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LATITUDINAL VARIATION IN THE RELATIONSHIP
BETWEEN ROSETTE DIAMETER AND FATE
IN COMMON MULLEIN (*VERBASCUM THAPSUS* L.)

There is currently a good deal of interest in the "biennial" life history. This stems from the fact that theoretical analysis of the selective advantage of alternate life histories predicts that biennials should seldom be favored relative to annual or perennial alternatives (Hart, 1977). However biennials often appear highly successful in terms of abundance, being both common and widespread, even though they constitute only a small proportion of any flora (Wisconsin, 1%, Struick, 1975; Carolinas at most 2%, calculated from Radford et al., 1968). Moreover, population studies of biennials usually have not revealed rigid two-year life histories but rather short variable prereproductive periods followed by senescence after fruiting, e.g. in *Daucus carota* (Holt, 1972; E. Lacey, pers. comm.), *Digitalis purpurea* (Oxley, from Harper and White, 1974), *Dipsacus fullonum* (Werner, 1975), *Carduus* sp. (J. Hamrick, pers. comm.) and *Hymenopappus* sp. (E. Evans, pers. comm.). Werner's (1975) study of *Dipsacus fullonum* from southwestern Michigan is the only detailed account of the factors related to death and flowering of rosettes of a biennial. Thorough descriptions of the conditions under which short-lived perennial monocarps are successful are necessary for the formation of a more adequate theory.

Biologists attempt to understand the evolution of life history traits mainly through a description of character variation and the correlation of this variation with environmental conditions. Although latitude is one of the most general sources of spatial differences in environmental conditions, plant intraspecific variation in life history traits correlated with this cline remains essentially unexplored. Accounts of latitudinal differences in plant life histories have been confined mostly to phenological observations of flowering time; McNaughton (1975) described latitudinal effects in other aspects of the population dynamics of *Typha latifolia*. Studies of physiological and morphological traits have shown that latitudinal variation affords valuable insights into the evolutionary response of plant populations to environmental pressures.

This paper describes the effects of latitude on the relationship between rosette diameter at the end of one growing season and a plant's fate in the next (death, continued vegetative growth, or flowering) for populations of the "biennial" species *Verbascum thapsus*.

MATERIALS AND METHODS

Verbascum thapsus L., common mullein, is classified as a biennial since it produces a broad leaved rosette its first growing season and later a tall (0.2 - 2.8m), usually unbranched, stalk bearing fruit on the upper third portion. Flowering is most common during its second growth season but possible any time from year one to year four (Reinartz, in prep.). Mullein is strictly monocarpic (always dying immediately after setting fruit). It is native to Eurasia and was apparently introduced very early to North America, becoming a wide-spread colonizer of recently disturbed habitats throughout the continent (n. Mexico to s. Canada).

During the period September 1976 to October 1977, 23 mullein populations were chosen for study. Ten were located in southern Canada between the Gaspé Peninsula of Quebec and Kenora, Ontario. This east - west line corresponds roughly to the northern limit of range for mullein in North America. Six populations were located in North Carolina. Seven populations were chosen close to the southern border of mullein's North American range; one in south Georgia and six in south Texas.

At each site a portion of the population large enough to contain at least 100 rosette plants was mapped each fall from 1977 to 1979 unless there were fewer than that number in the entire rosette population. Rosette diameters of mapped individuals were measured. Mapping in subsequent years provided information on whether the plant remained a rosette, flowered or died. Field data were obtained for a total of 3,571 plants.

Seed was collected from 20 randomly selected plants from each of four of the North Carolina populations. Similar collections were made from 10 randomly selected plants from each of four populations from each of the northern and southern latitudinal limits. A total of 4,400 plants were grown from this seed collection in a randomized block design in a garden located in Durham, North Carolina. Of these plants 1,385 survived to the end of the first growing season in 1978. Measurements of first season rosette diameters and subsequent fate were recorded for the common garden grown plants. Methodology is further detailed in Reinartz (in prep.).

RESULTS

The data from 23 field populations relating diameter and fate are presented in Table 1. Similar data for the common garden are shown in Table 2. The total number of rosettes in each diameter class is listed with the proportion that die, remain vegetative or flower the following season. Plants from each latitudinal region are tabulated separately. A strong association between rosette diameter and fate is apparent in both tables. It comes as no surprise that small rosettes have a higher probability of dying or remaining vegetative when compared with larger rosettes which flower more frequently since it has been shown for a number of species that size is positively related to reproductive potential. Very large rosettes ($>70\text{cm}$) however, consistently have a somewhat lower probability of survival than those in the more medial diameter classes.

G- (or log likelihood ratio-) statistics were calculated for each 3-way contingency table (latitude x diameter x fate) in order to test the null hypothesis that the association between rosette diameter and fate does not differ by latitude (Kullback, 1959; Sokal and Rohlf, 1969). More precisely, the null hypothesis is that the pattern of joint frequencies in the 10×3 contingency tables showing diameter and fate do not differ among the three latitudes. It was found that latitude had a highly significant effect on the diameter-fate relationship for both field ($G=358$, 36df; $p < .001$) and common garden grown plants ($G=98$, 36df; $p < .005$).

Both field and garden data show the same two major patterns of variation among latitudes: 1) as latitude increases so does the likelihood that plants in the smaller rosette classes will remain vegetative, and 2) the proportion of small rosettes that flower the following year increases as one samples more southerly populations. The second of these is expressed both as a lower size threshold for flowering in southern populations and as a generally increased flowering probability in smaller size classes.

	Latitudinal Region											
	North (48-50°N)				North Carolina (34-36°N)				South (27-31°N)			
Rosette diameter classes (cm)	Probabilities of remaining			N	Probabilities of remaining			N	Probabilities of remaining			N
	dying	a rosette	flowering		dying	a rosette	flowering		dying	a rosette	flowering	
<5	1.000	0	0	26	1.000	0	0	5	1.000	0	0	7
5-10	.672	.328	0	61	.859	.141	0	71	.590	.115	.295	61
11-20	.483	.279	.239	201	.555	.146	.299	164	.461	0	.539	154
21-30	.487	.221	.292	298	.276	.050	.673	199	.422	.010	.567	201
31-40	.240	.083	.677	313	.086	.025	.888	197	.398	0	.602	226
41-50	.288	.028	.684	288	.208	.026	.766	231	.277	0	.723	184
51-60	.188	.006	.807	181	.252	.033	.715	123	.288	0	.712	139
61-70	.119	0	.881	59	.139	0	.861	36	.167	0	.833	72
71-80	.227	0	.773	22	.286	0	.714	7	.364	0	.636	33
81-90	0	0	0	0	0	0	0	0	.417	0	.583	12
<5-90	.354	.122	.522	1449	.305	.057	.638	1033	.376	.008	.616	1089

Table 1. The proportion of plants in ten rosette diameter classes that die, remain vegetative rosettes, or flower in the following growing season for mulleins studied in three latitudinal regions. N = total number of plants in each latitude – size class. The bottom row of the table gives the combined proportions of each fate in each latitude.

DISCUSSION

The latitudinal trends described in mullein's diameter-fate relationship can be understood as evolutionary responses to variation in length of the growing season. Small rosettes from southern populations that set fruit in the following growing season undergo a period of vegetative growth in their flowering season before bolting (flowering stalk elongation) is initiated (Reinartz, in prep.). The long growing season in the south allows these plants to grow and store adequate food reserves for flowering early in their flowering season and still have time to flower and set fruit later within the same season. Mulleins at the northern range limit must begin bolting as soon as growth is initiated in order to have ample time to set fruit within the same season.

Northern plants that lack adequate reserves to begin bolting at the beginning of the season remain vegetative for that season. Mid latitude mulleins are intermediate with respect to both of these observed differences. More rapid closure of successional communities in the south probably exerts a selective pressure against prolonging the period of vegetative growth. This type of pressure would not be as intense on northern mullein populations.

Reproduction success is normally thought to be a monotonically increasing function of plant size (Harper and White, 1974; Stearns, 1976). For this reason the lowered probability of survival of the very largest rosette diameter classes is an unexpected trend. A small number of the very large mullein rosettes have been observed to initiate a slight amount of internodal elongation very late in the growing season. This was especially evident in southern populations which do not have as strict a requirement for vernalization as those further north (Reinartz, in prep.). These plants almost always die. This evidence suggests that occasionally large plants begin their enzymatic shift to the bolting state (Gleir and Caruso, 1973; 1977) toward the end of a growing season resulting in a lowered ability to become winter hardy. These phenological "mistakes" associated with extreme plant size further suggest a causative relationship between size and the initiation of flowering.

Plasticity in the growth rate of *Verbascum thapsus* renders plant size a more valuable predictor of subsequent fate than plant age. Plant age does, however, have some use as a predictor for two reasons: 1) most rosettes reach the critical size for flowering during their first year and flower during their second and 2) plants remaining rosettes at the end of their third growing season have an increased probability of dying without flowering regardless of their diameter (Reinartz, in prep.). Mulleins that do not flower until their third or fourth year are with very few exceptions individuals that have grown slowly as a result of highly competitive or resource poor conditions (Reinartz, in prep.). Cohorts of mullein that contain a high proportion of "triennials" are typically those that germinated one or two years after the initial population was established. The apparent size threshold for flowering in *V. thapsus* suggests that the initiation of bolting must be dependent at least in part on the accumulation of adequate stored food reserves. Slow growing plants require a longer accumulation period.

Rosette diameter classes (cm)	Latitudinal Region											
	North (48-50°N)				North Carolina (34-36°N)				South (27-31°N)			
	Probabilities of remaining			N	Probabilities of remaining			N	Probabilities of remaining			N
	dying	a rosette	flowering		dying	a rosette	flowering		dying	a rosette	flowering	
<5	1.000	0	0	6	1.000	0	0	3	1.000	0	0	1
5-10	.867	.133	0	15	.886	.114	0	44	.619	.143	.238	21
11-20	.500	.220	.280	50	.547	.132	.321	106	.460	.020	.520	50
21-30	.507	.133	.360	75	.266	.047	.688	128	.431	.015	.554	65
31-40	.253	.051	.696	79	.077	.015	.908	130	.375	0	.625	72
41-50	.274	.014	.712	73	.216	.026	.758	153	.288	0	.712	59
51-60	.174	0	.826	46	.247	.025	.728	81	.333	0	.667	45
61-70	.200	0	.800	15	.174	0	.826	23	.500	0	.500	22
71-80	.167	0	.833	6	.500	0	.500	6	.625	0	.375	8
81-90	0	0	0	0	0	0	1.000	1	.500	0	.500	2
<5-90	.367	.077	.556	365	.302	.049	.649	675	.409	.014	.577	345

Table 2. The proportion of plants in ten rosette diameter classes that die, remain vegetative rosettes, or flower in the following growing season for mulleins grown in a common garden from seed collected in three latitudinal regions. N = total number of plants in each latitude – size class. The bottom row of the table gives the combined proportions of each fate in each latitude.

The exact correspondence of frequency patterns between the field study and common garden experiment show that the differences found in the diameter-fate relationship are the result of evolution of latitudinal ecotypes. Phenotypic variation resulting from field environmental conditions would not have been expressed under uniform garden conditions if this variation had not had a genetic basis. The fact that such a large component of the variation among latitudes has a genetic basis suggests that this complex of traits has been under intense selection.

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