

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

III. Sex expression

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Summary. Browsed Canada yew (*Taxus canadensis*) populations have a higher proportion of males and a lower proportion of monoecious plants than unbrowsed yew populations. The proportion of monoecious plants increases with time following protection from browsing suggesting that deer browsing causes male-biased sex expression in Canada yew. In contrast, results from comparing browsed and unbrowsed populations, exclosure studies, and browse simulation experiments indicate that strobilus ratios and phenotypic gender of browsed yews may be female-biased. In part, these results correspond to the influence of size on sex expression in Canada yew; small yews tend to be male, but if monoecious, have female-biased strobilus ratios. Large yews are monoecious, but have male-biased strobilus ratios. There is, however, no consistent relationship between size and gender in Canada yew, suggesting that in some circumstances, yews shift allocation to female function in response to browsing.

Key words: Herbivory – *Taxus* – Sex expression – *Odocoileus* – Gerder

Studies of variation in sex expression among plants have emphasized the effect of plant status on sex expression within and among populations. Factors influencing plant status include stress, plant size, and plant age. One widely cited generalization is that stress favors maleness (Charnov 1982). Freeman et al. (1980) listed 17 cases where environmental stress (e.g. low soil moisture, high temperature) shifted sex expression from female to male. In several other examples increasing age, size, or soil nutrients resulted in a shift from male to female (e.g. Bierzychudek 1982). This suggests that individuals of many cosexual plant species are able to alter their sex expression or gender in response to changes in their sta-

tus, and that as their status “improves”, they will shift resources to female function.

There are exceptions to these trends. The proportion of males was higher in dry habitats for *Ephedra viridis* (Freeman et al. 1976), but no such relationship between soil moisture and plant sex ratio was observed in *E. trifurca* (Brunt et al. 1988). Moisture stress resulted in earlier initiation of ovulate strobili in *Pinus banksiana* (Riemenschneider 1985). In general, many coniferous species when young first produce ovulate strobili and produce their first staminate strobili when older or larger (Matthews 1963).

Female-biased sex expression was correlated with higher soil nitrogen in *Ambrosia artemisiifolia*, but relative male effort in ragweed increased with plant size (e.g., McKone and Tonkyn 1986). Relative maleness also increased with plant size in *Xanthium strumarium* (Solomon 1989). Finally, insect attack also has been shown to influence sex expression in conflicting ways. Herbivore attack resulted in male-biased sex expression in *Pinus edulis* (Whitham and Mopper 1985), but resulted in female-biased sex expression in umbelliferous species (Hendrix 1979; Hendrix and Trapp 1981).

In a previous study of sex expression in Canada yew (*Taxus canadensis* marsh.) considerable variation was observed among yew individuals within several populations. A pattern in this variation corresponded to size differences among plants. Small yews tended to be male, but if monoecious had female-biased strobilus ratios. Large yews were typically monoecious but had male-biased strobilus ratios (Allison 1991). Sex expression also showed significant annual variation. These results indicated that sex expression in Canada yew was responsive to differences in plant status. Phenotypic gender however, measured as maleness was weakly and inconsistently negatively correlated with plant size (Allison 1991).

The influence of browsing by white-tailed deer (*Odocoileus virginianus* Rafinesque) on Canada yew reproduction has also been examined. Although studies demonstrating the negative impact of deer on vegetative

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growth and density of plants are common (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), studies examining their impact on plant sexual reproduction are rare. In the first paper of this series the negative impact of deer browsing on absolute production of pollen, ovules, and seeds was discussed (Allison 1990a). The third paper of the series focuses on the impact of deer on the relative production of these parameters, i.e., sex expression. Results of simulated browsing experiments indicated that browsing reduced production of male strobili more than female strobilus production (Allison 1990a). This result suggested that browsing may affect yew sex expression by causing a shift to female function.

Study organism – Canada yew is a monoecious, evergreen, shrub native to the mixed conifer-hardwood forests of northeastern United States and southeastern Canada (Martell 1974). 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 these rooted branches can be traced under the litter layer, but eventually these connections rot. In high density populations the genetic relatedness of neighboring aboveground shoots can be difficult to determine due to this layering habit of Canada yew. In sampling yew reproductive effort in high-density populations, belowground connections were traced to the rotted end. This network of aboveground shoot systems was called a plant. The sex expression of an individual genet was estimated by combining the results from the connected shoot systems of the plant. In high density populations, therefore, a plant constituted an unknown proportion of a genet. In low density populations individual genets consisting of one or more branches are readily distinguished, and the sex expression of sample plants and genets is assumed to be equivalent.

The influence of browsing on yew sex expression was examined in two ways: (1) qualitatively – the proportion of monoecious, male, and female individuals and (2) quantitatively – by strobilus ratios and phenotypic gender (Lloyd and Bawa 1984).

Methods

Investigations of the impact of deer browsing on Canada yew sexual reproduction involved comparing browsed and unbrowsed populations of yew, excluding deer from previously browsed yew by using fenced plots, and simulating browsing on previously unbrowsed yews. Observations and experiments were performed at: (1) Cedar Creek Natural History Area, Anoka County, Minnesota, USA; (2) North Grey Cloud Island, Washington County, Minnesota, USA; (3) Root River, Fillmore County, Minnesota, USA; and (4) Apostle Islands National Lakeshore (APIS), Bayfield County, Wisconsin, USA.

Comparison of browsed and unbrowsed populations

Strobilus ratios and the proportion of male, female, and monoecious yews were compared in seven populations that differed in the presence or absence of deer. Four of these populations were located at APIS (Oak Island, Basswood Island, and Outer Island (closed) and Outer Island (gap)), other populations were located at North Grey Cloud, Root River, and Cedar Creek. Basswood, Oak, and Cedar Creek support deer herds while both Outer populations, Root River, and North Grey Cloud yew populations are unbrowsed. Study populations were chosen to minimize differences in forest composition and structure.

Transects were located systematically in each study area. Sampling points in each population were established at 10 m intervals along these transects at APIS and randomly at North Grey Cloud, Root River, and Cedar Creek. The yew plant nearest each point was selected for study. North Grey Cloud, Root River, and Outer Island populations have high-density yew populations while Basswood, Oak, and Cedar Creek have low density yew populations. The definition of a plant for these different populations is as described in the introduction.

For each plant the number of male and female strobili were counted. Student *t*-tests tested the null hypotheses that the mean proportion of male yew plants and the ratio of male strobili to female strobili did not differ significantly between deer present and deer absent populations. Data from 1985 were used for all populations with the exception of Root River and Cedar Creek. Data from 1985 were not collected at the Root River site, and heavy browsing by deer at Cedar Creek in 1985 resulted in almost no reproduction by browsed yews; data from 1984 were used from these two sites (Allison 1990a; Allison 1991).

Exclosure studies

On Basswood Island in Autumn 1983, 46 plants were paired on the basis of their size and Spring 1983 production of strobili. One member of each pair was assigned randomly 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" x 3" mesh size. Individual exclosures ranged in diameter depending on the diameter of the plant, but generally were twice the diameter of enclosed plants. Strobilus and seed production was measured for all plants in 1984, 1985, and 1986. Strobilus production only was recorded in 1987 and 1988.

Strobilus counts were analyzed using Wilcoxon's *W*-test on data within years. Data on proportion of males, females, and monoecious plants were analyzed using SPSS-X loglinear models procedure (PC-version). The null hypothesis was the probability of a plant being monoecious was not different in fenced and unfenced treatment groups and the probability did not change over time. The significance of main effects, two-way, and three-way interaction terms was tested by removing a particular term from the model and comparing the change in the maximum likelihood statistic with a chi-square statistic at one degree of freedom ($\alpha = 0.05$).

In Autumn 1981, a single deer-only exclosure (10 m x 40 m) was constructed of six-foot wire mesh fence to protect a portion of a small Canada yew population growing at Cedar Creek. Sample plants inside and outside the Cedar Creek exclosure were randomly chosen along transects. Strobilus and seed production of these plants was measured in each spring and summer from 1982 through 1987. Although there was no replication of treatment, the results from this study formed a useful adjunct to the exclosure study on Basswood Island.

Browse simulation experiment

The effect of deer browsing was simulated by clipping previously unbrowsed yews on Stockton Island of APIS. Deer were present on Stockton in the mid-1950's, but they went extinct on the island

in the early 1970's. Yews on Stockton are widely spaced and generally much larger than those on either Oak or Basswood Islands. This site was chosen because clipping treatments could be applied to entire genets.

As reproductive effort in Canada yew varies significantly with plant size (Allison 1991), 50 plants were selected each having a minimum of three major branches, one of which was at least one m in length. These plants were further subdivided 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 field observations of deer browsing and that recorded in the literature (King 1975). In browse classes with less than 100% removal, branches were clipped randomly until the designated amount of browse was removed. Plants were clipped once in the fall of 1983 and allowed to regrow without further clipping. Strobilus and seed production were recorded in 1984, 1985, 1986, and 1987 (control and 100% removal only).

Clipping data were summarized by strobilus ratios and by phenotypic gender (Lloyd 1980). Gender was calculated where $gender = (m_i/M)/(m_i/M + d_i/D)$ and is a measure of relative maleness on a scale of 0 (female) to 1 (male). Strobilus ratios were $\log(y+1)$ transformed and gender was arc-sin transformed prior to MANOVA to meet the assumptions of the models. Repeated measures analysis of variance on strobilus ratios was used on all treatment groups except the 100% removal group because of low strobilus production in the latter. Differences between control and 100% removal groups in 1985, 1986, and 1987 were tested by MANOVA.

Results

Qualitative sex expression

The proportion of males in populations with deer present was significantly higher than in populations where deer were absent (Table 1). Conversely, monoecious yews were relatively more abundant in populations where deer were absent. The proportion of monoecious yews increased over time in the fenced populations at both Basswood Island and Cedar Creek (Fig. 1). No such trend was discernible in unprotected yews. Loglinear analysis of the Basswood Island data showed a significant treatment by sex type by year interaction indicating a significant increase over time in the probability of fenced yews becoming monoecious. Furthermore this increase was linear; quadratic and higher order effects were not significant. Other significant terms in the final model were: sex type, sex type by year, and treatment (fenced or unfenced) by year.

Quantitative sex expression

Ratios of male to female strobili in deer-absent populations were relatively female-biased when compared to deer-present populations (Table 2). Deer exclusion resulted in an increase in the strobilus ratios of yews. At Basswood Island, the mean $\log_{10}(Y+1)$ strobilus ratio of unfenced plants was significantly female-biased rela-

Table 1. Males, females, and monoecious plants as a proportion of reproducing individuals in different yew populations by presence or absence of deer in 1985 (unless otherwise noted). Student's *t*-test on arc-sin transformed proportions tested the null hypothesis that the proportion of male yews in each population was the same in deer-absent populations and deer-present populations. Yews not producing strobili were excluded from the analysis

	<i>n</i> ^a	Males	Females	Monoecious
<i>Deer absent</i>				
Outer (closed)	86	0.23	0.01	0.76
Outer (gap)	25	0.04	0	0.96
Grey Cloud	31	0.03	0	0.97
Root River ('84)	26	0.08	0.04	0.88
<i>Deer present</i>				
Basswood	20	0.45	0.16	0.39
Oak	29	0.87	0	0.13
Cedar creek ('84)	66	0.60	0.12	0.38

$t = -5.51; p < 0.005$

^a number of plants producing strobili

Table 2. Strobilus ratios (male/female) of Canada yew populations differing in presence or absence of deer in 1985 (unless noted). Numbers are based on summing strobilus productions of all *n* plants. The student's *t*-test tested the null hypothesis that there was no difference between mean strobilus ratios of populations with deer present and deer absent

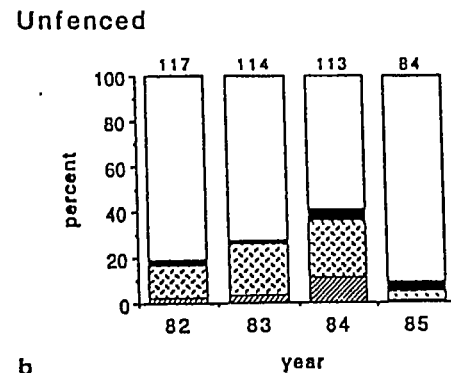
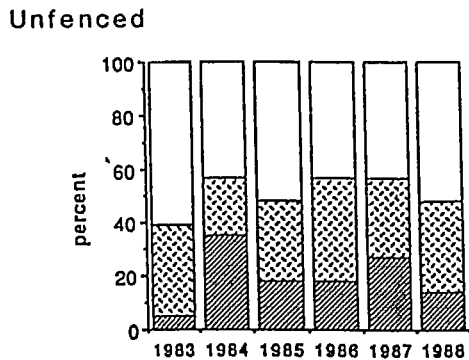
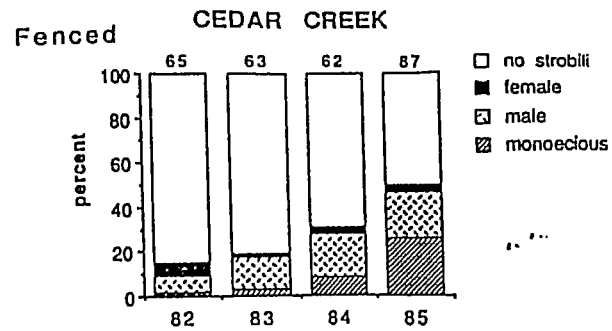
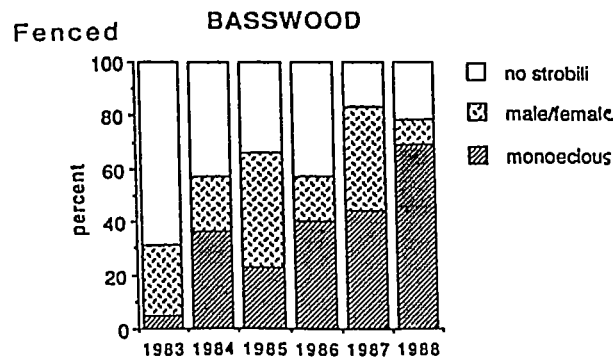
	<i>n</i> ^a	Strobili		
		Male	Female	Male/Female
<i>Deer absent</i>				
Outer (closed)	92	8063	1027	7.85
Outer (gap)	25	7244	1553	4.67
Grey Cloud	31	5394	700	7.71
Root River ('84)	26	7719	827	9.33
<i>Deer present</i>				
Basswood	50	34	18	1.89
Oak	38	340	103	3.30
Cedar Creek ('84)	113	237	49	4.84

$t = 2.97; p < 0.05$

^a Number of plants on which strobilus totals are based

tive to fenced plants in 1988 [0.32 vs 0.93, respectively ($\log_{10}(Y+1)$ transformed means); Wilcoxon's $W = 46.5$, $p < 0.001$]. This year was also the first year in which strobilus production differed significantly by treatment (Allison 1990a).

Repeated measures ANOVA (Winer 1971) of the simulated browsing experiment on Stockton Island showed that clipping reduced the floral sex ratio ($p < 0.05$). In particular, yews in the 50%-removal group had female-biased floral sex ratios relative to control yews in 1985 and 1986 in within year comparisons (see Table 3). In pairwise comparisons, control plants had significantly more male-biased strobilus ratios than 100% removal plants in 1985, 1986, and 1987 (Table 3). Results



a Year

b year

Fig. 1a, b. Change in frequency distribution over time of male, female, monoecious, and non-strobili-producing plants for protected and unprotected Canada yew plants: a) Basswood Island,

Apostle Islands National Lakeshore; b) Cedar Creek Natural History Area

Table 3. a Strobilus ratios and b phenotypic gender of Canada yew plants used in the browse simulation experiment on Stockton Island in 1985, 1986, and 1987. Means of strobilus ratios were transformed prior to MANOVA by $\log_{10} [(male+1)/(female+1)]$ which is equivalent to $\log_{10} (male+1) - \log_{10} (female+1)$. Gender values were arc-sin transformed prior to MANOVA. Back-transformed means for both strobilus ratios and gender are presented for ease of interpretation. Means with the same letters within columns are not significantly different at $\alpha=0.05$ for within year comparisons

a Strobilus ratios

Treatment	n	1985*	1986*	1987**
Control	10	6.2a	11.7a	9.1a
50% Removal	10	1.8b	5.0b	no data
100% Removal	8	0.6b	1.9	0.7b

b Phenotypic gender

Treatment	n	1985**	1986*	1987**
Control	10	0.57 ^a	0.55	0.58 ^a
50% Removal	10	0.34 ^a	0.40	no data
100% Removal	8	0.05 ^b	0.38	0.11 ^b

* $p < 0.05$

** $p < 0.005$

^a Not significant

of gender analysis were similar for comparisons between control and 100%-removal groups although there was no significant difference in 1986. No significant differences were observed in gender between control and other treatment groups in any year.

Discussion

Sex expression in Canada yew is complex, and this is reflected in the results of this study. In comparisons among populations, for example, deer browsing increases maleness in Canada yew populations when sex expression is measured qualitatively. When quantitative measures are used, however, femaleness increases as a result of browsing. Because comparisons among different populations cannot be rigorously controlled, they may confound several factors with the one of interest. For example, yews in deer-present populations are smaller and produce fewer strobili than those in deer-absent populations. These characteristics probably reflect deer impact also, and they are correlated with measures of sex expression in Canada yew (Allison 1991). The results of these comparisons, however, also are observed experimentally – in enclosure experiments and simulated browsing. Thus, the contradiction in the effect of deer on sex expression in yew appears to be real.

The effects of deer browsing presented here correspond to the relationship between size and sex expression (Allison 1991). Small yews or browsed yews tend to be male or, if monoecious, have relatively female-biased strobilus ratios. Large yews and unbrowsed yews tend to be monoecious, but have relatively male-biased strobilus ratios. The effect of deer browsing then is to cause browsed yews to have a sex expression similar to small unbrowsed yews.

The apparent contradiction in the effect of size (or browsing) on sex expression in Canada yew may be an artifact of the methods used in calculating the quantitative and qualitative measures of sex expression. For example, previous analysis suggested that gender in Canada yew may be dimorphic, consisting of male and female morphs; both morphs are monoecious (Allison 1991). I hypothesize that female morphs will tend to be monoecious at all sizes while male morphs will produce only male strobili when small. As they grow larger male morphs will become monoecious although their strobilus ratios will be strongly male-biased (Allison 1991). Strobilus ratios (male strobili/female strobili) as calculated in this study did not include small male morphs. Mean strobilus ratios of small yews will therefore only include female morphs having relatively female-biased ratios. Mean ratios of larger yews will include both male and female morphs, resulting in an apparent increase in the mean strobilus ratio of Canada yew with plant size.

Alternatively, strobilus ratios in unbrowsed yew populations average nine to one (male:female). Small yews average less than three strobili per plant. Such plants could, by chance alone, produce male strobili only increasing the proportion of "male" yews in populations consisting of relatively small yews.

Yews in browsed populations are smaller than yews in unbrowsed populations and produce fewer strobili per plant (Allison 1990a). Thus, a browsed population consisting principally of "small" plants will have more males, but female-biased floral sex ratios in those plants that are monoecious possibly because of the factors cited above. An unbrowsed population containing larger yews on average (Allison 1990a) will have a higher proportion of monoecious plants and a male-biased floral sex ratio of the monoecious plants. Measures of breeding type or floral sex ratios are often used as indicators of plant shifts in sex expression in response to environmental factors (e.g. Freeman et al. 1980; Barker et al. 1982). Based on these measures, a shift in yew sex expression in response to deer browsing on sex expression may be more apparent than real.

Phenotypic gender may be a more objective and inclusive measure of sex expression. Gender in Canada yew became female-biased in response to clipping. This difference was only significant in the 100% removal group, and the result was not observed in all years. Unlike strobilus ratios, phenotypic gender in Canada yew bears no strong or consistent correlation with plant size, and in those few significant cases the correlation was negative – the opposite of the trend observed for strobilus ratios (Allison 1991).

Deer browsing, at least at high intensities, therefore,

may cause a shift in sex expression qualitatively different than the size-related effects described above. If true, this would be consistent with the greater reduction in male than female strobili production resulting from clipping (Allison 1990a). On the other hand, all of the plants used in the clipping experiment were relatively large and showed no evidence of past browsing. Plants sampled in comparisons among populations and in enclosure experiments were smaller than average and chronically browsed. Small yews may react differently to the stress of browsing than large yews chosen for the simulated browse experiment. Small yews, for example, showed more flexible gender in year to year comparisons in unbrowsed populations than large yews (Allison 1991).

The adaptive significance of the apparent gender shifts in yew is difficult to interpret. Other studies finding size-based patterns in plant sex expression interpret these patterns in terms of size-advantage models (e.g. Charnov 1982). For hermaphrodite organisms these models predict that as an organism becomes larger it will shift allocation to the sex function which shows the greater increase in fitness with the increase in size. Allocation shifts to female function as size increases have been most commonly observed in plants (Charnov 1982), but a shift to male function in larger individuals has been recorded for some wind-pollinated species (e.g. Abul-Fatih et al. 1979; Solomon 1989; Ackerly and Jasienski 1990). For Canada yew, although there are distinctive trends in size and sex expression, these trends are contradictory or possibly artifacts (see above), making it difficult to readily apply such models to this species.

Shifts in plant sex expression due to herbivory may reflect the architectural arrangement of inflorescences on the plant and are not adaptive per se. For example, Whitham and Mopper (1985) found that insect herbivory on *Pinus edulis* resulted in a male shift in sex expression due to the arrangement of male and female strobili and the feeding behavior of the herbivore. Changes in sex expression correlated with plant architecture have also been observed in *P. contorta* (Smith 1981), *Xanthium* (Solomon 1989), and *Ambrosia* (Ackerly and Jasienski 1990). In Canada yew, female shifts in the gender of heavily browsed yew individuals also may reflect architectural patterns. Browsing stimulates the production of adventitious shoots; strobili on these shoots tend to be female (TD Allison, unpublished data). Additionally, dormant female strobili buds on unbrowsed branches may mature in response to browsing; no similar pattern has been observed for male strobili (TD Allison, personal observation). Neither of these observations, however, have been confirmed. No other patterns in the distribution of male and female strobili were observed in Canada yew plants.

Whether or not the shifts in sex expression of browsed yew individuals are adaptive, when expressed by an entire population these shifts may have negative consequences for individual fitness. For example, in 1983 on Basswood Island (deer present), only male strobili were produced by those plants producing strobili; no sexual reproduction occurred. Alternatively, shifts to female-biased strobilus ratios in a browsed population may re-

duce individual fitness if pollen availability is reduced to the point where seed production becomes pollen-limited (e.g., Allison 1990b).

In summary, the total effect of deer browsing on Canada yew reproduction is complex and involves more than one level of action. For example, at the individual level deer browsing can influence plant fitness by reducing absolute production of pollen, ovules, and seeds (Allison 1990a) and by affecting sex expression. Plant fitness can be decreased indirectly if pollen availability is reduced to the point where seed production is pollen limited (Allison 1990b). This effect involves a population-level response to deer browsing and is due to reductions in pollen production and plant density of the population, or by a population-wide shift in sex expression of individual yews to female-biased strobilus ratios. For the individual yew, the adaptive significance of this shift remains obscure.

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