Demography of clonal ostrich fern (*Matteuccia struthiopteris*). IV. Year four of a long-term study

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Introduction

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

In many plant species, recruitment through the production of vegetative offshoots (clonal growth) is an important method of establishment and spread (Silvertown and Lovett Doust 1993). Demographic profiles of a number of clonal plant species have been developed, but most are based on comparatively short-term studies (Jackson *et al*. 1985). Clonal ramets, like individual plants (genets), have individual demographic profiles (birth, death, size, reproductive capacity). Ramets differ in that they often remain attached to one another (via rhizomes or lateral roots), and may therefore remain physiologically interconnected (Watson 1986). Intraspecific competition in clonal species may be extremely important in regulating population density (see Kenkel 1993 and references therein). Clonal growth may result in the development of 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).

The biology of the ostrich fern is well known (Prange and von Aderkas 1985), but age-specific mortality rates and the longevity of clonal ramets are poorly known. While 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. The first three years of results from this study are reported in Kenkel (1994, 1995, 1996).

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, although it also occurs in the southern boreal forest in moist, nutrient-rich sites (Walshe 1980). The species prefers rich alluvial sites, and it particularly common on river plain fluvial deposits. It is a good indicator of soil moisture conditions, preferring moist by moderately drained soils (Mueller-Dombois 1964). In Manitoba, vegetative fronds have a stipe up to 40 cm in length and a blade to ca. 1 m in length. Individual ramets are erect rootstocks with a projecting crown of one or (usually) more fronds. Rootstocks are connected by a stout, persistent underground rhizome. Some ramets, usually the largest, produce separate and morphologically distinctive fertile fronds. These are thought to have a nutrient depletion effect on the vegetative fronds (Prange and von Aderkas 1985). In Manitoba, vegetative fronds complete their elongation in the last few weeks of May, and begin dying back in mid-August. Because low moisture and high light reduce frond height and dry mass, the species is considered to be 'shade-adapted' (Prange and von Aderkas 1985). Fertile fronds are persistent but uncommon. In New Brunswick, Prange and von Aderkas (1985) found that under shaded conditions only 1% of ramets produced fertile fronds, but that "in conditions of direct sunlight, a much higher percentage of plants (*sic*) develop fertile fronds".

Study Area

The ostrich fern population studied occurs in a gallery forest (known locally as Oxbow Woods) along a former oxbow of the Assiniboine River. The site is on University of Manitoba Field Station (Delta Marsh) property (50°11'N, 98°23'W, ca. 3 km south of Lake Manitoba). The study plot was located within an extensive monodominant stand of ostrich fern located near the Inkster Farm site. This gallery forest 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 ca. 20% organic matter content and a near-neutral pH. The forest understory is locally variable and quite patchy. Few other species were 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 ca. 1.5°C. July is the warmest month (mean of ca. 19°C), and January the coldest (ca. -20°C). Mean annual precipitation is ca. 50 cm, of which ca. 75% 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, and on August 23 of 1996.

Results

Vegetative Fronds: 1995 vs. 1996

Rootstock turnover in the 1995-1996 interval was somewhat higher than in previous years. Of the 248 rootstocks present in 1995, 18 had died by 1996. Fifteen new rootstocks were mapped in 1995, and an additional rootstock present in 1994 but recorded as 'dead' in 1995 was mapped. Thus a total of 246 rootstocks were mapped in 1995, down from 248 in 1994 but higher than the number recorded in 1993 (235 rootstocks) and 1994 (234 rootstocks). The total number of vegetative fronds has declined over time, from 1002 in 1993 (mean of 4.26 per rootstock), to 902 in 1994 (mean = 3.86), 886 in 1995 (mean = 3.57) and 879 (mean = 3.57) in 1996. Mean values are lower than the 6.75 fronds per rootstock reported in New Brunswick populations (Prange and von Aderkas 1985). As in previous years, most of the rootstocks that died between 1995 and 1996 were classed as 'small' (i.e. fronds much smaller than average, generally < 20 cm in height) in the previous year, and most produced only one vegetative frond. As in previous years, the correlations between the number of vegetative fronds produced by rootstocks between years (1995-1996) was statistically significant ($r = 0.636$, $p < 0.01$).

Fertile Fronds: 1994 vs. 1995

Population fecundity recovered from the very low level observed in 1995. In 1996, 18 fertile rootstocks were observed (7.3% fertility), compared to only 3 (1.2% fertility) in 1995. The 1996 results are similar to those obtained in 1993 and 1994 (26 rootstocks or 11.1% fertility and 21 rootstocks or 8.9% fertility, respectively). Thirty-one fertile fronds were produced in 1996, compared to only 4 in 1995. The 1996 value is similar to those observed in 1993 and 1994 (31 and 42 fertile fronds, respectively). Interestingly, all but two of the 18 rootstocks that were fertile in 1996 were also recorded as being fertile in the 1993 and/or 1994 surveys. As in previous years, fertile rootstocks produced a higher than average number of large, sterile fronds (mean = 6.2).

Four Year Trends: 1993-1996

An examination of data collected over the four years (1993-1996) reveals some interesting trends. The following is a brief summary:

1. Rootstock mortality rates are similar from year to year, averaging ca. 4%. If mortality within the population is random, this would result in complete turnover of the ramet population every ca. 25 years. However, individual ramets may be much more long-lived, since mortality occurs disproportionately among the smallest size classes. Indeed, four small rootstocks that were 'born' after 1993 were recorded as being 'dead' by 1996, suggesting that rootstock turnover rates are much higher in smaller rootstocks.
2. Mortality in the population is largely restricted to the smallest rootstocks. This is apparent from an examination of the number of fronds produced by each rootstock in the year before it died:

Number of Fronds in Year t	Number Dead in Year t+1
1	20
2	14
3	6
> 3	0

Of the 13 rootstocks that were present in 1993 but recorded as dead in 1996, most showed a steady decline the number of fronds produced over the four year period (Fig. 1). There are no cases of relatively 'healthy' and productive (> 3 fronds) rootstocks dying in the following year.

3. Correlations between the number of vegetative fronds produced per rootstock over time are consistently positive and statistically significant, although the correlation declines over time (n = 200):

	1993	1994	1995
1994	0.70		
1995	0.57	0.72	
1996	0.45	0.58	0.64

These results suggest that rootstock productivity shows positive temporal autocorrelation: large rootstocks tend to remain large, while small rootstocks tend to remain small.

4. Fertile rootstocks are usually large, producing on average ca. 6 large sterile fronds in addition to one or more fertile fronds. Interestingly, although only ca. 10% of rootstocks are fertile in a give year (1995 excepted), the same rootstocks tend to be fertile from year to year. Of the 33 rootstocks that were fertile at least once during the four year period (1993-1996), 12 were fertile only once while 21 were fertile for two or more years (9 over two years, 10 over three years, and 2 over all four years). This suggests that certain ramets are 'programmed' to be fertile, while the majority of the clone remains sterile.

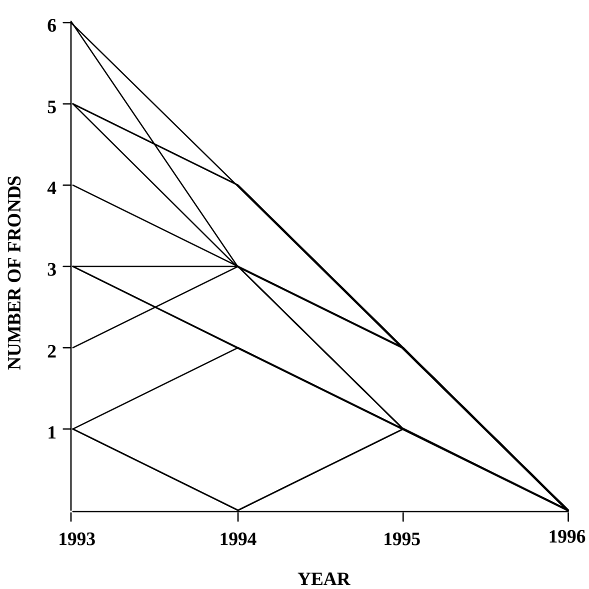

Figure 1. Changes over time in the 'size' (number of fronds) of 13 rootstocks that were alive in 1993 but recorded as 'dead' in 1996. Note that in 1995 (the year before death) all 13 rootstocks produced only 1 or 2 vegetative fronds.

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