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Does the shelterwood method to regenerate oak forests affect acorn production and predation?

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Abstract

The shelterwood system is one of the primary methods currently used to encourage regeneration of oak forests; yet, little is known about its influence on acorn production and predation. We compared acorn production, and predation by insects and mammals in stands of red oak (*Quercus rubra* L.) that were regenerated by the shelterwood method (50% canopy removal) to that of uncut (control) stands in the first year of production after the harvest treatment. In each plot, we measured stand and tree characteristics and estimated acorn production by using both acorn traps and a visual crown survey to place trees into productivity classes. Acorns collected in traps were examined to record the external and internal conditions, percentage of cotyledon damaged and the presence of insects. Exclusion cages were used to quantify acorn predation by mammals in harvested and control plots. Oaks in the shelterwood plots produced more acorns than oaks in uncut stands if the acorn crop was rated by the crown survey method, but not when production was measured with acorn traps. We found no evidence that the shelterwood method influenced acorn predation by insects or mammals. Visual examination of the exterior of the pericarp indicated that insects attacked 44% and 47% of the acorns in harvested and control plots, respectively. Most of the damage produced by insects was attributed to pip galls (cynipid wasps) and acorn weevils (*Curculio* sp.), which in most cases damaged more than 75% of the cotyledon. Squirrels and chipmunks were the primary mammals responsible for removing 50% of the acorns in the fall-spring whereas mice took 33% of the acorns. Use of the shelterwood method in conjunction with leaving the best acorn producers can be used to create the desired stand structure while maintaining or increasing acorn production and oak regeneration potential in the stand.

Keywords: *Quercus rubra*; Regeneration by shelterwood system; Seed production; Pre-dispersal seed predation; Post-dispersal seed predation

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1. Introduction

In Canada, red oak (*Quercus rubra* L.) occurs in the southeastern mixed coniferous–deciduous and deciduous forests, from east of Lake Superior to Nova Scotia. Although red oak can be a common main canopy species in these northern forests, it is hard to regenerate and sustain its current level of stocking in the overstory.

Many factors contribute to the difficulty of maintaining oak by natural regeneration in these forests. Typically, natural regeneration of red oak forests occurs after disturbances (e.g., fire) that open the forest canopy and understory, thus favoring oak seedling growth and recruitment into the overstory by providing more light in the forest understory (Crow, 1988; Dey, 2002). Fire suppression, however, has resulted in the displacement of oaks by more shade-tolerant species (Abrams, 1992), and historical trends suggest the replacement will continue (Nowacki et al., 1990). The natural regeneration of oaks is further complicated because acorn production by red oak is highly variable among individuals and fluctuates from year-to-year (2–7 years interval between large crops) for individual trees (Healy, 2002; Johnson et al., 2002). This natural variability in acorn production makes it hard to time silvicultural practices with a good seed crop to favor oak regeneration. Variability in seed production is due, in part, to the (1) inherent periodicity of good to bumper acorn crops, (2) differences in individual tree characteristics such as age, size of crown and crown dominance, (3) stochastic environmental factors that affect flowering, pollination and seed development, and (4) predation of oak flowers and acorns by insects and vertebrates (Christisen and Kearby, 1984; Sork et al., 1993; Dey, 1995). In addition, some red oaks are consistently good acorn producers, whereas others are not, although they may be dominant trees in the site (Healy et al., 1999; Healy, 2002; Johnson et al., 2002).

Crown size, health and vigor are major determinants of acorn production of oaks (Downs and McQuilken, 1944; Christisen, 1955; Sharp and Sprague, 1967; Goodrum et al., 1971; Sork et al., 1993). The potential to produce acorns is partially related to stand density and the degree crowns are exposed to direct sunlight (Johnson et al., 2002). Compared to forest-grown trees, open-grown oaks have (1) larger, wider crowns with greater surface area and volume, (2) more leaf area and foliage biomass, (3) higher densities of live, healthy branches, (4) greater live crown ratios, and (5) greater crown exposure to direct sunlight; all of which are correlated with acorn production.

Oak seedling establishment occurs mainly in years when production of sound acorns exceeds predation (Downs and McQuilken, 1944; Gysel, 1957; Christisen and Kearby, 1984). Predation by insects, mammals and birds may result in low acorn survival, especially in years of low to moderate acorn production (Marquis et al., 1976). It has been hypothesized that in years of mast production seed predators become satiated, leaving a greater number of seeds available for dispersal and germination (Murphy, 1968; Janzen, 1971). Insects can destroy the entire crop in low seed years, and a large proportion of the acorns in highly productive years (Galford et al., 1988). Many insects, such as weevils (e.g., *Curculio* spp., *Conotrachelus* spp.), moths (e.g., *Melissopus* spp.) and cynipid wasps, attack acorns causing damage that prevents germination (Kearby et al., 1986; Weckerly et al., 1989; Johnson et al., 2002). Mammals such as deer (Harlow et al., 1975), squirrels (Short, 1976), chipmunks (Pyare et al., 1993) and mice (Gómez et al., 2003) are known predators of acorns and can consume high proportions of the acorn crop in years of poor to moderate production (Sork, 1984). However, mammals and birds also play a beneficial role in oak seed dispersal, and their caching of acorns promotes germination (Darley-Hill and Johnson, 1981; Jensen and Nielsen, 1986).

Currently, the shelterwood system is one of the primary methods used to encourage the regeneration of oak forests (Hannah, 1987; Dey and Parker, 1996). To create the shelterwood for oak regeneration, trees are harvested from below (i.e., from the lower diameter classes first) until the desired overstory stocking is achieved. Non-oaks are preferentially removed, leaving co-dominate and dominate oaks in the overstory to produce acorns. Reductions in stand stocking may promote acorn production by providing more growing space for oak crown expansion and development, and by modifying environmental conditions that influence acorn production and predation. Few studies have scientifically evaluated the effects of thinning or shelterwood harvesting on acorn production of individual trees and stands, and their results were inconsistent. There is evidence that thinning oaks in young stands (e.g., 7–22 years old) may increase tree diameter growth and oak stocking in the upper crown classes (Johnson et al., 2002), thereby increasing the amount of acorn bearing crown area in the stand. Stand density, however, may be weakly related to acorn production because it has little influence on acorn crop size in years of poor production, and in years of high production, a few large, inherently good seed producers can generate the majority of a bumper acorn crop, irrespective of stand density (Greenberg and Parresol, 2002). In Massachusetts, Healy (1997) thinned young (i.e., 40 years old) stands to relate stand stocking to differences in acorn production where red oak was growing with white pine and red maple. It was found that reducing stand stocking from 100% to 40% (according to Gingrich, 1967) significantly increased acorn production per tree, and that differences between the thinned and uncut stands were the greatest in years of poor acorn production. At the stand-level, Healy (1997) reported that acorn production that was averaged over a 3-year period was not significantly different in thinned or uncut mature stands (62–82 years old) in New England, although on an annual basis, he observed that acorn yields were consistently greater in thinned stands than uncut stands; the lack of significance was attributed to large year-to-year variation in acorn production during his short sampling period. Because little is known about the influence of shelterwood harvesting on acorn production of individual trees and stands, we initiated a study to experimentally test for differences in acorn production and predation by insects and mammals between stands being regenerated by the shelterwood method and uncut stands in central Ontario.

2. Materials and methods

2.1. Study area and site description

The study area was located in central Ontario, Canada, in the Great Lakes-St. Lawrence forest region, an area characterised by mixed deciduous–coniferous forests where common tree species include red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), red oak, yellow birch (*Betula alleghaniensis* Britton), white ash (*Fraxinus americana* L.), white pine (*Pinus strobus* L.), red pine (*P. resinosa* Ait.), jack pine (*P. banksiana* Lamb.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The work was conducted in mature, oak-northern hardwood stands that had at least 30% of stand basal area in red oak and where no cutting had taken place in the past 20 years. Sites were located northeast of Papineau Lake (45°21′N, 77°48′W), Bangor Township, Hastings County, approximately 30 km northeast of Bancroft.

Before harvesting at the study site, the forest canopy was dominated by sugar maple, red oak, American basswood (*Tilia americana* L.), American beech, white ash, ironwood (*Ostrya virginiana* (Mill.) K. Koch), white pine and hemlock. For trees ≥ 5 cm diameter breast height (DBH), average stand basal area was 27.2 m^2/ha and density was 645 trees/ha. Overall, red oak accounted for 60% of stand basal area and 52% of stand stocking (Dey, 1995). DBH of the red oak in the overstory averaged 28.8 cm, and their ages ranged from 68 to 179 years (Guyette and Dey, 1995). The understory had a diversity of hardwood advance regeneration including sugar maple, red oak, red maple, ironwood, striped maple (*Acer pensylvanicum* L.), and American beech. However, sugar maple dominated the population of advance regeneration, comprising 82% of the more than 250,000 stems/ha. Red oak advance regeneration density was relatively low (9200 seedlings/ha) and the oak seedlings were small, averaging 2.2 mm in basal diameter (2.5 cm above ground level) and 15 cm in height.

2.2. Experimental design

This study was established within the framework of a larger investigation that was designed to evaluate silvicultural methods to regenerate red oak. We used a one-way ANOVA design to test for the effects of shelterwood harvesting on acorn production and predation. We randomly selected a subset of 10 experimental plots (60 m × 60 m) from the original experiment. Five plots were harvested by the shelterwood method (the treated plots). The other five plots were not harvested and left undisturbed (the control plots).

The shelterwood harvest occurred during the fall of 1993 through winter of 1994. We created the shelterwood by cutting trees from the lower crown classes until the residual crown cover was about 50% and basal area ranged from 5 to 7 m^2/ha. The small, inferior and subordinate trees were preferentially selected for harvest. Non-oak species were removed first where possible. The harvest resulted in a uniform canopy cover dominated by red oak. After the commercial timber harvest, all unmerchantable stems $\geq$ 2.5 cm DBH were cut in the spring of 1994.

2.3. Stand and tree variables

In each plot, we determined the density of oaks, and for each individual oak we measured DBH, total tree height, and crown diameter along the N–S (d_1) and E–W (d_2) axes through the tree trunk. Crown cover (the ground area covered by the crown) for each oak was estimated as $\pi d_1 d_2/4$ and was averaged for the plot. Total crown cover for a plot was estimated by adding the crown cover of each oak. Only trees with DBH $\geq$ 18 cm were used to estimate the average DBH, tree height and crown cover, because smaller red oak trees are unlikely to produce acorns (Dey, 1995; Greenberg, 2000).

2.4. Acorn production

Acorn production was estimated using two techniques. The first technique consisted of sampling falling acorns using traps in 1996 and 1997. Acorn traps consisted of squared-base funnels (1 m $\times$ 1 m) made of aluminium screen (mesh 1.25 cm $\times$ 1.25 cm), equipped with a cylinder (PVC tubing 15.5 cm inside diameter, and 30 cm in length) at the bottom of the funnel (opening of funnel 10 cm $\times$ 10 cm) to collect the acorns. In each plot, we installed one acorn trap per 120 m^2 of crown cover. Each trap was installed below the canopy of an oak tree selected at random (one acorn trap below each selected oak for a total of 86 traps). Acorn traps were emptied every 2 weeks from early August to the end of November. The total number of acorns collected in a trap provided an estimate of the number of acorns produced per m^2 of crown cover. Acorn production in a plot was estimated as the mean number of acorns produced per m^2 of crown cover multiplied by the total crown cover of oaks with DBH greater than 18 cm.

Acorn production was also estimated visually. Assessments were made by looking, with binoculars, at the canopy of each of the 86 selected oaks every year after treatment. Acorn production assessments were performed from 14 to 16 August 1996 and from 29 July to 2 August 1997 (no acorn production was recorded in previous years) prior to beginning of arboreal removal by animals, as suggested by Koenig et al. (1994). The same two observers conducted the assessment in both years. The rating of acorn abundance followed that of Christisen and Kearby (1984): (1) few to none; (2) poor (P): sparsely scattered acorns or no acorns; (3) P+ or F−; (4) fair (F): evenly distributed single acorns and small clusters; (5) F+ or G−; (6) good (G): evenly distributed acorns with numerous small and medium-sized clusters; (7) G+ or H−; (8) heavy (H): numerous medium- and large-sized clusters throughout the crown; and (9) bumper: very high acorn density over a large percentage of the crown. Theses production indices are correlated with acorn counts per square metre of northern red oak (Christisen and Kearby, 1984).

2.5. Acorn damage

Acorns collected in traps during 1996 were examined externally and their condition was recorded as healthy (typically green colour and with no evidence of external damage), insect infested or other (included acorns chewed or partially eaten by mammals, broken, mouldy, malformed, black instead of green or with abnormal cap). Each acorn was subsequently sliced in half and the condition of the cotyledon (healthy, blackened, collapsed, damaged by insect or other), percentage of cotyledon damaged (0%, 1–75% or >75%) and the presence of insects (identified to morphospecies when possible) were recorded. The proportion of acorns in each type of condition was estimated for each trap and averaged for the plot. These averages were used to make comparisons between treated (shelterwood harvest) and control plots. Voucher specimens of the insect morphospecies are deposited at the Great Lakes Forestry Centre in the collection of J.J. Turgeon.

2.6. Sampling of small mammals

Small mammals were sampled using Sherman and Longworth traps in all harvested and control plots during September–October 1996. A 5 × 5 grid of traps (12 m apart) was established in each plot. In each grid, traps were operated for four consecutive nights, followed by a resting period of 10 days and reset for another four-night period, providing a total trapping effort of 200 trap nights per plot. Traps were baited with peanut butter and checked daily between 07:00 and 11:00 am. Captured mammals were identified, marked, and released at the site of capture. Rodents were marked with numbered ear tags and shrews were toe-clipped. Abundance of small mammals was estimated as the number of original captures per 100 trap nights.

2.7. Mammalian predation on acorns

Exclusion cages were used to quantify mammalian predation on acorns in harvested and control plots. Cages were made with aluminium screen (7 mm × 7 mm). Three types of cages were employed: (1) open trays that allowed access to all vertebrate predators; (2) upright cylinders (32 cm diameter, 32 cm high) with two large opposite entrance holes (7 cm × 7 cm) at the base that excluded mid- to large-size mammals and birds, but allowed access by mice, voles, chipmunks, and squirrels; (3) upright cylinders with two small opposite openings (2.5 cm × 2.5 cm) that excluded all birds and mammals except mice and voles. Cages were set in a randomised block design within each plot. Five sets of three cages (one of each type, 1 m apart) were set in each plot following a regular pattern (one set in the centre and one set 25 m from each corner of the plot). Within a set, position of cages was established randomly. A total of 100 red oak acorns were placed into each cage on 17 October 1996. The number of acorns remaining in each cage was counted on 26–27 November 1996 and on 13 May 1997 to estimate predation during the fall and winter–spring, respectively.

2.8. Data analysis

Non-parametric tests were used in most situations because data sets had heterogeneous variances even after transformation. Mann–Whitney or *t*-test for unequal variances was used to compare plot characteristics and acorn conditions between treated and control plots. *G*-test was employed to test for differences in the frequency distribution of trees

Table 1
Oak density, the number of randomly selected oaks, mean DBH (±S.E.), mean height, mean crown area per oak tree, total crown area, and acorn production in treated (shelterwood harvest) and control plots of a deciduous forest in central Ontario (Canada)

Plot	Oaks/ha (oaks/plot)	Number of selected oaks	DBH[a] (cm)	Height[a] (m)	Crown area/tree (m^2)[a]	Total crown area (m^2)[b]	Acorn production per plot	
							1996	1997
Treated								
1	69 (24)	6	41.8 ± 2.1	24.4 ± 0.2	29.8 ± 3.2	716	71481	23509
2	194 (67)	13	31.1 ± 1.0	18.7 ± 0.2	24.5 ± 2.2	1632	95535	31259
3	11 (4)	1	34.9 ± 5.9	21.7 ± 1.2	31.2 ± 14.2	125	6500	16750
4	141 (51)	13	35.8 ± 1.4	23.8 ± 0.2	39.3 ± 3.6	2005	272834	48737
5	27 (9)	3	40.6 ± 4.9	23.5 ± 0.8	67.3 ± 15.9	606	2038	23229
Average	88 ± 35		36.7 ± 1.9	22.4 ± 1.0	38.4 ± 7.6	1021 ± 347	94078 ± 47456	28697 ± 5512
Control								
1	177 (46)	12	25.4 ± 1.6	15.4 ± 0.4	23.9 ± 2.5	1331	160053	35161
2	33 (12)	3	26.0 ± 0.5	26.0 ± 0.5	50.9 ± 10.3	611	40937	12627
3	19 (5)	2	36.9 ± 7.1	21.8 ± 1.6	45.6 ± 11.9	298	36803	9685
4	27 (10)	3	47.3 ± 4.8	24.2 ± 0.4	74.9 ± 13.1	749	42943	48435
5	330 (97)	24	24.4 ± 0.7	20.9 ± 0.3	25.5 ± 1.4	2713	219075	42278
Average	117 ± 61		35.3 ± 4.8	22.6 ± 1.7	48.4 ± 9.0	1239 ± 488	99962 ± 37764	29577 ± 7878

[a] Plot average based on all oak trees in the plot.
[b] Total crown area of oaks with DBH > 18 cm.

showing different acorn production ratings between treated and control plots; ratings were pooled when required. The relationship between acorn production in 1996 and DBH or crown cover was explored by regression analysis. *t*-Tests were used to compare the mean mammal abundance between harvested and control plots. Friedman's test for randomised blocks was used to test for differences in the number of acorns taken from open and exclusion cages. All values are given as mean ± 1 S.E. Minitab (V. 13) was used to perform most tests.

3. Results

3.1. Treatment effect on acorn production

The oak density ($t = 0.41$, $P > 0.695$), DBH ($t = 0.28$, $P > 0.793$), tree height ($t = 0.10$, $P > 0.922$), and total oak crown area ($t = 0.85$, $P > 0.424$) were similar between harvested and control plots (Table 1).

Visual inspection of oak canopies showed no acorn production in 1994 and 1995, thus, no acorn traps were deployed. First production of acorns after the shelterwood harvest treatment occurred in the fall of 1996 (3 years after treatment). In 1997, the crop was moderate in size, and it was significantly lower than the 1996 crop, as revealed by both the acorn production ratings ($G = 66.869$, $P < 0.001$) (Fig. 1a) and the estimated number of acorns produced per plot (97,020 ± 28,607 and 29,137 ± 4535 acorns per plot in 1996 and 1997, respectively; Mann–Whitney, $W = 132.0$, $P < 0.05$).

Based on acorn trapping, there was no evidence that the treatment affected the total number of acorns produced in a plot (Mann–Whitney, $W = 26.0$ and 28.0, $P > 0.5$, in 1996 and 1997, respectively) (Table 1). The production rating system, however, showed that the frequency distribution of trees differed between harvested and control plots, where oaks located in treated plots produced a larger crop than those in control plots ($G = 6.090$, $P < 0.05$ and $G = 11.044$, $P < 0.005$ in 1996 and 1997, respectively) (Fig. 1b and c). Crown cover explained little of the variation in the number of acorns produced per m^2 of crown cover by individual trees ($r^2 = 0.035$, $F = 4.04$, $P < 0.05$, $n = 85$) and DBH ($r^2 = 0.074$, $F = 7.69$, $P < 0.007$, $n = 85$).

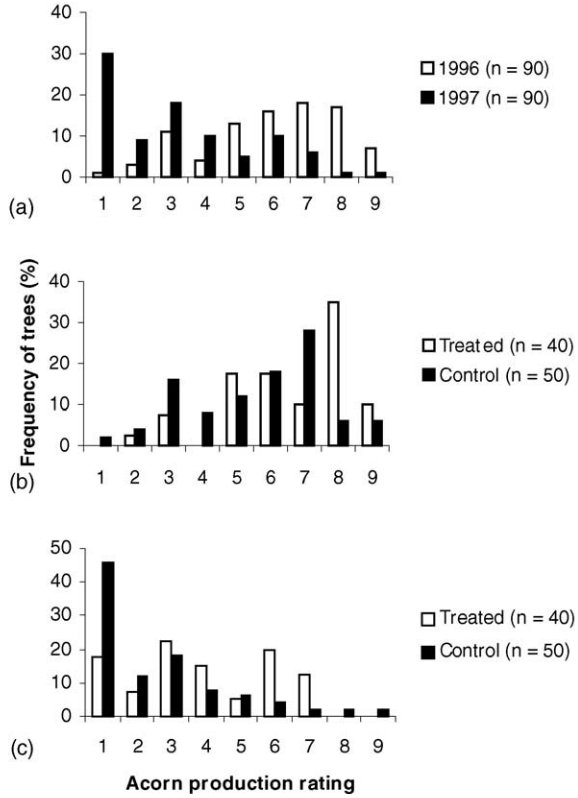

Fig. 1. Frequency distribution of oak trees from a deciduous forest in central Ontario (Canada) according to acorn productivity classes in 1996 and 1997 (a), and in treated (shelterwood harvest) and control plots in 1996 (b) and 1997 (c). The acorn productivity classes were: (1) few to no acorns; (2) poor production; (4) fair production; (6) good production; (8) heavy production; (9) bumper crop (see text for more details on classes 3, 5 and 7).

3.2. Treatment effect on insect predation of acorns

The shelterwood treatment had no significant effect on the proportion of acorns that showed evidence of external damage to the pericarp. The proportion of acorns in the healthy or various damage classes was similar in harvested and control plots (Table 2). The most common cause of external damage was insects as indicated by the presence of pip galls, insects under the acorn cup, and exit holes in the pericarp. Occasionally, a single acorn was attacked by more than one species of insect.

Shelterwood harvesting had no significant effect on the internal condition of acorns. The proportion of the trapped acorns that were healthy (i.e., with no

Table 2
Mean percentage of acorns (±1 S.E.) showing the most frequent external and internal conditions and insects morphospecies in five treated (shelterwood harvest) and five control plots of a deciduous forest in central Ontario (Canada)

Type of condition	Treated	Control	Mann–Whitney[a]
External condition of the pericarp			
Healthy	37.8 ± 4.4	44.4 ± 8.8	24.0
Insect damage[b]	44.1 ± 9.3	47.5 ± 11.4	28.0
Morphospecies 1 (Hymenoptera: pip gall)	30.0 ± 7.5	31.2 ± 9.5	28.0
Insects under cup	20.4 ± 2.4	19.7 ± 3.4	27.5
Exit hole or frass	10.4 ± 1.0	6.3 ± 1.2	18.0
Other[c]	18.1 ± 7.3	8.2 ± 3.2	34.5
Internal damage to the cotyledon			
Healthy	25.3 ± 5.7	34.1 ± 8.0	24.0
Collapsed cotyledon	27.3 ± 10.2	17.8 ± 5.0	31.0
Blackened cotyledon	15.9 ± 0.9	20.6 ± 3.6	24.0
Insect damage	31.1 ± 6.8	27.0 ± 2.1	34.0
Insect frass	14.9 ± 3.1	12.7 ± 2.3	33.0
Presence of insect	8.9 ± 2.5	8.3 ± 2.0	29.0
Morphospecies 2 (Hymenoptera: stone gall)	8.6 ± 3.1	9.1 ± 2.4	27.0
Galleries	1.2 ± 0.6	2.0 ± 0.7	24.0
Mouldy	0.4 ± 0.4	0.5 ± 0.4	–
Insect morphospecies found in acorns			
Morphospecies 1 (Hymenoptera: pip gall)	25.2 ± 6.7	22.1 ± 7.6	29.5
Morphospecies 2 (Hymenoptera: stone gall)	8.0 ± 2.9	8.8 ± 2.3	27.0
Morphospecies 3 (Diptera: *Resseliella* sp.)	8.9 ± 1.1	10.9 ± 2.3	24.0
Morphospecies 4 (Diptera: unidentified)	7.2 ± 2.5	6.4 ± 1.1	29.0
Morphospecies 5 (Diptera: *Resseliella* sp.)	11.0 ± 3.4	6.5 ± 1.5	33.0
Morphospecies 6 (Diptera: unidentified)	1.4 ± 0.2	1.2 ± 0.7	33.0
Morphospecies 7 (Coleoptera: *Curculio* sp.)	4.5 ± 1.4	4.4 ± 1.2	27.0
Other morphospecies[d]	1.1 ± 0.7	1.5 ± 1.2	29.0

[a] All test values were not significant at $\alpha = 0.05$.
[b] Occasionally, a single acorn supported the attack of more than one morphospecies. Thus, adding the proportion of acorns attacked by insects may result in a higher value than the total proportion of acorns damaged by insects.
[c] Includes acorns chewed or partially eaten by mammals, broken, mouldy, malformed, black instead of green or with abnormal cup.
[d] Includes morphospecies 8 (Coleoptera, *Conotrachelus* sp.), morphospecies 9 (Lepidoptera, unidentified), and morphospecies 10–12 (Diptera, unidentified).

evidence of internal damage) was similar in shelterwood harvest and control plots (Table 2). Similarly, the proportions of acorns in the other internal damage classes were not significantly different between the harvest treatments. The primary signs of internal damage included insect damage (frass, galls, galleries), and blackened or collapsed cotyledons. The proportion of damaged cotyledons did not vary ($F_{1,24} = 0.004$, $P > 0.5$) between the shelterwood and control treatments; however, there was a difference in the proportion of acorns showing different levels of cotyledon damage: most acorns had more than 75% of the cotyledon damaged followed by healthy and moderately damaged acorns ($F_{2,24} = 20.297$, $P < 0.001$) (Fig. 2). There was no treatment-damage interaction ($F_{2,24} = 1.296$, $P > 0.2$).

The proportion of acorns hosting insects did not differ among shelterwood-treated and control plots in the first year of acorn production. Approximately 49% and 45% of the collected acorns hosted insects in harvested and control plots, respectively. Insects found in acorns were at the larval stage and included morphospecies of Diptera (seven, two of which belong to the genus *Resseliella*), Hymenoptera (cynipid wasps, pip gall and stone gall), Coleoptera (*Curculio* sp. and *Conotrachelus* sp.), and Lepidoptera (Table 2). Most acorns were being exploited by a single morphospecies, but a low proportion hosted from 2 to 6 insect morphospecies ($16.4 \pm 2.8\%$ and

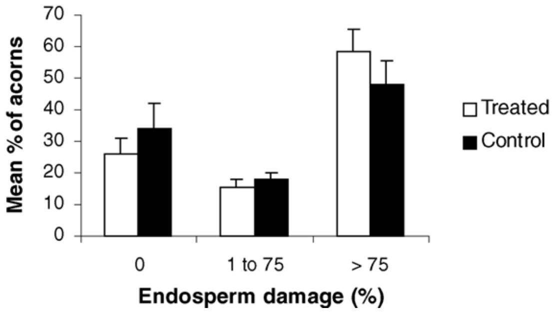

Fig. 2. Mean percentage of acorns with different levels of cotyledon damage in five treated plots (shelterwood harvest) and five control plots of a deciduous forest in central Ontario (Canada) during August–November 1996.

$15.1 \pm 2.8\%$ in treated and control plots, respectively). There was no evidence that the proportion of acorns being infested by the different insect morphospecies was affected by the treatment (Table 2).

3.3. Treatment effect on mammalian predation of acorns

Six mammal species were caught in the control plots and four in the harvested plots. *Peromyscus maniculatus* (deer mouse) and *Clethrionomys gapperi* (red-backed vole) were the most common species in both harvested and control plots (Table 3). There was no treatment effect on the total abundance of small mammals ($t = 1.04$, $P > 0.3$), and the abundance of *P. maniculatus* ($t = 1.91$, $P > 0.1$) and *C. gapperi* ($t = 0.76$, $P > 0.4$).

Acorn predation by mammals was not affected by the shelterwood treatment. The mean number of acorns removed from open cages (Mann–Whitney, $W = 28.0$, $P > 0.5$), cages with large entrances ($W = 27.0$, $P > 0.5$) and cages with small entrances ($W = 29.0$, $P > 0.5$) was similar between treated and control plots during the fall (Fig. 3a) and the fall-spring (open cages: $W = 31.0$, $P > 0.5$; cages with large entrances: $W = 30.0$, $P > 0.6$; cages with small entrances: 31.0, $P > 0.5$) (Fig. 3b). Thus, data were pooled for further analyses.

Squirrels and chipmunks were the primary predators responsible for the removal of acorns from exclosure cages, and acorn predation by vertebrates larger than squirrels was negligible. The number of acorns removed differed among cage types (fall: $S = 12.60$, $P < 0.002$; winter–spring: $S = 16.80$, $P < 0.001$) (Table 4). Thus, a similar number of acorns were taken from open trays (accessible to all vertebrate predators) and cages with large openings

Table 3
Number of small mammals caught in 100 trap nights in treated (shelterwood harvest) and control plots of a deciduous forest in central Ontario

Plots	*Clethrionomys gapperi* (red-backed vole)	*Peromyscus maniculatus* (deer mouse)	Others[a]	Total
Treated				
1	0.5	4.5	0	5.0
2	1.0	3.0	0.5	4.5
3	6.0	4.5	0.5	11.0
4	7.0	4.5	0	11.5
5	1.5	4.0	1.0	6.5
Control				
1	1.0	4.0	0.5	5.5
2	1.0	3.0	1.0	5.0
3	3.0	2.5	1.5	7.0
4	2.5	4.0	0.5	7.0
5	3.0	3.0	0	6.0

Trap effort was 200 trap nights per plot.
[a] Includes *Tamias striatu* (Eastern chipmunk), *Zapus hudsonian* (Jumping mouse), *Blarina brevicauda* (Short-tailed shrew), and *Sorex cinereus* (Masked shrew).

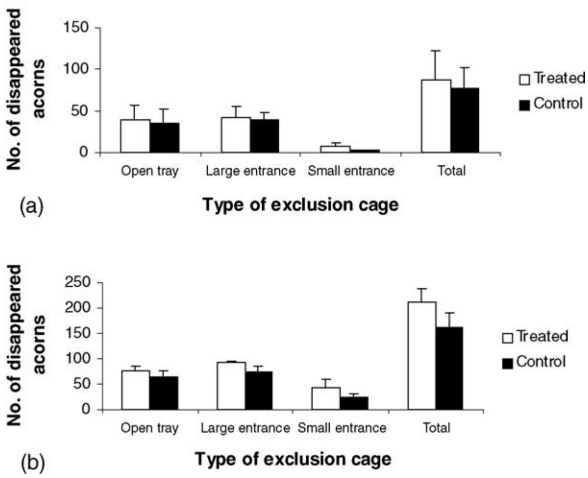

Fig. 3. Mean number of acorns removed from exclosures in five treated (shelterwood harvest) and five control plots of a deciduous forests in central Ontario (Canada) during the fall of 1996 (a), and the winter 1996–spring 1997 (b). Open trays allowed access to all predators, cages with large entrances (7 cm × 7 cm) excluded large mammals and cages with small entrances (2.5 cm × 2.5 cm) excluded large mammals, squirrels and chipmunks.

Table 4
Percentage of red oak acorns removed from exclusion cages

Predators that access cages	Type of exclosure	Fall 1996	Winter–spring 1997	Total
All vertebrates	Open tray (OT)	37.5	33.5	71.0
Squirrels + mice	Large openings (LO)	41.3	42.0	83.3
Mice	Small openings (SO)	6.3	26.9	33.2
Squirrels	LO − SO	35.0	15.1	50.1
Larger vertebrates	OT − LO	–	–	–

(excluded mid- and large vertebrates), showing no predation by animals larger than squirrels. More acorns were taken from cages with large openings (accessible to squirrels and mice) than from those having small openings (accessible to mice alone), indicating that squirrels removed a higher proportion of acorns than mice. Acorn removal from cages with large openings occurred primarily during the fall, whereas that in cages with small openings occurred during the winter–spring (Table 4). A similar number of acorns were taken from exclosures during the fall 1996 and the winter–spring 1997 from both open trays and cages with large openings, but more acorns were removed during the winter–spring than in the previous fall from cages that provided access only to mice ($\chi^2 = 14.096$, $P < 0.001$).

4. Discussion

4.1. Acorn production

Acorn production varied considerably (i.e., from no seed crop to mast production) over the 4-year period that acorn development was monitored. Acorn production by red oaks is known to be cyclical and to have pronounced year-to-year fluctuations (Downs and McQuilken, 1944; Sork et al., 1993; Healy, 2002). An average production of 3232 acorns per tree is considered a maximum yield for forest-grown red oak trees during mast production years (Downs and McQuilken, 1944; Sork et al., 1993). Our oaks yielded an average of 2583 acorns/tree (based on acorn production and number of oaks per plot) in 1996, which is close to the reported maximum yields. Acorn production in 1997 (average 772 acorns/tree) was typical of moderate nut yields for red oaks throughout North America (Downs, 1944; Sork et al., 1993).

The two techniques used to estimate acorn abundance led to different conclusions as to the influence of the shelterwood treatment on acorn production. The visual ratings suggested that trees in the harvested plots had significantly higher acorn production ratings than trees in control plots whereas trap counts indicated no influence of treatment on acorn production. Many factors may have contributed, either individually or in combination, to this difference of conclusion between assessment methods. One possibility is that the rates of arboreal acorn removal by animals (i.e., prior to or during acorn drop, but after visual assessment), which in some years can be important (Koenig et al., 1994; Johnson et al., 2002), may have been higher in treated than in untreated plots, thus leading to a higher abundance in treated at the time of visual rating but to equal abundance at the end of trap counts. Squirrels were observed often taking acorns from trees during our bi-weekly visits to empty acorn traps, and likely contributed to lower estimates of acorn production, especially in 1997, however, there is no evidence of differential activity between treated and untreated plots. Another possibility is that a differential trap placement in relation to the productive portion of the crown may have inadvertently occurred resulting in lower trap counts (than projected by the visual ratings) in treated than in untreated plots; but again there is no such evidence. One of the four circumstances in which Koenig et al. (1994) envisioned traps might be preferable to visual surveys was in stands with complete canopy closure, because under such conditions it is difficult to discriminate the crown of individual trees. This would be especially true in a mixed stand with dominant and co-dominant trees. Our visual ratings in control plots were often based on an examination of a small portion of the crown (some of which may not have been representative of the productivity of the tree) because of the restrictive view offered by the lower canopy. Ratings in treated plots, however, were established in almost all cases on a complete examination of the crown, thus, possibly leading to an underestimation of the acorn crop size in untreated plots compared to treated plots.

Typically, the shelterwood harvest reduced overstory canopy cover and increased crown exposure to direct light of individual oaks that were left after harvest. This may have promoted acorn production because the amount of direct sunlight has been correlated with increased acorn production in the exposed portions of the crown (Verme, 1953). Although individual variations in acorn production occur, trees with open-grown canopies usually produce larger acorn crops per unit of crown area than smaller crowned trees of similar age growing in shaded stands (Gysel, 1957). In our study, however, crown cover explained a low proportion of the variation in acorn production, based on acorn trap count data. In the southern Appalachians, Greenberg and Parresol (2002) found that acorn production per unit of crown area increased with increasing tree basal area in five oak species including red oak, and that basal area and crown area were highly and positively correlated. Red oak trees with DBH $\leq$ 25 cm produced significantly fewer acorns per m^2 of basal area than larger diameter trees (Greenberg, 2000), but acorn production tapered off when diameters exceeded 76 cm. Others have also noted increasing acorn production with increasing diameter up to a threshold size, beyond which production declines (Downs and McQuilken, 1944; Goodrum et al., 1971). In forest stands, maintaining stocking at the B-level should provide for full site utilization by overstory trees and give maximum growing space for oak crowns (Gingrich, 1967; Sampson, 1983).

We expected that acorn production would be higher in the shelterwood harvest plots than in the control plots because the crowns had been released and given more exposure to direct sunlight (Goodrum et al., 1971; Johnson, 1994; Dey, 1995; Healy, 2002). However, there was also little difference in crown area per tree between harvested and control plots. The period of time between the shelterwood harvest (1994) and the first notable acorn crop (1996) may have been too short for the oaks to respond by increasing their leaf area, foliage biomass, amount of fine branching and crown volume, and may have thus contributed to the weak relationship between crown area and acorn production. Younger, well-formed co-dominant or dominant oaks respond the most to thinning (Johnson et al., 2002). Small-crowned, older trees released from dense stands typically show delayed growth responses to thinning. The oaks in our study were forest grown all their lives, which ranged from 68 to 179 years. In contrast, Healy (1997) reported early benefits in acorn production by thinning younger (i.e., 40-years old) red oak stands, as acorn production in individual trees increased within 6 years following thinning. If we compare the actual crown area of our study oaks with the maximum crown area they may achieve in open-grown conditions, which are computed using the B-level stocking equation for red oak (Sampson, 1983), the forest-grown oak crowns were at 56.7% of their maximum crown area on the shelterwood plots, whereas oak crowns on control plots were 80.9% of their maximum potential. Individual tree crowns on the control plots were closer to achieving their maximum potential than those on the shelterwood. This difference in crown development may be an artefact of different disturbance histories and stand dynamics over the past 60 years or more, and it could be confounding harvest treatment effects on acorn production. In addition, Healy (1997) reported that differences in acorn production in thinned and uncut red oak stands were less evident in years of good acorn production. In our study, we measured acorn production in years that were considered to be good to bumper crop by most standards.

4.2. Insect and mammal predation on acorns

The impact of acorn predation varies with the size of acorn crops, with insects consuming higher proportions of the acorn crop in years of low to moderate production (Sork, 1984; Galford et al., 1988). Our study was conducted in a year of high acorn production. Thus, our results represent predation impacts when production is more likely to exceed losses to predation.

Insects attacking acorns destroyed most of the cotyledon tissue. We found that most of the insect-infested acorns lost more than 75% of their cotyledon. Damage to the cotyledon, however, may not always result in reduced viability, especially if the embryonic axis is undamaged, but the vigour is often decreased (Branco et al., 2002). Germination experiments revealed similar germination frequencies between partially consumed acorns and undamaged acorns, and a preference by mammals and insects to feed upon the basal rather than the apical portion of the acorn (Steele et al., 1993).

Overstory manipulations change microenvironment conditions such as surface soil temperature, soil moisture and atmospheric conditions (Dey and MacDonald, 2001), which may influence insect development and abundance, and thus insect damage to acorns. In our study, a reduction of 50% of the overstory in the harvested plots resulted in increased light intensity from pre-harvest levels of 1% to 35%, and increased surface soil temperature and daily variations compared to control plots (Dey and Parker, 1996). We found no difference between harvested and control plots in the proportion of acorns showing external or internal damage by insects. Similarly, Healy (1997) found no difference in the proportion of sound to unsound acorns in thinned and uncut red oak stands in Massachusetts.

We found that 75% and 66% of the acorns were internally damaged in harvested and control plots, respectively. Collapsed cotyledons (27% and 18% of the acorns in harvested and control plots, respectively) usually occurred in immature acorns where the acorn cap completely enclosed the nut, and we were unable to determine the causes. Most of the blackened cotyledons were associated with the presence of pip galls. Thus, 47% and 48% of the damage to red oak acorns could be attributed to insects in harvested and control plots, respectively. These values are consistent with the 46% reported by Marquis et al. (1976) in a site with high acorn production in Pennsylvania, the 41–61% found by Christisen and Kearby (1984) in Missouri, the 38% estimated by Gysel (1957) in Michigan, and the 52% average reported by Gibson (1982) for several years and localities in North America. Primary causes of damage by insects to red oak acorns (insect galls, acorn weevils of the genus *Curculio*, and acorn moths) were the same as those previously reported (Gibson, 1982; Kearby et al., 1986; Johnson et al., 2002). We recorded a low proportion of malformed acorns (3–6%), as was found by Christisen and Kearby (1984) (6%) and Gibson (1982) (4–8%).

Although acorn predation by vertebrates may vary with vegetation type (Leiva and Fernández-Alés, 2003) and habitat conditions (Fuchs et al., 2000), we found no harvest treatment effect on acorn predation by mammals. Many birds and mammals feed on acorns, and some of them play a key role in seed dispersal (Jensen and Nielsen, 1986). We estimated that squirrels and chipmunks took 50% and mice 33% of the acorns during the winter–spring, but we do not know whether these acorns were eaten or cached. Based on open trays, 37.5% of the red oak acorns were taken by vertebrate predators during the fall. Because the number of acorns removed from open trays was similar to that removed from cages with large entrances, we concluded that squirrels and chipmunks were the primary consumers of acorns during our study. Results from using partial and complete exclosures showed high loss of acorns to ungulates and especially to small mammals in Spain (Gómez et al., 2003; Leiva and Fernández-Alés, 2003).

4.3. Management implications

We found contrasting results regarding the effects of the shelterwood harvesting on acorn production, where a larger production was recorded in harvested than in control plots according to the crown survey but no significant difference was found based on the acorn trap counts. Detecting differences in acorn production in good seed crop years is difficult and may require a longer-term data set than most researchers are able to collect. High variation in annual acorn production and limited number of observed seed years often masks the effects of thinning on acorn production. Initial shelterwood cuts that reduce stand stocking to enhance acorn production will not likely significantly increase the number of acorns that survive predators, and thus are available to produce seedlings in the short-term.

Thinning or shelterwood harvesting in older stands may be less likely to increase acorn production because of lower tree vigour and growth potential related to senescence in mature trees. A more serious reality is that stand acorn production is reduced after harvesting because the better acorn producing trees were removed in the operation. Care must be taken not to remove the good acorn producers during the shelterwood harvest. Healy et al. (1999) and Healy (2002) have presented recommendations for identifying good acorn producers before conducting a thinning or shelterwood harvest.

There is growing interest in long-term retention of a low to moderately dense overstory and the creation of two-aged or multi-layered stands. Thinning that reduces the amount of oak crown in the overstory or that indiscriminately removes the inherently good producers can reduce stand production. If the good acorn producers are left after thinning, then stand density and harvesting are less likely to reduce stand acorn production (Healy, 2002). Use of the shelterwood method in conjunction with leaving the best acorn producers can be used to create the desired stand structure while maintaining or increasing acorn production and oak regeneration potential in the stand. We found that insect and mammalian predators took a large proportion of the acorn crop, but found no evidence that the shelterwood method to regenerate oak forests influenced the predation of red oak acorns by insects or mammals.

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