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Seed Predation by Yucca Moths on Semelparous, Iteroparous and Vegetatively Reproducing Subspecies of Yucca Whipplei (Agavaceae)

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ABSTRACT: *Yucca whipplei* subspecies are distinguished by differences in reproduction: spp. *whipplei* and ssp. *parishii* are semelparous, flowering once and dying; ssp. *caespitosa* is iteroparous, producing multiple rosettes which may flower in different years; ssp. *percursa* has clonal reproduction from rhizomes, and ssp. *intermedia* is intermediate to the latter two. Seed loss due to the symbiotic yucca moth *Tegeticula maculata* was not evenly distributed among subspecies, nor was such predation correlated with the mode of reproduction. Rather, the number of moth larvae per capsule was significantly negatively correlated with distance from the coast and average annual temperature. The number of larvae per capsule varied from 0-14. All subspecies had a percentage of fruits lacking larvae; this percentage was largest in the two semelparous subspecies where nearly half of their fruits were without larvae. There is some evidence that this is the result of egg or larval mortality early in development. Within an inflorescence, larvae in individuals of some subspecies showed a highly clumped dispersion and others a highly uniform dispersion.

Introduction

Yucca species are common in desert and scrub vegetation throughout the southwestern United States. There are over 40 species, ranging in growth form from acaulescent rosettes to aborescents, and distributed in arid environments from sea level to above 2500 m. *Yucca whipplei* is an acaulescent rosette shrub widely distributed in southern California scrub vegetation. It differs from other species of *Yucca* by floral and fruit characteristics as well as aspects of its pollination and life history.

All species of *Yucca* are dependent upon the pollinator services of yucca moths, which in turn depend entirely on yucca flowers for oviposition sites (Davis, 1967). *Yucca whipplei* has a species of moth restricted to it. This moth, *Tegeticula maculata* (Lepidoptera:Incurvariidae), is one of three in the genus; of the others T. *synthetica* is restricted to *Y. brevifolia* and T. *yuccasella* is common to all other species of *Yucca* besides *Y. whipplei* (Davis, 1967).

Yucca whipplei is also the only species in the genus with typically semelparous (monocarpic) subspecies. Haines (1941) described five subspecies based on more or less geographically contiguous populations with characteristic reproductive modes (Fig. 1). The semelparous ssp. *whipplei* (*typica* of Haines) and *parishii* are distinguished by size. Both produce a rosette of leaves, and after years of vegetative growth, they send up a single flower stalk; following fruiting, the entire plant dies. Subspecies *caespitosa* is iteroparous, producing multiple (4 to > 100) densely packed rosettes arising from axillary buds early in development. These rosettes are all attached to a small caudex and the individual rosettes are homologous to branches that die after flowering. Flowering does not begin until all rosettes are produced and thus time to initial flowering may be much longer than in semelparous forms. In any given year zero to several rosettes on a single plant may flower and die and thus the plant flowers repeatedly over many years. Subspecies *percursa* is a semelparous form that also reproduces vegetatively by rhizomes that may extend several meters. Populations with individuals that combine characteristics of both of the latter taxa are described as ssp. *intermedia.*

Hoover (1973) found that populations of mixed growth form, including single rosette, caespitose and/or rhizomatous, may occur throughout the range of *Yucca whipplei.* Our observations indicate that a low percentage of the individuals in most populations of the "semelparous" ssp. *whipplei* actually produce multiple rosettes. Thus the designations semelparous, iteroparous and vegetatively reproducing attached to each subspecies are best considered as the modal, or most common, condition found in that taxon.

Webber (1953) provided limited evidence from common garden experiments that these growth forms are genetically controlled. The fact that populations of one predominant growth form may have a small proportion of other types suggests the dominant form is being selectively maintained in that region. The adaptive significance of these different reproductive modes is unknown. Because differential seed predation can affect plant recruitment and consequently plant distribution (Louda, 1982), it could also have a selective role in determining reproductive mode. The purpose of this study was to investigate differences among subspecies in the extent and pattern of seed predation by the symbiotic yucca moth to determine if there are differences related to reproductive mode.

METHODS

Mature capsules were collected from populations throughout the range of each subspecies during the summer of 1978 (*see* Appendix 1). When possible, 15 capsules per individual and 15 individuals per population were collected although total sample sizes for a population were ultimately determined by availability.

Capsules were opened and the number of *Tegeticula maculata* larvae counted. Capsule length and wall thickness were measured, the latter with a vernier caliper. Seeds per locule and seeds destroyed per larvae were also recorded.

Population and subspecies differences were statistically analyzed with a one-way ANOVA. Correlations were evaluated with the Pearson Product Moment Correlation Coefficient. Climatological data used in correlations were obtained for the nearest station for each population from the Climatological Summary published by the National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, N.C.

RESULTS

Seed and fruit characteristics were significantly different among *Yucca whipplei* subspecies (Table 1). Seed weight was not obviously related to reproductive mode, as the heaviest seeds were produced by one semelparous subspecies (*parishii*) and these were

TABLE 1.—Seed and fruit characteristics of *Yucca whipplei* subspecies

Subspecies	Seed weight (mg) $\bar{X} \pm$ SD (N)	Capsule length (mm) $\bar{X} \pm$ SD (N)	Capsule wall thickness (mm) $\bar{X} \pm$ SD (N)	Seeds/locule $\bar{X} \pm$ SD (N)
whipplei	17.6 ± 4.9 (134)	30.2 ± 4.8 (617)	0.54 ± 0.16 (660)	31.6 ± 4.4 (242)
parishii	21.3 ± 7.3 (94)	30.8 ± 7.0 (423)	0.59 ± 0.26 (465)	28.8 ± 6.0 (303)
caespitosa	18.1 ± 4.6 (74)	26.8 ± 3.9 (399)	0.55 ± 0.13 (370)	24.9 ± 3.9 (244)
intermedia	18.0 ± 3.7 (113)	25.9 ± 3.7 (558)	0.46 ± 0.11 (550)	24.9 ± 3.9 (224)
percursa	16.0 ± 4.3 (108)	26.4 ± 3.2 (611)	0.47 ± 0.13 (535)	26.5 ± 3.4 (221)
P	<0.01	<0.01	<0.01	<0.01

significantly heavier than those of the other semelparous subspecies (*whipplei*). Seed weight was significantly correlated with elevation and distance from the coast of the site of collection (Table 2). Capsule length and number of seeds per locule were significantly higher for the two semelparous subspecies *whipplei* and *parishii* (Table 1). Both of these characteristics were significantly correlated with elevation and distance from the coast (Table 2). Capsule walls were significantly thinner on those from the more northern and/or coastal subspecies (Tables 1 and 2).

Number of yucca moth larvae per capsule was quite variable, ranging from 0 - 14. All five subspecies had highly significant differences among populations (Table 3). Population means varied from one larva for every two capsules to over four per capsule. The number of larvae per capsule showed no obvious relationship to reproductive mode; the iteroparous ssp. *caespitosa* was more similar to the two semelparous subspecies than to the other two subspecies. The highest number of larvae per capsule was in the more northern and coastal taxa, ssp. *intermedia* and ssp. *percursa* (Table 3). Number of larvae per capsule was negatively correlated with elevation, distance from the coast, total annual precipitation and average temperature (Table 2).

The year after these data were collected a population of ssp. *caespitosa* and a population of ssp. *percursa* were recollected. There were significantly ($P<0.01$) fewer larvae per capsule in both populations in 1979 than in 1978, though in both years the number from the *percursa* population was significantly ($P<0.01$) greater than that from the *caespitosa* population.

The number of seeds destroyed per larva was not significantly different between subspecies (Table 4). Across all subspecies, it was negatively correlated with seed weight ($r = -0.14$, $P<0.01$, $N = 3249$). Generally, less than 10% of the seeds were destroyed in populations of both semelparous and iteroparous subspecies (Table 4). However, the more northern and coastal populations of the rhizomatous ssp. *percursa* lost close to a quarter of their seeds to the yucca moth.

Particularly striking was the large number of capsules lacking a yucca moth larva in the two semelparous subspecies; 41% and 45% in ssp. *whipplei* and ssp. *parishii*, respectively (Fig. 2). Subspecies *caespitosa* had 30% without larvae whereas many fewer capsules lacked larvae in ssp. *intermedia* and ssp. *percursa*, 16% and 11%, respectively.

The pattern of larval dispersion varied among subspecies. The number of larvae per capsule was scored for 15 capsules from the same inflorescence, and the dispersion of larvae within the inflorescence was then tested for fit to the Poisson Distribution. This was done for 15 individuals randomly selected from throughout the range of each subspecies. The two semelparous subspecies had no individuals which deviated from randomness. A third of the ssp. *caespitosa* and ssp. *intermedia* individuals deviated significantly ($P<0.05$ with the chi-square test) in the direction of uniform dispersion. Subspecies *percursa* showed great variability with four of the 15 individuals significantly ($P<0.05$) uniform and four significantly ($P<0.01$) clumped.

TABLE 2.—Correlations of *Yucca whipplei* seed, fruit and seed predation characteristics with elevation, distance from the coast and climatic parameters for all subspecies combined

	N	Elevation r	Distance from coast r	Total-annual precipitation r	Average Annual temperature r
Seed weight	523	0.13**	0.35**	-0.02^{ns}	0.27**
Capsule length	2608	0.24**	0.45**	−0.09**	0.22**
Capsule wall thickness	2580	0.22**	0.38**	−0.11**	0.20**
Seeds/locule	1234	0.16**	0.32**	−0.11**	0.06^{ns}
Larvae/capsule	3050	−0.13**	−0.10**	−0.11**	−0.21**
Seeds/larva	3249	0.07^{ns}	0.05^{ns}	−0.10**	−0.06*

$^{ns}P>0.05$, $^{*}P<0.05$, $^{**}P<0.01$

DISCUSSIONS

On average, *Tegeticula maculata* destroy a relatively small proportion of *Yucca whipplei* seeds. However, the extent of seed loss is not evenly distributed thoughout the species; some populations averaged fewer than one larva for every other capsule whereas other populations averaged more than four larvae per capsule. Within a population, in 1 year, some individuals suffer little seed loss from moth predation whereas others are damaged extensively. Even within some inflorescences, larvae were not distributed randomly; ssp. *percursa* had some capsules with as many as 12 larvae and other capsules with none. It is possible that the ssp. *percursa* populations, due to their more northern distribution, have a longer flowering period and thus different parts of the inflorescence are available at times of differing moth abundance (Powell and Mackie, 1966).

The extent of moth predation is not closely tied to the type of reproductive mode common to the subspecies. The greatest extent of larval predation occurs in the more coastal and northern populations and is inversely correlated to average annual temperature. This pattern is similar to that observed for nonsymbiotic moth predation in the southern Californian shrub *Haplopappus squarrosus* (Louda, 1982). Louda suggested that the more moderate climatic conditions of coastal sites enhanced moth survival and this may be an appropriate explanation for the pattern with *Tegeticula maculata*. The fact that capsule wall thickness also increases with increasing annual temperature may reflect selection for increased larval protection since poor larval survival could adversely affect pollination success.

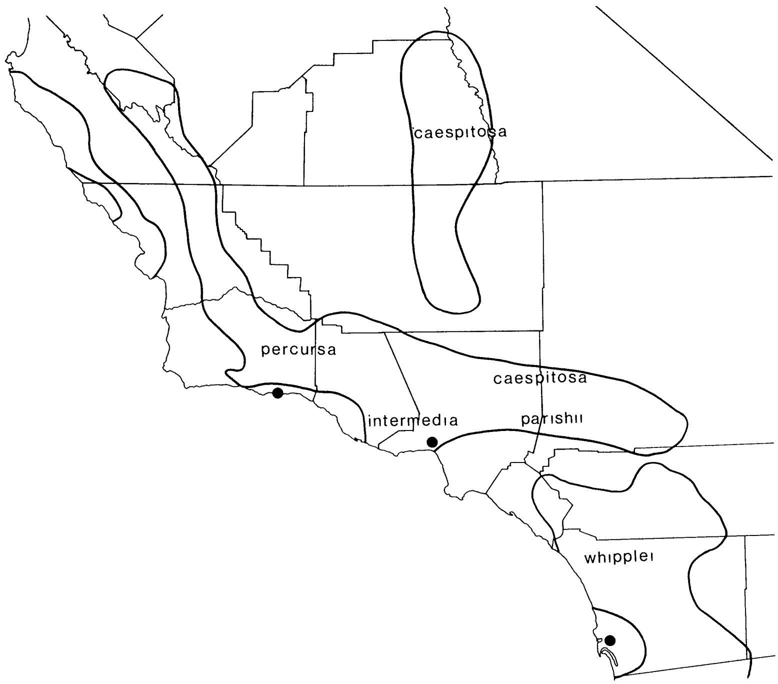

Fig. 1.—Geographical distribution of *Yucca whipplei* subspecies in southern California based on Haines (1941), Hoover (1973) and personal observations. (Localities indicated with dots are from left to right, Santa Barbara, Los Angeles, and San Diego.) Haines (1941) did not treat those populations in the southern Sierra Nevada though they appear to be quite similar to ssp. *caespitosa* with monocarpic individuals being frequent in most populations (J. Keeley, pers. observ.). Outside of California there are disjunct populations of monocarpic forms in Arizona and disjunct populations of multiple rosette forms in Baja California (Webber, 1953)

TABLE 3.—Number of *Tegeticula maculata* larvae per capsule for *Yucca whipplei* subspecies

Subspecies	Ssp. mean	Number	Larve/capsule Range of population means			P
			Lowest		Highest	
	$\bar{X}$ ± SD (N)	of populations	Pop. Id[1] $\bar{X}$ ± SD (N)		Pop. Id[1] $\bar{X}$ ± SD (N)	
whipplei	1.16 ± 1.30 (735)	14	(7) 0.50 ± 0.68 (20)	-	(6) 1.70 ± 1.50 (95)	<0.01
parishii	0.94 ± 1.08 (575)	7	(7) 0.48 ± 0.84 (85)	-	(1) 1.45 ± 0.94 (20)	<0.01
caespitosa	0.99 ± 0.95 (475)	7	(2) 0.69 ± 0.75 (145)	-	(7) 1.93 ± 1.34 (30)	<0.01
intermedia	1.83 ± 1.35 (645)	9	(6) 1.18 ± 0.70 (60)	-	(3) 2.06 ± 1.36 (105)	<0.01
percursa	2.61 ± 6.01 (620)	8	(1) 1.01 ± 1.03 (90)	-	(7) 4.43 ± 2.68 (40)	<0.01
P	<0.01					

[1]Population identification; locations are given in Appendix I

One characteristic that correlated with reproductive mode was the number of capsules lacking larvae; this was substantially greater for the two semelparous subspecies. Capsules with viable seeds (as shown by germination tests), but without *Tegeticula* larva, seem to be at odds with the dogma surrounding the obligate symbiosis between yuccas and their pollinator. Hypotheses that could account for capsules without larvae include: (1) those capsules were pollinated without the assistance (and oviposition) of *Tegeticula*; (2) *Tegeticula* pollinated those flowers but failed to oviposit in the ovary, or (3) *Tegeticula* pollinated them and oviposited in them but the egg or larva did not survive.

Data from the literature indicate that pollination without *Tegeticula* is not quantitatively important (Trelease, 1893; Coquillett, 1893; Wimber, 1958; Powell and Mackie, 1966; Acker and Udovic, 1981). Therefore, hypothesis #1 does not account for the large number of capsules lacking larvae encountered in this study.

Pollination by *Tegeticula*, but without oviposition, does occur (Wimber, 1965; Acker and Udovic, 1981), and may account for some of the capsules lacking larvae; therefore, hypothesis #2 cannot be ruled out. Why this might occur more commonly in the two semelparous subspecies is unknown.

Hypothesis #3 can account for some of the capsules lacking larvae. This is based on the observation that the moth oviposition leaves a scar on the external ovary wall (Trelease, 1893; Powell and Mackie, 1966). In our study the vast majority of capsules "lacking" larvae had an oviposition scar. Close examination showed that connected to this scar was a scar across the internal ovary wall and frequently, a barely developed but dead larva on the inside wall. Apparently, parasitism is not the cause of mortality (Davis, 1967). Why poor egg or larval survival would occur more frequently in semelparous subspecies needs further study.

In conclusion, there is no compelling evidence that differential seed predation by the yucca moth has affected the selection of reproductive modes in *Yucca whipplei* subspecies. Semelparous taxa do produce larger capsules with more seeds, and overall seed destruction tends to be lower than in other taxa. However, it is not known whether or not subspecies differ in total seed production per plant. Observations suggest there are no consistent differences in this regard, but demonstrating this is difficult since *Yucca whipplei* populations show tremendous annual variability in flowering and fruiting. The semelparous forms differ from other taxa in that a much greater proportion of their capsules escape seed predation entirely. The fact that this appears to stem from poor larval survival raises the intriguing question of whether or not certain *Yucca whipplei* taxa have the ability to affect larval survival and thus regulate moth density.

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TABLE 4.—Seed destruction by *Tegeticula maculata* larvae for *Yucca whipplei* species

Subspecies	Seeds/larva $\bar{X} \pm$ SD (N)	Percentage of seeds destroyed[1] Lowest population	Highest population
whipplei	9.7 ± 3.1 (833)	2.5	8.7
parishii	8.5 ± 2.5 (525)	2.4	7.1
caespitosa	9.0 ± 2.7 (253)	4.2	11.6
intermedia	8.6 ± 3.4 (1090)	6.8	11.9
percursa	8.8 ± 4.1 (548)	5.6	24.5
	$P<0.01$		

[1]Calculated as (seeds/larva) x (larvae/capsule) ÷ (seeds/locule) x (6 locules)

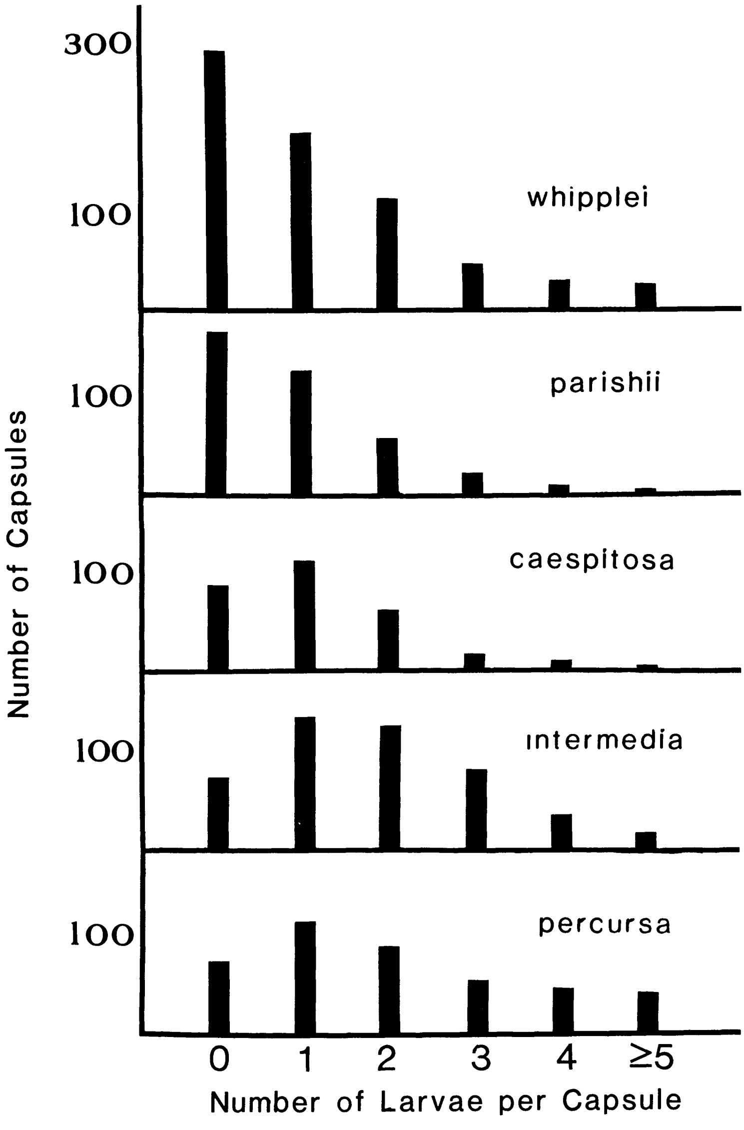

Fig. 2.—Distribution of number of *Tegeticula maculata* larvae per capsule for *Yucca whipplei* subspecies

APPENDIX I

LOCATIONS OF YUCCA WHIPPLEI POPULATIONS

	Elevation (m)	Distance from coast (km)
ssp. *whipplei*		
1. Modjeska Canyon Road, Orange Co.	450	22
2. Lake Elsinore, Riverside Co.	450	30
3. R-3 So. of Hemet, Riverside Co.	450	60
4. Hwy. 243 N of Idyllwild, Riverside Co.	750	85
5. Banner, San Diego Co.	925	70
6. Fallbrook, San Diego Co.	300	20
7. Ramona, San Diego Co.	450	50
8. Poway, San Diego Co.	600	17
9. Lomas, Santa Fe, San Diego Co.	50	2
10. Lawson Valley, San Diego Co.	625	35
11. Guatay, San Diego Co.	1500	65
12. Dulzura, San Diego Co.	575	35
13. Tecate, San Diego Co.	700	38
14. Campo, San Diego Co.	775	60
ssp. *parishii*		
1. Head of San Gabriel Canyon, Los Angeles Co.	925	45
2. Mouth of San Gabriel Canyon, Los Angeles Co.	450	45
3. La Canada, Los Angeles Co.	760	40
4. Angeles Crest Hwy, Los Angeles Co.	1500	50
5. Redlands, San Bernardino Co.	425	120
6. W of Mountain Home Village, San Bernardino Co.	1225	140
7. N of Highland, San Bernardino Co.	925	130
ssp. *caespitosa*		
1. Agua Dulce, Los Angeles Co.	750	60
2. Escondido Canyon, Los Angeles Co.	750	60
3. Hubbard Road, Los Angeles Co.	750	60
4. Aliso Canyon, Los Angeles Co.	975	60
5. Big Pines, Los Angeles Co.	1225	75
6. Mt. Gleason, Los Angeles Co.	1675	55
7. Placerita Canyon, Los Angeles Co.	600	50
ssp. *intermedia*		
1. N of San Fernando Pass, Los Angeles Co.	600	50
2. Glendale, Los Angeles Co.	250	30
3. Coldwater Canyon Rd, Los Angeles Co.	300	15
4. Las Virgenes Rd, Los Angeles Co.	150	5
5. Encinal Canyon Rd, Los Angeles Co.	450	5
6. W of Cabrillo State Beach, Ventura Co.	50	1
7. Camarillo, Ventura Co.	75	15
8. Moorpark, Ventura Co.	250	25
9. Piru, Ventura Co.	250	45
ssp. *percursa*		
1. S end of Cuyama Valley, Ventura Co.	1100	50
2. S of Refugion Rd, Santa Barbara Co.	350	5
3. S of Buelton, Santa Barbara Co.	250	10
4. Happy Canyon Rd, Santa Barbara Co.	400	25
5. N end of Cuyama Valley, San Luis Obispo Co.	300	30
6. Twitchell Reservoir, San Luis Obispo Co.	150	10
7. W of Morro Bay, San Luis Obispo Co.	1025	75
8. W of Priest Valley, Monterrey Co.	450	70

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