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

II. Pollen limitation: an indirect effect

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Summary. Hand-pollination significantly increased seed production in a Canada yew (*Taxus canadensis*) population that had been browsed previously by white-tailed deer (*Odocoileus virginianus*) indicating that pollen availability limited seed production in this population. Hand-pollination did not significantly increase seed production in a population never browsed by deer. Deer-browsing significantly reduces yew density and pollen production, which in turn results in reduced pollination and seed production. Pollen limitation of yew seed production is an indirect effect of deer browsing on Canada yew and results from an interaction between the direct effect of deer browsing and the pollination syndrome of Canada yew. Artificially created female yews had lower seed set than monoecious yews when yew seed production was pollen-limited, but not when pollen did not limit seed production.

Key words: Herbivory – Indirect effects – Plant – Pollen limitation – *Taxus*

The total effect one species has on another species includes both direct and indirect effects (Vandermeer 1980; Tilman 1983). Indirect effects are typically transmitted through other species, but they also may result when factors having direct effects interact with characteristics of species that are incidental to the direct interaction. For example, the efficiency of wind-pollination is assumed to depend on high levels of pollen production and/or high density of conspecifics (e.g. Faegri and van der Pijl 1983). Evidence from a variety of sources supports this assumption (e.g., Bateman 1947; Lemen 1980; Allison 1990). A factor may directly effect a wind-pollinated species by reducing the density or pollen production of the population. This factor will also have an indirect effect on individuals in that population if the decline in plant density or pollen production reduces pollen availability to where seed production becomes pollen-limited. This assumes that seed production in the wind-pollinated species typically is not pollen-limited.

The impact is indirect because an individual wind-pollinated plant does not have to be directly affected by the ecological factor. Rather it suffers decreased reproductive success due to the reduced pollen production or density of conspecifics that are directly affected. I have examined this hypothesized indirect effect in my study of the influence of deer browsing on the reproductive ecology of Canada yew (*Taxus canadensis* Marsh.), a wind-pollinated, coniferous shrub.

The abundance of Canada yew has been considerably reduced by the browsing of white-tailed deer *Odocoileus virginianus* and moose *Alces alces* throughout eastern North America during the past few decades (Spiker 1935; Stearns 1951; Curtis 1959; Pimlott 1965; Snyder and Janke 1976). I have shown previously that browsing has a direct negative impact on sexual reproduction in Canada yew (Allison 1987). I propose that, in addition to this direct effect, deer-browsing has an indirect effect on the reproductive success of yew individuals by reducing density and pollen production of yew populations to the point where pollen availability limits seed production of the population.

I performed this research at the Apostle Islands National Lakeshore, an archipelago of 21 islands near Bayfield, Wisconsin, USA (90° 45′ W longitude, 46° 50′ N latitude; hereafter referred to as Islands). Several of the Islands experienced rapid buildups of deer herds in the mid-1940's and early 1950's. Other Islands had few or no deer during this period. Hunting pressure, declining browse supply, and a series of harsh winters in the early 1960's all contributed to a decline in the deer herds on

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Table 1. Change in total browse stem density and density of Canada yew as a percentage of total browse stem density of Islands of different deer history Browse stems are defined as all woody stems between 0.6 m and 2.1 m. Data are sorted by forest type. See Beals, et al. (1960) for details on methods of data collection and vegetation typing. Data adapted from Beals and Cottain (1967)

	1956–57		1966	
	% Yew Density	Total Density (stems/ha)	% Yew Density	Total Density (stems/ha)
Islands Supporting Deer				
White cedar type				
South Twin	7	785	0	1065
Rocky	8	546	0	553
Yellow birch-balsam fir-sugar maple type				
South Twin	43	4105	0	1566
Rocky	52	2470	0	1391
Sugar maple-hemlock type				
Stockton	10	447	0	6249
Oak	5	8302	0	1277
Island without deer				
Yellow birch-balsam fir-white cedar type				
Devil's Island	62	6625	71	13,533
Devil's Island	100	672,458	93	54,893

Table 2. 1985 mean male strobilus production, nearest neighbor distance, pollination success, and seed set (number seeds per ovule) of Canada yew populations with different deer browsing histories. All differences between populations with deer (past or present) and populations without deer in pollination success and seed set are significant at $P<0.05$ with the exception of Outer (gap) and Cedar Creek seed set. See Allison (1990) for details concerning data calculations

Site	n[a]	Male Strobilus Production	Nearest Neighbor Distance (m)	Pollination Success	Seed Set
With deer (past or present)					
Apostle Islands					
Basswood	50	0.5	3.13	0.231	0.103
Oak	38	3.0	0.86	0.485	n.d.[b]
Rocky	54	1.9	3.13	0.463	0.134
Cedar Creek	87	1.0	0.15	0.473	0.284
No deer					
Apostle Islands					
Outer (closed)	92	22.2	0.11	0.853	0.393
Outer (gap)	25	163.3	0.03	0.932	0.212
North Grey Cloud	31	87.3	0.03	0.913	0.309

[a] Number of plants sampled
[b] no data

most of the Islands. At present deer are found in low numbers on Oak and Basswood Islands (Brander 1983; TD Allison, unpublished work).

Beals et al. (1960) studied the impact of deer on Apostle Islands' vegetation and showed that as browsing intensity (estimated by a browse index) increased, Canada yew abundance decreased. Furthermore, yew densities continued to decrease over time on islands with deer, but remained high on islands without deer (Table 1; Beals and Cottam 1967). Production of male strobili and seeds, plant density (estimated as nearest neighbor distance), pollination success (proportion of ovules pollinated), and seed set are significantly lower in Canada yew populations that have experienced heavy deer browsing when compared to yew populations that have not been browsed (Table 2; Allison 1990). I also have determined that pollination success and seed set are strongly correlated with yew spacing and pollen production (Allison 1990).

I performed a series of hand-pollination experiments in island populations of Canada yew having deer histories to determine if pollen availability limited yew seed production; pollen limitation would reflect an indirect effect of deer on the reproductive success of Canada yew.

Methods

I hand-pollinated individuals of Canada yew on Rocky Island and Basswood Island in 1984 and on Rocky Island and Outer Island in 1985. Basswood Island currently has a small deer population, Rocky Island now has no deer, but had high deer densities in the mid-1950's and early 1960's, and Outer Island has never had deer (Brander 1983). Plant density, production of male strobili, pollination success, and seed set for each study population in 1985 are included in Table 2 (see Allison 1990 for details). Study populations were located in sugar maple-yellow birch forests approximately 20 m from the shoreline.

I chose 20 individual plants each on Rocky Island in 1984 and Outer Island in 1985 that had at least four female strobili, or ovules, per plant. Maximum ovule number per plant was 70 on these two islands. I paired plants on the basis of stem length and ovule number; ten pairs of plants (or 20 plants total) were set up on each island. Plants within pairs were randomly assigned to treatment or control groups. On Rocky Island in 1985, due to difficulties in finding enough plants having the minimum ovule number, I assigned 9 plants each to hand-pollination and control groups in a completely randomized design.

On Basswood Island, plant density and ovule production were low, and I could not find enough plants to satisfy the previously stated criterion on minimum ovule number per plant. Instead, I brushed the ovules of nine plants with pollen collected from other yew plants located in the study area. Results of the hand-pollination were compared with data collected from 21 yew plants on Basswood Island used in a comparative study (Allison 1987).

I dusted the ovules of treatment plants with pollen collected the previous day from male strobili of yews not included in the experiment. The receptivity of ovules and the viability of pollen at the time of hand-pollination were unknown. Previous tests of this procedure resulted in high ($n=500+$ ovules: $\bar{X}>90\%$) pollination success for all plants treated and indicated that brushing alone did not stimulate seed development.

I performed all hand-pollinations in mid-May of 1984 and again in mid-May of 1985. In mid-June of each year, I counted the number of developing and non-developing ovules in the treatment and control groups of each study population. Developing ovules were easily distinguished from non-developing ovules by color and size; the former were enlarged and green while the latter were yellow and small. I measured seed production in late summer; individual plant seed set was calculated as a percentage of ovule production.

Although Canada yew is principally monoecious, male and female plants occur in low proportions in natural populations (Allison 1987). In addition, it is the only monoecious member of the genus *Taxus* (den Ouden and Boom 1965; Dallimore and Jackson 1967). I wanted to determine if there was any reproductive advantage of monoecious plants over dioecious plants at low yew density. Therefore, in conjunction with the 1985 hand-pollination experiment on Rocky Island, I created female plants by removing all immature male strobili from eight plants randomly assigned to this treatment group.

I was unable to create females on Outer Island as most male strobili had opened before I arrived on the island. I estimated the importance of self-fertilization in high-density yew populations, by removing immature male strobili from nine randomly selected plants in a population at North Grey Cloud, Minnesota, USA (92° 56′ W longitude, 44° 46′ N latitude) in Spring 1986 (Allison 1987). Pollination success and seed set of these "females" were compared with nine randomly selected control plants.

The hand-pollination data were analyzed with the University of Minnesota's analysis of variance program, IVAN (Weissberg and Koehler 1982) with the exception of the 1984 Basswood Island data and the 1985 seed data for Rocky Island. I transformed individual plant percentages prior to analysis by the arcsine square root transformation (Sokal and Rohlf 1981). I analyzed Rocky island 1985 seed production data with Wilcoxon's 2-sample test comparing hand pollinated plants versus control plants and control plants versus "female" *T. canadensis*. The proportion of ovules pollinated and seeds produced for Basswood Island treatment and control plants were analyzed by the G-test (Sokal and Rohlf 1981).

Table 3. Percentages of pollination success, seed set, and maturation levels of Canada yew plants used in hand-pollination experiments on Rocky, Basswood, and Outer Islands. Data were analyzed by ANOVA's based on arcsine transformed percentages with the exception of Rocky Island 1985 and Basswood Island seed set which were analyzed as described in Methods. P-values at the base of columns for each island refer to the results of statistical comparisons between or among treatments. Rocky Island 1985 treatments with different superscripts are significantly different at $P<0.05$. Percentages listed below have been back-transformed

Site	n^1	Pollination Success	Seed Set	Maturation Level
Rocky Island – 1984				
Control	10	39.7	16.4	46.3
Hand-pollinated	10	93.2	48.5	54.0
		$P<0.005$	$P<0.001$	$P>0.50$
Rocky Island – 1985				
"Females"	8	17.8[a]	10.8[a]	51.6
Control	9	46.2[b]	25.1[b]	52.0
Hand-pollinated	9	94.9[c]	41.1[c]	43.3
		$P<0.001$	$P<0.008$	$P>0.50$
Basswood Island – 1984				
Control	21 (86)[2]	22.1	12.8	57.9
Hand-pollinated	9 (30)	76.7	26.7	34.8
G (adj.) =		27.9	2.78	2.24
		$P<0.005$	$P<0.10$	$P>0.10$
Outer Island – 1985				
Control	10	91.0	53.8	66.7
Hand-pollinated	10	93.1	55.3	62.0
		$P>0.50$	$P>0.50$	$P>0.50$

[1] number of plants per treatment group
[2] number of ovules in each group

Results

Seed set of hand-pollinated plants on Rocky Island was almost three times greater than seed set of control plants in 1984 and two-thirds greater in 1985 (Table 3). Hand-pollination also significantly increased pollination success, but not seed set of treatment plants on Basswood Island in 1984 (Table 3) although seed set was greater in treatment plants as a group. Hand-pollination did not significantly increase the pollination success or seed set on Outer Island (Table 3).

Monoecious control plants on Rocky had significantly greater pollination success (2.6X) and seed set (2.3X) than female yews in 1985 (Table 3). Nine randomly chosen monoecious controls had significantly greater pollination success than nine females in the high density yew population of North Grey Cloud, MN (0.86 versus 0.78; untransformed means: $P<0.05$; Mann-Whitney U), but no significant difference in seed set was observed. Maturation levels (ripe seeds as a proportion of ovules pollinated) did not differ significantly among treatments in any study population.

Increases in seed production in 1985 due to hand-pollination or self-pollination (comparing control plants to females) on Rocky Island were not at the expense of ovule or seed production the following year. I recorded ovule and seed production of all treatment plants on Rocky in 1986. All plants showed an increase in ovule production in 1986 over 1985, and there was no difference in the relative amount of this increase by treatment (G-test on proportion of total ovules produced by year = 0.15: $P>0.5$). There also was no significant difference in 1986 seed set among plants by 1985 treatment.

Discussion

The data support the conclusion that pollen limits seed production in the low density yew population of Rocky Island, but pollen does not limit seed production in the high density Outer Island population. Pollen may also be limiting on Basswood Island, but the difference in seed set between hand-pollinated plants and control plants was not significant according to the G-test. Pollination success is lower on Basswood Island than all other populations I have studied (Allison 1987). The results of the statistical analysis suggest that a larger sample size would increase the likelihood of detecting increased seed set following hand-pollination on Basswood.

Higher seedling recruitment in low-density populations versus high-density populations could counteract differences observed in seed set. I observed, however, the greatest seedling recruitment in the high density population of North Grey Cloud, Minnesota, USA. Differences in seed set seem to be reasonable estimates of differences in reproductive success between low and high density yew populations.

Hand-pollination will enhance seed set if the naturally occurring level of pollen is insufficient. It has been suggested, however, that to provide a true demonstration of pollen limitation, long-term reproduction or sur-

vival of treated plants should not be reduced as a result of the short-term increase in seed production that results from hand-pollination (Janzen et al. 1980; Willson and Burley 1983). In this study, seed production data from Rocky Island in 1986, the year following hand-pollination, indicated no immediate reduction in reproductive effort in Canada yew as a result of hand-pollination.

Monoecious yew (controls) had significantly higher seed set than artificially created female yews on Rocky Island. This result strongly indicates that, all other things being equal, monoecious yews have greater fitness than dioecious yews, at least when pollen is limiting. As Canada yew is the only monoecious member of the genus *Taxus*, I hypothesize that low pollen availability was a selective force in the evolution of monoecy in Canada yew from a dioecious *Taxus* ancestor.

A striking aspect of this experiment is the lack of significant difference between treatments in abortion levels (1 – maturation level). Differences in abortion levels between hand-pollinated plants and control plants might be expected and has been cited as evidence of resource limitation of seed production (e.g. Schemske et al. 1978; Lovett Doust et al. 1986). For example, hand-pollinated plants might be expected to have higher abortion levels than control plants if seed production in the former becomes resource-limited. Alternatively, control yew plants might have higher abortion levels because of potentially higher selfing levels than hand-pollinated plants and the obligately outcrossed female yews. In conifers, increased selfing often leads to higher abortion levels (see Willson and Burley 1983 and references cited therein). Earlier work, however, detected no evidence of this form of inbreeding depression in Canada yew (Allison 1987).

In summary, these experiments show that: (1) pollen availability typically does not limit seed production in unbrowsed Canada yew populations; and (2) the reduction in plant density and male strobilus production caused by past or current deer browsing has reduced pollen availability to where seed production in these yew populations is potentially pollen-limited.

High deer populations in the 1950's and 1960's drastically reduced the density of Canada yew on several Islands (Table 1; Beals et al. 1960). Studies of browsed yew populations and the results of simulated browsing experiments showed that browsed yews produce fewer male strobili, ovules, and seeds than plants in unbrowsed populations (Allison 1987). Pollination levels and seed set in browsed populations are lower than in unbrowsed populations, and the hand-pollination experiments indicate that this is due to lower pollen availability in browsed populations. Thus, the lower seed production in browsed populations may be due not only to the direct effect of browsing on Canada yew reproduction (Allison 1987), but the indirect effect caused by the reduction in pollen availability.

This indirect effect of browsing resulted from the constraints inherent in the wind-pollination syndrome of Canada yew, a characteristic which is incidental to the direct interaction between deer and Canada yew. Furthermore, the results of the hand-pollination experiments on Rocky Island show that the indirect effect of deer browsing may persist in yew populations well after browsing has ceased. Deer disappeared from Rocky Island in the early 1970's (Brander 1983), but the seed production of individual plants is still reduced, in part, as a result of low pollen availability that resulted from past deer browsing. Yews on Rocky Island are small and widely spaced and may reflect a population that is expanding following release from severe deer browsing in the past.

Both direct and indirect effects may be felt concurrently, but, as this study shows, the indirect effect may persist long after the direct effect has ended. Such a result has important consequences for determining the factors that influence the *current* ecological characteristics of populations.

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