

Shoot Demography in New England Populations of *Maianthemum canadense* Desf.

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Summary. The demography of shoots of eight populations of a herbaceous perennial exhibiting clonal growth, is presented. The study was done along an elevational gradient, from a more open secondary mixed forest to a denser, more mature stand. Most shoots lived one to three years on the average, but shoots as old as twelve years were found. Large variation in formation and mortality of shoots was observed among plots and years. Yearly trends in the mortality rates of site replicates showed a higher correlation than rates of shoot formation. Although the density of shoots was highest in the drier sites, the turnover of shoots was highly variable and apparently uncorrelated with site location. Age structures revealed a tendency of longer-lived and higher reproductive activities among shoots from more mesic sites. It is hypothesized that environmental rather than density controls are primary causes of the population dynamics observed in this species.

Introduction

A large number of forest floor herbs exhibit a type of growth usually referred to as vegetative reproduction which consists of the formation of a series of identical copies of a basic growth unit along a rhizome axis. These units behave like individual plants in that they perform the productive and reproductive functions generally used to define an individual. The long list of species growing by means of modular replication and the endless diversity of mechanisms by which this replication is accomplished (Abrahamson 1980) indicates that this is an important ecological and evolutionary phenomenon.

The demography of shoots is an important aspect of the population biology of plants (White 1979). The shoots are the units of growth and reproductive performance of the plant since they gather the energy and substances that are invested both in vegetative and sexual reproductive structures. Therefore, analysis of their behavior in the field is essential for the understanding of the relationships between growth and reproduction as well as the constraints imposed upon seed production under different environments.

Silva (1978) found that in *Maianthemum canadense*, an herbaceous perennial abundant on the floor of the temperate forests of northeastern North America, the erect shoots behave as modular units exhibiting relative independence in their growth and reproductive activities. This paper reports on a study of the

demography of erect shoots¹ in populations of this species. The aim of this study is to analyze the shoot life history dynamics through time of several populations along a gently sloping hill-side.

Materials and Methods

The study was conducted at the Concord Field Station of Harvard University in Bedford, Massachusetts. The forest is very diverse, consisting basically of a mixture of deciduous hardwoods and coniferous evergreen trees. *M. canadense* is found in almost all forest stands at the Station, from wet to dry areas and from early secondary successions to older forests. In the spring of 1975, two 1 m² plots 0.5 m apart were demarcated at each of four different sites along a transect comprising several different forest habitats. These sites were designated A, B, C, and D, and the plots sequentially designated from 1 to 8. Permanent plots were not set up at the extreme wet end of the transect, but some sampling was conducted there (site E). A schematic view of the gradient is present in Fig. 1.

A metallic plotter (Abrahamson 1973) was positioned on top of the pipes and used to determine shoot coordinates. Within a subsection of each plot (0.25 m² in A and B; 0.40 m² in C and D) every shoot was marked with a numbered flag. In the remainder of the plot only reproductive shoots were marked by flags. Coordinates of the marked shoots were determined with the aid of a metallic plotter (Abrahamson 1973). Identifica-

¹ In this paper we will refer to the erect shoots simply as "shoots"

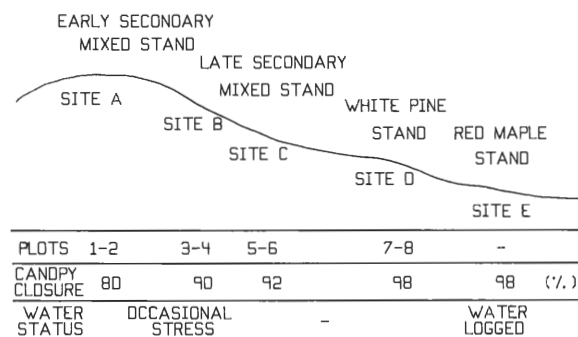


Fig. 1. Diagram of the study sites as a function of canopy closure and water status showing some ecological features, summarized from Silva (1978). Canopy closure is an estimate of the percent full sun reaching *M. canadense* after leaves on the deciduous trees had formed

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tion of new and old shoots was made quite easy with the marker flags and we feel that the frequency of misidentification was insignificant. All marked shoots were monitored from early spring to early fall at four week intervals from 1975 to 1977. From this relatively frequent sampling, it was determined that over 90% of the new shoots emerge before July; this justified a reduced monitoring regime in subsequent years. In 1978, populations were censused in May and August and in June in 1979 and 1980. Plots 1 and 2 were abandoned in 1979 and 1980. Extreme care was taken to minimize disturbance of the populations adjacent to the sample area because rhizomes could be growing into the plot from the surroundings.

A relatively unambiguous enumeration procedure was used to determine the rates of shoot formation and mortality. New shoots originated either from differentiation of the rhizome tip or seed germination. Seedlings could be readily identified by their characteristically small size (leaf length < 2 cm) and lack of rhizome. Mortality could only be detected with certainty at the beginning of each growing season when marked shoots fail to produce new leaves and visual inspection revealed no living tissue. In a few cases, "dead" shoots restarted growth from lateral buds, but they never persisted for more than one season.

Erect shoots of *M. canadense* exhibit a developmental pattern which can be used to determine their age and reproductive history. In any one growing season erect shoots may develop into either vegetative or sexual shoots. Vegetative shoots are characterized by a single leaf subtended by two, or less frequently, three bud scales. A bud, visible under low magnification, is formed in the axil of the leaf. The yearly production of lateral buds and leaf and bud scale scars is a consistent morphological key to the age of the erect shoot. Whereas the apical meristem remains in the bud of a vegetative shoot, the sexual shoot is the product of determinant growth of this meristem. Continuation of growth of these shoots is through lateral bud development. This lateral development is easily visible on the erect shoots.

Measurements of the daily photosynthetic active radiation were made several times on days with little or no cloud cover throughout the 1976 and 1977 growing seasons using LI-500/190M Integrators with quantum probes, LI-190s, (Lambda Instruments Co.). Soil moisture was measured gravimetrically in 1975 in 5 cm diameter cores. The depth of the cores (approx. 5 cm) corresponded to the root zone.

Results

Light and Water

Four measurements, each of 48 h duration, were made during sunny days from June to September at each of sites A through D. The average quantity of light reaching *M. canadense* decreased down the hill with 15% of full sun at site A and 5, 6, and 2% at sites B, C, and D respectively. Thus, there is a general decrease in light flux down the hillside.

Additional measurements of the daily light flux were made simultaneously at each plot in sites A and C at five points during the growing season (Fig. 2a). There was fairly good correspondence between the adjacent plots within these two sites. However, the positioning of the sensor within a plot, at least in site D, was found to be critical (Fig. 2b). At the level of *M. canadense* a two-fold difference in daily solar flux was recorded on certain days over a 0.5 m distance.

Soil moisture availability generally increased down the slope of the hill (Table 1), with site D experiencing little or no drought

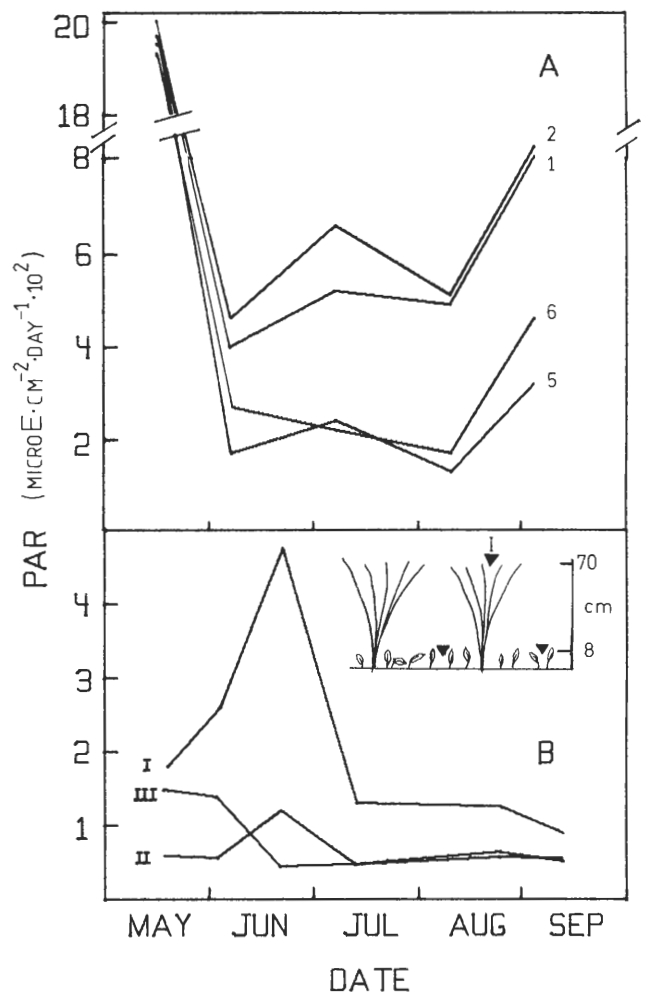


Fig. 2. A Photosynthetically-active radiation (*PAR*) measured simultaneously at site A (plots 1 and 2) and C (plots 5 and 6) during the 1977 growing season. B *PAR* at three locations (positions indicated in inset) in site D

Table 1. Soil moisture measured in 1975. *N*=2. Range is in parentheses

Site	May 22	June 25	July 22	August 27
g H ₂ O·g d.w. soil ⁻¹				
A	0.91 (0.06)	0.73 (0.33)	0.39 (0.11)	0.49 (0.20)
B	1.80 (0.29)	0.58 (0.00)	1.09 (0.41)	0.90 (0.30)
C	0.92 (0.13)	0.97 (0.05)	0.49 (0.04)	0.62 (0.18)
D	2.70 (0.01)	2.04 (0.12)	1.83 (0.87)	3.11 (0.53)

during the six years of observation. (Although no data was obtained for site E, it was the only site that experienced water-logging during the spring months.) Rainfall prior to these measurements was typical of the local climate with 1–3 cm falling within the two week period prior to measurement. Additional moisture estimations made in 1977 using gypsum blocks showed similar trends along the elevational gradient (Silva 1978).

Leaf Activity

Leaves emerged in early April when the average temperature was about 15 C. Population C emerged two weeks earlier than the others, but by the second week of May all populations were

indistinguishable in their phenological stage, with leaves fully spread and inflorescences well developed. The length of photosynthetic activity varied considerably within populations with the time of the onset of senescence ranging from mid-July to mid-September. The average length of the active period of leaves varied from year to year and also from population to population. Population D (plots 7 and 8) showed more longevous leaves and the least yearly fluctuations. Shoots under denser canopies and wetter soils had their leaves functioning for several weeks longer than those from drier, more open conditions.

Density, Formation and Mortality

Yearly summaries of density, mortality, and formation of shoots are presented in Fig. 3. Densities generally increased from the bottom of the hill to the top, paralleling the increase in daily solar irradiance and drought stress. Densities ranged from below 250 m^{-2} in plot 8 to greater than 800 m^{-2} in plots 2 and 3. The six year trend in density was not consistent among all plots. Plots 2, 3 and 4 showed fairly steady declines, plot 6 increased, whereas the others did not show a trend.

Because *M. canadense* is both rhizomatous and perennial, standardized measures of shoot formation and mortality give an indication of the average performance of shoots in the populations. Formations of new shoots are expressed as the percent of shoots in a population at y_0 that produced daughter shoots in y_1 {i.e. births (y_1)/density (y_0) \times 100}. Mortality was measured as the percent of shoots that did not emerge the following year. High year to year variation in percent formation and mortality was evident in nearly all plots (Fig. 3). Comparing sites B, C and D, the narrowest range was observed in site B, although it showed differences of up to twofold. Plot 5 exhibited a fivefold increase in percent formation from 1979 to 1980 but its putative "replicate", plot 6, showed a slight decline. There was no correlation between percent formation and percent mortality for pooled data.

To suggest the relevant spatial scale to which demographic parameters respond, the yearly trends in formation, mortality and density were tested for similarity among all plots and between adjacent plots within sites (Table 2). Chi-square tests showed no homogeneity among populations 1 and 2 from 1975–78 or population 3–8 from 1975–80. The behavior of the paired plots within sites was strongly heterogeneous for the three measures in site C; in sites A and D, the chi-squares for the numbers of new shoots were non-significant whereas in sites A and B the density chi-squares were non-significant. Coefficients of determination of the standardized measures of formation and mortality (from Fig. 3) were calculated to test the strength of the yearly trends between adjacent plots within each of the four sites (Table 2). In three sites the yearly trends in percent mortality were highly correlated ($r^2 > 0.85$) between plots. This contrasts with a general lack of correlation of the percent formation measurements made between adjacent plots.

The survivorship of individuals present in 1975 in the eight plots is presented in Fig. 4. The decay rates of these populations, expressed as the time to 30% survival, ranged from 1.5 years in plot 5 to 4 years in plot 4. There was no apparent sorting of site replicates in terms of average decay or degree of deviation from log-linearity.

Survivorship of uniform age cohorts from plots 3 to 8 (Fig. 5) also tended to be log-linear although in some years there are important deviations. A comparison of survivorship during the first two years of the three cohorts within each plot showed marked differences in all plots except plot 4, indicating that

Table 2. Significance of among-plot comparisons for density, mortality, and formation using chi-square analysis and coefficients of determination. Data are chi-squares (d.f.), significance^a, and r^2

Sites	Density	Formation	Deaths	% Formation	% Mortality
A-D 1975-78	133 (21) ***	44.9 (14) ***	303 (14) ***	--	--
B-D 1975-80	210 (25) ***	101 (20) ***	250 (20) ***	--	--
A 1975-78	5.68 (3) n.s.	1.86 (2) n.s.	6.41 (2) *	--	--
B 1975-80	3.27 (5) n.s.	10.2 (4) *	9.79 (4) *	--	--
C 1975-80	56.8 (5) ***	72.8 (4) ***	30.4 (4) ***	--	--
D 1975-80	32.6 (5) ***	8.45 (4) n.s.	79.4 (4) ***	--	--
	0.58	0.80	0.99	0.55	0.93
	0.91	0.31	0.82	0.25	0.88
	0.03	0.10	0.46	0.16	0.85
	0.36	0.02	0.11	0.27	0.06

^a * $p < 0.05$; *** $p < 0.001$

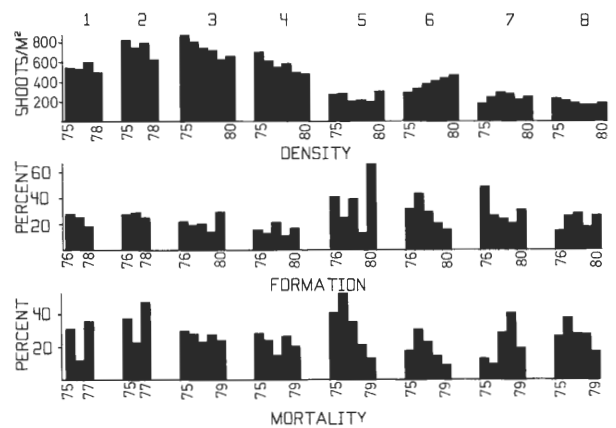


Fig. 3. Yearly variation in density, percent formation and percent mortality of shoots in the eight plots

survivorship was closely tied to environmental conditions and that age specific mortality rates had a relatively high variance.

Age Structure of Shoots

These results include site E, but do not include site B. Twelve years was the oldest age found among shoots (site C). The average age of each population is: A = 2.1; C = D = 2.9; and E = 3.4. To analyze the differences in age structure between populations, the samples from each site were pooled. The distributions are presented in Fig. 6. A non-parametric multiple comparison test based on Wilcoxon-Mann-Whitney statistics (Sokal and Rohlf 1969) was used to compare the four distributions. The age structure of population A was significantly different from the other three and was skewed to the left. The age structure of population E was also significantly different from the rest, with a more important representation of older ages. In both cases, the level

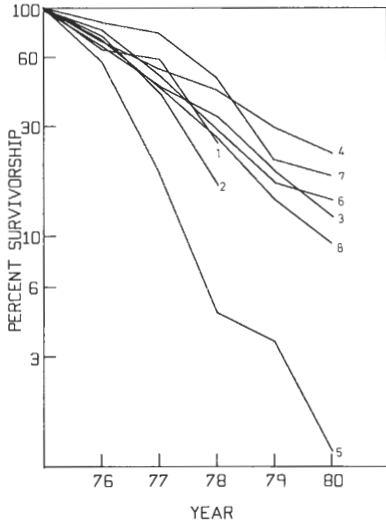


Fig. 4. Depletion curves for the 1975 mixed-age cohorts from plots 1-8

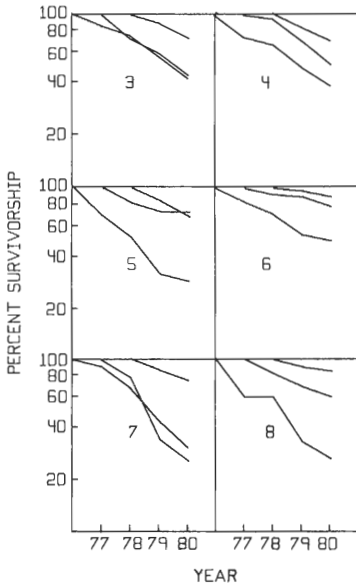


Fig. 5. Survivorship curves for new shoots formed in 1976, 1977 and 1978

of significance is $p < 0.05$. The age distributions of populations C and D did not differ significantly from each other, and were intermediate between the other two.

Reproductive Growth

Figure 7 shows the proportion of shoots that flowered each year and the number of fruits produced per flowering shoot for three years in each of the eight plots. Despite variations between years, there was a clear indication that populations from plots 5 and 6 (site C) and from plot 8 (site D) flowered more than those from the other plots during the period of study. In 1976 fewer shoots bloomed in all populations, but those shoots generally had more fruits.

The age distribution of flowering shoots is strongly dependent on the location of the population (Fig. 8). Flowering in population A was restricted to the first two-year classes and this was the only population in which one-year old shoots bloom. Popula-

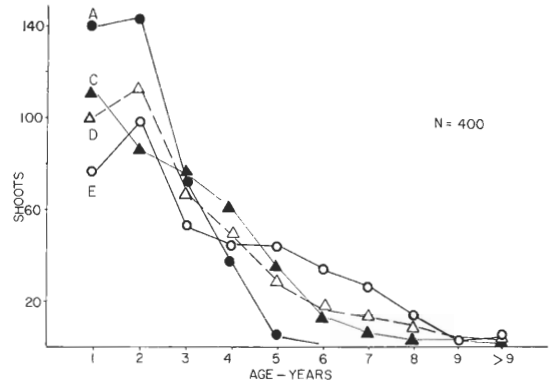


Fig. 6. Age-structure of four shoot populations in sites A, C, D, and E

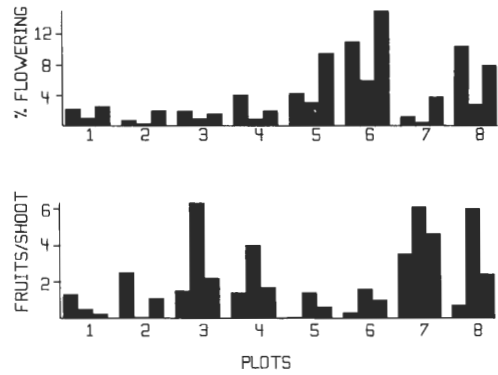


Fig. 7. Percent of the total population flowering and number of fruits produced per flowering shoot in each plot for each one of the three years, 1975-77

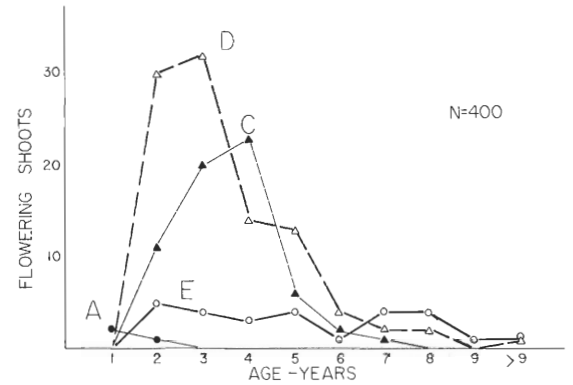


Fig. 8. Flowering schedule of each of the four populations (A, C, D, and E) expressed as number of flowering shoots in each age-class from a sample of 400 shoots

tion E showed a totally different schedule, with flowering evenly distributed throughout all ages, with the exception of the one-year class. As was the case with age-structure, the flowering schedules of populations C and D were very similar to each other, with peaks at the four-year class in population C and the three-year class in population D.

Table 3. Proportion of shoots formed before 1979 that initiated reproductive shoots at least once between 1975 and 1980

Site	Plot	Total # shoots	% that flowered
B	3	343	7
	4	254	8
C	5	165	12
	6	159	35
D	7	200	9
	8	154	12

Table 4. Number of shoots that were reproductive at least once before 1979 and flowered n years

Plot	n			
	1	2	3	4
3	35	2	0	0
4	49	1	0	0
5	35	6	0	0
6	73	29	7	1
7	14	3	0	0
8	28	11	1	0

The initiation of sexual shoots was only observed in a fraction of the shoots in the study site. A measure of that fraction for each of the six plots for which six years of data exist is presented in Table 3. Only shoots appearing before 1979, i.e. those which were three years old at the end of the study, were counted because of the low probability of finding reproductive shoots during the first two years of existence. The greatest proportion of shoots that flowered occurred in plot 6 and generally in site C. The drier and denser site B exhibited the lowest proportion of shoots that initiated sexual shoots at least once.

Individual shoots of *M. canadense* may flower more than once in their lifetime. The frequency of reproductive events weighs heavily on the potential for seed output by shoots. As shown in Table 4, of those shoots that flowered at least once, 2 to 33% flowered more than once. The proportion of shoots flowering multiple times depended on the plot. The most flowering occurrences in this sample was four times for one shoot in plot 6. The distributions in Table 4 are unfortunately but necessarily biased in two directions² but we feel that the general conclusions are not affected.

Discussion

The demographic components of the populations of *M. canadense* reported here operate on several different spatial scales. We have defined these as ranging from locality patterns that are similarly expressed across all sites, down to patterns that are determined across parts of meters, i.e. at the scale of the plots. These correlations to the spatial scale can allow us to formulate hypotheses concerning the causality of the responses.

The rate of initiation of flowering was the only response that was consistent among all plots. We were able to define so-called "good" years and "bad" years for this reproductive component. The relative number of fruits per reproductive shoot during three years was consistent across all sites except site A. This indicates that the initiation and fulfillment of sexual reproduction is susceptible to climatic and/or biological factors which overwhelm the hillside gradient. The cause of the inverse correlation between flowering percentage and fruit yield is unknown. Based on the architecture of *M. canadense*, we feel that resource limitation does not account for the depressed yield because the proportion of flowering shoots in the population is small. A more plausible explanation depends on pollinator availability. *M. canadense* is primarily, if not obligately outcrossed (Silva 1978) by *Bombus* spp. (personal observations). A change from year to year in the relative abundance of pollinators should be reflected in the fruit yield.

The average density of the plots increased with increasing irradiation and decreasing soil moisture. A similar trend was expressed by the average leaf area (Silva 1978) with the leaves in the moister sites being up to three times the area of the leaves at the top of the hill.

The change in density is a function of the mortality and formation rates. The mortality rates from year to year showed a certain fidelity toward the site location. This was not seen in the formation rates. The data support a view of alternative causalities of the two rates. Mortality is dependent on site characteristics, i.e. those which are distributed a few meters over the forest floor, whereas formation reflects factors specific to individual plots. Data do not exist which would allow us to define their respective causes.

There are however two possible, though not mutually exclusive, explanations for the lack of coordinated behavior between adjacent plots. The first involves the assumption of steady-state populations. *M. canadense* is a fairly vigorous woodland perennial. It can spread vegetatively across the forest floor quickly. It is not known whether the vigor of the individuals in the zones of invasion is different from that in stable or senescent zones as has been found by Watt (1947) for *Pteridium aquilinum*. We were not able to determine where, relative to population origins and directions of spread, the eight plots were located. Nor do we know the intensity of the gradient from mature, presumably steady-state sites to sites of colonization or senescence. If demographic differences result from differing levels of maturity, they may be measured over meters or parts of meters.

The lack of a correlation may also be due to microenvironmental heterogeneity. Light, water, and nutrients are known to be distributed very heterogeneously on and in forest soils through space and time (Anderson 1968; Usher 1970). Measurements show that soil moisture and light flux may differ within and between sites (Silva 1978; Table 1 and Fig. 2). It is possible that the light flux through the canopy, drainage patterns through the litter, and distribution and supply rates of nutrients, are sufficiently different across one or two meters to elicit concurrently different rates of formation and mortality of shoots in adjacent plots.

This hypothesis has important implications in the evolution of the architecture and development of rhizomatous plants because a single genet may experience large differences in the level of resources. *M. canadense* is a highly abundant herb in many E. Massachusetts woods. Moreover, it has a comparatively broad ecological amplitude (considerably broader than that presented here). The adaptability to large habitat differences may allow

² Because these data include the 1975 mixed-age cohort it is not known whether any of those shoots flowered prior to the start of the study. Also, those shoots still alive at the end of 1980 did not have their full life span recorded. We are not able to assess the direction and magnitude of these unknowns

this species to support relatively high densities across small scale environmental gradients. An important unanswered question is whether this behavior is supported primarily by phenotypic plasticity or genetic variability.

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