

The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* marsh.)

I. Direct effect on pollen, ovule, and seed production

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Summary. Canada yew (*Taxus canadensis*) populations currently browsed by white-tailed deer (*Odocoileus virginianus*) or browsed by deer in the past had significantly lower production of male strobili, female strobili, and seeds than unbrowsed yew populations. Exclosure studies showed that protected yews produced significantly more male and female strobili than unprotected yews, but only after several years of protection. Seed production did not respond as readily to protection from deer perhaps because of reduced pollination levels in browsed yew populations. Previously unbrowsed yews were clipped at different levels of removal of available browse (control (no removal), 25%, 50%, 75%, and 100% removal) to simulate deer browsing. Reduction in male strobilus production was linearly related to clipping intensity in three years of observation. Female strobilus production was significantly reduced only at the 100% level of removal. Intermediate levels of clipping may have even stimulated production of female strobili. Analysis of covariance, with previous year's branch production as the covariate, showed no significant effect of clipping on male strobilus production except in the 100% removal group. Female strobilus production showed no such covariance with branch production. Effects of clipping on seed production could not be reliably assessed in 1984 and 1985 due to low seed production. Seed production in 1986 was significantly reduced only in the 100% removal group. Field observations of deer browsing of Canada yew indicate that 100% levels of removal are typical of natural levels of browsing.

Key words: Herbivory – *Odocoileus* – Sexual reproduction – *Taxus* – Woody plant

(*Odocoileus virginianus* Rafinesque) and moose (*Alces alces*) on vegetative growth and density of plants (De Boer 1947; Aldous 1952; Krefting and Stoeckeler 1953; Graham 1958; Beals et al. 1960; Ross et al. 1970; Marquis 1974; Anderson and Loucks 1979), but few studies have examined the effect of vertebrate herbivores on plant sexual reproduction. This reflects the bias of researchers interested in woody plants that have silvicultural importance or have importance for game animals. The relationship between plant fitness and the negative effects of herbivory on vegetative growth are not clearly known.

The few studies on vertebrate herbivore impact on sexual reproduction have shown different results. Edwards (1985) recorded reduced seed production of *Aralia nudicaulis* plants browsed by moose while Katsma and Rusch (1980) found compensation in fruit production of apple tree branches subjected to simulated browsing. Paige and Whitham (1987) measured increased fruit and seed production of browsed *Ipomopsis aggregata* relative to unbrowsed plants.

In this paper I describe the effects of deer browsing on the reproductive effort of Canada yew (*Taxus canadensis* Marsh.). Reproductive effort was estimated as the production of male strobili, female strobili, and seeds. I compared reproductive effort in browsed and unbrowsed populations of yew, recorded changes in reproductive effort over time in chronically browsed yews protected from deer browsing, and measured the effect of simulated browsing (by clipping) on the reproductive effort of previously unbrowsed yews. Because of the difference in browsing history of yews used in the latter two experiments, the effects of these different treatments on changes in yew reproductive effort may be qualitatively different.

Numerous studies have demonstrated the negative impact of vertebrate herbivores, such as white-tailed deer

Study organism

Canada yew is a monoecious, evergreen, coniferous shrub of the mixed conifer-hardwood forests of north-eastern United States and southeastern Canada. Yew

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is a highly preferred winter browse of white-tailed deer, and the abundance of yew throughout its range has been severely reduced by heavy deer browsing during the mid-20th century (Spiker 1935; Braun 1950; Stearns 1951; Curtis 1959; Beals et al. 1960; Martell 1974).

Reproductive effort in Canada yew is readily estimated by counting male and female strobili and seeds. Male "flowers" (or strobili) are excellent indicators of pollen production by individual yew plants (Allison 1987). Female strobili are uniovulate and after fertilization produce a stony seed that is surrounded by a red, fleshy, aril-like structure. There is a slight, but non-significant, tendency for female strobili to be located on branches closer to the shoot apex than male strobili (Allison, TD, unpublished data).

Canada yew individuals reproduce vegetatively by layering when their arching branches are pressed to the ground surface and take root. Side branches, growing in different directions than that of the main stem axis, cause the plant to spread along the forest floor. Connections between the rooted branches can be traced under the litter layer, but eventually these connections rot. In low density populations individual plants, or genets, consisting of one or more branches are readily distinguished. In high density populations the genetic relatedness of neighboring plants, or more appropriately, shoot systems, is difficult to determine due to this layering. In this study, I defined a yew plant as a stem or shoot system emanating from the forest litter. Each plant consisted of one to four major branches which diverged from one another just above the litter. In low density populations, a plant represented the entire genet. In high density populations, a plant constituted an unknown proportion of a genet.

Study site

The majority of observations and experiments on Canada yew reproduction were made at the Apostle Islands National Lakeshore, Wisconsin, USA (46°50' N latitude, 90°45' W longitude; hereafter referred to as Islands). The Islands comprise a 21-island archipelago off the southwest shore of Lake Superior. The Islands are edaphically similar; soils have developed from lacustrine deposits and glacial till derived from Lake Superior sandstone (Brander 1983). Deer populations began to increase on several of the Islands in the mid-1940's and peaked in the mid-1950's (Brander 1983). Aerial observations showed deer population densities varied considerably among the Islands (Fig. 1). Some of the Islands had dense populations while others had few deer or none at all. Deer populations declined in the mid-1960's and early 1970's and went extinct on many of the Islands. At present deer are found on two of the Islands (TD Allison, unpublished work).

I sampled Canada yew on four islands that had different deer histories: Basswood Island; Rocky Island; Otter Island; and Outer Island. I chose these four islands because they supported similar vegetation, but had different deer histories. Basswood Island, for example, still has deer and yews on this island show sign of chronic,

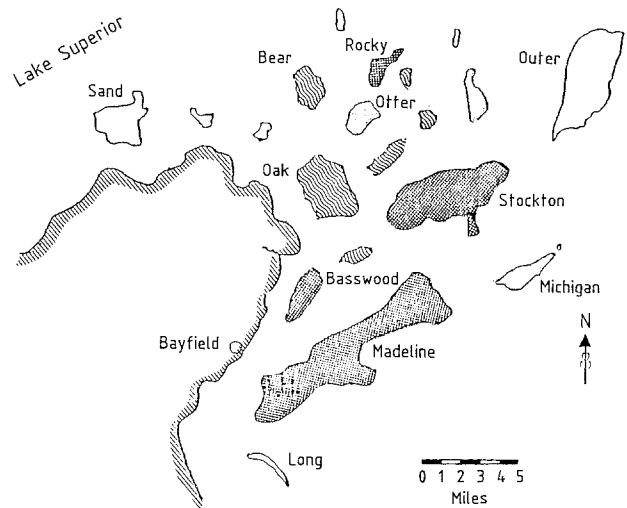


Fig. 1. Apostle Islands National Lakeshore and estimated deer densities of the Islands during the mid-1950's. Estimates are based on Beals et al. (1960) and Brander (1983). □ None; ▒ Low; ▓ Medium; ■ High

Table 1. Area, location, and deer history of Apostle Islands study sites. Number in parentheses refers to the area of the study population. Populations are listed in order of assumed deer impact (highest to lowest)

Site	Area (ha)	UTM coordinates	Deer history
Basswood Island	767 (2.3)	673 700 mE/5192 500 mN	Moderate deer density in 1950's. A few deer still on the island.
Rocky Island	440 (1.5)	676 500 mE/5211 000 mN	High deer density in the 1950's. Deer are no longer present on the island.
Stockton Island	4070 (3.0)	686 700 mE/5198 100 mN	High deer population in the 1950's. Deer currently absent.
Otter Island	533 (1.0)	675 100 mE/5206 000 mN	Low deer densities in 1950's. Deer no longer present.
Outer Island	3200 (1.4)	695 500 mE/5216 600 mN	No deer observed during major herd build-up of the 1950's. No deer currently present.

heavy browsing. The other three islands no longer have deer or never had deer. They range in past deer impact from high (Rocky) to low (Otter) to none (Outer). To minimize variation due to local differences in vegetation, soils, and microclimate, study populations on these islands were located in *Acer saccharum*-*Betula lutea* for-

ests approximately 20 m from the shoreline. Specific information on each island's deer history is listed in Table 1.

Methods

Comparison of browsed and unbrowsed populations

In Spring 1983, I systematically located transects in the study population on each island. Sampling points were established at 10 m intervals along these transects and the yew plant (as defined earlier) nearest each point was selected for study. I established enough transects to sample a minimum of 50 plants in each island population. In all, five transects were established on Outer Island, six on Rocky Island, seven on Otter Island, and ten on Basswood.

In 1983, 1984, and 1985, I counted the number of male strobili, female strobili, and seeds produced on all sample plants. I determined the number of branches for each plant sampled on the four islands and calculated means of male strobilus, female strobilus, and seed production on a per branch basis for each island population. Male and female strobilus production data were $\log_{10}(Y+1)$ transformed prior to analysis by ANOVA; seed production data were analyzed by non-parametric Mann-Whitney U tests (Sokal and Rohlf 1981).

Because size influences reproductive effort in Canada yew (Allison 1987) and deer may influence plant size, I measured the basal diameter of each plant. Two measures of the diameter were taken at right angles to each other with calipers, and I averaged them to obtain the stem diameter.

Exclosure studies

On Basswood Island (deer present) in Fall 1983, 46 plants were paired on the basis of their size and Spring 1983 production of strobili. I then randomly assigned one member of each pair to treatment (fenced) or control (unfenced) for a total of 23 pairs. Plants were fenced individually with four-foot wire mesh fence having a 2" × 3" mesh size. Individual exclosures ranged in diameter depending on the diameter of the plant, but generally were twice the diameter of enclosed plants. I measured strobilus and seed production of all plants in 1984, 1985, and 1986. Strobilus production only was recorded in 1987 and 1988.

An exclosure study also was started at Cedar Creek Natural History Area, East Bethel, Minnesota, USA in fall 1981. A single 10 m × 40 m exclosure was constructed of six-foot wire mesh fence to protect a portion of a Canada yew population. Individual yew plants inside and outside the exclosure were randomly selected, and male and female strobilus production and seed production were counted for each plant from 1982 to 1987. Although there was no replication of treatment, the results from this study formed a useful adjunct to the exclosure study on Basswood Island. In particular, the accessibility of Cedar Creek during winter enabled me to make observations on the pattern of winter deer browsing.

Browse simulation experiment

I simulated browsing by clipping previously unbrowsed yews on Stockton Island (Fig. 1; Table 1). I chose this site because yews were widely spaced, and I could apply clipping treatments to entire genets.

As reproductive effort in Canada yew varies significantly with plant size (Allison 1987), I first selected 50 plants each having a minimum of three major branches, one of which was at least one m in length. I further subdivided these plants by grouping them in five size-based blocks, each block consisting of ten plants similar in stem length and/or having a similar number of branches. Five clipping treatments were then randomly assigned to plants within

each block; there were two replicates per treatment per block. Treatment levels were control (no clipping), 25%, 50%, 75%, and 100% removal of available browse. The latter was defined as all twigs with a diameter <3 mm. This diameter was chosen on the basis of my field observations of deer browsing and the literature (King 1975). In browse classes with less than 100% removal, I randomly clipped branches until the designated amount of browse was removed. Plants were clipped once in Fall 1983 and allowed to regrow without further clipping. I recorded strobilus and seed production in 1984, 1985, and 1986.

Results of strobilus and seed counts were analyzed using SPSS MANOVA (Hull and Nie 1981) and repeated measures analysis of variance (Winer 1971) in a randomized complete block design. Data for the control, 25%, 50% removal, and 75% removal groups were square root transformed prior to analysis. The variance of the 100% removal group was unequal to the other treatment groups, despite transformation. Consequently, it was not included in the statistical analysis, but was compared to the other treatment means by non-parametric tests.

In 1985, I estimated pollination levels (proportion of ovules pollinated) of treatment plants in 1985. Pollinated ovules were swollen and green and easily distinguished from unpollinated ovules which were yellow and unchanged in size. Proportions were arc-sine transformed prior to MANOVA.

Results

Comparison of browsed and unbrowsed populations

Male strobilus production was significantly greater on Outer Island than the other three islands in all years (Table 2). Female strobilus, or ovule, production on Outer Island and Otter Islands was significantly greater than Rocky or Basswood Islands in all years. Basswood and Rocky Island ovule production were not significantly different according to Tukey's Honest Significant Difference (Snedecor and Cochran 1967). Numbers of seeds

Table 2. Mean male and female strobilus production, and seed production per branch for different populations of the Apostle Islands. Superscripts indicate islands that differ significantly at $P < 0.05$. Analyses of data were based on $\log_{10}(Y+1)$ transformed data. Arithmetic means are presented for ease of interpretation. Standard errors of the untransformed means are listed in parentheses

Island	n^1	Male strobili	Female strobili	# seeds
1983				
Outer	50	87.3 (23.3) ^a	5.6 (1.0) ^a	2.5 (0.5) ^a
Otter	55	16.9 (4.0) ^b	4.8 (2.2) ^a	1.1 (0.3) ^b
Rocky	54	10.7 (5.3) ^c	0.8 (0.4) ^b	0.2 (0.1) ^c
Basswood	50	1.6 (0.7) ^d	0.04 (0.02) ^c	0
1984				
Outer	50	113.6 (30.8) ^a	9.2 (2.0) ^a	3.6 (0.8) ^a
Otter	54	22.9 (5.4) ^b	5.7 (1.2) ^a	2.0 (0.5) ^a
Rocky	54	22.6 (10.5) ^b	1.7 (0.8) ^b	0.6 (0.3) ^b
Basswood	51	2.8 (0.9) ^c	1.4 (0.4) ^b	0.2 (0.1) ^b
1985				
Outer	92	77.2 (15.1) ^a	9.9 (2.4) ^a	3.9 (1.0) ^a
Otter	57	10.7 (2.2) ^b	5.3 (1.0) ^a	2.9 (0.7) ^a
Rocky	97	12.3 (5.1) ^b	0.8 (0.3) ^b	0.1 (0.1) ^b
Basswood	50	0.6 (0.2) ^c	0.3 (0.1) ^b	0.04 (0.03) ^b

¹ n = number of plants sampled

produced in the different populations showed a trend nearly identical to that of ovule production except that significantly more seeds were produced on Outer Island than Otter in 1983 and Basswood Island yews produced no seeds in that year. In general, there is a linear decreasing trend in the production of male strobili, ovules, and seeds and the hypothesized increasing level of deer impact.

Mean basal diameter of yews on Outer Island was greater than that of the other 3 islands; I found no differences in basal diameter among Rocky, Otter, and Basswood Islands. Previous analysis indicated that basal diameter was consistently the best predictor of male strobilus production for unbrowsed yews (e.g., $R^2=0.83$ for Rocky Island; Allison 1987). On Basswood Island, however, basal diameter had no significant relationship with male strobilus production ($R^2=0$).

Exclosure experiments

Repeated measures analysis (Winer 1971) of male and female strobilus production on Basswood Island showed a significant effect of exclusion on both male ($P<0.02$) and female strobilus production ($P=0.01$) and a significant treatment by year interaction ($P<0.001$ for male strobilus production; $P<0.05$ for female strobilus production). There was a significant year effect on male strobilus production, but no such effect on female strobilus production (Fig. 2). These results are qualitatively similar to those observed at Cedar Creek. At the latter site, there was a significant treatment by year interaction for both male and female strobilus production ($P<$

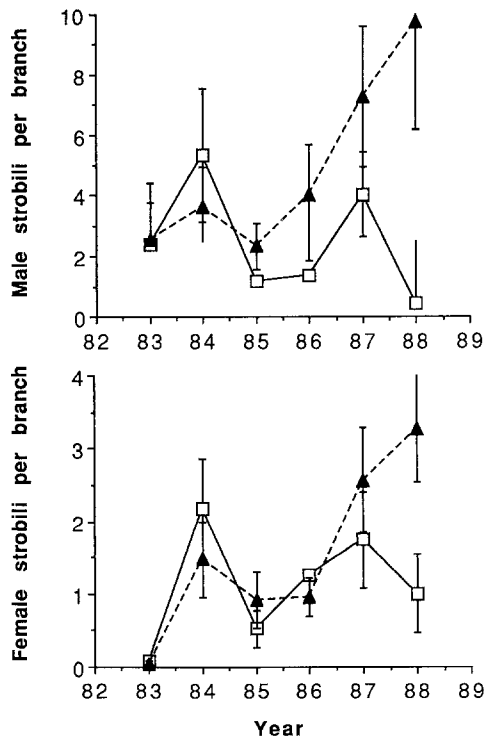


Fig. 2. Male and female strobilus production versus time of protected and unprotected yews at Basswood Island. Plotted values are arithmetic means that were transformed prior to ANOVA (see text). Error bars are one standard error. Note differences in the scale of the "Y" axis in male and female strobilus plots. —□— control; —▲— protected

0.001). For within year comparisons at Cedar Creek, male and female strobilus production were first significantly higher in protected yews beginning in 1985 – the fourth year of deer exclusion. There was no significant difference in strobilus production between fenced and unfenced yews at Cedar Creek when averaged over the five years of the experiment ($P=0.51$ for male strobili; $P=0.24$ for female strobili).

Seed production at Basswood and Cedar Creek was low in protected and unprotected yews in all years measured and, therefore, treatment effects could not be assessed reliably. I do not have seed production data from Basswood Island for 1987 or 1988; the latter year is the first year that male and female strobilus production levels were significantly higher in protected yews. At Cedar Creek protected plants produced 20 seeds in 1985 – greater than the total of all sample plants at Cedar Creek (protected and unprotected) in the three previous years combined.

Browse simulation experiment

With the exception of the 25% removal group, male strobilus production in all treatment groups was significantly lower than the control group in all three years. The 25% removal group was greater than the control group in 1986 although this difference was not significantly different (Fig. 3a). Repeated measures ANOVA of control, 25%, 50% and 75% removal groups showed that male strobilus production changed significantly over the 3 years ($P<0.001$), but there was no significant treatment by year interaction ($P=0.11$). The latter result suggests that clipping did not affect the response of plants to the effects of different years. Male strobilus production of the 100% removal group was significantly lower than all treatment groups in all years ($P<0.001$).

Ovule production did not differ significantly among

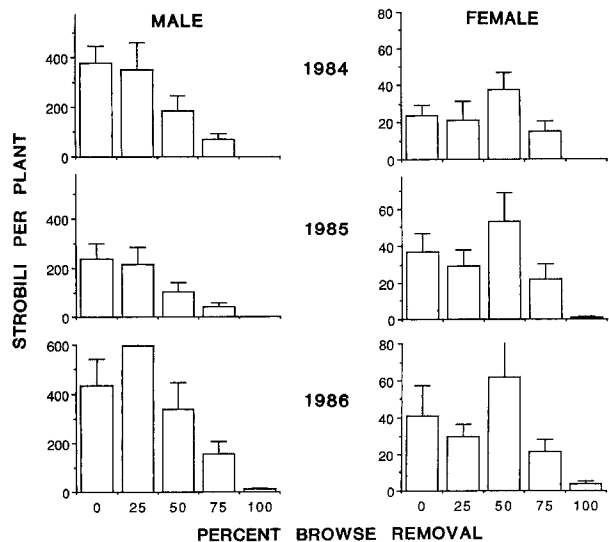


Fig. 3. Male and female strobilus production by treatment and year for the browse simulation experiment. Values graphed are arithmetic means that were transformed prior to MANOVA (see text). Error bars are one standard error based on within treatment standard deviations. Data were analyzed according to MANOVA according to a randomized complete block design. Blocks were constructed as described in Methods

Table 3. 1984 seed set (seed production as a proportion of ovules produced), 1985 pollination success (percent ovules pollinated), and 1986 seed production and seed set by treatment of yews in browse simulation study. 1985 and 1986 percentage data were arc-sin transformed prior to MANOVA. Means shown here are back-transformed for ease of interpretation. Treatments with different superscripts are significantly different at $P < 0.05$

Treatment	<i>n</i>	1984 Seed set*	1985 Percent pollinated**	1986 Seeds/Plant	1986 Seed set***
Control	10	0.167 (234) ^a	65.4 (41.9–85.5) ¹	14.2 ^a (6.2–26.6) ¹	28.2 (14.5–44.5) ¹
25% Removal	9	0.037 (191) ^b	46.1 (23.7–69.4)	10.5 ^a (5.5–17.9)	23.8 (5.7–50.5)
50% Removal	10	0.045 (377) ^b	64.0 (40.5–84.4)	13.6 ^a (7.5–22.1)	23.8 (9.9–40.5)
75% Removal	9	0 (136) ^c	47.4 (24.8–70.5)	7.6 ^{ab} (3.7–14.0)	23.0 (2.9–53.5)
100% Removal	8	0 (1)	n/a	4.6 ^b (3.2–6.7)	18.9 (0–68.0)

* $G(\text{adj.}) = 51.7$; $P < 0.005$; total ovules produced is listed in parentheses

** $P = 0.39$ of MANOVA

*** $P = 0.88$ of MANOVA

¹ 95% confidence range

those treatments analyzed (repeated measures ANOVA; $P = 0.07$). The trend in ovule production strongly suggests that it was not depressed at intermediate levels of clipping; only the 100% removal group showed significantly reduced ovule production (Fig. 3b). There was no significant year effect ($P = 0.13$) or treatment by year interaction ($P = 0.79$) in ovule production.

Seed production was highly variable among years on Stockton, making analyses of differences in seed production among treatments unreliable. Few seeds were produced in 1984 and 1985. I summed 1984 seed production of all plants within treatment groups and compared by the G-test (Sokal and Rohlf 1981) the proportion of seeds produced versus ovules produced (Table 3). Control plants ripened a significantly greater proportion of seeds than the 25% and 50% removal groups. The 75% removal group produced no seeds. The 100% removal group was not included in the analysis because only one ovule was produced.

There were no significant differences among treatments in 1985 pollination levels ($P = 0.39$; Table 3); the 100% removal group was not included in the analysis as it produced very few ovules in that year. Essentially no ripe seeds were produced by all plants in 1985. Predation on developing seeds may have been responsible for the failure of this seed crop (Allison, TD, personal observation).

In 1986, seed production in all plants was considerably higher. The 100% removal group produced significantly fewer seeds than all other treatment groups with the exception of the 75% removal group (Table 3). No other comparisons among treatment groups were significantly different. There were no differences among treatments in percent seed set (number of seeds produced per ovule).

Assuming strobilus buds are distributed evenly on the plant, 50% removal of the available browse over the winter, should decrease strobilus production an average of 50% the following spring. I performed t-tests to determine if the Spring 1984 census of strobilus production of clipped plants differed significantly from expected results given a certain rate of removal in Fall 1983. For example, the 1984 mean of the 25% removal group (observed production) was compared to the 1984 mean of the product of {control group samples $X(1-0.25)$ } (expected production) by the student t-test.

Expected 1984 levels of male strobilus production did not differ significantly from observed 1984 levels for any treatment. For female strobilus production, the results of the Spring 1984 census were significantly different from expected production for all treatments ($P < 0.05$) except for the 100% treatment group.

Male strobilus production and branch production of the previous year are significantly correlated on Stockton Island ($r = 0.97$), and clipping significantly reduced the number of branches produced in 1984 ($P < 0.001$). Analysis of covariance showed no significant effect of clipping on 1985 male strobilus production when adjusted for 1984 branch production, except in the 100% removal group. No significant covariance relationship was observed between ovule production and the previous year's branch production of treatment plants.

I had measured male and female strobilus production of 20 plants in Spring 1983 prior to clipping (four plants in each treatment group). In Spring 1987, I measured the strobilus production of these plants in control and 100% removal groups. Male strobilus production of the four control plants sampled in 1983 had increased an average of 22% by 1987; female strobilus production increased over 350%. In the 100% removal group, male strobilus production was 83% lower in 1987 than in 1983; female strobilus production was 42% lower.

Discussion

Deer browsing removes overwintering strobilus buds located on branches removed by deer. These buds are initiated the previous summer and would typically have matured the following spring. Browsed yews might respond to the loss of immature strobili by initiating and/or maturing additional buds during the late winter and early spring after browsing but before the "flowering" period. Comparing observed and expected 1984 strobilus production levels by treatment tests for this type of response. The results indicate that browsed yews do not replace male strobilus buds removed the previous winter by deer browsing, but that female strobilus buds are replaced. This suggests that browsed yews compensate by increasing female effort.

Deer browsing may also influence Canada yew reproduction by altering resource allocation to sexual reproduction. As new branches are produced during the

growing season following browsing, new strobilus buds are also initiated. Browsed plants may initiate fewer or more strobilus buds per branch than unbrowsed plants. On Stockton Island, the census of strobilus production the second spring after clipping (i.e., 1985) potentially measured this effect.

The significant covariance between male strobilus production and the previous year's branch production suggests that there is no effect of browsing on the production of male strobili beyond the impact of browsing on branch production. The fewer branches produced by a plant the fewer male strobili it produces; there appears to be no significant change in the relative allocation by browsed plants to growth and male function. The lack of covariance between branch production and female strobilus production suggests that, once again, the influence of browsing on female function is more complex.

The results of the clipping experiment suggest that the impact of deer browsing on male strobilus production is linearly related to browsing intensity. It also suggests that yews compensate for deer browsing by increasing ovule production. I do not know the mechanism of this compensation, but it is possible that more than one mechanism is involved. For example, during my spring counts I have observed dormant buds on individual yews which are morphologically similar to female strobilus buds. Clipping (and browsing) may stimulate the maturation of these otherwise dormant buds which remain on unbrowsed stems the following spring. Hence the lack of agreement between observed and expected female strobilus production in 1984.

Further compensation may occur as new strobili are differentiated during the growing season following browsing; browsed yews may produce more female strobili than unbrowsed yews per unit vegetative growth. The lack of covariance between ovule production and the previous year's branch production of browsed yews supports this conclusion, particularly as there is a significant relationship between these two variables in unbrowsed yew populations (Allison 1987).

Compensation by plants for the effects of herbivory typically has been recorded in the form of increased maternal effort. For example, removal of primary umbels increased seed set in secondary and tertiary umbels in *Pastinaca sativa* (Hendrix 1979; Hendrix and Trapp 1981). Katsma and Rusch (1980) found that apple trees produced more fruit per inflorescence in the summer following simulated deer browsing. Paige and Whitham (1987) recorded overcompensation by *Ipomopsis aggregata* in fruit and seed production in response to deer and elk browsing. Hormones and nutrients in herbivore saliva have been implicated as the stimuli for plant compensation (McNaughton 1983). No saliva effect was mimicked in this study, in Paige and Whitham (1987), or in Katsma and Rusch (1980). Thus, although herbivore saliva may enhance plant compensation it is not necessary for compensation to occur.

Although Canada yew may compensate for the removal of female strobili by deer, the evidence indicating compensation in seed production is less conclusive and difficult to evaluate due to low seed production in some

years. The greater proportion of seeds produced by control yews on Stockton Island in 1984 suggests that simulated browsing depresses maturation levels of clipped plants. Seed production, therefore, may be reduced by clipping in the year immediately following treatment. Few seeds were produced in 1985 and treatment effects on seed production could not be evaluated although clipping did not influence pollination levels. Only the 100% removal group had significantly lower absolute and percent seed production than the control group in 1986. The lack of difference in 1986 absolute seed production among the remaining groups, however, may be explained by compensation in ovule production alone, in part because there were no differences in seed set among treatments.

Comparative and exclosure studies do not provide direct evidence for compensation. Levels of male strobilus, female strobilus, and seed production of browsed populations in these studies were most comparable to the 100% removal group of the Stockton Island browse simulation experiment. My own observations of recently browsed yews indicate 100% removal is the most common natural level of browsing intensity. For example, on Basswood Island, two unprotected plants together produced 73 male strobili in 1984. They were the only plants browsed during the winter of 1984-85 on Basswood Island. In Spring 1985 these two plants produced no male strobili. In contrast, the fenced yews paired with the two previous plants produced a total of 24 male strobili in 1984 and 20 male strobili in 1985. Intermediate levels of browsing, at which compensation was observed in clipping experiments were not observed in the field.

The comparative study and exclosure experiment show that at natural levels of deer browsing, both female and male reproductive effort are significantly reduced. They also suggest that browsing may alter sex expression of browsed yews. Browsed yews have female-biased sex expression relative to unbrowsed yews (Allison 1987).

Exclosure studies at Basswood Island and Cedar Creek indicate that chronically browsed yews recover slowly following release from browsing. This rate of increase, at least over the length of the study is linear for both male and female strobilus production. The increase in seed production of protected plants at Cedar Creek appears directly related to increases in ovule production, although the proportion of ovules developing as seeds is significantly lower than that recorded in unbrowsed populations (Allison 1987). Clipped yews also recover slowly following release from browsing. In 1987, four years after clipping, male strobilus production in 100% removal plants was only 6.1% of control plant production.

The slow recovery of Canada yew following release from browsing may reflect the complete defoliation of yew by deer that is characteristic of natural browsing intensity. Yews retain their foliage for up to eight years (T.D. Allison, unpublished work). Leaves are major storage organs in many evergreen species (e.g., Kozłowski and Keller 1966; Chapin 1980), and the loss of photosynthetic capacity and resource storage that the needles represent may be difficult to replace in the short term.

Considerable annual variation was observed in male and female strobilus production at Basswood Island and Cedar Creek. This variation reflects, in part, natural variation in strobilus production in Canada yew (Allison 1987), but it also reflects variation in yew vulnerability to deer browsing. This vulnerability, in part, reflects the amount and duration of snow cover, and consequently, the amount of protection yews receive during the browse season. As deer do not dig through the snow for Canada yew (Allison, TD, personal observation), plants covered by snow are typically protected from deer-browsing. Yews not covered by the snow pack, on the other hand, are vulnerable.

At Cedar Creek, for example, mean snow depth over a 119 day period of the 1983–84 winter was approximately 41 cm. Only four yews were browsed during that winter, and these plants were significantly taller than unprotected yews that were not browsed (46.8 cm vs 16.6 cm, respectively; $P < 0.001$; oneway ANOVA). In the winter of 1984–1985, snow cover exceeded mean plant height only 10 days, and all plants outside the enclosure were browsed that winter. The following spring male and female strobilus production decreased almost 100% among unprotected yews (e.g., 1.65 male strobili per branch in 1984 versus 0.09 male strobili per branch in 1985).

In conclusion, deer browsing reduces male and female strobilus production and seed production in Canada yew although intermediate levels of browsing may result in compensation of ovule, and consequently, seed, production. The decrease in male strobilus production due to browsing may interact with the pollination syndrome of Canada yew. Pollen availability in this wind-pollinated species is significantly correlated with pollination success and seed set (Allison 1990); pollen availability is, in part, a function of male strobilus production. Canada yew reproductive success, therefore, may be indirectly reduced if seed production becomes pollen-limited due to browsing-related decreases in pollen production. The slow recovery of Canada yew pollen production following release from deer browsing suggests that this indirect effect may persist long after the direct effect (deer browsing) has been removed. Low seed production in browsed populations may therefore reflect both direct and indirect effects of deer browsing. The full impact of deer browsing on Canada yew reproductive success requires consideration of this indirect effect.

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