Factors Limiting Northern Red Oak Reproduction in Pennsylvania

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Abstract: When harvested, upland oak forests of northwestern Pennsylvania generally regenerate to new forests dominated by non-oak species. In 1988, the Northeastern Forest Experiment Station began to identify and learn to manipulate factors that limit the establishment and development of northern red oak (*Quercus rubra* L.) seedlings in second-generation stands on high-quality sites. The study includes three replications located within the Moshanon State Forest and four replications within the Allegheny National Forest on the unglaciated section of the Allegheny Plateau in northwestern Pennsylvania. Each replication includes six plots in which two each were cut to 40 and 60% relative density and two left uncut. One plot of each overstory density level was fenced to exclude deer and one-half of every plot was herbicided to control herbaceous cover and competing hardwoods. The major causes of regeneration failure in oak stands are low numbers and/or small size of oak advance reproduction. The small number of natural red oak seedlings results from infrequent seed crops and destruction of acorns by insects, deer, and small mammals. Deer, small mammals, and insects contribute to slow development and mortality of established seedlings.

INTRODUCTION

The difficulty in regenerating oaks, particularly on the higher quality sites, is widespread throughout all oak forests of eastern North America. Crow and Isebrands (1986) pointed out that this is neither recent nor limited to eastern North America. This problem has been recognized, discussed, and researched for more than 60 years in both the United States and Europe and we still are unable to reproduce oak forests consistently. Moreover, the problem is most acute on higher quality sites where foresters most want to grow oak, especially northern red oak.

Most oak regeneration failures are attributed to the absence of adequate amounts of advance regeneration or the inability of oak to outgrow competitors when released (Sander 1988; Crow 1988). The conditions that led to the establishment of oak types on these better sites are lacking. If natural regeneration is present, natural succession is progressing toward conversion to fast-growing, intolerant, mesic northern hardwood species such as black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), and sweet birch (*Betula lenta* L.). The problem is intensified in oak stands on the Allegheny Plateau in northwestern Pennsylvania where large populations of white-tailed deer have influenced the development of forest vegetation over a long period (Marquis and Brenneman 1981).

In 1988, the Northeastern Forest Experiment Station began a study in northwestern Pennsylvania to identify the biotic and environmental limitations on the establishment and development of red oak seedlings. This study also will seek to determine how these limitations might be manipulated to encourage red oak in second-generation stands. The effects of deer, rodents, insects, light, competition from herbaceous and woody species, site, stand composition, and acorn availability

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are some of the factors being evaluated. It is our purpose here to discuss limitations for northern red oak regeneration, especially those encountered in northwestern Pennsylvania, and explain how this study is designed to investigate them. After 4 years, we have gained a considerable understanding of the factors that limit the establishment and early development of red oak seedlings. However, the conclusions presented here are preliminary at this time and further results must await longer term evaluation.

All replications of this study are located on the unglaciated Allegheny Plateau in northwestern Pennsylvania. We established three replications on the Moshannon State Forest (CLR) in Clearfield County that have completed four growing seasons. In addition, four replications located within the Allegheny National Forest (ANF) have undergone three growing seasons. Two of these ANF replications are in Warren County and two are in Elk County. All study sites are characterized as having good soils and uniform, gentle-rolling topography. They range from 2,000 to 2,300 feet above sea level and are typical of conditions on the Allegheny Plateau. The cool-moist climate is similar at all locations with about 140 frost-free days each year. Rainfall averages about 4 inches per month throughout the growing season and the average growing season temperature is 61°F. Because of ample rainfall, cool temperatures, and much summer cloud cover, soil moisture rarely becomes limiting until late in the growing season. These are excellent growing sites for northern red oak.

Although the soils vary somewhat from replication to replication, they are essentially similar. In general, they are medium textured, moderately well drained, and have 24 to 30 inches of effective rooting depth with good structure and permeability. None of the plots has a soil physical limitation for red oak regeneration, such as severe surface rockiness, shallow depth to bedrock, coarse soil texture, high perched water tables, or excessive slope steepness on south-facing aspects. The forest floor is typically a duff mull, with 2 to 3 inches of litter, a thin fermentation layer, and about 1 inch of humus that grades abruptly into the mineral soil beneath. The plots are equally good for growing oaks as they are for the other associated hardwoods and represent sites that are extremely difficult to regenerate to northern red oak.

All CLR and ANF research sites were located in similar fully stocked stands dominated by northern red oak. These stands were about 80 years old and had no evidence of recent cutting. The CLR stands averaged 137 ft^2 of basal area in 355 trees (1.0 inches dbh and larger)/acre and 13.8 inches dbh. Relative stand density was 87% of the average maximum stocking expected in undisturbed stands of similar size and species composition. Northern red oak made up 55% of the stand basal area with a maximum tree size of 32 inches dbh. White (*Quercus alba* L.), black (*Q. velutina* Lam), and chestnut (*Q. prinus* L.) oaks added 2% more basal area, with red and sugar maples (*Acer saccharum* Marsh.) making up an additional 32%. The other associated overstory species were mainly black cherry, white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow-poplar (*Liriodendron tulipifera* L.), and cucumbertree (*Magnolia acuminata* L.). The ANF stands averaged 139 ft^2 of basal area in 422 trees/acre and 14.5 inches dbh. Relative stand density was 89%. Northern red oak accounted for 49% and white and chestnut oaks 6% of the stand basal area. Red maple and black cherry contributed another 32% to the stand basal area. The balance of the overstory was mostly sugar maple, American beech, yellow-poplar, cucumbertree, and white ash. The largest ANF tree was a 34-inch-dbh red oak.

METHODS

The field layout consists of a randomized complete block split-plot design with six, 4-acre main plots in each replication. The main plot treatments include three levels of residual overstory stand density, with and without fencing. These overstory treatments included two plots each uncut and two plots each cut to 40 and 60% relative density. One plot of each density was then fenced with a

6-strand, high-voltage, electric fence to exclude deer. One-half of each main plot received a broadcast herbicide treatment of 2 lb a.i. glyphosate and 1.5 oz a.i. sulfometuron methyl/acre to control herbaceous cover and competing hardwood species. The other half was not sprayed. All trees on all plots that were smaller than 5.5 inches dbh were cut and the stumps (except for those few oaks cut) treated with 2% Garlon in fuel oil to prevent sprouting. This was done to reduce competition for advance regeneration development from the mid-crown overstory. Each replication then had 12 treatment combinations on 2-acre subplots for a total of 24 acres/replication. Since there are seven replications, the study encompasses 168 acres in total.

Great care was exercised in selecting study sites with fully stocked stands approaching maturity with no recent cutting, at least 15% northern red oak, and no mountain-laurel. We also wanted stands of medium to good site quality (site index of 60 to 75 base age 50), and no site limitations to oak seedling establishment. Within each replication, all six plots were located so as to have uniform topography with similar slope steepness and aspect, soils that were similar, and uniform stand conditions.

Initially, 100% overstory inventories by species and 1-inch dbh classes were completed for each 2-acre subplot. These were used to develop a marking guide for each plot to determine the trees that needed to be retained. Care was taken to closely match the residual stands as to species composition and stand structure on fenced and unfenced plots of each residual density in a replication, and to match the overstory on the herbicided and unherbicided halves of each 4-acre plot. As far as consistent with the above, the objective always was to retain as much red oak as possible in the largest size classes.

These procedures were designed to create basic plots on which we could investigate the process of red oak regeneration rather than merely observing results of practices applied in the forest. In these plots, the limiting factors to the establishment of northern red oak seedlings could be evaluated, manipulated, and made unlimiting. The major limiting factors under investigation and the corrective measures applied are listed in Table 1.

Table 1.—Factors limiting oak regeneration and corrective measures

Limiting factors	Corrective measure
Light and other environmental factors limit seedling establishment	Partial overstory removal to vary light and other factors
Deer eat acorns and/or seedlings	Exclude deer with high-voltage electric fences
Understory interference limits seedling	Eliminate understory with herbicide
Acorns not produced by parent stand	Measured and reasons for failure determined
Small mammals consume acorns and/or seedlings	Small mammals excluded on subplots and acorns supplied
Insects destroy acrons and/or seedlings	Insect populations measured and species identified
Forest floor inhibits seedling establishment	Direct seed intact litter, burned and scarified subplots
Other species outcompete oak seedlings	Measured and correlated with light0

EXPERIMENTAL DESIGN

The overall study consists of three main experiments. The first experiment deals with the processes controlling the establishment and development of natural red oak seedlings as affected by acorn supply, manipulation of light by cutting the overstory, elimination of deer browsing by fencing, control of understory interference and competition with herbicide, and insects. This is an intensive investigation to learn the biology of red oak regeneration. The second experiment deals with the impacts of insects and small mammals on acorn predation, seedling establishment, and future seedling development, and how these impacts are affected by intact litter, burning, and soil disturbance in relation to light and competing vegetation. This is a major study that probes the biological factors that may be responsible for the lack of natural oak seedlings and their failure to accumulate as advance regeneration over a wide range of environmental conditions. The third experiment deals with underplanting red oak seedlings as a way of establishing advance regeneration, and also with the insects, large mammals, and small mammals that can affect seedling survival and development. Supplementary experiments deal specifically with determining the important insects that affect acorns while attached to the tree and after they have fallen to the forest floor, causes for the lack of consistent acorn crops, and ways to overcome on-site limitations for seedling establishment, such as the effectiveness of electric fences to exclude deer.

Natural Regeneration Experiment

The natural regeneration experiment evaluates the effects of overstory density, deer browsing, and competition control on the establishment and growth of natural red oak regeneration. Natural regeneration populations are measured annually on 15 permanent, 6-foot-radius plots in each 2-acre treatment plot. On the fenced plots only, individual red oak seedling development as affected by insects and small mammals in relation to light level (overstory density) and competition is further evaluated to learn why red oak advance regeneration does not increase in abundance. Acorn crop size on these plots is estimated annually by cap counts and by direct observations of acorns on the ground in autumn. Causes of acorn crop failure are determined by direct crown observations beginning at time of flowering and continuing through maturation in the following year. Insect populations within the plots are determined each year during peak insect damage periods (to acorns on the ground) by pitfall trapping. The plots also are frequently visited to observe the course of stand development and to determine causal factors governing the direction of stand development.

Direct Seeding Experiment

The direct seeding experiment evaluates the impact of small mammals, insects, light, competition control, litter, and acorn placement on seedling establishment from direct-sown acorns. This experiment is located only in the fenced cutting level plots where deer are excluded. Each herbicided and unherbicided subplot contains two 14-foot by 42-foot installations, one of which is surrounded by a rodent-proof exclosure. Within each installation, acorns were placed on top of the forest floor (O_1 horizon) or 1 inch deep in the mineral soil under three litter treatments: intact forest floor, burning of the forest floor, and scarification (mixing of the forest floor with mineral soil to a depth of 8 inches). Burying acorns at a 1-inch depth simulates the caching of acorns by small mammals and rodents. These treatment combinations provide 72 different treatments.

Red Oak Underplanting Experiment

The red oak underplanting experiment evaluates the impacts of overstory density, deer browsing, and competition control on the survival and development of planted seedlings. Further, red oak seedlings were planted in the herbicided and unherbicided, unfenced plots with tree shelters for protection from deer browsing. Planting represents a way of quickly establishing seedlings in areas that may lack red oak advance regeneration. Tree shelters were developed to protect planted seedlings from deer browsing but also are reported to enhance seedling survival and early height growth (Tuley 1983, 1985). This experiment is designed to determine not only the factors that affect initial survival and development of planted red oak with and without tree shelters, but also those factors that inhibit or may prevent seedlings from attaining dominance in the future stand after final overstory removal. Seedlings are subject to routine annual measurements of height growth and survival, and also are evaluated during the growing season to determine the causes of mortality and/or poor development, particularly from the impact of insects.

Limiting Factors

Limitation to northern red oak seedling establishment can be arranged into three categories: (1) acorn production, (2) acorn predation and desiccation, and (3) seedling predation and competition.

Acorn Production

Of course, for obvious reasons acorns must be produced in order to have seedlings. However, acorn production is notoriously erratic and unpredictable (Sharp and Chisman 1961), varying from species to species, tree to tree, location to location, and year to year (Olson and Boyce 1971). Bumper crops occur irregularly and may be as infrequent as 10 years apart (Downs and McQuiklin 1944). Besides knowing the factors that control acorn production, it is important to learn what happens to those acorns that are produced, what prevents them from developing into seedlings, and what prevents the development of seedlings from acorns that germinate.

Acorn crops were estimated from acorn-cap counts each year from 1988 to 1992 on the CLR plots and from 1990 to 1992 on the ANF plots. Caps were counted on 30 systematically located 1 ft^2 plots in each fenced 4-acre plot. The annual per acre acorn crop for the CLR plots averaged 104, 105, 129 and 25 thousand for each plot from 1988 to 1991, respectively. The ANF plots averaged 46 and 58 thousand per acre, respectively, for 1990 and 1991. There were no acorns produced on any plot in either location in 1992.

Acorns develop only from fertilized flowers, never from unfertilized flowers by asexual means. Oaks have imperfect flowers and are monoecious. Staminate and pistillate flowers are borne separately on the same tree and depend on wind for dissemination of pollen. Oaks produce abundant staminate flowers nearly every year, but the number of pistillate flowers may vary greatly from year to year. The causes of cyclic flower production are not fully understood, but weather and genetics often are implicated (Sharp and Chisman 1961; Sharp and Sprague 1967; Olson and Boyce 1971). Thus, a lack of pistallate flowers may contribute to poor acorn production in some years, though flower abortion also is high in most years (McQuilken 1983). Unfavorable weather conditions at the time of pollination during flower development are among the probable causes; wind, late frost, prolonged rain, relative humidity, and temperature have been shown to influence pollination (Sharp and Chisman 1961). Unfertilized pistillate flowers abort, and oak flowers occasionally are killed by late spring frosts (Sharp and Sprague 1967). We observed a freeze that killed the entire crop of staminate flowers in May 1991 and resulted in the total acorn crop failure in 1992 reported above. Since similar freezes and hard frosts in late spring are common on the Allegheny Plateau, this is likely an important limitation to acorn production for the region.

Insects are another likely cause of oak flower abortion and hence reduced acorn production. In a Missouri study, rapid flower abortion and abscission was observed in May and early June, which corresponded with the time of pollen shed and pollination. But the abortion also may have been related to the feeding behavior of treehoppers, which are sucking insects of the family *Membracidae*. Adult treehoppers were observed with their stylets inserted into the stigmas of oak pistillate flowers. The flowers turned from green to brown within a week and aborted (Cecich et al. 1991). Apparently, the treehopper can pierce the female flower, causing physical damage, or perhaps inhibiting salivary compounds are injected that promote abortion. We have not observed this damage in northwestern Pennsylvania, but neither have we looked for it. Such damage is extremely difficult to see without physically being in the tree canopy at frequent intervals.

Finally, acorn production within a stand may be limited simply because there are only a few oaks available that produce seed. Not all trees produce acorns and some are consistently poor acorn producers. Some have few to none, even in good mast years, while others produce small or no acorn crops because of their small crown size, subordinate crown position, or poor health (Downs and McQuilkin 1944; Sharp and Sprague 1967). If acorn production is a management goal, whether for mast production or seed source, it is important to select "leave trees" in the thinnings or other partial cuttings that are good acorn producers.

Even when acorns are produced, there are still many damaging agents that destroy them or can prevent their germination. The *Curculio* weevil attacks maturing acorns while they are still attached to the trees. After dropping to the forest floor, acorns are prize food for many animals and birds including white-tailed deer, chipmunks, squirrels, mice, turkeys, and blue jays (Downs and McQuilkin 1944; Gysel 1957; Marquis et al. 1976; Darley-Hill and Johnson 1981; Galford et al. 1988, 1991). If not eaten, exposed acorns not covered by forest litter can quickly desiccate. Acorns also are targets for insects and other arthropods that live in the forest floor.

Curculio weevils probably are the best known "worms" that attack acorns. Each year they destroy about half of the acorn crop (Galford et al. 1988). Arend and Scholz (1969) found that *Curculio* larvae infected up to 90% of the fallen acorns. The adult females bore a hole in the immature acorn pericarp (shell) while it is still attached to the tree and oviposit inside. The eggs hatch and the larvae feed on the acorn cotyledons. After abscission, when the acorn is on the ground, the larvae emerge by chewing a characteristic hole in the pericarp. The larvae overwinter in the soil and pupate in the spring or early summer. The adults then emerge from the soil and mate, and the female deposits eggs in the new acorns developing on the trees, completing the life cycle (Gibson 1982; McQuilkin 1983). Not all acorns infected with *Curculio* weevils are destroyed. However, seedlings resulting from "weeviled" acorns often are less vigorous and may have poor survival because some of the cotyledonary reserve has been consumed. In a collection of 536 acorns from the 1989 bumper crop, about 25% were infected with *Curculio* weevils. Of the infected acorns, 53% germinated and produced seedlings. About 12% of that 1989 bumper crop was destroyed while still on the trees.

Acorn Predation

Upon falling to the ground, acorns are subject to intense predation by several species of gound insects and millipedes. Two important species that damage germinating acorns were caught in pitfall traps in 1989 and 1990: the weevil *Conotrachalus posticatus* Boheman and the nitidulid or sap beetle *Stelidata octomaculata* Say. Acorn samples collected near the pitfall traps revealed that the radicle tips of 50% of the acorns had been eaten by larvae of the acorn moth *Valentinia glandulella* Riley, and that 60% of the acorns were infested with moth larvae. Although previously not considered a major problem, the acorn moth now must be considered a major pest of germinating acorns in Pennsylvania (Galford 1986a; Galford et al. 1991). Millipedes are another previously unreported pest of germinating acorns. Up to 17% of the acorn radicles in areas with heavy acorn crops were damaged in 1991 by millipedes (Galford et al. 1992).

In a companion study, acorns were sown on the forest floor surface and buried both under wire cages (rodent protected) and outside wire boxes. Rodents destroyed virtually every acorn outside of the boxes so that insect activity could not be evaluated. However, for those acorns under the wire boxes, insects destroyed 92% of the acorns on the surface but only 8% of those that were buried. Of 1,800 acorns surface sown under hardware cloth boxes, desiccation destroyed 30% and mice pilferred another 7%. Thus, 1,139 (63%) of the acorns germinated but only 152 (13%) of those germinating survived insect destruction and grew into seedlings. The insect damage was primarily by the acorn moth and the *Conotrachelus* weevil. Most of the newly rooted seedlings were killed due to heavy weevil feeding on the radicles and shoots. On some seedlings, sap beetles ate the tender top shoots, destroying any chance for the acorn to resprout. Acorn placement and rodent protection did result in significant differences in seedling number, acorns taken by rodents, and acorn destroyed by insects. There were no differences due to overstory density or herbicide treatment (Galford et al. 1991).

As mentioned previously, acorns on the ground are heavily predated by a variety of mammals and birds. Arboreal-feeding birds and squirrels reportedly consume as much as 25% of any mature acorn crop (Downs and McQuilkin 1944; Gysel 1957). Our own observations confirm that white-tailed deer are major consumers of acorns. In nothwestern Pennsylvania, deer are plentiful with county populations estimated to range from 21 to 32/mi^2. This is an average of eight animals/mi^2 over the winter carrying-capacity goal as determined by the Pennsylvania Game Commission.[2] This large deer population consumes many acorns. Gray squirrels are less important as acorn predators than chipmunks and mice simply because there are fewer squirrels. In most years, intense predation by birds, mammals, and insects destroy nearly all of the acorn crop, especially in years when the mast croop is poor to average. Two years after treatment, there were an average of more than 700 northern red oak seedlings per acre on the CLR fenced plots and less than 300 on the unfenced plots. Although it is not possible to distinguish between acorn and seedling consumption by deer, the net difference between the fenced and unfenced number does suggest the deer impact on oak seedling density.

Acorn predators such as chipmunks, mice, squirrels, and blue jays also disperse acorns. These animals transport acorns, often over considerable distances, to caching sites and bury ("plant") them. These buried acorns are protected from deer, other small mammals and insects, and from dessication. Many cached acorns are subsequently retrieved and consumed, but many are not. Since cached acorns generally are in locations favorable for germination, unretrieved acorns often germinate and produce seedlings. Most new oak seedlings become established only in years of good to bumper acorn crops (Olson and Boyce 1971; Watt 1979); these are years when many more acorns are cached than are retrieved. Janzen (1971) recognized predation as the necessary "cost" to the plant of the essential benefit--dispersal/planting--of acorns provided by these animals.

Seedling Predation and Competition

In those infrequent years of bumper seed crops, some acorns may escape damage and germinate, but even abundant germination does not ensure adequate stocking of oak seedlings. Any new seedlings must survive deer browsing, clipping by small mammals, insect attack, low light, and usually a combination of these. If they survive, the oak seedlings still must compete with faster growing associated hardwood regeneration. The contrast in the number of red oak seedlings per acre reported above for the fenced and unfenced CLR plots suggests the impact that deer exert on oak regeneration.

When white-tailed deer populations exceed levels above 18/mi^2 in the deciduous forests on the Allegheny Plateau, species richness and abundance of herbaceous and woody vegetation decline.[3]

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[2] Unpublished data, William Palmer, Pennsylvania Game Commission, 1992.

[3] Personal communication, David S. deCalesta, Northeastern Forest Experiment Station, Warren, PA, 1992.

Large deer herds have influenced forest vegetation development in northwestern Pennsylvania over a long period. As a result, understory vegetation is sparse in most uncut stands and new seedlings are severely browsed, causing shifts in species composition or reduced stocking. Most understories are dominated by hayscented fern (*Dennstaedia punctilobula* (Michx.) Moore), striped maple (*Acer pensylvanicum* L.), American beech root suckers or if tree seedlings are present, by black cherry, red maple, or sweet birch (Marquis et al. 1976; Marquis and Brenneman 1981). There are few if any oak and those few do not respond vigorously enough to compete.

The total impact of insect damage on the survival and growth of understory oak seedlings is largely unknown. Insect outbreaks occasionally cause visible mortality, but damage is usually moderate, subtle, and cummulative. Many seedlings simply fail to leaf out in the spring after a couple of years of insect damage. From the 1,800 acorns surface sown under hardware cloth boxes, 422 seedlings became established initially, but 64% of these were subsequently destroyed by insects. Most of these new seedlings were killed due to heavy *Conotrachelus* weevil feeding on the radicles and shoots. Some damage was attributed to nitidulid or sap beetles in concert with the weevils (Galford et al. 1991). Another weevil, *Barypeithes pellucidus* Boheman, was found to be a pest of new seedlings by girdling the stems (Galford 1986b, 1987). In Ohio, more than 20% of the new oak seedlings were topkilled at least once by this weevil (Galford et al. 1988).

In addition to eating acorns, rodents also feed on new seedlings. From a group of new oak seedlings, we observed that rodents had chewed the tops off of 66% (Galford et al. 1991). In other areas, more than 80% of the new seedlings had been chewed off one or more times (Galford et al. 1988); many of these shoots are consumed. Acorn germination is hypogeal, that is, the cotyledons remain in place attached at the base of the new seedling stem. We believe that at least some new seedlings are destroyed by rodents retrieving the residual cotyledon.

Despite these factors that limit acorn production and oak seedling establishment, acorns do germinate and some new oak seedlings become established. However, few of these survive more than a year or two. Surviving stems remain small, generally less than 1 foot tall. Dieback is to ground level and resprouting is frequent. Surviving stems grow more slowly and are unable to respond as vigorously to attack as non-oak understory components. Dieback and mortality generally has been attributed to too little light and inadequate moisture (Korstian 1927; Merz and Boyce 1956; Olson and Boyce 1971; McQuilkin 1975). On the Allegheny Plateau, there are few northern red oak seedlings and these are small and slow growing. They do not do well in competition with other hardwoods such as black cherry, red maple, white ash, and sweet birch. And few will gain dominance in the emerging second-generation stands. The fenced CLR plots averaged 7,200 seedlings/acre of commercial species 2 years after treatment. Of these, 26% were taller than 1 foot. In contrast, the unfenced plots averaged 5,100 seedlings/acre and 12% were taller than 1 foot. Red maple was the most abundant species followed by black cherry. As reported above, these plots had about 700 and 300 red oak seedlings/acre in the fenced and unfenced plots, respectively, with about 1% and 0.1% of them taller than 1 foot.

SUMMARY

Harvested upland oak forests of northwestern Pennsylvania generally regenerate to new forests dominated by non-oak species such as black cherry, red maple, and sweet birch. The major causes of regeneration failures in oak stands are low numbers, low vigor, and/or small size of oak advance reproduction. Natural regeneration of northern red oak is limited by infrequent acorn crops and the destruction of large numbers of acorns by animals (white-tailed deer, chipmunks, mice, and birds) and insects, and by desiccation. Deer browsing, small mammals, insects, low light, competition from other fast-growing hardwoods, and usually a combination effect from several of these contribute to slow development and mortality of established oak seedlings. These conclusions are based on 3 years of observation of the ANF plots and 4 years of the CLR plots, respectively. Final conclusions await longer term evaluations.

LITERATURE CITED

Arend, J.L., and H.T. Scholz. 1969. Oak forests of the Lake States and their management. USDA For. Serv. Res. Pap. NC-31.

Cecich, R.A., G.L. Brown, and B.K. Piotter. 1991. Pistillate flower abortion in three species of oak. P. 578 in McCormick, L.H., and K.W. Gottschalk (eds.). Proc., 8th central hardwood forest conf. March 3-6, 1991, Pennsylvania State Univ., University Park.

Crow, T.R. 1988. Reproduction mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)--a review. For. Sci. 34: 19-40.

Crow, T.R., and J.G. Isebrands. 1986. Oak regeneration - an update. P. 73-86 in Proc., integrated pest management symposium for northern forests. Univ. Wisconsin Coop. Ext. Serv., Madison.

Darley-Hill, S., and W.C. Johnson. 1981. Acorn dispersal by the blue jay (*Cyanocitta cristata*). Oecologia 50: 231-232.

Downs, A.A., and W.E. McQuilkin. 1944. Seed production of southern Appalachian oaks. J. For. 42: 913-920.

Galford, J.R. 1986a. Primary infestation of sprouting chestnut, red and white oak acorns by *Valentinia glandulella* (Lepidoptera:Blastobasidae). Entomol. News 97: 109-112.

Galford, J.R. 1986b. The weevil *Barypeithes pellucidus* (Coleoptera: Curculionidae) feeds on northern red oak, *Quercus rubra* seedlings. Entomol. News 97: 113-114.

Galford, J.R. 1987. Feeding habits of the weevil *Barypeithes pellucidus* (Coleoptera:Curculionidae). Entomol. News 98: 163-164.

Galford, J.R., J.W. Peacock, and S.L. Wright. 1988. Insects and other pests affecting oak regeneration. P. 219-225 in Smith, H.C., A.W. Perkey, and W.E. Kidd, Jr. (eds.). Proc., guidelines for regenerating Appalachian hardwood stands. May 24-26, 1988, West Virginia Univ., Morgantown. Soc. Am. For. Publ. 88-03.

Galford, J., L.R. Auchmoody, H.C. Smith, and R.S. Walters. 1991. Insects affecting establishment of northern red oak seedlings in central Pennsylvania. P. 271-280 in McCormick, L.H., and K.W. Gottschalk (eds.). Proc., 8th central hardwood forest conf. March 3-6, 1991, Pennsylvania State Univ., University Park.

Galford, J.R., L.R. Auchmoody, R.S. Walters, and H.C. Smith. 1992. Millipede damage to germinating acorns of northern red oak. USDA For. Serv. Res. Pap. NE-667.

Gibson, L.P. 1982. Insects that damage northern red oak acorns. USDA For. Serv. Res. Pap. NE-492.

Gysel, L.W. 1957. Acorn production on good, medium, and poor oak sites in southern Michigan. J. For. 55: 570-574.

Janzen, D.H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst. 2: 465-492.

Korstian, C.F. 1927. Factors controlling germination and early survival in oaks. Yale Univ. Sch. of For. Bull. 19.

Marquis, D.A., and R. Brenneman. 1981. The impact of deer on forest vegetation in Pennsylvania. USDA For. Serv. Gen. Tech. Rep. NE-65.

Marquis, D.A., P.L. Eckert, and B.A. Roach. 1976. Acorn weevils, rodents, and deer all contribute to oak regeneration difficulties in Pennsylvania. USDA For. Serv. Res. Pap. NE-356.

McQuilkin, R.A. 1975. Growth of four types of white oak reproduction after clearcutting in the Missouri Ozarks. USDA For. Serv. Res. Pap. NC-116.

McQuilkin, R.A. 1983. Silvical factors affecting the regeneration of oaks and associated species in Pennsylvania. P. 37-65 in Proc. 1983 Penn State forestry issues conf. March 15-16, 1983, Pennsylvania State Univ., University Park.

Merz, R.W., and S.G. Boyce. 1956. Age of oak seedlings. J. For. 54: 774-775.

Olson, D.F., Jr., and S.G. Boyce. 1971. Factors affecting acorn production and germination and early growth of seedlings and seedling sprouts. P. 44-48 in Oak Symp. Proc. August 16-20, 1971, Morgantown. USDA For. Serv., Northeast. For. Exp. Stn., Upper Darby, PA.

Sander, I.L. 1988. Guidelines for regeneration Appalachian oak stands. P. 189-198 in Smith, H.C., A.W. Perkey, and W.E. Kidd, Jr. (eds.). Proc., guidelines for regenerating Appalachian hardwood stands, May 24-26, 1988, West Virginia Univ., Morgantown. Soc. Am. For. Publ. 88-03.

Sharp, W.M., and H.H. Chisman. 1961. Flowering and fruiting in the white oaks. I. Staminate flowering through pollen dispersal. Ecology 42: 365-372.

Shart, W.M., and V.G. Spraque. 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. Ecology 48: 243-251.

Tuley, G. 1983. Shelters improve the growth of young trees in the forest. Q. J. For. 77: 77-87.

Tuley, G. 1985. The growth of young oak trees in shelters. Forestry 58: 181-195.

Watt, R.F. 1979. The need for adequate advance regeneration in oak stands. P. 11-17 in Holt, H.A., B. C. Fischer (eds.). Proc., regenerating oaks in upland hardwood forests. Purdue Univ. Res. Found., West Lafayette, IN.