TEMPORAL VARIATION IN SPOROPHYTE FERTILITY IN *DRYOPTERIS INTERMEDIA* AND *POLYSTICHUM ACROSTICHOIDES* (DRYOPTERIDACEAE: PTERIDOPHYTA)

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ABSTRACT

A long-term demographic study to assess temporal variation in two common New England ferns, *Dryopteris intermedia* (Evergreen wood fern) and *Polystichum acrostichoides* (Christmas fern) focused on fertile leaf production by the reproductively mature sporophyte. Over an eight-year period only 29.9% of the leaves in a *D. intermedia* crown were fertile, while for *P. acrostichoides* significantly more (48.0%) of the leaves in the crown were fertile. Annual values of the percentage of plants with fertile leaves for *D. intermedia* ranged from 42% to 77% and for *P. acrostichoides* from 57% to 93% reflecting significant annual variation, possibly related to winter weather conditions. Only 16% of *D. intermedia* and 14% of *P. acrostichoides* sporophytes were fertile every year of the study. Transitions from fertile plant status to sterile plant status occurred in 15% of the *D. intermedia* observations and 14% of the *P. acrostichoides* observations. For both species, when a sterile year followed a fertile year the number of leaves in the crown decreased by approximately half a leaf. Determining the causes of such high levels of variability in plant fertility will be necessary before the role of ferns in any ecosystem can be fully understood.

INTRODUCTION

Long-term monitoring of marked individuals can provide insight into the life history of a species (Harper, 1977) as well as providing a solid basis for future experimental research (Noss, 1999). Werth & Cousens (1990) emphasized the importance of long-term studies of ferns in order to understand mortality and differential fitness, and noted that very little information is available on the life spans and generation times of ferns. There have been several short-term studies of the life history of sporophytes of specific temperate understory fern species. Field research on various aspects of the temperate fern life cycle has been reported for *Blechnum spicant* (L.) Smith (Cousens, 1973, 1981), *Thelypteris dentata* (Forsskål) E. P. St. John, *Woodwardia virginica* (L.) Smith, *Osmunda regalis* L. (Bartsch & Lawrence, 1997) and *Polystichum acrostichoides* (Michaux) Schott (Greer & McCarthy, 2000). Studies exceeding 12 years in length have been conducted on selected species of *Botrychium* (Montgomery, 1990; Johnson-Groh, 1999). Sato (1990) followed leaf production for more than nine years in *Polystichum braunii* (Spenner) Fée, *P. tripteron* (Kunze) Pr.and *Dryopteris crassirhizoma* Nakai. Few other long-term studies have considered annual variation in temperate fern life history characteristics.

Of the seven fern life history classes identified by Cousens *et al.* (1988) the reproductively mature sporophyte class has the greatest impact on ecosystem processes. Spore production, controlled by the mature sporophyte, is a significant element of the reproductive effort for ferns (Greer & McCarthy, 2000) and may also limit establishment of the next generation (Peck, 1980). Though few quantitative studies have addressed temporal variation in fertile leaf production it is assumed that most mature ferns reliably release spores every year (Sheffield 1996). Siman *et al.* (1999) state that fertility is the rule for mature individuals of most ferns but note that the genus *Pteridium* is an exception. A few short-term studies have also noted variation from this generally accepted assumption. Cousens (1988) reported that marked adult fertile plants had been observed reverting to adult sterile plant status. This was based on a study of *Woodwardia areolata* (L.) T. Moore (= *Lorinseria areolata* (L.) C. Presl.) which lasted 30 months (Cousens, *et al.*, 1988). Sato (1990) used counts of number of veins off the leaf midrib (NV) to assess chronological age. He observed a year-to year decrease in NV in about 20% of comparisons of overwintered leaves to the newly emerged leaf cohort in individuals of *D. crassirhizoma* and *P. tripteron*, but not in *P. braunii*. Greer & McCarthy (2000) found that not all reproductively mature individuals of *P. acrostichoides* produced at least one fertile leaf in each of the two years of their study.

This exploratory study of the reproductively mature sporophyte of two temperate species was undertaken to extend our knowledge of annual variation in plant fertility in a long-term study lasting eight years. The goals were to 1) determine what percentage of the leaves produced by an individual each year were fertile, 2) assess the number of plants in a sample population that produced at least one fertile leaf from year to year, 3) examine levels of consistency in the annual sequence of fertile and sterile leaf production, 4) compare patterns of temporal variation for two different species, and 5) compare any observed temporal patterns to relatively short term local climate parameters.

STUDY SPECIES

Two temperate ferns common in northeastern forests of the USA were chosen for comparative study: *Dryopteris intermedia* (Willdenow) A. Gray, the Evergreen wood fern, and *Polystichum acrostichoides*, the Christmas fern. Leaves of *D. intermedia* are described as monomorphic by Montgomery & Wagner (1993) while those of *P. achrostichoides* exhibit strong sterile-fertile leaf dimorphism, with the fertile leaf exhibiting a distinctive terminal segment of spore-bearing leaflets that are greatly reduced in size compared to the proximal sterile leaflets (Wagner, 1993). Both species have short internodes so that the leaves form a distinctly tufted crown around the shoot apex.

MATERIALS AND METHODS

Sporophyte fertility was observed over an eight-year period from 1993 to 2000 in a secondary, mixed-hardwood forest approximately 15 m above sea level in the town of Dresden, Lincoln County, Maine (USA) using methods developed for long-term studies of fern demography in a tropical forest at the Luquillo Long Term Ecological Research site in Puerto Rico (Sharpe, 1997). The sample population consisted of 31 individuals of *D. intermedia* and 14 individuals of *P. acrostichoides* which were considered reproductively matures as they had produced spores at least once during the eight-year study period. Of those monitored, 24 individuals of *D. intermedia* and nine individuals of *P. acrostichoides* were fertile in 1993, the first year of the study. Each plant was identified by a numbered plastic stake and a small segment of colored, plastic-covered wire attached to a leaf base and transferred annually to one of the leaves in the next year's cohort of leaves. Annual observations of sporophytes were made during the last week in August to insure that all leaves had fully expanded.

All leaves in the current year cohort were counted and each leaf was classified as sterile or fertile. To calculate a crown fertility perecentage for each sporophyte, the number of fertile leaves was compared to total number of leaves in the crown. Percentage of the plants fertile each year was determined by comparing the number of plants with at least one fertile leaf present in the crown to the total number of plants observed each year. Temporal patterns of fertile leaf production were further evaluated by noting the sequence of changes in plant fertility status, observed seven times within the eight-year monitoring period for each plant. Year-to-year transitions in plant fertility status were classified as FF (fertile to fertile), SS (sterile to sterile), FS (fertile to sterile) and SF (sterile to fertile). These categories are illustrated with an example of an individual plant which happened to experience all four types of plant fertility transitions (Figure 1). The number of continuous years a plant was sterile following and preceding a fertile year was also noted.

In order to evaluate whether relatively short term weather patterns could have an effect on plant growth, values for mean daily minimum and maximum temperatures, precipitation and snowfall were taken from records of the NOAA weather station located within 100 km of the study site in Portland Maine. Climate data were analyzed separately for summer (May through October) and winter (November through April). These analyses did not show significant variation in mean daily summer temperatures and precipitation. However, winter temperatures had significantly lower mean daily minimums in 1994 and 1996. Snowfall was significantly higher in the winter of 1996. Furthermore, there was a major cyclic disturbance in the form of an ice storm in

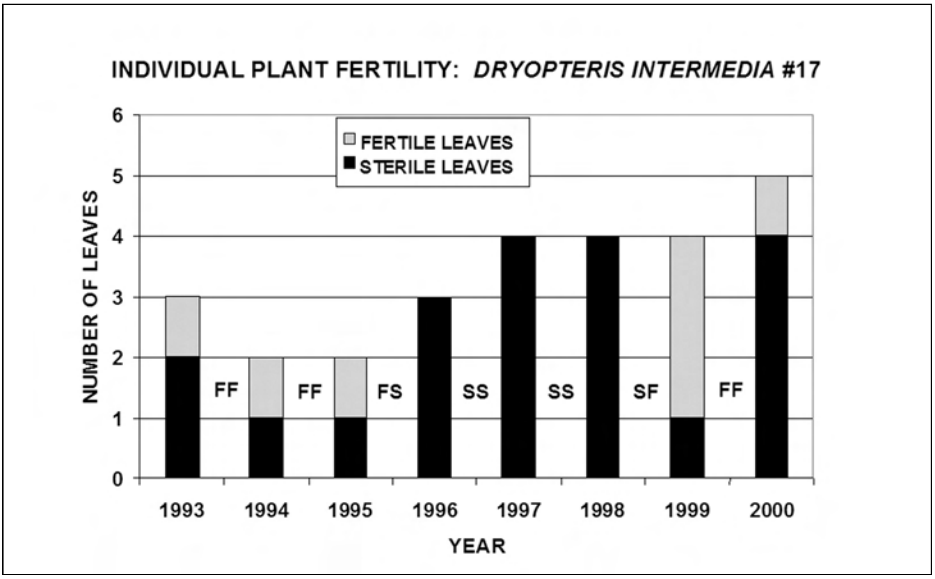

Figure 1. Profile of the fertile and sterile leaves present in the crown of a sample individual (#17) of *Dryopteris intermedia* for each of the eight years the plant was monitored. Plant fertility status transitions are noted between bars (SS = Sterile/Sterile, SF = Sterile/Fertile, FF = Fertile/Fertile, FS = Fertile/Sterile) for this sporophyte which happened to experience all four of the possible year-to-year transitions.

February 1998 (Darwin *et al.*, 2004).

Data analysis

Means and standard error of the means (SE) were calculated for crown fertility for each plant using data collected each year (N = 8). Standard error of the means were chosen to show variation because of the small sample sizes. All percentages were arcsine transformed before statistical tests were applied. To factor out variability among marked individuals, Repeated Measures Analysis of Variance (RMA) was used to evaluate year-to-year differences in the percent of crown fertile. A one sample t-test was used to compare plant fertility and transition type percentages from year to year for each species. Paired t-tests were used to compare the different fertility characteristics for the two species. Data were analyzed using Statistix 8 (Analytical Software, 2003).

RESULTS AND DISCUSSION

Crown fertility

In eight years of monitoring these populations, observations of crowns that were composed entirely of fertile leaves were unusual for both species. Of 360 individual annual flushes of leaves observed in this study, only eight individual leaf cohorts of *Dryopteris intermedia* and 18 of *Polystichum acrostichoides* were completely fertile. Fewer than half the leaves produced by these reproductively mature plants were fertile and the mean percentage of leaves in the crown that were fertile is significantly lower for *D. intermedia* than for *P. acrostichoides* (Table 1). Neither species in this study approached 100% fertile leaf production. This could be a function of the chronological age of these plants, which is unknown. If they are all relatively young plants, perhaps the ability to produce a full cohort of fertile leaves had not yet occurred. If they are all relatively old plants, then possibly the ability to produce a full cohort of fertile leaves had been lost. Although no increasing or decreasing pattern can be seen by comparing the percentages from year to year, perhaps eight years is too small a segment of the total life span to observe such patterns. It is also possible that full fertile leaf production is not possible in the specific habitat where these plants were growing. It is possible that each species has an intrinsic limit on fertile leaf production by reproductively mature plants which integrates its habitat requirements and need for vegetative support tissue. While there are reports of high percentages of crown fertility in some temperate ferns, for example in *Leptopteris hymenophylloides* (Sussex, 1958), low crown fertility has also been observed in *Matteuccia struthiopteris* (Von Aderkas & Green, 1986). In a study undertaken in southern Siberia, Gureyeva (2001) found that environmental factors may severely limit spore production by ferns and Cousens (1973) noted population differences in fertile leaf production by *Blechnum spicant*.

There were year-to-year differences in crown fertility. The annual mean percentage of leaves that were fertile within the crown ranged from 21.9% to 38.9% for *D. intermedia* and from 37.6% to 60.6% for *P. acrostichoides* with little concordance between species in the pattern of annual increases and decreases (Table 1). *Dryopteris intermedia* had the highest total fertile leaf production in 1994 following one of the two coldest winters of the study and had the lowest total fertile leaf production following the ice storm in 1998. In contrast, *P. acrostichoides* had the lowest fertile leaf production in 1996 following one of the two coldest winters of the study and exhibited no unusual response after the ice storm. Investigations into the specific triggers for fertile leaf production have been recommended by Wagner & Wagner (1977) and could identify potential environmental factors involved. For example, it has been

TABLE 1. Summary of annual variation in crown and plant fertility for reproductively mature sporophytes of *Dryopteris intermedia* and *Polystichum acrostichoides*. N is the number of plants measured. One-sample t-tests are used to compare years for percentage of plants and transition type percentages. Repeated measures analysis of variance is used to compare years for individual percentage of crowns fertile. Paired t-test is used to compare the year-to-year differences between species. Significant differences are indicated by * (P < 0.0500), ** (P < 0.0100) and *** (P < 0.0010).

Year	Fertile leaves in crown N	Percentage of crown (mean)	Percentage of plants fertile	Transition type percentages SS	SF	FF	FS
Dryopteris intermedia							
1993	31	35.1±4.87%	77%	–	–	–	–
1994	31	38.9±5.88%	71%	10%	13%	58%	19%
1995	31	33.9±5.09%	71%	13%	16%	55%	16%
1996	31	22.9±5.11%	48%	23%	7%	42%	29%
1997	31	35.1±4.63%	77%	23%	29%	48%	0%
1998	31	21.9±5.35%	42%	23%	0%	42%	36%
1999	31	23.8±4.58%	55%	39%	19%	36%	7%
2000	31	27.3±4.12%	68%	26%	19%	48%	7%
All	248	29.9±1.68%	64%	22%	15%	47%	15%
F/t		F = 1.88	t = 11.52	t = 6.11	4.10	14.49	3.28
df		7	7	6	6	6	6
P		0.0748	<0.0001 ***	0.0009 ***	0.0063 **	<0.0000 ***	0.1637
Polystichum acrostichoides							
1993	14	49.6±10.64%	64%	–	–	–	–
1994	14	41.4±9.73%	71%	23%	23%	46%	23%
1995	14	44.2±10.85%	71%	15%	15%	54%	15%
1996	14	37.6±11.99%	57%	33%	0%	58%	8%
1997	14	50.4±11.28%	71%	17%	25%	50%	8%
1998	14	52.7±10.27%	79%	14%	21%	57%	7%
1999	14	60.6±9.14%	93%	0%	21%	71%	7%
2000	14	47.4±9.01%	71%	0%	7%	64%	29%
All	112	48.0±1.71%	72%	12%	16%	58%	14%
F/t		F = 0.56	t = 12.97	t = 2.84	4.57	15.22	4.19
df		7	7	6	6	6	6
P		0.7891	<0.0001 ***	0.0295 *	0.0038 **	<0.0000 ***	0.0057 **
Species comparisons							
t		-4.57	-1.22	1.22	-0.31	-1.76	0.38
df		7	7	6	6	6	6
P		0.0026 **	0.2603	0.2696	0.7702	0.1298	0.7186

demonstrated in greenhouse studies (Siman & Sheffield, 2002) that under field conditions individuals do not necessarily produce the maximum number of fertile leaves possible each year. In a year-long study of *Polypodium vulgare* L. in the United Kingdom, field-grown and greenhouse-grown plants from identical genetic stock were compared by Siman & Sheffield (2002). The indoor population showed a four-fold increase in new leaves, mostly fertile, emerging in a wave pattern thought to represent three annual cohorts for field grown plants as compared to the outdoor population. There do appear to be limits to fertile leaf production which may be consistent within species over an extended period of time. Experiments similar to this one done by Siman & Sheffield (2002) would confirm these limitations.

Plant fertility

Of 248 individual leaf cohorts of *D. intermedia* observed during the eight years of the study, 64% included at least one fertile leaf, while for 112 cohorts of *P. acrostichoides* the percentage was 72% (Table 1). The percentage of plants in the population that produced at least one fertile leaf each year ranged from a low of 42% in 1998 to a high of 77% in 1993 for *D. intermedia,* a range from the lowest year to the highest of 35%, reflecting significant year-to-year variation. For *P. acrostichoides* there were also significant year-to-year differences, with a range from the lowest year (1996) to the highest year (1999) of 36% (Table 1). For *D. intermedia,* the lowest percentage of plant fertility occurred following the ice storm. A paired comparison of annual plant fertility percentages did not detect a significant difference between the two species (Table 1).

Annual sequence of plant fertility status

There are some elements of life history than can only be determined by making repeated observations of marked individuals over a long period of time. One of those elements is the year-to-year change in an individual sporophyte's fertility status. Overall, a plant was sterile one year as well as the next (SS) 48 times in the 217 observations of transition for *D. intermedia* (Table 1). Of these SS transitions, 9 (3 plants) occurred before a plant produced its first fertile leaf while for all others (81%) the SS transition occurred after the plant had produced at least one fertile leaf. For *P. acrostichoides*, SS transitions occurred 11 times out of 98 transition observations, with one plant (of 14) accounting for all of the SS transitions that occurred before a fertile leaf was produced. Thus 89% of the SS transitions for *P. acrostichoides* occurred after a fertile leaf had been produced. Sterile to fertile (SF) transitions occurred in 15% of the *D. intermedia* observations and 16% of the *P. acrostichoides* observations (Table 1).

Fertile to fertile (FF) transitions occurred in 47% of the *D. intermedia* observations and 58% of the *P. acrostichoides* observations (Table 1). A small percentages of all *D. intermedia* plants observed produced fertile leaves only once or twice, while all *P. acrostichoides* individuals produced at least one fertile leaf during three or more years (Table 2A). Although all plants in this study were reproductively mature, only 16% of the individuals of *D. intermedia* and 14% of the individuals of *P. achrostichoides* produced at least one fertile leaf during each of the eight years of the study (Table 2A). Of the sporophytes of *D. intermedia* which were fertile at the start of the study in 1993, 75% were fertile in 1994 while only 21% were consistently fertile through 2000, the last year of the study (Table 2B). Of the sporophytes of *P. acrostichoides* which were fertile in 1993, 67% were fertile in 1994, compared to the 60.8% sequential reproducers observed in a two-year study of this species in southeastern Ohio by Greer & McCarthy (2000). By 2000, only 22% of the *P. acrostichoides* the individuals that were fertile in 1993 could be called sequential reproducers. Thus, as the number of years a plant is monitored increased, the percentage of sequential reproducers decreased at approximately the same rate for both species (Table 2B).

Fertile to sterile transitions (FS) reverse the more common trend of fertile-to-fertile transitions in the chronological maturation of a reproductively mature sporophyte described by Sheffield (1996). However, plants that were fertile one year and produced

TABLE 2. Comparison of fertility and sterility frequencies for reproductively mature sporophytes of *D. intermedia* and *P. acrostichoides* observed for an eight-year period from 1993 to 2000. Table A includes all plants which became fertile during the eight-year monitoring period. Table B includes only plants which were fertile in 1993.

Years	*D. intermedia*	*P. acrostichoides*
A. Number of years that individuals are fertile		
1	7%	0%
2	3%	0%
3	16%	21%
4	12%	7%
5	16%	21%
6	19%	14%
7	9%	21%
8	16%	14%
B. Number of consecutive years that fertile individuals remain fertile		
1	100%	100%
2	75%	67%
3	63%	67%
4	38%	56%
5	38%	56%
6	29%	44%
7	25%	44%
8	21%	22%
C. Number of fertile/sterile transitions per individual		
1	54%	50%
2	32%	37%
3	14%	13%
D. Span of sterile years after and before a fertile year		
1	60%	60%
2	20%	20%
3	8%	10%
4	8%	10%
5	4%	0%

no fertile leaves the next year (FS) were seen in 15% of the *D. intermedia* observations and 14% of the *P. acrostichoides* transition observations. For *D. intermedia*, 70% of the individuals reverted to sterile status from fertile status (FS) at least once during the eight-year monitoring period, while 57% of *P. acrostichoides* individuals had FS transitions. For approximately half of the plants of both species an FS transition occurred only once (Table 2C). Given that a plant must transition back to fertile status in order to become sterile again, the maximum number of FS transitions possible in an eight-year study is three. This maximum number of FS transitions was noted for 14% of the observations for *D. intermedia* and 13% of the FS observations for *P. acrostichoides*. The span of years that a previously fertile sporophyte remained sterile ranged from one to five for *D. intermedia* and one to four for *P. acrostichoides* (Table 2D). For both species the majority (60%) remained sterile for only one year (Table 2D). Of the FS transitions for *Dryopteris intermedia* (Table 1), most occurred in 1998 (36%), following the ice storm and in 1996 (29%), following a winter with very low daily minimum temperatures (Table 1). For *P. acrostichoides* most FS transitions (29%) occurred in 2000 (Table 1).

Crown size and changes plant fertility status

Changes in crown size can be related to the annual transitions to and from fertile leaf production. Plants maintained a stable crown size following FF transitions (Table 3). Crown size was also stable for SS transitions for *D. intermedia*, though it increased for *P. acrostichoides*. However, following FS transitions, individual plants produce a significantly smaller sterile crown by over half a leaf (Table 3). Following SF transitions, the increase in the size of the fertile crown is also significant for *D. intermedia*, with an increase in *P. acrostichoides* as well (Table 3). Thus, even for the same individuals, the number of leaves in the crown increases with a shift from plant sterility to fertility. On a smaller scale than that observed experimentally by Siman & Sheffield (2002), it appears that when field conditions favor above-average fertile leaf production for *D. intermedia* and *P. acrostichoides*, more leaves are produced.

TABLE 3. Comparison of changes in crown sizes for transitions in plant fertility status from one year to the next. Significant differences are indicated by * (P < 0.0500) and ** (P < 0.0100).

Transition	*Dryopteris intermedia*				*Polystichum acrostichoides*			
	N	Mean difference	t	P	N	Mean difference	t	P
Fertile/Fertile	101	-0.040±0.186	-0.21	0.8314	53	-0.076±0.294	0.26	0.7982
Sterile/Sterile	48	-0.021±0.210	-2.25	0.0308*	11	+0.727±0.304	-1.13	0.2793
Fertile/Sterile	35	-0.571±0.254	3.20	0.0031**	13	-0.539±0.475	1.16	0.2654
Sterile/Fertile	33	+0.727±0.227	-0.10	0.9212	15	+0.333±0.287	2.39	0.0379*
Min/Max		-4/+6				-7/+5		
F		3.57				1.12		
P		0.0149*				0.3438		

CONCLUSIONS

The most striking observations to emerge from this temporal study of annual variation in individual plant fertility are 1) the overall low level of fertile leaf production in both species with very few observations of whole crown fertility, 2) the inconsistency of the percentage of the crown which is fertile from year to year, 3) significant differences in the number of plants that are fertile from year to year for each species, a phenomenon possibly linked to winter weather conditions, 4) the difference between species in the overall percentage of plants that are fertile 5) the similarities between species with respect to the annual patterns in changes of the percentages of fertile plants and transitions in plant fertility status 6) the significant year-to-year variation in the percent of the population that experiences a fertile to fertile plant status transition, 7) expansion of individual crown size when fertile leaves are produced, and reduction of crown size when a fertile plant fails to produce fertile leaves the following year. Most of these characteristics of fertile leaf production could not have been known without annual monitoring of marked individuals. Though eight years seems to be a relatively short time compared to the life span of long-lived sporophytes, it was possible to quantify several previously untested assumptions about sporophyte growth.

The original intention of this study was to determine if annual variability in plant fertility could be detected in field populations of sporophytes of temperate species. With the exception of general observations relating to significant local weather patterns, no attempt was made to determine the cause of any observed variation. It is certainly clear from these results that there can be a high level of annual variability in fertile leaf production in temperate ferns. It is also clear that observing a sporophyte only once can lead to a number of erroneous assumptions about its past life history status. A plant with no fertile leaves cannot automatically be assumed to be an immature plant. A plant with one fertile leaf may or may not have been producing fertile leaves longer than one with a 100% fertile crown. A plant that is fertile may or may not be fertile the following year. A population that has the same proportion of fertile plants from one year to the next may still reflect numerous changes due to independent changes in the fertility status of individual plants. While the two species chosen for observation in this study may differ in the overall number and timing of fertile leaves produced, there was a striking similarity in the frequency of the different types of year-to-year transitions in plant fertility status.

Fundamental to understanding of all of these observations is a knowledge of the specific process that determines whether an emergent leaf will be fertile or sterile (White 1971). The current exploratory study, limited as it was to simply observing the reproductive sporophyte, has provided few clues about the stimuli behind the observed patterns. The differences between species detected in this long-term field study of just two species indicate that for each species the fertility triggers may be different. Significant year-to-year variation in plant fertility suggests that environmental factors may be important. Annual variation may be related to climate factors but the relatively short time span of the study and the many potential microhabitat influences require experiments to properly assess these observations.

More long-term field studies are needed as the differences between these two species suggest that the patterns of leaf and plant fertility can vary widely. Because the limitations on observing plants in the field were unknown at the start of this study, sample sizes of plants for which data was available for all eight years were small by the end of the study, especially for *P. acrostichoides*. The number of plant fertility transitions from fertile to sterile taking place after a plant had become reproductively mature could only be observed a maximum of three times in an eight-year period, limiting the potential for identifying underlying causes. Only one large cyclic event occurred during the study, limiting the potential for generalizations about disturbance effects.

The length of study was limited because of the choice of study site. It was conducted on private land which changed hands after eight years and was no longer accessible for research. For long-lived perennials, a long-term study should encompass a large part of the life span of a sporophyte, and should ideally extend to 100 years or more. As indicated by Werth & Cousens (1990), a long-term study should be conducted at a site guaranteed to be in place for the long-term. The Long Term Ecological Research (LTER) program (Van Cleve & Martin 1991) which has extended world-wide from its original designation of sites in the United States can provide such stable study locations for future long-term studies. The LTER sites also provide for maintenance of standardized data sets long-term which allows for continual monitoring of marked individuals beyond the lifetime of a single individual researcher. The availability of LTER data on the internet also facilitates supplemental short-term studies and experiments based on earlier observations, another recommendation made by Werth & Cousens (1990). Long-term natural experiments such as this one rely on inference from uncontrolled climate data. Although this approach does not have the rigor of a controlled experiment, it does document variation under real environmental conditions. Another advantage of conducting both long and short term studies at an LTER is the continual monitoring of climate parameters as well as other abiotic and biotic environmental characteristics which can be related to an individual researcher's observations about ferns.

This long-term study of fertility in two wintergreen fern species from the same forest showed different patterns of annual variation, suggesting that any future ecological assumptions about ferns must account for differences among fern species. Studies of populations of both *D. intermedia* and *P. acrostichoides* throughout their ranges are needed and other life history stages could exhibit such amplitudes of annual variability as well. Long-term field monitoring and additional experimentation with other fern species will be necessary before the ecological generalizations hoped for by Harper (1982) can be made.

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