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Inter- and Intralocular Distribution of Yucca Moth Larvae in *Yucca whipplei* (Agavaceae)

Pollination of *Yucca* species is dependent upon the services of a moth in the genus *Tegeticula* (Trelease 1893). In this mutualistic relationship the moth is in turn dependent upon the flowers for oviposition sites. Previous studies have shown that the number of moth larvae, and consequently seed loss, are highly variable, among *Yucca* species (Keeley et al. 1984).

Yucca whipplei is a common species on shallow soils throughout the foothills of southern California and the southern Sierra Nevada. This species is distinct from other yuccas in that it is the only one with monocarpic reproduction, i.e., dying after reproduction, (at least in two of the five subspecies, see Haines 1941). In addition, while the majority of *Yucca* species are pollinated by *Tegeticula yuccasella, Y. whipplei* has a different species of moth (*T. maculata*) restricted to it. A recent study of yucca moth seed predation on *Yucca whipplei* (Keeley et al. 1986 press) has shown that the distribution of moth larvae is highly variable, among subspecies, among individuals within populations, and even among capsules within an inflorescence.

This variation prompted an investigation into the distribution of moth larvae within the fruits of *Yucca whipplei.* Two questions are addressed. 1) For fruits with more than a single moth larva, are the larvae randomly distributed among the six locules in the fruit? 2) Within a locule, are larvae randomly distributed along the length of the capsule?

Methods

Mature capsules were collected from plants throughout the range of *Yucca whipplei* (see Keeley et al. 1986 for localities). Capsules were opened and the relative distribution of larvae within capsules was indicated by numbering each of the six locules beginning with the first locule in which a larva was encountered and noting this number for each subsequent larva. Distribution of larvae within locules was described by measuring the distance from the base of the capsule to the nearest seed destroyed.

Results

To determine if multiple larvae within a capsule were randomly distributed between locules, the number of capsules with only two larvae were used to determine the proportion of larvae in the adjacent locule vs. nonadjacent locules. If larvae are randomly distributed in a capsule with six locules, the probability that a second larva would be adjacent to an occupied locule would be 2/5, and 3/5 that it would occur in a non-adjacent locule. The Chi-square test for goodness of fit showed no significant departure from expectation ($P > 0.05$, $N = 180$). Thus, moth larvae were randomly distributed among locules within a capsule.

The distribution of larvae within a single locule, however, was highly skewed.

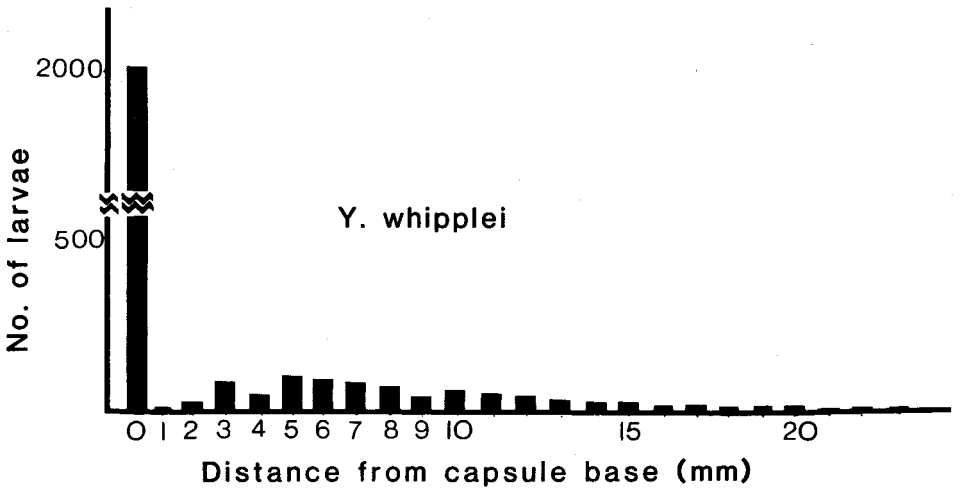

Fig. 1. Distribution of *Tegeticula maculata* larvae within locules of *Yucca whipplei* fruits (sample size: N = 2912 larvae).

The Chi-square tests for goodness of fit showed a highly significant departure from normality ($P < 0.01$). As seen in Fig. 1, the vast majority of moth larvae in *Yucca whipplei* fruits were situated at the base of the capsule.

Due to this very skewed distribution the question arose as to whether this was a characteristic of *Yucca* species in general. The intralocular distribution of larvae was determined from data collected previously (Keeley et al. 1984) for nine other *Yucca* species from the southwestern U.S. These included species with dehiscent capsular fruits (*Y. angustissima, Y. elata, Y. glauca, Y. reverchoni*) and species with indehiscent baccate fruits (*Y. baccata, Y. brevifolia, Y. schidigera, Y. schottii, Y. torreyi*). Fig. 2 shows the intralocular distribution of larvae for one of these

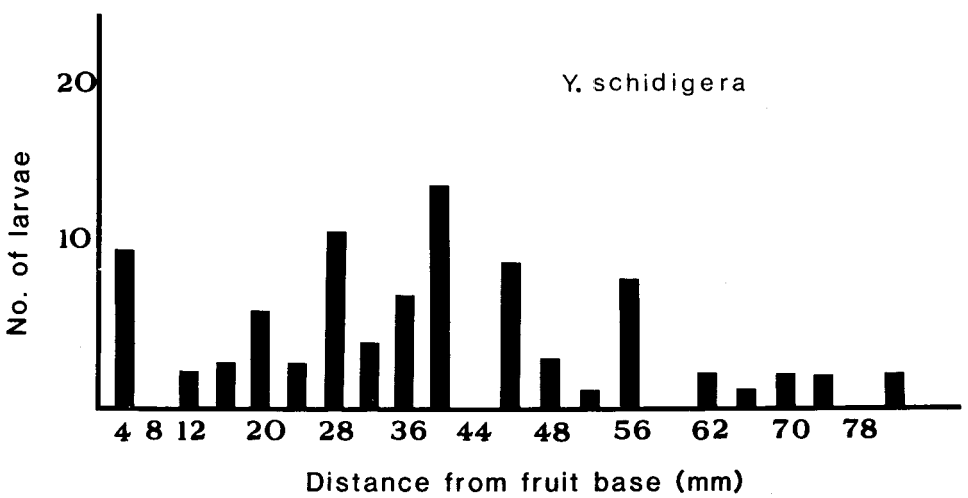

Fig. 2. Distribution of *Tegeticula yuccasella* larvae within locules of *Yucca schidigera* fruits (sample size: N = 82 larvae).

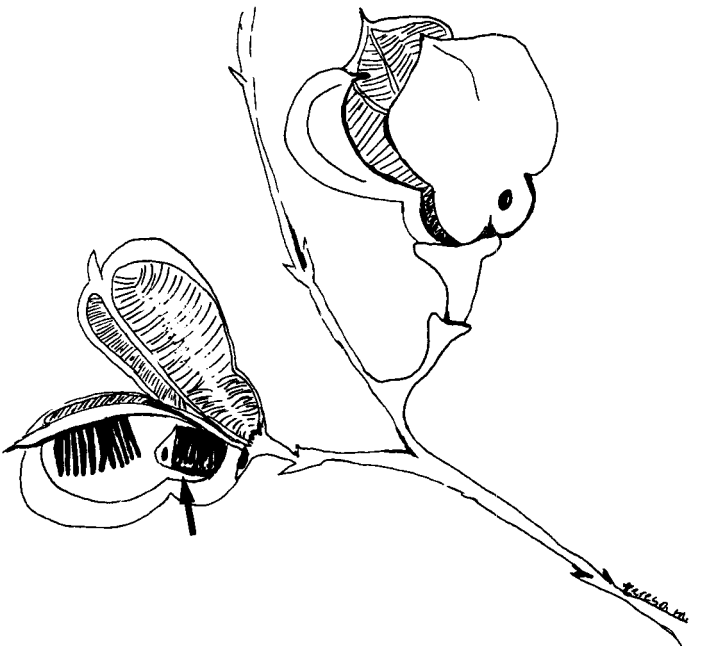

Fig. 3. Open capsules of *Yucca whipplei* illustrating the typical site of oviposition (point of constriction of the capsule), larval chamber (arrow) consisting of destroyed seeds glued together and most common position of the larval chamber within the capsule by Teresa Montygierd-Loyba.

species which closely resembles the pattern observed for the other eight species. For all nine of these species the distribution of larvae along the length of the capsule did not depart significantly from normality ($P > 0.05$).

Discussion

Particularly intriguing is the distribution of larvae within the locules of *Yucca whipplei* (Fig. 1). The highly skewed distribution of moth larvae in *Y. whipplei* capsules is in marked contrast to the intralocular distributions of the larvae in nine other *Yucca* species from the southwestern U.S. These other nine species represent most of the range of variation in the genus with respect to fruit characteristics.

There are characteristics unique to *Yucca whipplei* which could explain the highly skewed intralocular distribution of larvae in this species but not in others. For example differences in floral structure could affect oviposition location; in *Y. whipplei* flowers, the stamens tend to spread whereas in other yuccas they are erect or appressed to the carpel. Behavioural differences in oviposition site and/or orientation of larvae may be involved as *Y. whipplei* has a unique *Tegeticula* species. One characteristic of *T. maculata* that could be involved is the fact that the larvae of this species produce a silk that glues together the remains of the seeds they eat and thus forms a chamber (Fig. 3). Experiments have shown that if these chambers, rather than being situated at the base of the capsule, are artificially placed higher up, they act as a plug and block the dispersal of all seeds situated beneath them (A. Meyers and J. Keeley, unpublished data). This is due

to the fact that the upright capsules do not open completely and, due to a rudimentary false septum the seeds must escape upwards (McKelvey 1947). The positioning of larval chambers at the base of the capsules is apparently due to the orientation of the feeding larva since the female typically oviposits near the middle, as evidenced by direct observation (Trelease 1893) or presence of apparent oviposition scars (J. Keeley personal observation).

In other *Yucca* species the moth larvae may not create a seed dispersal problem for two reasons. In the baccate-fruited species the fruits are indehiscent and thus the position of the larvae should not have any effect on ultimate seed dispersal. In the other *Yucca* species with dehiscent capsules, the yucca moth (*Tegeticula yuccasella*) larvae are larger and do not produce a silk which binds the seed remains together into a chamber; thus less seed debris is left behind and since it is not glued together it disperses as well as or better than good seeds.

It is concluded that non-random orientation of moth larvae within the locules of *Yucca whipplei* fruits has been selected for as a means of enhancing the dispersal of seeds not consumed by the yucca moth.

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