wood 1938; Barnett 1977). White-footed and other species of mice usually eat acorns where they are found rather than storing them for later use (Smith and Reichman 1984; Sork 1984), and nearly every acorn scatterhoarded by wood mice (*Apodemus speciosus* and *A. argenteus*) (Miyaki and Kikuzawa 1988) and *Peromyscus* spp. (Sork 1984) is later recovered and consumed or placed in nest burrows. Often, acorns that are not retrieved are damaged severely by mice and thus rendered inviable (Smith 1962). Miyaki and Kikuzawa (1988) observed a maximum dispersal distance of 27 to 37 m for *Apodemus*, and Sork (1984) estimated that 36 to 58 percent of northern red oak acorns were cached or consumed by small rodents within approximately 18 m of the parent tree.

Microorganisms

Fungi, bacteria, and other microorganisms associated with northern red oak acorns have received little attention. Winston (1956) completed the only published account of microbiotics in northern red oak acorns and described several genera of organisms in limited detail. Researchers have identified organisms in other species of oak. For example, drippy nut disease (*Erwinia quercina*) has been isolated from California live oak (*Quercus agrifolia*) and interior live oak (*Q. wislizenii*) acorns (Hildebrand and Schroth 1967). The fungus that causes black rot (*Ciboria batschiana*) has been identified in English oak (*Q. robur*) and sessile oak (*Q. petraea*) acorns (Delatour and Morelet 1979), and Vozzo (1984) isolated *Epicoccum purpurascens* and *Fusarium solani* fungi from water oak (*Q. nigra*) acorns.

Acorn germination

Like all acorns in the *Erythrobalanus* subgenus, northern red oak acorns are characterized by a period of dormancy before germination (Bonner and Vozzo 1987). In laboratory trials, it was necessary to stratify fully hydrated northern red oak acorns for 4 to 6 weeks in moist storage at 2° to 5°C to break dormancy. Sound, undamaged northern red oak acorns have a moisture content of 50 to 60 percent and germinative capacity of 75 to 90 percent (Korstian 1927), germination of *Erythrobalanus* acorns is best when the moisture content falls to 40 percent and concentrations of crude fat and total carbohydrates peak (Bonner and Vozzo 1987). Germinative capacity is reduced substantially by further desiccation (Korstian 1927; Hodges and Gardiner 1993), and viability may be lost when the moisture content falls to 15 to 25 percent and remains there (Korstian 1927; Bonner and Vozzo 1987). Because acorns must imbibe water after dormancy for the pericarp (seedcoat) to rupture (Peterson 1983), dry spring weather can be particularly damaging. Rehydration after a period of desiccation can restore viability (Bonner and Vozzo 1987), suggesting that wet spring weather might reverse the effects of dry winter conditions.

Table 1.—Summary of studies of removal of acorn crops from the ground by vertebrates

Reference	Oak species	Technique	N	Period observed	Percent removed	Vertebrate responsible
Wood (1938)	<i>Quercus prinus</i>	Acorn cap counts	Varied ^a	Acorn drop to November	87.0	<i>Pitymys pinetorum</i> , <i>Sciurus carolinensis</i>
Cypert and Webster (1948)	<i>Q. nigra</i> <i>Q. phellos</i>	Marked acorns on open-ground plots	Varied ^a	24 hours	5.6	<i>Peromyscus</i> spp., <i>Glaucomys volans</i> , <i>Quiscalus quiscula</i> , <i>Colaptes auratus</i>
Christisen and Korschgen (1955)	<i>Q. stellata</i> <i>Q. alba</i> <i>Q. velutina</i> <i>Q. marilandica</i>	Acorn traps and open-ground plots compared	Varied ^a	Acorn drop to January	21.5 37.2 4.0 18.9	Not specified
Krajicek (1955)	<i>Q. rubra</i>	Unprotected on top of litter or on soil surface	640	Late fall to mid-May	100.0	Unspecified rodents
Gysel (1957)	Good sites: <i>Q. rubra</i> , <i>Q. alba</i> Med. Site: <i>Q. velutina</i> , <i>Q. alba</i> Poor sites: <i>Q. velutina</i>	Acorn traps and open-ground plots compared	Varied ^a	Acorn drop to December	8.0 17.0 13.0 18.0 47.0	<i>Sciurus niger</i> (based on photographic devices and direct observation)
Krajicek (1960)	<i>Q. velutina</i> <i>Q. macrocarpa</i> <i>Q. alba</i> <i>Q. rubra</i>	Litter kept intact Litter removed	320 per species	Late fall to mid-May	99.8 100.0	Unspecified rodents
Tryon and Carvell (1962a)	<i>Q. alba</i> <i>Q. rubra</i>	Acorn traps and open-ground plots compared	Varied ^a	Acorn drop to mid-November	58.6 50.2	Not specified
Tryon and Carvell (1962b)	<i>Q. alba</i> <i>Q. rubra</i>	Acorn traps and open-ground plots compared	Varied ^a	Acorn drop to mid-November	50.0	Not specified
Shaw (1968a)	<i>Q. petraea</i>	Acorn traps and cap counts compared	Varied ^a	Acorn drop to mid-November	63.0	Not specified

^aReported as proportion of total acorn crop consumed.

Table 2.—Summary of research using screens, barriers and other devices to exclude vertebrate acorn predators based on body size

Reference	Oak species	Technique	Remarks
Korstian (1927)	<i>Q. rubra</i> (other species also used)	Acorns planted under screens that failed to exclude small rodents	Unspecified, small rodents removed 100 percent of planted acorns. No difference in survival on plots screened from larger vertebrates and unprotected plots.
Shaw (1968b)	<i>Q. petraea</i>	Buried and unburied exclosures with and without top screening	Exclosures accessible only to small mammals suffered same rate of loss as open-control plots. Wood mice (<i>Apodemus sylvaticus</i>) and bank voles (<i>Clethrionomys glareolus</i>) were responsible.
Marquis and others (1976)	<i>Q. rubra</i>	Exclosures used to exclude vertebrates based on body size	53 percent germination of acorns fully protected from deer and rodents; 9 percent germination if protected from deer only; 2 percent germination if not protected. Unspecified small mammals and white-tailed deer (<i>Odocoileus virginianus</i>) were responsible.
Kikuzawa (1988)	<i>Q. mongolica</i>	Frames with different sizes of mesh used to protect acorns	Exclosures accessible only to small mammals suffered same rate of loss as open-control plots. <i>Clethrionomys rufocanus</i> , <i>Apodemus argentius</i> , and <i>Apodemus speciosus</i> were responsible.
Borchert and others (1989)	<i>Q. douglasii</i>	Exclosures used to exclude vertebrates based on body size	Exclosures accessible to smallest vertebrates suffered the highest predation rates. Botta pocket gophers (<i>Thomomys bottae</i>), deer mice (<i>Peromyscus maniculatus</i>), and other unspecified species of mice were responsible.
Gribko (1995a)	<i>Q. rubra</i>	Exclosures used to exclude vertebrates based on body size	Exclosures accessible only to small mammals suffered same rate of loss as open-control plots. White-footed mice (<i>Peromyscus leucopus</i>), deer mice, eastern chipmunks (<i>Tamias striatus</i>) and southern flying squirrels (<i>Glaucomys volans</i>) were responsible.

Temperature also is critical during dormancy and germination; no germination occurs until temperatures are consistently above 4.5 °C (Korstian 1927). Germination is best when nighttime temperatures average 10 °C and daytime temperatures average 18 °C. Both excessive heat and excessive cold can damage acorns (Korstian 1927; Hodges and Gardiner 1993). Temperatures of 26.5 °C at night and 35 °C during the day are too high for optimal germination (Korstian 1927). Periods of fluctuating temperatures, especially in the spring, can be particularly detrimental (Gribko 1995b). Early thaws often stimulate premature radicle emergence; subsequent subfreezing temperatures kill back the tender radicles. Affected acorns may send out a second radicle though, in the absence of cool, wet weather in spring, the early splitting of the seed coat exposes the cotyledons to desiccation reducing the germination rate.

A layer of leaf litter or soil greatly enhances acorn germination by providing a cool, moist, stable environment (Korstian 1927; Shaw 1968b; Sander and others 1983; Crow 1988). This protective layer reduces desiccation and encourages the growth of microorganisms that may aid germination by softening the pericarp (Bonner and Vozzo 1987). Because acorns from oaks of the subgenus *Leucobalanus* germinate in autumn when litter depths peak, they may derive the maximum benefit of litter accumulations. In studies of chestnut oak (*Quercus prinus*), litter was essential for germination even under dense overhead shade (Barrett 1931). Seedling establishment was best when the depth of loose unincorporated leaf litter was 2 to 4 cm. Olson and Boyce (1971) suggested that deeper, looser litter at the time of germination may explain why Carvell and Tryon (1961) found that white oak regeneration was five times greater than northern red oak regeneration given equal seed crops.

While not always affording protection from vertebrate predators, a thin layer of soil enhances germination of northern red oak acorns on exposed slopes in dry years (Gribko 1995a). Acorns of several species buried in a California foothill woodland germinated regardless of aspect, shade, or early spring weather; those sown on the surface were more susceptible to overheating and desiccation (Griffin 1971). A planting depth of 3 cm in mineral soil, approximately the depth acorns are cached by gray squirrel (*Sciurus carolinensis*) (Thorn and Tzilkowski 1991), was suggested by Sander and others (1983). It is important that site conditions be considered because acorn burial in consistently wet soils can reduce the germination rate (Shaw 1968b).

Acorn germination usually is good in uncompacted, moist, well-drained mineral soil that allows penetration by the developing radicle (Griffin 1971; Matsuda and McBride 1986; Walters 1990). Because radicles are unable to penetrate soil that has been compacted at the surface (Korstian 1927), soil disturbance can enhance the establishment of oak regeneration (Carvell and

Tryon 1961; Arend and Scholz 1969) and soil scarification has been suggested to improve initial and possibly long-term survival of seedlings (Minckler and Jensen 1959; Scholz 1959). In the absence of compaction, the humus layer generally should be left intact because it keeps the soil surface porous and retains moisture (Carvell and Tryon 1961).

Thick, dense, unincorporated litter or grass that suspends the acorn above the soil surface prevents the radicle from reaching mineral soil (Arend and Scholz 1969; Griffin 1971; Borchert and others 1989). Burning has been suggested to remove excessive litter (Johnson 1974; Brose and others 1999) and create a more favorable site for acorn burial by vertebrates (Galford and others 1988). However, substantial numbers of acorns were destroyed in fall burns (Korstian 1927; Auchmoody and Smith 1993).

Initial survival and early growth of seedlings depend primarily on stored food reserves in the cotyledons (Grime and Jeffrey 1965; Musselman and Gatherum 1969; Kormanik and others 1998). Accordingly, many observers have reported strong correlations between acorn weight and the size and vigor of first-year seedlings (Korstian 1927; McComb 1934; Shaw 1968a; Farmer 1980). Soil moisture also is critical in the first year (Core 1971), particularly before the development of taproots and in the presence of competing herbaceous vegetation (Carvell and Tryon 1961; Kolb and others 1990). Initially, shading has little negative impact on oak seedlings and may even enhance establishment in dry environments (Barrett 1931; Borchert and others 1989). However, once cotyledon reserves are depleted and seedlings depend on photosynthate, light often becomes limiting (Crow 1988). The mechanisms involved in the long-term survival and development of oak seedlings are beyond the scope of this report, but it is worth noting that absent management intervention, northern red oak seedlings persist in the understory only for several years (McGee 1967; Olson and Boyce 1971; Loftis 1988; Hodges and Gardiner 1993).

Interactions of Factors Affecting Seedling Establishment

The interaction of factors that affect oak seedling establishment has been the focus of much speculation but little study. For example, it has been suggested that populations of *Curculio* and *Conotrachelus* weevils may be regulated by predation by small mammals on larvae, larvae-infested acorns, and pupae. Weevil larvae of both genera exit acorns after feeding and burrow into the soil to pupate. Depending on the species, they may overwinter as pupae or as adults. In laboratory trials, *Peromyscus* and northern short-tailed shrew (*Blarina brevicauda*) readily burrowed through soil to a depth of 15 cm to prey on pupae (Semel and Andersen 1988). Mice consumed about 5.4 larvae per hour versus 6.5 for shrew. On the basis of these results, it was suggested that

predation on larvae during and after periods of low acorn production might retard the growth of the weevil population, though there have been no controlled field investigations. In addition, gray squirrel (Weckerly and others 1989a) and *Peromyscus* (Semel and Andersen 1988) ate significant numbers of both weevil-infested and noninfested acorns during laboratory trials. Unfortunately, the ecological implications of these observations have received little attention.

It also has been suggested that the impact of acorn insects may depend at least partially on the size of the acorn crop (Downs and McQuilken 1944; Christisen 1955; Beck and Olson 1968; Schopmeyer 1974; Christisen and Kearby 1984). Research to date indicates that light acorn crops are more heavily infested by *Curculio* and *Conotrachelus* weevils than heavy crops (Gibson 1972; Marquis and others 1976; Galford and others 1988). These observations may indicate that acorn weevils do not adapt their breeding behavior to take full advantage of bumper crops; as a result, populations may be regulated primarily by the size of the smallest acorn crops. The dynamics of acorn weevil populations have not been studied in detail so few conclusions should be drawn.

The effect of crop size on vertebrate acorn predation also is of interest. The synchronous production of large seed crops followed by one or more years of small crops may allow oaks to take advantage of mammalian seed dispersal (Downs and McQuilken 1944). The irregular production of large crops is assumed to satiate populations of acorn predators (Janzen 1971). In years of low or average production, many vertebrates act as predators, whereas in years of high production, they function as dispersal agents when hoarding and then failing to use excess acorns. Sork (1983) listed two criteria that must be met if satiation is functioning in a seed predator-prey system: seed disappearance must be a function of seed density, and seed predation should eventually decline at high seed density. In studies involving pignut hickory (*Carya glabra*) (Sork 1983) and northern red oak (Sork 1984; Gribko 1995a), there was no evidence of predator satiation. High seed production slowed but did not stop total predation of nuts and nearly total predation was observed even in areas where acorn production was very high.

The intensity of vertebrate acorn predation also may be related to specific site factors. Acorns of several species tend to be removed more quickly from forests with intact canopies (Kikuzawa 1988; DeLong and Yahner 1991). Site productivity also may play a role in vertebrate predation rates; Gysel (1956) observed higher rates of vertebrate crop damage on less productive sites. However, an intact canopy on a high-quality site does not always lead to low rates of predation and high seedling recruitment. In the Western United States, seedling recruitment of blue oak (*Quercus douglasii*) was positively associated with increased canopy cover and more mesic

microclimate at low elevations but negatively associated with these factors on a higher elevation site with more overstory oaks (Borchert and others 1989). As acorns were more available, vertebrate predation apparently was more pronounced and the advantages of improved microsite were eliminated. Likewise, in the Appalachians, a high proportion of large northern red oaks in the overstory and the relative availability of acorns of any species resulted in higher rates of predation of northern red oak acorns (Gribko 1995a).

Acorn predation by vertebrates also may be affected by weather conditions. During two winters of light snow in West Virginia, the entire northern red oak acorn crop was removed by small mammals (Gribko 1995a). By contrast, much of the crop remained in place on the soil surface during a winter of deep consistent snowpack, resulting in a wave of seedling establishment.

Summary

Despite the volume of information available, a clear understanding of the mechanisms involved in the successful seedling reproduction of northern red oak and other oak species is needed. The knowledge to date and gaps in this knowledge can be summarized as follows:

- Northern red oak acorn production is highly variable and the mechanisms involved are only partially understood. Late spring freezes and insects that damage flowers reduce crop size. Methods for predicting the size of acorn crops are only beginning to be developed and are limited to empirical within-year estimates.
- Site conditions and microsite variability are assumed to have minimal influence on seedling establishment, though factors such as soil moisture have not been studied rigorously.
- In some years, especially years of low production, a large proportion of the acorn crop is infested with *Curculio* weevils and other insects. The potential for healthy seedling production from infested acorns has not been investigated thoroughly. Moreover, the population dynamics of these insects, including the effects of weather, small mammals, and site conditions, are poorly understood.
- *Conotrachelus* weevils and nitidulid sap beetles infest large numbers of northern red oak acorns as they germinate in the spring. However, there are few data on the population dynamics of these insects and the degree of regulation afforded by small mammals and unfavorable spring weather.
- Little is known about the role of microorganisms and secondary insects that potentially affect acorn viability.

- Large numbers of acorns are removed from the ground and directly from the tree by vertebrate predators. However, little is known about the effect of acorn availability on vertebrate foraging behavior or whether small mammals are effective as dispersal agents. There is some evidence that site productivity and canopy cover affect vertebrate predation rates, but the mechanisms driving these effects are not known. The impact of winter weather patterns, particularly constancy of snow cover, on the behavior of vertebrate acorn predators may have important consequences yet remains largely unexplored.

To sustain oak forests throughout the eastern and central hardwood regions, long-term research is needed on the biotic and abiotic factors that affect establishment of northern red oak seedlings. Objectives should include the intensity of predation on acorns by vertebrates; the impact of autumn and spring infestations of insects on acorn crops (with an emphasis on weevils of the genus *Curculio* and *Conotrachelus*); the role of pathogens that infect northern red oak acorns and their impact on acorn crops; the effects of soil moisture, soil temperature, and weather patterns (including depth and duration of snowpack) on seed germination and seedling establishment; the relationship between crop size and seedling establishment; and how these factors interact.

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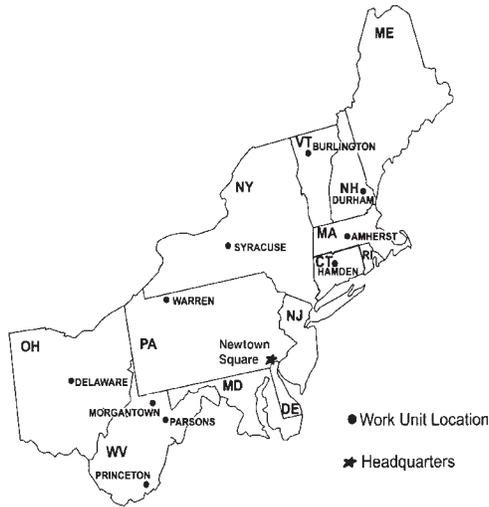
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Gribko, Linda S.; Schuler, Thomas M.; Ford, W. Mark. 2002. **Biotic and abiotic mechanisms in the establishment of northern red oak seedlings: a review.** Gen. Tech. Rep. NE-295. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 18 p.

This review of literature pertaining to the biotic and abiotic mechanisms in the establishment of northern red oak seedlings is designed to aid forest managers and researchers interested in sustaining the oak component of the eastern and central hardwood forest regions. Recommendations for future research are presented.

Keywords: northern red oak, acorn production, acorn dispersers, acorn germination.





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