

# STUDIES ON THE POPULATION BIOLOGY OF THE GENUS *VIOLA*

## IV SPATIAL PATTERN OF RAMETS AND SEEDLINGS IN THREE STOLONIFEROUS SPECIES

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### SUMMARY

(1) The spatial pattern of demographic variables of ramets and seedlings in sixteen populations of *Viola blanda*, *V. pallens* and *V. incognita* were analysed using a variety of approaches (area and distance methods, G-tests of heterogeneity based on area counts, neighbourhood analysis, spatial autocorrelation) The variables considered were the position of ramets in space and time, emergence and mortality of ramets and seedlings

(2) Emergence of new seedlings is clumped in space The seedlings tend to be more numerous in areas where the overall ramet density is low, indicating that seed germination or seedling emergence or both are inversely correlated with overall density of ramets Seedling survival is affected by density

(3) Ramets one year-old or older appear to be aggregated or randomly distributed in space

(4) The pattern of emergence of new ramets from stolons and the pattern of ramet death is random in space and not density dependent

(5) It is proposed that seedling germination or survival or both are density dependent, but that the pattern of adult ramet distribution, vegetative production of new ramets and ramet mortality is more sensitive to environmental variables such as light, water and nutrients which are known to be unevenly distributed on the forest floor

(6) The concept of 'safe site' for seed germination has little predictive value in these populations of *Viola*

### INTRODUCTION

A large number of understorey herbs of the temperate forests of central, eastern and north-eastern North America are characterized by vegetative spread by rhizomes of different lengths and diameters (Sparling 1964, 1967, Bell 1974, Abrahamson 1975, Anderson & Loucks 1975, Sohn & Policansky 1977, Bell & Tomlinson 1980, Silva, Kana & Solbrig, in press) The prevalence of species with the same growth pattern in the forest understorey is probably an indication that this growth pattern is especially well suited to the forest environment

Vegetative spread and its possible adaptive significance has been discussed by Bell (1974, 1976), Harper & White (1974), Harper (1977), Bell, Roberts & Smith (1979), Harper & Bell (1979), and Bell & Tomlinson (1980) According to these authors, vegetative spread is much more economical than seed dispersal in removing the daughter plant from the competitive influence of its parent There are, of course, inherent costs such as the lack of genetic recombination and reduced ability to disperse to far-away places

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Many species have precise rhizome branching patterns while others have a more 'opportunistic' pattern of growth (Bell & Tomlinson 1980). Species of violet that spread by stolons (slender, underground rhizomes) belong to this last group. Stolons in violets are formed from axillary leaf buds and grow for an indeterminate distance before the apical meristem bends upward and produces a short shoot with leaves and reproductive structures. From the axil of one or more leaves of the new ramet, new stolons may be produced that repeat the process. The direction of the new stolon bears no relation to that of the parent one.

One approach to the study of the adaptive nature of vegetative spread is to analyse the architecture of rhizome growth. Another is to investigate the distribution of ramets in two dimensional space and its variation in time. The second of these approaches is particularly suitable for violets because both rhizome length and branching angle vary unpredictably. In this, the fourth article on the population biology of species of eastern North American violets, we describe the spatial distribution of ramets and seedlings and of birth, death and plant size of three closely related species, *Viola blanda* Wild, *V. pallens* Brainerd and *V. incognita* Brainerd, and their change in time. This study complements a demographic analysis of these species (Newell, Solbrig & Kincaid 1981).

## MATERIALS AND METHODS

Sixteen populations of three related stoloniferous species, *Viola blanda*, *V. pallens* and *V. incognita*, were studied at three different localities: seven populations on the Island of Newfoundland, five populations in Massachusetts and four populations in western North Carolina (Table 1, Fig. 1). All the plots contained very few plants other than violets.

At each site plots were established. These differed in size from 25 × 50 cm to 100 × 100 cm according to the density of ramets. The plots in Massachusetts were visited at fortnightly intervals during a 4-year period (1976–1979) while the ones in Newfoundland were visited only once or twice during the study, and the ones in North Carolina were visited at 2–4 week intervals during one year (1979).

For each ramet in a plot the spatial coordinates were obtained and at each visit presence or absence and, if present, the number of leaves and number of reproductive structures were recorded. For those plots where results from more than one year are available, the pattern of births and deaths was analysed. In the Massachusetts plots, seedlings were studied as well.

Four different methods were chosen to determine the spatial distribution of seedlings, old and new emerging ramets and deaths: (1) spatial analysis using both area and distance methods, (2) *G*-tests of heterogeneity in the vicinity of new and dead plants compared to that around survivors, (3) correlation of individual ramet size with a variety of neighbourhood variables (neighbourhood analysis), (4) spatial autocorrelation of ramet size.

### *Spatial analysis (area and distance methods)*

Only intensity of spatial pattern (i.e. measures of density, cover or biomass) and not of grain (i.e. patch size) were computed (Pielou 1977). Preliminary results using hierarchical analysis of variance (i.e. block-size analysis—Greig-Smith 1952, Kershaw 1957, Ripley 1978) showed no evidence of patchiness within these populations. Five measures of spatial pattern were used. We consider them in turn.

TABLE 1 Plot identity number, locality, plot size and size of populations of three species of *Viola* studied

Plot number	Locality	Plot size (cm)		Population in 4 years			
				1976	1977	1978	1979
<i>Viola blanda</i>							
111	Harvard Forest, Petersham, Massachusetts	100 × 100	Total	113	113		
			New ramets		40		
			Dying ramets	40			
113	Harvard Forest, Petersham, Massachusetts	100 × 100	Total	115	138	58	25
			New ramets		24	7	
			Dying ramets	31	61	35	
			Seedlings		30		
			Dying seedlings		28		
122	Harvard Forest, Petersham, Massachusetts	100 × 100	Total	179	257	156	58
			New ramets		80	26	
			Dying ramets	20	115	121	
			Seedlings		18		28
			Dying seedlings		18		
131	Concord Field Station, Bedford, Massachusetts	100 × 50	Total	140	233	225	291
			New ramets		79	55	124
			Dying ramets	36	52	66	
			Seedlings		50	9	24
			Dying seedlings		20		
132	Concord Field Station, Bedford, Massachusetts	100 × 50	Total	99	166	154	307
			New ramets		69	21	74
			Dying ramets	22	28	24	
			Seedlings		20	7	113
			Dying seedlings		12		
191	Coweeta Experiment Forest, North Carolina	100 × 50	Total				111
192	Coweeta Experiment Forest, North Carolina	100 × 50	Total				39
193	Balsam Gap, Blue Ridge Parkway, North Carolina	50 × 50	Total				65
<i>Viola pallens</i>							
481	Parson's Pond, Newfoundland	50 × 50	Total			127	
482	Badger Alder Thicket, Newfoundland	50 × 50	Total			17	
491	Lake Powhatan, North Carolina	50 × 25	Total				106
<i>Viola incognita</i>							
681	Parson's Pond, Newfoundland	100 × 50	Total			40	
682	Birchy Alder Thicket, Newfoundland	50 × 50	Total			111	
			Dying ramets			29	
683	Birchy Alder Thicket, Newfoundland	100 × 50	Total			66	
			Dying ramets			13	
684	Badger Alder Thicket, Newfoundland	50 × 50	Total			105	
			Dying ramets			5	
685	Badger Alder Thicket, Newfoundland	50 × 50	Total			34	

*Variance/mean quotient, V/M*

The mean number of plants and the variance in circles of 8-cm radius around 100 random points (at least one radius from the plot border) were calculated. The radius of 8 cm was chosen to be large enough to include several plants and small enough to be able to take large numbers of samples within a plot. Computer simulations showed that overlap of

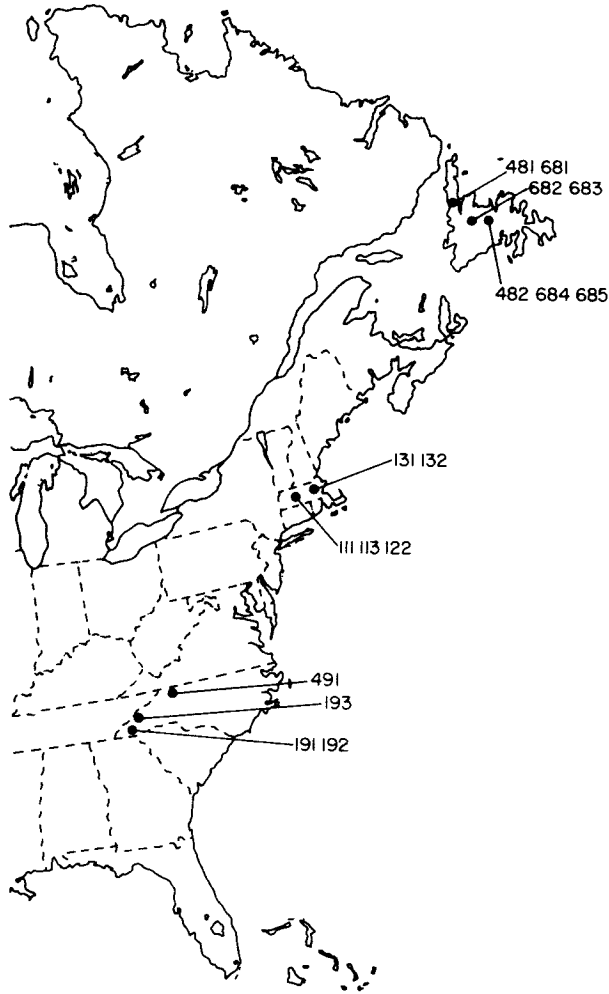


FIG 1 Location of the study-populations of *Viola blanda*, *V. pallens* and *V. incognita*. The three-digit numerals identify plots. Further details are given in Table 1

the circles, which occurred most often in the small plots, did not change the significance level of the tests. The dispersion index  $\{\sum_{i=1}^n (x_i - \bar{x})^2 / \bar{x}\}$  which approximates the distribution of  $\chi^2$  with  $n - 1$  degrees of freedom (Skellam 1952) was used to test the significance of deviations from randomness.

#### *Fit to the Poisson distribution*

*G*-tests (Sokal & Rohlf 1969), with (*G*<sub>adj</sub>) and without (*G*) adjustment for continuity, were used to compare the frequency distribution of plants in circles of 8-cm radius around 100 random points (again, at least one radius from the plot border) with the Poisson distribution.

#### *Pielou Index, $\alpha$* (Pielou 1959, Mountford 1961)

For 100 random points in each population,  $\alpha = \pi d \bar{w}$ , where  $d$  = density,  $\bar{w}$  = mean square of  $n$  distances from a random point to the nearest neighbour was calculated. To test

the significance level for the departure from random expectation ( $\alpha = 1.0$ ), a  $\chi^2$  test was used (Skellam 1952)

*Hopkins Index, A* (Hopkins 1954)

This is given by  $A = \sum_{j=1}^n P_j^2 / \sum_{j=1}^n I_j^2$  where  $P_j$  = distance from a random point to the nearest individual, and  $I_j$  = distance from a random plant to its nearest neighbour. To satisfy the assumptions of the Poisson distribution, the areas swept in searching for the nearest plant around random points and plants, respectively, must be independent. This reduces the sample size to approximately one-third of the total population. Significant departure from expectation ( $A = 1.0$ ) was determined by using the tables of the incomplete beta-function (Pearson 1934) for sample sizes below fifty and the tables of the normal curve probability integral (Pearson 1914) otherwise.

*Hill Index,  $\iota$*  (Hill 1973)

This is given by the formula  $\iota = (\text{variance} - \text{mean}) / (\text{mean})^2$ . It has the important property of remaining roughly constant under random thinning. Simulations were run using randomly distributed individuals to study the variability of  $\iota$  under random thinning.

*Tests of heterogeneity (based on area counts)*

In order to detect the influence of neighbours on birth and death of ramets and seedlings, the density of individuals within a circle of given radius around new plants or around plants which had died during the same year was calculated. New plants or plants that had died in previous years were excluded. These frequency distributions of density were compared with similarly obtained distributions for plants of the mixed-age cohort that survived from the previous year in the case of new plants, or around plants of that cohort still alive in the following year in the case of deaths. The comparison was made with the  $G$ -test of heterogeneity (Sokal & Rohlf 1969). Similar calculations were made using the number of leaves—a measure of plant size—in circles of given radius. In addition, circles of different radius were used in all computations. Age effects on mortality were studied in similar fashion: the age distribution of surviving plants was compared with the age distribution of plants that had died during the same year.

*Correlation between individual plant size and measures of interference (neighbourhood analysis)*

Around each plant (excluding those within one radius of the plot border) circles were drawn, and within each circle the number of plants, their distance from the centre and their size (measured by the number of leaves) were used to calculate five different interference measures:

$$(1) \sum_{j=1}^n \frac{S_j \cos d_j}{S_{\max}}, \quad (2) \sum_{j=1}^n S_j / S_{\max}, \quad (3) \sum_{j=1}^n 1/d_j,$$

$$(4) \sum_{j=1}^n 1/d_j^2, \quad (5) \sum_{j=1}^n S_j / (d_j^2 S_{\max}),$$

where  $d_j$  = distance of the individual to the centre of the circle (in cm),  $S_j$  = number of leaves on the  $j$ th plant,  $S_{\max}$  = maximum observed number of leaves per plant in the population,  $n$  = number of plants within a circle. The interference measures were chosen

according to results reported by Ross & Harper (1972), Harper (1977), Mack & Harper (1977), Antonovics & Levin (1980) and personal observations of violet populations

### *Spatial autocorrelation*

Spatial autocorrelation analysis tests whether the observed value of a nominal, ordinal or interval variable at one locality is independent of the values of the variable at neighbouring (not necessarily adjacent) localities (Sokal & Oden 1978a,b) The distance between pairs to be correlated must be chosen and different weights may be used

Two autocorrelation coefficients have been calculated Moran's (1950)  $I$  and Geary's (1954)  $c$  These are given by

$$I = \frac{n \sum_{k=1}^n \sum_{j=1}^n w_{kj} z_k z_j}{W \sum_{j=1}^n z_j^2}$$

$$c = \left( \frac{n-1}{2W} \right) \frac{\sum_{k=1}^n \sum_{j=1}^n w_{kj} (x_k - x_j)^2}{\sum_{j=1}^n z_j}$$

where  $z_j = x_j - \bar{x}$ ,  $x_k$  = value of variable  $x$  for locality  $k$ ,  $x_j$  = value of variable  $x$  for locality  $j$ ,  $\bar{x}$  = mean of  $x$  for all localities,  $w_{kj}$  = weight given to the edge between localities  $k$  and  $j$ , and  $W = \sum_{k=1}^n \sum_{j=1}^n w_{kj}$

The value of  $I$  ranges between  $-1.0$  (maximum negative autocorrelation) and  $+1.0$  (maximum positive autocorrelation) with  $-(n-1)^{-1} \approx 0$  (if  $n$  is sufficiently large) for no autocorrelation The values of  $c$  range between  $0$  (maximum negative autocorrelation) and an undefined large positive value The expected value for no autocorrelation is  $1.0$

For the computation, the number of leaves per plant was used as the variable  $x$  Connections were established by joining every plant in the population with every plant at a chosen range of distances The weight applied to a pair of connected plants was  $1.0$ , as no justifiable function of plant interaction is known In some cases, other weights (functions (1) and (4) of the neighbourhood analysis) were used in addition By calculating the spatial autocorrelation coefficient for a sequence of distance ranges, correlograms were obtained which might reveal the size of patches of similar sized plants, if there were such patches The behaviour of the indices was also followed through time

Statistical tests (Cliff & Ord 1973) for the significance of the departure of the indices from expectation were used These calculations were performed under assumptions of random distribution of data The results of these tests were then compared with computations of the variability of plant size (mean, standard deviation, coefficient of variation) in a given year and through time, as well as with maps of distributions of plant size in space and through time

## RESULTS

### *Spatial analysis*

The principal objective of this analysis is to learn whether there is a discernible spatial pattern to the distribution of plants in the populations studied We asked that question for

the entire population, for ramets of different sizes, for new ramets, for new seedlings, for dying ramets and for dying seedlings

### *Spatial distribution of all ramets in space and through time*

Different indices gave different results (Table 2) This shows that it is dangerous to rely on just one index to determine spatial distributions Recent comparisons of different area

TABLE 2 Measures of pattern intensity and significance level of their departure from randomness for adult plants of three species of *Viola* in sixteen plots Results for only one year in each plot are presented,  $n = 100$  except for Hopkins Index †

Plot number	Year	V/M Index	G	Poisson Gadj	d f	Pielou Index, $\alpha$	Hopkins Index, $A$	$n$
<i>V. blanda</i>								
111	1977	1.46**	18.7**	13.3	7	1.22**	1.88**	43
113	1977	2.75***	86.3***	67.5***	11	1.91***	1.98***	53
122	1977	2.19***	51.0***	32.3**	15	1.70***	1.15	67
131	1977	2.14***	69.5***	47.7***	24	2.76***	1.00	45
132	1977	2.33***	67.3***	47.8***	21	2.02***	1.08	65
191	1979	1.11	21.1*	13.7	12	1.36***	1.71***	39
192	1979	1.80***	35.9***	28.6***	7	1.28***	1.88	16
193	1979	2.14***	62.3***	39.1***	16	1.86***	1.20	18
<i>V. pallens</i>								
481	1978	2.52***	88.9***	57.2***	25	3.33***	1.02	31
482	1978	3.96***	173***	156.8***	9	2.15***	—	—
491	1979	0.83	23.2	16.9	30	5.26***	1.13	17
<i>V. incognita</i>								
681	1978	0.90	3.8	5.3	4	1.75***	0.93	7
682	1978	2.33***	90.0***	56.2***	26	2.67***	0.90	28
683	1978	3.44***	126***	77.0***	19	1.22**	1.09	25
684	1978	2.16***	70.0***	43.3**	21	2.54***	0.65	27
685	1978	2.29***	51.4***	28.2*	13	0.94	1.08	13

† d f for V/M Index are 99, d f for Pielou Index are 200 for Tables 2–7 Probability levels are indicated in all tables as follows \*,  $P \leq 0.05$ , \*\*,  $P \leq 0.01$ , \*\*\*,  $P \leq 0.001$ , no asterisk for  $P > 0.05$ ,  $n$  = sample size in all Tables

and distance methods (Holgate 1965, 1972 Diggle, Besag & Gleaves 1976, Goodall & West 1979, Byth & Ripley 1980) indicate that the Hopkins Index,  $A$ , is the most reliable, except where the aggregation is slight only Two general conclusions can be reached

First, populations of individual plants are either aggregated or randomly distributed (Table 2, Fig. 2) Random distribution means that no evidence of departure from randomness is found (despite our large sample sizes) The dispersion Index, V/M (and also the Pielou Index,  $\alpha$ ) show in many cases significant aggregation of individual ramets, but only 14% of the populations studied (four out of twenty-nine) show significant aggregation with all indices No case of significant regular dispersion was observed There are no obvious differences among the three species analysed

The Harvard Forest, Massachusetts populations of *V. blanda* are the most aggregated Nine out of ten cases show positive aggregation if the dispersion Index alone is used, and five out of ten show positive aggregation with all indices. On the other hand, the *V. blanda* and *V. pallens* populations from North Carolina show the least aggregation as only two out of four show positive aggregation with the dispersion Index, and none show positive aggregation with all indices As sample sizes were sufficiently large, differences in density have no influence on the results

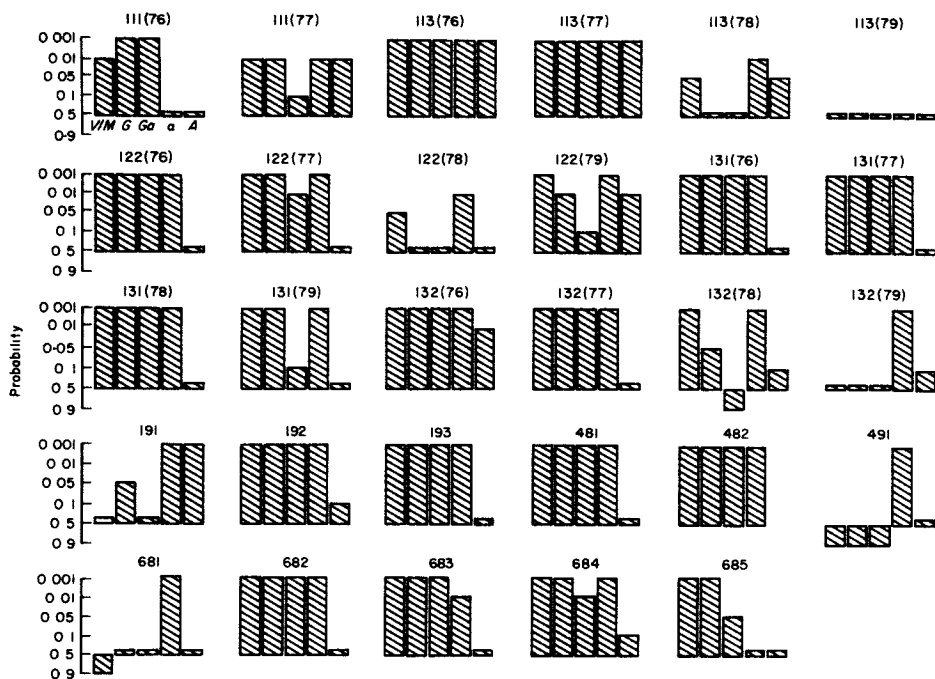


FIG 2 Results of tests with five indices for deviations from randomness of pattern. From the left the columns represent  $V/M$ ,  $G$ ,  $Gadj$ , Pielou and Hopkins Index, represented as  $V/M$ ,  $G$ ,  $Ga$ ,  $\alpha$  and  $A$  respectively. For details, see text. Bars above 0.5 indicate aggregation, below 0.5 regularity. Above each set of five tests, the three-digit number is the identity of the plot (and population). The number in parentheses represents the year. The vertical scale is integral and non-linear.

Secondly, thinning (i.e. ramet mortality) within populations is random, that is, it is not concentrated in any area of the population. When a particular (mixed age) cohort is followed through time (Table 3), no significant differences in the spatial distribution of surviving plants can be detected (compared with random thinning in computer simulations) even though a trend towards a decrease in the values of the  $V/M$  and Pielou Index,  $\alpha$ , is present which indicates a very slight tendency towards a more even spatial distribution of surviving ramets. Nevertheless, the changes in Hill's  $i$  are not greater than values obtained

TABLE 3 Measures of pattern intensity of mixed age cohorts of adults of two species of *Viola* followed through 4 yr. Only one time series for each plot is presented,  $n$  (sample size) = 100, — indicates no record made

Plot number	$V/M$				Pielou Index, $\alpha$				Hill Index, $i$			
	1st year	2nd year	3rd year	4th year	1st year	2nd year	3rd year	4th year	1st year	2nd year	3rd year	4th year
<i>V. blanda</i>												
111	1.41	1.72	—	—	1.04	1.21	—	—	0.17	0.47	—	—
113	2.34	2.50	1.45	1.00	1.72	1.50	1.02	0.87	0.61	0.96	0.67	0.00
122	2.60	2.32	1.48	1.22	1.33	1.22	1.37	1.16	0.37	0.34	0.26	0.70
131	2.19	1.96	2.23	2.34	1.67	1.58	1.52	1.59	0.21	0.25	0.42	0.70
132	3.05	2.52	2.41	2.24	1.83	1.47	1.25	1.23	0.46	0.43	0.44	0.42
<i>V. incognita</i>												
682	2.33	2.21	—	—	2.67	2.30	—	—	0.15	0.19	—	—
683	3.44	4.79	—	—	1.22	2.83	—	—	0.79	1.49	—	—
684	2.16	2.20	—	—	2.54	2.44	—	—	0.12	0.13	—	—



in computer simulations using randomly distributed individuals and random thinning. Also the percentage of populations showing aggregation, when the spatial distribution of surviving plants is analysed, indicates random distribution of deaths from year to year. There are no differences between the species analysed.

*Spatial distribution of ramets of different sizes in space and through time*

For this study (Table 4), the population was arbitrarily divided into 'large' ramets (approximately the upper 10–30% of the population in terms of number of leaves) and

TABLE 4 Measures of pattern intensity and significance level of their departure from randomness for different sized adult plants of three species of *Viola* in fifteen plots. Results for one year of observation only are presented,  $n = 100$  except for Hopkins Index. Plant size is measured by the number of leaves. The sizes tested overlap: a plant with 3 leaves is included in both the  $\leq 3$  and  $\geq 3$  categories.

Plot number	Year	Plant size (leaves)	V/M Index	G	Poisson Gadj	df	Pielou Index, $\alpha$	Hopkins Index, $A$	$n$
<i>V. blanda</i>									
111	1977	$\leq 3$	1.58***	21.1**	14.8*	7	1.19*	1.60*	39
		$\geq 3$	1.15	2.6	0.4	4	1.10	2.95**	15
113	1977	$\leq 3$	2.36***	56.0***	42.8***	10	1.77***	2.61***	49
		$\geq 3$	1.89***	28.1***	21.7***	5	2.10***	2.73*	9
		$\geq 4$	1.60***	13.3***	10.2*	3	1.99***	—	—
122	1977	$\leq 3$	1.80***	32.5*	16.6	13	1.29***	1.13	64
		$\geq 3$	1.70***	30.9**	20.6*	11	1.25**	1.30	52
		$\geq 4$	1.13	3.1	0.7	5	0.97	1.67	21
131	1977	$\leq 3$	1.86***	40.8**	26.3	18	2.13***	1.59**	46
		$\geq 4$	1.53***	29.2***	21.2***	7	1.46***	1.14	16
		$\geq 5$	1.18	6.1	4.1	3	1.85***	—	—
132	1977	$\leq 3$	1.55***	24.6*	12.8	13	1.16*	1.38	36
		$\geq 4$	1.70***	36.9***	28.2***	10	1.35***	1.86**	29
		$\geq 5$	0.96	8.3	7.7	4	0.86	0.90	11
191	1979	$\leq 3$	1.31*	19.6	12.9	12	1.39***	2.10***	37
		$\geq 3$	0.72	14.6*	11.2	6	0.79	0.78	11
192	1979	$\leq 3$	1.86***	34.6***	26.3***	7	1.25**	3.16***	14
		$\geq 3$	1.13	9.6*	6.5	3	0.87	2.13	7
193	1979	$\leq 3$	1.70***	34.8***	23.5*	12	1.45***	1.50	16
		$\geq 3$	1.84***	34.9***	28.4***	8	1.85***	2.23	7
		$\geq 4$	1.87***	41.7***	38.3***	4	2.05***	—	—
<i>V. pallens</i>									
481	1978	$\leq 3$	2.21***	75.8***	55.2***	21	2.62***	1.27	27
		$\geq 4$	1.28*	23.9***	20.8***	4	1.54***	—	—
		$\geq 5$	1.15	14.4***	12.6*	4	1.07	—	—
491	1979	$\leq 3$	1.17	53.6**	38.4	29	4.67***	1.06	17
		$\geq 3$	1.26*	41.4***	35.9***	4	0.76	—	—
<i>V. incognita</i>									
681	1978	$\leq 2$	0.85	5.4	6.8	3	1.66***	1.16	7
		$\geq 2$	1.00	4.4	2.8	2	1.71***	—	—
682	1978	$\leq 2$	2.31***	78.9***	42.5*	25	2.41	1.50	26
		$\geq 2$	1.75***	38.1***	28.1**	13	1.55***	2.08	12
683	1978	$\leq 3$	4.87***	168***	107***	19	1.44***	1.71	18
		$\geq 4$	1.32*	12.5*	8.6	4	1.15*	1.38	7
		$\geq 10$	1.36**	7.2	3.3	3	1.13*	—	—
684	1978	$\leq 2$	2.13***	69.7***	48.7***	21	2.47***	0.70	27
		$\geq 2$	0.78	17.4*	13.5	9	0.98	1.30	12
685	1978	$\leq 3$	1.85***	30.7***	15.6	11	0.86	1.61	11
		$\geq 3$	0.88	2.4	3.5	5	0.82	1.01	5

'small' ramets, or into 'very large', 'large' and 'small' ones. The reason for the separate analysis of size classes is the significant advantage that large plants have both in terms of survival and fecundity (Newell, Solbrig & Kincaid 1981). No significant differences in the pattern of distribution of different sized plants could be detected, however, either on a geographical or time series basis although the index values for larger plants are in a majority of cases slightly smaller than are the values for smaller plants of the same population. Thinning is random also for plants of similar size (results not shown here)

#### *Spatial distribution of new ramets*

A large majority of the index statistics (Table 5) fail to show evidence of non-randomness in space of the sites of new ramets in all populations. No change in the spatial distribution of survivors occurred with time (results not shown here)

TABLE 5 Measures of pattern intensity and significance level of their departure from randomness for new ramets of *Viola blanda* in five plots,  $n = 100$  except for Hopkins Index

Plot number	Year	V/M Index	G	Poisson Gadj	df	Pielou Index, $\alpha$	Hopkins Index, $A$	$n$
111	1977	0.87	3.3	2.8	3	1.08	0.58	13
113	1977	0.94	2.0	2.0	2	1.32***	1.74	9
	1978	1.40**	8.7*	5.8	2	1.39***	—	—
122	1977	1.00	11.2	7.4	5	1.15*	1.16	30
	1978	0.96	3.0	2.2	4	0.93	0.91	9
131	1977	2.74***	93.4***	71.0***	12	1.67***	2.13**	28
	1978	1.04	12.0	8.5	6	1.10	2.09	17
	1979	2.81***	111***	76.3***	24	2.08***	1.43	33
132	1977	0.84	5.5	3.5	8	0.95	0.93	30
	1978	0.92	3.1	3.3	3	1.19*	0.92	5
	1979	1.40**	21.8**	17.8*	8	1.70***	1.79*	21

#### *Spatial distribution of seedlings*

Significant aggregation was detected (Table 6) in the distribution of seedlings in most populations analysed, and no significant change in the distribution of survivors occurred on the five time sequences observed (results not shown here)

#### *Spatial distribution of deaths*

Sufficient results (three years) exist only for the Massachusetts populations, the sample

TABLE 6 Measures of pattern intensity and significance level of their departure from randomness for seedlings of *Viola blanda* in four plots,  $n = 100$  except for Hopkins Index

Plot number	Year	V/M Index	G	Poisson Gadj	df	Pielou Index, $\alpha$	Hopkins Index, $A$	$n$
113	1977	2.24***	41.1***	34.5***	5	1.70***	4.29***	12
	1979	1.81***	17.3***	12.1***	2	3.11***	—	—
122	1977	1.28*	4.7	1.1	3	3.57***	4.73***	7
	1979	1.75***	21.2***	11.8*	5	3.72***	2.84***	13
131	1977	4.14***	205***	167***	14	2.15***	3.56**	17
	1978	1.38**	24.2***	21.2***	2	1.31***	—	—
	1979	2.83***	86.2***	72.4***	7	1.99***	5.33***	6
132	1977	1.75***	22.6***	15.1***	5	1.75***	—	—
	1978	1.73***	25.1***	22.1	3	1.24**	—	—
	1979	0.93	13.0	9.4	9	1.52***	1.15	29

TABLE 7 Measures of pattern intensity and significance level of their departure from randomness of (a) dying ramets and (b) dying seedlings of two species of *Viola* in eight plots,  $n = 100$  except for Hopkins Index

Plot number	Year	V/M Index	G	Poisson Gadj	d f	Pielou Index, $\alpha$	Hopkins Index, $A$	$n$
(a) Dying ramets								
<i>V. blanda</i>								
111	1976	0.79	8.5*	9.5*	3	1.02	2.73**	15
113	1976	1.57***	13.8***	9.7*	4	1.18*	1.37	11
	1977	2.40***	56.6***	43.2***	7	2.04***	5.95***	24
	1978	1.16	5.6	2.6	3	1.47***	2.11	13
122	1976	1.88***	21.1***	11.7*	5	1.34***	0.82	8
	1977	2.19***	60.5***	48.0***	10	1.01	1.09	47
	1978	1.44**	16.7	7.5	9	1.06	1.51*	48
131	1976	1.80***	40.4***	29.6***	8	1.04	2.09***	14
	1977	2.09***	40.6***	29.3***	9	1.44***	1.38	19
	1978	2.08***	45.0***	32.2***	12	1.50***	1.66	22
132	1976	1.38**	10.7*	8.8	4	1.12	1.84	5
	1977	1.08	10.1*	9.4	4	0.86	0.50	10
	1978	1.74***	26.1***	18.9**	6	1.11	3.74**	10
<i>V. incognita</i>								
682	1978	2.21***	52.5***	41.0***	10	1.20*	1.73	8
683	1978	2.04***	56.2***	37.7***	4	2.94***	—	—
684	1978	0.84	2.2	2.9	2	0.87	—	—
(b) Dying seedlings								
<i>V. blanda</i>								
113	1977	2.04***	30.3***	19.6***	5	1.58***	4.68***	11
122	1977	1.28*	4.7	1.1	3	3.57***	5.77***	7
	1978	0.90	1.3	1.2	1	0.71	—	—
131	1977	5.85***	156***	119***	12	2.51***	21.06***	9
	1978	1.41**	20.1***	17.1***	2	0.82	—	—
132	1977	1.37**	11.4**	7.5	3	1.64***	—	—
	1978	2.00***	35.2***	31.0***	3	0.99	—	—

sizes of the Newfoundland population were too small for definite statements. For the populations analysed (Table 7), the distribution of dying ramets in space is not different from that of all ramets. The spatial distribution of dying seedlings is mostly aggregated as were the seedlings themselves.

### Tests of heterogeneity

The principal objective of this analysis is to learn whether there is an effect of the density of neighbouring ramets within a given circle on birth and death of individual ramets or seedlings or both. Either the number of plants present in a given year or the number of leaves per plant was used for calculating the density within the circles.

### Effect of density on births

When seedlings and new ramets are considered together (Table 8, Fig 3(a)), no significant difference in the 'average' density of neighbours within circles of different radii surrounding new plants and established plants could be detected. If ramets alone are considered, the same results are obtained. Of 160 tests (radii of 3, 5, 8 and 10 cm) only 17 showed significant heterogeneity at  $P \leq 0.05$  (results not shown here). When seedlings are considered by themselves, however, in those cases where the sample size is over 30, a significant difference between seedlings and ramets is found (Table 8). In effect, seedlings emerge mostly in areas where ramet density is low, usually where there are no or

TABLE 8 Heterogeneity *G*-tests comparing the frequency of plants of *Viola* present in a given year in a circle of given radius around plants at least 1 yr-old with those around seedlings born in that year See text for further details

Plot number	Year	Number of adults	Number of seedlings	Plant number considered alone		Plant size considered also	
				<i>G</i>	df	<i>G</i>	df
(a) Radius = 3 cm							
113	1977	99	29	4.5	3	13.5	10
122	1977	221	17	1.6	4	15.0	12
	1979	26	28	1.3	1	1.3	1
131	1977	154	41	20.8***	7	36.4*	20
	1979	211	20	12.9	8	21.0	20
132	1977	134	15	5.4	5	18.9	16
	1979	170	100	13.6*	5	23.6	20
(b) Radius = 5 cm							
113	1977	97	27	9.8	6	20.8	18
122	1977	209	16	11.7	9	19.0	25
	1979	25	28	11.0**	2	11.2*	4
131	1977	139	29	42.4***	15	63.3*	42
	1979	186	17	30.4*	17	44.4*	31
132	1977	128	14	9.1	9	28.7	30
	1979	154	84	18.2**	9	35.7	31
(c) Radius = 8 cm							
113	1977	83	24	28.6***	10	32.1*	20
122	1977	195	14	15.5	14	26.9	45
	1979	22	26	4.3	3	4.9	5
131	1977	118	35	59.9***	23	103***	67
	1979	146	13	29.6	32	41.0	65
132	1977	119	11	15.2	18	40.4	55
	1979	135	59	22.2	17	80.4*	58

only one or two violet ramets within a 3- or 5-cm radius circle (Fig 3(a)) When the density of ramets surrounding 1-yr-old seedlings is compared to the density of ramets surrounding all other ramets, no significant difference can be detected, indicating that the 'open' spaces where seedlings emerged are filled within the year by new ramets or seedlings or both (results not shown here) Considering plant size and plant number rather than plant number alone within circles does not affect the results

#### *Effect of density on deaths*

Ramet death appears to be independent of the density of surrounding ramets (Table 9, Fig 3(b)) as there is no significant difference in the density of ramets in circles surrounding living and dying ramets in all populations and years analysed and for circles of different sizes Only 11 out of 128 tests showed significant differences at  $P \leq 0.05$  (results not shown here)

There is, however, some effect of the density of neighbours on the mortality of seedlings in cases where the density of seedlings is sufficiently high (Table 9) The results are similar if the size of neighbours is considered also

Age has no influence on the mortality of ramets, though it has on seedlings A high proportion die during the first year (results not shown here) This confirms the results of Newell, Solbrig & Kincaid (1981)

#### *Correlation between individual plant sizes and measures of interference (neighbourhood analysis)*

The objective in this part of the analysis is to see how much of the variance in plant size

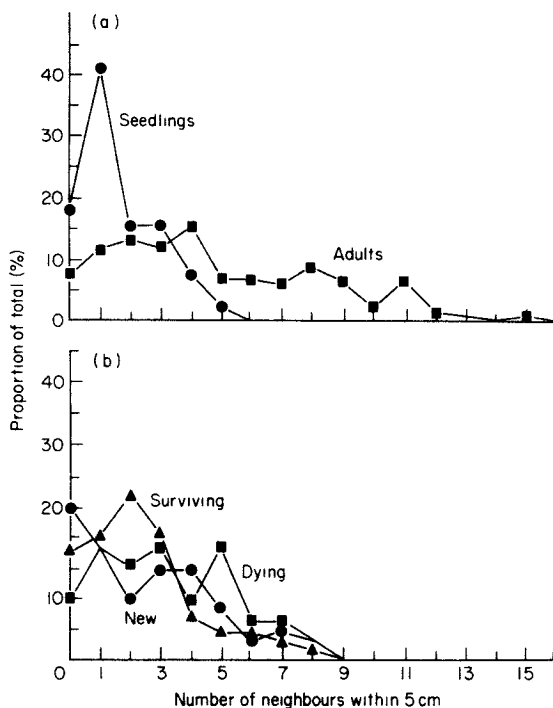


FIG 3 Distribution of number of plants of *Viola blanda* in 1977 in plot 131 within circles of 5 cm radius around (a) adults and seedlings and (b) around new ramets, ramets at least one year old (surviving ramets) and dying ramets

TABLE 9 Heterogeneity *G*-tests comparing the frequency of plants of *Viola blanda* present in a given year in a circle of given radius around plants present in 1977 and surviving until 1978 with those around seedlings that died in 1977. See text for further details

Plot number	Year	Sample size		Plant number		Plant size	
		Number of survivors	Number of dying seedlings	considered only	<i>G</i>	considered also	<i>G</i>
				<i>G</i>	<i>df</i>	<i>G</i>	<i>df</i>
(a) Radius = 3 cm							
113	1977	99	27	16.8**	7	17.4	10
122	1977	221	17	3.0	4	13.8	12
131	1977	154	18	51.1***	21	59.0***	30
132	1977	134	9	11.7	10	17.1	24
(b) Radius = 5 cm							
113	1977	97	25	23.3***	8	27.7	18
122	1977	209	16	9.9	9	24.2	25
131	1977	140	18	30.5	33	57.5	42
132	1977	128	9	21.1	25	22.5	44
(c) Radius = 8 cm							
113	1977	83	22	18.1	11	28.0	29
122	1977	195	14	17.2	14	31.4	45
131	1977	119	17	33.2	49	38.4	50
132	1977	119	6	18.8	27	27.6	59

can be explained by the number and size of close neighbours. Several sizes of circles were used. For each, a total of twenty-eight sets of results (three species, eleven sites for 1 yr,

one for 2 yr, one for 3 yr, and three for 4 yr) were analysed. The correlation between the five interference measures (1) to (5) (p 277) and individual plant size was calculated. Most of the sets of results contained more than fifty samples but, for 10-cm radius circles, only twelve tests out of 140, involving five of the twenty-eight sets of results, fell below the nominal  $P = 0.05$  level. Samples of random numbers might be expected to give almost as many nominally 'significant' results as this. Similar results were found for other sizes of circle. Even in cases where the  $F$ -test was significant ( $P \leq 0.001$ ), the proportion of the variance in plant size explained by regression on the interference measures was very low.

TABLE 10. Spatial autocorrelation and plant size statistics for mixed age cohorts through time (circle radius = 10 cm, weight = 1) for two species of *Viola*. The Indices  $I$  and  $c$  are defined in the text.

Plot number	Base year	Elapsed time (yr)	$n$	$\bar{x}$	SD	SD/ $\bar{x}$ (%)	$I$	$c$	
<i>V. blanda</i>									
111	1976	0	113	2.12	2.49	118	0.10	0.94	
		1	73	2.22	1.04	47	0.02	0.35***	
113	1976	0	115	2.15	2.47	115	0.15***	0.82	
		1	84	2.32	3.26	140	0.07	0.43***	
		2	38	1.34	0.53	40	-0.01	0.05***	
		3	15	1.27	0.70	56	-0.01	0.02*	
		1977	0	138	1.81	2.22	122	0.15***	0.90
122	1978	1	49	1.29	0.54	42	0.00	0.06***	
		2	18	1.22	0.65	53	-0.01	0.02*	
		0	58	1.22	0.56	46	0.12	0.78	
122	1976	1	19	1.21	0.63	52	-0.05	0.18*	
		0	179	2.45	2.65	108	0.01	0.91	
		1	159	2.96	3.01	102	0.04	0.44***	
		2	86	1.57	0.68	43	0.01	0.09***	
		3	18	1.11	0.47	42	0.00	0.01**	
		1977	0	257	2.65	2.92	110	-0.02	0.96
		1	124	1.50	2.17	145	0.01	0.10***	
		2	24	1.08	0.41	38	0.00	0.01**	
		1978	0	156	1.40	1.78	127	0.11*	0.90
		1	29	1.07	0.37	34	-0.01	0.13**	
131	1976	0	140	2.09	2.08	99	-0.01	1.00	
		1	104	3.21	3.65	114	0.06	0.32***	
		2	78	2.95	3.50	119	0.02	0.30***	
		3	53	3.34	1.47	44	-0.02	0.25***	
		1977	0	233	2.76	2.95	107	0.07	0.83*
		1	161	3.20	3.44	107	0.05	0.38**	
		2	107	3.47	3.72	107	0.01	0.27***	
132	1978	0	225	2.91	3.30	113	0.02	0.99	
		1	143	3.49	3.91	112	-0.01	0.44***	
		0	99	2.61	2.93	112	0.03	0.91	
		1	77	3.88	3.49	90	-0.01	0.28***	
		2	66	4.14	4.06	98	0.00	0.20***	
132	1977	3	61	3.51	4.37	125	-0.01	0.16***	
		0	166	3.13	3.42	109	0.03	0.94	
		1	126	3.93	4.30	109	0.02	0.37***	
		2	104	3.51	3.65	104	-0.01	0.16***	
		1978	0	154	3.62	4.03	111	0.05	0.91
		1	120	3.47	3.88	112	0.01	0.28***	
<i>V. incognita</i>									
682	1978	0	109	1.51	0.63	42	-0.03	1.03	
		1	81	1.73	0.67	39	0.25***	0.42***	
683	1978	0	66	5.24	8.88	170	0.33***	0.30***	
		1	53	7.26	12.98	179	0.33***	0.30***	
684	1978	0	106	1.51	0.56	37	-0.01	1.04	
		1	101	1.62	0.61	38	-0.05	1.10	

*Spatial autocorrelation*

The goal of this analysis is to determine if plants of similar size are more (or less) likely to be found growing together (or at certain distances) than would be expected by chance

In only 14 out of 138 tests was a nominally 'significant' ( $P = 0.05$ ) positive or negative autocorrelation of plants of similar size found for any distance range even when different weights were used. No differences among species or geographical regions were discovered.

When the values of the spatial autocorrelation coefficients for survivors of populations are compared from year to year, however, it is apparent that while Moran's Index,  $I$ , does not change (i.e. it stays around zero), Geary's Index,  $c$ , decreases steadily from year to year and tends toward zero in all populations indicating a tendency for the surviving plants in a neighbourhood to become more similar in size even when the total overall variability in plant size is not declining (Table 10). This means there is a tendency for scattered large and small individuals to be replaced by patches of large and patches of small individuals.

## DISCUSSION

The exhaustive analysis of the distribution of ramets and seedlings in space and time has yielded three important results. First, emergence of new seedlings (in cases when the sample size is large) tends to be clumped in space, and furthermore, in such cases the seedlings are more numerous in areas where the overall ramet density is low, indicating that seed germination or seedling emergence or both is inversely correlated with overall density of ramets. Seedling survival is affected by density. Secondly, ramets one-year-old or older appear to be aggregated or randomly distributed in space. Thirdly, the pattern of emergence of new ramets from stolons and the pattern of ramet death is random in space and not density dependent.

In previous studies (Cook 1979, Newell, Solbrig & Kincaid 1981), it was shown through direct field observation and experimental manipulation that survival of seedlings of *Viola blanda* declines as density increases. In those studies, as well as in experiments with the related species *V. sororia* Willd. (Solbrig in press), it was demonstrated that survival of seedlings is strongly size-dependent and that growth rate is lower where density is high. The present study indicates that the density effect operates through interactions of close neighbours.

Seedling germination, growth and survival depend on a variety of factors. According to Cook (1979, 1980) predation and insufficient soil moisture are the most frequent causes of death in populations of violets. To these may be added insufficient light and nutrients, although at present we do not know how important these are. Since ramets compete with seedlings for soil moisture and nutrients and they can shade seedlings, the negative effect of ramet density on seedling survival is most likely effected through competition for water, nutrients and light.

Harper (1977) has proposed the concept of the 'safe site' which he envisions as that place which provides a seed with the necessary stimuli for breaking dormancy and the resources and environment necessary for germination. In the case of the species of violet under study, a necessary but probably not sufficient characteristic of a safe site is a low density of ramets. As the local density varies with time, it follows that the distribution of safe sites in the population also varies with time. In other words, a safe site has both a spatial and a temporal dimension. As there is no way of predicting when ramet density will be sufficiently low for seedling establishment, in this case a safe site can only be determined

*a posteriori* which diminishes considerably the usefulness of the concept as it becomes tantamount to saying that a safe site is where a seed has germinated

If seedling germination and establishment are inversely related to density, the spatial distribution of the ramets in the population should tend towards evenness. However, this is not the case. Ramets are distributed at random, or they tend towards a clumped distribution. This indicates that although seedling establishment is strongly affected by density, vegetative ramet establishment is not. This is confirmed by the present study. Our analysis also indicates that ramet death (thinning) in the population is not necessarily concentrated in areas of the population where density is high. Where a mixed-age cohort of ramets is followed through time (that is when the distribution of survivors alone is followed) the values of the spatial indices tend to decrease, but not sufficiently to alter the basic random or aggregated nature of the plant distribution. The same is true if only plants of certain sizes are considered. This indicates only a slight tendency towards evenness, possibly as a result of interference. However, the *G*-tests of heterogeneity did not detect any effect of density on ramet emergence or death and the correlation between individual ramet size and several measures of interference was either non-significant or it explained less than 31% of the variance in plant sizes indicating that interference among ramets is very slight. The spatial autocorrelation as well as maps of distributions of plant sizes also confirm this result. This is a significant and critical difference between the demography of ramets and seedlings.

An interesting result apparent in all three of the spatial autocorrelation analyses, the coefficient of variation, and the spatial distribution maps for plant sizes (following mixed age cohorts through time) is the fact that the surviving plants in a circle tend to become of similar size (though not necessarily the same for all surviving plants). This indicates the possible existence of phenotypic selection forces at a scale of a few centimetres.

In a previous study (Newell, Solbrig & Kincaid 1981), it was determined that ramet survivorship is largely age-independent but strongly size-dependent, so is fecundity. Laboratory growth studies with these and other species (Solbrig in press) show that violets have the potential of growing to much larger sizes and at a much faster rate when presented with sufficient light, water and nutrients. Laboratory studies also indicate that genetic variation in growth rate is very low (Ducker 1981, Solbrig in press). The large differences in size observed in the field between individuals are, therefore, most likely due to differences in the environment in which the ramets grow.

Given that only plants that find themselves in a favourable environment can attain a large size, and given the fact that those sites are unevenly distributed (at a small scale) on the forest floor (Anderson 1964, Likens & Borman 1977), it follows that a selective advantage must accrue to the plant that reaches such a favourable site. From the plant's point of view, however, favourable microsites are randomly distributed in space and time. Producing stolons that scatter new plants (ramets) in space and time can be seen as a strategy to place ramets in favourable microsites. It may be that stolon tips can sense areas of high nutrient, water or light flux, increasing the probability of placing ramets in favourable sites, but the evidence so far is inconclusive (Clapham 1945, Wareing 1964).

Violet ramets can exchange carbon through the stolons, and the flow of carbon within and between ramets is governed by the relative strength of sink and sources (S. J. Newell, unpublished results). New ramets, are therefore, not necessarily dependent for survival on availability of local resources as is the case with seedlings. This probably explains the difference between the rate of survival of new ramets and that of seedlings, and why emergent ramets are less affected by density than are seedlings.



In summary, the stoloniferous habit in these species may be considered an adaptation to the paucity and uneven distribution of resources in and on the forest floor, and a mechanism to extend the life span of the genotype in an environment where seedling establishment is infrequent and unpredictable (Schaffer 1974, Stearns 1977)

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