Notes and Discussion

Seed Predation Due to the Yucca-moth Symbiosis

Abstract: All species of *Yucca* (Agavaceae) require the pollinator services of a species of moth in the genus *Tegeticula* (*Lepidoptera*: Incurvariidae). These moths oviposit in the ovary of the plants and the larvae are entirely dependent upon *Yucca* seeds for food. The extent and distribution of larval seed predation was examined in nine *Yucca* species in the southwestern United States. The proportion of seeds destroyed by the yucca moth ranged from 3% in *Y. schidigera* from coastal southern California to 45% in one population of *Y. angustissima* from southern Utah. This sampling was done in 1979 at which time the *Y. schidigera* population averaged 0.6 larvae per fruit and the population of *Y. angustissima* averaged 9.3 larvae per fruit. A second sampling of these populations in 1982 averaged 0.5 for *Y. schidigera* and 5.6 for *Y. angustissima.* Several species showed significant differences between populations in the number of larvae per fruit. Contrary to expectation, based on the dogma that fruit production is dependent upon *Tegeticula* pollination (which is always followed by oviposition), a large number of fruits were found without larvae. The proportion varied greatly between populations but was as high as two thirds of all fruits in some populations. Observations suggested that these flowers had been pollinated by *Tegeticula* and the moths had oviposited in them but that the eggs failed to hatch.

Introduction

The *Yucca*-moth pollination interrelationship is a classical example of symbiosis. There are over 40 species of *Yucca* (Agavaceae) and apparently all are completely dependent upon the pollinator services of a species of moth in the genus *Tegeticula* (Lepidoptera:Incurvariidae). These moths in turn are entirely dependent upon *Yucca* seeds as food for their developing larvae.

Three species of *Tegeticula* are currently recognized: *T. maculata* specific for *Yucca whipplei, T. synthetica* specific for *Y. brevifolia* and *T. yuccasella* common to all the remaining *Yucca* species (Davis, 1967). All three moths have broadly similar behaviors (Riley, 1892; Trelease, 1983; Powell and Mackie, 1966; Aker and Udovic, 1981). Adults emerge in the spring (or early summer) in association with the flowering of the local *Yucca* species. Following copulation within the *Yucca* flower, the female gathers pollen and flies to another *Yucca* plant. Immediately after ovipositing in the ovary of the *Yucca* flower the female moth deposits part of her pollen on the stigma of the same flower. The egg hatches in a week and the larva feeds on the developing ovules. At approximately the time of fruit ripening the larva bores a hole through the ovary wall and exists by lowering itself to the ground on a silk thread.

The extent of seed loss incurred by the *Yucca* plant has not previously been studied in detail. George Engelmann (who published the first account of the *Yucca*-moth interrelationship in 1872) stated in some unpublished notes that in one capsule he found half a dozen larvae and "all the seeds eaten" (Anonymous, 1974). Trelease (1893) noted that a female deposits no more than six eggs to an ovary "so that there is rarely more than one larva to each tier (locule) of seeds and consequently a fair percentage of seeds are allowed to come to maturity." Riley (1892), however, found as many as 21 larvae in a single fruit. Rau (1945) noted in *Y. filamentosa* the number of *Tegeticula yuccasella* larvae per fruit varied from 0-12 with an average of 4.9. He found that each larva destroyed 18-25 seeds and in some fruits all seeds were destroyed, whereas others had "hundreds of good seeds ready for dissemination." Powell and Mackie (1966) found that *Yucca whipplei* fruits harbored 0.4 larvae per fruit and consumed an average of 14.3% of the seeds. For *Y. filifera,* Davis (1967) found "one or two larvae per pod (sometimes none) and rarely over three." Wallen and Ludwig (1978) noted for *Y. baccata* that "of the seeds in infected fruits," 27% were consumed by yucca moth larvae, with an average of 7.5 larvae per fruit.

The purpose of this study was to gather information on the extent of seed predation by *Tegeticula* larvae for nine *Yucca* species in the southwestern U.S. and to determine whether differences in extent of predation were related to fruit or seed characteristics. The species were selected to represent most of the range of variation in the genus with respect to fruit type (baccate and capsular), growth form (acaulescent to arborescent), elevational distribution (0-2500 m), vegetational types (desert scrub, grassland, woodland) and geographical distribution (California to Texas).

METHODS

Fruits were collected from populations of the nine *Yucca* species described below during early August 1979. Sample sizes were largely determined by availability of material. Less common species and ones which fruited poorly in 1979 were sampled less than others.

Fruits were opened and examined for *Tegeticula* larvae and, for a subsample, the number of seeds destroyed by a single larva was recorded. Fruit length was measured and, for a subsample the number of seeds in one of the six locules was recorded. Weights also were recorded for a sample of air-dried seeds.

In some populations of *Yucca angustissima* and *Y. glauca* the seeds had begun to disperse and so the number of larvae was estimated by recording exit holes in the fruit. This is a reliable estimate as all *Tegeticula* larvae leave just a single exit hole. Potentially this could overestimate the number of *Tegeticula* larvae since it is not known if other insects produce such holes in the *Yucca* fruit. Occasionally other larvae were encountered in fruits, but these were easily distinguished from the very distinctive *Tegeticula* larvae.

A smaller sampling of fruits was made in July 1982. At this time the species with the highest number of larvae per fruit and the species with the lowest number of larvae (from the 1979 sampling) were resampled to assess the extent of year-to-year consistency in *Yucca* moth seed predation. *Yucca angustissima* was one of the two species resampled, and at this time all fruits were collected prior to seed dispersal and thus direct observation of *Tegeticula* larvae (rather than exit holes) was possible.

Yucca species.—Five indehiscent baccate fruited species (*Yucca baccata, Y. brevifolia, Y. schidigera, Y. schottii, Y. torreyi*) and four dehiscent capsular fruited species (*Y. angustissima, Y. elata, Y. glauca, Y. reverchoni*) were studied (names according to Webber, 1953). Populations sampled are shown in Appendix I. *Yucca baccata* is an acaulescent species ranging from southeastern California to SE Texas (750-2200 m) in grassland and open woodlands. *Yucca brevifolia* is a desert scrub tree of southeastern California, western Arizona and southern Utah (450-1800 m). *Yucca schidigera,* a low caulescent species commonly associated with chaparral and other scrub vegetations, ranges from coastal southern California to Arizona (0-1800 m). Only coastal populations from southern California were sampled as nearly all interior populations failed to fruit in 1979. *Yucca schottii* is an arborescent component of oak woodlands of southeastern Arizona and adjacent New Mexico (1200-2100 m). *Yucca torreyi* is a caulescent species of open scrub in New Mexico and Texas (600-1500 m).

Yucca angustissima, an acaulescent species of grasslands and open scrub vegetation is distributed from N-central Arizona to southern Utah (750-2300 m). *Yucca elata* is an arborescent species of desert grasslands and scrub vegetation ranging from western Arizona to central Texas (450-1800 m). *Yucca glauca* is an acaulescent species widely distributed in grasslands throughout the plains states (200-2200 m). *Yucca reverchoni* is an acaulescent plant of rocky, open, scrub vegetation in central and southern Texas (300-1300 m).

RESULTS

Seed and fruit characteristics were not significantly different ($P > 0.05$) between populations of the same species and, therefore, are presented by species in Table 1. The species with fleshy baccate fruits had larger fruits and fewer, heavier seeds than the species with dry capsules. Seed weight varied between species by more than an order of magnitude (8-139 mg), and was positively related to fruit length ($r = 0.86$, $p < 0.01$, $N = 9$) with the Pearson Product Moment Correlation and negatively correlated with number of seeds per locule ($r = -0.75$, $P < 0.01$, $N = 9$).

The average number of *Tegeticula* larvae per fruit for the 23 populations of *Yucca* ranged from less than one to more than nine (Table 2). Four of the species had significant population differences in number of larvae per fruit. However, the number of seeds destroyed per larva did not differ between populations of the same species (data not shown). For baccate species the average number of seeds per larva ranged from 6.0-8.9 and from 14.8-19.6 in capsular species, and is undoubtedly a function of seed size; seed weight was negatively correlated with seeds destroyed per larva ($r = -0.85$, $P < 0.01$, $N = 9$).

The percentage of seeds destroyed by *Tegeticula* for the 23 populations (Table 2) was estimated as the (number of larvae per fruit X seeds per larva) ÷ (seeds per locule X 6). Clearly, the impact of *Tegeticula* is quite variable, ranging from 3-45% of the seed production. In some species, seed loss occurred from other causes such as seed abortion or other predators (not quantified here), and thus the impact of *Tegeticula* seed predation might represent a somewhat greater proportion of the seeds actually dispersed.

Even within populations the extent of damage from *Tegeticula* was quite variable. The distribution of larvae among fruits showed a highly significant departure from the Poisson Distribution for 19 of the 23 populations (four populations were excluded due to the small sample size). In all instances the departure from randomness was in the direction of clumped (as evidenced by the $\frac{S^2}{\bar{X}} > 1$). Within the same population some fruits had as many as 16 larvae whereas others were completely free of *Tegeticula* (Table 2). In fact, in the majority of populations 33% or more of the fruits lacked larvae entirely and in some populations up to 66% of the fruits were free of *Tegeticula* (Table 2).

A 2nd-year sampling of the number of *Tegeticula* larvae was made for population ii of *Yucca angustissima,* which had the highest number of larvae per fruit, and for population ii of *Y. schidigera,* which had one of the lowest numbers of larvae per fruit.

In this second sampling the *Yucca angustissima* population remained higher than any of the previously sampled populations ($\bar{X} = 5.6 \pm 4.4$, n = 75) and the *Y. schidigera* population was lower ($\bar{X} = 0.5 \pm 1.5$, n = 75) than other previously sampled populations.

DISCUSSION

In light of the dogma surrounding the *Yucca*-moth symbiosis, the observation of large numbers of fruits with viable seeds (as shown by germination experiments) but without a *Yucca* moth larva is surprising. Hypotheses that could account for such a large proportion of fruits lacking larvae include: (1) These fruits resulted from self-pollination or pollination by agents other than *Tegeticula;* (2) *Tegeticula* pollinated these fruits but failed to oviposit in them, or (3) *Tegeticula* pollinated and oviposited in them but the egg or young larva died.

The possibility of self-pollination or pollination by agents other than *Tegeticula* has been examined for various *Yucca* species (for review, *see* Wimber, 1958; Powell and Mackey, 1966; Davis, 1967). In summary, most species are self-compatible to some degree and a few species apparently have a very limited capacity for self-pollination, though this seems to be quantitatively insignificant. Other insects are known to visit *Yucca* flowers, but none have been observed to act as pollinators. The general consensus in the literature seems to be "that the great majority of yuccas would never bear fruit if it were not for the deliberate act of pollination performed by the *Tegeticula* moths" (Davis, 1967). If this is true, then the absence of larvae in a fruit is most likely due to either the failure of *Tegeticula* to oviposit successfully or produce viable larvae as suggested by hypotheses 2 and 3. Observations made on *Y. schidigera* fruits in 1982 suggest that indeed egg and/or larval viability may be the major reason for fruits lacking larvae. This is based on the fact that in many yuccas the female yucca moth often causes a noticeable constriction of the fruit due to tissue damage at the site of oviposition (Riley, 1892; Trelease, 1893; Webber, 1953). Examination of mature *Y. schidigera* fruits lacking larvae revealed that all had a prominent constriction associated with scar tissue extending across the ovary wall. Microscopic examination of a

TABLE 1.—Seed and fruit characteristics for the nine *Yucca* species

	Seed weight (mg)	Fruit length (mm)	Seeds/locule
	$\bar{X} \pm$ SD(n)	$\bar{X} \pm$ SD(n)	$\bar{X} \pm$ SD(n)
Baccata species			
Y. baccata	$93^a \pm 21$ (54)	$89^a \pm 32$ (39)	$23^{ab} \pm 7$ (4)
Y. brevifolia	$99^a \pm 21$ (100)	$69^b \pm 9$ (155)	$26^a \pm 3$ (31)
Y. schidigera	139 ± 38 (100)	$87^a \pm 16$ (161)	$20^b \pm 4$ (35)
Y. schottii	28 ± 11 (100)	$65^b \pm 18$ (145)	$23^{ab} \pm 8$ (106)
Y. torreyi	117 ± 32 (100)	73 ± 19 (299)	$20^b \pm 6$ (55)
Capsular species			
Y. angustissima	23 ± 6 (100)	56 ± 11 (226)	$51^c \pm 8$ (16)
Y. elata	$17^b \pm 6$ (100)	49 ± 12 (454)	$50^c \pm 9$ (89)
Y. glauca	$16^b \pm 4$ (100)	52 ± 8 (80)	$53^c \pm 11$ (17)
Y. reverchoni	8 ± 3 (100)	34 ± 6 (182)	34 ± 8 (39)
P	<0.01	<0.01	<0.01

Species with the same superscript are not significantly different ($P > 0.05$ with Fisher's LSD) subsample showed the presence of the very distinctive *Tegeticula* egg where the oviposition scar terminated on the inside of the ovary wall. Thus, these fruits were apparently pollinated by *Tegeticula* and oviposited in but the egg did not hatch.

The fact that some populations of *Yucca* have many fruits free of *Tegeticula* larvae and other populations have few fruits lacking larvae may be related to a number of reasons. Perhaps populations of *Tegeticula* in some regions have lower egg viability than populations in other regions or possibly a certain level of egg viability is common throughout the range of *Tegeticula* and thus the proportion of fruits lacking larvae is a function of moth density. On the other hand, some *Yucca* populations may be capable of inhibiting the hatching of *Tegeticula* eggs and thus "regulating" *Tegeticula* densities in their population.

TABLE 2. — *Tegeticula* larvae per fruit and estimated percentage of seeds destroyed for populations of the nine *Yucca* species. The range of number of *Tegeticula* larvae per fruit and percentage of fruits without larvae are given for each population

	Population	$\bar{X} \pm$ SD (n)	Percentage of seeds destroyed	Range of larvae/fruit	Percentage of fruits without larvae
Baccata species					
Y. baccata	i	$2.1 \pm 2.8(15)^{cd}$	10	0-7	27
	ii	$2.5 \pm 4.4(24)^{cde}$	12	0-16	58
Y. brevifolia		$1.4 \pm 1.5(155)^{c}$	7	0-6	39
Y. schidigera	i	$0.6 \pm 0.9(80)^{a}$	3	0-4	65
	ii	$0.6 \pm 0.9(81)^{a}$	3	0-4	64
Y. schottii	i	$0.7 \pm 1.1(83)^{ab}$	5	0-5	64
	ii	$1.6 \pm 1.6(62)^{c}$	10	0-5	31
Y. torreyi	i	$1.1 \pm 1.8(49)^{abc}$	8	0-7	49
	ii	$0.8 \pm 1.4(74)^{ab}$	6	0-7	68
	iii	$0.6 \pm 1.0(57)^{a}$	4	0-3	68
	iv	$1.6 \pm 1.7(119)^{c}$	11	0-8	42
Capsular species					
Y. angustissima	i	$3.2 \pm 2.4(51)^{ed}$	15	0-11	6
	ii	$9.3 \pm 4.4(48)$	45	3-17	0
	iii	$4.8 \pm 4.4(131)$	23	0-15	11
Y. elata	i	$3.4 \pm 2.8(118)^{e}$	22	0-12	10
	ii	$1.1 \pm 1.4(80)^{bc}$	7	0-9	48
	iii	$2.2 \pm 1.4(26)^{cd}$	14	0-11	35
	iv	$1.5 \pm 1.3(119)^{c}$	10	0-4	29
	v	$1.2 \pm 1.8(25)^{bc}$	8	0-3	36
	vi	$1.8 \pm 2.7(88)^{c}$	12	0-16	49
Y. glauca		$1.4 \pm 1.9(80)^{c}$	7	0-8	50
Y. reverchoni	i	$2.2 \pm 2.0(47)^{cd}$	18	0-7	30
	ii	$1.5 \pm 1.7(135)^{c}$	12	0-7	39

Species with the same superscript are not significantly different ($P > 0.05$ with Fisher's LSD)

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APPENDIX 1.—Location of *Yucca* populations used in this study

Baccata species		Population
Y. baccata	i.	Southeastern boundary of Zion National Park, Kane Co., Utah
	ii.	10 km W of Payson, Gila Co., Arizona
Y. brevifolia		5 km W of Lancaster, Los Angeles Co., California
Y. schidigera	i.	5 km W of Leucadia, San Diego Co., California
	ii.	5 km NE of National City, San Diego Co., California
Y. schottii	i.	East boundary of Chiricahua National Monument, Cochise Co., Arizona
	ii.	Portal, Cochise Co., Arizona
Y. torreyi	i.	Quitman Mountains, E of McNary, Hudspeth Co., Texas
	ii.	20 km E of Marathon, Brewster Co., Texas
	iii.	15 km E of Marathon, Brewster Co., Texas
	iv.	30 km E of Marathon, Brewster Co., Texas
Capsular species		
Y. angustissima	i.	5 km W of Hurricane, Washington Co., Utah
	ii.	Southeastern boundary of Zion National Park, Kane Co., Utah
	iii.	30 km S of Page, Coconino Co., Arizona
Y. elata	i.	20 km SE of Fredonia, Coconino Co., Arizona
	ii.	10 km E of Camp Verde, Gila Co., Arizona
	iii.	35 km NE of Globe, Gila Co., Arizona
	iv.	Oracle Junction, Pinal Co., Arizona
	v.	Wilcox, Cochise Co., Arizona
	vi.	Paradise, Cochise Co., Arizona
Y. glauca		75 km W of Clinton, Roger Mills Co., Oklahoma
Y. reverchoni	i.	15 km W of Eldorado, Schleicher Co., Texas
	ii.	50 km S of Vernon, Wilbarger Co., Texas

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