
Population Sex Ratios, Population Mixtures and Fecundity in a Clonal Dioecious Macrophyte, *Vallisneria Americana*

Author(s): Jon Lovett Doust and Gerald Laporte

Source: *Journal of Ecology*, Jun., 1991, Vol. 79, No. 2 (Jun., 1991), pp. 477-489

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/2260727>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Ecology*

JSTOR

POPULATION SEX RATIOS, POPULATION MIXTURES AND FECUNDITY IN A CLONAL DIOECIOUS MACROPHYTE, *VALLISNERIA AMERICANA*

JON LOVETT DOUST AND GERALD LAPORTE

Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada N9B 3P4

SUMMARY

(1) Sex ratios and plant densities were determined for three populations of *Vallisneria americana* in the Detroit River–St Clair River system (Great Lakes Basin, North America). Line transects were made at each of the three sites, and for each individual its location, sex (where possible), leaf number and number of connected ramets were recorded. In this clonal aquatic macrophyte, the majority of ramets (58–72%) did not flower. The flowering ramets were significantly male-biased in their sex ratio, ranging from a male:female ratio of 9.9:1 at the northernmost, upstream site, to 3.2:1 at the southernmost site. Sites differed in the density of shoots present.

(2) Female plants had significantly greater mass and more leaves than males at each site. This suggests that female ramets need to be larger before they are capable of flowering. Approximately half of all male flowers examined at the three sites were sterile (lacked pollen).

(3) Plants collected at the beginning of the growing season were raised in experimental pools, and all combinations of plants from the three natural populations, including representatives of each population alone, were allowed to grow for the season. Plant fitness was assessed when female flowers were exposed to pollen from their home site, or to pollen from all combinations of alien sites in addition to their home-site pollen.

(4) Ramet densities in each pool were identical at the outset of the experiment; by final harvest, however, the ranking of the densities in the pure culture pools had become the same as the ranking of densities at the three field sites. This suggests that populations may be differentiated in their relative extents of clonal growth.

(5) Fruit set in the experiment was comparable to field results, but seed set fruit⁻¹ was lower than in the field, suggesting pollen limitation. Certain treatments produced greater numbers of shoots (pools containing only plants collected from Sarnia, and pools having mixtures which included plants from Sarnia). As a direct result of its greater clonal growth, plants from Sarnia also produced the greatest number of fruits per unit area. The pattern of results for fecundity suggested that hybrid vigour may have been occurring in some combinations.

INTRODUCTION

The interplay between sexual reproduction and clonal growth in dioecious plant species has been the subject of several recent investigations. It has been shown that

males and females often differ in other ways than simply the primary sex organs. Such 'secondary sex characteristics' have included the phenology of flowering and growth (Miller & Lovett Doust 1987; Lovett Doust, O'Brien & Lovett Doust 1987; Lovett Doust & Lovett Doust 1987, 1988), and concentrations of secondary chemicals (L. Lovett Doust, J. Lovett Doust & M. Cervone, unpublished). In addition, it has generally been found that male individuals or male ramets produce greater numbers of flowers inflorescence⁻¹ and more inflorescences plant⁻¹ than females (Bawa & Opler 1975; Webb 1976; Lovett Doust & Lovett Doust 1988). In general, the greater *subsequent* cost of maturing fruits and ovules has been identified as an evolutionary pressure favouring the production of fewer flowers by females.

An overriding characteristic of most aquatic macrophytes is a very effective means of clonal growth. Cook (1987) ventures to call this clonal growth 'aggressive' vegetative spread. In essence, this means that vegetative growth is extremely proliferative and usually dominates population dynamics in aquatic weeds. In nine of the twelve important aquatic weeds reviewed by Cook (1987), no seed set at all was found. Indeed, Cook indicates that in natural populations of three species (*Elodea*, *Hydrilla* and *Lagarosiphon*) one rarely finds males and females cohabiting single areas. Clearly, in such circumstances, opportunities for gene mixis may be strongly hindered by aggressive clonal spread.

Dioecious species have sometimes shown spatial segregation according to environmental gradients, or patchiness of environmental conditions (e.g. Grant & Mitton 1979; Cox 1981; Lovett Doust, O'Brien & Lovett Doust 1987; Bierzychudek & Eckhart 1988). Iglesias & Bell (1989) surveyed ten heteromorphic species in southern Quebec and concluded that clonal growth might obscure associations (or segregation) between the sexes.

In this paper we describe sex ratios, growth and reproductive biology in natural populations of *Vallisneria americana*. Plants collected from three different sites were also raised experimentally. Fitness components and distance-dependent effects were examined in groups of plants grown in replicate tanks either alone or in two- or three-way combinations of the three populations.

MATERIALS AND METHODS

Species and study sites

Vallisneria americana Michx. (Hydrocharitaceae) is a dioecious, perennial, aquatic macrophyte (Cook *et al.* 1974). It is a stoloniferous species capable of extensive clonal growth; most individuals within a population appear to remain vegetative (Titus & Stephens 1983; and see below). Pollination in this species is a remarkable process; indeed, the elaborate pollination mechanism of this plant was cited in earlier centuries by William Paley as an indication of the handiwork of God (see Cox 1988; Cox & Knox 1989). Whereas the female flower remains connected to the parent plant by a long spiral peduncle, male inflorescences, containing many minute (0.75 mm) flowers enclosed by a short-peduncled spath, open their sheaths and release their flowers as small 'boats' which rise to the surface. The male flowers are then left to the vagaries of surface tension and water currents (for details see Svedelius 1932; Cox & Knox 1989). Pollen is kept dry throughout this, and pollination is effected by wave action which moves the bubble that forms around the unwettable inner

surface of the female flower (Kausik 1939). With such a random and potentially wasteful means of pollen dispersal, there is a possibility that pollen supplies may limit fruit and ovule production in the field.

Vallisneria americana occurs on submerged, freshwater substrates (Sculthorpe 1967). A rosette of leaves is formed and stolons may arise in leaf axils. The ribbon-like leaves are narrow (3–10 mm wide), and elongated, although the length of leaves is variable. Leaf length (up to 2 m) seems to depend on the depth and the movement of the water; leaves of different sizes appear to be characteristic of particular habitats (Wylie 1917; Sculthorpe 1967).

In females, the peduncle of the pistillate flower is formed in a leaf axil, and it grows as a loose spiral coil reaching to the water surface (Wilder 1974). The coiling seems to ensure that the flower will reach the surface even if the water level changes drastically. It is essential that the female flower lies at the water surface if it is to be pollinated successfully (Sculthorpe 1967). The peduncle grows slowly at first, but later grows at a rate of up to 2 cm h^{-1} and continues to do so for 1–3 days. At flowering, three pinkish-white sepals are formed, 5 mm wide and 2–3 mm long, surrounding three smaller petals. The fruits may grow to a length of 5–15 cm. After pollination the female peduncle usually becomes more tightly coiled than previously, retracting and submerging the developing fruit.

Vallisneria americana was sampled from three separate locations along the St Clair River–Detroit River system of the Great Lakes Basin, near Windsor, Ontario and Detroit, Michigan. Site 1, near Sarnia, Ontario ($42^{\circ}37' \text{ N}$, $82^{\circ}28' \text{ W}$) was a marshy delta in the St Clair River. The second site was approximately 80 km downstream at Peche Island ($42^{\circ}50' \text{ N}$, $82^{\circ}50' \text{ W}$), where Lake St Clair flows into the Detroit River. The third site was 6 km beyond that, on the western shore of Turkey Islet ($42^{\circ}11' \text{ N}$, $83^{\circ}28' \text{ W}$), just beyond Fighting Island in the Detroit River, 7 km north of Lake Erie.

Sampling

At each site, on dates between the end of June 1989, and early August 1989, a series of 10–25 m rectangular transects (30 cm wide) was surveyed. All plants were excavated along the transects at intervals of 10 cm. The total lengths of transects were 37 m, 122 m and 140 m at the Sarnia, Turkey Is. and Peche Is. sites, respectively. (Lengths reflect the differing sizes of the three natural populations.) Along each transect every *Vallisneria* shoot was sampled, and the following data were recorded: plant sex (if flowering—otherwise noted as vegetative), number of inflorescences, number and lengths of leaves, and number of stolons attached to the plant.

Thirty each of male, female and vegetative plants were sampled from two of the three sites (Sarnia and Turkey Islet). Plants were separated into leaves, roots, stolons and inflorescences, oven-dried to constant weight at 60°C , and weighed with a Mettler microbalance.

Clone size

Two indirect estimates of clone size were made. One is a minimum measure based on the assumption that a change of sex along the transect represents the start of a new clone. ‘Male strings’ (i.e. sequences of male and vegetative plants that are not

interrupted by a female shoot) and 'female strings' were counted for all transects. The lengths of purely male or purely female or vegetative strings were also determined for all transects.

Reproductive output

A random sample of 100 fruits was collected from each site. The length and weight of each fruit were recorded. Seeds were carefully dissected from the ovary, noting from which section of the ovary they came (distal, middle or proximal third). Seeds were counted in a scaled grid under a dissecting microscope (at 20 \times magnification). The seeds were categorized as viable, undeveloped or aborted. Viable seeds were recognizable as those having a rough, light-brown testa. Undeveloped seeds were tiny specks; they were *c.* 0.2–0.1 times the size of viable seeds, white in colour and lacked a rough testa. Aborted seeds had a brown testa, but were shrivelled and smaller in volume than the viable seeds. The viability of seeds fitting the criteria for viable and aborted seeds was checked with tests using tetrazolium chloride (Malone 1967). Seeds were also collected from fruits in the experimental pools (see below) and analysed in the same way as those from natural populations.

Forty male inflorescences were collected just before anthesis from each of the three sites. From these inflorescences, approximately 250 individual flowers were stained in Coomassie Brilliant Blue G-250, and then kept in distilled water for 24 h. The number of pollen grains flower⁻¹ was then determined.

Experimental pools

An experiment was conducted to examine the effects upon components of fitness (fruit set and seed set) when female flowers were exposed to pollen of plants from their own natural population or from plants coming from the other two sites studied in the field, or from both sources. Twenty-eight plastic pools (2 m in diameter and 62 cm deep) were arranged in a random block design, outdoors in an open field in Essex County, Southern Ontario. There were no detectable gradients in the field in terms of temperature, light quantity or quality, or humidity. Sediment from a single site was used (to a depth of approximately 12 cm). The plants used in the experiment were collected from the three field sites (described above) in late June 1989. Four replicate pools, each containing forty plants, were set up for each of the following mixtures: (i) all plants from Sarnia, (ii) all plants from Turkey Is., (iii) all plants from Peche Is., (iv) twenty plants each from Sarnia and Peche Is., (v) twenty plants each from Sarnia and Turkey Is., (vi) twenty plants each from Peche Is. and Turkey Is., (vii) thirteen plants from each of the three populations and one plant chosen randomly. Before transplanting, the numbers and lengths of leaves and the diameter of rosettes were determined for each plant. Each plant was uniquely identified with coloured wire so that its subsequent fate could be monitored. Pools were filled with water and this was topped up every day as necessary, until the final harvest of the experiment on 15 October 1989.

At the end of the experiment, the numbers of shoots in each pool were counted and all fruits were collected. Fruit lengths were measured and the number of seeds fruit⁻¹ determined. Treatments were compared using analysis of variance.

RESULTS

Transects

In all, 8137 plants were sampled from the field transects (Table 1). This represents an average density of 90.7 plants m^{-2} . Of these, 2284 were male, 594 female, and the majority, 5259, were vegetative. The overall sex ratio of flowering plants was significantly male biased, 3.9:1 ($\chi^2 = 164$, $P < 0.001$). Between sites, there were differences in plant density, the ratio of vegetative to sexual plants, and the sex ratio (Table 1). The male-biased sex ratio was greatest at the Sarnia population (9.9:1), and similarly the proportion of vegetative plants was greatest at this site.

The mean number of leaves plant^{-1} was significantly greater ($P < 0.01$) for females than for males (Table 2), and leaf number on vegetative plants (5.4) was significantly lower than both of these ($P < 0.001$). The greatest number of male flowers $\text{inflorescence}^{-1}$ was found at Peche Is. (1418); this was significantly greater than at Turkey Is. (1170), and this in turn was significantly greater than at Sarnia (817). Male sterility appeared to be commonplace—about half of the male flowers at each site lacked pollen (Table 2). In flowers which bore pollen, approximately similar numbers of pollen grains were found in all three populations (c. 67 grains flower^{-1}) (Table 2).

There were significant differences in both absolute and proportionate distribution of biomass in males, females and vegetative plants, and there were some differences in total biomass but no significant difference in proportionate biomass between the populations (Table 3). Females had significantly greater total biomass, and had proportionately more biomass in inflorescences and roots, and less in stolons and leaves, than did males. Vegetative plants had about half the biomass of sexual plants, and allocated proportionately more of their biomass to leaves. Plants at the Sarnia site had significantly less total biomass plant^{-1} compared with plants at the Turkey Is. site.

Clone size

By the minimum estimate of clone size, male strings (i.e. sequences of male and vegetative plants that are not interrupted by a female shoot) are significantly larger than female strings at all three sites in terms of number of shoots (Table 4). However,

TABLE 1. Number and reproductive status of *Vallisneria americana* plants at three sites in the Huron–Erie Corridor.

Number of plants	Sarnia	Peche Is.	Turkey Is.	Total
Vegetative	1359	2245	1655	5259
Sexual	492	1204	1182	2878
Male	447	921	916	2284
Female	45	283	266	594
M:F ratio	9.93	3.25	3.44	3.85
% Vegetative	73.4	65.1	58.3	64.6
Ramets m^{-2}	166.8	82.4	77.5	90.7

TABLE 2. Characteristics (mean \pm 1 S.E.) of male and female plants of *Vallisneria americana* at three sites in the Huron–Erie Corridor.

	Sarnia		Peché Is.		Turkey Is.	
	Male	Female	Male	Female	Male	Female
No. of leaves ramet ⁻¹	8.1 \pm 0.08	9.2 \pm 0.25	8.3 \pm 0.08	10.1 \pm 0.17	8.5 \pm 0.12	9.6 \pm 0.17
No. of inflorescences ramet ⁻¹	1.8 \pm 0.04	1.7 \pm 0.12	1.9 \pm 0.03	2.1 \pm 0.05	2.2 \pm 0.03	2.0 \pm 0.07
No. of ovules fruit ⁻¹		167.7 \pm 3.6		278.4 \pm 7.4		324.4 \pm 6.8
No. of male flowers inflorescence ⁻¹	817 \pm 59.2		1418 \pm 83.7		1170 \pm 90.4	
% of male flowers that are sterile	53.4		49.1		52.3	
No. of pollen grains per fertile male flower	68.1 \pm 4.8		65.5 \pm 5.2		67.9 \pm 7.3	

TABLE 3. Biomass of male and female plants of *Vallisneria americana* in two sites in the Huron–Erie Corridor. *n* = 30 in each case.

	Sarnia			Turkey Is.		
	Male	Female	Vegetative	Male	Female	Vegetative
Mean (\pm 1 S.E.) biomass (mg)						
Leaves	98 \pm 12	109 \pm 11	72 \pm 11	159 \pm 15	182 \pm 16	132 \pm 13
Stolons	107 \pm 11	69 \pm 4	43 \pm 4	163 \pm 13	100 \pm 5	86 \pm 5
Roots	165 \pm 16	226 \pm 18	56 \pm 15	250 \pm 22	370 \pm 27	110 \pm 13
Reproductive structures	22 \pm 3	53 \pm 4		34 \pm 5	93 \pm 9	
Total biomass	392	457	171	606	744	328
Proportionate distribution of biomass (%)						
Leaves	25.0	23.8	42.1	26.2	24.5	40.0
Stolons	27.3	15.1	25.1	26.9	13.4	26.2
Roots	42.1	49.5	32.8	41.3	49.7	33.5
Reproductive structures	5.6	11.6		5.6	12.5	
Root:shoot ratio*	2.27:1	1.82:1	1.38:1	2.14:1	1.71:1	1.48:1

* Ratio of below-ground parts (roots and stolons) to above-ground parts (leaves and reproductive structures).

when male and female strings are examined in terms of the percentage of vegetative shoots within each, there are no significant differences between the sexes. The number of shoots in ‘pure’ or contiguous male- or female-flowering, or vegetative strings are also shown in Table 4; in each case vegetative strings are significantly larger, with pure males having more ramets than pure female strings.

Reproductive output

The total number of seeds and the total number of viable seeds were greatest in fruits from Peche Is., followed by those from Turkey Is. and then Sarnia (Table 5).

TABLE 4. The number of shoots in male and female strings (sequences of male plus vegetative, or female plus vegetative shoots that are not interrupted by a shoot of opposite sex) of *Vallisneria americana*, and the number of contiguous male, female and vegetative shoots (‘pure’ strings) at the three sites. Values in the same column that differ significantly (*P* < 0.05) are designated with different superscripts.

	Sarnia	Peche Is.	Turkey Is.
String			
male	44.32 ^a	23.39 ^a	20.83 ^a
female	6.28 ^b	7.80 ^b	7.80 ^b
Pure string			
male	1.57 ^c	1.75 ^c	1.79 ^c
female	1.35 ^d	1.56 ^d	1.47 ^d
vegetative	4.10 ^e	3.19 ^e	2.65 ^e

TABLE 5. Contents of fruits (numbers of seeds) from female plants of *Vallisneria americana* at three sites in the Huron–Erie Corridor. Values in the same row that do not differ significantly ($P < 0.05$) are designated with the same superscript.

	Sarnia	Peché Is.	Turkey Is.
Fruit length (cm)	11.1 ^b	11.3 ^b	10.2 ^a
Total no. of seeds	167.1 ^a	287.9 ^c	233.5 ^b
Total no. of viable seeds	155.7 ^a	282.0 ^c	226.2 ^b
% Viable	93.1 ^a	98.0 ^c	96.9 ^b
Position within fruit			
Proximal (basal or peduncular end)			
Undeveloped	3.4 ^b	0.9 ^a	1.1 ^a
Aborted	0.8 ^a	1.2 ^a	1.1 ^a
Viable	44.7 ^a	94.7 ^c	72.3 ^b
Mid			
Undeveloped	0.8 ^a	2.3 ^c	1.4 ^b
Aborted	0.8 ^a	1.0 ^a	1.1 ^a
Viable	61.0 ^a	100.6 ^c	80.3 ^b
Distal (stylar end)			
Undeveloped	3.0 ^b	1.1 ^a	1.5 ^a
Aborted	1.1 ^a	0.9 ^a	1.1 ^a
Viable	50.2 ^a	86.7 ^c	73.6 ^b
Total (for fruit)			
Proximal	48.8 ^a	96.8 ^c	74.5 ^b
Mid	62.6 ^a	103.9 ^c	82.7 ^b
Distal	54.3 ^a	88.8 ^c	76.3 ^b

Seeds from Peché Is. had the greatest percentage viability. In the proximal and distal portions of the fruit, Sarnia fruits consistently had slightly greater numbers of non-developed seeds, whilst in all three portions, fruits from Peché Is. had the greatest number of viable seeds (Table 5). The number of aborted seeds did not differ significantly between sites or between sections of the fruit; but the number of viable seeds was always greatest in the mid section.

Experimental pools

The rank order of shoot densities achieved by the end of the season, in the pools containing pure cultures from each site corresponded to that of the densities encountered under field conditions, despite identical starting densities. Pools containing Sarnia plants developed the greatest density (the number of ramets in these pools increased almost fivefold over the 3.5 months of the experiment), and there was no significant difference between the pools containing only plants from Peché Is. or Turkey Is. (Table 6). Treatments involving plants from combinations of sites including Sarnia had increased shoot densities, whereas the combination of plants from Peché Is. and Turkey Is. was decreased. The greatest biomass ramet⁻¹ was reached in the mixture of Sarnia and Peché Is. plants, as was the greatest biomass genet⁻¹ (Table 6).

Fruits from pools containing pure Turkey Is. plants were greatest in length (Table 6); fruits from plants in all the combinations followed, and smallest of all were fruits of

TABLE 6. Comparison of plant growth and reproduction of *Vallisneria americana* in experimental pools. Plants were grown in pure cultures and mixtures including all combinations of the three source populations. The source populations of plants in each treatment are: S = Sarnia, P = Peche Is., T = Turkey Is. Values in the same row that do not differ significantly ($P < 0.05$) are designated with the same superscript.

	Population source						
	S	P	T	S/P	S/T	P/T	S/P/T
No. of shoots m^{-2}	107.4 ^d	30.7 ^a	26.9 ^a	56.7 ^b	65.1 ^c	32.7 ^a	43.6 ^{ab}
No. of shoots $pool^{-1}$	195.8 ^d	56.0 ^a	49.0 ^a	103.5 ^b	118.8 ^c	59.7 ^a	79.5 ^{ab}
No. of fruits $pool^{-1}$	17.5 ^c	5.5 ^a	6.0 ^a	5.5 ^a	8.3 ^b	3.3 ^a	4.3 ^a
Length of fruit (cm)	7.49 ^a	7.00 ^a	8.25 ^b	7.86 ^a	7.91 ^a	7.83 ^a	7.73 ^a
No. of fruits shoot ⁻¹	0.09 ^a	0.10 ^a	0.12 ^a	0.05 ^a	0.07 ^a	0.06 ^a	0.05 ^a
No. of seeds fruit ⁻¹	105.5 ^a	89.6 ^a	121.7 ^{ab}	140.3 ^b	113.7 ^{ab}	148.7 ^b	118.4 ^{ab}
Total no. of seeds $pool^{-1}$	1846.1 ^d	492.5 ^a	730.3 ^b	771.5 ^{bc}	943.4 ^c	490.6 ^a	508.9 ^a
Clonal growth rate*	4.89 ^d	1.13 ^a	1.23 ^a	2.59 ^{bc}	2.97 ^c	1.49 ^a	2.00 ^b
Dry mass ramet ⁻¹ (mg)	162 ^a	187 ^a	205 ^a	230 ^b	148 ^a	216 ^{ab}	165 ^a
Dry mass genet ⁻¹ (mg)	1041 ^d	453 ^{ab}	571 ^{ab}	810 ^c	492 ^{ab}	689 ^b	414 ^a

* The starting density of 40 plants $pool^{-1}$ is represented by a value of 1.0. Values > 1.0 indicate net clonal growth.

plants from the pure Sarnia and pure Peche Is. pools. Seed set fruit⁻¹ differed between sites and combinations of sites. Plants from Peche Is. combined with plants from either Turkey Is. or Sarnia ranked first, followed by plants from Turkey Is. alone, and the combination of plants from all three sites. Plants from pools that were entirely from Sarnia or entirely from Peche Is. ranked last in terms of seed set. Seed set fruit⁻¹ was generally lower than under field conditions.

When the production of viable seeds is tallied according to position within the fruit (Table 7), it is apparent that the productivity of the proximal and mid-sections is significantly lower for the plants from Peche Is., in isolation. There are no significant differences between treatments (mixtures) in terms of viable seed production in the distal (stylar) portion of the fruit.

TABLE 7. Distribution of viable seeds of *Vallisneria americana* according to their position within a fruit, in the experimental pools. The source populations of plants in each treatment are: S = Sarnia, P = Peche Is., T = Turkey Is. Values in the same row that do not differ significantly ($P < 0.05$) are designated with the same superscript.

Position within fruit	Population source						
	S	P	T	S/P	S/T	P/T	S/P/T
Proximal (basal or peduncular end)	27.3 ^b	13.7 ^a	34.8 ^b	44.4 ^b	34.2 ^b	43.8 ^b	31.2 ^b
Mid	38.6 ^{ab}	34.5 ^a	42.2 ^{ab}	48.2 ^{ab}	40.9 ^{ab}	54.1 ^b	43.5 ^{ab}
Distal (stylar end)	39.6 ^a	41.2 ^a	44.7 ^a	47.6 ^a	38.6 ^a	50.8 ^a	43.6 ^a

DISCUSSION

There is some sexual dimorphism in *Vallisneria americana*, but with the exception of primary sexual characteristics these differences are quantitative rather than qualitative. For example, leaf number and biomass leaf⁻¹ were significantly greater in females. However, patterns of biomass allocation are not particularly useful in early diagnosis of sex because they are not evident until plants are in flower, and, for females, they are highly dependent on pollination success.

According to the minimum estimate of clone size, male strings are significantly larger than female strings at all three sites (Table 4). When male and female strings are examined in terms of the percentage of vegetative shoots within each there are, however, no significant differences between the sexes. This contrasts with *Rhus typhina*, where females were found to contain more vegetative ramets (Lovett Doust & Lovett Doust 1988). However, this result for *Vallisneria* is probably in part a reflection of the strongly male-biased ratio of flowering ramets; it is likely that some of the vegetative shoots that appear to be part of male clones may in fact be ramets of non-flowering female clones. Allozyme surveys currently under way should clarify the true extent of clones, and should allow a more-accurate assessment of the frequency of flowering and vegetative ramets in male and female clones. By the second estimate of clone size, pure male strings are significantly longer than pure female strings. This is in agreement with the finding of Sullivan & Titus (1990) that male plants produce significantly more vegetative buds per g dry mass than do females (although they produce significantly fewer than do vegetative plants).

Because there are no secondary sexual characteristics identified for *Vallisneria* that would allow us to identify which of the vegetative plants will turn out to be males and which will be females, the genet sex ratio is not yet known. However, the sex ratio as expressed by flowering plants (the tertiary sex ratio) is strongly male-biased. This supports the generalization of Lloyd (1973) that male-biased sex ratios are to be expected in long-lived polycarpic perennials (although shoots of *Vallisneria* are annual, and the longevity of *Vallisneria* genets is unknown). In a clonal species male bias may be due to greater reproductive costs for females, seen as relatively greater survival by male ramets, a larger size threshold before females can flower, differing competitive ability for males and females, or differing rates of clonal growth between males and females as a consequence of greater costs incurred by females as they mature fruits (Lovett Doust & Lovett Doust 1988). Sullivan & Titus (1990) reported a strong relationship between growth and clonal growth in males and vegetative plants but noted an inverse relationship between fruit production and clonal growth in females. This is indicative of a trade-off between the more costly sexual reproduction of females and their clonal growth, whereas reproductive costs for males may make a less significant impact on their clonal growth.

In a study of *Vallisneria* in upper New York State, Titus & Stephens (1983) reported a flowering frequency of 24%. This was comparable to the frequency of flowering at Sarnia, although the proportion of flowering plants increased in our study in the more southerly sites. The frequency of sexual shoots that are female follows the same geographic trend. It may be that female ramets must reach a certain size threshold before they can flower, and fewer female ramets are able to reach that size in Sarnia. There are several possible explanations for this. The growing season was approximately 3 weeks delayed at Sarnia, compared to Peche Is. and Turkey Is.

Furthermore, there may be a significant gradient of chemical pollutants which are present in greater concentrations near Sarnia (a major petrochemical manufacturing area) than they are downstream. There may actually be selection for asexual reproduction over sexual reproduction if sexually produced offspring are more vulnerable to detrimental genotoxic exposure.

Bierzchudek (1989) compared sexual and asexual populations of *Antennaria parviflora*, a dioecious perennial herb of alpine meadows. She cloned sexual and apomictic females and grew each genotype in six growth-chamber environments varying in temperature and moisture levels. Bierzchudek found that asexual plants (apomicts) were less sensitive to environmental extremes than sexual plants: their survivorship, flower-head production and biomass were all significantly greater than for sexuals. It is possible that Sarnia plants have been selected to follow a phenology differing from that of the plants at the other two sites; indeed, they form ramets that are smaller, on average, than those of the other populations studied here. If the threshold for flowering as a female is fairly constant between populations, it may be that female Sarnia plants are simply less likely to attain that threshold because of developmental constraints, resulting in greater emphasis on clonal growth for the maintenance of that population. There is yet another factor that may be in operation here. Ramets at the Sarnia site were at almost twice the density of ramets at the other two sites. The reduced sexual expression, and increased male bias at Sarnia may have been due to inter-ramet competition, causing plants to grow less, and therefore to be less likely to flower, particularly if they were female. A number of studies are under way to explore these hypotheses. The relative response of each population to exposure to organic contaminants typical of the Huron–Erie Corridor of the Great Lakes Basin is being assessed (M. Biernacki, unpublished). Work in progress (T. K. Mal, unpublished) explores the level of genetic diversity in each of the sites through allozyme electrophoresis. In addition, studies involving reciprocal transplants and replants between the sites are in progress (M. Biernacki, unpublished). These studies should provide an explanation of the performance of plants at Sarnia, but in a larger sense should elucidate many aspects of the population biology of aquatic plants.

Experimental results

The Sarnia plants showed the greatest vegetative vigour in isolation and also in combination with plants from other sites. They also produced the greatest number of viable seeds, both in isolation and, generally, in combination with plants from the other sites (Table 6). There is some evidence from natural populations that matings between neighbouring plants can result in reduced seed set, lower seed weight and reduced seed viability (Price & Waser 1979; Levin 1981, 1984; Waser & Price 1983; Redmond, Robbins & Travis 1989).

In natural populations of a clonal dioecious species it is possible that neighbours are closely related, resulting in inbreeding depression. In the experimental pools two of the 'pure cultures' of plants from single sites (Peché Is. and Sarnia) showed the lowest fruit length and seed set fruit^{-1} . Conversely the mix of plants from these two sites showed the second-highest fruit length and number of seeds fruit^{-1} for combinations of plants in the experiment. The number of seeds fruit^{-1} was generally lower in the experiment than in the field; this suggests that ovule number fruit^{-1}

was pollen limited. A further indication of pollen limitation is the observation that viable seed set is comparable in the stylar section of fruits in all treatments, whereas there are some significant differences between treatments in the mid and proximal sections of the fruit (Table 7). The depth of the pools was shallower than water depth in the field and the leaves readily reached the surface of the water. Leaves at the surface of the water probably restrict the mobility of the male flowers and thus limit the efficiency of pollination.

The overall production of seeds pool⁻¹ (Table 6) indicates that Sarnia plants were by far the most productive per unit area, and per initial plant established in the experiment, because of their considerably greater clonal growth. In *Vallisneria*, the production of flowers seems to be strongly coupled to clonal growth; indeed the number of flowers ramet⁻¹ is similar between sites and between the sexes. The greater clonal growth of Sarnia plants therefore resulted in greater fecundity in the experiment. Sarnia plants were not performing at this level in the field, however. *Vallisneria* at Sarnia was sampled in dense patches; it is likely that these plants have the potential for considerable clonal growth and consequent sexual reproduction, but that potential is realized only in years when environmental conditions favour their growth either through an extended growing season, or in areas where *Vallisneria* is at low density.

ACKNOWLEDGMENTS

We thank the Banwell family of 'Banland', Essex County, who generously provided the land, water and water troughs necessary to maintain the experiment. Kathryn Bondy, Ben Doctor and Patrick McNiven-McKenna assisted with field-work. Lesley Lovett Doust, James White and two referees provided valuable comments on the manuscript. The research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERCC) and the Ontario Ministry of Natural Resources.

REFERENCES

- Bawa, K. S. & Opler, P. A. (1975). Dioecism in tropical forest trees. *Evolution*, **29**, 167–179.
- Bierzychudek, P. (1989). Environmental sensitivity of sexual and apomictic *Antennaria*: do apomicts have general purpose genotypes? *Evolution*, **43**, 1456–1466.
- Bierzychudek, P. & Eckhart, V. (1988). Spatial segregation of the sexes of dioecious plants. *American Naturalist*, **132**, 34–43.
- Cook, C. D. K. (1987). Vegetative growth and genetic mobility in some aquatic weeds. *Differentiation Patterns in Higher Plants* (Ed by K. M. Urbanska), pp. 217–225. Academic Press, London.
- Cook, C. D. K., Gut, B. J., Rix, E. M., Schnellner, J. & Seitz, M. (1974). *Water Plants of the World*. Dr W. Junk, The Hague.
- Cox, P. A. (1981). Niche partitioning between the sexes of dioecious plants. *American Naturalist*, **117**, 295–307.
- Cox, P. A. (1988). Hydrophilous pollination. *Annual Review of Ecology and Systematics*, **19**, 261–280.
- Cox, P. A. & Knox, R. B. (1989). Two-dimensional pollination in hydrophilous plants: convergent evolution in the genera *Halodule* (Cymodoceaceae), *Halophila* (Hydrocharitaceae), *Ruppia* (Ruppiaceae), and *Lepilaena* (Zannichelliaceae). *American Journal of Botany*, **76**, 164–175.
- Grant, M. C. & Mitton, J. B. (1979). Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution*, **33**, 914–918.
- Iglesias, M. C. & Bell, G. (1989). The small-scale spatial distribution of male and female plants. *Oecologia*, **80**, 229–235.
- Kausik, S. B. (1939). Pollination and its influences on the behavior of the pistillate flower in *Vallisneria spiralis*. *American Journal of Botany*, **26**, 207–211.

- Levin, D. A. (1981). Dispersal versus gene flow in plants. *Annals of the Missouri Botanical Garden*, **68**, 233–253.
- Levin, D. A. (1984). Inbreeding depression and proximity-dependent crossing success in *Phlox drummondii*. *Evolution*, **38**, 116–127.
- Lloyd, D. G. (1973). Sex ratios in sexually dimorphic Umbelliferae. *Heredity*, **31**, 239–249.
- Lovett Doust, J. & Lovett Doust, L. (1988). Modules of production and reproduction in a dioecious clonal shrub, *Rhus typhina*. *Ecology*, **69**, 741–750.
- Lovett Doust, J., O'Brien, G. A. & Lovett Doust, L. (1987). Effect of density on secondary sex characteristics and sex ratio in *Silene alba* (Caryophyllaceae). *American Journal of Botany*, **74**, 40–46.
- Lovett Doust, L. & Lovett Doust, J. (1987). Leaf demography and clonal growth in female and male *Rumex acetosella*. *Ecology*, **68**, 2056–2058.
- Malone, C. R. (1967). A rapid method for the enumeration of viable seeds in the soil. *Weeds*, **15**, 381–382.
- Miller, J. S. & Lovett Doust, J. (1987). The effects of snail grazing and plant density in female and male spinach plants. *New Phytologist*, **107**, 613–621.
- Price, M. V. & Waser, N. M. (1979). Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*. *Nature*, **277**, 294–297.
- Redmond, A. M., Robbins, L. E. & Travis, J. (1989). The effects of pollination distance on seed production in three populations of *Amianthium muscaetoxicum* (Liliaceae). *Oecologia*, **79**, 260–264.
- Sculthorpe, C. D. (1967). *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.
- Sullivan, G. & Titus, J. E. (1990). Relating asexual reproduction to growth and fruit production in a submersed plant. *Bulletin of the Ecological Society of America*, **71**, (Suppl.), 339.
- Svedelius, N. (1932). On the different types of pollination in *Vallisneria spiralis* L. and *Vallisneria americana* Michx. *Svensk Botanisk Tidskrift*, **26**, 1–12.
- Titus, J. E. & Stephens, M. D. (1983). Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. *Oecologia*, **56**, 23–29.
- Waser, N. M. & Price, M. V. (1983). Optimal and actual outcrossing and the nature of plant–pollinator interaction. *Handbook of Experimental Pollination Biology* (Ed by C. E. Jones & R. J. Little), pp. 341–359. Van Nostrand Reinhold, New York.
- Webb, C. J. (1976). Flowering periods in the gynodioecious species *Gingidia decipiens* (Umbelliferae). *New Zealand Journal of Botany*, **14**, 207–210.
- Wilder, G. J. (1974). Symmetry and development of pistillate *Vallisneria americana* (Hydrocharitaceae). *American Journal of Botany*, **61**, 846–866.
- Wylie, R. B. (1917). The pollination of *Vallisneria spiralis*. *Botanical Gazette*, **75**, 191–202.

(Received 8 October 1990; revision received 14 March 1991)