Variable demography in relation to germination time in the annual plant *Tagetes micrantha* Cav. (Asteraceae)

Jorge González-Astorga[1,2] & Juan Núñez-Farfán[1,3]
[1]*Departamento de Ecología Evolutiva, Instituto de Ecología, UNAM, México, D.F., México (e-mail: far-fan@servidor.unam.mx); (*[2]*Present address: Jardín Botánico Clavijero, Instituto de Ecología, Veracruz, México;* [3]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA*

Abstract

This study tests whether variability in a life history trait such as emergence time has ecological and evolutionary significance in seasonal environments due to their relationship with fitness components. The population dynamics of nine different cohorts of seedlings emergence were analyzed in a natural population of the annual herb *Tagetes micrantha* Cav. (Asteraceae). Temporal variation in seedling emergence was related to the pattern of precipitation, while spatial variation could be related to topographical heterogeneity. Plants that emerged at the beginning of the season (early germination) had lower probabilities of survivorship than those that emerged at the end of the season (late germination). In contrast, plants that emerged early had, on average, higher fecundity than those that emerged late. The net result of these contrasting patterns of survival and fecundity constitute a life history trade-off in *T. micrantha*.

Introduction

Demographic studies deal with quantitative aspects of birth, growth, and mortality rates in populations (Harper 1977). Demographic studies of plants have attempted to describe population dynamics of species in particular habitats and to obtain insights regarding the microevolutionary processes that affect the life history parameters (Bradshaw 1984; Stearns 1977, 1992). Three such parameters that determine the temporal and spatial dynamics in annual plants (Symonides 1987) are seedling establishment, survivorship, and reproductive differences among adults. In particular, it has been demonstrated that variability in establishment could cause differences in fitness among annual plants (Baskin & Baskin 1972; Abul-Fatih & Bazzaz 1979; Marks & Price 1981; Watkinson 1981; Venable et al. 1987; Kalisz 1986; Molina 1986; Morales 1986; Cabrales-Vargas 1991; Philippi 1993) and, therefore, may promote life-history trade-offs

among fitness components (see Venable 1984; Kalisz 1986).

The timing of seed germination is a life history trait of early expression in plants' ontogeny, and thus is expected to affect many other characters of late expression, like fecundity and survivorship. Variation in germination time is related to seed morphology variation in *Heterosperma pinnatum*, and germination time is associated with fecundity and survival; also a trade-off between fecundity and survival has been documented (Venable et al. 1987). However, the importance the timing of germination has in determining the fitness of an individual relative to others in the population can not be anticipated without considering variation in environmental conditions. Venable (1984) proposed that the interplay between physical and biotic environmental variation might determine the mode of natural selection on germination time. For example, variability in the time of emergence could be affected by intra- and interspecific competition (Arthur et al. 1973). In addition, physical

factors like photoperiod, temperature, and soil moisture, also affect the timing of germination (Newman 1963; Cruden 1974; Baskin & Baskin 1985; Baskin & Baskin 1988). Environmental variation determines in a great extent how selection affects genetic variation and the evolution of ecologically important characters. The relationship between adaptive variability of organisms and variability in the environment is an issue of major importance for current studies of evolutionary ecology (Mosseau et al. 2000).

The goal of this study was to relate phenotypic variation in germination time of *Tagetes micrantha* in Central Mexico to environmental factors, and to determine how such variation affects two major components of fitness (survival and reproduction). *T. micrantha* is a summer annual that occurs in dense patches in the study region. Therefore, we hypothesized that early-germinating cohorts would have an advantage in fitness relative to late-germinating cohorts by minimizing negative effects of competition on survival and reproduction.

Methods

Plant species and study site

Tagetes micrantha (L.) Cav. (Asteraceae) is a small herbaceous (10–40 cm in height) annual plant species, distributed throughout Central Mexico and common in the mountains that surrounds the basin of Mexico City. Also, this species is found in New Mexico and Arizona (Rzedowski & Rzedowski 1985). *T. micrantha* is often found in open areas of pine-oak forests and in human disturbed places such as grasslands and paths. This study was carried out in the Pedregal de San Angel Ecological Preserve (84 ha), the southern limit of the Valley of Mexico (Rzedowski 1954). The site is rocky, with a highly complex topography produced by the consolidation of lava flows erupted from the Xitle volcano 2500 years ago. The vegetation is a xerophilous scrubland (Rzedowski 1954), with little soil development. Soil accumulates in small flat areas and in crevices, and in these places *T. micrantha*, together with grasses and other annuals, form dense stands in the summer (Núñez-Farfán et al. 1994). The site is markedly seasonal with average annual precipitation and temperature of 800 mm and 15.5 °C, respectively (García 1988). The rains commonly begin by the end of May, although it varies among years, and end by November.

Germination of *T. micrantha* occurs soon after the beginning of the rains or after a single storm (González-Astorga & Núñez-Farfán, pers. obs., 1988–1999). Germination continues until August. Having indeterminate growth, reproduction of *T. micrantha* begins early in the season and continues throughout November, when either drought or the first frost kills it.

Sampling

In the spring of 1989 (dry season), twenty randomly selected plots (25 × 25 cm) were established in an area of 20 ha that corresponds to the research zone of the Pedregal's Preserve. The emergence of seedlings of *T. micrantha* was monitored once the rains had begun. All seedlings that emerged in each plot after the first rains were marked with plastic, color-coded rings to indicate the cohort. By censusing the quadrats at about 10 days intervals, nine cohorts were distinguished.

Seedling survival was recorded every ten days, on average. At the end of the reproductive season, all surviving plants were collected and individually placed in paper bags to later determine the total number of seeds. Mortality data were used to construct cohort survivorship curves, and total seed number per plant of each cohort was used to obtain mean fecundity.

Data analysis

Association between precipitation and seedling emergence was tested by means of a regression analysis (Sokal & Rohlf 1995; Zar 1999). Spatial and temporal patterns of seedling emergence of *T. micrantha* were analyzed by obtaining the coefficient of aggregation $CA = \sigma^2/X$ where σ^2 and X are the variance and mean in the time of germination, respectively (Pielou 1977; Zar, 1999). For the spatial analysis, for a given census date, all seedlings emerged in each quadrat were taken into account. For the temporal analysis, data of seedlings emerged in a given quadrat through time were used. Deviations of CA from unity were tested by means of a *t*-test (Smith 1996). A sequential Bonferroni for multiple comparisons was carried out at an experimentwise error rate of 5% (Rice 1989; Sokal & Rohlf 1995).

To assess the dynamics of mortality through time, survivorship curves were analyzed by adjusting a log linear model (Healy 1988). The equation that describes mortality through time is $\ln N(t) = a + bt + ct^2$, where $N(t)$ is the number of surviving individuals at time t; a is the *y*-intercept and is related to the
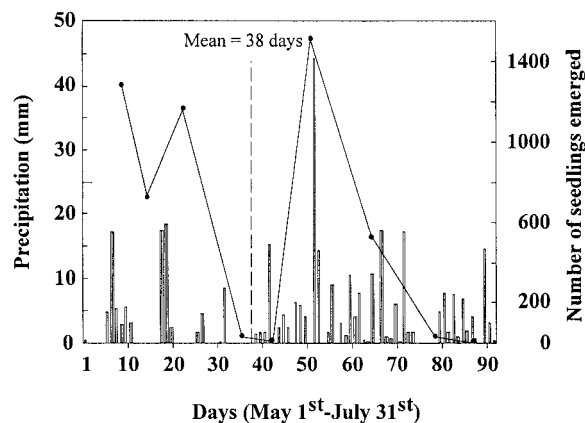
Figure 1. Temporal variation in seedling emergence of *Tagetes micrantha* (continuous line) in relation to precipitation (bars) in the Pedregal de San Angel, Mexico.

number surviving individuals at t_0 (N_0); b is the linear regression coefficient, which, if significantly different from zero, describes a type II mortality curve (constant mortality rate). Finally, c is the quadratic, non-linear, regression coefficient that if significant and negative suggest a type I survivorship curve (lower rates of mortality during young and juvenile stages). If c were positive, a type III survivorship curve is suggested and a higher rate of mortality in early stages is expected than the constant rate of mortality through time (Deevey 1947; Silvertown & Lovett Doust 1993). To assess the significance of linear and quadratic regression coefficients an experimentwise error rate ($\alpha = 0.05$) was carried out (Rice 1989).

Differences in average fecundity per plant among cohorts were assessed by means of a one-way ANOVA. Comparisons among cohorts were determined using the Student Newman-Keuls test (SNK) for multiple comparisons and the probability of Type I error was controlled using the Bonferroni adjustment procedure (Sokal & Rohlf 1995; Underwood 1997).
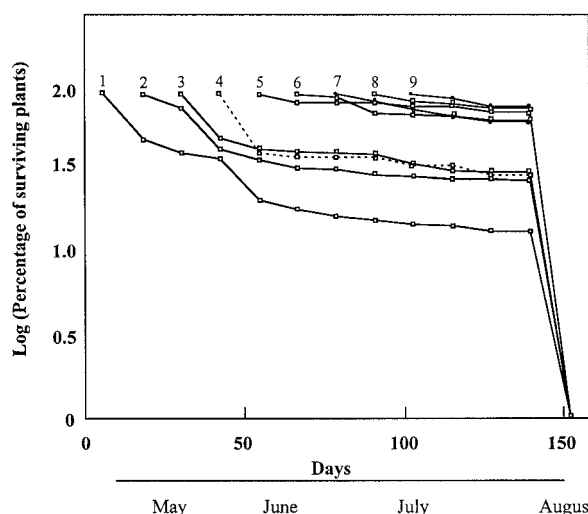

Figure 2. Survivorship curves for nine emergence cohorts in the annual plant *Tagetes micrantha* in the Pedregal de San Angel Preserve. Each number corresponds to that of cohort.

Results

Variable germination time

Germination of *T. micrantha* began at the onset of the rainy season (ca. May 9, 1989) and ended by the middle of rainy season (July 31). Sixty percent of the seedlings emerged during the first month (Table 1). Mean seedling emergence time was 38 days, although great variation was observed also (S.D. = 22.5 days; Figure 1). The pattern of seedling emergence showed a relationship with precipitation. A linear regression of the number of emerged seedlings per cohort as a function of the cumulative amount of rain between cohorts (i.e., every nine days) indicated a significant positive relationship ($F_{1,7} = 11.34$, $P = 0.012$), and explained about 62% of variance in seedling emergence ($R^2 = 0.618$).

Spatial and temporal variation in seedling emergence

Great spatial and temporal heterogeneity in seedling emergence was found (Table 2). Without considering mortality, densities attained values as high as 28.04 (quadrat 9) or as low as 0.88 seedlings cm^{-2} (quadrat 5). Similarly, the pulses of emergence varied from site to site on a given date or through time in a given site (Table 2). All the temporal and spatial aggregation coefficients, as estimated by the ratio Variance/Mean, were significantly higher than 1, indicating that seedling emergence in *T. micrantha* oc-

Table 1. Temporal dynamics of emerged plants of *Tagetes micrantha* in the in the Pedregal de San Angel Preserve during 1989.

Cohort	Date of emergence	Days after beginning of rains	Emerged seedlings	Cumulative number of plants (%)
1	May 9	5	1281	1281 (24.0)
2	15	11	753	2034 (38.0)
3	23	24	1146	3180 (59.6)
4	June 5	31	43	3223 (60.4)
5	12	38	17	3240 (60.7)
6	20	52	1518	4758 (89.2)
7	July 4	66	524	5282 (99.0)
8	18	73	32	5314 (99.6)
9	27	84	17	5331 (100)
			$\Sigma = \mathbf{5331}$	

Table 2. Spatial (among quadrats) and temporal (among dates, t_i) variation in seedling emergence of *Tagetes micrantha* in the Pedregal de San Angel, Mexico.

Quadrat	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	X	σ^2/X (temporal)	t_{obs}	Density (ind. cm^{-2})
1	16	79	81	1	0	1	17	0	0	21.67	52.64	292.11	7.80
2	19	102	23	7	0	4	24	0	0	19.89	52.64	292.09	7.16
3	4	19	103	1	1	14	55	1	8	22.89	52.20	289.65	7.92
4	3	20	92	1	1	13	43	2	0	19.44	48.18	266.87	7.00
5	17	8	0	0	0	0	0	0	0	2.78	12.76	66.52	0.88
6	30	0	0	0	0	0	0	0	0	3.33	30.00	164.05	1.20
7	15	30	59	4	0	34	121	2	1	29.56	53.13	294.89	10.64
8	7	7	25	0	0	4	0	0	3	5.11	12.54	65.30	1.84
9	236	230	123	4	5	90	11	2	0	77.89	124.20	696.93	28.04
10	48	82	104	14	2	29	17	2	0	33.11	42.70	235.89	11.92
11	40	5	5	0	0	18	0	2	0	7.78	23.04	124.67	2.80
12	21	19	100	4	0	71	63	10	1	32.11	41.45	228.84	11.56
13	32	38	82	1	1	81	76	0	2	34.78	38.28	210.87	12.52
14	144	26	58	5	5	145	2	5	1	43.44	83.14	464.63	15.64
15	263	56	43	0	0	130	7	0	1	55.56	142.48	800.35	20.00
16	133	17	7	1	0	3	0	0	0	17.89	105.91	593.46	6.44
17	19	1	44	0	0	308	43	0	4	46.56	213.51	1202.10	16.76
18	137	0	5	0	0	303	15	6	0	51.78	209.39	1178.80	18.64
19	15	0	101	0	2	173	16	0	0	34.11	110.46	619.19	12.28
20	85	14	91	0	0	97	14	0	4	33.89	55.28	307.05	12.20
X	64.0	37.6	57.3	2.1	0.8	75.9	26.2	1.6	–				
σ^2/X (spatial)	89.9	74.1	28.7	5.3	2.7	112	36.9	4.8	–				
t_{obs}	1252.2	1034.9	393.83	62.38	25.28	1581.0	509.75	44.36	32.81				

X, Mean number of recruited seedlings on each census time (see Table 1); σ^2/X, Coefficient of aggregation (CA); t_{obs}: t-Student observed, where $t_{obs} = (\sigma^2/X - 1)/(\sqrt{2}/n - 1)$. d.f. for spatial and temporal CA were 19 and 8, respectively. All CA were statistically significant greater than one ($P < 0.05$) after a sequential Bonferroni test.

Table 3. Coefficients of the log-linear fitted curves of the survivorship curve of each germination cohort of *T. micrantha* in the Pedregal de San Angel.

Cohort	Constant (a)	Linear coefficient (b)	Quadratic coefficient (c)
1	7.382*	−0.3646*	+0.01264*
2	6.887*	−0.3241*	+0.01083*
3	7.204*	−0.2734*	+0.00765*
4	3.693^{ns}	−0.1822*	+0.00226^{ns}
5	2.545^{ns}	+0.2103*	−0.03145^{ns}
6	7.048*	+0.2037*	−0.04278*
7	5.890*	+0.3164*	−0.06897*
8	2.908	+0.5614	−0.11830
9	2.152	+0.8292	−0.20190

*Significant at a 5% experimentwise error rate; $P < 0.01$, ns, non significant.

curred in pulses, both spatially and temporally (cf. Figure 1).

Survivorship

Pattern of survival differed between early and late cohorts. The first three cohorts had high mortality in the juvenile stages, while last cohorts showed high survival during the first stages (Figure 2). Globally, almost 40% (2103 out of 5331 plants) of the emerged plants survived until the end of the season. However, the first cohort had the lowest value of survival (14.2%), while the fifth and ninth cohorts had the highest (82%). In contrast, longevity was 154 days for plants the first cohort but only 74 days for those in the latest cohort (see Figure 2).

Log-linear adjustments of survival through time indicated significant and positive quadratic coefficients for the first three cohorts, suggesting a pattern of mortality type III (Table 3). In contrast, cohorts 6–7 showed a type I survivorship curve (negative *c* coefficient). Cohorts 4 and 5 had an intermediate pattern between cohorts 1–3 and 6–7. Finally, pattern of survival of the last two cohorts was similar to cohorts 6 and 7 but the coefficients were not significant due to the power of the test (i.e., fewer censuses for cohorts that emerged late).

Fecundity

A total of 2103 plants survived until the end of the season and significant differences in average fecundity per plant among cohorts of *T. micrantha* were found (one-way ANOVA; $F_{(8,2102)} = 97.06$; $P << 0.001$).
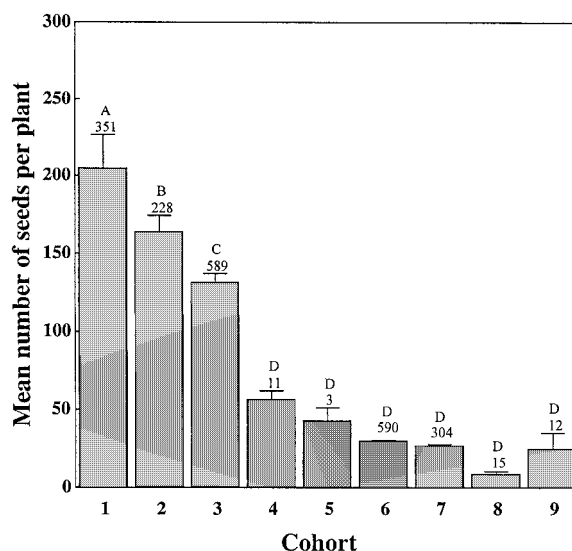

Figure 3. Average fecundity (+1 S.E.) of plants of *Tagetes micrantha* from different cohorts. Numbers above the bars represent the sample size and different letters indicate statistically significant differences ($P < 0.05$; see Methods).

The average fecundity of plants from the first three cohorts was an order of magnitude higher than that of cohorts fourth to ninth (Figure 3). Yet, average fecundity of the three first cohorts was significantly different among them, while the remaining cohorts did not differed in average fecundity per plant (Figure 3).

Discussion

The results of this study clearly demonstrated great temporal and spatial variability in germination time in the annual herb *Tagetes micrantha*. Furthermore, an ecological trade-off between survival and fecundity was detected in relation to seedling emergence time, as striking differences in survivorship and fecundity among cohorts were detected. Phenotypic variation in life history traits such as emergence time, is ecologically and evolutionarily important due to its effect in determining life-time fitness and how selection might affect fitness components (Baskin & Baskin 1972; Abul-Fatih & Bazzaz 1979; Marks & Price 1981; Watkinson 1981; León 1985; Kalisz 1986; Molina 1986; Morales 1986; Cabrales-Vargas 1991; Philippi 1993; Venable 1984; Venable et al. 1987).

Temporal and spatial variation in emergence time in Tagetes micrantha

It has been argued that heterogeneous environments promote the maintenance of phenotypic and genetic variation (Hedrick 1986). Thus, phenotypic variation in emergence time can be the result of both genetic variation (i.e., differences among genotypes) and phenotypic plasticity (see Schlichting & Pigliucci 1998). First, in the studied population, a close relationship between pattern of seedling emergence and amount of precipitation was found. Second, there here is evidence that genetic variation in emergence time exists in this population (González-Astorga & Núñez-Farfán, unpublished data). Thus, temporal variation in germination in this species can, in part, be the result of individual variation in the threshold level of soil moisture that triggers germination (see Dominguez & Dirzo 1995).

In contrast, spatial variation in germination is caused by the heterogeneity in topography and plant cover (e.g., rock versus small flat areas; pers. obs.). The highest densities of *T. micrantha* in the Pedregal of San Angel were found in sites with deeper soils without perennials (e.g., quadrats 13–15, 17–20), than in exposed rocky sites, with a thin soil layer (e.g., quadrats 5, 6, 8 and 11) (see Table 2). Spatial environmental heterogeneity can be of particular importance in producing variance in relative fitness among individuals, even at small scales (Kalisz 1986; Stratton 1994).

Temporal and spatial variation in plant density may promote competition within patches or microsites, and thus selective pressures may vary accordingly. Successful reproductive phenotypes in sites with deep soils can be unsuccessful in sites with rocky soils, and thus spatial variation in plant density may promote the evolution of phenotypic plasticity and/or the maintenance of genetic variation in germination time (Schlichting 1986; Sultan 1987).

Survivorship and fecundity

The results of this study demonstrate that variation in plant emergence time in *T. micrantha* produces a life history trade-off, with early emergence favoring the fecundity component of fitness and late emergence favoring the survival component. Thus, other factors being equal, natural selection should favor phenotypes that minimize survivorship costs and maximize average fecundity. We stress that the variable demography of the different cohorts of emergence has profound implications for the evolution of this life history trait. However, environmental heterogeneity (i.e., timing, pattern and amount of precipitation, microsites) suggests that the results of selection may vary temporally and spatially. Thus, in order to determine if variation in germination time is adaptive, the analysis of the mode, intensity, and direction of selection across generations is needed (Mosseau et al. 2000). Also, experimental studies are needed to determine the potential for the evolution of fitness reaction norms in relation to a varying environment (Schlichting & Pigliucci 1998).

Acknowledgements

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