Demography of clonal Ostrich Fern (*Matteuccia struthiopteris*): a five year summary

Norm C. Kenkel
Department of Botany, University of Manitoba
Winnipeg, Manitoba R3T 2N2

Introduction

This contribution summarizes the first five years of a long-term investigation into the demography and spatio-temporal dynamics in a clonal ostrich fern population (*Matteuccia struthiopteris*) at Oxbow Woods, Delta, Manitoba. The study was initiated in the fall of 1993 (year 1).

In many plant species, the production of vegetative offshoots (clonal growth) is an important method of establishment, spread and perpetuation (Silvertown and Lovett-Doust 1993). Clonal ramets, like individual plants (genets), have individual demographic profiles (e.g., birth, death, size, reproductive capacity). However, ramets differ from genets in that they often maintain underground connections (rhizomes or lateral roots) and so remain physiologically interconnected (Watson 1986). A number of demographic profiles of clonal plant species are available, but the majority are based on comparatively short-term data (Jackson *et al.* 1985).

Clonal growth often results in large, dense stands consisting of a single genotype, even though many genets may have initially been present (Langer *et al.* 1964). This appears to be the case in the clonal bracken fern (*Pteridium aquilinum*), which often forms large, genetically uniform stands in burned areas in Finland (Oinonen 1967). This suggests that intraspecific competition may be extremely important in regulating population densities (see Kenkel 1993 and references therein). The basic biology and ecology of Ostrich Fern is well known (Prange and von Aderkas 1985) but the population dynamics of the species (e.g., age-specific mortality rates, longevity of clonal ramets) remain poorly understood. Whereas a number of studies have demonstrated that the size and proximity of neighbours can affect growth rates of individuals in a population (Kenkel 1991), very few investigations have integrated spatial interactions with demographic processes.

The objective of this long-term study is to relate individual ramet productivity (ramet size), reproduction (fertile frond production), and longevity to the size and proximity of ramet 'neighbours' within the stand. Results from the first four years of this study are reported in Kenkel (1994, 1995, 1996, 1997).

Matteuccia struthiopteris (L.) Todaro

This fern species is a member of the family Polypodiaceae. It is commonly known as the Ostrich Fern, or more generally as 'fiddle heads' after the edible young frond shoots. A large clonal species, ostrich fern occurs throughout much of northern North America and Eurasia. It often forms extensive, monodominant stands in moist deciduous forests, but it also occurs in the southern boreal forest in moist, nutrient-rich sites (Mueller-Dombois 1964, Walshe 1980, Odland 1992). The species prefers rich alluvial sites, and is particularly common on river plain fluvial deposits. It is a good indicator of soil moisture conditions, showing a strong preference for moist, moderately drained soils (Mueller-Dombois 1964, Odland 1992). In Manitoba, vegetative fronds have a stipe up to 40 cm in length and blades to 1 m in length. Individual ramets are erect rootstocks with a projecting crown of one or (usually) more fronds. Rootstocks are connected by stout, persistent underground rhizomes that generally occur within the upper 15 cm of the soil profile. A small number of ramets in the clone (usually the largest) produce separate, morphologically distinct fertile fronds that are thought to have a nutrient depletion effect on vegetative fronds. Under shaded conditions in New Brunswick, only about 1% of ramets produced fertile fronds, but "in conditions of direct sunlight, a much higher percentage of plants (*sic*) develop fertile fronds" (Prange and von Aderkas 1985). In Manitoba, vegetative fronds complete their elongation in the last few weeks of May, and begin dying back by mid-August to early September. Low soil moisture and high light reduce frond height and dry mass, and the species is considered to be 'shade tolerant' (Prange and von Aderkas 1985).

Study Area

The Ostrich Fern population studied occurs in a gallery forest (known locally as Oxbow Woods) near an abandoned channel of the Assiniboine River. The site is on University Field Station (Delta Marsh) property (50°11'N, 98°23'W, circa 3 km south of Lake Manitoba). The study plot was located within an extensive monodominant stand of Ostrich Fern near the Inkster farm site. The overstory is dominated by mature Bur Oak (*Quercus macrocarpa*) and Green Ash (*Fraxinus pennsylvanica*). Younger individuals of Manitoba Maple (*Acer negundo*) occur at low abundance. Soils in the Oxbow Woods are rich clay-loams, with approximately 20% organic matter content and a near-neutral pH. The forest understory is locally variable and quite patchy. Few other species are found within the study plot, but in adjacent areas (where Ostrich Fern is not present) conspicuous understory species include *Aralia nudicaulis*, *Carex assiniboinensis*, *Rhus radicans*, *Osmorhiza longistylis*, *Actaea rubra* and *Rudbeckia laciniata*. Löve (1959) characterizes most of these species as having an 'eastern' floristic affinity.

The climate of the area is humid sub-continental, with short warm summers and long cold winters. Mean annual temperature is circa 1.5°C. July is the warmest month (about 19°C), and January the coldest (about -20°C). Mean annual precipitation is about 50 cm, three-quarters of which falls as rain.

Materials and Methods

A 5 x 5 m study plot was located in a dense, monodominant population of Ostrich Fern. Other understory species were present at very low abundance and cover, and abiotic conditions (soils, degree of shading by trees) within the plot were uniform. All ramet rootstocks within the study plot were numbered with a small red 'flag' and their locations mapped. Mapping was accomplished by measuring the distance (± 1 cm) to each of the four corner posts of the study plot. The law of cosines was then used to obtain the spatial coordinates of each rootstock. For each rootstock, the sizes (three classes: 'full', 'half' and 'small') and number of vegetative fronds were recorded. For fertile rootstocks, the number of new (current year) and older (previous years) fertile fronds were recorded. Mapping and recording of rootstocks was performed from August 3-7 of 1993, August 9-10 of 1994, August 1-3 of 1995, August 23 of 1996, and August 1 of 1997.

Results

Vegetative Fronds and Rootstocks: 1993 to 1997

The total number of vegetative rootstocks was relatively invariant over time, ranging from 208 in 1994 to 245 in 1995 (Table 1). However, the number of vegetative fronds declined over time, from 1,002 in 1993 to 824 in 1997 (a decrease of about 18%). This is reflected in the decline in the mean number of vegetation fronds per rootstock (Table 2). Frequency distributions of the number of vegetative fronds per rootstock indicate that distributions in 1993 and 1994 were not skewed, but those in 1995 through 1997 were positively skewed (Fig. 1, Table 2).

Table 1. Five year trends in the number of vegetative and fertile fronds and rootstocks.

	1993	1994	1995	1996	1997
No. vegetative rootstocks	214	208	245	228	229
No. fertile rootstocks	21	26	3	18	5
Total no. rootstocks	235	234	248	246	234
No. vegetative fronds	1,002	902	886	879	824
No. fertile fronds	31	42	4	31	7
Total. no. fronds	1,033	944	890	910	831
Percent vegetative rootstocks	8.94	11.11	1.21	7.32	2.14
Percent fertile fronds	3.00	4.45	0.45	3.41	0.84

Table 2. Distribution of vegetative fronds on all rootstocks.

Number of fronds	1993	1994	1995	1996	1997
Mean	4.26	3.85	3.57	3.57	3.52
CV (%)	40.0	40.2	44.5	49.9	47.1
Skewness	-0.07	0.06	0.34	0.28	0.15

Demography of Rootstocks

Rootstock turnover in the population is low. Of the 235 rootstocks present in 1993, 189 (about 81%) were still alive in 1997 (11 died in 1994, 9 in 1995, 12 in 1996 and 14 in 1997). Twelve new rootstocks were 'born' in 1994, 20 in 1995 (3 of which died in 1996, and 3 more in 1997), 15 in 1996, and 5 in 1997. Thus rootstock 'births' generally match deaths. The annual rate of rootstock turnover is approximately 5%.

Interannual Correlations in Number of Vegetative Fronds per Rootstock

For the n = 189 rootstocks that remained alive from 1993-1997, one-year lag correlations in the number of fronds per rootstock were generally r > 0.7 (Table 3). The exception is 1995-1996, with a correlation of r = 0.607. These results suggest that the number of fronds produced by a given rootstock in year X is largely predictable from the number produced in the previous year. Interannual correlations decline with increasing year-lag, reaching a low of r = 0.368 for the five-year lag (1993-1997).

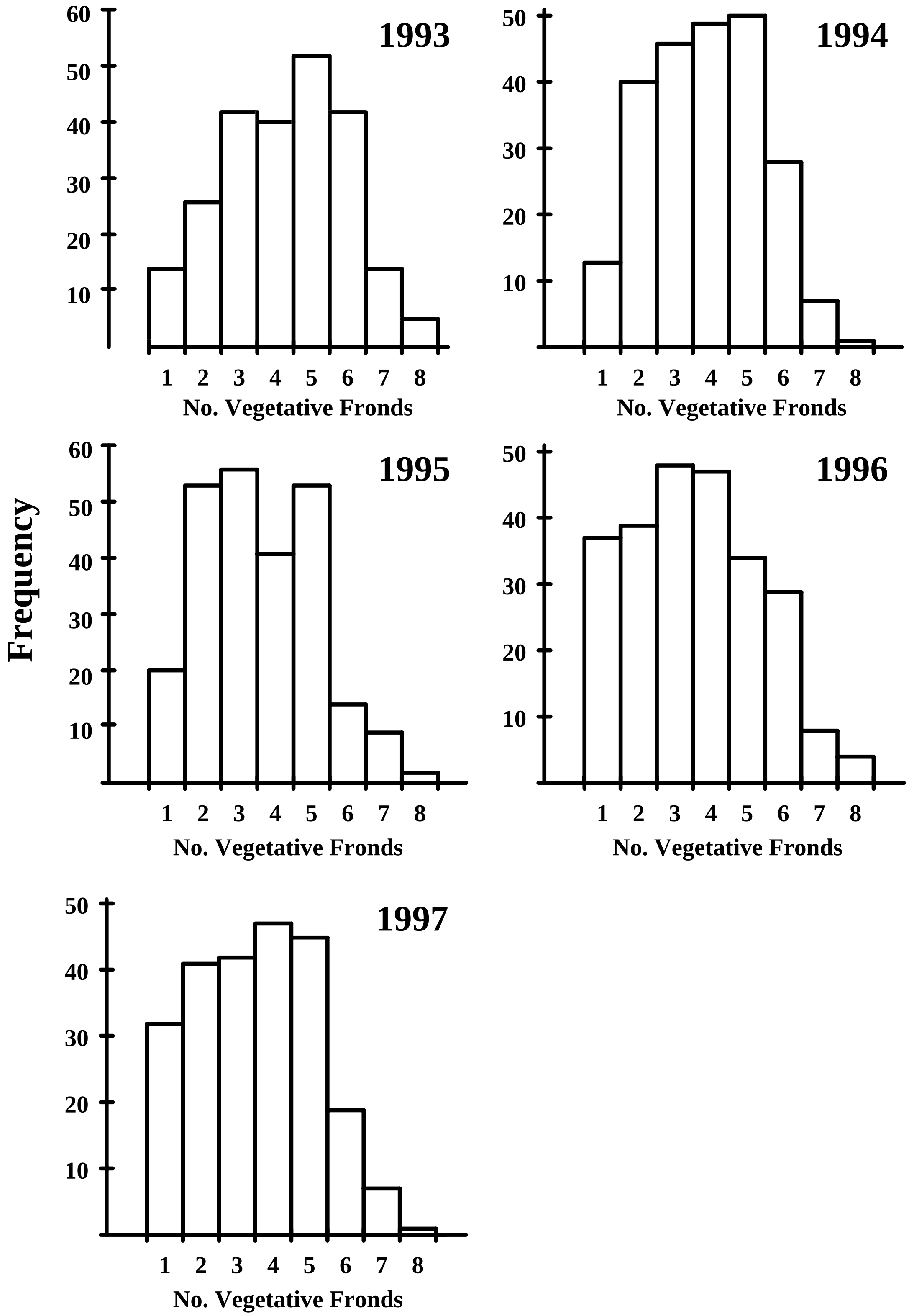

Figure 1. Frequency histograms of the number of vegetative fronds per rootstock in a population of clonal Ostrich Fern, for the years 1993-1997.

Table 3. Interannual correlations (n = 189) in the number of vegetation fronds per rootstock, 1993-1997.

	1993	1994	1995	1996
1994	0.703			
1995	0.560	0.709		
1996	0.471	0.596	0.607	
1997	0.368	0.512	0.565	0.719

Table 4. Distribution of the number of fertile fronds on fertile rootstocks.

No. fertile fronds	1993	1994	1995	1996	1997
1	13	14	2	8	3
2	6	8	1	7	2
3	2	4	0	3	0
Mean no. fertile fronds	1.48	1.62	1.33	1.72	1.40

Fertile Fronds and Rootstocks: 1993 to 1997

The total number of fertile rootstocks varied considerably from year to year, from lows of 3 and 5 (1995 and 1997, respectively) to 26 in 1994 (Table 1). In all years, the majority of fertile rootstocks had one or two fertile fronds, and none had more than three (Table 4). A total of 34 rootstocks were fertile in at least one of the five years 1993-1997 (Table 5). Of these, 22 (or about 65%) were fertile for at least two years, and 12 (or about 35%) were fertile for at least three years. Of the 32 rootstocks that produced fertile fronds in the most fertile years (1993, 1994 and 1996), 22 (or about 69%) were fertile in at least two of those three years. These results indicate that only a small proportion of the population is fertile in any given year, and that fertile rootstocks often remain so for two or more years. Fertile rootstocks are generally large, producing above-average numbers of vegetative fronds (Table 5).

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Table 5. Summative profile of the 34 rootstocks that were fertile at least once during the five year period, 1993-97.

Years fertile	No. fertile fronds ‘93	‘94	‘95	‘96	‘97	No. vegetative fronds ‘93	‘94	‘95	‘96	‘97
5	2	1	2	3	2	6	6	6	6	5
4	2	2	1	1	8	7	7	6	6	
4	1	2	1	1	7	6	5	6	6	
4	1	3	1	2	7	6	5	6	5	
3	3	2	2	8	6	6	6	7		
3	3	2	1	7	6	5	8	5		
3	2	3	1	8	7	7	7	7		
3	1	1	3	6	6	6	6	7		
3	1	1	2	6	5	4	3	4		
3	1	1	2	7	6	4	7	7		
3	1	2	1	6	6	4	6	5		
3	1	2	2	6	5	5	6	5		
2	2	1	6	5	7	3	5			
2	1	1	7	6	6	1	1			
2	1	1	4	6	4	3	3			
2	1	1	5	7	4	5	5			
2	1	1	6	4	4	5	2			
2	3	3	6	6	7	8	5			
2	2	2	6	6	5	6	4			
2	1	2	5	5	5	7	4			
2	1	1	8	6	6	6	5			
2		1	2	6	6	7	7	7		
1	2		6	5	5	4	3			
1	2		7	6	6	5	5			
1	1		6	5	4	3	1			
1	1		6	5	7	6	5			
1	3	7	7	6	8	7				
1	2	7	6	6	6	2				
1	1	5	4	2	1	3				
1	1	6	7	6	6	5				
1	1	6	6	6	5	4				
1		1	7	5	5	4	5			
1		1	3	1	2	4	3			
1		1	6	7	8	7	6			

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