

The Biological Flora of Canada.

6. *Matteuccia struthiopteris* (L.) Todaro, Ostrich Fern

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Matteuccia struthiopteris (L.) Todaro is a fern which occurs throughout the north temperate and sub-boreal zones of the northern hemisphere including all provinces and territories of Canada, the northern U.S., Japan, China, Siberia west to Scandinavia, Belgium, France and parts of the Alps. Its occurrence may be considered as an indicator of moist eutrophic soils where the water table is generally within 1.5 m of the soil surface. The young vegetative fronds or “fiddleheads” that emerge in the spring have been a traditional part of the diet of the Malecite Indians of New Brunswick. These fiddleheads are an edible, nutritious vegetable that is considered to have potential as a cultivated crop.

Key Words: *Matteuccia struthiopteris*, Ostrich Fern, biology, ecology, physiology, distribution, economic importance.

1. Name.

Matteuccia struthiopteris (L.) Todaro 1866; tribe Onocleioideae; Aspidiaceae (Lloyd 1971);

M. pensylvanica (Willd.) Raymond 1950;

Pteretis pensylvanica (Willd.) Fernald 1945;

Ostrich Fern, Fougère-à-l'autruche.

2. Description of the Mature Plant

(a) *Raunkiaer life-form*. Hemi-cryptophyte. Clonal herb with fronds ascending from a short, erect rhizome; fronds dimorphic, with deciduous sterile fronds and persistent fertile fronds; reproduces by spores and rhizomes.

(b) *Shoot morphology*. Base of the plant a stout erect rhizome, heavily surrounded by the persistent stipe bases, average height 15 cm with maximum of 60 cm if regularly covered by alluvial deposits, deeply perforated by pockets abaxial to frond bases (Mekel 1938); fronds dimorphic, appearing spirally on the erect rhizome; winter-deciduous sterile fronds appearing first, may be followed by persistent fertile fronds; sterile fronds up to 3 m long, stipes up to 4 cm long, deeply channelled on upper side, covered with ramenta when young; blade oblong lanceolate, 17–60 cm wide, gradually reduced toward the base, abruptly reduced at the tip; rachis deeply grooved on the upper side; pinnae broadly linear, acuminate ascending, 20 to many pairs, deeply pinnatifid into oblong, blunt segments, 7–9 pairs of veins in each segment; stout, black, horizontal rhizomes appearing from the base of the erect rhizome, produced from detached meristems located in strict relation to the underlying vasculature (Wardlaw 1943, 1946), covered with black, linear, acuminate, slightly grooved cataphylls, 2–4 cm long, 0.4–1.0 cm wide (Figure 1).

(c) *Root morphology*. The roots arise adventitiously on the erect and horizontal rhizomes (Ogura 1972). The overall root system is a dense fibrous mass that is restricted to the top 30 cm of soil. Roots have unicellular root hairs and are black and wiry with diameters of 0.6–2.0 mm (Lloyd 1971).

(d) *Sporophyll morphology*. Persistent fertile fronds shorter than sterile fronds, eventually dark brown when mature, narrowly oblanceolate, 30–70 cm long, 2.5–6 cm wide; stipe and rachis grooved as in sterile frond; pinnae not over 7 mm wide, inrolled margins, venation free; sori dorsal on the veins, several to a segment, covered by the margins, with a membranous indusium; sporangia with 21–30 indurated annulus cells, spores 64 per sporangium, bilateral, chlorophyllous, with perispores, 47–73 μ m long (Lloyd 1971).

(e) *Subspecies*. None.

(f) *Varieties and forms*. A form *pubescens* (Terry) Clute, characterized by the presence of hairs and scales on the rachis, is known from the Gaspé (Fernald 1935). Tryon (1939) stipulated that if this form was to be recognized, the criteria must be the presence of hairs and scales on the back or sides of the rachis rather than the mere presence of hairs. Morton (1950), who did not recognize the form *pubescens*, pointed out that the presence of

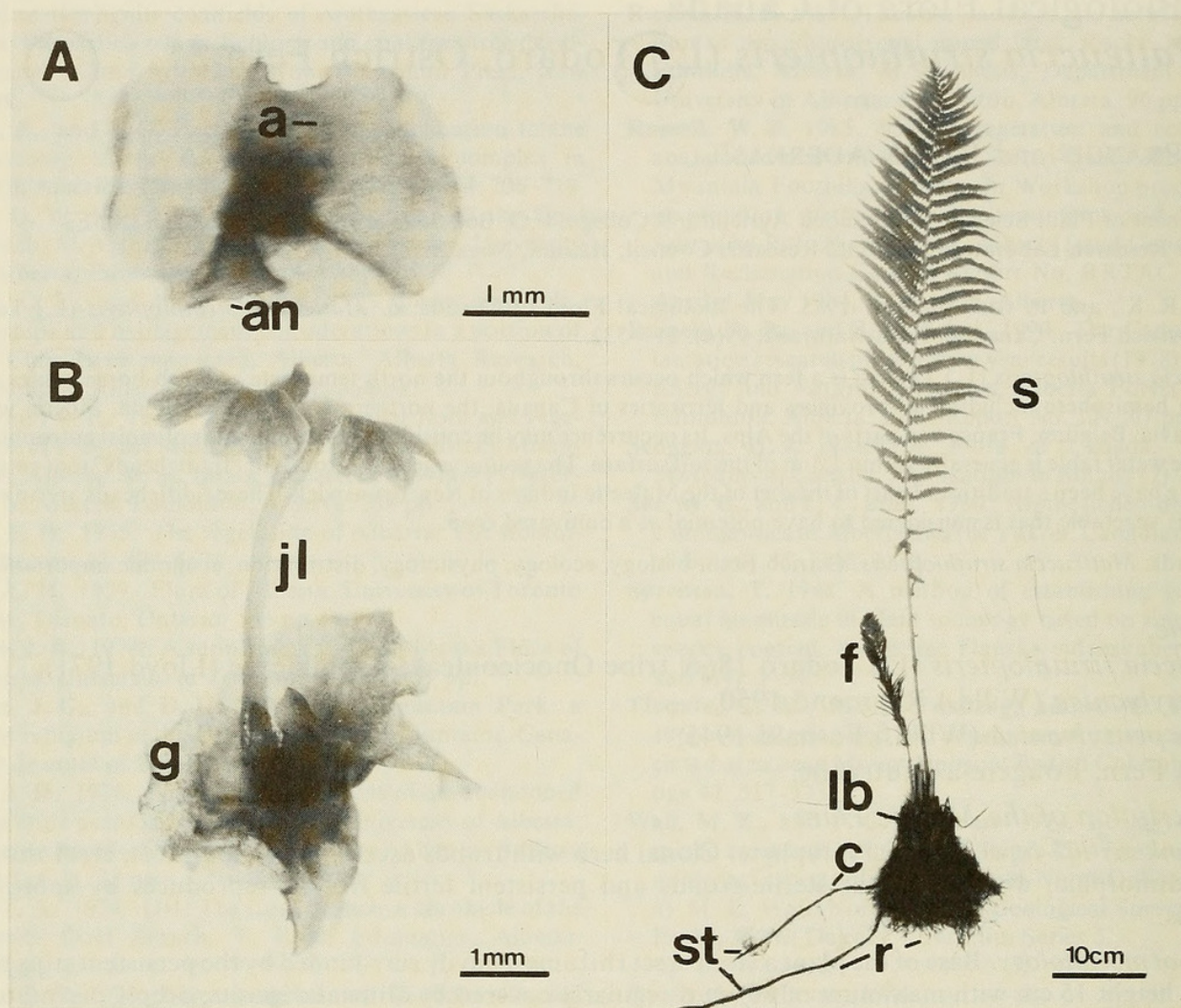


FIGURE 1. Stages in the life-cycle of the Ostrich Fern. A. Gametophyte with archegonia (a) in the central anterior, and antheridia (an) in the basal portions. B. First leaf of juvenile sporophyte (jl) which is still partially dependent on the gametophyte (g) for nutrition. C. Mature sporophyte with large sterile fronds (s) and smaller fertile ones (f). Both types are eventually shed, only the leaf bases (lb) remaining, protecting stem and apex. Stolons (st), which have cataphylls (c) at intervals along their length, arise from the main rhizome. Roots (r) develop extensively from the rhizome but only intermittently along the stolons.

hairs was common to most specimens of *M. struthiopteris*, as did Tryon (1939). Another form of *M. struthiopteris* is *obtusilobata*, which has obtusely shaped pinnules (Fernald 1935). Form *foliacea*, in which the leaves are intermediate between sterile and fertile fronds, and the European equivalents *hypophylloides* and *epiphyllloides* (Luerksen 1889) are not thought to constitute good forms, as such intermediate leaves are known to occur in *M. struthiopteris* following surgical removal of the leaves (Goebel 1888) or adverse environmental conditions (Atkinson 1911). Forms recorded for European, but not North American, populations of the Ostrich Fern include *furcata* Baenitz, in which the frond apex has bifurcated, *daedala* Sauter, in which the apex has repeatedly bifurcated, and *serrata* Baenitz, the leaves of which have serrated edges (Hegi 1965).

(g) *Ecotypes*. None reported.

(h) *Chromosome numbers*. Numbers (n) of 39 (Fabbri and Menicanti 1970; Kurita 1976; Love 1976) ca. 40 (Britton 1953) and 40 (Friebel 1933; Okuno 1936; Sorsa 1958; Mitui 1965) have been reported.

3. Distribution and Abundance

(a) *Geographic range*. The Ostrich Fern occurs as a native plant throughout the north temperate-sub boreal zone of the northern hemisphere, including North America, Siberia, southern China, Japan, Iran, Scandinavia,

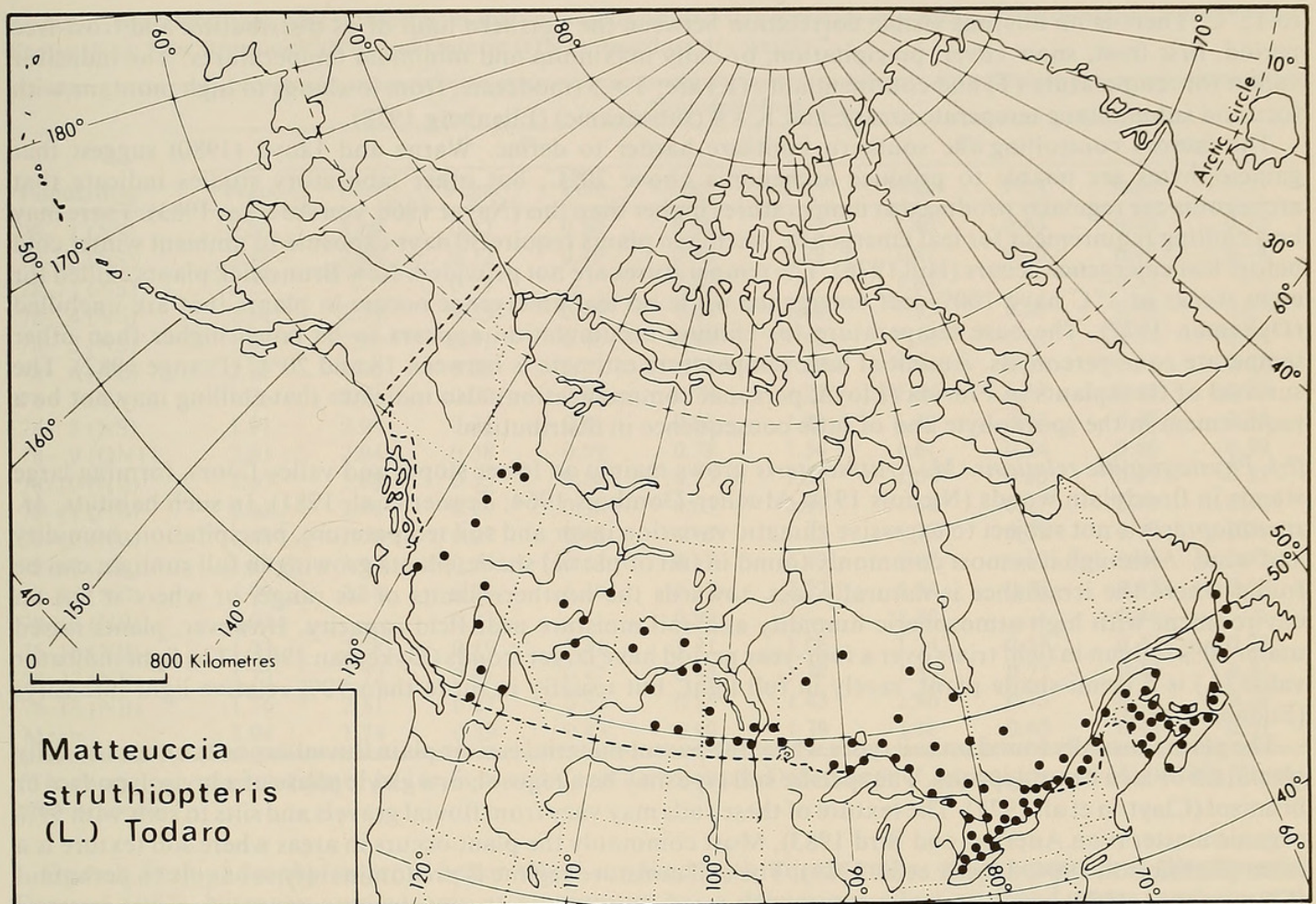


FIGURE 2. Canadian distribution of *Matteuccia struthiopteris* from specimens in DAO (Canada Department of Agriculture, Ottawa, Ontario), CAN (National Museum of Canada, Ottawa, Ontario), NFLD (Memorial University, St. John's, Newfoundland), NSAC (Nova Scotia Agricultural College, Truro, Nova Scotia), ACAD (Acadia University, Wolfville, Nova Scotia) and maps in Cruise (1972), Roland and Smith (1969) and Scotter and Cody (1979).

eastern and central Europe, extending westward to eastern Belgium and France, parts of the Alps, central Yugoslavia and Sicily (Todaro 1866; Lawalrée 1964; Hultén 1968, map; Lloyd 1971). In North America it is distributed from western Newfoundland to southern Alaska, Virginia, Ohio, Indiana, Illinois, Missouri, South Dakota and British Columbia (Lloyd 1971; Scoggan 1978; Tryon and Tryon 1982, map). In Canada, it is found in all provinces and territories (Figure 2) but it is most abundant from New Brunswick west to southern Quebec and southern Ontario.

(b) *Altitudinal range.* *M. struthiopteris* grows from near sea level to 4000 m elevation (Lloyd 1971). The highest recorded elevation in Canada is 732 m near Dawson Creek, British Columbia (DAO #200053). In Scandinavia *M. struthiopteris*-dominated grey alder woods are found in the prealpine belt (Hamet-Ahti 1963). They are most common at lower altitudes, such as in the *Alnus incana* forests below 650 m elevation in Røldal, Norway. The Ostrich Fern occurs in plant associations up to 750 m but the abundance decreases (Odland 1981).

4. Physical Habitat

(a) *Climatic relations.* In North America the northern limit of *M. struthiopteris* distribution may be related to temperature. Scoggan (1978) characterized its distribution as low subarctic and high temperate, extending from the -3.91°C isotherm of mean annual temperature in the north, to the ca. 7.21°C isotherm in southern British Columbia and the Niagara peninsula of southern Ontario. Using climatological maps in Fremlin (1974), the northern limit is visually correlated with: i) a minimum 1500 degree-day growing season (above 5.6°C), ii) a growing season (days with mean temperature above 5.6°C) which starts no later than 20 May and ends before 1 October, and iii) mean annual soil temperature 2.2 to 8.3°C as well as a mean summer soil temperature of 8.3

to 15°C. There is no obvious visible correlation between the northern limit of its distribution and frost-free period, first frost, snow cover, precipitation, or daily maximum and minimum temperatures. The indicator values for temperature (T) and continentality (K) are: T = 5 (moderate; from lowlands to high montane with focus on submontane temperate areas), and K = 4 (suboceanic) (Ellenberg 1978).

The factors controlling the southern limit are harder to define. Warne and Lloyd (1980) suggest that gametophytes are unable to produce archegonia above 20°C, but other laboratory studies indicate that archegonia are regularly produced at temperatures higher than this (Nayar 1968; von Aderkas 1983). There may be a chilling requirement for leaf emergence. Michigan plants require 30 days exposure to ambient winter cold before leaf emergence occurs (Hill 1976). The temperatures are not provided. New Brunswick plants chilled for eight weeks at 1°C have 100% leaf emergence while no leaf emergence occurs in plants that are unchilled (Dykeman 1977). The base temperature for chilling accumulation appears to be much higher than other temperate zone perennials. An initial base temperature estimate is between 18 and 20°C (Prange 1982). The survival of transplants in Florida (Lloyd, personal communication) also indicates that chilling may not be a requirement in the sporophyte and of little consequence in distribution.

(b) *Physiographic relations.* *M. struthiopteris* grows mainly on lower slopes and valley floors, forming large stands in floodplain woods (Nichols 1918; Mueller-Dombois 1964; Tessier et al. 1981). In such habitats, *M. struthiopteris* is not subject to excessive climatic variation in air and soil temperature, precipitation, humidity and wind. Although it is most commonly found in full or partial shade, plants growing in full sunlight can be found where the irradiance is naturally less, towards the northern limits of its range, or where it has an environment with high atmospheric humidity and soil moisture near field capacity. However, plants raised under 70% full sun in field trials over a four-year period have larger fronds (Dykeman 1981). The light indicator value (L) is 5 (semi-shade plant, rarely in full light, but usually in more than 10% relative light intensity) (Ellenberg 1978).

The plant is usually found on soil types where the parent material is river plain fluvial deposits or occasionally glacial till or lacustrine deposits. The specific soil type may be a regosol, or a gleyic phase of a luvisol, podzol or brunisol (Clayton et al. 1977). The texture of these soils may vary from fluvial gravels and silts to soils with 59% organic matter (von Aderkas and Bird 1983). Most commonly the plant occurs in areas where soil texture is a loam (Gabrielson 1964; Tessier et al. 1981). The soil moisture regime is predominantly subaquic to perhumid (Clayton et al. 1977).

(c) *Nutrient and water relations.* *M. struthiopteris* is considered by some to be a calcicolous species (Wherry 1920, 1921; Fernald 1921; Pesola 1928; Lloyd 1971), although this has not been confirmed by other studies (Gabrielson 1964; Roberts-Pichette 1971; Porfirev 1975; Söyrinki and Saari 1980). The plant is usually absent wherever the parent material is predominantly non-calcareous, e.g. eastern Newfoundland, Atlantic coast of Nova Scotia and southern New Jersey (Chrysler and Edwards 1947). Soils occupied by *M. struthiopteris* tend to have very high calcium content (Prange 1981; Tessier et al. 1981; von Aderkas and Bird 1983).

M. struthiopteris can tolerate soils with a broad range of pH (Prange 1981). Gabrielson (1964) reported that Ostrich Fern occurs on soils with pH ranging from 4–7.5, with the best growth on sites at pH 5.1 and 5.4. Prange (1980) found that increasing soil pH from 5.1 to 6.5 and to 7.4 had no significant effect on frond number, frond length and frond fresh or dry weight in mature plants. The pH indicator value is 7 (from light acidic to light basic soils; never on very acidic sites) (Ellenberg 1978). There is evidence that suggests that very low pH may cause Mn toxicity in ferns (Hou 1950).

M. struthiopteris is a very good indicator of soil moisture conditions since it grows neither on saturated soils nor on soils that dry out during the growing season, preferring moist, well-drained soils instead (Mueller-Dombois 1964; Porfirev 1975). The soil moisture indicator value (F) is 7 (moist but not wet soils) (Ellenberg 1978).

Analysis of vegetative leaves of wild plants near Dresden, German Democratic Republic and plants raised in various botanical gardens indicated that *M. struthiopteris* is a silicon accumulator (Höhne and Richter 1981). Partitioning of mineral elements, between different organs, was studied by Stetsenko and Tabachnyi (1982).

Chemical analyses of macronutrient concentrations in mature fertile and vegetative fronds of 18 different populations of *M. struthiopteris* from Nova Scotia, New Brunswick and Ontario, which had been transplanted to the Nova Scotia Agricultural College four years previously, show greater differences between vegetative and fertile fronds than amongst populations (Table 1). Fertile fronds have higher N, P, K and lower Ca and Mg concentrations than vegetative fronds. A growth chamber study supports these results and also shows that fertile fronds have a nutrient depletion effect on vegetative fronds (Prange 1980).

TABLE 1. Macronutrient concentrations in mature vegetative and fertile fronds of *Matteuccia struthiopteris* from Nova Scotia (NS), New Brunswick (NB) and Ontario (ONT), based on dry weight.^a

Population	Concentration (%)									
	N		P		K		Ca		Mg	
	Veget	Fert	Veget	Fert	Veget	Fert	Veget	Fert	Veget	Fert
78- 1 (NS)	2.00	3.00	0.42	0.50	0.95	1.52	1.40	0.63	0.40	0.32
78- 2 (NS)	2.38	2.85	0.32	0.49	0.90	1.29	1.87	0.70	0.45	0.34
78- 3 (NS)	2.27	—	0.34	—	1.07	—	1.84	—	0.53	—
78- 4 (NS)	2.19	2.74	0.23	0.49	1.03	1.46	1.93	0.68	0.45	0.27
78- 5 (NS)	1.67	2.51	0.31	0.46	0.88	1.42	1.32	0.61	0.34	0.34
78- 6 (NB)	1.99	2.06	0.32	0.27	0.92	1.17	1.74	0.59	0.53	0.32
78- 7 (NS)	1.76	2.91	0.30	0.48	0.78	1.27	1.44	0.63	0.42	0.33
78- 8 (NS)	1.91	2.98	0.31	0.51	0.88	1.40	1.40	0.67	0.38	0.34
78- 9 (ONT)	2.03	2.94	0.38	0.59	0.79	1.54	1.61	0.84	0.46	0.39
78-10 (NB)	1.67	2.68	0.35	0.51	0.75	1.53	1.69	0.65	0.45	0.33
78-11 (NB)	2.03	2.78	0.29	0.36	0.63	0.91	1.52	0.77	0.49	0.30
78-12 (NB)	1.88	2.76	0.27	0.46	0.67	1.23	1.79	0.59	0.47	0.31
78-13 (NB)	1.89	3.19	0.21	0.43	0.87	1.43	1.87	0.69	0.46	0.32
78-14 (NB)	1.99	2.16	0.29	0.30	1.12	2.22	1.64	0.53	0.43	0.22
78-15 (NB)	2.01	—	0.23	—	0.99	—	1.87	—	0.44	—
78-16 (NB)	1.73	2.78	0.19	0.41	1.21	1.06	1.74	0.57	0.37	0.23
78-17 (NB)	1.73	2.72	0.21	0.47	0.95	1.39	1.64	0.77	0.37	0.31
78-18 (NB)	1.76	2.81	0.27	0.53	0.85	1.43	1.86	0.75	0.52	0.27
Mean	1.94	1.74	0.29	0.45	0.90	1.39	1.68	0.67	0.44	0.31

^aTissue analyses were performed by the Soils and Crops Laboratory, Department of Agriculture and Marketing, Truro, Nova Scotia.

Ostrich Fern sporophytes grow better when supplied with nitrate rather than ammonium (Prange and Ormrod 1982). Nitrogen applied only as ammonium has a deleterious effect on frond water relations and growth. Ammonium reduces frond fresh and dry weights, water use, frond water potential and frond diffusive resistance. However, plants grown in nutrient solution containing both ammonium and nitrate grow normally (Prange 1981). Soils with a low pH or that are water-logged inhibit nitrate production and could limit the distribution and growth of *M. struthiopteris*. The nitrogen indicator value (N) is 7 [more often on nitrogen-rich than moderate or poor sites] (Ellenberg 1978).

5. Plant Communities. The Ostrich Fern is found in plant communities which have high moisture and nutrient-rich soil conditions. In temperate zones such conditions are usually found along floodplains.

Mueller-Dombois (1964, 1965), in his study of forest habitat types in southeastern Manitoba, uses *M. struthiopteris* as an indicator of the *Ulmus-Matteuccia* habitat type, which he characterizes as a forest hardwood type occurring on very moist, eutrophic, alluvial bottomlands where soil surfaces are only 0.6 to 1.2 m above the stream level in mid-summer. In a study at the Cent-iles area of the St. Lawrence River, Tessier et al. (1981) identify *M. struthiopteris* as a character species for a variant of the *Acer saccharinum-Fraxinus pennsylvanica-Ulmus americana* plant community. This community is also characterized by having a water table level fluctuating from +10 cm in spring to -50 cm in summer. They consider this variant to be the most developed of the variants within this community, and the last in the sequence of succession of vegetation. *M. struthiopteris* has been found in plant communities other than bottomland hardwood forests. Curtis (1959) lists it in nine Wisconsin plant communities, with maximum frequency (11%) in the northern sedge community. Maycock and Curtis (1960) place *M. struthiopteris* in the dry-mesic, mesic and wet-mesic segments of the boreal conifer-hardwood forests of the Great Lakes region, with frequency values of 5, 10 and 9%, respectively.

In communities where *M. struthiopteris* is present, the dominant tree cover may be deciduous and/or coniferous (Table 2). There may be no tree cover at all, as in the Wisconsin study (Curtis 1959). Species that occur in four of the studies summarized in Table 2 are *Fraxinus nigra*, *Ulmus americana*, *Alnus rugosa*, *Cornus stolonifera*, *Prunus virginiana* and *Onoclea sensibilis*. Of these, only *F. nigra*, *U. americana* and *O. sensibilis* appear to reach their greatest frequency in the same communities as *M. struthiopteris*. Although *O. sensibilis* appears on many of the same sites as *M. struthiopteris*, the two species rarely overlap, because the sensitive fern

TABLE 2. Species-stand table showing the frequency of vascular plants in selected plant communities in which *Matteuccia struthiopteris* was present. Data were taken from: 1) wet-mesic stands in boreal conifer-hardwood forests of the Great Lakes region (Maycock and Curtis 1960); 2) northern sedge meadow stands in Wisconsin (Curtis 1959); 3) hardwood forests on alluvial sites in Manitoba (Mueller-Dombois 1964, Appendix IV); 4) hardwood forests on alluvial sites on islands in the St. Lawrence River between Trois-Rivières and Montreal (Tessier et al. 1981); and 5) Ostrich Fern stands in Maine (Gabrielson 1964). Any species occurring in only one study was not included.

Study Number	1	2	3	4	5
Number of stands	43	35	5	?	22
Trees					
<i>Abies balsamea</i> *	V**	—	—	—	I
<i>Acer saccharinum</i>	—	—	—	V	I
<i>Betula lutea</i>	III	—	—	—	I
<i>Betula papyrifera</i>	V	—	I	—	II
<i>Carya cordiformis</i>	I	—	—	I	—
<i>Fraxinus americana</i>	II	—	—	II	—
<i>F. nigra</i>	III	—	V	I	III-V
<i>F. pennsylvanica</i>	—	—	V	II	—
<i>Picea glauca</i>	V	—	I	—	—
<i>Populus balsamifera</i>	II	—	III	I	—
<i>P. tremuloides</i>	IV	—	II	—	—
<i>Quercus macrocarpa</i>	I	—	I	—	—
<i>Q. rubra</i>	III	—	—	—	I
<i>Thuja occidentalis</i>	IV	—	—	—	I
<i>Tilia americana</i>	II	—	—	I	—
<i>Tsuga canadensis</i>	III	—	—	—	I
<i>Ulmus americana</i>	III	—	V	IV	I
Shrubs					
<i>Alnus rugosa</i>	III	—	I	I	I
<i>Cornus stolonifera</i>	I	—	IV	III	I
<i>Corylus cornuta</i>	IV	—	III	—	I
<i>Ilex verticillata</i>	I	—	—	II	—
<i>Lonicera oblongifolia</i>	I	—	I	—	—
<i>Prunus virginiana</i>	IV	—	V	I	I
<i>Rhamnus alnifolia</i>	I	—	III	—	—
<i>Ribes triste</i>	III	—	IV	—	—
<i>Rubus idaeus</i>	III	—	III	—	I
<i>Spiraea alba</i>	I	III	—	I	I
<i>Symphoricarpos occidentalis</i>	I	—	I	—	—
<i>Viburnum cassinoides</i>	I	—	—	I	—
<i>V. lentago</i>	I	—	V	I	—
<i>V. rafinesquianum</i>	I	—	III	—	—
<i>V. opulus</i> var. <i>trilobum</i>	I	—	V	—	—
Herbs					
<i>Achillea millefolium</i>	I	—	—	—	I
<i>Actaea pachypoda</i>	I	—	—	—	I
<i>A. rubra</i>	IV	—	III	—	—
<i>Alopecurus pratensis</i>	III	I	—	—	—
<i>Amphicarpa bracteata</i>	I	—	—	II	—
<i>Anemone quinquefolia</i>	III	—	I	—	—
<i>Apocynum androsaemifolium</i>	II	—	—	I	I
<i>Aralia nudicaulis</i>	V	—	III	—	I
<i>Arisaema atrorubens</i>	II	—	—	III	I
<i>Asarum canadense</i>	II	—	IV	—	—
<i>Aster ciliolatus</i>	II	—	II	—	—
<i>A. lateriflorus</i>	III	—	—	I	—
<i>A. puniceus</i>	I	III	—	—	—
<i>Athyrium filix-femina</i>	IV	—	—	—	II
<i>Botrychium virginianum</i>	III	—	I	—	—
<i>Brachyelytrum erectum</i>	III	—	—	II	—

TABLE 2. Species-stand table (concluded).

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Study Number	1	2	3	4	5
Number of stands	43	35	5	?	22
<i>Calamagrostis canadensis</i>	I	V	I	I	—
<i>Caltha palustris</i>	I	—	II	—	—
<i>Carex intumescens</i>	II	—	—	I	—
<i>Cicuta maculata</i>	I	II	—	—	—
<i>Cinna latifolia</i>	I	—	IV	—	—
<i>Cirsium arvense</i>	I	—	—	—	I
<i>Convolvulus sepium</i>	—	—	—	I	I
<i>Echinocystis lobata</i>	—	—	—	I	I
<i>Equisetum arvense</i>	III	II	—	—	I
<i>E. sylvaticum</i>	III	—	I	—	—
<i>Eupatorium purpureum</i>	I	V	—	II	—
<i>Fragaria virginiana</i>	V	—	III	—	I
<i>Galium boreale</i>	I	—	III	—	—
<i>G. trifidum</i>	—	II	—	I	—
<i>G. triflorum</i>	IV	—	V	—	—
<i>Gaultheria procumbens</i>	I	—	—	—	I
<i>Heracleum lanatum</i>	I	—	I	—	I
<i>Impatiens capensis</i>	II	II	—	II	—
<i>Iris versicolor</i>	—	—	III	I	I
<i>Laportea canadensis</i>	I	—	—	V	—
<i>Lilium canadense</i>	I	—	—	—	I
<i>Lycopus americanus</i>	I	III	—	I	—
<i>L. uniflorus</i>	I	III	—	—	—
<i>Lysimachia ciliata</i>	—	—	—	I	I
<i>Maianthemum canadense</i>	V	—	IV	—	II
<i>Matteuccia struthiopteris</i>	I	I	V	II	V
<i>Mentha arvensis</i>	—	—	III	I	—
<i>Mimulus ringens</i>	—	I	—	I	—
<i>Mitella nuda</i>	IV	—	I	—	—
<i>Onoclea sensibilis</i>	I	III	—	V	III-V
<i>Osmunda claytoniana</i>	II	—	—	—	I
<i>O. regalis</i>	—	—	—	III	I
<i>Petasites palmatus</i>	III	—	I	—	—
<i>Polygonum coccineum</i>	—	II	—	I	—
<i>P. sagittatum</i>	I	III	—	—	—
<i>Polypodium virginianum</i>	I	—	—	I	—
<i>Prenanthes alba</i>	II	—	—	—	I
<i>Rhus radicans</i>	I	—	—	—	II
<i>Rubus pubescens</i>	V	—	V	I	—
<i>Sanicula marilandica</i>	III	—	II	—	—
<i>Scutellaria lateriflora</i>	I	—	—	I	—
<i>Stellaria media</i>	—	—	—	III	I
<i>Taraxacum officinale</i>	II	—	—	—	I
<i>Thalictrum dasycarpum</i>	I	II	—	—	—
<i>T. pubescens</i>	—	—	—	IV	III-V
<i>Thelypteris palustris</i>	—	III	—	II	—
<i>Uvularia sessilifolia</i>	II	—	—	—	II
<i>Vicia americana</i>	I	—	I	—	—
<i>Viola pubescens</i>	II	—	—	—	I

*Nomenclature follows Scoggan (1978).

**Braun-Blanquet frequency (constancy) scale: I, < 20%; II, 20.1 to 40%; III, 40.1 to 60%; IV, 60.1 to 80%; V, 80.1 to 100%.

generally occupies wetter microtopographic sites (Roberts-Pichette 1971; Tessier et al. 1981). These sites are subject to greater spring flooding (Tessier et al. 1981).

In Eurasia, *M. struthiopteris* occurs in sites very similar to those in North America, although the associated species are different (Englert 1970; Porfirev 1975). In central European forest stands, *M. struthiopteris* is considered a characteristic species of Alno-Padion (*Alnus incana-Prunus padus*) (Mueller-Dombois and Ellenberg 1974; Rasbach et al. 1978) or Alno-Ulmion (*Alnus incana-Ulmus glabra*) (Hamet-Ahti 1963, Ellenberg 1978) plant alliances. Generally, such forest types are found by river beds, brooks and other places with a high, stable water table. The tree layer may be dominated by *Alnus incana*, *Betula pubescens*, *Fraxinus excelsior*, *Picea abies*, or *Ulmus glabra* (Odland 1981). A detailed study by Odland (1981) of plant communities of Roldal, Norway, indicated that *M. struthiopteris* is dominant in two types of *Alnus incana* forest; tall herb/fern type and *M. struthiopteris* type. The latter is much poorer in species (21.7 spp./25 m²) than the former 30.5 spp./25 m²), due to the total dominance of the Ostrich Fern. The *M. struthiopteris* type of *Alnus incana* forest is restricted to shady, moist, hillsides and according to Odland (1981) it should be treated as a separate association from alluvial forests. In the U.S.S.R., *M. struthiopteris* is found in coniferous, mixed and deciduous forests which are found in localities with high water table and eutrophic conditions suitable for the nitrophilous plants of these communities (Porfirev 1975).

Other descriptions of plant communities in which *M. struthiopteris* is found are also referred to in Nichols (1918), Szafer (1966), Walter (1974), Taylor and MacBryde (1977), Soyrinki and Saari (1980), von Aderkas and Bird (1983) and Gauvin and Bouchard (1983).

6. Growth and development

(a) *Morphology.* Embryogenesis and juvenile development in the Ostrich Fern occur in a manner typical of other leptosporangiate ferns (Campbell 1887). *M. struthiopteris* develops three kinds of leaves: cataphylls, (found only on stolons), sterile and fertile fronds. Fertile fronds do not appear until the third year, and then only irregularly. Sobey and Barkhouse (1977) report a maximum growth rate of less than 1 cm/yr for "thick rhizomes" which probably are the thickened erect rhizomes. Dykeman (1982a) reports erect rhizome growth rates of 0.5 to 2.0 cm/yr. The growth rate of horizontal rhizomes is much greater, and plants with intact rhizomes up to 3 m in length have been excavated in Hants County, Nova Scotia (von Aderkas, unpublished). Horizontal rhizomes are produced from detached meristems on the stem after one year. Detached meristems are groups of meristematic cells derived from the apical meristem, occurring at the junction of two meristemes. The longevity of horizontal and erect rhizomes is unknown.

(b) *Physiology.* Prange (1980) has shown that vegetative fronds generally complete their elongation in 15 to 20 days. Both high photosynthetic photon flux density (PPFD) (418 $\mu\text{mol m}^{-2}\text{s}^{-1}$), and low moisture (30–60% of field capacity) reduces frond height. Low soil moisture also decreases the fresh and dry weights of both vegetative and fertile fronds, thus providing further evidence that soil moisture is a critical factor limiting the plant's distribution.

Measurements of photosynthesis, dark respiration, frond diffusive resistance, water potential, osmotic potential and pressure potential in well-watered fronds of various ages up to 28 days old have been reported by Prange et al. (1984). These physiological measurements are summarized in Table 3. In fronds up to nine days of age, nighttime diffusive resistances are similar to daytime resistances (ca. 550 s m⁻¹). These then increase to

TABLE 3. Net photosynthesis at light saturation (600 $\mu\text{mol m}^{-2}\text{s}^{-1}$), dark respiration, light compensation point, pre-dawn frond water potential, osmotic potential, pressure potential, diffusive resistance and mid-day diffusive resistance in fronds from 3 to 24 days old (mean \pm standard error) (adapted from Prange et al. 1984).

Parameter	Frond age (days)			
	3	6–8	15–16	22–24
Net photosynthesis ($\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	—	134 \pm 6	221 \pm 10	195 \pm 15
Respiration ($\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	—	71 \pm 2	16 \pm 1	9 \pm 2
Light compensation point ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	—	50	10	7
Pre-dawn frond water potential (kPa)	-332 \pm 57	-103 \pm 44	-379 \pm 29	-390 \pm 65
Pre-dawn frond osmotic potential (kPa)	-837 \pm 72	-942 \pm 64	-1892 \pm 129	-1493 \pm 51
Pre-dawn pressure potential (kPa)	505 \pm 33	839 \pm 73	1513 \pm 103	1104 \pm 5
Pre-dawn diffusive resistance (s m ⁻¹)	—	557 \pm 26	941 \pm 100	1246 \pm 99
Mid-day diffusive resistance (s m ⁻¹)	—	365 \pm 12	338 \pm 19	389 \pm 17

ca. 1250 s m^{-1} at full frond expansion. This shift could be due to either cuticular wax deposition or a change in stomatal functioning. Osmotic and pressure potentials reach their lowest and highest values, respectively, as the frond reaches full expansion at ca. 16 days. At this time, net photosynthesis peaks and then gradually declines, while dark respiration reaches a low steady value. The results indicate that *M. struthiopteris* is a typical shade-adapted plant with a maximum net photosynthetic rate of ca. $220 \mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

The effect of a mild water stress on immature and mature *M. struthiopteris* fronds has been reported in terms of water status and frond elongation (Prange and Ormrod 1983) and frond gas exchange (Prange et al. 1983). A mild soil water stress of ca. -0.15 MPa is sufficient to significantly reduce elongation in immature fronds and net photosynthesis, dark respiration, internal carbon dioxide concentration and diffusive conductance in fronds of both ages. The residual resistance to carbon dioxide flux is not significantly affected by either mild water stress or frond age. A wild water stress reduces frond water potential in immature fronds but produces an increase in mature fronds, which is the reverse of the typical response. In most agricultural plants, wilting occurs in the older leaves first.

(c) *Phenology*. The swelling of the croziers begins towards the end of April in Nova Scotia, with the first leaves appearing above the crown by the middle of May. In cooler areas this is delayed. Full leaf expansion occurs by the middle of June, with fertile fronds appearing late in that month through to the beginning of autumn. Smaller sterile fronds often appear towards the end of the summer. The fronds begin to brown in early autumn and die back with the first frost. The leaves do not abscise, but remain attached to the leaf-bases until removed either by flooding, or some other agent. In subsequent years, the large leaf bases serve as storage organs or trophopods (Wagner and Johnson 1983).

From autumn until spring the crown remains dormant. During autumn and winter, dormant plants were brought into the greenhouse at weekly intervals. The mean weekly air temperature in the greenhouse ranged between 18.2 and 23.0°C . The minimum PPFD was ca. $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ provided by high pressure sodium lights. These plants produced some new emergent fronds on 4 November and reached 100% emergence by 18 November. Throughout the rest of the winter the frond emergence rate, expressed as the daily average rate of development as defined by Nooden and Weber (1978), continued to increase (Prange, unpublished). This suggests that the plants continued to benefit from exposure to cold after the chilling requirement, to break dormancy, was satisfied. Small crowns and horizontal rhizomes appear to have little or no dormancy because they continue to grow in the autumn if placed in a greenhouse or growth chamber.

7. Reproduction

(a) *Spore production and dispersal*. Sporangia develop on the underside of the fertile frond, the pinnules of which curl around the sori, thereby giving protection (Bower 1923). The gradate sori are minutely indusiate. Meiosis occurs during early summer, for example, 1 July in southern Ontario (Britton 1953). Each sporangium produces 64 spores. Spores are mature by late summer or the beginning of the autumn, but are not released until winter and the following spring. The sporangia open by the drying of a slightly oblique annulus. Initially, the propagules are both whole sporangia and free spores, as excavation of snow profiles in Massachusetts revealed (Klekowski 1979), but later, as the surrounding pinnule breaks down, free spores are released. Each fertile frond is estimated to produce between $1 \times 10^5 = 1 \times 10^6$ spores (Farrar 1976).

Dispersal is by two methods: air and water dispersal of spores, and water dispersal of crowns and/or stolons from populations along riverbanks. Establishment of young plants from gametophytes has not been studied, for in spite of the prodigious production of spores per fertile frond, very few spores germinate. Gametophyte development in nature is dependent on conditions of high humidity (von Aderkas 1983).

The production of fertile fronds per plant is quite variable. Only 1% of shaded plants along the floodplain of the Five Mile River near South Maitland, Nova Scotia developed fertile fronds (von Aderkas, unpublished). The number of fertile fronds produced per plant is also proportional to the size of the plant. It is our observation that in conditions of direct sunlight, a much higher percentage of plants develop fertile fronds. Growth chamber studies show that fertile fronds production is greatest under high PPFD ($418 \mu\text{mol m}^{-2} \text{ s}^{-1}$), and soil moisture conditions [100% field capacity] (Prange 1980).

(b) *Spore viability and germination*. Fresh spores of *M. struthiopteris* germinate at temperatures from 5 to 30°C (Klebs 1917; Hill and Wagner 1974; Warne and Lloyd 1980). The germination rate of spores shed in December and those shed in March stayed at 95% (Farrar 1976). Development of a gametophyte with sex organs takes from two to three weeks in laboratory conditions (von Aderkas 1983). The germination of *M. struthiopteris* spores is light-dependent (Klebs 1916; Pietrykowska 1962; Mohr and Holl 1964; Jarvis and Wilkins 1973). A low percentage of spores, e.g. less than 43%, is able to germinate in the dark but light greatly

increases the germination rate, e.g. 70–91%. All wavelengths between 400 and 750 nm promote germination, but two major peaks of promotion occur at 550 nm and 625 nm, and a minor peak at 450 nm (Jarvis and Wilkins 1973).

Gantt and Arnott (1965) and Jarvis and Wilkins (1973) report that spore viability is maintained for at least 18 months and up to two years when stored in a dark, dry environment at 3 to 5°C. Jarvis and Wilkins (1973) report reduced viability at -10°C or room temperature. Barker and White (1964) freeze-dried spores and observed no drop in viability after three months storage.

Gantt and Arnott (1965) examined germination and early gametophyte growth using histochemistry and electron microscopy. They showed that the dormant spores contain no starch but it accumulates in the chloroplasts after the spores are exposed to light. During germination the abundant protein granules are broken down and disappear. The degradation of protein body reserves by proteolytic enzyme activity has been studied by Cohen and DeMaggio (1983).

(c) *Gametophyte development.* The prothallus initially develops into a small heart-shaped plant. Detailed description of the cell pattern lineages was recorded by Döpp (1927). Under controlled conditions sexual maturity is attained approximately three weeks after germination. Sex expression of Ostrich Fern populations is largely determined by density and age (von Aderkas 1983). Individual plants develop slower than plants at moderate densities. With increasing age, more hermaphrodites are observed, allowing the possibility of intra- and inter-gametophytic mating. Gametophytes respond to a bracken pheromone, antheridiogen, which induces male sex organ formation (Döpp 1950), but do not produce such a compound themselves (Döpp 1962). Strictly male plants arise from gametophytes arrested at a juvenile stage (von Aderkas 1983). Plants will grow in either liquid or solid inorganic media. Mutations in gametophyte development have been studied from populations beside polluted and unpolluted rivers in Massachusetts. The frequency of somatic mutations is much higher along the river known to be contaminated with high levels of polychlorinated biphenyls (Klekowski and Klekowski 1982).

Gametophytes raised in culture frequently give rise to apogamous features such as single leaves, sporangia and glandular scales. This sort of development is markedly promoted by sucrose. However, the occurrence of complete apogamous plants is very rare (von Aderkas 1984a).

In culture, gametophytes may develop from the cut edges of juvenile leaves and, when mated, produce polyploid sporophytes (von Aderkas, unpublished).

In the wild, gametophytes develop very slowly and consequently the proportion of female plants is much lower than in culture (von Aderkas 1983). Prothalli are particularly susceptible to desiccation from which they do not recover (Pickett 1914).

(d) *Vegetative reproduction.* Stolons develop from detached meristems on the rhizome stem and generally grow parallel to the soil surface. The stimulus for reorientation of the apex of the stolon and the onset of crown development is not known, but may be brought about by exposure of the apex to light. A stand of *M. struthiopteris* is spread by the colonization of the surrounding soil by these stolons. If the apex of the stolon is damaged, plants develop from the detached meristems.

Studies of detached meristems (Wardlaw and Alsopp 1948) suggest that emergence may be affected by soil oxygen concentration. The rate of development increases with O₂ concentration up to 45%. Soil pH may also play a role (Prange 1983). Soil media with a pH between 6.5 and 7.1 are the most productive in terms of emerged meristems, time of emergence, plant numbers and fresh weight.

8. Population Structure and Dynamics

(a) *Dispersion patterns.* Populations of sporophytes within a community generally show a clumped or contagious distribution. In denser stands, in which *M. struthiopteris* is the dominant species, frequently found along floodplains in parts of the Maritimes, there is a strong tendency towards a regular distribution in which self-shading plays an important role. When soil moisture varies on a microenvironmental level from aquatic to perhumid, patchiness is readily apparent.

(b) *Age distribution.* Age-specific mortality rates and longevity in different habitats have not been reported for the Ostrich Fern. Sporophytes are thought to be "potentially immortal", as the distribution of plants showing the same type of heterogeneity for a somatic mutation may be very extensive within a population (Klekowski and Klekowski 1982). By vegetative propagation, a clone is established which may form quite an extensive stand. At present, it is difficult to determine the age of individual ramets, particularly erect rhizomes, as there are neither clear age indicators, such as yearly additions of regular numbers of leaf bases, nor visible differences

TABLE 4. Width distribution of sporophytes selected from a stand of *Matteuccia struthiopteris* along the Five Mile River, Hants County, Nova Scotia, Canada (N = 140) (von Aderkas, unpublished).

	Plant width (cm)							
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7+
Percentage of plants	0	10.0	11.4	27.1	25.6	22.1	3.5	0

between annual additions beyond the present year. The difficulties of ageing ferns by numbers of existing leaf bases is clearly outlined by Tanner (1983).

(c) *Size distribution.* Preliminary data from a Nova Scotia population in an *Ulmus-Fraxinus-Acer* community along a floodplain indicates that size distribution is rather skewed (Table 4). The smaller plants (1-3 cm) are the recent additions to the population. There is a lack of plants smaller than 1 cm in width because new additions are from underground rhizomes which turn upwards, and not from sporophytes of sexual origin. Maximum plant width did not exceed 7 cm. This size limit does not represent a maximum, which once attained is followed by rhizome death. The growth habit of erect rhizomes is much like that of a tree fern: once a certain width is reached, the plant continues to grow upwards, retaining approximately the same width. The average height of fronds in this same population was 85 cm, ranging in final size from 33-159 cm. The average number of fronds per plant was 6.75 ± 2.3 and ranging from 2-13. The average total leaf dry weight per plant was 22.9 g, ranging from 1.6 to 72.3 g (von Aderkas, unpublished). Under controlled cold room conditions, large individual crowns have a greater survival rate during dormancy than small individual crowns (Prange 1982).

(d) *Growth and turnover rates.* Populations of the Ostrich Fern are long-lived. In Raifa, U.S.S.R., Porfirev (1975) noted that *M. struthiopteris* maintained the same ground cover from 1925 to 1956, in spite of the change of the plant associates from those of a *Picea* stand, in which *Tilia* was sub-dominant, to one in which *Tilia* was dominant and *Picea* sub-dominant. This he took as further evidence that soil moisture conditions are more important than the type of plant community in determining the presence or absence of *M. struthiopteris*.

(e) *Successional role.* Braun (1950) states that the successional series of communities on floodplains in the Hemlock-White Pine-Northern Hardwoods Region includes transition from elm-black ash to maple-elm-basswood-yellow birch, which in turn becomes maple-yellow birch-hemlock or maple forest. The herbaceous layer of the first community, elm-black ash, includes an abundance of *M. struthiopteris*. In subsequent seral stages, which reflect increasing elevation, less flooding and lower water tables, *M. struthiopteris* is not mentioned. Tessier et al. (1981) described the succession of vegetation on islands in the St. Lawrence River that are subjected to periodic flooding and concluded that the community sequence is controlled primarily by the depth of the water table. The climax floodplain community, which contains *M. struthiopteris*, along with *Acer saccharinum*, *Fraxinus pennsylvanica* and *Ulmus americana*, is mainly determined by small changes in microtopography in relation to the water table. Recently, the almost complete destruction of *Ulmus americana* by Dutch elm disease has led to increases in the other dominants.

9. Interaction with other Species

(a) *Competition.* In the most vigorous stands of *M. struthiopteris*, the plants form a dense stand that reduces light at ground level to a level insufficient for growth of competitors. If the soil becomes water-logged, *M. struthiopteris* is frequently replaced by *Onoclea sensibilis*. On sites that are drier or receive more radiation, *M. struthiopteris* is replaced by *Solidago*, *Rubus* and *Eupatorium* species, and grasses (Dykeman 1982a).

(b) *Symbiosis.* Boullard (1957) reported the presence of endomycorrhizae in the sporophyte of *M. struthiopteris*. In a more detailed study of roots, Berch and Kendrick (1982) quite commonly found unspecified vesicular arbuscular mycorrhizae. No ectomycorrhizae were observed, but a variety of fungal endophytes were present. None of these endophytes are necessary for the growth of the plant as sporophytes grow quite well in sterile culture. No mycorrhizal organisms are associated with gametophytes (Boullard 1957).

(c) *Predation and parasitism.* The following insects are listed as feeding on *M. struthiopteris* (Balick et al. 1978): Diptera — *Chirosia hystricina* Rondani; Aphididae — *Amphorophora ampullata* Buckton, *A. laingi* Mason; Hymenoptera — *Blasticotoma filiceti* Klug, *Strombocerus delicatulus* (Fallen), *S. lineata* (Christ.), *S. struthiopteridis* (Forsius); and Lepidoptera — *Papipema* sp.

Various diseases and fungi have been recorded on plants by Gregor (1938), Stevenson (1945), Anonymous

(1960), Connors (1967), Gourley (1983) and von Aderkas and Brewer (1983). *M. struthiopteris* is the host for the uredinial and telial stages of the rust *Uredinopsis struthiopteridis* Stormer ex Diet. Other fungi reported include: *Herpobasidium struthiopterides* (Rostr.) Lind., *Sclerotium deciduum* Davis, *Dothidella osmundae* (Pk. and Clint.) Sacc., *Sphaerothyrium filicinum* Bub., *Taphrina struthiopteris* Nishida (leaf blister), *Phoma exigua* Desm. var. *foveata* (gangrene), *Ceratobasidium anceps* (Bres. and Sacc.) Jackson, *Cyphella capula* (Holmskj.) Fr., *Dasyscyphus carestianus* (Rabh.) Sacc., *Leptothyrium litigiosum* (Desm.) Sacc. and *Solenia filicina* Pk.

Dodder, *Cuscuta europaea* L., has been found to parasitize the fern (Gams 1938).

(d) *Toxicity and allelopathy*. None reported to date.

10. *Evolution and Migration*. There are two other species in the genus (Lloyd 1971): *M. orientalis* (Hook.) Trev., and *M. intermedia* C. Chr. The former occurs in Siberia, Japan, Korea, throughout China to Assam, India and Sikkim. The latter is found from south-central and southeastern China to Tibet, Sikkim and northeastern India. Many of the morphological characteristics of *M. intermedia* are intermediate between *M. struthiopteris* and *M. orientalis*. Lloyd (1971) suggests that *M. intermedia* is a tetraploid species, and probably an allopolyploid derivative of a cross between diploid *M. orientalis* and *M. struthiopteris*. He also suggests that *M. intermedia* has two separate origins by different hybridizations of the same two parent species because there are two morphological forms of *M. intermedia* that are geographically separated.

In North America the Ostrich Fern probably migrated into the northern part of its habitat from the southern United States following the retreat of the last glacial ice.

11. Response Behavior

(a) *Fire*. *M. struthiopteris* does not occur in fire-prone habitats.

(b) *Grazing and harvesting*. Sheep and cattle are known to eat both young and old fronds. Continual grazing leads to reduced vigour and eventually death of the plant. One of the effects of repeated annual harvesting in the Fredericton area of New Brunswick is a drop in the vigour of plants (Roberts-Pichette 1971).

(c) *Flooding*. When *M. struthiopteris* is found along floodplains, it is subject to inundations, especially in the spring. Flooding probably benefits the Ostrich Fern by depositing new soil and organic debris (Dykeman 1982a). Freshets also play a role in dispersal of rhizomes.

(d) *Drought*. The effect of drought on the sporophyte has not been investigated. However, in nature gametophytes growing on soil which dried out as the growing season progressed quickly dried up and died (von Aderkas 1983). This decrease in humidity had no noticeable effect on the surrounding sporophytes.

(e) *Herbicides*. Doohan (1982) screened herbicides for the Ostrich Fern and observed no injury when Glyphosate and Simazine were applied to dormant crowns. Glyphosate, Simazine, Dicamba, Cyanazine and Terbacil all injured the Ostrich Fern when applied to expanded foliage.

12. Relationship to Man

The young fronds of *M. struthiopteris* have been eaten in North America by the indigenous population. They have been used as a spring tonic (Smith 1957). There is some evidence that the Abenaki Indians ate the roasted crown (Medsger 1938). The croziers, or fiddleheads, have been eaten as a spring vegetable by European colonists in New Brunswick since 1784 (Fisher 1825), and later, in the New England area. According to Gams (1938) the Norwegians used the Ostrich Fern in the making of beer. This species has been listed as a vermifuge in Russia (Komarov 1934). In eastern North America, fresh fiddleheads are a spring market vegetable. Canned and, more recently frozen fiddleheads have become available throughout the year. The tonnage of fiddleheads harvested increased greatly with the sale of the frozen product (von Aderkas 1984b).

M. struthiopteris fiddleheads are neither toxic nor carcinogenic as shown in laboratory studies on rats (Newberne 1976). They are an excellent source of nutrition (Bushway et al. 1982). A 100 g portion of wet fiddlehead greens will furnish 25, 13, 2, 46 and 71% of the U.S. Recommended Dietary Allowance (RDA) for niacin, riboflavin, thiamin, vitamin C and vitamin A, respectively. The percent RDA of the mineral elements supplied by a 100 g serving of fiddleheads would be 4% calcium, 10% magnesium, 13% phosphorus, 11% iron and 4% zinc. The fibre content represents a substantial proportion of the solids content, and could contribute to dietary fibre intake. Because of their low sodium content (0.5 mg/100 g) Ostrich Fern fiddleheads are suitable for salt-restricted diets. The fiddleheads are comparable in nutritional quality to many common green vegetables.

Gellerman et al. (1972) report the occurrence of arachidonic acid and 5,8,11,14,17-eicosapentaenoic acids in *M. struthiopteris*. These highly unsaturated fatty acids, although required by higher animals, are not synthe-

sized by them except when appropriate precursors are provided in the food. These acids are not found in seed plants, but occur in lower plants. Arachidonic acid is found in all sporophyte tissues at levels of 5.8–9.8%.

Recently there has been interest in both management of wild Ostrich Fern populations (Roberts-Pichette 1971; Dykeman 1982a) and field cultivation (Dykeman 1981, 1982b). Research on *M. struthiopteris* has been coordinated by the Atlantic Fiddlehead Research Organization.

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Literature Cited

- Aderkas, P. von. 1983. Studies of the gametophytes of *Matteuccia struthiopteris* (ostrich fern) in nature and in culture. Canadian Journal of Botany 61: 3267–3270.
- Aderkas, P. von. 1984a. Promotion of apogamy in *Matteuccia struthiopteris* (L.) Todaro (ostrich fern). American Fern Journal 74: 1–6.
- Aderkas, P. von. 1984b. The economic history of the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro). Economic Botany 38: 14–23.
- Aderkas, P. von, and D. Brewer. 1983. Gangrene of the ostrich fern caused by *Phoma exigua* var. *foveata*. Canadian Journal of Plant Pathology 5: 164–167.
- Aderkas, P. von, and C. J. Bird. 1983. The habitat of the ostrich fern (*Matteuccia struthiopteris*) in Nova Scotia and Prince Edward Island. Proceedings of the Nova Scotian Institute of Science 33: 131–135.
- Anonymous. 1960. Index of plant diseases in the United States. U.S. Agricultural Handbook Number 165. 531 pp.
- Atkinson, G. F. 1911. The relation between the sterile and fertile leaves of dimorphic ferns. Fern Bulletin 4: 33–35.
- Balick, M. F., D. G. Furth, and G. Cooper-Driver. 1978. Biochemical and evolutionary aspects of arthropod predation on ferns. Oecologia 35: 55–89.
- Barker, W. G., and R. G. White. 1964. Retention of viability in lyophilized spores of fiddlehead fern, *Matteuccia pensylvanica*. American Fern Journal 54: 87–89.
- Berch, S. M., and B. Kendrick. 1982. Vesicular-arbuscular mycorrhizae of southern Ontario ferns and fern-allies. Mycologia 74: 769–776.
- Boullard, B. 1957. La mycotrophie chez les ptéridophytes: Sa fréquence, ses caractères, sa signification. Le Botaniste 41: 5–187.
- Bower, F. O. 1923. The ferns. Volume 1. Cambridge University Press, Cambridge. 359 pp.
- Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co. 596 pp.
- Britton, D. M. 1953. Chromosome studies on ferns. American Journal of Botany 40: 575–583.
- Bushway, A. A., A. M. Wilson, D. F. McGann, and R. J. Bushway. 1982. The nutrient composition of fresh fiddlehead greens. Journal of Food Science 47: 666–667.
- Campbell, D. H. 1887. The development of the ostrich fern. Memoirs of the Boston Society of Natural History 4: 17–52.
- Chrysler, M. A., and J. L. Edwards. 1947. The ferns of New Jersey. Rutgers University Press, New Brunswick, New Jersey. 201 pp.
- Clayton, J. S., W. A. Ehrlich, D. B. Cann, J. H. Day, and I. B. Marshall. 1977. Soils of Canada. Volumes 1 and 2. Research Branch, Canada Department of Agriculture.
- Cohen, H. P., and A. E. DeMaggio. 1983. Proteolytic enzyme activity in spores of the ostrich fern. Plant Physiology 72 (supplement 1): 99.
- Connors, I. L. 1967. An annotated index of plant diseases in Canada and fungi recorded on plants in Alaska, Canada and Greenland. Canada Department of Agriculture, Research Branch, Publication 1251. 381 pp.
- Cruise, J. 1972. Spring harvest — the fiddlehead, a gourmet delight. Ontario Naturalist 11: 18–23.
- Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 pp.
- Doohan, D. J. 1982. Screening herbicides for the ostrich (fiddlehead) fern. Pp. 115–116 in 1981 Adaptive Research Reports. Plant Industry Branch, New Brunswick Department of Agriculture and Rural Development.
- Döpp, W. 1927. Untersuchungen über die Entwicklung von Prothallien einheimischer Polypodiaceen, Pflanzenforschung 8: 1–58.
- Döpp, W. 1950. Eine die Antheridienbildung bei Farnen fördernde Substanz in den Prothallien von *Pteridium aquilinum* (L.) Kuhn, Berichte der deutschen botanischen Gesellschaft 63: 139–147.
- Döpp, W. 1962. Weitere Untersuchungen über die Physiologie der Antheridienbildung bei *Pteridium aquilinum*. Planta 58: 483–508.
- Dykeman, B. W. 1977. Breaking of dormancy in the ostrich fern sporophyte. New Brunswick Department of Agriculture and Rural Development, Plant Industry Branch, 1977 Research Report. 3 pp.
- Dykeman, B. W. 1981. Effects of shade on growth and development of the ostrich fern. Pp. 119–123 in Adaptive Research Reports, New Brunswick Department of Agriculture and Rural Development, Plant Industry Branch.

- Dykeman, B. W.** 1982a. Management of native stands of the ostrich fern. A discussion paper. New Brunswick Department of Agriculture and Rural Development, Plant Industry Branch. Manuscript Report. 13 pp.
- Dykeman, B. W.** 1982b. Cultivated fiddleheads. An economic projection. New Brunswick Department of Agriculture and Rural Development, Plant Industry Branch. Manuscript Report. 20 pp.
- Ellenberg, H.** 1978. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Ulmer. 981 pp.
- Englert, K.** 1970. *Matteucia struthiopteris* und *Equisetum pratense* in den Innauen. Berichte der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora 42: 199.
- Fabbri, F., and F. Menicanti.** 1970. Sul numero cromosomico di *Matteuccia struthiopteris* (L.) Todaro. Caryologia 23: 673-676.
- Farrar, D. R.** 1976. Spore retention and release from overwintering fern fronds. American Fern Journal 66: 49-52.
- Fernald, M. L.** 1921. The Gray Herbarium expedition to Nova Scotia. Rhodora 23: 130-171.
- Fernald, M. L.** 1935. Critical plants of Ontario and Michigan. Rhodora 37: 197-222.
- Fernald, M. L.** 1945. Botanical specialties of the Seward forest and adjacent areas of southeastern Virginia. Rhodora 47: 93-142.
- Fisher, P.** 1825. History of New Brunswick. Reprint 1921, Historical Society of New Brunswick, St. John. 133 pp.
- Fremelin, G., Editor.** 1974. The atlas of Canada. Fourth edition. Macmillan Co., Canada Department of Energy, Mines and Resources and Information Canada. 254 pp.
- Friebel, H.** 1933. Untersuchungen zur Cytologie der Farne. Beiträge zur Biologie der Pflanzen 21: 167-210.
- Gabrielson, F. C., Jr.** 1964. A survey of the ostrich fern, *Matteuccia struthiopteris* (L.) Todaro. M.Sc. thesis, University of Maine, Orono. 74 pp.
- Gams, H.** 1938. Oekologie der extratropischen Pteridophyten. Pages 382-419 in Manual of pteridology. Edited by F. Verdoorn. Martinus Nijhoff, The Hague.
- Gantt, E., and H. J. Arnott.** 1965. Spore germination and development of the young gametophyte of the ostrich fern (*Matteuccia struthiopteris*). American Journal of Botany 52: 82-94.
- Gauvin, C., et A. Bouchard.** 1983. La végétation forestière du Parc du Mont-Orford, Québec. Canadian Journal of Botany 61: 1522-1547.
- Gellerman, J. L., W. H. Anderson, and H. Schlenk.** 1972. Highly unsaturated lipids of *Mnium*, *Polytrichum*, *Marchantia*, and *Matteuccia*. Bryologist 75: 550-565.
- Goebel, K.** 1888. Ueber künstliche Vergrünung der Sporophylle von *Onoclea struthiopteris* Hoffm. Bulletin of the Torrey Botanical Club 15: 86-89.
- Gourley, C. O.** 1983. An annotated index of the fungi of Nova Scotia. Proceedings of the Nova Scotian Institute of Science 32: 75-295.
- Gregor, M. J. F.** 1938. Experimental morphology. Pages 105-140 in Manual of pteridology. Edited by F. Verdoorn. Martinus Nijhoff, The Hague.
- Hämet-Ahti, L.** 1963. Zonation of mountain birch forests in northernmost Fennoscandia. Annales Societa Vanamo 34: 1-127.
- Hegi, G.** 1965. Illustrierte Flora von Mittel-Europa: I. Carl Hanser, Munich. 528 pp.
- Hill, R. H.** 1976. Cold requirements of several ferns in southeastern Michigan. American Fern Journal 66: 83-88.
- Hill, R. H., and W. H. Wagner, Jr.** 1974. Seasonality and spore type of the pteridophytes of Michigan. Michigan Botanist 13: 40-44.
- Höhne, H., and B. Richter.** 1981. Untersuchungen über den Mineralstoff und stickstoffgehalt von Farnkrautern. Flora 171: 1-10.
- Hou, H.-Y.** 1950. The chemical composition of certain ferns and fern allies of central Pennsylvania. American Fern Journal 40: 233-240.
- Hultén, E.** 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford, California. 1008 pp.
- Jarvis, S. J., and M. B. Wilkins.** 1973. Photoresponses of *Matteuccia struthiopteris* (L.) Todaro I. Germination. Journal of Experimental Botany 24: 1149-1157.
- Klebs, G.** 1916. Zur Entwicklungs-Physiologie der Farnprothallien: Erster Teil. Sitzungsberichte der Heidelberger Akademie der Wissenschaften B 7(4): 1-82.
- Klebs, G.** 1917. Zur Entwicklungs-Physiologie der Farnprothallien: Dritter Teil. Sitzungsberichte der Heidelberger Akademie der Wissenschaften B 8(7): 1-104.
- Klekowski, E. J., Jr.** 1979. The genetics and reproductive biology of ferns. Pages 133-170 in The experimental biology of ferns. Edited by A. F. Dyer. Academic Press, New York.
- Klekowski, E. J., Jr., and E. Klekowski.** 1982. Mutation in ferns growing in an environment contaminated with polychlorinated biphenyls. American Journal of Botany 69: 721-727.
- Komarov, V. L.** 1934. Flora of the USSR. Volume 1. Archegoniatae and Embryophyta. Israel Program for Scientific Translations, Jerusalem.
- Kurita, S.** 1976. Chromosome numbers of some Japanese ferns. La Kromosomo 2: 69-76.
- Lawalrée, A.** 1964. *Matteuccia* Tod. Page 19 in Flora Europea. Volume 1. Lycopodiaceae to Platanaceae. Edited by T. G. Tutin, V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters and D. A. Webb. Cambridge University Press.
- Lloyd, R. M.** 1971. Systematics of onocleoid ferns. University of California Publications in Botany 61: 1-93.

- Löve, A. 1976. IOPB chromosome number reports LIII. *Taxon* 25: 483–500.
- Luerssen, C. 1889. Rabenhorst's Kryptogamenflora. Vol. III. Die Farnpflanzen oder Gefäßbündel Kryptogamen (Pteridophyta). Kummer, Leipzig. 906 pp.
- Maycock, P. F., and J. T. Curtis. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. *Ecological Monographs* 30: 1–35.
- Medsger, O. P. 1938. Edible wild plants. Macmillan, New York.
- Mekel, J. C. 1938. Die Entwicklung des Stammes von *Matteuccia struthiopteris*, insbesondere die der Höhlungen. *Recueil de Travaux Botaniques Néerlandais* 30: 627–724.
- Mitui, K. 1965. Chromosome studies on Japanese ferns (I). *Journal of Japanese Botany* 40: 117–124.
- Mohr, H., and G. Holl. 1964. Die Regulation der Zellaktivität bei Farnvorkeimen durch Licht. *Zeitschrift der Botanik* 52: 209–211.
- Morton, C. V. 1950. Notes on ferns of the eastern United States. *American Fern Journal* 40: 245–248.
- Mueller-Dombois, D. 1964. The forest habitat types of southeastern Manitoba and their application to forest management. *Canadian Journal of Botany* 42: 1417–1444.
- Mueller-Dombois, D. 1965. Eco-geographic criteria for mapping forest habitats in southeastern Manitoba. *Forestry Chronicle* 41: 188–206.
- Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Toronto. 547 pp.
- Nayar, B. K. 1968. The prothallus of *Matteuccia pensylvanica*. *British Fern Gazette* 10: 26–29.
- Newberne, P. M. 1976. Biologic effects of plant toxins and aflatoxins in rats. *Journal of the National Cancer Institute* 56: 551–555.
- Nichols, G. E. 1918. Vegetation of northern Cape Breton Island. *Transactions of the Connecticut Academy of Arts and Sciences* 22: 249–467.
- Nooden, L. D., and J. A. Weber. 1978. Environmental and hormonal control of dormancy. Pages 222–268 in *Dormancy and developmental arrest*. Edited by M. E. Clutter. Academic Press.
- Ogura, Y. 1972. Comparative anatomy of vegetative organs of pteridophytes. Second edition. Pp. 1–502 in *Encyclopedia of plant anatomy*. Volume 7, Part 3. Edited by H. Linsbauer. Gebrüder Borntraeger, Berlin.
- Odland, A. 1981. Pre- and subalpine tall herb and fern vegetation in Røldal, West Norway. *Nordic Journal of Botany* 1: 671–690.
- Okuno, S. 1936. Chromosome in some sporophyll-bearing ferns. *Botanical Magazine (Tokyo)* 50: 332–337.
- Pesola, V. 1928. Kalsium karbonaattii kasvimaantietelli senä tekijänä suomessa. (Calcium carbonate as a factor in the distribution of plants in Finland.) *Annales Societa Vanamo* 9: 1–246.
- Pickett, F. L. 1914. Some ecological adaptations of fern prothallia — *Camptosorus rhizophyllus* Link. and *Asplenium platyneuron* Oakes. *American Journal of Botany* 1: 477–498.
- Pietrykowska, J. 1962. Investigation on the germination of spores of the fern *Matteuccia struthiopteris* (L.) Tod. *Acta Societa Botanica Polska Warschau* 31: 437–447.
- Porfirev, V. S. 1975. (The synecology of *Matteuccia struthiopteris* Todaro, Pteridophyta: An indicator of underground soil water). Pages 337–342 in *Vodnyi obmen v osnovnykh tipakh rastitel'nosti SSSR: kak element krugovorota veshchestva i energii*. Edited by G. I. Galazii. Akademya Nauk SSSR, Sibirskoe Otdelenie, Limnologicheskii Institut, Irkutsk.
- Prange, R. K. 1980. Responses of the ostrich fern, *Matteuccia struthiopteris* (L.) Todaro, to lime, soil moisture and irradiance. *Proceedings of the Nova Scotian Institute of Science* 30: 171–181.
- Prange, R. K. 1981. Internal and external factors affecting frond growth in the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro). Ph.D. thesis, University of Guelph, Guelph, Ontario. 135 pp.
- Prange, R. K. 1982. Breaking of dormancy in the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro). National Research Council of Canada Contract Report No. 081-051/1-6306. 43 pp.
- Prange, R. K. 1983. Improvement of propagation systems — ostrich ferns. National Research Council of Canada Contract Report No. OSC82 – 00412. 22 pp.
- Prange, R. K., and D. P. Ormrod. 1982. Effects of ammonium and nitrate nutrition on the ostrich fern (*Matteuccia struthiopteris*). *Canadian Journal of Plant Science* 62: 195–201.
- Prange, R. K., and D. P. Ormrod. 1983. Differential response in the water status of immature and mature fronds of the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro) to a mild water stress. *Plant Physiology* 72: 96–98.
- Prange, R. K., D. P. Ormrod, and J. T. A. Proctor. 1983. Effect of water stress on gas exchange in fronds of the ostrich fern (*Matteuccia struthiopteris* (L.) Todaro). *Journal of Experimental Botany* 34: 1108–1116.
- Prange, R. K., D. P. Ormrod, and J. T. A. Proctor. 1984. Effect of frond age on frond elongation, gas exchange and water relations in the ostrich fern (*Matteuccia struthiopteris*). *Canadian Journal of Botany* 62: 2094–2100.
- Rasbach, K., H. Rasbach, and O. Wilmanns. 1978. Die Farnpflanzen Zentraleuropas. Second edition. Gustav Fischer, Stuttgart. 304 pp.
- Raymond, M. 1950. Quelques entités mineures nouvelles de la flore du Québec. I. *Le Naturaliste Canadien* 77: 55–71.
- Roberts-Pichette, P. 1971. Fiddleheads in New Brunswick. ARDA Project 33906, New Brunswick Department of Agriculture and Rural Development, Fredericton. 33 pp.
- Roland, A. E., and E. C. Smith. 1969. Flora of Nova Scotia. Nova Scotia Museum, Halifax, Nova Scotia.

- Scoggan, H. J.** 1978. The flora of Canada. National Museums of Natural Sciences, Publications in Botany 7. National Museums of Canada, Ottawa, Ontario. 1711 pp.
- Scotter, G. W., and W. J. Cody.** 1979. Interesting vascular plants from southeastern Yukon Territory. *Canadian Field-Naturalist* 93: 163–170.
- Smith, N. N.** 1957. Notes on the Malecite of Woodstock, New Brunswick. *Anthropologica*, series 1, 5: 1–40.
- Sobey, D. H., and P. Barkhouse.** 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick – Nova Scotia border region. *Canadian Field-Naturalist* 91: 377–383.
- Sorsa, V.** 1958. Chromosome studies on Finnish Pteridophyta. I. *Hereditas* 44: 541–546.
- Söyrinki, N., and V. Saari.** 1980. Die Flora im Nationalpark Oulanka, Nord-Finnland. *Acta Botanica Fennica* 114: 1–150.
- Stetsenko, N. M., and Y. Tabachnyi.** 1982. Alkaline and earth alkaline elements of some species of ferns. *Ukrainskii Botanichnii Zhurnal* 38: 37–40.
- Stevenson, J. A.** 1945. Ferns and fungi. *American Fern Journal* 35: 97–104.
- Szäfer, W.** 1966. The vegetation of Poland. Pergamon Press, London. 738 pp.
- Tanner, E. V. J.** 1983. Leaf demography and growth of the tree-fern *Cyathea pubescens* Mett. ex Kuhn in Jamaica. *Botanical Journal of the Linnean Society* 87: 213–227.
- Taylor, R. L., and B. MacBryde.** 1977. Vascular plants of British Columbia: a descriptive resource inventory. University of British Columbia Press, Vancouver. 754 pp.
- Tessier, C., A. Maire, et A. Aubin.** 1981. Étude de la végétation des zones riveraines de l'archipel des Cent-îles du fleuve Saint-Laurent, Québec. *Canadian Journal of Botany* 59: 1526–1536.
- Todaro, A.** 1866. Synopsis plantarum acotyledonearum vascularium sponte provenientium in sicilia insulisque adjacentibus. Panormi. 52 pp.
- Tryon, R. M.** 1939. Notes on the ferns of Wisconsin. *American Fern Journal* 29: 5.
- Tryon, R. M., and A. M. Tyron.** 1982. Ferns and fern allies, with special reference to tropical America. Springer-Verlag, New York. 857 pp.
- Wagner, W. H., and D. M. Johnson.** 1983. Trophopod, a commonly overlooked storage structure of potential systematic value in ferns. *Taxon* 32: 268–269.
- Walter, H.** 1974. Die vegetation Osteuropas. Nord- und Zentralasiens. Gustav-Fischer, Stuttgart. 452 pp.
- Wardlaw, C. W.** 1943. Experimental and analytical studies of pteridophytes I. Preliminary observations on the development of buds on the rhizome of the ostrich fern (*Matteuccia struthiopteris* Tod.) *Annals of Botany, New Series* 8: 173–188.
- Wardlaw, C. W.** 1946. Experimental and analytical studies of pteridophytes VII. Further observations on bud development in *Matteuccia struthiopteris*, *Onoclea sensibilis* and species of *Dryopteris*. *Annals of Botany, New Series* 10: 117–132.
- Wardlaw, C. W., and A. Alsopp.** 1948. Experimental and analytical studies of pteridophytes XII. The effect of different concentrations of oxygen on inactive and active meristems of ferns. *Annals of Botany, New Series* 12: 157–168.
- Warne, T. R., and R. M. Lloyd.** 1980. The role of spore germination and gametophyte development in habitat selection: temperature responses in certain temperate and tropical ferns. *Bulletin of the Torrey Botanical Club* 107: 57–74.
- Wherry, E. T.** 1920. The soil reactions of certain rock ferns — I. *American Fern Journal* 10: 15–22.
- Wherry, E. T.** 1921. The soil reactions of the ferns of woods and swamps. *American Fern Journal* 11: 5–16.

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