PROC. N.S. INST. SCI. (1980)
Volume 30, pp. 171-181

RESPONSES OF THE OSTRICH FERN, *MATTEUCCIA STRUTHIOPTERIS* (L.) TODARO, TO LIME, SOIL MOISTURE, AND IRRADIANCE

ROBERT K. PRANGE
Department of Biology
Nova Scotia Agricultural College
Truro, N.S., B2N 5E3

Mature sporophytes of *Matteuccia struthiopteris* were grown in controlled environment chambers at 3 lime [$Ca(OH)_2$] levels, 2 soil moisture levels, and 2 irradiance levels. The effects of these treatments on vegetative and fertile frond fresh and dry weights, frond height and frond nutrient concentrations were measured. Soil moisture had the greatest effect and was the only variable affecting frond weight. Increased irradiance reduced frond height but increased the number of plants producing a second set of fronds. Liming had no effect on frond weight, number, or height. It interacted with soil moisture and irradiance in their effect on frond nutrient concentrations. Fertile fronds had a nutrient depletion effect on the vegetative fronds and higher concentrations of nitrogen, phosphorus, and potassium than vegetative fronds. Calcium levels in the fertile and vegetative fronds were unaffected by any of the variables. The association of *M. struthiopteris* with calcareous soil may be due to the soil's effect on another stage in the fern's life cycle, such as spore germination, gametophyte growth, or fertilization.

Introduction

The ostrich fern, *Matteuccia struthiopteris* (L.) Todaro [=*Pteretis pensylvanica* (Willd.) Fern.] is widely distributed in temperate North America and Eurasia (Lloyd 1971). In North America it is sometimes designated var. *pensylvanica* (Willd.) Morton because of the larger stature and uniformly brown scales on the frond stipe. *M. struthiopteris* is dimorphic, producing sterile photosynthetic fronds early in the spring, followed 1 to 2 months later by fertile, nonphotosynthetic fronds on some of the plants.

M. struthiopteris is most commonly found in shady habitats on or near river flood plains where the soil is moist and high in nutrients (Mueller-Dombois 1964; Porfir'ev 1975). There are also reports that it occurs only on calcareous soils. It is absent from the noncalcareous Atlantic coast of Nova Scotia (Roland & Smith 1969) and the eastern half of Newfoundland. Several reports indicate the greatest abundance of ostrich fern on limestone soils and gypsum outcrops (Chrysler & Edwards 1947; Fernald 1921; Roland & Smith 1969). However, both naturally occurring and transplanted plants have been observed growing on sites of acid pH, under conditions of full sunlight and/or low moisture (Gabrielson 1964; R.K. Prange, unpubl.).

Although *M. struthiopteris* is generally not regarded as a food plant, the Maliseet Indians of the Penobscot and Saint John River Valleys of Maine and New Brunswick have traditionally utilized the "fiddleheads" (young vegetative fronds) as a spring vegetable. Since the United Empire Loyalists first settled in the region the taste for "fiddleheads" has grown considerably and today the annual commercial harvest of "fiddleheads", obtained entirely from wild populations, is estimated to be 225,000 kg. The demand for this vegetable has exceeded the supply and there is an obvious need to domesticate and cultivate *M. struthiopteris*. In order to do this a greater understanding of its responses to environmental variables must be known. It is especially important to understand the nature of the requirement for soil moisture, irradiance and calcium. This experiment examines the response of the ostrich fern to these variables under controlled environment conditions.

Methods

Forty-eight dormant plants of *M. struthiopteris* were collected in early May from a population growing on the grounds of the Nova Scotia Agricultural College, Truro, Nova Scotia. These were grown for 45 days in controlled environment chambers at 3 lime, 2 soil moisture, and 2 irradiance levels with 4 replicates (plants) of each treatment.

Each plant was planted in a pot 25 cm in diameter containing sterilized greenhouse soil composed of 62% compost, 25% peat moss, 13% sand by volume, with 250 ppm 20% superphosphate. To determine the effect of calcium, 3 levels of $Ca(OH)_2$ were applied: (a) 0 g kg^{-1} of soil; (b) 2 g kg^{-1}; and (c) 4 g kg^{-1}. The pH of each lime treatment was recorded at the beginning, after 27 days and at the end of the experiment (45 days).

Within each lime treatment, 2 levels of plant water stress were applied by controlling soil moisture. A condition of low water stress (high soil moisture) was obtained by maintaining the soil moisture near 100% field capacity by applying distilled water daily until it dripped out the bottom of the pots. A condition of high water stress (low soil moisture) was provided by reduced watering. Daily measurements of the soil were made with a JLM soil moisture probe and the plants were not watered until the moisture probe reading dropped to the 30-40% value between field capacity and permanent wilting point, when water was applied slowly until the level reached 50-60%. Six soil samples were taken from the pots and measured on a pressure plate. At tensions of 30 kPa (field capacity) and 1500 kPa (permanent wilting point) the soil moisture was 20.7% and 11.5% of the dry weight, respectively.

The plants were grown in 2 Conviron walk-in controlled environment chambers, both set at 20°C, 70-80% relative humidity, and 16:8 h light:dark photo-period. Light was supplied by 40-W incandescent bulbs (25% input wattage) and 110- and 215-W cool-white fluorescent lamps (75% input wattage), 1.16 m above the tops of the pots. The irradiance, as measured by a Li-Cor LI-185A quantum meter O.65 m below the lights, was 160 μmol m^2s^{-1} in the low irradiance chamber and 418 μmol $m^{-2}s^{-1}$ in the high irradiance chamber.

Throughout the course of the experiment, 1 vegetative frond from each plant was regularly measured for total height by pulling the frond to its maximum length along a meter stick. At the end of the experiment, the heights of all the fronds were recorded. The fronds were harvested and, following fresh and dry weight determination (55°C for 72 h), were analyzed by the Soils and Crops Laboratory, Nova Scotia Department of Agriculture and Marketing, for percent nitrogen, calcium, magnesium, potassium and phosphorus.

During the experiment vegetative fronds appeared on all the plants and near the end of the experiment some plants also produced fertile fronds. These fertile fronds were analyzed separately for dry and fresh weights and foliar nutrient concentrations.

After harvesting, the plants were kept in the controlled environment for 4 weeks to determine the effects of the experiment on subsequent production of fronds. During this period, all of the pots were watered to field capacity, leaving only 2 variables, irradiance and lime.

The results were examined statistically using a 1-, 2-, and 3-way analysis of variance (ANOVA). Standard errors (SE) were included for data that were not significant in the ANOVA or not subjected to a statistical test.

Table I. Significant levels of F^1 for effects of liming, soil moisture and irradiance on frond weight, number, height, and mineral composition.

Source	df[2]	Fresh weight		Dry weight		Vegetative fronds						
		Total	Fertile	Total	Fertile	Fronds/ plant	Height	N %	K %	P %	Mg %	Ca %
Irradiance (I)	1	NS	NS	NS	NS	NS	**	**	**	**	NS	NS
Lime (L)	2	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS
Moisture (M)	1	**	*	**	*	NS	**	**	**	*	NS	NS
I x L	2	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS
I x M	1	NS	NS	NS	NS	NS	**	NS	*	NS	NS	NS
L x M	2	NS	NS	NS	NS	NS	NS	**	**	*	NS	NS
I x L x M	2	NS	NS	NS	NS	NS	NS	NS	**	NS	NS	NS
Error	36											
Total	47											

1—Variance ratio test for homogeneity of means
2—Degrees of freedom

NS —Not significant at 5% level.
* —Significant at 5% level.
** —Significant at 1% level.

Results

Soil pH levels during the experiment varied little within each lime treatment. The soil pH's (±SE) for the lowest to highest lime levels were 5.1±0.2, 6.5±0.1 and 7.4±0.1, respectively. Since liming had an effect on soil pH but no significant effect on calcium levels in the fronds (Table I), the significant effects of liming noted In Table I could really be due to changes in soil pH.

The fresh and dry weights of both the vegetative and fertile fronds were significantly affected by the soil moisture level (Table I; Fig 1). High soil moisture, compared to low soil moisture, increased fresh and dry weights of vegetative fronds by 47% and 70% respectively and of fertile fronds by 461% and 510% respectively.

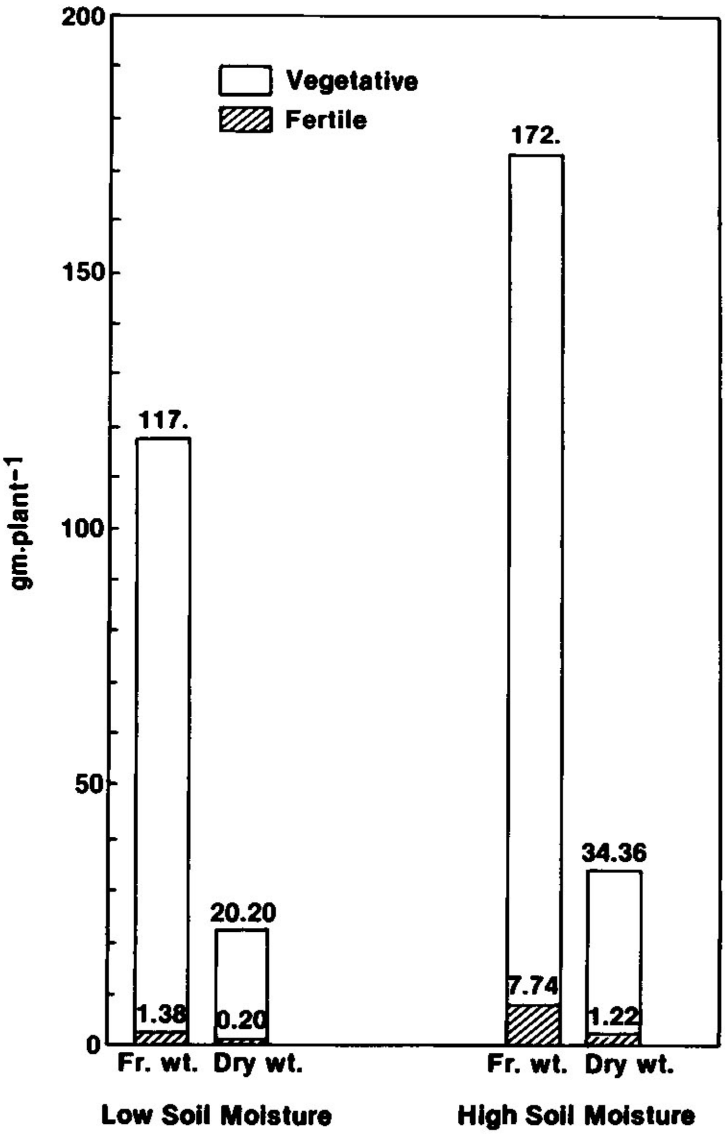

Fig 1. Effect of soil moisture on frond production (fresh and dry weights)

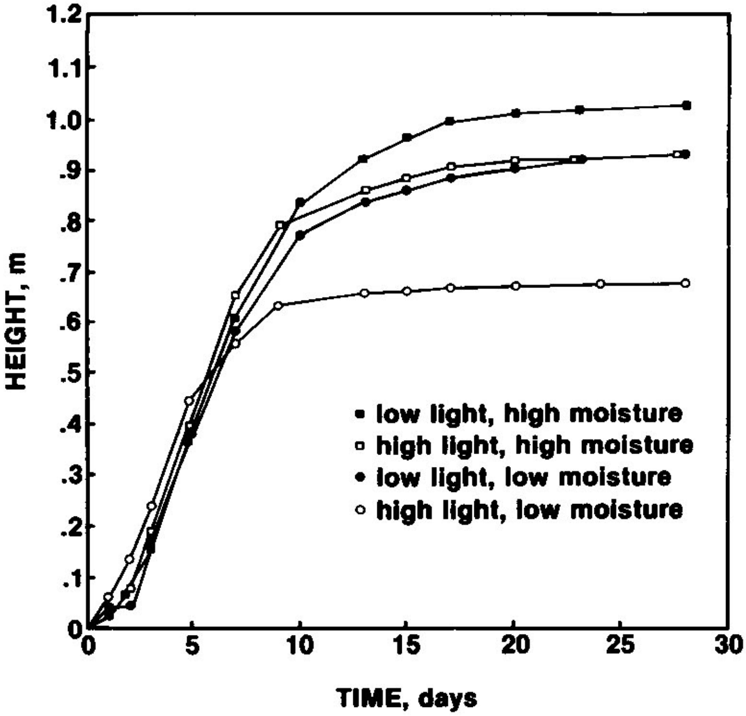

Fig 2. Effect of soil moisture and irradiance on frond height. High light = 418 μmol $m^{-2}s^{-1}$; low light = 160 μmol $m^{-2}s^{-1}$.

Both soil moisture and irradiance significantly affected frond height (Table I). Increasing soil moisture increased the height, whereas increasing irradiance decreased height by almost the same amount (Fig 2). In the first 5 days after germination, high irradiance combined with low moisture produced the greatest rate of frond elongation but after 5 days the fronds had completely opened, increasing the surface area for transpiration. This treatment had the slowest rate of elongation for the remainder of the experiment. Fronds in the high irradiance treatments developed more brown tips than in the low irradiance treatments.

Changes in fresh and dry weights were not due to changes in number of fronds produced (Table I). The number of fronds per plant was nôt significantly different in any of the treatments (Mean$\pm$SE = 6.40$\pm$0.33 fronds/plant).

The percent nitrogen in the vegetative fronds was less at the high irradiance (Table II). Lime and soil moisture treatments interacted (Table III). At the high soil moisture level, concentrations of nitrogen and phosphorus dropped with lime level and at the low soil moisture level they increased. The low soil moisture level had a higher mean value (1.95%) for nitrogen than the high soil moisture level (1.45%).

The ANOVA of the percent potassium concentrations in the vegetative fronds indicated a significant 3-way interaction among the irradiance, lime, and soil moisture treatments (Tables I, IV). This 3-way interaction can be seen by examining the responses of potassium concentration at the 2 g kg^{-1} lime level in Table IV. At this lime level the low soil moisture plants had their lowest potassium concentration and the high soil moisture plants had their highest potassium concentration. This interaction of lime and soil moisture was more noticeable at the high irradiance level than the low irradiance level.

Table II. Effect of irradiance on percent nitrogen and phosphorus in vegetative fronds.

	Irradiance (μmol $m^{-2}s^{-1}$)	
	160	418
Nitrogen (%)	1.89	1.52
Phosphorus (%)	.28	.22

Table III. Effect of interaction between soil moisture and liming on percent nitrogen and phosphorus in vegetative fronds.

	Soil Moisture			
	Low		High	
Lime (g kg^{-1})	N (%)	P (%)	N (%)	P (%)
0	1.66	.25	1.52	.24
2	2.07	.26	1.48	.27
4	2.12	.30	1.36	.18

Table IV. Effects of liming, soil moisture and irradiance on percent potassium in vegetative fronds.

	Irradiance (μmol $m^{-2}s^{-1}$)					
	160			418		
Soil	Lime (g kg^{-1})			Lime (g kg^{-1})		
Moisture	0	2	4	0	2	4
low	1.54	1.18	1.74	1.17	.90	1.63
high	1.31	1.32	1.20	.96	1.58	.88

The percent phosphorus in the vegetative fronds had a similar pattern to percent nitrogen. That is, increased irradiance decreased the phosphorus concentration (Table II) and liming and soil moisture interacted on phosphorus concentrations (Table III). In the lime X moisture interaction, the values were similar at 0 g kg^{-1} and 2 g kg^{-1} between moisture levels. However, at 4 g kg^{-1} the phosphorus concentration was most affected by soil moisture, with the highest phosphorus concentration at the low soil moisture level and the lowest at the high soil moisture level.

Even though the lime levels were established by $Ca(OH)_2$, the percent calcium concentration in the vegetative fronds was not significantly affected. The mean calcium concentration ($\pm$ SE) was 1.14 $\pm$ 0.04%.

The percent magnesium in fronds was significantly affected by an interaction between irradiance and lime (Tables I, V). At the high irradiance level, the magnesium concentration was greatest at lime treatment 0 g kg^{-1}, whereas plants grown at low irradiance had high magnesium concentrations at lime treatments 0 and 4 g kg^{-1}.

Table V. Effect of interaction between irradiance and liming on percent magnesium in vegetative fronds.

Lime (g kg^{-1})	Irradiance (μmol m^{-2}s^{-1}) 160	418
0	.18	.22
2	.15	.15
4	.18	.15

A comparison of vegetative fronds from infertile plants, vegetative fronds from fertile plants, and fertile fronds (Table VI) showed that plants that produced fertile fronds had greater fresh and dry weight of vegetative fronds than did infertile plants. The presence of fertile fronds also decreased the concentration of nitrogen, potassium, and phosphorus in the vegetative fronds on the same plant. Calcium and magnesium concentrations in the vegetative fronds remained the same, regardless of the presence of fertile fronds. Compared with vegetative fronds, fertile fronds had higher concentrations of nitrogen, potassium, and phosphorus; magnesium was similar; and calcium was considerably lower.

After the fronds were harvested and the plants were watered to the high soil moisture level, fronds appeared on some of the original plants and also from new plants (Table VII). The total number of plants producing a second set of fronds was substantially greater in high irradiance (n=30) than in low irradiance (n=10). Although not recorded, the number of fronds per plant was fewer than in the first set.

Discussion

Soil moisture, lime, and irradiance produced significant responses in *M. struthiopteris*. Soil moisture had the greatest effect. The significant reduction in fresh and dry weights of both frond types at low soil moisture indicates that this is the major factor limiting distribution to habitats with a constant water supply as previously

Table VI. Comparison of vegetative fronds on infertile plants, vegetative fronds on fertile plants, and fertile fronds. Number in brackets is the sample size.

Parameter	Vegetative fronds on sterile plants (Mean ± SE)	Vegetative fronds on fertile plants (Mean ± SE)	Fertile fronds (Mean ± SE)
Fresh wt (g/plant)	127.00 ± 9.15 (34)	171.66 ± 19.27 (14)	15.62 ± 3.49 (14)
Dry wt (g/plant)	22.58 ± 1.53 (34)	36.67 ± 3.95 (14)	2.44 ± .58 (14)
Nitrogen (%)	1.84 ± .06 (34)	1.35 ± .07 (14)	2.18 ± .13 (12)
Potassium (%)	1.41 ± .06 (34)	1.14 ± .09 (14)	2.03 ± .04 (11)
Phosphorus (%)	0.27 ± .01 (34)	0.20 ± .02 (14)	0.38 ± .02 (12)
Calcium (%)	1.13 ± .03 (34)	1.17 ± .04 (14)	0.16 ± .01 (12)
Magnesium (%)	0.17 ± .01 (34)	0.16 ± .01 (14)	0.20 ± .01 (11)

Table VII. Production of a second set of fronds from the original plants, and production of new plants.

	Irradiance (μmol $m^{-2}s^{-1}$)					
	160			418		
	Lime (g kg^{-1})			Lime (g kg^{-1})		
	0	2	4	0	2	4
Original Plants	2	0	0	8	7	8
New Plants	2	2	4	4	2	1

suggested by Mueller-Dombois (1964) and Porfir'ev (1975). Porfir'ev (1975), in his study of the ostrich fern distribution and ecology in the USSR, stated that *M. struthiopteris*, regardless of its geographical location, was associated with a continuous flow of soil underground water rich in oxygen and minerals. On a 0.1-hectare plot which he studied for 7 years, the dry weight of the above-ground biomass varied from 18.3 to 58.6 g m^{-2} (ca. 3.29 - 18.17 g/plant), depending on soil moisture during the growing season. In the same study the projected cover of each fern, which varied from 0.18 to 0.31 m^2, also depended on soil moisture.

Frond height had a positive response to soil moisture and a negative response to irradiance. Difference in height with irradiance is typical of leaves in shade and sun (Boardman 1977; Hariri & Brangeon 1977). In the fern *Pteris cretica*, increasing irradiance was related to increased dry matter per unit surface area, reduced leaf water content, and thicker leaves (Hariri & Brangeon 1977). As the difference in leaf height could not be related to reduction in total frond dry weight in my experiment, higher irradiance probably would not increase frond production, and would probably reduce the height even more. This reduction in height has been observed in plants transplanted to a field plot at the Nova Scotia Agricultural College in which the plants were not shaded.

Even though none of the treatments resulted in any significant difference in the number of fronds produced during the experiment, the number of plants producing a second set of fronds (Table VII) was increased at higher irradiance. This is similar to my observations on the field plot at the Nova Scotia Agricultural College where plants growing in full sun during the first year produced more fronds per plant in the second year.

Soil pH, which was altered by the amount of lime added, could be the explanation for significant differences in the foliar mineral concentrations with lime level. The effect of liming varied among the elements and always involved an interaction with soil moisture or irradiance.

Higher irradiances tended to decrease concentrations of nutrients such as nitrogen and phosphorus as has been shown for other plants (Boardman 1977). However more research must be done to further understand the mechanisms involved, because irradiance had little effect on potassium and none on calcium contrary to other observations (Boardman 1977).

The positive effect of low soil moisture on percent nitrogen and phosphorus is noteworthy. As this effect interacted with lime levels, it could result from differences in availability of these nutrients in the soil. This soil-moisture effect was most noticeable at the highest lime level. The lower nutrient concentrations in the high moisture treatment could be partly the result of a "dilution effect" caused by greater carbohydrate production.

The accumulation and depletion of nitrogen, phosphorus and potassium in the fertile and vegetative fronds, respectively, suggests that the production of fertile fronds acted as a strong sink, translocating a portion of these 3 mobile nutrients from the vegetative fronds.

Magnesium, although a mobile ion (Bukovac and Wittwer 1957), may not show a similar difference between fertile and vegetable fronds because its main function is in the chlorophyll molecule and the CO_2-fixing enzyme, ribulose bisphosphate carboxylase, and the fertile fronds are considered to have little, if any, photosynthetic activity.

The production of fertile fronds, which were formed on larger than average plants, was related to high soil moisture perhaps because such conditions would allow sufficient production of carbohydrates in the vegetative fronds to nourish the nonphotosynthetic fertile fronds. The relationship between sufficient carbohydrate production in the vegetative fronds and fertile frond production in *M. struthiopteris* was first suggested by the experiments of Atkinson (1896) and Goebel (1905).

More recent evidence, however, indicates that nitrogen, in addition to carbohydrate, can influence fertile frond production. In cultured fronds of *Todea barbara*, sucrose supplemented with nitrate enhanced fertile frond production (Sussex & Steeves 1958). Harvey and Caponetti (1974), using cultured *Osmunda cinnamomea* leaf primordia, concluded that ammonium and not nitrate was necessary, in the presence of high sucrose concentrations, to induce sporangia. Fertile fronds in this study also accumulated phosphorus and potassium. Therefore, the overall nutritional balance of the fronds is important.

Even though liming had no significant effect on production of vegetative and fertile fronds, the possibility still remains that germination of spores or growth and fertilization of gametophytes requires a calcareous substrate and alkaline soil pH. The pH range of natural sites (Gabrielson 1964) is within the optimum pH for fern spore germination in culture media, which is usually in the range of pH 4.5 to 7.5 (Dyer 1979; Page 1979). Evans and Bozzone (1977; 1978) have shown that in *Pteridium aquilinum* (bracken fern), sperm motility and fertilization in the gametophyte were reduced at pH 5.8 and 4.2, respectively. They were reduced even more by the addition of anions such as sulfate, nitrate, and chloride, which are the dominant anions in precipitation, especially in "acid rain" regions. It is also possible that the apparent preference of *M. struthiopteris* for calcareous soils and soil pH close to neutrality is really due to the greater availability in acid soil of elements such as iron, aluminum, or manganese which could be toxic to *M. struthiopteris* (Hou 1950).

In summary,

1. Of the three variables examined, soil moisture had the greatest effect on the production of vegetative and fertile fronds.
2. Irradiance did not affect frond weights in the first set of fronds but it did influence height and nutrient levels and increased the production of subsequent fronds.
3. Liming had no effect on growth and only indirectly affected nutrient levels through interaction with soil moisture and irradiance.
4. Fertile frond production was associated with treatments which resulted in greater vegetative frond production, suggesting the need for higher carbohydrate levels for fertile frond induction. Fertile fronds also had a nutrient depletion effect on the sterile fronds, resulting in higher concentrations of nitrogen, phosphorus, and potassium in the fertile fronds. Only calcium had a lower concentration in the fertile fronds than in the vegetative fronds.

Acknowledgements

Support for this research was provided by Research Grant No. 70 from the Nova Scotia Agricultural College Research and Innovative Demonstration Committee. Helpful comments by D.P. Ormrod, J. McLachlan, D.W. Larson and the technical assistance of Gwen Williams are gratefully acknowledged.

References

Atkinson, G.F. 1896. The probable influence of disturbed nutrition on the evolution of the vegetative phase of the sporophyte. *Am. Nat.* 30: 349-357.

Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28: 355-377.

Bukovac, M.J. and **Wittwer, S.H.** 1957. Absorption and mobility of foliar applied nutrients. *Plant Physiol.* 32: 428-435.

Chrysler, M.A. and **Edwards, J.L.** 1947. *The Ferns of New Jersey*. Rutgers Univ. Press, New Brunswick, N.J.

Dyer, A.F. 1979. The culture of fern gametophytes for experimental investigation. In *The Experimental Biology of Ferns* (ed. A.F. Dyer). Academic Press, New York, pp. 253-305.

Evans, L.S. and **Bozzone, D.M.** 1977. Effect of buffered solutions and sulfate on vegetative and sexual development in gametophytes of *Pteridium aquilinum*. *Am. J. Bot.* 64: 897-902.

Evans, L.S. and **Bozzone, D.M.** 1978. Effect of buffered solutions and various anions on vegetative and sexual development in gametophytes of *Pteridium aquilinum*. *Can. J. Bot.* 56: 779-785.

Fernald, M.L. 1921. The Gray Herbarium expedition to Nova Scotia. *Rhodora* 23: 136-186.

Gabrielson, F.C., Jr. 1964. *A Survey of the Ostrich Fern,* Matteuccia struthiopteris *(L.) Todaro.* MSc Thesis, Univ. of Maine, Orono, Me.

Goebel, K. 1905. *Organography of Plants*, Part II. Oxford Univ. Press, Oxford.

Hariri, M. and **Brangeon, J.** 1977. Light-induced adaptive responses under greenhouse and controlled conditions in the fern *Pteris cretica* var. *ouvrardii* I. Structural and infrastructural features. *Physiol. Plant.* 41: 280-288.

Harvey, W.H. and **Caponetti, J.D.** 1974. *In vitro* studies on the induction of sporogenous tissue on leaves of cinnamon fern. III. The role of reduced nitrogen. *Can. J. Bot.* 52: 2611-2614.

Hou, H.-Y. 1950. The chemical composition of certain ferns and fern allies of central Pennsylvania. *Am. Fern J.* 40: 233-240.

Lloyd, R.M. 1971. Systematics of the onocleoid ferns. *Univ. Calif. Publ. Bot.* 61: 1-86.

Mueller-Dombois, D. 1964. The forest habitat types of southeastern Manitoba and their application to forest management. *Can. J. Bot.* 42: 1417-1444.

Page, C.N. 1979. Experimental aspects of fern ecology. In *The Experimental Biology of Ferns* (ed. A.F. Dyer). Academic Press, New York, pp. 551-589.

Porfir'ev, V.S. 1975. (The synecology of *Matteuccia struthiopteris* Todaro Pteridophyta: An indicator of soil underground waters). In *Vodnyi obmen v osnovnykh tipakh rastitel'nosti SSSR kak element krugovorota veshchchestva i energii, pp. 337-342.*

Roland, A.E. and **Smith, E.C.** 1969. *The Flora of Nova Scotia*. Nova Scotia Museum, Halifax. N.S.

Sussex, I.M. and **Steeves, T.A.** 1958. Experiments on the control of fertility of fern leaves in sterile culture. *Bot. Gaz.* 119: 203-208.