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Reproductive biology of the monoecious clonal shrub *Taxus canadensis*¹

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WILSON, P. (Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303), M. BUONOPANE (Department of Biology, Bates College, Lewiston, ME 04240) AND T. D. ALLISON (Department of Forestry and Wildlife, University of Massachusetts, Amherst, MA 01002). Reproductive biology of the monoecious clonal shrub *Taxus canadensis*. Bull. Torrey Bot. Club 123: 7–15 1996.—Strobilus production, pollination, and maturation were studied in *Taxus canadensis*, a procumbent clonally-spreading shrub. Plants that produced many cones had greater shoot growth; no obvious tradeoff between sexual effort and vegetative growth was observed. *T. canadensis* is monoecious, but plants showed considerable variation in phenotypic gender. Because related species are dioecious, we hypothesize that *T. canadensis* evolved from a dioecious ancestor. Monoecy may have been favored as a means of assuring pollination via selfing; the proportion of ovules pollinated was positively correlated with the number of male cones on a plant. Selfing may be at the cost of inbreeding depression; 26% of the female cones aborted, about twice the percentage of the dioecious *Taxus cuspidata*. Application of nutrient fertilizer did not reduce the abortion percentage. Seed and aril maturation in *T. canadensis* occurred over a three month period, much more gradually than in *T. cuspidata*. Removal of the seeds, probably by antagonistic rodents, was very rapid and thorough in *T. canadensis*. Asynchronous ripening and monoecy may help reduce seed predation by rodents by reducing the conspicuousness of “fruiting” displays relative to the dioecious species.

Key words: monoecy, phenotypic gender, pollination limitation, reproductive allocation, seed abortion, seed consumption, *Taxus canadensis*.

Detailed studies of the reproductive biology of wind-pollinated woody plants have lagged behind those of showy meadow herbs. In the present study, on *Taxus canadensis* Marsh., we provide data relating to several topics that have received much attention from authors who were mainly focusing on other types of plants: (1) strategies of monoecy versus dioecy (Bawa 1980, 1994; Muenchow 1987; Thomson and Brunet 1990), (2) life history allocation to growth and reproduction (Delph 1990; Primack and Hall 1990; Cippollini and Whigham 1994), (3) ecological variation in the degree of pollination limitation (Zimmerman and Pyke 1988; Young and Young 1992; Wilson et al. 1994), (4) the abortion of immature seeds (Stephenson 1981; Willson and Burley 1983), and (5) seed predation versus effective seed dispersal (Janzen 1971; Price and Jenkins 1986). *Taxus canadensis*

adds a distinct perspective on these issues, which we will speculatively relate to each other by outlining an integrated shift in the reproductive system of *T. canadensis* away from that of other *Taxus* species.

Taxus canadensis is a monoecious evergreen shrub native to mixed conifer-hardwood forests of the northeastern United States and southeastern Canada (Allison 1991). It is the only monoecious member of its genus, and monoecy in this case almost certainly arose from dioecy (see Discussion). Male and female cones are initiated during the summer in the axils of leaves, and they overwinter as buds. In the spring, ovules are fertilized by wind-dispersed pollen. Unpollinated ovules remain small and become whitish-yellow, thus distinguishing them from developing nascent seeds. Throughout the summer some cones abort, with first the receptacle and then the seed coat becoming shriveled and yellow. The seed, receptacle, and pedicel of these aborted cones eventually fall off the plant. Mature female cones consist of a single seed surrounded by a fleshy red aril.

Taxus canadensis spreads clonally. Procumbent branches take root resulting in plants that expand horizontally. Branch by branch, the clone spreads along the forest floor, sometimes

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Table 1. List of study sites.

Site	N ^a	Males counted	Females counted	Fertilizer experiment	Site description
Templeton	51	Yes	Yes	Yes	Roadside, mixed hardwood-conifer canopy, dense patch.
Riceville Road	72	Yes	Yes	No	On a steep hill, dense, next to pasture, in a pine stand.
Riceville Pond	50	No	Yes	No	Open, relatively high light, roadside, mixed canopy.
Nelson Road	44	No	Yes	Yes ^b	On a hill, mixed hardwood-conifer canopy.
Nelson Brook	50	No	Yes	No	Next to brook, moist, mixed hardwood-conifer canopy.

^a Number of "plants" sampled = rooted branches (see text).

^b Possible effects on fruit maturation were not followed.

forming huge patches. In our study, a "plant" was considered to be one shoot system emanating from the forest litter. Our study plants were well spaced, but some of them may have been separate ramets of the same genet.

Taxus canadensis, though poisonous to humans, is a winter forage for deer and moose (Allison 1990a). Birds are assumed to act as dispersal vectors, eating the red aril and voiding the seed at some distance from the parent plant. Studies on other species of *Taxus* have shown that seeds fed to birds and spit out or excreted can later germinate (Barkowiak 1978). Not much information is available concerning seed predation by rodents, but Bartkowiak (1978) cites squirrels as eating *Taxus* seeds, and Allison (pers. obs.) has often noted rodent teeth marks and has observed chipmunks, squirrels, and mice eating *Taxus canadensis* seeds.

Methods. We studied *Taxus canadensis* at five sites in north-central Massachusetts, as described in Table 1. At each site, approximately fifty plants (i.e., rooted shoot systems) were chosen at random distances along parallel transects and tagged. In late May, we recorded for each plant the number of male cones, the number of female cones, and the number of withering, presumably unfertilized ovules, which we distinguished from pollinated immature seeds on the basis of color. Due to the late date of sampling, the counts of male cones are only estimates—some of the male cones may have already fallen off—and at three of the five sites the number of males cones could not be determined with satisfactory certainty (Table 1).

In late June, we collected data on size and growth for each plant at the five sites. The basal diameter at ground level was measured with cal-

ipers twice, with the measurements taken perpendicular to each other. The mean of these two numbers was used to represent plant size. New (1994) growth was measured as the length of the five longest sprig tips, which were lighter green in color and softer in texture than previous years' growth. The average of these five numbers was used as an indication of the amount of growth.

Seed development was closely monitored on the twelve plants at the Templeton site that had ten or more ovules. To test for nutrient limitation of seed maturation, half the plants were given about one pint of Rapid Grow[®] fertilizer every two weeks from mid-June until the end of "fruiting" in September. At the beginning of July, we tagged each branchlet that bore a female cone, and we recorded the condition of the cone every two to three days. Cones were scored as (1) green and healthy but not yet with a red aril, (2) having a red aril, (3) removed leaving only the receptacle or pedicel stub, or (4) yellow and aborting. Very few were unaccounted for. For comparison, we also followed seed maturation and removal on a stand of cultivated *Taxus cuspidata*, which is a dioecous upright tree. The same procedure for marking and scoring female cones was used.

In order to evaluate whether or not rodents eat *Taxus* arils and seeds, we live-trapped a *Peromyscus maniculatus* underneath a clone of *T. canadensis*. This was done after the peak in seed maturation but while some seeds were still ripening. We placed the animal in a bucket with five mature *T. canadensis* cones and periodically observed what had been eaten.

Results. GENDER. Phenotypic gender was calculated following Lloyd (1980; Lloyd and Bawa

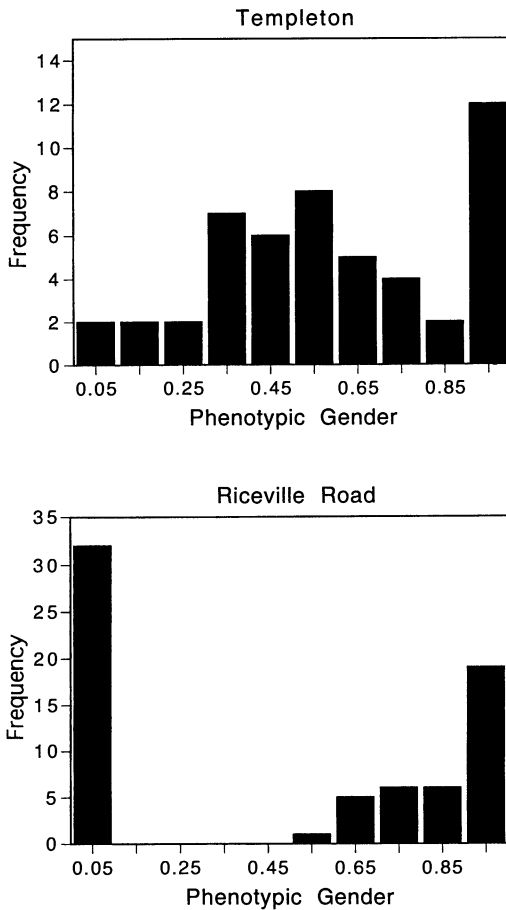


Fig. 1. Frequency distribution of phenotypic gender (*sensu* Lloyd and Bawa 1984) of *Taxus canadensis* for Templeton and Riceville Road. Gender ranges from 0.0 (female function) to 1.0 (male function).

1984; Allison 1991) as being the proportion of male to female cones relative to male and female representation in the rest of the population. An all-female plant would have a value of 0.0, an all-male plant a value of 1.0. The distributions of phenotypic gender were tested for deviations from unimodality using a statistic proposed by Engelman and Hartigan (1969) and calculated for *Taxus canadensis* in northern Wisconsin by Allison (1991). Phenotypic gender at the Templeton site was not significantly different from unimodal ($P > 0.05$), but it did show considerable variation among plants, with a large number of hermaphrodites and some plants that were essentially all male (Fig. 1, upper panel). The Riceville Road site was significantly and distinctly bimodal ($P < 0.05$) with individuals strongly tending to be either male or female

(Fig. 1, lower panel). At both sites, intrapopulation differences are evident in the percentage of male and female plants. The two sites also differed in gender, with Templeton having a higher percentage of male plants and Riceville Road a higher percentage of female plants.

GROWTH AND REPRODUCTION. We were interested in whether there was a negative (tradeoff) relationship, a positive (general vigor) relationship, or no consistent relationship between cone production and vegetative growth. In this and other analyses, the number of cones was square-root transformed, since the square roots of cone numbers were more or less normally distributed. Furthermore, since larger plants naturally produce more cones than smaller plants, we attempted to remove the effect of size in two ways. First, we divided the number of cones (after transforming) by the basal diameter of the plant. In relating female reproductive output to growth, all five sites showed a weak but persistent positive correlation (Fig. 2a, left panel). This relationship was significant for Riceville Road and marginally significant for Nelson Brook (see Fig. 2 for statistics). Plants that did not grow very much also did not produce many female cones; plants that grew more produced either few or many female cones, and those that produced few tended to be plants that were predominantly male (Fig. 2a). We also adjusted for basal diameter in a second type of analysis: we combined data from all the sites and calculated a partial correlation of the rank of female cone production against the rank of growth, holding basal diameter and population constant. In this analysis, $r = 0.224$ ($N = 262$; $P < 0.001$). For the two sites where we scored male cone production, Templeton and Riceville Road, we looked for a correlation between male reproductive output and growth. We found positive correlations between growth and the square root of the number of male cones divided by basal diameter. This was significant for Templeton when all plants were included, and was significant for Riceville Road when only male plants were included (Fig. 2b, right panel).

POLLINATION SUCCESS. The percentage of female cones that developed after the receptivity stage, hereafter "pollination success," varied among populations. Templeton and Nelson Road had close to 100% pollination success while Riceville Road and Riceville Pond showed only 50–60% median pollination success. Nelson Brook had a median pollination success of 74%

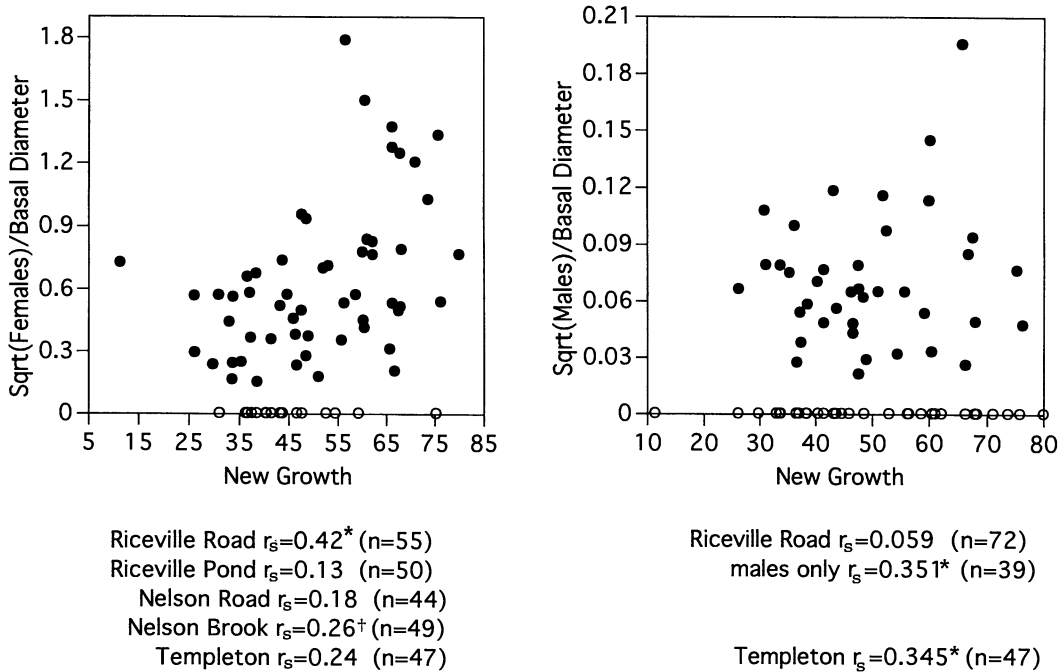


Fig. 2. Comparison of reproductive output and growth for *Taxus canadensis* at Riceville Road. Sqrt = Square root transformed. Spearman's Rank correlation coefficients are given for all five populations ($^+P < 0.1$; $*P < 0.05$). Open circles indicate male individuals on the left panel and female individuals on the right panel.

(Table 2). The sites also differed in the amount of variation in pollination success among plants within each population. For example, Templeton showed little variation with most plants experiencing high pollination success. Riceville Road, however, displayed very broad variation, with a bimodal distribution of success. There were many plants with a pollination success of less than 5% and many with a pollination success close to 100%, as well as variation between the extremes (Fig. 3). Pollination success was positively correlated with the number of male cones produced (Templeton and Riceville Road combined $r_s = 0.57$; $N = 93$; $P < 0.001$). A plant with a high number of male cones will have a high pollination success, but a plant with a low

number of male cones might experience high or low pollination success (Fig. 4).

SEED MATURATION, ABORTION, AND PREDATION. Aril and seed ripening was very gradual in *Taxus canadensis* (Fig. 5, upper panel). At the Templeton site, seed ripening extended over a period of three months. There was an early wave of maturation at the beginning of July, but maturation soon slowed, and the last aril did not turn red until the end of September. In addition to maturing gradually, the ripe "fruits" were spatially scattered within and among ramets and did not produce a showy display. The abortion rate was 26% overall; it ranged from 50% to 8%, and there was no significant effect of nutrient fertil-

Table 2. Among-site variation in pollination success.

	No. ovules pollinated Total no. of ovules	Median pollination success ^a	N ^b
Templeton	$\frac{423}{449} = 94\%$	1.0	(51)
Riceville Road	$\frac{324}{1213} = 27\%$	0.6	(72)
Riceville Pond	$\frac{341}{572} = 60\%$	0.5	(47)
Nelson Road	$\frac{661}{712} = 93\%$	0.96	(37)
Nelson Brook	$\frac{175}{235} = 75\%$	0.74	(50)

^a Kruskal-Wallis $\chi^2 = 45.13$ (4 df); $P < 0.001$.

^b Number of "plants" sampled = rooted branches (see text).

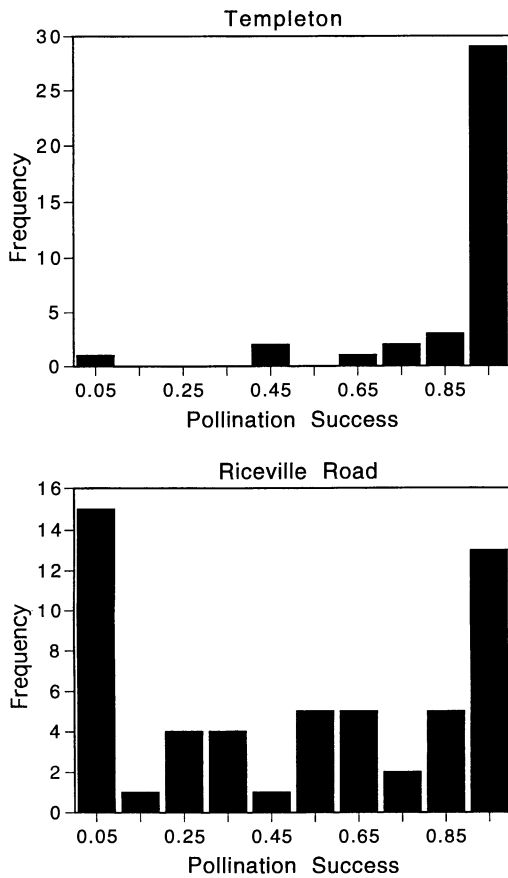


Fig. 3. Frequency distribution of pollination success for *Taxus canadensis* for Templeton and Riceville Road.

izer addition on the proportion aborted (angularly transformed; $t = 0.777$ with 10 df; $P = 0.455$). Most of the abortion happened well after the first arils of other seeds on a plant had turned red. In our study (unpubl. data) of the dioecious species *Taxus cuspidata*, maturation was much more simultaneous with most arils on a plant turning red in the period of a few days (Fig. 5, lower panel). Also the cones were produced in dramatic clusters on the trees. The abortion rate was lower, 13%, and abortion occurred before the other cones matured—also most of this abortion occurred on one plant, unlike the situation in *T. canadensis*. Only three of the 189 cones that we followed were removed by animals. Most arils became mushy or rotten several weeks after becoming red, and then the cones fell to the ground. In *Taxus canadensis* when an aril turned red, the cone was generally removed very quickly by animals: the median time to re-

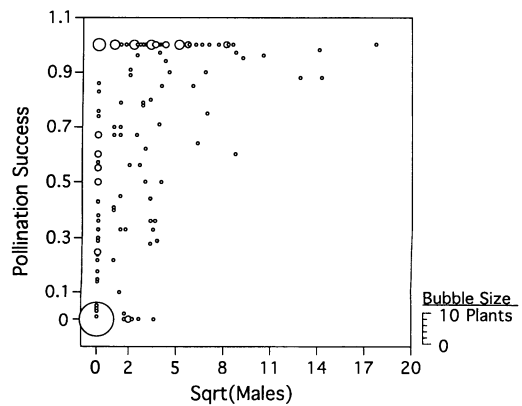


Fig. 4. Pollination success of female cones on abundance of male cones for Templeton and Riceville Road combined. Sqrt = Square root transformed. Each bubble represents one to several plants, as indicated by size.

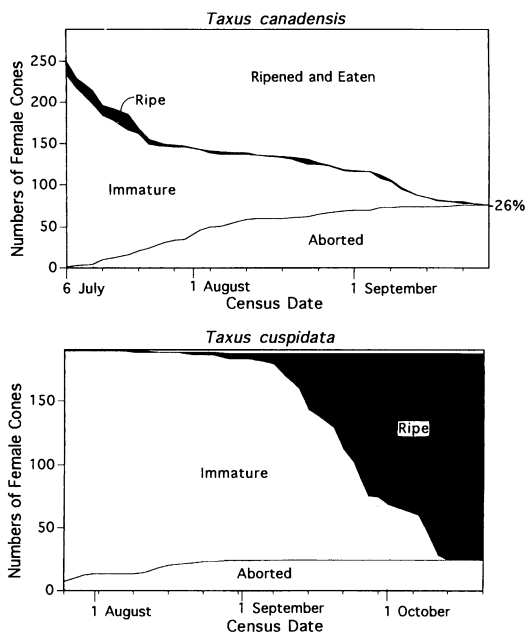


Fig. 5. Cumulative seed maturation and abortion. For *Taxus canadensis*, there were 13 cones that were eaten before they matured, and they are not included in the graphed data. “Ripe” means having an aril that was seen as having some red or in a few cases estimated as likely to turn red before the next census; it does not mean the arils and seeds had reached full size, which for *T. canadensis* most never did. All numbers on the graph are based on pooling all censused plants in the population, but there were not major differences among plants in *T. canadensis*. For *Taxus cuspidata*, the several declines in number of immature cones are a result of different individuals maturing their cones on different weeks; even when these individuals are pooled the simultaneous maturation is dramatic compared to *T. canadensis*.

removal was 2.3 days (one census unit), the mean 3.8 ± 2.72 SD ($N = 74$). Fifty-one percent of cones were removed when they had been green in the previous census ($N = 184$). These typically were well developed, and some of them may have been removed after turning red but before we recorded them as such. We could not tell directly whether cones were being removed by birds that might disperse the seed or by rodents, but in numerous instances we found gouged arils with the seed removed and pedicel stubs that seemed to have been cut by a sharp tooth, not broken by merely having the aril plucked. Our captive deer mouse ate all five cones that we provided, leaving only the intact receptacles. The first was eaten after 1 hour and 22 minutes, and when we left the mouse alone and returned some 4 hours later, the remaining four cones were eaten, again with the receptacles left intact.

Discussion. Our results on gender distribution confirm the findings of Allison (1991) from sites in the Apostle Islands of Lake Superior. In both regions, and hence probably for the species as a whole, there is a dioecious tendency toward bimodal gender. This tendency may be a phylogenetic holdover from a dioecious ancestry. All other species of *Taxus* seem to be usually dioecious (*T. baccata* and *T. cuspidata*—pers. obs.; *T. brevifolia*—Taylor and Taylor 1981; *T. floridana*—Godfrey 1988; *T. globosa*—Standley and Steyermark 1958; *T. sumatrana*—de Laubenfels 1978; *T. chinensis*, *T. wallichiana*, and *T. yunnanensis*—Botanical Institution Chinese Academy of Sciences, Beijing, 1972, and Cheng *et al.* 1978). Furthermore, related genera are dioecious such that a phylogenetic analysis of character evolution unambiguously infers the three hypothetical common ancestors below *Taxus* to have been dioecious (Hart 1987; Donoghue 1989). It is, therefore, almost certain that *Taxus canadensis* is secondarily monoecious.

What ecological conditions might be functionally associated with the change in breeding system toward monoecy? Most discussions of the strategic stability of monoecy versus dioecy have focused on evolution in the opposite direction, that is, from cosexuality to dioecy. For instance, the arguments presented by Bawa (1980), Givnish (1980), Muenchow (1986), and Charlesworth and Charlesworth (1978) all center on possible reasons for the sexes becoming separated. The arguments, however, can be turned

around. Two non-mutually exclusive theories seem reasonable for *Taxus canadensis*: (1) monoecy may have been favored because it allowed for self-pollination in plants that had become frequently pollen limited (Allison 1990b); and (2) dioecy may have been no longer favored because the ecology of seed dispersal and survival no longer made it advantageous to have as many “fruits” as possible concentrated on half the plants (Bawa 1980; Givnish 1980). Both chronic pollen limitation and chronic seed predation may in turn be due to the prostrate, outwardly spreading, clonal habit.

Life history theory typically assumes that there is a tradeoff between reproductive effort and vegetative growth (Willson 1983; Stearns 1992; Reekie and Bazzaz 1992). Our results do not support this assumption. We found positive correlations between cone production and the length of new shoots, even holding plant size constant. This could be accounted for by a number of mechanisms (Reekie and Bazzaz 1987). There seems to be more variance in general vigor affecting both growth and reproduction than in any tradeoff between growth and reproduction. Of course, there may still be a negative genetic or evolutionary correlation, but most of the variance among plants seems to be in how much resource they have acquired, not in how they allocate it (van Noordwijk and de Jong 1986). This suggests that the plants that are best at spreading clonally may also be those that are best able to afford producing large numbers of male and female cones. Such a complex positive correlation cannot be proven without a controlled experiment, but the census data do point in that direction. The plants that grew more, and probably have spread out more, also produced more cones and probably sired and set more seed.

Our pollination-success results indicate that some of our populations were experiencing pollen limitation (see also Allison 1990b, 1990c, 1993), but, interestingly, some parts of those populations showed high pollination success. Considerable variation must therefore exist in the availability of airborne pollen at a very local scale. Substantial site-to-site differences in pollination limitation have been found in insect and bird pollinated species (see references in Wilson *et al.* 1994, p. 285; Wilson 1995). Our results provide an example of such variation in a species with wind dispersed pollen. Some of this variation among sites may be explained by variation in levels of selfing associated with the

degree of monoecy. As the number of male cones increased pollination success also increased. Selfing may have prevented pollen limitation in some plants and in some sites. Specifically, pollination did not limit female function at Templeton where plants were mostly hermaphrodites or males, whereas pollination was limiting for some plants at Riceville Road where there were large numbers of essentially female plants. It is quite possible that, if *Taxus canadensis* were still dioecious, it would be chronically pollen limited. The architecture of the species seems to act against adequate cross-pollination: layering increases the size of clones horizontally rather than vertically, and plants are very close to the ground as well as protected by a dense overstory such that pollen grains may not have far to fall in air that is rarely turbulent. Individuals that were able to become cosexual may have been favored after the evolution of this growth form.

The high rates of seed abortion that exist in many plants are a curious feature to explain (Stephenson 1981). Several explanations have been proposed. Conceivably it is because plants are hedging their bets in favor of stupendously good years when resources are so plentiful that they are able to mature all their seeds (Ehrlén 1993). Or perhaps it is because mother plants are choosing to mature the best embryos from a larger field of candidates (Casper 1988; Bertin and Peters 1992). Or perhaps some embryos are genetically inviable on their own, either because of inbreeding or genetic bad luck (Lee 1988). Seed abortion in *Taxus canadensis* was 26% at our study site in Massachusetts, and this confirms the high levels of abortion observed by Allison (unpubl. data) in Minnesota and Wisconsin. Almost all of the abortion happened *after* many of the cones that would develop had already completely matured. Light limitation may play a role. Aborted cones are a bit smaller than fully mature cones—the seed is perhaps half as large, and there is no aril. Still it is hard to believe that not maturing them is energetically imposed. In addition, we found no evidence from our nutrient fertilizer study that abortion was due to lack of mineral nutrients. The explanation that seems the most reasonable and would be related to differences between the species in mating system is seed failure due to selfing. Allison (1990c) did an experiment showing that female cones on emasculated plants (where selfing was prevented) has similar abortion rates to monoecious plants (where

pollination success was higher presumably because of selfing; see also Allison 1993). His experiment did not test whether or not there is inbreeding depression given equal pollination by self and outcross pollen. Monoecy may yet be shown to be at the cost of increased abortion due to inbreeding depression.

Seed predation was exceedingly high in our study of *Taxus canadensis*. Although we have not discovered a way of directly distinguishing between removal of seeds by birds versus rodents, we believe rodent attack was overwhelming, as is quite possibly the case for many understory plants (Heithaus 1981). Because *T. canadensis* plants are procumbent, the cones are produced close to the ground where they are easily accessible to mice and chipmunks. We found dozens of instances of what we interpreted as teeth marks. And we know that rodents will eat seeds and arils of *T. canadensis*. Some seeds are even eaten before they mature, and most do not stay on the plant for more than a few days after developing a red aril. It would be interesting to do an experimental study of how distance from the ground and number of ripe cones affect removal rates by rodents and birds. There is no indication that large “fruit” crops would be especially attractive to birds who might disperse the seeds. There is no indication that birds are attracted to the seeds of *T. canadensis* at all. Thus, Givnish’s (1980, 1982) theory for the evolution of dioecy could work in reverse for the evolution of monoecy in *T. canadensis*: allocating energy to male function probably does not lower the fruit crop below any threshold of attractiveness to beneficial birds but it might to antagonistic mammals (on the quality of mammals as seed dispersers/predators see Smith et al. 1986; Davidar and Morton 1986; Carr 1992). The very gradual and scattered presentation of “fruit”—much more gradual and scattered than in *Taxus cuspidata*—might well reflect an ecology in which a lone cone has a greater chance of not being eaten than a cone on a heavily laden plant, in which case the female gain curve would be convex, not concave, and monoecy would be favored (Charnov 1982).

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