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Characteristics of Sites Occupied by Wild Lily-of-the-Valley, *Maianthemum canadense*, on Hill Island, Ontario

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One hundred and thirteen sites on an island in the Thousand Islands region of the St. Lawrence River were studied to determine the environmental factors active in controlling the local distribution of *Maianthemum canadense* var. *canadense* (Wild or False Lily-of-the-Valley). The plant occurred most frequently in areas with moderate shade and evaporation and with a low cover of graminoid plants. Standing crop was negatively correlated with levels of evaporation, and positively correlated with penetration of light through the tree canopy and soil phosphorus. Analysis of interspecific associations indicated a positive correlation between the presence of *Maianthemum canadense* and the following species: *Tsuga canadensis, Acer saccharum, Carya ovata, Solidago caesia,* and *Pteridium aquilinum*. A negative correlation was detected with *Rumex acetosella* and *Deschampsia caespitosa*.

Key Words: Autecology, *Maianthemum canadense*, Wild or False Lily-of-the-Valley, Ontario, environmental factors, interspecific association, distribution.

The distribution of a plant species is limited by external factors which include soil and climate and by its reproductive strategy and biotic interactions. The 'realized niche' of a species (Hutchinson 1958), the 'space' in which its individuals live, may be delimited by one circumscribing factor such as grazing pressure, or by several interrelated environmental factors.

In the Thousand Islands region of the St. Lawrence River the distribution of *Maianthemum canadense* is patchy. The region is situated at the heart of the North American distribution of the plant, hence it would not be expected that macroclimatic factors would be responsible for this pattern. At the same time, however, casual observations suggest that plant–soil relationships also are not important in producing pattern. While growth from rhizomes would explain small scale clumping, it cannot account for the larger scale patchiness that is evident. Therefore one might hypothesize that biotic interactions are of primary importance in developing pattern within the region.

This paper reports on the influence of a number of physical and biotic factors on the local distribution of *Maianthemum canadense* within the Thousand Islands region. While it is not possible to determine the mechanisms controlling distribution with field work such as presented here, it is possible to suggest which factors may be most active in determining local distribution. Further experimental testing is required to determine causal relationships.

The Plant

Maianthemum canadense var. *canadense* (Liliaceae) is a small herbaceous perennial with creeping rhizomes and is a rhizome geophyte. In Ontario, Sparling (1964) showed that *Maianthemum canadense* attains maximal leaf biomass and flowers in May, then maintains this biomass throughout the summer. Vegetative reproduction is important (Silva et al. 1982), and Whitford (1949) assumed that large clumps, which may be up to 6 m in diameter, are clones. Sobey and Barkhouse (1977) found the yearly growth increment of rhizomes to be 15–30 cm/yr, hence if a large clump had a single seed as its origin it could be 30 to 60 years old. Two varieties of the plant are known to occur in eastern Ontario (Beschel et al. 1970; Kawano et al, 1967, 1968; Ingram 1966) but all individuals encountered within the study area were *Maianthemum canadense* var. *canadense*.

The Study Area

The study area is located at the southern tip of Hill Island, Leeds County, Ontario. Hill Island is part of the Frontenac Axis, being primarily composed of granite, but partly overlain by Ordovician sandstone and a patchy cover of sand and gravel (Wynne-Edwards 1962). Both granite and sandstone outcrop in the study area. Local climate is moderated by the presence of Lake Ontario, so that the number of growing days is comparable to that occurring south of London, Ontario. The average continuous frost-free period is between 140 and 150 days and the duration of snow cover is highly variable (Hirvonen and Woods 1978). The effect of aspect and a steep microrelief is to create marked differences in microclimate, with southwest facing slopes being dry and warm while slopes with a northeasterly aspect are cooler and wetter. The possible influence of such microclimatic gradients on the distribution of tree species further west on the Frontenac Axis was studied by Jafri (1965). Species common to both Jafri's study and this study include *Tsuga canadensis* (Eastern Hemlock), *Pinus strobus* (Eastern White Pine), *Acer saccharum* (Sugar Maple), *Quercus alba* (White Oak), and *Carya ovata* (Shagbark Hickory).

The parent materials of Hill Island include deep glacio-fluvial and glacio-lacustrine sediments, some alluvium, and organic deposits. However, in the study area soils are exclusively shallow with numerous bedrock outcrops. Plant cover is discontinuous because of patches of rock. Soil texture is predominantly sandy.

The communities occurring in the study area closely resemble those found elsewhere in the region by Hirvonen and Woods (1978). Occurring on or bordering the most exposed rocky outcrops, moss and lichen communities dominate with small patches of soil being colonized by drought-tolerant plants such as *Rumex acetosella* (Sheep Sorrel). Where soil is sufficient to support more extensive growth, well-drained southeasterly aspects are characterized by a sparse incidence of *Pinus strobus*, *Pinus rigida* (Pitch Pine), *Juniperus virginiana* (Eastern Red Cedar), *Quercus borealis* (Red Oak), and a dense mat of *Deschampsia caespitosa* (Tufted Hairgrass).

In less arid areas a mixed woodland community characterized by *Pinus strobus*, *Quercus borealis*, and *Acer rubrum* (Red Maple) can be found. This community generally has a sparse canopy, thereby allowing species such as *Solidago caesia* (Blue-Stemmed Goldenrod), a number of graminoid species, and some shrubs including *Prunus serotina* (Black Cherry), *P. virginiana* (Choke Cherry) and *Amelanchier arborea* (Juneberry) to occur. These communities may also support seedlings of *Carya ovata* and *Acer saccharum*. More moist depressions often harbour luxuriant growth of *Pteridium aquilinum* (Bracken Fern).

Moist sites occurring in large depressions and on north and easterly exposures are characterized by one of two communities: a predominantly coniferous forest consisting of *Pinus strobus* and *Tsuga canadensis*, with lesser occurrences of *Acer rubrum*, *Quercus borealis*, and sparse herbs; or alternatively a deciduous forest characterized by a large number of species, including *Acer rubrum*, *Acer saccharum*, *Quercus borealis*, *Carya ovata*, *Fraxinus americana* (White Ash), and *Tilia americana* (Basswood). Here the understory is shaded, and supports a lush growth of *Parthenocissus inserta* (Virginia Creeper).

Materials and Methods

Because of numerous cliffs and rock outcrops, placing random sampling plots on a grid proved impossible. Accordingly a trail following, but not restricted to, major pockets of soil was blazed before the plants emerged in the spring. One hundred and thirteen points were marked at regularly spaced intervals along the trail and, when growth commenced, circular plots were established. If individuals or clones of *Maianthemum canadense* occurred within 5 m of the marked point a plot was established to include the closest individual or clone. Otherwise the plot was established at the point itself. Using this technique it was possible to obtain a sufficiently large number of sites (72) in which the plant occurred. The size of plots varied for the various parameters measured at each site. The 113 sites were scattered within an area of 6.5 ha.

Throughout eight weeks of the 1976 summer season, four Piché atmometers were run, two on a protected northeastern slope and two on an exposed southwestern slope. Evaporation values from the two atmometers for each slope were averaged to give two standard curves running for the eight weeks. The northeast curve was arbitrarily assigned a relative evaporation value of 10.0 while the southwest curve was assigned a relative evaporation value of 20.0. Evaporation at each of the 113 sites was measured with atmometers for at least one week and compared to the standard points for that week. Relative evaporation values for each site were then assigned, based upon a comparison with the two standards. Values ranged from 3.8 to 30.2. This use of standard atmometers is comparable to the method used by Wolfe et al. (1949).

Light penetrating through the forest canopy was determined as total irradiance at ground level, reported as percentage intensity of full sunlight reaching ground level under cloudless conditions in mid August. This method ignores all subtlety in measuring light intensity (Evans 1966; Sparling 1964) but allowed a rapid comparison of the effects of the tree canopy to be made.

Bedrock was identified at the nearest outcrop. The transition from granite to sandstone was sharply marked, so no errors are thought to have been made. Soil depth was measured down to 20 cm; points with deeper soil being recorded as > 20 cm. Soil samples of a standard volume were collected from the top 20 cm of soil after removal of the litter. This zone included all the rooting depth of the plant.

Samples were analyzed at the Ontario Soil Testing Laboratory, University of Guelph, for pH, K, P, Mg, Ca, and texture. All samples were dried at 90° C and sieved through 2 mm mesh. Soil pH was determined by the addition of sufficient distilled water to create a soil paste 20 minutes prior to measurement (Allen et al. 1974; Black et al. 1965). Ammonium acetate (pH 7.0) extractable K, Mg, and Ca were prepared with a 1:10 soil extractant ratio, agitated for 15 minutes and filtered through Whatman 42 filter paper. Determination was accomplished by atomic absorption spectrophotometry. Phosphorus was extracted with sodium bicarbonate (0.5 M buffered at a pH of 8.5 in NaOH) with a soil extractant ratio of 1:20, agitated for 30 minutes, and filtered through Whatman 42 filter paper. Determination was accomplished with a Techman Autoanalyzer.

All woody species within a radius of 5 m and all herbs within a radius of 1 m of each sampling point were recorded. Cover of graminoid plants was estimated as a percentage within the 1 m radius. Graminoid plants included non-flowering grasses and young sedges. Aside from *Maianthemum canadense* other herbs did not produce a continuous dense cover.

After cessation of growth, in mid-September, all shoots of *Maianthemum canadense* occurring in an area of 3.5 m^2 centred on each sampling point were harvested. All shoots rising above litter were counted and cut off just above the over-wintering bud. Standing crop biomass was then determined after drying to constant weight at 90° C.

The full data set (n = 113) was divided into two subsets, M + for those sites where *Maianthemum canadense* was present (n = 72) and M – where it was absent (n = 41). The T-test was utilized to determine if the M + and M – subsets were clustered on different portions of each of the full environmental gradients encountered (testing for the significance of the difference in the two means, M + and M –, for each environmental parameter). Possible relationships between standing crop and the continuous environmental factors were examined by regression analysis and association between the presence of *Maianthemum canadense* and non-continuous variables (presence or absence of other species, soil texture and bedrock) was determined by the chi-square test.

Results

Individuals of *Maianthemum canadense* were found growing in the full environmental gradient of relative evaporation as represented by the M + and M – sites (Figure 1A), but there was a concentration of plants in the more humid sites. The mean evaporation value for M + sites was significantly lower ($p < 0.01$) than that for the M – sites. *Maianthemum canadense* did not occur in the most densely shaded sites, but occupied the remainder of the environmental gradient including fully open sites (Figure 1B). Most of the sites were clustered in the lightly shaded portion of the gradient and the mean light penetration estimate for M + sites was significantly lower ($p < 0.01$) than for M – sites. While *Maianthemum canadense* survived where the cover from graminoid plants was 100% it tended to cluster at the other end of the gradient where cover of grasses and/or sedges was least (Figure 1C). The mean value of graminoid cover for M + sites was significantly lower ($p < 0.01$) than that for M – sites.

Soil depth appeared to be unimportant in determining the presence of *Maianthemum canadense*. The plant occurred in any depth of soil, provided some soil was present. More M + sites were found on sandstone than would be expected randomly ($p < 0.01$), but this cannot be attributed directly to the type of bedrock. It was found that sandstone sites generally showed low evaporation and moderate shading which are also the preferred portions of these gradients. This relationship may result from the fact that all sandstone sites were located on the more protected northeast exposure. It is, however, difficult to be sure that the sandstone itself, due to its pervious nature, does not produce a more moist, and hence more suitable, growing site. Soil texture and pH were not associated with the presence of the plant.

The mean soil concentration of Mg, Ca, P, and K at M + sites was not significantly different from that for M – sites ($p > 0.15$, Table 1). The gradients for Ca and Mg were fully exploited by the plant, indicating that the plant did not select subsections of the full gradient encountered in the study stie. The frequency polygon for phosphorus (Figure 1D) shows a slight clustering of M + sites in a restricted portion of the gradient, but this did not result in a significant difference in the M + and M – means ($p = 0.36$).

Table 1 also gives the mean, standard deviation, and range of *Maianthemum canadense* standing crop biomass for M + sites. Simple regression analysis of the M + data (continuous variables only) demonstrated that only the relative evaporation was significantly and negatively correlated with biomass ($p < 0.01$). As several scatter diagrams indicated a possible logarithmic relationship between the dependent and independent variables, simple regression analyses were performed with biomass as the dependent variable versus the natural log of all the

TABLE 1. Mean above-ground biomass of *Maianthemum canadense* at M + sites and mean concentrations and T-test significance levels for the difference in mean concentrations of available soil nutrients in sites with (M +) and without (M −) *Maianthemum canadense* on Hill Island, Ontario. St. crop = standing crop. Plot area = 3.5 m^2.

Variable	*Maianthemum canadense* Present (n = 72) mean ± SD	Range	*Maianthemum canadense* Absent (n = 41) mean ± SD	Range	T-test Significance Level
M. canadense st. crop (g/plot)	2.4 ± 2.0	0.05 - 11.05	—	—	—
Potassium (ug/g)	105 ± 45	40 - 260	104 ± 40	36 - 200	0.91
Phosphorus (ug/g)	60 ± 28	15 - 120	54 ± 27	13 - 120	0.36
Calcium (ug/g)	384 ± 263	125 - 1700	486 ± 404	125 - 1900	0.15
Magnesium (ug/g)	58 ± 34	15 - 156	64 ± 46	12 - 200	0.45

independent variables (except pH). In these analyses, the natural log values of the relative evaporation values were negatively correlated, and the natural log values of the light penetration were positively correlated with biomass ($p < 0.04$ and $p < 0.02$ respectively). The other factors measured were not significantly related to biomass ($p > 0.211$).

Multiple regression analysis of the untransformed data demonstrated that the light penetration estimate was the best predictor of biomass. The residuals from this regression were best explained by soil potassium followed by the relative evaporation value, percent graminoid cover, and the remaining soil characteristics. Only the inclusion of the first variable in the multiple regression equation was significant at the 5% level and only a small portion of the total variance was explained ($R^2 = 0.13$ for the significant variable, $R^2 = 0.23$ for all remaining variables) and only a small portion of the total variance was explained.

Multiple regression analysis was repeated using the natural log of each independent variable (except pH). Relative evaporation proved to be the best predictor of biomass, while percent light penetration and soil phosphorus explained a significant portion of the residuals ($p < 0.05$). Thirty eight per cent of the total variation was explained ($R^2 = 0.38$) by the first three variables, and 48% ($R^2 = 0.48$) after inclusion of the remaining five variables in the analysis.

Sixty species of trees (as seedlings), shrubs, herbs, ferns, and mosses were found within the smaller plots and 19 species of trees occurred within the larger plots. Table 2 lists the species present in 10 or more plots together with their frequency of occurrence and an indication of their association with the presence or absence of *Maianthemum canadense*. Less common herbs included the spring-flowering plants such as *Trillium grandiflorum* (White Trillium), *Polygonatum pubescens* (Solomon's Seal), and *Smilacina racemosa* (False Solomon's Seal). *Maianthemum canadense* was found to be positively associated with the trees *Tsuga canadensis, Acer saccharum,* and *Carya ovata* and with *Solidago caesia* and *Pteridium aquilinum*. It was negatively associated with *Rumex acetosella* and *Deschampsia caespitosa*.

Discussion

Of the eleven factors investigated, three were found to be significantly correlated with the presence or absence of *Maianthemum canadense* ($p < 0.01$): percent light penetrating through the forest canopy, the relative evaporation estimate, and cover by graminoid plants. Bedrock type was also associated with the presence or absence of *Maianthemum canadense*; however, its significance may have been a result of other factors. Over 80% of M + sites occurred where there was little graminoid cover, moderately low evaporation, and moderate shading. *Maianthemum canadense* also tended to occur more frequently in the middle of the soil phosphorus gradient, although it did grow throughout the full gradient of concentrations sampled.

Maianthemum canadense was not normally present in sites where graminoid cover was high, but when it did occur in such sites no significant relationship existed between standing crop biomass and graminoid cover. If the *Maianthemum canadense* – graminoid relationship were directly competitive, resulting in reduced growth of *Maianthemum canadense*, a negative correlation would be expected (Cable 1969; Bell and Nalewaja 1968; Simms and Mueller-Dombois

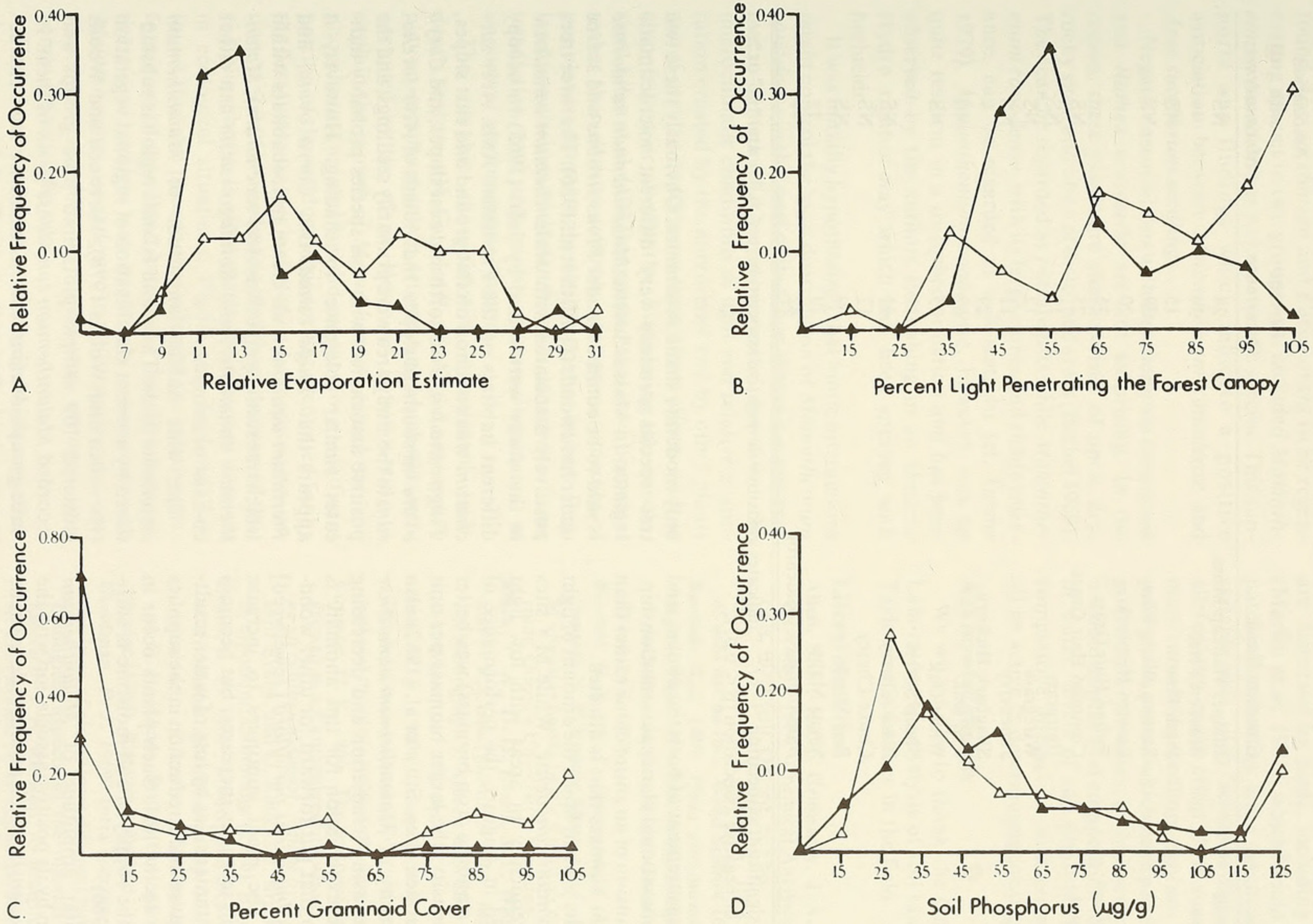

FIGURE 1. Frequency distribution of the relative evaporation estimate (1A), percent light penetrating the forest canopy (1B), percent cover by graminoid species (1C), and soil phosphorus concentrations (1D) at sites with (n = 72) and without (n = 41) *Maianthemum canadense*. Plots with solid triangles represent the relative frequency of occurrence of sites with *Maianthemum canadense* (M +), while plots with open triangles represent sites without *Maianthemum canadense* (M –). For A, B, and C, the mean for M + sites is significantly lower than the mean for M- sites ($p < 0.01$), indicating that *Maianthemum canadense* is selecting restricted portions of the environmental gradient encountered. For D, however, the M+ and M– means are not significantly different ($p = 0.36$). Note the greater range in relative frequencies indicated in C.

TABLE 2. Percent frequency of occurrence and association between *Maianthemum canadense* and plant species occurring in 10 or more of the 113 sample sites in the Hill Island study area.

Species	Common Name	Percent Occurrence	Association with *M. canadense*
Polytrichum commune	Juniper Haircap Moss	24	NS*
Pteridium aquilinum	Bracken Fern	34	++
Pinus rigida	Pitch Pine	15	NS
Pinus strobus	Eastern White Pine	39	NS
Tsuga canadensis	Eastern Hemlock	20	+
Deschampsia caespitosa	Tufted Hair Grass	35	--
Deschampsia flexuosa	Common Hair Grass	25	NS
Agrostis hyemalis	Hairgrass	12	NS
Poa compressa	Wiregrass	12	NS
Amelanchier arborea	Juneberry	11	NS
Carya ovata	Shagbark Hickory	29	+
Quercus borealis	Red Oak	62	NS
Quercus alba	White Oak	25	NS
Rumex acetosella	Sheep Sorrel	11	--
Prunus serotina	Black Cherry	43	NS
Prunus virginiana	Choke Cherry	12	NS
Acer rubrum	Red Maple	9	NS
Acer saccharum	Sugar Maple	39	++
Solidago caesia	Blue-stemmed Goldenrod	42	++

*"NS" indicates no significant association "+" or "–" indicates a positive or negative association ($p < 0.05$), and "++" or "--" indicates a positive or negative association ($p < 0.01$).

1968). Possibly measurement of both the above- and below-ground biomass could clarify this relationship, unless it is the expansion of an entire clone rather than the individual shoot biomass that is affected.

Cover of all plants present limits the amount of light reaching *Maianthemum canadense*. While M + sites occurred more frequently in areas with low light intensity (measured in August), the performance of shoots (judged by standing crop biomass) was better with high light intensity; the larger biomass per unit area was found in open sites. Silva et al. (1982) also found that the density of *Maianthemum canadense* increased with increasing irradiation and decreasing soil moisture. The explanation for this anomaly is possibly similar to that put forward for other woodland herbs such as *Impatiens parviflora* [Jewelweed] (Coombe 1966). The plant continues to increase assimilation as light intensity increases, but becomes limited at high light intensities by loss of water resulting in stomatal closure and a reduction in the supplies of carbon dioxide to the leaf. Such plants occur in open sites only if the supply of soil moisture is sufficient (Rackham 1966).

The wide habitat amplitude of *Maianthemum canadense* is shown by its positive association with the conifer, *Tsuga canadensis*, which produces deep shade throughout the season and with the deciduous tree, *Carya ovata*, which produces little shade in spring and only moderate shade in summer. Obviously these two tree species produce very different microclimatic regimes. In Massachusetts *Maianthemum canadense* is said to be common under *Pinus strobus* and scarce under hardwoods (Griffith et al. 1936). The three trees positively associated with *Maianthemum canadense* in this study were found by Jafri (1965) to occupy different habitats on the Frontenac Axis. *Acer saccharum* was common on flat ground and east slopes, *Tsuga canadensis* on north and east slopes, and *Carya ovata* on southern slopes. Individuals of *Acer saccharum* in the study area were primarily seedlings, and the positive association with this species probably indicates similar tolerance to shading. However, it appears that *Tsuga canadensis, Carya ovata,* and *Pteridium aquilinum* all create microhabitats within which tree seedlings (such as *Acer saccharum*), *Maianthemum canadense*, and *Solidago caesia* can either co-exist or compete.

The wide habitat amplitude of *Maianthemum canadense* in the Thousand Islands region is substantiated by a recent classification of regional vegetation (Hirvonen and Woods 1978). Hirvonen and Woods clustered 109 sample plots into nine groups and recorded *Maianthemum canadense* in six of them. In three groups, *Maianthemum canadense* was a characteristic species. One of these, the *Tsuga* group, repeats our positive association with *Tsuga canandensis* on a larger scale. The positive association with *Pteridium aquilinum* in our plots was also found in the *Aralia-Carpinus* group. Finally, Hirvonen and Woods (1978) found *Acer saccharum* and *Carya ovata* to be regenerating species in two groups that included *Maianthemum canadense* as a characteristic species. This supports our findings which indicate a positive association between *Maianthemum canadense* and *Acer saccharum* seedlings.

Negative associations with *Deschampsia caespitosa* and *Rumex acetosella* are not surprising. In the region, these plants are characteristic of open, dry, rocky sites, and often of disturbed areas (Bechel 1969). They can be regarded as r-strategists while *Maianthemum canadense*, with its large clones and shade tolerance, can be regarded as a K-stategist (cf. Grime 1979). *Maianthemum canadense*, however, can be quite resilient in a disturbed situation and has been observed by the authors flourishing in an Ontario Hydro right-of-way which had been sprayed with herbicide.

It was initially hypothesized that biotic interactions might control the local distribution of *Maianthemum canadense* in this part of its range, where it is not near macro-climatic limits. Apparently, however, the microclimatic conditions of light and relative evaporation created by the microrelief and by other plants are of greater importance than direct effects such as competition or allelopathy. Supporting this conclusion, Silva et al. (1982) suggested that environmental rather than density controls were primary causes of population demography characteristics in New England populations of *Maianthemum canadense*. Solar irradiation and soil moisture were implicated as important environmental factors.

The edaphic characteristics investigated (soil, depth, texture, pH, Ca, Mg, P, and K) did not seem to play an important role in determining which sites were occupied by the plant. However, in attempting to explain the growth of *Maianthemum canadense*, soil phosphorus (natural log) did account for a significant portion of the residual variance not accounted for by the first two variables included in the regression equation ($p < 0.05$). Goodman (1969) has commented that soil phosphorus is often the most important nutrient in ecological situations; Pigott and Taylor (1964) found that soil phosphorus affected the relative performance of woodland herbs and that *Deschampsia caespitosa*, which was negatively associated with *Maianthemum canadense* in this study, did not respond to additions of phosphorus, nitrogen, or a combination of the two.

Factors not measured in this study which may affect the pattern of local distribution include the annual regime of microclimate and snow cover, the concentrations of other soil nutrients such as nitrogen, and reproductive strategy, to name a few. For example, it is known that some *Maianthemum canadense* seeds are dispersed by birds, including the ruffed grouse (Martin et al. 1951), which would tend to produce a patchy distribution. Even assuming seeds reached all suitable sites, such factors as disease, predation, and allelopathy could affect their success, or *Maianthemum canadense* seedlings may not be capable of competing with plants which have pre-empted the suitable micro-sites. However, in the Thousand Islands region, it would appear that competition for light, availability of water, levels of soil phosphorus, and possibly a competitive interaction with graminoid species may all be active in determining local distribution.

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