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STUDIES ON THE POPULATION BIOLOGY OF THE GENUS *VIOLA*

III THE DEMOGRAPHY OF *VIOLA BLANDA* AND *VIOLA PALLENS*

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SUMMARY

(1) All ramets one-year or older of *Viola blanda* and *V pallens* were enumerated at regular intervals for up to 4 yr in two New England forest sites Each seedling was similarly enumerated, and each leaf and reproductive structure in twenty plants was marked and their fate recorded at weekly intervals

(2) Calculations were made of population flux, age distribution, survival, and life expectancy for ramets one-year or older and for seedlings

(3) At one site, fluctuation in population size was small compared with the large number of individual ramets gained and lost but at the other site the population declined and eventually disappeared

(4) On average individual ramets lived for 4½ years

(5) The rate of seed production and the probability that a ramet will survive is a function of ramet size

INTRODUCTION

The work reported here is part of a study the objective of which is to investigate the mechanism of adaptation of three species of violet (*Viola sororia*§, *V blanda* and *V pallens*) to the low light flux of the forest floor The approach combines demography, ecophysiology and genetics and is centred upon a life cycle analysis Details of the overall design are presented in Solbrig, Newell & Kincaid (1980) In this article we report on the demography from seed germination to seed production and on the size of the soil seed bank of two closely related species, *V blanda* and *V pallens* The results of a similar study on *V sororia* were presented in a previous article (Solbrig, Newell & Kincaid 1980)

In the study on *V sororia* it was found that there was a constant annual risk of death superimposed upon a seasonal cycle with greater mortality during May to September, inclusive, than during the winter months when the plants were inactive It was also found that seedling and adult survival and fecundity are primarily a function of size In a subsequent study (Solbrig 1981), it was shown that in *V sororia* the size attained and growth rate have low heritability and that the observed size hierarchy is regulated by availability of environmental resources

Viola blanda and *V pallens* differ from *V sororia* in the extent of vegetative propagation Although *V sororia* can produce new ramets asexually, it does so infrequently in nature *Viola blanda* and *V pallens*, on the other hand, habitually produce new ramets vegetatively, this form of propagation being much more common than establishment of seedlings

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§ Nomenclature follows that of Fernald (1950)

In this paper we report on the demography, from seed germination to seed production, and on the size of the soil seed bank of several populations of *V blanda* and *V pallens* in New England We then compare and contrast them with *V sororia* We are especially interested in learning whether the differences in growth habit are correlated with differences in the habitat where these species are found

METHODS

The present study initiated in 1976 has been conducted at two principal localities the Concord Field Station in Bedford, Massachusetts, which is about 32 km north-west of Boston, and Harvard Forest in Petersham, Massachusetts, 97 km west of Boston At each of these localities one study site, in deciduous woodland, was chosen The soils were shallow brown-earths with little persistent litter The top-most layer of mineral soil had pH 5–7 and near 100% base-saturation

Demography

Four 1 × 0 5 m permanent quadrats were established in Concord and eight 1 × 1 m quadrats were established in Petersham, and within them each violet plant was identified by a plastic marker and tagged in late summer 1976 The size of the quadrats was governed by density considerations, the smaller ones corresponding to the denser population at Concord Starting in the spring of 1977 and continuing for 3 yr until 1979, each population was visited every one or two weeks during the growing season from May to September and monitored for a variety of demographic variables

Biomass distribution

At each site, a 10 × 10 m area adjacent and as similar to the permanent quadrats as possible was selected for destructive sampling At each sampling date, ten 20 × 20 cm squares were randomly chosen and all vegetation (including underground parts) removed Violet plants in each sample were divided into four categories nonreproductive plants, with and without new stolons, and reproductive plants, with and without new stolons The plants were counted, separated into underground structures (roots and old stolons), leaves reproductive structures (flowering buds, flowers or fruits or both) and new stolons, and oven dried at 80 °C for 24 h and weighed

At the end of the 1977 growing season, the plants in one of the demography quadrats (number 111) at the Harvard Forest were dug up and the position of stolons in relation to ramets mapped and recorded Subsequently the dry weight of the below-ground biomass, the leaves and the reproductive organs was measured

Standard techniques were followed for estimating the soil seed bank Counts were made of the number of apparently undamaged seeds, but no tests of viability were made The methods are described in detail in Solbrig, Newell & Kincaid (1980) where details followed in studying the demography of seedlings, adults and plant parts can also be found

DESCRIPTION OF *VIOLA BLANDA* AND *V PALLENS* AND THEIR ENVIRONMENT

Viola blanda, the sweet or woodland white violet, is a common species in the understorey of deciduous and coniferous forests in North America from western Quebec to Minnesota and southward through New York, New England and through the Appalachian Mountains

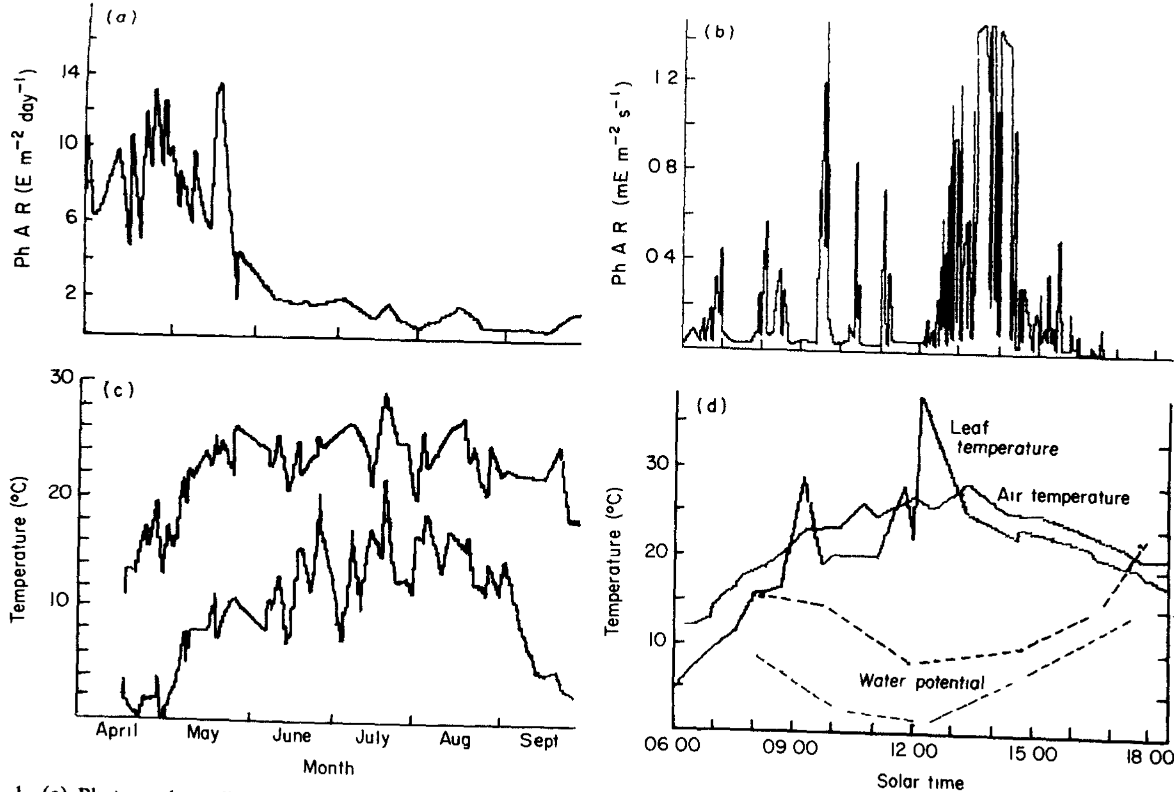

FIG 1 (a) Photosynthetically active radiation flux (Ph A R) integrated over 24 h through the growing season at the same point in the Concord Field Station *Viola blanda* site Sixty readings span 177 measuring days (b) Ph A R flux for 31 May 1977 at the Harvard Forest *V blanda* site Note the low background of radiation and the short duration bursts of high light flux created by sun flecks (c) Maximum (upper line) and minimum (lower line) air temperature and soil temperature at 5 cm depth (dots) for the Concord Field Station *V blanda* site during 1978 (d) Air temperature and temperature of a *V blanda* leaf during 31 May 1977 Leaf temperature remains below air temperature except during periods of high light flux Dashed lines show the upper and lower values of leaf water potential of three leaves chosen at random at hourly intervals during the day to northern Georgia *Viola pallens*, the smooth white violet, is found near bogs and other wet localities in the north-eastern United States and eastern Canada

The leaves of *Viola blanda* are characteristically heart-shaped, 2–4 cm long and 2–5 cm wide, slightly hairy on the upper surface and have glabrous petioles up to 15 cm long *Viola pallens* has leaves which are similar to *V blanda* in shape with usually glabrous blades and pubescent petioles The flowers of both species are white with narrow petals The capsules of *V blanda* are purplish, those of *V pallens* are green When *V blanda* and *V pallens* grow together, *V pallens* is always found in the wetter soils, often those with standing water early in the spring Both species produce long, slender, unbranched stolons that terminate in new ramets Single cleistogamous flowers are produced from a few nodes of the rhizome Each ramet may produce one or more stolons, but only one in each leaf axil Because of their stoloniferous growth both species tend to form mats that are often but not always, very dense and with few or no individuals of other species in them

In May or early June both species produce the characteristic white chasmogamous flowers and later, from June to August, they produce inconspicuous cleistogamous flowers The leaves and aerial parts of the plants yellow and die during August and September, earlier and more rapidly if there is a drought

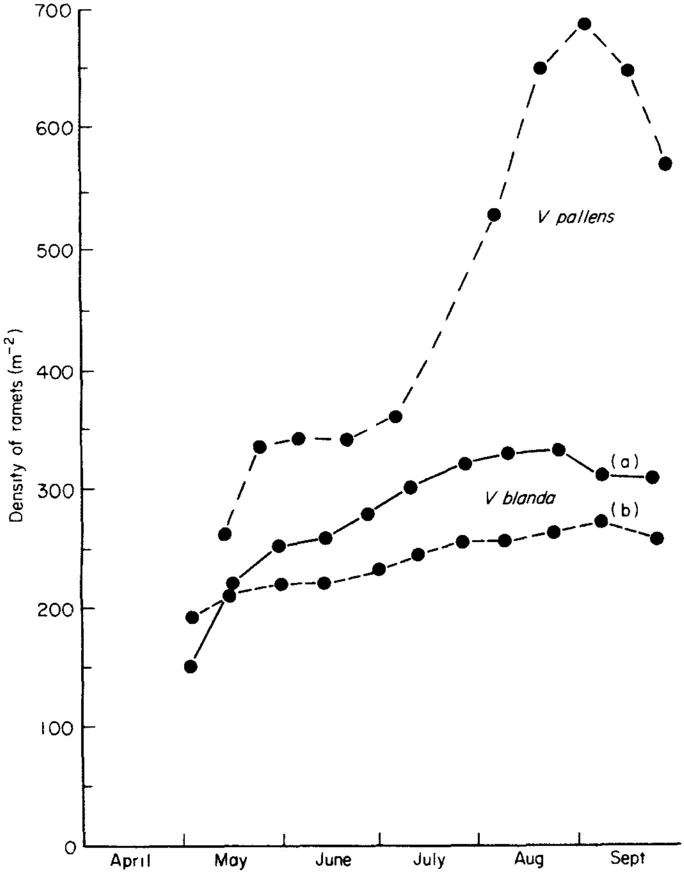

FIG 2 Density of ramets for two 0 5 m^2 plots, (a) and (b), of *Viola blanda* and one 0 5 m^2 plot of *V pallens* at the Concord Field Station site in 1977

These species overwinter as stolons Differences of up to a month in time of first emergence were recorded over the study period, so it seems likely that emergence of leaves and flowers in spring is triggered by temperature and not by photoperiod At the time of emergence of *V blanda* and *V pallens* and for the first month of growth, the leaves of trees and shrubs have not expanded and the light flux is much higher than it is during the middle and late part of the season since the tree and shrub canopy closes between the end of May and the end of June (Fig 1) Temperature increases steadily between April and June Over a 2-yr period, represented by 104 measurements, the average maximum temperature was 22 8 °C and the average minimum 11 1 °C Average soil temperature at 5 cm depth was 15 °C This indicates that plants are exposed to a moderate physical environment during the growing season with leaves experiencing the range of temperatures bounded by the maximum and minimum values in Fig 1 (Curtis 1979)

In *Viola blanda* the period of active growth, both in terms of initiation of growth and of leaf production, coincides with the time of maximum light flux (Fig 2) In *Viola pallens*, however, a flush of production of new ramets was observed towards the end of the growing season (Fig 2) Both species grow in a highly variable light environment Light varies both daily and seasonally as well as in space, even over very short distances Individual 24-h time-averaged values of photosynthetically active radiation (Ph A R 0 4–0 7 μm) varied from a maximum of 268 $\mu E\ m^{-2}\ s^{-1}$ at the beginning of May to a minimum of 14 $\mu E\ m^{-2}\ s^{-1}$ at the end of August After the canopy closes the daily light regime can be characterized by a low background of Ph A R (about 10 nE $m^{-2}\ s^{-1}$) punctuated by bursts of sun flecks concentrated around midday, these sun flecks may exceed 415 W m^{-2} (solar) or 1 4 mE $m^{-2}\ s^{-1}$ (Ph A R), a relatively high flux density Leaf temperature (Fig 1) is typically below air temperature. Resistance of leaves to diffusion of water vapour shows the expected trend of high resistance in the early morning, followed by a decrease in mid-morning and a gradual increase during the afternoon

RESULTS

Soil seed bank

The soil seed bank was estimated at four times over a period of one year at both study sites The results (Table 1) show that the density of seeds was approximately 300–500 m^{-2} in the soil at the Concord Field Station site and 300–400 m^{-2} at the Harvard Forest site except for a value of 1486 m^{-2} during the spring of 1977 The distribution of seeds in the soil is clumped, which may be due to the fact that ants transport the seeds to their nests (Beattie & Lyons 1975, Culver & Beattie 1978) The soil seed bank at these two sites is larger than that of *V sororia* for which the density of seeds was less than 100 m^{-2} (Solbrig, Newell & Kincaid 1980)

TABLE 1 Soil *Viola* seed bank (seeds m^{-2} to 5 cm depth)

	Harvard Forest site	Concord Field Station site
Spring 1977	1486	530
Summer 1977	318	530
Autumn 1977	318	295
Spring 1978	413	530
Mean	634	471

Seed germination and seedling survival

Seedlings were studied during 1977 and 1978 at six permanent 1 m^2 quadrats at the Harvard Forest site and two 0 5 m^2 quadrats at the Concord Field Station site In three of the Harvard Forest quadrats, all the vegetation (including roots and rhizomes) was removed, the other five quadrats were left undisturbed The number of seedlings emerging differed from site to site In 1977 in the Concord Field Station site, density of emerging seedlings in permanent quadrats was 76 m^{-2} (Table 2), at the Harvard Forest site it was 37 seedlings m^{-2} at three undisturbed quadrats (Table 3), and 39 seedlings m^{-2} emerged in the three quadrats where the vegetation was removed (Table 4) The density of emerging seedlings at the wetter but denser Concord Field Station sites was about twice that in the Harvard Forest sites Seedling survival was also much higher at the Concord Field Station where 79% of the 1977 cohort of seedlings survived to the end of the first growing season and 43% of the 1977 cohort survived to the end of the second growing season At the Harvard Forest, only 13% of the seedlings survived to the end of the first growing season and only 5% were alive at the end of the second growing season in the undisturbed quadrats In the quadrats from which the vegetation was removed, 45% survived the first growing season and 9% were alive at the end of the second growing season Removal of the cover of adult plants doubled the proportion of seedlings which survived (Fig 3) The beneficial effect on survival of the removal of competing vegetation is most likely through lowered competition for water as attested by the much higher survival of seedlings at the Concord Field Station quadrats even without adult vegetation removal There is also independent evidence of drought as a major source of death among seedlings (Cook 1979), the other principal cause being herbivore grazing (Cook 1979, Ducker 1981, Schellner, Newell & Solbrig 1982)

TABLE 2 Germination and survival of cohorts of seedlings of *Viola blanda* in two 0 5-m^2 permanent quadrats at the Concord Field Station site

Cohort	Survival 1977									
	3 May	16 May	1 June	13 June	30 June	13 July	27 July	10 Aug	29 Aug	8 Sept
3 May 1977	59	52	51	50	50	48	48	47	47	47
16 May		8	8	8	8	8	8	8	7	7
13 June				6	6	5	5	4	4	4
30 June					2	2	1	1	1	1
*13 July 1977						1	1	1	1	1
Total	59	60	59	64	66	64	63	61	60	60

	Survival 1978					
	12 May	26 May	11 June	3 July	18 July	1 Aug
3 May 1977	30	30	28	28	28	27
16 May	5	5	4	4	2	2
13 June	4	4	4	4	4	4
30 June	1	1	0	0	0	0
*13 July 1977	1	0	0	0	0	0
Total	41	40	36	36	34	33

* No seedling germination after this date

TABLE 3 Germination and survival of cohorts of seedlings of *Viola blanda* in three 1-m² permanent quadrats at the Harvard Forest site

Cohort	Survival 1977								1978				
	19 May	25 May	9 June	23 June	7 July	28 July	12 Aug	8 Sept	7 May	20 May	2 June	14 June	6 July
19 May	21	17	15	15	15	12	9	2	1	1	1	0	0
25 May		33	30	30	22	17	7	3	2	2	2	2	2
9 June			11	11	11	11	11	1	1	1	1	1	1
23 June				19	17	13	9	3	1	1	1	1	1
7 July					5	3	3	1	1	1	1	0	0
28 July						8	4	2	1	1	1	1	1
* 8 Sept								1	0	0	0	0	0
Total	21	50	56	75	70	64	43	13	7	7	7	5	5

* No seedling germination after this date

TABLE 4 Germination and survival of cohorts of seedlings of *Viola blanda* in three 1-m² permanent quadrats with vegetation removed at the Harvard Forest site

Cohort	Survival 1977								1978					
	19 May	25 May	9 June	23 June	7 July	28 July	12 Aug	8 Sept	7 May	20 May	20 June	23 June	20 July	22 Aug
19 May	65	62	55	55	51	49	47	35	16	16	16	16	15	8
25 May		26	24	21	20	19	16	12	5	5	5	3	3	3
9 June			7	7	7	7	4	1	0	0	0	0	0	0
23 June				6	4	1	0	0	0	0	0	0	0	0
7 July					8	4	1	1	0	0	0	0	0	0
*28 July						6	4	0	0	0	0	0	0	0
Total	65	88	86	89	90	86	72	49	21	21	21	19	18	11

* No seedling germination after this date

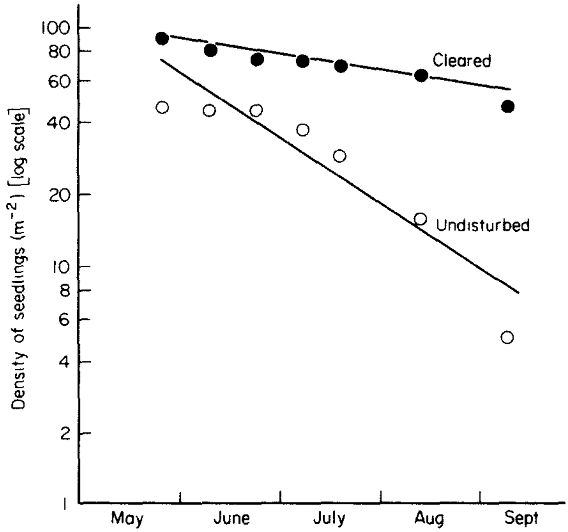

FIG 3 Seedling mortality for two cohorts of *Viola blanda* at the Concord Field Station site in adjacent 1 m^2 plots, one undisturbed (unfilled circles), the other with all adult vegetation, including violets, removed (filled circles)

The population of one-year old or older ramets

Viola blanda

A summary of the population flux for the three Harvard Forest quadrats and the two Concord Field Station quadrats is presented in Table 5 Data are presented for 4 yr at the Concord Field Station but for only 3 yr at the Harvard Forest because most of the plants

TABLE 5 Population flux in *Viola blanda* All but (h)–(j) are for individual quadrats, 1 0 m^2 each at Harvard, 0 5 m^2 each at Concord

	Harvard Forest site				Concord Field Station site		
Quadrat number	113	122	124	*All three*	131	132	*Both*
(a) Number of ramets at beginning of study*	115	179	100	394	141	200	341
(b) Number of ramets at the end of study†	45	97	106	248	194	200	394
(c) Net change	−70	−82	6	−146	53	0	53
(d) Rate of change	0 39	0 54	1 06	0 63	1 38	0	1 16
(e) New ramets during study	52	114	93	259	303	193	496
(f) Ramets lost during study	122	196	87	405	250	193	443
(g) Ramets present at start alive at end of study	28	58	54	140	52	61	113
(h) Percentage survival of plants in (a) (g/a × 100)	24 3	32 4	54 0	35 5	36 9	30 5	33 1
(i) Expected time for complete turnover in years (years of study/(100 − h) × 100)	2 6	2 9	4 3	3 1	4 8	4 3	4 5
(j) Percentage mortality of all individuals (f/k × 100)	65 9	66 9	45 1	62 0	56 3	49 1	52 9
(k) Total plants recorded in study	167	293	193	653	444	393	837

* August 1976

† August 1978 for Harvard Forest site and August 1979 for Concord Field Station site

at the Harvard Forest quadrats did not emerge in 1979 for undetermined reasons By 1980, most plants in the Harvard Forest population were dead Tables 6 and 7 show survival and age structure for all quadrats from 1976 to 1979

The ramet density in single quadrats varied from 74 to 244 m^{-2} at the Harvard Forest (Table 6) and from 282 to 560 m^{-2} at the Concord Field Station (Table 7) The differences in density are probably due to the fact that the Harvard Forest site is drier than the Concord Field Station site The density of ramets varied in all quadrats from year to year (Fig 4) Heterogeneity tests show the density differences to be statistically significant ($\chi^2 = 14\ 7$, 4 d f, $P < 0\ 01$ for the Harvard Forest quadrats, $\chi^2 = 79\ 3$, 3 d f, $P < 0\ 001$ for the Concord Field Station quadrats)

Although there are fluctuations in density from year to year, the overall pattern fits best a Deevey type II mortality curve (Fig 5) The same conclusion was reached for *Viola sororia* (Solbrig, Newell & Kincaid 1980), although the conclusion was more firmly based for *V sororia* than it is for *V blanda* because there were more years of observation Mortality is not uniform in time, being slightly greater during the growing season especially during summer months The results also indicate that mortality is not the same in all size classes (as measured by the number of leaves per plant) (Table 8)

TABLE 6 Survival and age structure of *Viola blanda* populations in 1-m^2 quadrats at the Harvard Forest site

Cohort	Quadrat number	Survival through 1976	1977	1978
1976 and older	113	115	84	43
	122	179	158	88
	124	100	87	71
	All three	*394*	*329*	*202*
1977	113		43	22
	122		86	39
	124		65	33
	All three		*194*	*94*
1978	113			9
	122			28
	124			28
	All three			*65*
Total		394	523	361

TABLE 7 Survival and age structure of *Viola blanda* populations in 0 5 m^2 quadrats at the Concord Field Station site

Cohort	Quadrat number	Survival through 1976	1977	1978	1979
1976 and older	131	141	103	75	53
	132	200	77	67	41
	Both	*341*	*180*	*142*	*94*
1977	131		80	59	38
	132		72	55	44
	Both		*152*	*114*	*82*
1978	131			97	63
	132			47	42
	Both			*144*	*105*
1979	131				126
	132				74
	Both				*200*
Total		341	332	400	481

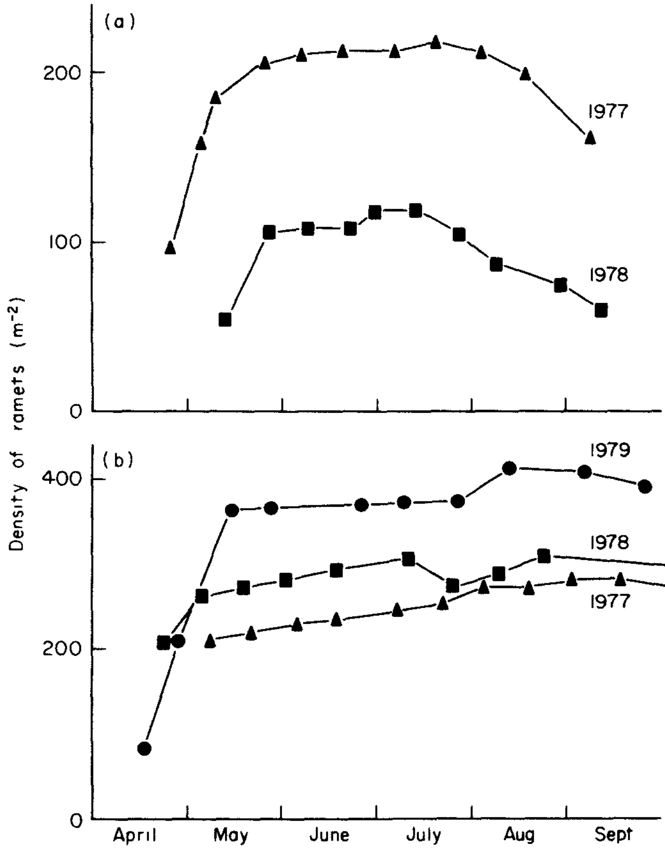

FIG 4 (a) Density of ramets of *Viola blanda* in (a) the 1 0 m^2 quadrat number 122 at the Harvard Forest site and (b) the 0 5 m^2 quadrat number 131 at the Concord Field Station site In June 1977 the density of plants was about the same in both quadrats

TABLE 8 Mortality for ramets of *Viola blanda* with different numbers of leaves at the Harvard Forest site

Number of leaves	1977 Initial number	1977 Mortality (% yr^{-1})	1978 Initial number	1978 Mortality (% yr^{-1})
1	83	34	40	75
2	129	12	79	51
3	113	9	107	36
4 and 5	31	16	79	22

Viola pallens

For this species we possess demographic observations for one year only The very high rate of recruitment combined with the high ramet density (1400 m^{-2}) was the reason for the abandonment of further demographic observations on this species as it was impossible to accurately identify surviving individuals in the spring of 1978

The population of leaves

Plants grow by the production of repetitive structures One such structure is the leaf Leaves of *Viola blanda* and *V pallens* are ephemeral structures which are continually formed from Aprıl to late summer (August or early September) when growth ceases ın response to low temperature or water stress or both Leaves can dıe as a result of fungal growth or drought stress or they may be eaten, or they may yellow and dıe from other causes

Table 9 represents the average leaf number per plant for five quadrats of *V blanda* and one of *V pallens* durıng July over a 4-yr perıod, and Fıg 8 shows the densıty of leaves ın three quadrats at dıfferent dates over a 3-yr or 4-yr perıod Between the two sıtes there ıs a marked dıfference ın the densıty of leaves produced and there were also dıfferences between years There are also marked dıfferences ın the average number of leaves per ramet between sıtes and between years The dıstrıbutıon of plants wıth dıfferent number of leaves ıs not Gaussıan (Fıg 6) but ıt ıs not log-normal or Poısson eıther Fıgure 7 shows the dıstrıbutıon of bırth and death of leaves of *V blanda* (assessed by leaf area) throughout the year for twenty randomly selected ındıvıdual plants durıng 1977, 1978 and 1979 for one quadrat at the Concord Fıeld Statıon sıte New leaves are produced throughout the season, but at a decreasıng rate, leaf mortalıty ıs nearly lınear untıl the end of the season

TABLE 9 Mean leaf number per plant for random samples (n = 20) from five quadrats of *Vıola blanda* and one of *V pallens*

	Harvard Forest sıte *V blanda*			Concord Fıeld Statıon sıte *V blanda*		*V pallens*
Quadrat number	113	122	124	131	132	231
July 1977	2 2	2 2	3 3	3 1	3 4	3 1
July 1978	0 7	0 8	1 4	2 9	3 0	–
July 1979	–	–	–	2 8	2 7	–

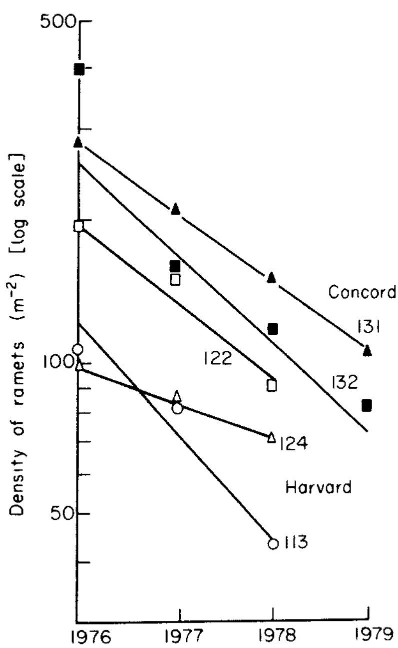

FIG 5 Survıval of ramets of *Vıola blanda* (of varıous age) present ın 1976 ın three (numbered) quadrats at the Harvard Forest and two at the Concord Fıeld Statıon sıtes

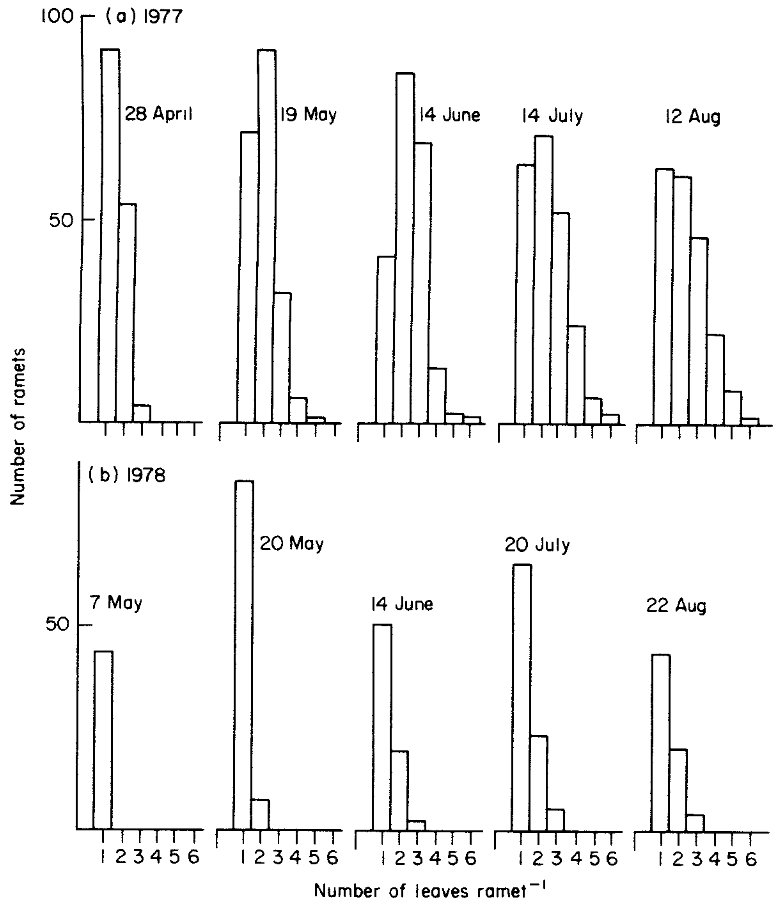

FIG 6 Frequency distribution of plants of *Viola blanda* with different number of leaves in the 1 m^2 quadrat number 122 at the Harvard Forest site during (a) 1977 and (b) 1978

Consequently, the actual number of living leaves increases steeply early in the season levelling off about mid-summer between early July and early August

Leaf loss

It is of interest to know how much leaf surface is lost (by grazing, etc) As Table 10 and Fig 8 show, during the three years of observation, there was substantial variation in the number of leaves attacked In quadrat 131, 36% of the leaves had been partially destroyed by the end of the 1977 growing season, 14% in 1978 and 40% in 1979 There was also variation between quadrats quadrat 132 always had a higher percentage of attacked leaves that did quadrat 131 (48%, 26% and 53% in 1977, 1978 and 1979 respectively) Similar variation was observed in the Harvard Forest quadrats

The number of damaged leaves increased throughout the season The extent of leaf surface consumed varied from 10% to almost 40% The maximum number of attacked leaves in *V pallens* during 1977 was 30%, well within the range of damage experienced by *V blanda*

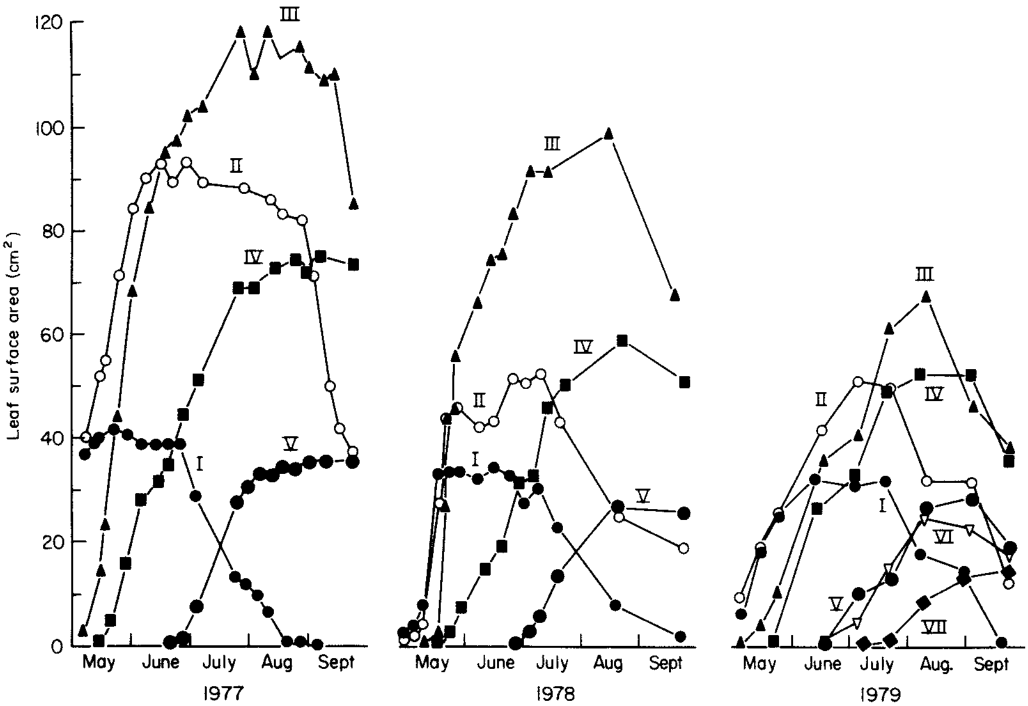

FIG 7 Mean leaf surface area for twenty plants of *Viola blanda* in quadrat number 131 at the Concord Field Station site by node (roman numeral I–VII) for 3 yr

Seed production

Seed production varied from quadrat to quadrat and from year to year (Table 11) The rate of seed production was low (fewer than twenty-three seeds per ramet per year) The Concord Field Station quadrat, in particular number 132, produced more seeds than did the Harvard Forest quadrats, both on a quadrat and an individual plant basis This is probably related to the apparently more favourable environmental conditions of the Concord Field Station quadrats which had a higher density of ramets, more leaves per plant and more fruits per plant As was the case with *V sororia* (Solbrig, Newell & Kincaid 1980), the number of fruits per plant is approximately exponentially related to the number of leaves (Fig 9) The same is true for *V pallens* The one population of this species that was monitored produced, on the average, more fruits than did *V blanda* (Table 11)

Stolon production

Stolon production was measured in 1977 on Harvard Forest plants of *V blanda*, growing outside the demographic plots, by destructive sampling and likewise in 1978 on *V pallens* plants growing outside the demographic plots Table 12 shows that for *V blanda* only 28% of sample plants had stolons and that only 6% of all sampled plants had more than one stolon These plants were the large plants with several leaves Stolons are borne in the axils of leaves, one to a leaf commencing usually with the third leaf In *V pallens* the distribution of plants with new stolons was similar to that observed in *V blanda*, except that a slightly greater proportion (40%) of all sampled plants had new stolons New

TABLE 10 Predation on leaves of *Viola blanda* in 0 5 m^2 quadrats at the Concord Field Station site (131, 132) and in 1 m^2 quadrats at the Harvard Forest site (113, 122, 124) and on leaves of *V pallens* in a single 0 5 m^2 quadrat at the Concord Field Station site during 1977 and 1978 N = Total number of leaves, P = number showing some damage, BP = number of bare petioles

	Quadrat 131			Quadrat 132			Quadrat 113			Quadrat 122			Quadrat 124			*V pallens* 321		
1977	N	P	BP	N	P	BP	N	P	BP	N	P	BP	N	P	BP	N	P	BP
19 May	267	6	7	244	39	16	188	22	13	279	66	7	304	99	11	320	0	16
9 June	330	29	8	325	45	21	179	80	11	488	87	15	320	88	9	428	16	6
7 July	387	60	14	409	156	12	200	102	11	500	110	8	419	124	1	534	115	4
4 Aug	358	116	20	378	145	65	190	81	4	457	159	12	371	125	7	703	162	52
8 Sept	289	104	17	339	161	73	106	67	19	288	45	14	259	62	8	486	106	27
1978																		
29 April	108	1	2	140	–	–	–	–	–	–	–	–	–	–	–			
19 May	284	4	14	310	2	1	29	2	4	43	18	5	96	15	9			
9 June	410	1	5	366	8	4	47	10	10	93	50	12	131	58	47			
7 July	498	72	4	388	30	11	50	14	12	129	65	58	155	74	18			
4 Aug	543	92	13	515	57	13	57	16	5	106	67	14	133	94	8			
8 Sept	303	42	13	385	98	22	25	15	2	70	45	10	89	87	12			

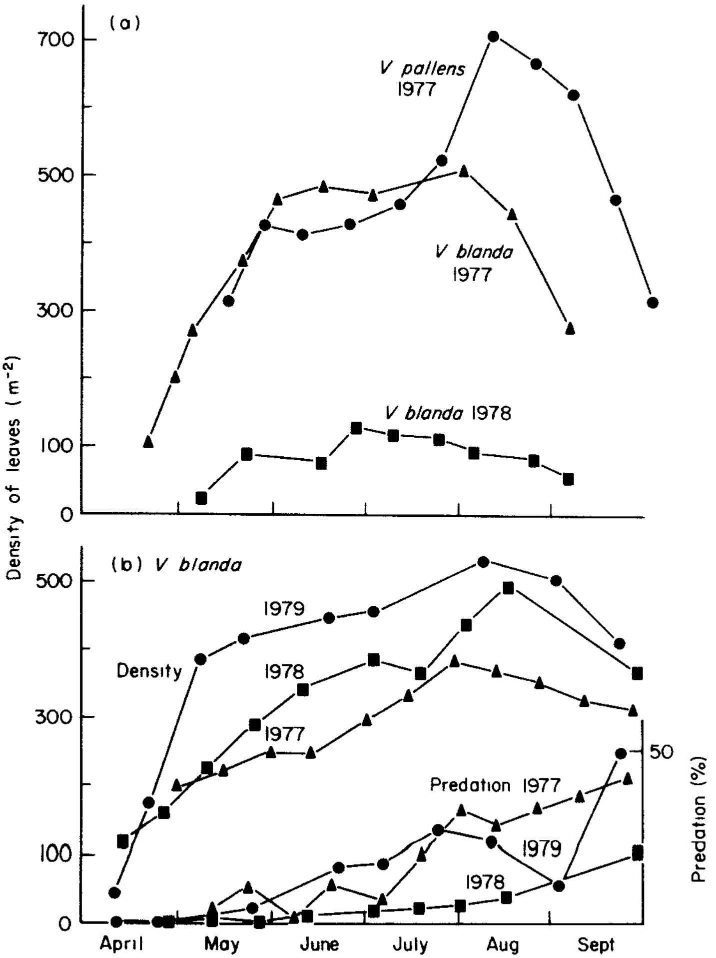

FIG 8 (a) Density of leaves for quadrat number 122 of *Viola blanda* during 1977 and 1978 at the Harvard Forest site, and for *V pallens* in 1977 (b) Upper three lines, density of leaves for quadrat number 132 of *V blanda* at the Concord Field Station site during 1977, 1978 and 1979, lower three lines, proportion of leaves eaten in the same populations during the same 3 yr

stolons are formed fairly regularly throughout the year in *V blanda* (with perhaps a slightly larger proportion in the spring), while in *V pallens*, stolon production increases throughout the year (Table 12)

Biomass allocation

The total dry weight of the Harvard Forest quadrat number 111 with a density of 89 ramets m^{-2} at time of harvest was 68 g The average dry weight of a ramet (including its rhizome) was 0 76 g Only 2 4% of the biomass of quadrat 111 (1 65 g) was devoted to vegetative spread (new rhizomes and associated buds and incipient leaves)

Viola blanda allocates about 90% of its biomass to roots and shoots (Fig 10) and 10% or less to reproductive functions Of this last amount, 60% is in new stolons and 40% in fruiting structures In *V pallens*, on the other hand, close to 15% of the biomass is in reproductive tissues, almost all in stolons (Fig 10)

TABLE 11 Number of fruits produced per quadrat, per year, and per plant of different sizes in four plots of *Viola blanda* and one of *V pallens* at the Harvard Forest (HF) and Concord Field Station (CFS) sites N = Total number of plants, F = total number of fruits, F/PL = average number of fruits per plant

Leaves per plant	CFS *V blanda* quadrat number 131									CFS *V blanda* quadrat number 132								
	1977			1978			1979			1977			1978			1979		
	N	F	F/PL	N	F	F/PL	N	F	F/PL	N	F	F/PL	N	F	F/PL	N	F	F/PL
1	26	0	0 00	43	1	0 02	80	1	0 01	15	1	0 07	9	1	0 11	44	2	0 05
2	51	1	0 02	49	0	0 00	46	0	0 00	18	7	0 39	41	11	0 27	35	27	0 77
3	53	2	0 04	53	4	0 08	46	5	0 11	36	19	0 53	72	19	0 26	46	36	0 78
4	24	6	0 25	38	3	0 08	31	1	0 03	43	16	0 37	17	15	0 88	45	19	0 42
5+	1	0	0 00	11	1	0 09	22	3	0 14	15	8	0 53	6	12	2 00	24	5	0 21
All	155	9	0 06	194	9	0 05	225	10	0 04	127	51	0 40	145	58	0 40	194	89	0 46

Leaves per plant	HF *V blanda* quadrat number 113						HF *V blanda* quadrat number 122						CFS *V pallens* quadrat number 321		
	1977			1978			1977			1978			1977		
	N	F	F/PL	N	F	F/PL	N	F	F/PL	N	F	F/PL	N	F	F/PL
1	37	5	0 14	40	0	0 00	64	4	0 06	76	2	0 03	101	14	0 14
2	31	9	0 29	5	1	0 20	71	8	0 11	32	1	0 03	109	48	0 44
3	17	6	0 35	1	0	0 00	52	8	0 15	5	0	0 00	64	57	0 89
4	10	3	0 30	–	–	–	24	2	0 08	–	–	–	34	44	1 29
5	2	0	0 00	–	–	–	8	3	0 38	–	–	–	11	18	1 63
All	97	23	0 24	46	1	0 02	219	22	0 10	113	3	0 03	319	181	0 57

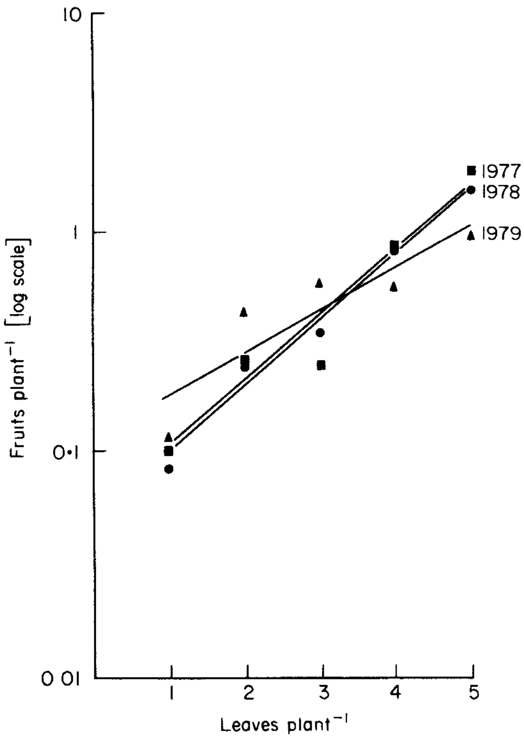

FIG 9 Relationship between number of fruits plant^{-1} and number of leaves plant^{-1} for quadrat number 132 of *Viola blanda* at the Concord Field Station site in 1977, 1978 and 1979

TABLE 12 Number of ramets of *Viola blanda* with a given number of stolons at the Harvard Forest site in 1977

Date	Stolons 0	1	2	3	Total number of plants	Mean number of stolons plant^{-1}
23 June	11	15	2	1	29	0 76
7 July	67	20	11	2	100	0 48
21 July	89	25	2	0	116	0 25
4 Aug	89	24	9	0	122	0 34
20 Aug	65	19	5	1	90	0 36
1 Sept	84	21	1	1	107	0 24
All dates	405	124	30	5	564	0 35
Percentage of all stolons	72	22	5	1		

DISCUSSION

Populations of seedlings and of mature plants of *V blanda* exhibit a negative exponential type of mortality, a conclusion in line with the results obtained by us with *V sororia* (Solbrig, Newell & Kincaid 1980) and with the behaviour of other species (Tamm 1948, Rabotnov 1956, 1958, Antonovics 1972, Sarukhan & Harper 1973, Harper & White 1974, Sarukhan 1980, Cook 1980) Deaths in populations of leaves of *V blanda*, *V pallens* and *V sororia* were concentrated in the old age classes This implies that mortality of ramets, but not of leaves, is age independent However, mortality of ramets is inversely correlated with the size of the ramets as measured by the number of leaves a plant has

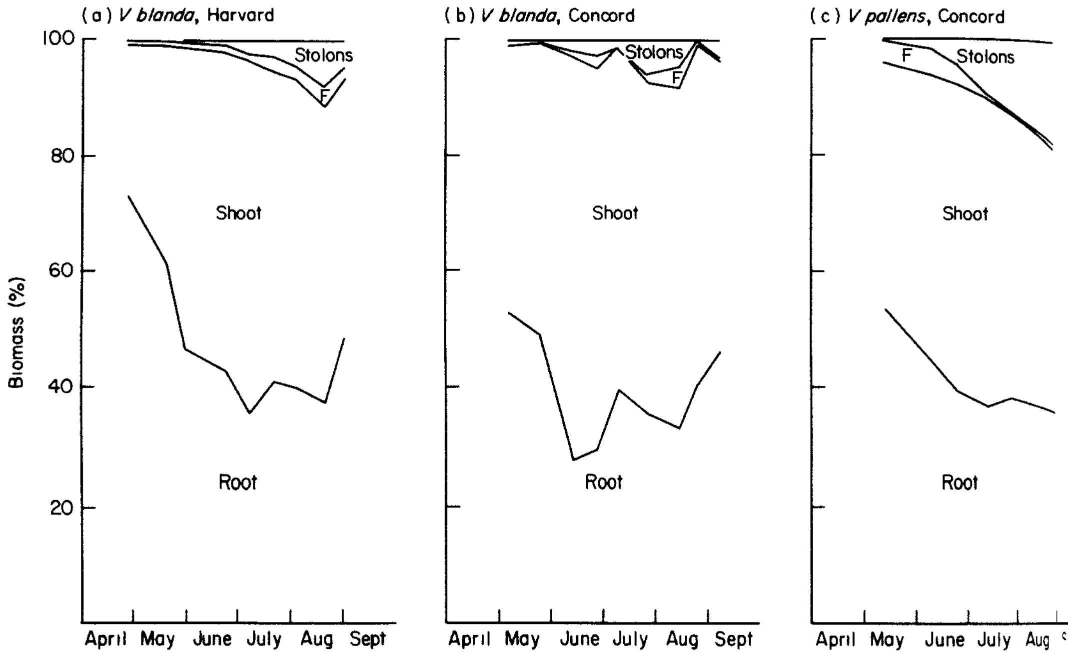

FIG 10 Proportion of biomass in different organs of *Viola blanda* at (a) the Harvard Forest site, (b) the Concord Field Station site, and (c) for *V pallens* at the Concord Field Station site F = flowers and fruits

This also corresponds with what has been reported for other species (Werner 1975a, b, Ford 1975, Rabinowitz 1979, Solbrig 1981) Fecundity apparently is also size- and not age-dependent Size and not age appears then to be the better predictor of life table components

A characteristic of the observations made on the life table components of these species is their very large variance Consequently, the above statements are only tentative So, for example, number of seedlings emerging in a quadrat varied from year to year and within a year between quadrats including adjacent ones Likewise there were remarkably large variations in fecundity So, in 1977, ramets in quadrat number 132 at the Concord Field Station site produced an average of 0 40 fruits per plant while those in quadrat number 131, less than a metre away, produced only 0 06 fruits per plant No obvious macro- or micro-environmental factor can be identified to account for these differences This contrasts with results obtained with the one population of *V sororia* studied by us (Solbrig, Newell & Kincaid 1980) which showed a remarkably constant mortality and fecundity over an 8-yr period of observation in all observed demographic characteristics excepting new seedling emergence

The population of *V blanda* from the drier Harvard Forest site had a lower density than had the one from the Concord Field Station site As a whole the population showed lower seedling establishment and lower seedling and ramet survival and lower fecundity The replacement rate was insufficient to maintain the population and, by spring 1981, the population was reduced to less than one hundred individual ramets, less than ten of them within the permanent quadrats We have no exact way of determining the reasons for this decline Among possible causes are

(1) Drought The Harvard Forest site is very dry and 1978 was an especially dry year

(2) Disease Many of the plants were infected by a fungus during 1977 It produced fruiting bodies on the leaves These leaves yellowed and died early

(3) Human activity Although great care was taken to minimize the effect of the frequent visits, considerable soil compaction in the area surrounding the quadrats was visible at the end of 3 yr of visits

Any of these causes singly or combined, might account for the demise of the Harvard Forest population of *V blanda*

In comparing the life history of *V blanda* and *V pallens* with that of *V sororia* several points are of interest First, the three species are remarkably similar in their leaf morphology and dimensions The flowers are also very similar although of different colours All these species exhibit the same general phenology and the same type of explosive seed dispersal mechanism and have myrmecochorous seeds They grow in the same general type of mixed deciduous forest characteristic of the eastern United States Their geographical ranges are slightly different *Viola pallens* has the widest distribution extending west to British Columbia, the other two species growing generally from Quebec to Minnesota and south along the Appalachian Mountains to Georgia and the Carolinas *Viola pallens* grows in wetter sites than either *V blanda* or *V sororia* do, and *V sororia* appears to grow in more disturbed sites although this is difficult to quantify

Viola sororia differs markedly from *V blanda* and *V pallens* in its almost exclusively sexual mode of reproduction, while the other two species dedicate almost equal amounts of biomass to sexual and asexual reproduction The population of *V sororia* monitored by us produced an average of 0 78 fruits per plant over a 2-yr period, *V pallens* produced 0 57 fruits per plant in the one year in which it was monitored (1977), while the *V blanda* population produced 0 22 fruits per plant at the Concord Field Station and only 0 10 fruits per plant at the Harvard Forest. As mentioned, *V sororia* produces essentially no ramets by vegetative means, but *V blanda* produced 0 35 stolons per plant at the Harvard Forest site in 1977, each of which could potentially give rise to a new ramet

Another difference in the life table is the probability of survival of ramets *Viola sororia* ramets have an average life span of a little over 10 yr, while *V blanda* ramets live on the average only slightly over 4 yr Survival is size dependent in both species, but is not normally distributed in either species

In brief, it appears that the production of new ramets in *V blanda* (and *V pallens* but we possess fewer data for that species) is mostly by asexual means, while it is exclusively by sexual means in *V sororia* Asexual reproduction in *V blanda* is accompanied by lower seed production and lower ramet survival

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