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Self-fertility in Canada yew (*Taxus canadensis* Marsh.)[1]

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ABSTRACT

Allison, T. D. (Department of Plant Biology, The Ohio State University, Marion, OH 43302). Self-fertilization in Canada yew (*Taxus canadensis* Marsh.). Bull. Torrey Bot. Club 120: 115–120. 1993.—Self-fertility was examined in a Canada yew (*Taxus canadensis*) population in southeastern Minnesota. Bagged yew branches and unbagged control branches showed no significant differences in seed production, proportion of pollinated seeds that matured, or seed masses. Greater than 99% of male strobili were located on current growth, but a significant proportion of female strobili (>33%) were located on growth two years or older. There was no consistent trend in location of these strobilus types on higher or lower branches. Results from other studies examining consequences of monoecy in Canada yew support the conclusions of this study that Canada yew is self-fertile and that self-pollination enhances seed production when pollen is limiting.

Key words: *Taxus canadensis,* self-fertilization, plant reproductive biology, pollination biology.

The effects of self-pollination in gymnosperms often are expressed by such post-zygotic phenomena as early embryo abortion (indicated by reduced seed production or the presence of unfilled seeds), lower seed masses, and/or reduced seedling growth. These phenomena characterize inbreeding depression—the reduction in fitness resulting from self-fertilization. Inbreeding depression is apparently caused by the expression of recessive lethal, or otherwise deleterious, alleles in offspring produced by self-fertilization (e.g., Dobzhansky *et al.* 1977).

Many coniferous species show some form of inbreeding depression following self-pollination (Snyder 1968; Sorensen 1970, 1971; Dorman and Squillace 1974; Ledig and Fryer 1974). Other conifers, however, show little if any negative effect of self-pollination (Fowler 1965a), and there can be considerable variation in self-fertility within species that otherwise show inbreeding depression (Hanover 1975).

I have examined various aspects of the pollination ecology of Canada yew (*Taxus canadensis*) (Allison 1990a, 1990b). This species is the sole monoecious member of the genus *Taxus* (den Ouden and Boom 1982), and it is of interest to ask whether Canada yew is self-fertile or shows any indication of inbreeding depression. Such questions are relevant to understanding the adaptive significance of monoecy in an otherwise dioecious genus.

Study Organism. Canada yew is an evergreen shrub indigenous to the mixed conifer-hardwood forests of northeastern United States and southeastern Canada. The male and female reproductive structures (hereafter referred to as strobili) typically begin to develop in the late summer in the leaf axils of the year's current growth (Dupler 1917). Maturation of the strobili and pollination of female strobili occur the following spring. Female strobili are uniovulate and when fertilized produce a single ripe seed that is surrounded by a red, fleshy, aril-like structure. Seed ripening begins in late July or early August and continues for 6–8 weeks into early fall.

The growth form of Canada yew is diffuse; branches are typically ascending and rarely arborescent (see Fig. 1). Vegetative propagation of Canada yew occurs when these ascending branches are pressed to the ground and take root. Axillary branches off the main stem axis may also take root, causing the plant to spread along the forest floor (Figs. 1 and 2). Connections between these rooted branches, or shoot systems, can be traced under the litter layer, but eventually these connections rot. In high-density populations of Canada yew genetic relatedness of neigh-

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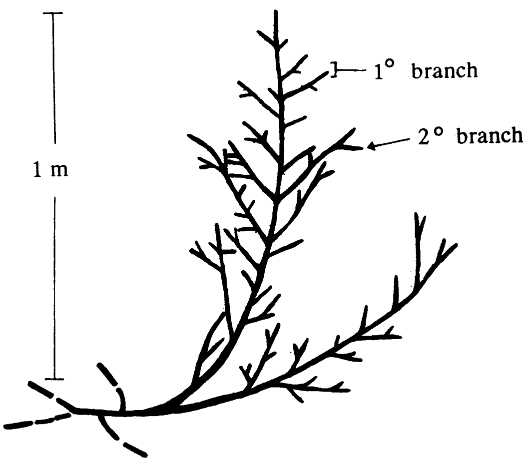

Fig. 1. Skeleton view of a hypothetical shoot system of Canada yew. Primary and secondary branches as described in the text are indicated. For mapping strobilus position, primary branches were numbered consecutively beginning with the shoot tip. With the exception of the shoot tip, primary branches are equivalent to axillary branches. Dashed lines correspond to belowground connections to other yew shoot systems.

boring plants, or more appropriately, shoot system networks is difficult to determine because of this layering habit.

Methods. Field work was performed at North Grey Cloud Island, Minnesota (92°56′W longitude, 44°46′N latitude) and at the Apostle Islands National Lakeshore, Bayfield, Wisconsin (90°45′W longitude, 46°50′N latitude).

In Spring 1984 and 1985 at North Grey Cloud, I paired terminal branches of neighboring yew plants, or shoot systems, (eight in 1984 and nine in 1985) that contained both female strobili and male strobili. I had determined that these plants were not connected belowground. I randomly assigned one member of the pair of branches to the treatment or control group. Treatment branches were enclosed in parchment "Pollen-tector" bags (Carpenter Paper Company, Des Moines, IA 50302). Branches were bagged while male strobili were immature; no pollen had been shed in the population prior to bagging. Only a portion of the branch could be covered by the bag, and I labeled the location of the end of the bag with a tag. The number of ovules on treatment and control branches ranged from nine to 40. I bagged four additional branches, each on a separate plant, from which all male strobili had been removed to determine whether female strobili developed in the absence of pollination and to measure the extent of pollen leakage into the bags.

Bags were removed one month after the pollen shedding season had ended. I counted the number of developing seeds on bagged and unbagged branches. Developing seeds were easily distinguished by their swollen, green appearance from non-developing seeds which were yellow and unchanged in size. No mortality of developing seeds had occurred by this time. I assumed, therefore, that this census was a measure of pollination success. I measured seed production by counting seeds or empty receptacles that indicated the re-

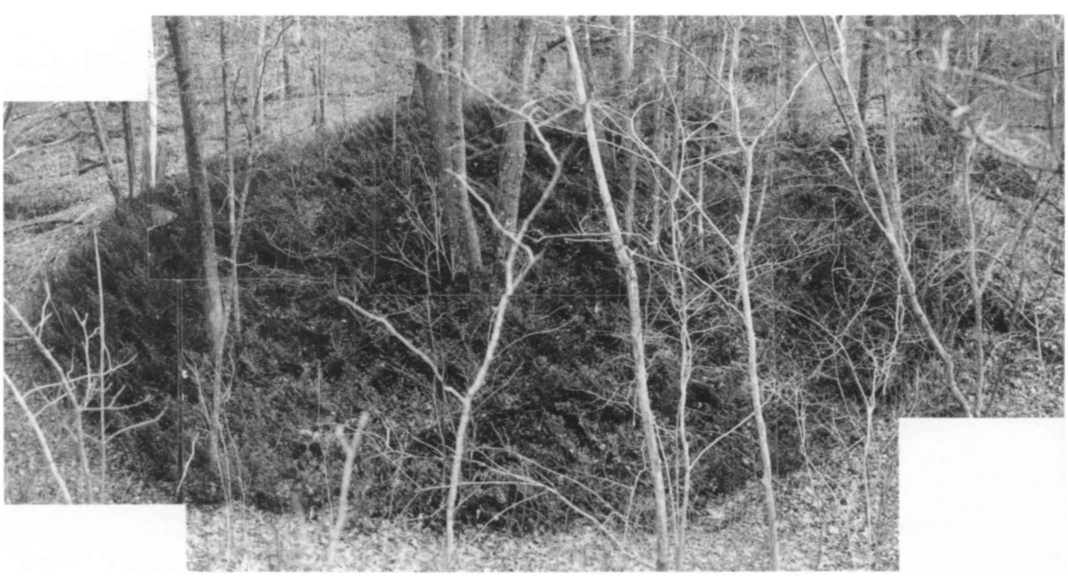

Fig. 2. A dense Canada yew colony.

Table 1. Mean and standard deviation of (a) pollination success (pollinated ovules expressed as a proportion of total ovules), (b) seed set (ovules producing seeds expressed as a proportion of total ovules, and (c) mature seed production expressed as a proportion of pollinated ovules for bagged and unbagged Canada yew branches at Grey Cloud, MN 1984 and 1985. "n" refers to the number of branches. Analyses were performed on arcsin $\sqrt{Y}$ square root transformed data. Results presented in the table have been back-transformed. An asterisk by the mean or standard deviation indicates a significant difference between treatments for that parameter in that year.

		Pollination success		Seed set		Proportion of matured seeds	
	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1984							
Bagged	8	0.78*	.07	0.23	.02	0.39	.14*
Unbagged	8	0.97*	.03	0.24	.01	0.25	.01*
1985							
Bagged	9	0.45**	.15	0.14*	.08	0.50	.31*
Unbagged	9	1.00**	.02	0.34*	.02	0.35	.02*

* $P < 0.05$.
** $P < 0.005$.

moval of a ripe aril and seed. All available ripe seeds on treatment branches were collected, removed from their arils, and air-dried for at least 6 months. Air-dried seeds were weighed to the nearest milligram.

I compared the effects of treatment on the proportion of ovules pollinated (pollination success), proportion of total ovules matured as seeds (seed set), and proportion of pollinated ovules matured as seeds (maturation level). Student's *t*-tests (Sokal and Rohlf 1981) were performed on arcsin $\sqrt{Y}$ transformed proportions; Wilcoxon's matched pairs signed ranks test was used for treatment comparisons when treatment variances were unequal (Sokal and Rohlf 1981).

I recorded the branch position of male and female strobili on seven plants in a Canada yew population on Stockton Island of the Apostle Islands. I designated the terminal branch as branch one and then numbered all distal primary branches (those coming off the main stem axis) in sequence (i.e., branch two, branch three, etc.) down to the base of the stem (Fig. 1). Both the branch number and the number and sex of strobili on the branch were recorded. I compared the median branch (the location of 50% of male or female strobili) of each strobilus type using Wilcoxon's two sample test (Sokal and Rohlf 1981).

Results and Discussion. Negative effects of self-fertilization on plant fitness can be expressed in a variety of ways: (1) reduced seed production resulting from the low fertilization of ovules or low maturation percentages; (2) reduced seed masses and a greater proportion of unfilled seeds; and (3) low seed germination and seedling vigor. I was unable to germinate *Taxus* seeds during the course of this study, so the relationship between seed germination, seedling growth, and selfing in Canada yew remains unresolved. Seeds of all members of the genus *Taxus* have tenacious dormancy (Rudolf 1974; Melzack and Watts 1982).

SEED PRODUCTION. Unbagged branches had a significantly greater pollination success than bagged branches in both 1984 and 1985 (Table 1). Bagged branches also had a significantly lower seed set in 1985, but there was no significant difference in 1984. Maturation levels of bagged branches were higher in both 1984 and 1985 but these differences were not significant.

Pollination success in bagged branches ranged from 33% to 100% in 1984 and from 6% to 94% in 1985, but the variances in pollination success did not differ significantly by treatment. The lower pollination success of bagged branches could reflect reduced pollen transfer within the bags rather than differences in self-fertility. Variances in maturation levels were significantly greater in bagged branches ($P < 0.05$) in both years (Table 1). This could reflect differences in levels of inbreeding depression among yews.

In branches bagged without male strobili, 1.7% of the ovules began developing one month after pollen shedding, but none of the developing ovules matured into seeds. Parthenocarpy, the development of fully formed, empty seeds in the absence of pollination, has been reported in the genus *Taxus* (Orr-Ewing 1957), but in this experiment, I cannot rule out the possibility of pollen leakage into the bags. However, the rarity of

Table 2. Mean seed masses in mg (and 1 SE) of bagged and unbagged branches in Grey Cloud, MN Canada yew population for 1984 and 1985. The number of seeds in each treatment is indicated by n.

	1984		1985	
	n	mass	n	mass
Bagged	11	30.94* (1.15)	31	26.13 (0.44)
Unbagged	25	28.09 (0.75)	21	26.96 (0.72)

* $P < 0.05$.

developing ovules in branches bagged without male strobili indicates that the vast majority of ovules developing and maturing as seeds on branches bagged with male strobili were self-pollinated.

SEED MASSES. Seeds of bagged branches were significantly heavier in 1984; no difference in seed masses was observed in 1985 (Table 2). Seed masses have been shown to be positively correlated with early seedling development in *Pinus strobus* (Spurr 1944). Sorensen and Miles (1974), however, noted that 1st year growth of selfed progeny was 18% to 21% lower than open-pollinated progeny in Douglas-fir (*Pseudotsuga menziesii*) even though the selfed seeds of this species showed negligible differences in seed mass compared to open-pollinated seeds. A lack of inbreeding depression in *Taxus* seedlings, therefore, cannot necessarily be inferred from seed mass data alone.

I collected 102 ripe seeds from treatment plants over two years. Fourteen of these seeds were empty, but the proportion of unfilled seeds did not differ between bagged and unbagged plants ($\chi^2 = 0.12$). A high proportion of unfilled seeds is a strong indication of high levels of self-pollination in plants that suffer from inbreeding depression (Sarvas 1962). Based on this criterion, treatment yews show little evidence of inbreeding depression when compared to control yews.

STROBILUS LOCATION. Thirty-five percent of the primary branches in the seven measured Canada yew plants had both male and female strobili; the rest had either male or female strobili. Typically, within a primary branch system, either male or female strobili only were located on secondary branches, but a low percentage (<5%) of secondary branches had both male and female strobili. Greater than 99% of the male strobili were located on current growth (branch tissue produced the previous growing season). More than 33% of the female strobili were located on growth two years or older. I have observed this latter phenomenon in all Canada yew populations that I have studied although the percentage varies from population to population (Allison unpublished data). The median branch for male strobili was lower than the median branch for female strobili in four of seven plants. One plant had a lower median branch for female strobili, and in two plants there was no significant difference in the median branch for the two strobilus types.

In conifers, male strobili are typically located on lower branches (Smith 1981), and this has been suggested as a means of reducing self-pollination in monoecious species (Fowler 1965b). I did a simple statistical test that showed a slight tendency for spatial separation of male and female strobili in Canada yew. More detailed analysis might have shown differences in their distribution, but the growth form of Canada yew renders such differences superfluous. Canada yew lacks strong apical dominance, and axillary branches within a shoot system are often only slightly lower than the terminal branch of the main shoot axis (Fig. 1). In addition, Canada yew has limited vertical growth; plants spread horizontally forming large dense clones. Ovules on one ramet or shoot probably receive large quantities of pollen from male strobili on other shoots within the clone.

Female strobili within a plant may appear up to 12 days prior to the maturation of male strobili. Pollen dispersal may occur over a time period as short as 24 hours (Allison personal observation). I do not know if differences in timing of maturation reduce self-pollination.

The results indicate that Canada yew is self-fertile, and that there are no obvious barriers to self-pollination under natural conditions. The failure of this study to detect inbreeding depression can be explained in two ways. First, there is a high degree of selfing in natural populations of Canada yew. Ovules on unbagged branches may have received considerable self-pollen from the same branch or from genetically identical but separate shoot systems. High density Canada yew populations, such as at Grey Cloud, may consist of a low number of genetically distinct individuals spreading clonally. Nearest neighbors donating pollen to ovules on unbagged branches could be members of the same genet.

If the above is the case, it would be more appropriate to say that I was comparing the effects of between-ramet and within-ramet pollination. Many of the seeds produced by unbagged branches could also have resulted from self-pollination.

and both treatment and control groups could be showing the negative effects of selfing. Female plants that I created in 1986 at Grey Cloud had significantly lower pollination percentages, but not seed production, than monoecious controls, indicating that significant within-plant pollination occurs even in a high density yew population (Allison 1990b). To adequately test the effect of self fertilization, branches without male strobili should be bagged and pollen from genetically different yews applied to the ovules.

In another experiment, emasculated yews in a low density yew population at the Apostle Islands did not have higher maturation levels than monoecious yews (Allison 1990b). Both groups were naturally pollinated. Monoecious yews had higher seed production than female yews, and this difference presumably was due to selfing. Female yews in this population were all outcrossed. This result suggests that outcrossed seeds are not more likely to mature than selfed seeds.

A second, and not mutually exclusive, hypothesis is that Canada yew has low genetic variability and has not accumulated a significant proportion of lethal recessive genes. Electrophoresis, for example, detected no genetic polymorphisms in red pine (*Pinus resinosa*), which is highly self-fertile (Fowler 1965a, 1965b; Fowler and Morris 1977). Full evaluation of both hypotheses await further study.

Finally, as mentioned previously, Canada yew is the only monoecious member of the genus *Taxus*, and given the self-fertility of Canada yew, it is of interest to speculate on the adaptive significance of Canada yew's mating system. Ghiselin (1969) proposed that hermaphroditism (of which monoecy in plants is one type) may enhance reproductive success when potential mates are scarce. It is widely assumed that the effectiveness of wind-pollination is dependent on conditions that promote high concentrations of airborne pollen (Whitehead 1983), and there is a strong relationship between pollen production, plant spacing, and pollination in Canada yew (Allison 1990a). Monoecy in Canada yew may, therefore, be selectively advantageous under conditions of reduced pollen availability (or the low abundance of male "mates"). This hypothesis is supported by the greater seed production of monoecious Canada yews relative to female yews when pollen limits seed production (Allison 1990b).

It is not known whether monoecy is the derived or ancestral trait in the genus *Taxus*, but the presence of dioecy in all other *Taxus* species (and possibly the other members of the family Taxaceae) suggests that the most parsimonious explanation is that monoecy is a derived trait. Answers to questions concerning the evolutionary origin (or maintenance) of monoecy within the genus *Taxus* as well as the genetic variability of Canada yew require further study.

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