AUTUMN PREDATION OF NORTHERN RED OAK SEED CROPS

Kim C. Steiner[1]

Abstract: Production and autumn predation of northern red oak acorns was measured over four years in five Pennsylvania stands dominated by this species. Mean annual production was 41,779/acre, of which an average of 7.9% was destroyed by insects or decay following insect attack, and an average of 38.6% was destroyed or removed by vertebrates. White-tailed deer appeared to be the dominant vertebrate consumer of acorns.

INTRODUCTION

Numerous factors contribute to the well-known difficulty of regenerating northern red oak (*Quercus rubra* L.) (Crow 1988), but the frequent lack of seedlings even after good seed crops (Steiner and others 1993) suggests that acorn predation may be a particularly important limitation. Unfortunately, northern red oak's heavily provisioned seed, which plays such a large role in the post-germination growth patterns and ecological response of the species (Kolb and Steiner 1990, Kolb and others 1990), is also an extremely attractive food source for granivorous vertebrates and insects. Losses to seed predators are usually large (Beck 1993).

Despite a fairly large body of literature on the production and loss of northern red oak (NRO) acorns, there is still uncertainty about the relative importance of various acorn consumers because of conflicting results and inconsistent methodology. Many published studies have been based upon inadequate samples of trees, stands, or years (*e.g.*, Korstian 1927), all of which are now known to be large sources of variation not only in acorn yield but also in the relative importance of various sources of acorn loss (Olson and Boyce 1971). In other studies, there has been no accounting of acorns lost entirely from the site, creating an underestimate for some agents of loss and an overestimate of others. This appears to have been the case in the classic and otherwise excellent study by Downs and McQuilkin (1944). In others, the use of acorn traps without parallel counts of loss from ground plots has undoubtedly resulted in underestimates of loss to ground-feeding vertebrates (Christisen and Korschgen 1955). Also, in many studies, rates of predation by insects have been reported on the basis of acorns collected (presumably after some predation by vertebrates) rather than on the basis of total production, and no distinction has been made between insect infestation and failure to germinate because of insect attack. Finally, it is not always clear in published reports whether several-year average losses to predation are means of annual percentages, which give undue weight to the very high proportion of predation in years when acorn production is very low, or represent cumulative loss to various agents as expressed on an annual basis. This study of production and autumn predation of seed crops in NRO in five stands over a four-year period was undertaken to clarify our understanding of this portion of the regeneration process, specifically the fate of fully developed acorns during the months of autumn.

METHODS

The study was performed in five forest stands located over a broad portion of central Pennsylvania, two in the Ridge and Valley region and three on the Allegheny Plateau. Northern red oak was the dominant species in the overstory of each stand, with a mean of 49.3% (range 39.8 to 67.8) of stand basal area. Other common species were *Acer rubrum*

---

[1]Professor of Forest Biology, School of Forest Resources, Pennsylvania State University, Ferguson Building, University Park, PA 16802. The author wishes to gratefully acknowledge the able and generous assistance of Brian Joyce and Jim Zaczek. Thanks also to Marc Abrams, Todd Bowersox, Ellen Manno, Richard Yahner, and two anonymous reviewers for their comments on an earlier draft of the manuscript.

(mean = 24.8%) and other oaks (15.2%), including *Q. alba*, *Q. prinus*, *Q. velutina*, and *Q. coccinea*. At the beginning of the study, stand mean ages of dominant and codominant NRO ranged from 70 to 123 years. More information on the characteristics of these stands may be found in Steiner and others (1993).

At each research site, a study area of 3.5 to 4.3 acres in size was delineated in October 1990 by marking corner trees. In November of each year from 1990 through 1993, the size of the NRO seed crop was determined by the cap-count method (Shaw 1974) performed in 4.31-ft^2 (0.40 m^2) ground plots. At each study site, approximately 75 quadrats were located at fixed intervals on equally spaced transects that covered the entire study area. Although most caps had fallen by the time counts were made, usually in the second or third week of November, a small number of unfallen caps sometimes remained in the tree crowns. The density of these was estimated by surveying an estimated 10-foot square portion of the canopy directly above each quadrat with binoculars, and ground counts were revised upward as needed. Depending upon year and site, unfallen caps amounted to 0 - 11% of total production. In addition to detached acorn caps, the number of fresh acorns was counted, omitting those that remained firmly attached to their caps, which were typically undersized and considered to have been aborted before full maturity. Fresh acorns were tallied by two categories: 1) intact or 2) partially consumed (by small rodents) at the proximal end of the nut. Acorns with <30% of cotyledons removed were assumed to be viable, subject to germination tests; those with >30% consumed were tallied as having been lost to vertebrate (rodent) predation. Coefficients of variation for acorn and cap counts averaged 12.8% of stand/year means.

Each fresh, detached acorn cap was assumed to represent a viable acorn, excluding losses to vertebrate and insect predation. Differences between counts of caps and counts of fresh acorns were attributed to predation by vertebrates feeding on the ground or in tree tops prior to the November measurements. At the time of production counts in November, samples of fresh acorns were collected from each site for viability analysis. Except where no fresh acorns could be found, sample sizes ranged from as few as 18 to as many as 897, with an average of 170. Sample sizes of fewer than 100 acorns represented *all* the acorns that could be found on the site. Acorns were collected without regard to any external evidence of injury, including insect infestation. Acorn samples were fully hydrated and stored at -1.0°C until February, when they were planted in flats of moist peat moss in the greenhouse for determination of viability. In April or May, after germination had ceased, nongerminants were cut open and classed by apparent cause of death. Germination failure averaged 44.0% in acorns that had been partially consumed by rodents, and this loss was attributed to vertebrate predation. All other germination failures were attributable directly or indirectly to insects (decaying acorns were assumed to have become infected through insect attack [Oak 1993]), and this was the basis for estimated acorn losses to insect predation. Insect-infested acorns that successfully produced a seedling were not counted as lost to predators.

Signs of foraging by white-tailed deer (*Odocoileus virginianus*), especially in years of abundant acorn production, suggested that this species caused much of the loss to vertebrates. To estimate loss by deer *vs.* other vertebrates, a five-strand electrified fence was installed around two noncontiguous plots at one of the research sites on 17-18 August 1993, prior to acorn dissemination. Each plot enclosed about one-fourth of the total study area at the site, and two similar-sized plots were left unfenced. The four plots enclosed almost identical basal areas of NRO. In addition to the normal assessment of acorn production in November, the plots were remeasured five weeks later on 17 December to determine the progressive loss of acorns from fenced *vs.* unfenced plots. Where possible, the statistical significance of differences between means was determined by t-test, analysis of variance, or paired comparisons t-test.

RESULTS AND DISCUSSION

The NRO seed crop, based upon counts of fresh caps, varied from 540/acre to 198,510/acre among the four years of the study and all five stands. Mean annual NRO acorn production for all stands and years was 41,779/acre (Table 1), or 725 per ft^2 basal area of NRO. Every stand exceeded this level of production in at least one year of the four. Table 1 shows mean annual acorn production averaged across stands. The years 1991 and 1992 had relatively low production, and the years 1990 and 1993 had relatively high production. Although stands varied considerably in mean annual production, as shown in the following tabulation, only the main effect of years was statistically significant ($P < 0.05$) in analysis of variance for total production:

Stand number	Mean annual acorn production, 1990-93 (acorns/acre)
I	32,652
II	23,515
III	78,023
IV	55,200
V	19,505

The contribution of stand to variation in seed crop size was only 18% as large as the contribution of years, even though study sites were separated by as much as 66 miles. In simple terms, there was a tendency for good or poor seed crops to occur simultaneously at all sites. Downs and McQuilkin (1944) found the same result over a seven-year period of study in two stands separated by 100 miles.

Table 1. -- Production and autumn predation of northern red oak acorns from 1990 through 1993, averaged over five Pennsylvania stands. Means within a row that share the same letter are not significantly different at $P < 0.05$.

Year	Pre-November Vertebrate loss	Acorns present in November		Total Production
		Nonviable	Viable	
1990	47,740 a	3,610 b	31,426 a	82,776
1991	9,284 a	1,488 b	1,454 b	12,226
1992	3,790 a	370 b	454 b	4,614
1993	3,626 c	7,780 b	56,094 a	67,500
Mean	16,110 a	3,312 b	22,357 a	41,779

Over all years and stands, the number of viable acorns remaining on the ground in November averaged 22,357/acre (Table 1), or 53.5% of mean annual production. Acorns that were not viable in November as a direct or indirect result of insect infestation averaged 7.9% of production. Of a total of 469 acorns that failed to germinate in viability trials, 66.3% had been attacked by *Curculio* spp. and 4.3% by *Callirhytis*. Most of the remainder were rotten, though a small percentage was infested with acorn moths. Rotten acorns were assumed to be decayed as a result of attack by insects, some of which could also have been *Curculio*. Thus, the percentage loss attributable to *Curculio* could be underestimated.

This study's mean loss of 7.9% of potential production to insects is considerably lower than the 24 - 35% insect infestation rates for NRO acorns reported in many long-term studies (Beck 1977, Downs and McQuilkin 1944, Tryon and Carvell 1962). This is due in part to the methodological discrepancies mentioned in the introduction, especially 1) the expression by others of insect infestation as a percentage of recovered acorns rather than total production and 2) the difference between occurrence of infestation and failure to germinate as a result of infestation. Walters and Auchmoody (1993) found that 53% of acorns attacked by *Curculio* spp. were able to germinate and produce seedlings. In addition, some acorns that had been infested with insects in the present study may have been consumed or cached by vertebrates and thus counted against that source of acorn loss. Linda Gribko (personal communication) found that *Peromyscus* spp. consumed weeviled acorns as readily as sound acorns in the study reported by Gribko and Hix (1993). In any event, it appears that the loss of potential NRO reproduction solely attributable to autumn-feeding insects may be considerably less than commonly supposed. Of course, insects may also contribute to losses at other stages of the reproduction process.

Autumn predation of the seed crop by vertebrates averaged 38.6% of production. Vertebrates were a significantly ($P < 0.05$) more important agent of acorn loss than insects for the four-year study period. Of course, some of the acorns that appeared to have been consumed by vertebrates before November may have been merely cached in a location suitable for germination. However, this fraction still represents a potential loss (most cached acorns are consumed), and in fact total autumn and winter losses to vertebrates (net of spring germination) have consistently exceeded 38.6% (Steiner, unpublished data). Downs and McQuilkin (1944) found an average of 24% of acorns damaged by rodents or birds *at the time of dissemination.* Subsequent predation by vertebrates from ground plots is not clearly described in their report, but in one bumper crop year only 18% of production (five oak species) remained on the ground by mid-winter. Tryon and Carvell (1962) found an average loss to arboreal and ground-feeding vertebrates of 50.2% over a four-year period of study.

Peromyscus leucopus (white-footed mouse) is a common small rodent at all five study sites (Yahner and Steiner, unpublished data). Some evidence suggests that this and a related species are important predators of NRO acorns (Gribko and Hix 1993). According to Verme (1956), *P. leucopus* typically consumes a portion of the cotyledons by feeding through a hole chewed in the cap end of the acorn. In this study, such partial feeding typically amounted to perhaps a little more than one-third of the cotyledons, leaving the embryo and most of the food reserves intact. In fact, Verme found that white-footed mice *always* consumed only a portion of NRO acorns, suggesting that partially consumed acorns may be an accurate measure of predation by this species (other than caching). Such acorns amounted to an average of only 3.9% of mean annual production in this study, and many of those were still capable of germination. This suggests relatively light predation by *Peromyscus*, although additional acorns may have been removed and cached or consumed in burrows or tree cavities. Other information also indicates that this species may have relatively minor importance as a seed predator. Verme (1956) reported an average consumption of 1.8 acorns/day when *Peromyscus leucopus* was fed a diet of only acorns. Using his assumed density of 7 mice/acre (which appears liberal in light of the census data reported by Jensen [1982] and Thorn and Tzilkowski [1991]), this species would have consumed less than 3% of the average annual acorn production in this study by the time production was measured in mid-November.

Other potentially important vertebrate predators that are known to be present at or near the study sites include gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), white-tailed deer, wild turkeys (*Meleagris gallopavo*), and black bears (*Ursus americanus*). The acorns of NRO are generally avoided by blue jays, which can be heavy predators on oaks with smaller acorns (Bossema 1979, Darley-Hill and Johnson 1981, Scarlett and Smith 1991). In 201 hours on site for the measurements reported here, there were 7 gray squirrels sighted, 8 eastern chipmunks, 3 white-tailed deer, and no wild turkeys or black bears. Despite the documented potential for heavy acorn removals by gray squirrels (Thorn and Tzilkowski 1991), population densities of this animal can be quite low (Healy 1988). From my own experience as a squirrel hunter, the infrequency with which squirrels and chipmunks were sighted in this study, despite a sometimes abundant source of food, is rather typical of deep-woods Pennsylvania stands such as these.

In contrast to small mammals, signs of deer foraging were abundant on the study plots, especially when acorn production was high. The study area that was partially fenced to exclude deer in August 1993 provided an estimate of the relative impact of deer foraging on the NRO seed crop. By mid-December, a significantly ($P < 0.05$) higher percentage of the total NRO seed crop of 45,920/acre remained on fenced plots (65.4%) compared to unfenced plots (32.3%).

Furthermore, some undetermined proportion of the acorns lost within fenced areas was also a result of deer feeding, based upon the presence within fenced areas of disturbed leaf litter, masticated pericarps, and droppings. In other words, some of the losses attributed to small vertebrates were actually caused by deer. These observations indicate that deer accounted for at least 48.9%, and probably more, of total removals by vertebrates by mid-December.

Downs and McQuilkin (1944) obtained a similar result in another study area with high deer densities (18 - 32 per square mile). They concluded that deer were far more important than rodents as predators of acorns. Pennsylvania deer densities are higher than this prior to hunting season in late November (37/mi^2 in 1992 according to a personal communication from William Palmer, Pennsylvania Game Commission), but it is impossible to draw direct a direct comparison without knowing the basis for estimating density. Indirect evidence also suggests that deer are more important consumers of acorns than other vertebrates known to feed heavily on acorns, at least in Pennsylvania. Pennsylvania Game Commission estimates of population densities and animal weights indicate that mean deer biomass per forested acre is about 10 times that of gray squirrels and 60 times that of bear and turkeys (William Palmer and William Drake, personal communications). In Missouri, acorns made up 46% of the food consumed by deer during September, October, and November (Christisen and Korschgen 1955). Of course, feeding preferences vary among animals. However, the known tendency of deer to feed heavily on acorns, coupled with their overwhelming biomass abundance (in Pennsylvania) compared to other major consumers, suggests that they must necessarily have a disproportionate influence on acorn predation.

CONCLUSIONS

In five stands with a mean NRO stocking of 49% of total basal area, the annual production of mature acorns averaged 41,779/acre over a five-year period. Yearly variation in seed crop size was about five times as important as stand-to-stand differences. The number of viable acorns remaining on the ground in November averaged 53.5% of mean annual production. Of the 46.5% loss, only 7.9% was caused by insect attack or by fungal or bacterial infection following insect attack. This figure is less than other published figures for insect predation of NRO, which should be regarded as overestimates for reasons explained. The remaining 38.6% of acorn production was removed by vertebrates. In a stand that was partially fenced to exclude deer in 1993, deer predation accounted for a minimum of 48.9% of total acorn removals by vertebrates by mid-December. Other evidence supports a conclusion that deer were the dominant consumers of NRO acorns on these sites.

LITERATURE CITED

Beck, D. E. 1977. Twelve-year acorn yield in southern Appalachian oaks. USDA Forest Service Res. Note SE-244, 8 pp.

Beck, D. E. 1993. Acorns and oak regeneration. IN, Oak Regeneration: Serious Problems and Practical Recommendations (pp. 96-104), USDA Forest Service Gen. Tech. Rep. SE-84, 319 pp.

Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behavior 70: 1-117. h-h2

Christisen, D. M., and L. J. Korschgen. 1955. Acorn yields and wildlife usage in Missouri. Trans. N. Am. Wildl. Conf. 20: 335-357.

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

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.

Gribko, L. S. and D. M. Hix. 1993. The effect of small rodents on northern red oak acorns in north-central West Virginia. Proc. 9th Central Hardwood Forest Conference (pp. 400-408), USDA Forest Service Gen. Tech. Rep. NC-161, 515 pp.

Jensen, T. S. 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. Oecologia 54: 184-192.

Kolb, T. E. and K. C. Steiner. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. For. Sci. 36: 34-44.

Kolb, T. E., K. C. Steiner, L. H. McCormick, and T. W. Bowersox. 1990. Growth response of northern red oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. For. Ecol. Manage. 36: 65-78.

Korstian, C. F. 1927. Factors controlling germination and early survival in oaks. Yale Univ. School of Forestry Bull. No. 19, 115 pp. + plates.

Oak, S. W. 1993. Insects and diseases affecting oak regeneration success. IN, Oak Regeneration: Serious Problems and Practical Recommendations (pp. 105-111), USDA Forest Service Gen. Tech. Rep. SE-84, 319 pp.

Olson, D. F., Jr. and S. G. Boyce. 1971. Factors affecting acorn production and germination and early growth of seedlings and seedling sprouts. Oak Symposium Proceedings (pp. 44-48), USDA Forest Service, Northeastern Forest Experiment Station.

Scarlett, T. L. and K. G. Smith. 1991. Acorn preference of urban blue jays (*Cyanocitta cristata*) during fall and spring in northwestern Arkansas. The Condor 93: 438-442.

Shaw, M. W. 1974. The reproductive characteristics of oak. IN, M. G. Morris and F. H. Perring (eds), The British Oak: Its History and Natural History (pp. 162-181). Botanical Society of the British Isles, Hampton, England.

Steiner, K. C., M. D. Abrams, and T. W. Bowersox. 1993. Advance reproduction and other stand characteristics in Pennsylvania and French stands of northern red oak. Proc. 9th Central Hardwood Forest Conference (pp. 473-483), USDA Forest Service Gen. Tech. Rep. NC-161, 515 pp.

Thorn, E. R. and W. M. Tzilkowski. 1991. Mammal caching of oak acorns in a red pine and a mixed-oak stand. In, Proc. 8th Central Hardwood Forest Conf. (pp. 299-304), USDA Forest Service Gen. Tech. Rep. NE-148, 605 pp.

Tryon, E. H., and K. L. Carvell. 1962. Acorn production and damage. W. Va. Agric. Exp. Stn. Bull. 466T, 18 p.

Verme, L. J. 1956. Acorn consumption by chipmunks and white-footed mice. J. Mammal. 38: 129-132.

Walters, R. S. and L. R. Auchmoody. 1993. Factors limiting northern red oak reproduction in Pennsylvania. Proc. 9th Central Hardwood Forest Conference (pp. 271-280), USDA Forest Service Gen. Tech. Rep. NC-161, 515 pp.