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VARIATION IN SEX EXPRESSION IN CANADA YEW (*TAXUS CANADENSIS*)¹

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Sex expression was measured in several Canada yew (*Taxus canadensis* Marsh.) populations of the Apostle Islands of Wisconsin and southeastern Minnesota to determine the extent of variation within and among populations. Sex expression was recorded qualitatively (monoecious, male, or female) and quantitatively (by male to female strobilus ratios or standardized phenotypic gender). No discernible trends in differences in sex expression among populations or habitats were recorded. Trends in sex expression of individuals within populations were complex. Small yews tended to be male or, if monoecious, had female-biased strobilus ratios. Large yews were monoecious but had male-biased strobilus ratios. Phenotypic gender, recorded as relative maleness, however, was negatively, but weakly, correlated with plant size. Gender distribution in four of five populations was bimodal, suggesting that cosexual populations consist of male and female morphs. Strobilus ratios of individuals in Apostle Island populations showed significant annual variation, but gender for these same plants was significantly correlated from year to year. Annual adjustments in gender were most pronounced in small yews. The results indicate that relative investment in male and female reproductive structures by Canada yew individuals is responsive to environmental variation, but sex expression also has a proximate genetic component.

Several studies have shown that plants of cosexual species (containing individuals producing both pollen and ovules) vary widely in their relative male and female reproductive effort. Lloyd (1980) developed the concept of standardized phenotypic gender to provide a quantitative measure of this variation. According to this measure, a plant's gender ranges from 0.0 (female) to 1.0 (male) and is the contribution of male function (pollen) and female function (ovules and seeds) to a plant's fitness relative to other members of the population.

The variation in gender among individuals within a population, or gender distribution, suggests mechanisms by which sex expression in a plant population is determined. For example, in many plant species gender distribution is unimodal or monomorphic; functional gender may vary widely and continuously among individuals (Primack and Lloyd, 1980;

McKone and Tonkyn, 1986) in response to environmental variation or changes in plant size or vigor. Such variations in gender among individuals are not necessarily genetic. Alternatively, bimodal, or dimorphic, gender distributions also have been recorded in angiosperms where a cosexual plant population consists of male and female morphs (Lloyd, 1980). Female morphs, for example, may produce both pollen and seeds, but they comprise a discrete group of the population that reproduces primarily through seeds.

Dimorphic plant species are of special interest because they represent extremes in gender specialization. Lloyd (1980), for example, has suggested that dimorphic or discontinuous gender distributions indicate genetic differentiation within a population reflecting incipient or stalled evolution of dioecy. Studying dimorphic plant species should therefore illuminate conditions by which dioecy might evolve from monoecy or vice versa.

To date, dimorphic gender has not been recorded for any cosexual gymnosperm species, but this could reflect the lack of application of Lloyd's approach to this taxonomic group. The ratio of ovulate and staminate strobili (referred to hereafter as female and male strobili), however, does vary widely within gymnosperm species (Sarvas, 1968; Schoen, Denti, and Stewart, 1986), and these ratios vary according to environmental differences (Freeman et al.,

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1981) and in response to changes in plant size and vigor (Matthews, 1963; Smith, 1981; Whitham and Mopper, 1985). In this paper I describe annual and geographic variation in sex expression in Canada yew (*Taxus canadensis* Marsh.), a shrubby, monoecious gymnosperm. I recorded sex expression in Canada yew qualitatively (e.g., male, female, and monoecious) as well as quantitatively by standardized phenotypic gender (Lloyd, 1980) to assess the relative usefulness of these measures in understanding sex expression in Canada yew.

Species in the genus *Taxus* are principally dioecious, and the seeds are bird-dispersed (Chamberlain, 1966). Givnish (1980) hypothesized that dioecy in gymnosperms was linked with bird-dispersal of seeds. Canada yew, however, is monoecious, or cosexual, and is an exception to Givnish's hypothesis. Because of its unique position in the genus *Taxus*, it is of interest to examine variation in sex expression among Canada yew individuals in order to better understand the evolutionary and ecological significance of its mating system.

In addition, the study of sex expression in Canada yew is relevant to the debate concerning the importance of environmental vs. genetic impacts on gender. *Taxus* is cited as altering sex expression in response to environmental changes (Freeman, Harper, and Charov, 1980). Careful quantitative observations of the sex expression of individuals over extended periods of time is required to resolve this issue.

Canada yew is a monoecious, or cosexual, evergreen shrub of the mixed conifer-hardwood forests of northeastern United States and southeastern Canada (Martell, 1974). Male and female strobili are initiated during the summer and typically reside singly in leaf axils of branches produced that year. The male strobilus consists of 5–14 peltate microsporophylls attached to a central axis. Each microsporophyll contains two to ten microsporangia (Dupler, 1919). The female strobilus is uniovulate; the ovule is borne on a secondary shoot of a short primary shoot (Dupler, 1920). After fertilization the ovule develops into a stony seed that is surrounded by a red, fleshy, aril-like structure. Seed ripening in yew populations begins in late July or early August and continues for 6 to 8 weeks into early fall.

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 or shoot sys-

tems can be traced under the litter layer, but eventually these connections rot. In low-density populations, individual genets consisting of one or more branches are readily distinguished. In high-density populations the genetic relatedness of neighboring plants, or more appropriately, shoot system networks, is difficult to determine due to this layering habit. In sampling reproductive effort in high-density populations, I traced belowground connections to the rotted end. The sex expression of an individual genet was estimated by combining the results from connected shoot systems of the plant. In high-density populations, therefore, a plant constituted an unknown proportion of a genet.

Canada yew is a preferred winter browse of white-tailed deer (*Odocoileus virginianus* Rafinesque) (e.g., Beals, Cottam, and Vogl, 1960). All data on sex expression in Canada yew were collected from populations where current deer browsing was minimal or nonexistent. Browsing by deer significantly modifies sex expression in Canada yew (Allison, 1987).

MATERIALS AND METHODS

Reproductive effort in Canada yew was estimated by counting the number of male and female strobili and seeds produced by individual plants. This approach assumes that variation among individuals in the number of pollen grains per strobilus or the mass of seeds is low relative to the mean of these parameters (e.g., Stanton, 1984; Thompson, 1984; McKone and Tonkyn, 1986; McKone, 1989). The size of male strobili and seeds varied significantly among individuals within populations, but not among the different populations sampled (Allison, 1987). The range of variation was small (C.V. = 13.3% for male strobili and 11.1% for seed masses), however, indicating that counts of male strobili, female strobili, and seeds were reasonable estimates for comparisons of reproductive investment among individual yews and yew populations.

I sampled yew reproductive effort primarily at the Apostle Islands National Lakeshore, Wisconsin, USA (46°50'N latitude, 90°45'W longitude; hereafter referred to as Islands). The Islands comprise a 21-island archipelago located on the southwestern shore of Lake Superior. The Islands are edaphically similar; soils have developed from lacustrine deposits and glacial till derived from Lake Superior sandstone (Brander, 1983). As part of a larger study of sexual reproduction in Canada yew (Allison, 1987) I chose three different island populations

for study: Rocky Island, Otter Island, and Outer Island.

On each island, I systematically located transects and recorded reproductive effort in yew plants (defined above) located at 10-m intervals along these transects. On Rocky Island, yews were widely spaced (nearest neighbor distance = 3.13 m; Allison, 1990). Consequently, I was able to sample entire genets on Rocky Island. Populations on the other two islands were dense. Beginning in the spring of 1982 at the Island populations I counted the number of male and female strobili produced by each plant. Seed production was recorded for each plant in late summer. Each plant was resampled in 1983, 1984, and 1985, and additional plants were sampled on each island. A maximum of 98 plants was sampled on Rocky Island, 57 on Otter Island, and 92 on Outer Island. Yew plants were also sampled on Rocky Island in 1986. In 1984 I estimated the size of each plant by measuring shoot length and basal diameter. The latter was measured at a point immediately below the lowest living branch of each shoot system since this criterion could be applied consistently to all plants.

Geographic variation in yew sex expression was estimated by additional sampling with the same methods in two high-density yew populations located in southeastern Minnesota: North Grey Cloud Island (44°46'N latitude, 92°56'W longitude) (sampled in 1984 and 1985) and Marion, Minnesota, along the Root River (43°55'N latitude; 92°22'W longitude) (sampled in 1983 and 1984).

All censuses in the different populations were made on plants growing in the forest understory to minimize differences in reproductive effort resulting from gross differences in light and mineral resources. To estimate the influence of resources on sex expression on Outer Island, I randomly selected plants within large gaps created by beaver cutting. The same measurements were made on plants at this site as at other sites. I hereafter refer to this site as Outer Is. (gap); yew plants sampled in the understory of Outer Island are referred to collectively as Outer Is. (closed).

All data were analyzed by one-way ANOVA with site as the main effect. Analyses were based on $\log_{10}(Y + 1)$ -transformed values to equalize variances. Strobilus ratios of individual yews were transformed before ANOVA by $\log_{10}[(\text{male strobili} + 1)/(\text{female strobili} + 1)]$.

I calculated standardized phenotypic gender for plants in each population (Lloyd, 1980; Lloyd and Bawa, 1984). Gender was calculated as

$$\frac{m_i/M}{(f_i/F + m_i/M)}$$

where m_i equals the number of male strobili produced by plant i , f_i equals the number of female strobili or seeds produced by plant i , and M and F equal the total number of male strobili and female strobili or seeds, respectively, produced by the whole population. As calculated here, gender is a measure of the maleness of a plant and ranges from 0.0 (female) to 1.0 (male).

I used a test statistic proposed by Engleman and Hartigan (1969) (cited in McLaughlin, 1989) to test whether observed gender distributions for all populations were unimodal, representing monomorphic gender. Gender for these populations was sorted from lowest to highest and then divided up into two clusters $N - 1$ times where N is the number of plants in the population. For example:

$$\begin{matrix} (x_1)(x_2 \dots x_N) \\ (x_1, x_2)(x_3 \dots x_N) \\ \vdots \\ (x_1 \dots x_{N-1})(x_N) \end{matrix}$$

For each cluster pair, I calculated B/W which is the ratio of between- to within-cluster sums of squares:

$$B/W = \frac{n_1 n_2 (x_1 - x_2)^2}{[s_1^2(n_1 - 1) + s_2^2(n_2 - 1)](n_1 + n_2)}$$

where n_1 and n_2 are the sample sizes for the two clusters, x_1 and x_2 are the sample means, and s_1^2 and s_2^2 are the sample variances. To test the null hypothesis of a unimodal distribution (gender is monomorphic), the maximum B/W is used. When $N > 8$, $\ln(B/W_{\max} + 1)$ is normally distributed with a mean of $[-\ln(1 - 2/\pi) + 2.4/(N - 2)]$ and a variance of $1/(N - 2)$ (McLaughlin, 1989). The probability of obtaining a maximum value of B/W by chance can be estimated by scaling $\ln(B/W + 1)$ (Snedecor and Cochran, 1967) and comparing it to tables for the standard normal distribution. If B/W_{\max} has a low probability of occurrence ($P < 0.05$), this suggests that the population consists of two discrete gender clusters, or male and female gender groups, i.e., gender is bimodal.

Kendall's tau (Conover, 1980) was calculated to measure year-to-year gender correlation, or concordance, for individual yews. Phenotypic gender, as defined by Lloyd (1980), is an estimate of the relative genetic contribution of a cosexual plant from male and female function. Consequently, a plant's gender is dependent on the sex expression of other members of the population. Change in the relative allocation to pollen and seeds by one plant, for example, can change the gender of another plant

TABLE 1. Means \pm 1 SE of yew plants for Canada yew reproductive and vegetative parameters by site. Means within a column having different letters differ significantly at $P < 0.05$ using Tukey's Honest-Significant Difference. All means are on a per branch basis and were $\log_{10}(Y + 1)$ -transformed prior to ANOVA. Male and female strobilus production, seed production, and basal diameter are presented as arithmetic means. Male/female strobilus ratios are presented as back-transformed means

Site	N ^a	Male strobili	Female strobili	Seeds	Male/female strobilus ratio	N ^b	Basal diameter (mm)
1983							
Root River	21	296.3 \pm 68.4a	22.0 \pm 7.6a	5.5 \pm 2.8a	11.9 \pm 1.4a		
Outer Island (closed)	50	87.3 \pm 23.3b	5.6 \pm 1.0a	2.5 \pm 0.5a	10.5 \pm 1.2a		
Otter Island	55	16.9 \pm 4.0c	4.8 \pm 2.2b	1.1 \pm 0.3	3.2 \pm 1.2b		
Rocky Island	54	10.7 \pm 5.3d	0.8 \pm 0.4c	0.2 \pm 0.1	4.6 \pm 1.3b		
1984							
Root River	26	296.9 \pm 94.3ab	31.9 \pm 7.9a	8.0 \pm 2.8a	5.6 \pm 1.3ab	32	11.4 \pm 0.7b
Grey Cloud	28	156.6 \pm 33.0a	27.1 \pm 5.1ab	7.0 \pm 2.1a	10.7 \pm 1.3a	42	9.9 \pm 0.4bc
Outer Island (gap)	14	560.6 \pm 113.6a	58.5 \pm 17.4a	23.9 \pm 8.1	15.5 \pm 1.6a	21	17.0 \pm 0.8a
Outer Island (closed)	50	113.6 \pm 30.8b	9.2 \pm 2.0b	3.6 \pm 0.8ab	7.9 \pm 1.2a	99	9.2 \pm 0.4c
Otter Island	54	22.9 \pm 5.4c	8.5 \pm 1.2b	2.0 \pm 0.5b	2.6 \pm 1.2b	77	6.3 \pm 0.3d
Rocky Island	54	10.7 \pm 5.3d	1.7 \pm 0.4c	0.6 \pm 0.1c	7.8 \pm 1.2a	54	6.2 \pm 0.4d
1985							
Grey Cloud	31	146.8 \pm 28.2ab	19.0 \pm 4.2b	6.0 \pm 1.3ab	8.5 \pm 1.2a		
Outer Island (gap)	25	289.8 \pm 50.7a	62.1 \pm 10.7a	13.2 \pm 2.4a	4.5 \pm 1.2ab		
Outer Island (closed)	92	77.2 \pm 15.1b	9.9 \pm 2.4bc	3.9 \pm 1.0b	7.1 \pm 1.2a		
Otter Island	57	10.7 \pm 2.2c	5.3 \pm 1.0c	2.9 \pm 0.7b	1.8 \pm 1.2b		
Rocky Island	98	12.3 \pm 5.1c	0.8 \pm 0.3d	0.2 \pm 0.1c	6.2 \pm 1.2a		

^a Number of plants sampled.

^b Number of branches sampled.

even though the latter has not altered its absolute investment in male and female function. To estimate the extent of gender change in Apostle Island yews, I arbitrarily designated plants that showed a gender shift of >0.4 gender units (on a scale of 0 to 1) as showing "flexible" gender. By using a shift of this magnitude, I ignored the minor changes in gender of plants that resulted primarily from changes in sex allocation of other members of the population.

RESULTS

Geographic variation in sex expression—Male and female strobilus production, seed production, and plant size varied significantly among populations (Table 1). ANCOVA with basal diameter as the covariate still showed significant site effects ($P < 0.001$) on strobilus and seed production. There is less variation among populations in strobilus ratios; only Otter Island in all 3 years and Rocky Island in 1983 had significantly lower ratios of male to female strobili than the other populations (Table 1). Year-to-year production of strobili and strobilus ratios of individual plants varied signif-

icantly (repeated measures ANOVA; $P < 0.001$ for all comparisons). Finally, there was a significant, positive correlation between male strobilus production and seed production in five of six populations, but the strength of the correlation varied widely ($r^2 = 0.14$ to 0.86).

Canada yew plants (as defined in Materials and Methods) are either male, female, monoecious, or nonflowering (Table 2). In 1983 and 1984 the proportion of these types did not differ significantly among five of the six populations sampled (Table 2). The vast majority of individuals sampled in these populations were monoecious. Only 3% of all plants sampled were female. Outer and Otter Island populations had significantly more males in 1985 than North Grey Cloud and Outer Is. (gap), but monoecious plants were still in the majority (72% of reproducing individuals) in these two populations. A higher proportion of male yews occurred on Rocky Island, but this island was not included in the statistical analysis because Rocky Island yews included whole genets. Plants in the other four populations represented an unknown proportion of a genet.

Mean basal diameters of the different breeding types were significantly different by ANO-

TABLE 2. Variation in qualitative sex expression within and among different Canada yew populations. Rocky Island yews were not included in the statistical analysis for reasons as described in the Results section. G-statistics test for homogeneity of distribution of reproducing individuals among populations and were adjusted for Williamson's correction

Site	Males	Females	Monoecious	Non-flowering
1983				
Root River	2	1	17	1
Outer Is. (closed)	8	0	37	5
Otter Island	11	1	36	8
Rocky Island	9	2	15	28
G _{adj.} = 3.35; P > 0.50				
1984				
Root River	2	1	23	0
Grey Cloud	4	0	24	0
Outer Is. (gap)	3	0	11	0
Outer Is. (closed)	10	1	39	0
Otter Island	8	3	37	7
Rocky Island	17	0	17	20
G _{adj.} = 2.19; P > 0.50				
1985				
Grey Cloud	1	0	30	0
Outer Is. (gap)	1	0	24	0
Outer Is. (closed)	20	1	65	6
Otter Island	13	4	33	7
Rocky Island	28	2	21	47
G _{adj.} = 19.04; P < 0.005				

VA ($P < 0.001$) for both Otter and Outer Islands and Rocky Island. Small yews tended to be nonreproducing, large yews were generally monoecious, and yews of intermediate size were single-sexed and typically male (Fig. 1). The smallest yews on Outer and Otter Islands were an exception to this trend.

Yews usually produce only male strobili when first reaching reproductive maturity. During 4 years of censusing on Rocky Island, 20 yews reproduced for the first time; 18 of these plants were male, one plant was female, and one plant was monoecious.

Gender variation within populations—The vast majority (87%) of yews in all populations combined produced more male strobili than female strobili, although there was considerable variation within populations. Untransformed strobilus ratios (male/female) of individual plants ranged from 1.0 to >200. Analysis of B/W_{max} indicates that gender distribution in the Root River population in 1984 and in three of four Canada yew populations in 1985 was bimodal (Table 3); only the gender distribution of Grey Cloud did not differ significantly from a unimodal distribution. Gender distributions for Otter and Outer Is. (closed)

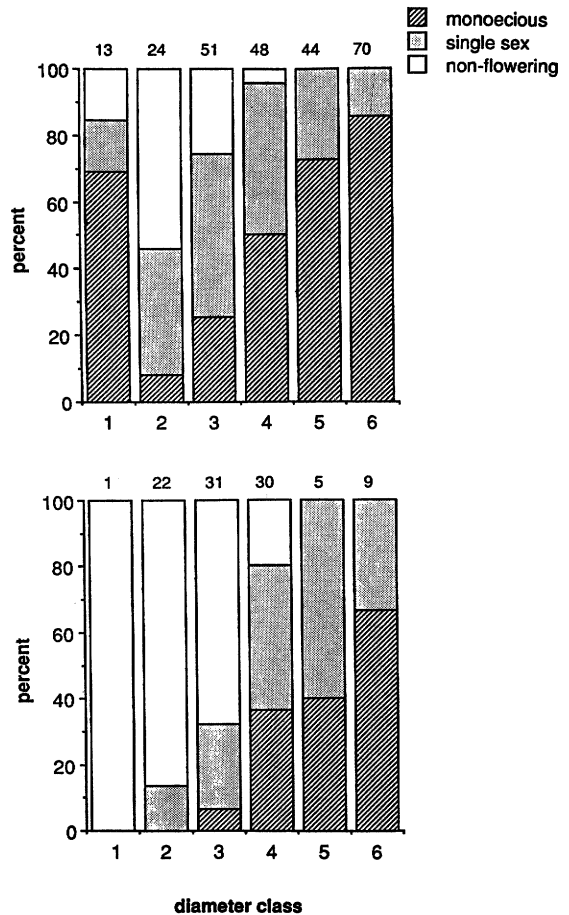


Fig. 1. Breeding type of shoot systems by diameter size class, for Apostle Island yews. Diameter classes increase in 2-mm increments beginning with 2 mm: class 2 = 2–4 mm; class 3 = 4–6 mm; class 4 = 6–8 mm; class 5 = 8–10 mm; and class 6 > 10 mm. (a) Outer (closed) and Otter Islands combined—multiple shoots per plant ($N = 250$); and (b) Rocky Island—whole genet ($N = 98$). Numbers above columns are numbers of plants in each diameter class.

yew populations in 1985 are portrayed in Fig. 2; these populations had the largest sample sizes of reproducing individuals. Distributions for Apostle Island populations were similar in showing a preponderance of male or male-biased yews and an additional, but smaller, peak below 0.5.

There is no significant relationship between gender and the number of strobili produced by a plant. Gender is negatively correlated with plant size on Rocky Island and Outer Is. (closed) (e.g., Fig. 3), but not on Otter Island. The correlation is weak ($r^2 = 0.03$ to 0.19) and appears due largely to the abundance of small males. When males are excluded there is a significant but weak, positive correlation between plant size and the ratio of male to female strobili

TABLE 3. Mean gender and variance of presumed male and female clusters (or "morphs") for Apostle Islands populations and Grey Cloud in 1985 and Root River in 1984. B/W_{max} was calculated as described in Materials and Methods and tests the null hypothesis of a unimodal distribution

Cluster	Outer Island	Otter Island	Rocky Island	Grey Cloud	Root River
Female					
x	0.2570	0.2625	0.2112	0.2658	0.1390
s ²	0.0246	0.0338	0.0825	0.0556	0.0123
N	40	20	8	12	10
Male					
x	0.9278	0.8728	0.9214	0.7568	0.7038
s ²	0.0071	0.0281	0.1041	0.0660	0.0235
N	46	25	22	19	16
B/W_{max}	7.53 ^a	3.15 ^b	4.25 ^b	3.82 ^c	4.24 ^b

^a $P < 0.002$.

^b $P < 0.01$.

^c $P < 0.10$.

(e.g., Outer Island (closed): $r^2 = 0.13$; $P < 0.001$), and strobilus ratios and the number of strobili produced by a plant (e.g., Outer Is. (closed) $r^2 = 0.29$; $P < 0.001$).

Annual variation in sex expression—The breeding type of individual plants changed annually, and most changes were in single-sexed individuals. For example, on Outer Is. (closed) and Otter Island (all yr), male and female yews

changed breeding status 44% of the time compared to 15% of the time for monoecious yews. Most of the changes in the breeding status of single-sex yews were to monoecy or nonflowering status. "Sex reversal" (changes from male to female or vice versa) in these two populations occurred four times in 4 years; two of these were from female to male. Changes in monoecious plants were typically to male (23 of 30 changes) and less frequently to female (6 of 30). One plant became nonflowering. Male plants became monoecious in 19 of the 28 changes that occurred in this group. Only one plant remained female for 2 consecutive years (out of eight occurrences); male plants remained male in consecutive years 61% of the time.

Gender based on male and female strobilus

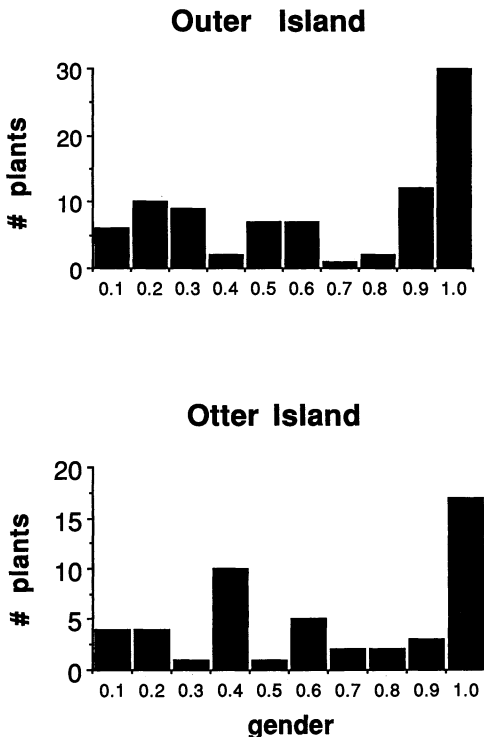


Fig. 2. Frequency distribution of gender for (a) Outer Island—1985 and (b) Outer Island—1985. Gender was calculated as defined in text (1.0 = male only).

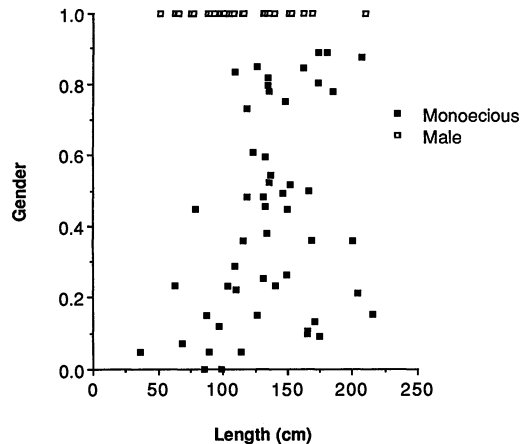


Fig. 3. Gender vs. length of plant (as defined in Materials and Methods), for monoecious and male Canada yew plants on Outer Island (closed)—1985. Gender was calculated as defined in Materials and Methods and ranges from 0.0 (female) to 1.0 (male).

TABLE 4. Kendall's nonparametric correlation of gender for different years for Rocky Island, Otter Island, and Outer Island (closed). Gender was calculated using male and female strobilus production as indices of paternal and maternal effort for all populations. Correlations for Outer Island were also performed on gender calculated using seeds produced as the indicator of female effort. *N* refers to the number of plants on each island included in the analysis

	1982	1983	1984	1985
Rocky Island (<i>N</i> = 16)				
1983	0.1333			
1984	0.3162	0.4462 ^a		
1985	0.3917 ^a	0.3233 ^a	0.2751 ^a	
1986	0.2333	-0.0254	0.2624 ^a	0.0936
Outer Island (closed) - (female strobili) (<i>N</i> = 46)				
1983	0.4412 ^a			
1984	0.3158	0.3034 ^a		
1985	0.6013 ^a	0.4038 ^a	0.5691 ^a	
Outer Island (closed) - (seeds) (<i>N</i> = 46)				
1984		0.3393 ^a		
1985		0.2949 ^a	0.4141 ^a	
Otter Island (<i>N</i> = 44)				
1984		0.3179 ^a		
1985		0.3922 ^a	0.4684 ^a	

^a Indicates significant concordance at $P < 0.05$.

production showed significant concordance in 15 of 21 year-by-year comparisons; gender concordance in Otter Island, Outer Is. (closed), Root River, and Grey Cloud yews was significant in 10 of 11 cases (Table 4). Kendall's tau for Grey Cloud and Root River were 0.6217 (1984 to 1985) and 0.6000 (1983 to 1984), respectively ($P < 0.001$), and these were not included in Table 4. Concordance was typically low in all populations (e.g., Table 4). Calculations using the number of ripe seeds as an index of female effort for Outer Is. (closed) gender yielded results similar to those when female strobili were used (Table 4). Significant year to year correlation in gender of individual yews is in contrast to the significant annual variation in strobilus ratios described above.

Seven percent to 18% of plants within a population had major gender shifts (as described in Materials and Methods) between years. On Outer Is. (closed) and Otter Island, plants that showed "flexible" gender between 1983 and 1984 (the interval with the greatest number of changes) were significantly smaller than plants that showed relatively little or no gender change (one-way ANOVA; $P < 0.005$) between those 2 years. Gender shifts from male (gender = 1.0) to female (gender = 0.0) and vice versa in Canada yew occurred in <2% of all observations, but in all cases these shifts involved small

yews that produced only one or two strobili per year.

DISCUSSION

Canada yew, despite being listed as monoecious (e.g., Chamberlain 1966), comprises single-sexed individuals as well. The latter were recorded on Rocky Island, where entire genets were sampled, indicating that the presence of single-sexed Canada yew individuals in natural populations is not an artifact of sampling only a portion of a genet in high-density populations. When quantitative measures are taken into account, however, the complexity of sex expression in Canada yew makes generalizations about underlying patterns of sex expression in this species difficult.

Some trends are apparent in the data, but these are weak or often contradicted by alternative measures of sex expression. For example, qualitative measures in Island populations indicate clearly that femaleness (recorded as a shift from male to monoecy) increases with plant size. Female gender is only weakly correlated with plant size, however, and if strobilus ratios are used as the measure of sex expression, the trend is reversed. The measures of plant size used in this study may not accurately reflect plant status, but it is apparent that gender variation among yew individuals cannot be explained simply by size differences.

Flexibility in yew gender is suggested by significant annual variation in strobilus ratios of individual yews indicating that a plant's sex allocation is responsive to environmental variation. Significant concordance of gender in individual yews, however, also suggests a proximate genetic component to yew sex expression (e.g., Primack and McCall, 1986). The largest gender fluctuations occurred in smaller yews; large yews showed relatively little gender flexibility.

The population with the lowest gender concordance was Rocky Island. Yews in this population were significantly smaller on average than yews in all other populations, and consequently one would predict greater gender adjustments in Rocky Island yews. A small yew produces few strobili, and the addition of one or two strobili (male or female) can have large effects on that plant's gender. In general, it is not clear whether large shifts in gender reflect true gender adjustments or random changes in allocation patterns. Greater yearly variation in the gender of small or young plants also has been observed in the oil palm (*Elaeis guineensis*) (Williams and Thomas, 1970) and lodgepole pine (*Pinus contorta*) (Smith, 1981).

Sex-reversal, or gender phase change (sensu Lloyd and Bawa, 1984), has been reported in dioecious *Taxus* and has been cited as evidence for environmental determination of sex expression in this genus (Freeman, Harper, and Charnov, 1980). Those cases of sex reversal in dioecious *Taxus*, however, typically involved the appearance of male branches on female plants (i.e., chimeras) or the reverse, on hybrid yews (Keen and Chadwick, 1954). This suggests that "sex-reversal" in this genus involves a disruption of the genetic sex-determining mechanism (sensu Lloyd and Bawa, 1984), perhaps resulting from hybridization, rather than environmental effects. Evidence for environmental determination of sex in *Taxus* is weak and inconclusive.

The principal effort in this study was to collect data in similar habitats: Outer Is. (gap) was an exception to this. Yews in the latter population, where light intensity was higher, showed a trend toward more female-biased gender. This was observed in other species (Freeman et al., 1981; Charnov, 1982 and references cited therein), although the difference here was not significant, possibly due to small sample sizes. No geographic differences (southeastern Minnesota vs. northern Wisconsin) in strobilus proportions were detected, and only Otter Island had consistently different strobilus ratios (more female-biased) than other populations. This result is hard to interpret, however, as current environmental differences among Island populations are not obvious. Historical factors such as past land-use or deer browsing history of the Islands may be important (Brander, 1983; Allison, 1987).

The most interesting result of this study is the bimodal gender distributions recorded in most study populations. This result suggests that Canada yew populations are dimorphic consisting of male and female morphs. Bimodal, or dimorphic, gender would indicate gender specialization and a pronounced genetic component to sex expression in Canada yew (Lloyd and Bawa, 1984). As Fig. 3 indicates, the difference between morphs is not dramatic, and the bimodal distributions may be an artifact of the preponderance of male yews (0.9 to 1.0 gender) in Apostle Island populations. Many of these plants are small, and they show the greatest gender fluctuations. Although the abundance of males is relatively constant from year to year, the male plants are not necessarily the same individuals. Gender distribution in the Root River population also was bimodal, however, and did not have the high frequency of male yews.

In general, the bimodal distributions are dif-

ficult to interpret because of the gender flexibility discussed earlier. Perhaps individual yews have a genetically defined tendency toward male or female gender, but have a limited ability to modify gender that declines with age. It will be necessary to separate the effects of age and plant size from genetic components of sex expression to determine conclusively that gender in Canada yew is bimodal.

If Canada yew gender is bimodal, it would be the first reported case of dimorphic gender in gymnosperms. The potential for dimorphic gender in Canada yew is particularly intriguing given the prevalence of dioecy in *Taxus*. Geographic distributions in the genus (Ferguson, 1976) and cladistic analysis of gymnosperms (Donoghue, 1989) support the hypothesis that dioecy is the ancestral trait in *Taxus* and that cosexuality in Canada yew is derived.

Dioecy in many plant species is genetically determined (see Charnov, 1982). If Canada yew's ancestor was dioecious and if dioecy is genetically determined in *Taxus*, it could explain the genetic component of Canada yew gender. Bimodal gender in Canada yew would be a remnant of this species' dioecious heritage. In turn, it would suggest that in the evolution of a cosexual yew species from a dioecious ancestor, there was selection for the ability of individuals to modify gender, i.e., gender flexibility. Cosexual individuals have been reported as rare in natural populations of European yew (*Taxus brevifolia*) (Pridnya, 1984). Occasional production of male branches on females, or vice versa, in hybrid yews, suggests a proximate mechanism for the evolution of cosexuality in *Taxus*.

Close examination of the ecological differences between Canada yew and other members of the genus could suggest hypotheses concerning the evolution of Canada yew from a dioecious ancestor. Givnish (1980), for example, hypothesized, in part, that dioecy is prevalent in bird-dispersed gymnosperms, like *Taxus*, because the concentration of resources into "fruit" would have a disproportionate effect on a plant's female fitness. The increased efficiency of seed dispersal with large "fruit" crops would result in a convex female gain curve favoring the evolution of gender specialization (e.g., Charnov, 1982).

Several characteristics of Canada yew may reduce the hypothesized female fitness gains associated with gender specialization. Individuals of this species are the smallest in the genus, their seeds ripen over an extended period of 6 to 8 weeks, and pollen occasionally limits their seed production (Allison, 1990). Canada yew also layers extensively; individuals increase in

size horizontally rather than vertically, and they become fragmented as underground connections rot. Any fitness advantages gained by gender specialization to improve seed dispersal may be counteracted by any or all of the above characteristics of this species.

Understanding the selective mechanisms for a hypothesized reversion to cosexuality in Canada yew is relevant to the current controversy concerning the evolution and maintenance of dioecy. This debate has typically focused on pathways from cosexual to fully dioecious taxa; hypotheses for this pathway involve outcrossing advantages, sexual selection, and ecological correlates (e.g., Givnish, 1980; Thomson and Barrett, 1981; Bawa, 1982; Willson, 1982). Studying the ecological circumstances where dioecy breaks down, such as the hypothesized case of Canada yew, could resolve some of the questions surrounding this debate, although to my knowledge this evolutionary pathway has rarely been considered. Cosexual, or monoecious, taxa occur in other predominantly dioecious gymnosperm genera such as *Ephedra* and *Juniperus*. Cosexual species in these genera may have bimodal gender, and they may provide additional ecological correlates to determine the mechanisms involved in the evolution of monoecy from dioecy and vice versa.

LITERATURE CITED

- ALLISON, T. D. 1987. The reproductive biology of Canada yew (*Taxus canadensis* Marsh.) and its modification by herbivory. Ph.D. thesis, University of Minnesota. Minneapolis.
- . 1990. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). II. Pollen limitation: an indirect effect. *Oecologia* 83: 530–534.
- BAWA, K. S. 1982. Outcrossing and the incidence of dioecism in island floras. *American Naturalist* 119: 866–871.
- BEALS, E. W., G. COTTAM, AND R. J. VOGL. 1960. Influence of deer on vegetation of the Apostle Islands, Wisconsin. *Journal of Wildlife Management* 24: 68–80.
- BRANDER, R. B. 1983. Environmental assessment: natural resources inventory and management—Apostle Islands National Lakeshore, Wisconsin. Apostle Islands National Lakeshore, Department of Interior, Wisconsin, unpublished report.
- CHAMBERLAIN, C. J. 1966. Gymnosperms, structure and evolution. Dover Publications, New York.
- CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.
- CONOVER, W. J. 1980. Practical nonparametric statistics. Wiley and Sons, New York.
- DONOGHUE, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43: 1137–1156.
- DUPLER, A. W. 1919. Staminate strobilus of *Taxus canadensis*. *Botanical Gazette* 68: 345–364.
- . 1920. Ovuliferous structures of *Taxus canadensis*. *Botanical Gazette* 69: 492–520.
- ENGELMAN, L., AND J. A. HARTIGAN. 1969. Percentage points of a test for clusters. *Journal of the American Statistical Association* 64: 1647–1648.
- FERGUSON, D. K. 1976. Some current research on fossil and recent taxads. *Review of Palaeobotany and Palynology* 26: 213–226.
- FREEMAN, D. C., K. T. HARPER, AND E. L. CHARNOV. 1980. Sex change in plants: old and new observations and new hypotheses. *Oecologia* 47: 222–232.
- , E. D. MCARTHUR, K. T. HARPER, AND A. C. BLAUER. 1981. Influence of environment on the floral sex ratio of monoecious plants. *Evolution* 35: 194–197.
- GIVNISH, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34: 959–972.
- KEEN, R., AND L. C. CHADWICK. 1954. Warn propagators to watch for sex reversal in *Taxus*. *American Nurseryman* 100: 13–14.
- LLOYD, D. G. 1980. Sexual strategies in plants III. A quantitative method for describing the gender of plants. *New Zealand Journal of Botany* 18: 103–108.
- , AND K. S. BAWA. 1984. Modification of the gender of seed plants in varying conditions. *Evolutionary Biology* 17: 255–338.
- MARTELL, A. M. 1974. Canada Yew. In J. D. Gill and W. M. Healy [eds.], Shrubs and vines for northeastern wildlife, 158–160. *USDA Forest Service General Technical Report NE-9*, Northeastern Forest Experiment Station, Upper Darby, PA. 180 pp.
- MATTHEWS, J. D. 1963. Factors affecting the production of seed by forest trees. *Forestry Abstracts* 24: 1–13.
- McKONE, M. J. 1989. Intraspecific variation in pollen yield in brome grass (Poaceae: *Bromus*). *American Journal of Botany* 76: 231–237.
- , AND D. W. TONKYN. 1986. Intra-population gender variation in common ragweed (Asteraceae: *Ambrosia artemisiifolia* L.), a monoecious, annual herb. *Oecologia* 70: 63–67.
- MCLAUGHLIN, R. L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *American Naturalist* 133: 654–670.
- PRIDNYA, M. V. 1984. Phytocenotic status and structure of the Khosta Common-yew population in the Caucasus Biosphere Reserve. *Ekologiya* 1: 3–8.
- PRIMACK, R. B., AND D. G. LLOYD. 1980. Sexual strategies in plants IV. The distributions of gender in two monomorphic shrub populations. *New Zealand Journal of Botany* 18: 109–114.
- , AND C. MCCALL. 1986. Gender variation in a red maple population (*Acer rubrum*: Aceraceae): a seven-year study of a “polygamodioecious” species. *American Journal of Botany* 73: 1239–1248.
- SARVAS, R. 1968. Investigations on the flowering and seed crop of *Picea abies*. *Communicationes Instituti Forestalis Fenniae* 67: 1–84.
- SCHOEN, D. J., D. DENTL, AND S. C. STEWART. 1986. Strobilus production in a clonal white spruce seed orchard: evidence for unbalanced mating. *Silvae Genetica* 35: 201–205.
- SMITH, C. C. 1981. The facultative adjustment of sex ratio in lodgepole pine. *American Naturalist* 118: 297–305.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods, 6th ed. Iowa State University Press, Ames, IA.
- STANTON, M. L. 1984. Seed variation in wild radish:

- effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105–1112.
- THOMPSON, J. N. 1984. Variation among individual seed masses in *Lomatium grayi* (Umbelliferae) under controlled conditions: magnitude and partitioning of the variance. *Ecology* 65: 626–631.
- THOMPSON, J. D., AND S. C. H. BARRETT. 1981. Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. *American Naturalist* 118: 2443–2449.
- WHITHAM, T. G., AND S. MOPPER. 1985. Chronic herbivory; impacts on architecture and sex expression in pinyon pine. *Science* 228: 1089–1091.
- WILLIAMS, C. N., AND R. L. THOMAS. 1970. Observations on sex differentiation in the oil palm *Elaeis guineensis* L. *Annals of Botany* 34: 957–963.
- WILLSON, M. F. 1982. Sexual selection and dicliny in angiosperms. *American Naturalist* 119: 579–583.