

## Fruit abortion in *Yucca elata* and its implications for the mutualistic association with yucca moths

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The yucca moth *Tegeticula yuccasella* is the sole pollinator of *Yucca elata*, and relies on yucca fruits to complete its life cycle. A high percentage of pollinated flowers aborts, killing the *T. yuccasella* eggs and larvae in them. We examined patterns of fruit production and abortion in *Y. elata*, and related these patterns to vegetative characteristics, moth abundance, and environmental conditions. We studied 38 inflorescences throughout their flowering period, during one season in southern New Mexico, USA. Each night we recorded the number of flowers opening, the number of fruit formed, the relative abundance of yucca moths, and climatic conditions. We monitored 11786 flowers, resulting in 699 mature fruit. Large inflorescences produced more, but proportionately fewer fruit than small inflorescences. Inflorescences flowering late in the season produced proportionately more fruit than inflorescences flowering early. Only 6.6% (extremes 1.4–15.1%) of flowers produced mature fruits. Hand-pollination of all flowers on inflorescences did not significantly increase the proportion of flowers that developed into mature fruit. Fruit production appeared to be resource-, not pollinator-limited. Ninety per cent of observed moth-pollinated flowers aborted ( $N=31$ ), resulting in the death of moth eggs and larvae laid in the flowers. Neither yucca moth abundance or climatic conditions correlated with fruit production. Inflorescences usually developed mature fruit from flowers opening during a 'window' of consecutive nights, lasting for five nights on average (36% of the flowering period of an inflorescence). The timing of the window of fruit production was highly variable and unpredictable: mature fruits were produced from flowers opening at the beginning, in the middle, or at the end of the flowering period of an inflorescence. The results for *Y. elata* do not support existing hypotheses that attempt to explain patterns of selective fruit production. High rates of abortion of initiated fruit, and the apparently unpredictable pattern of fruit production by individual inflorescences, may stabilize the mutualistic interaction by preventing yucca moths from hyper-ovipositing flowers that have a high probability of developing into mature fruits. A risk-spreading strategy of oviposition is likely to be more successful for the moth than multiple ovipositions per flower.

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The obligate mutualistic association between species of *Yucca* (Agavaceae) and moths of the genera *Tegeticula* and *Parategeticula* (Prodoxidae) has been described by a number of researchers (reviews by Baker 1986, Addicott et al. 1990, Powell 1992). Powell (1992) described the general association as follows: female yucca moths emerge from pupation at the base of yucca plants, copulate, and collect pollen which is carried in specialized mouthparts. Females then fly to another inflorescence, oviposit into the ovary of a newly opened flower, then pollinate the flower by placing some of the collected pollen on the stigmatic surface. In most species of *Yucca*, including *Y. elata* Engelm., pollination only occurs if pollen is pushed down the stigmatic tube, and does not occur without the deliberate actions of the moth. The moth larvae feed exclusively on yucca seeds, so are only assured of a food supply if the pollinated flower develops into a mature fruit. However, the yucca moth larvae do not eat all the seeds, and both the *Yucca* and the yucca moth achieve sexual reproduction from the interaction.

Despite the fame of this mutualistic interaction (Baker 1986), detailed studies of flowering, fruit production, and pollinator abundance of only three species of yuccas have been reported (*Y. whipplei* – Powell and Mackie 1966, Aker and Udovic 1981, Udovic 1981, Udovic and Aker 1981, Aker 1982a,b, *Y. glauca* – Kingsolver 1984, Fuller 1990, and *Y. schottii* – Powell 1984). These studies (and others) on a diversity of species of *Yucca*, have consistently noted that as a result of high rates of abortion of initiated fruits, yuccas produce mature fruits from less than 10% of the flowers on an inflorescence. Three ultimate reasons for low fruit:flower ratios in yuccas are possible: (1) fruit production is pollinator-limited; (2) insufficient resources prevent the development of mature fruit from all pollinated flowers; or (3) low quality or low quantity of pollen prevents successful pollination of flowers.

Whatever the explanation for low fruit:flower ratios, it has important implications for yucca moths since flower and fruit abortion results in the death of yucca moth eggs. Natural selection adjusts the life-history strategy of moths to maximise life-time reproductive success. Superficially it would appear that moths should place eggs in flowers that are most likely to develop into mature fruit. A moth that could predict which flowers were most likely to develop into mature fruit would have higher reproductive success. Hyper-oviposition of a flower may lead to larval crowding in fruit and increased larval mortality. So moths should also select flowers that have not been oviposited in by other females. Alternatively, if moths cannot predict which flowers will develop into mature fruit when pollinated, or cannot tell if a flower has previously been oviposited in, they should spread the risk of reproductive failure by laying a few eggs in many different flowers (Kingsolver 1984, Addicott et al. 1990).

Predictable patterns of fruit abortion in yuccas will therefore be of great significance to yucca moths. A number of general hypotheses (reviewed by Stephenson

1981) have been proposed to explain proximate patterns of fruit abortion in plants. Fruits are more likely to abort if they are: (1) damaged or have fewer seeds (Lee and Bazzaz 1982, Bookman 1984, Stephenson and Winsor 1986); (2) further from the source of nutrients (i.e., at the distal end of the inflorescence – Wyatt 1982, Copland and Whelan 1989); (3) late to be initiated (Wyatt 1980); (4) pollinated with unsuitable pollen (Stephenson 1981, Bookman 1984, Stephenson and Winsor 1986). All of these hypotheses explain predictable patterns of fruit abortion. If any of these patterns occurs in *Y. elata*, yucca moths should be able to key-in on flowers that have a greater chance of becoming mature fruit. For example, they should avoid hyper-ovipositing a flower (Hypothesis 1), they should oviposit in proximal and/or early opening flowers (Hypotheses 2 and 3), or should pollinate flowers with outcross pollen (Hypothesis 4).

Our objectives were to test both ultimate and proximate causes of fruit abortion in *Y. elata*, and relate these patterns to the life history of yucca moths. We determined:

- (1) The fruit:flower ratio for individual inflorescences, and whether fruit production was either pollinator-limited or resource-limited.
- (2) Whether the pattern of fruit abortion is consistent with any of the hypotheses outlined above, and predictable for yucca moths.

Pollen-limitation and the associated hypothesis of pollen compatibility are not addressed in this study.

## Methods and materials

### Biology of *Yucca elata*

*Yucca elata* occurs throughout western Texas, southern New Mexico, southern Arizona and the northern states of Mexico (Campbell and Keller 1932). *Yucca elata* is iteroparous, but individuals do not flower every year, having alternate pulses of vegetative growth and flowering (Smith and Ludwig 1978). *Yucca elata* also reproduces by vegetative growth resulting in a clonal cluster of plants. We defined an 'individual' as a unit comprising a caudex (stem) and rosette (crown), and a 'clone' as a clump of 1–10 individuals that were contiguous in space, and at least 3 m from another clump. Individuals are 1–2 m high and produce a single inflorescence 1–2 m long so the inflorescence is held 2–4 m above the ground.

The styles of *Y. elata* form a floral tube with the stigmatic surface located a few mm inside the tube. Moths must push pollen down inside the floral tube to affect pollination (Riley 1892, James et al. 1993). Flowers open at night, are receptive to pollen only during their first night of opening, and are partially self incompatible (James et al. 1993). Flowers that were pollinated had the potential to develop into fruits, but many of

these abort. We distinguish between pollinated flowers that aborted and fruit that reached maturity by using the terms 'initiated fruit' and 'mature fruit', respectively. The number or proportion of mature fruit an inflorescence produced was called 'fruit set'.

*Tegeticula yuccasella* (Riley) appears to be the only pollinator of *Y. elata* in southern New Mexico (James et al. 1993). The ovaries of the flowers have six locules, each containing 50–70 ovules (Hoffman et al. unpubl.). Moths oviposit once in one or more of the locules, and a single flower may be oviposited and pollinated by a number of moths (James et al. 1993). Although *T. yuccasella* is widespread, it is morphologically variable across its range (Miles 1983, Powell 1984), and the complex may represent more than one species.

### Study site

The study was conducted during one flowering season (May–June 1990) of a *Y. elata* population 2 km east of New Mexico State University, Las Cruces, New Mexico, USA, on the southwest side of Tortugas Mountain (106°42' W, 32°17' N). The 2.3 ha study site was located on a sandy ridge-crest flanked by arroyos, and surrounding areas had relatively coarse-grained gravelly soils compared with the ridge crest. The density of *Y. elata* was much higher on the sandy ridge crest than in the surrounding area. The study site supported 250 *Y. elata* plants, which produced around 500 inflorescences in the 1990 season.

In mid-May, when flowering stems were developing, one inflorescence on each of 100 clones was chosen at random: the first inflorescence chosen was at the approximate center of the population. Thereafter, inflorescences were chosen by moving a random distance (in m) and a random direction (compass bearing) to the next clone. If the random distance and direction did not coincide with a *Yucca* clone, we selected the nearest clone. The inflorescences were randomly assigned to various hand-pollination experiments ( $N = 62$ , James et al. 1993), and to the phenology study ( $N = 38$ ). Flowering for the population began on the night of 14 May, and finished on 24 June, giving a total of 42 nights of flowering. Flowering in the phenology study group began on 17 May (night 4) and ended on 21 June (night 39).

### Fruit:flower ratios

Thirty-eight inflorescences were examined daily for 35 d to determine flowering phenology and fruit set patterns. Each inflorescence was inspected every morning by CDJ and MTH using 3-m step-ladders. Every flower that had opened the previous night was color coded. Within five d the flower had either abscised or had initiated development into a fruit. If a fruit was developing, it was possible to determine the night on which that flower was polli-

nated because *Y. elata* flowers are only receptive to pollination on the first night of opening (James et al. 1993). Hence, we noted the color-code and carefully tagged the fruit indicating the night of pollination. Many of the initiated fruits subsequently abscised. We could not keep accurate records of the number of initiated fruits that abscised. After 4–5 weeks we counted the number of mature fruit per inflorescence. This procedure generated data on the number of flowers available for pollination each night, the number of mature fruits produced from flowers open each night, and the proportion of flowers that matured fruit.

### Oviposition frequency and fruit abortion

Our aim was to establish the number of times individual flowers were oviposited in and pollinated by moths, and to determine the frequency of abortion of these moth-pollinated flowers. Inflorescences were cleared of yucca moths resting in flowers in the afternoon by manual removal, and were bagged with nylon insect netting to ensure that flowers opening that night would not be pollinated or oviposited in before observations began. Netting was removed at  $\approx 2030$  hr and flowers were observed for two h. A small pocket flashlight, shining obliquely onto an inflorescence was used to observe moths. Although we did not determine the effect of the light on the moths' behavior, there appeared to be little disruption. We recorded the number of times that an ovary of a flower was oviposited in, the number of times a flower was pollinated, and the number of different female moths that oviposited into and pollinated a flower. Once a flower was observed being pollinated by a yucca moth, the flower was numbered and monitored for the remainder of the observation period. Inflorescences that had been monitored were cleared of moths and rebagged at the end of a night's observations, thereby preventing further pollination and oviposition of tagged flowers. The number of these flowers that developed into mature fruit was counted. Three inflorescences were monitored over five nights (nights 16–20) resulting in 69 oviposition observations of 31 flowers.

### Hand pollination experiments

To test whether fruit set was pollinator limited, we hand-pollinated all flowers on four inflorescences with pollen from two other plants (see James et al. 1993 for details of hand pollination methods), and counted the number of mature fruit that developed. Inflorescences were bagged before the first flower opened and remained bagged throughout their flowering period to prevent yucca moths from pollinating flowers.

Table 1. Vegetative and phenological statistics for 38 *Yucca elata* inflorescences.

Characteristic	$\bar{x} \pm \text{SD}$	(Extremes)
Duration of flowering (nights)	13.6 $\pm$ 1.9	(11–20)
Number of flowers/inflorescence	310.2 $\pm$ 254.8	(57–1366)
Number of mature fruit/inflorescence	18.4 $\pm$ 14.2	(2–74)
Proportion of flowers producing mature fruit	6.6 $\pm$ 2.8%	(1.4–15.1%)
Number of nights during which fruits were produced <sup>1</sup>	5.3 $\pm$ 2.3	(1–10)
Proportion of flowering period during which fruits were produced	39.2 $\pm$ 16.2%	(7.7–76.9%)

<sup>1</sup> Total number of nights from which mature fruit resulted.

### Temporal patterns of fruit production

From our phenological data we were able to determine the night on which a mature fruit had been initiated. Patterns of fruit set were correlated with the abundance of yucca moths on a given night, and environmental conditions.

The relative abundance of yucca moths was determined by counting moths in 300 flowers on ten inflorescences at 2200 hr each night from 23 May to 14 June (nights 9–31). The inflorescences and the flowers on each inflorescence were chosen haphazardly each night, but tended to be biased away from small inflorescences. Male and female moths were not distinguished during these censuses but casual observations confirmed that female *T. yuccasella* were present during the entire flowering period. The false-yucca moth, *Prodoxus quinquepunctellus*, was not present on the study site. These data were used to calculate the relative abundance of yucca moths for each night of the flowering period (number of moths per flower), and to estimate the number of moths an inflorescence may have received over its entire

flowering period. To do this, we multiplied the number of flowers open on an inflorescence on a given night by the average number of moths per flower for that night, and summed this value over all nights an inflorescence flowered. The resulting index, termed moth-nights, estimates the relative number of pollination events an inflorescence may have received, and is similar to the visitation index of Udovic (1981).

Temperature, wind speed, and rainfall were recorded at a weather station 1 km from the study site. These data were correlated with phenology data to examine individual and population patterns of flower and fruit production.

All statistical analyses were done using StatView II®.

## Results

### Fruit:flower ratios

Flower and fruit production data for 38 *Y. elata* inflorescences are summarized in Table 1. The number of fruits produced by an inflorescence was correlated with the size of the inflorescence ( $r=0.82$ ,  $P < 0.001$ ; Fig. 1A). The proportion of flowers that became mature fruit was 6.6% ( $\pm$ SD 2.8%), and was not correlated with inflorescence size ( $r=-0.29$ ;  $P=0.08$ ; Fig. 1B). Hence, large inflorescences had more flowers and more fruit, but did not produce proportionately more fruit than small inflorescences.

### Fruit position

Flowers did not open in sequential order from bottom to top of an inflorescence, or inner to outer ends of inflorescence branches. On any one night, flower buds could simultaneously open at the top, bottom and middle sections of an inflorescence. We could not detect a sequential pattern of flower opening or fruit initiation. Mature fruits were produced at many positions on an inflorescence, and were not clumped in any particular region.

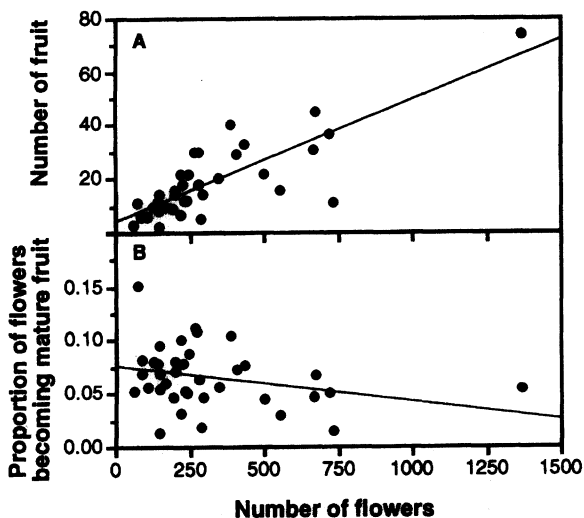


Fig. 1. Correlations between the size of an inflorescence and: the number of fruit produced (A); the proportion of flowers that produced mature fruit (B).  $N=38$  inflorescences for both figures.

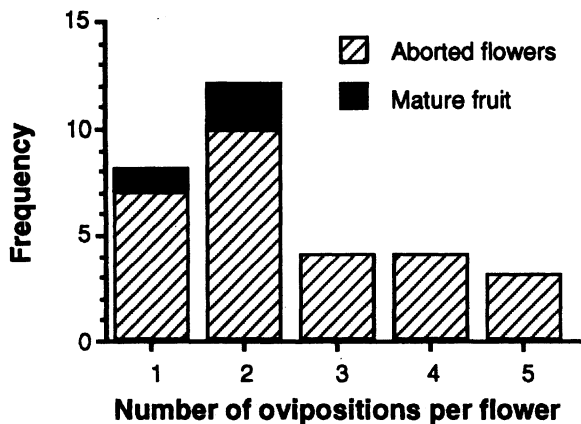


Fig. 2. Frequency distribution of the number of ovipositions in 31 individual flowers of *Y. elata*, and the proportion of flowers that became mature fruit.

### Oviposition frequency and fruit abortion

Thirty-one flowers were observed being oviposited in and pollinated by 11 individual female *T. yuccasella*. Female moths usually oviposited in one or two locules (20 of 31 observations), however one female oviposited in five of the six locules. Oviposition was followed by pollination except in three cases (69 observations) where moths had previously oviposited in and pollinated the same flower. Only three of the 31 flowers that were observed being oviposited in and pollinated set fruit; the remainder (90%) aborted (Fig. 2). The pollinated flowers that did develop into mature fruit had been oviposited in once or twice only. There were insufficient data to test whether flowers oviposited in many times (>3) are more likely to abort. Only 10% of the moth-pollinated flowers developed into mature fruit (Fig. 2), and on average an inflorescence produced mature fruit from 6.6% of flowers (Table 1), so we estimate that *T. yuccasella* pollinated 60–70% of the flowers in the population.

### Hand pollination

The proportion of flowers developing into mature fruits on four inflorescences in which all the flowers were hand-pollinated, was 7.9% (Table 2). This was not significantly different from that observed in the natural population (compared with four randomly selected in-

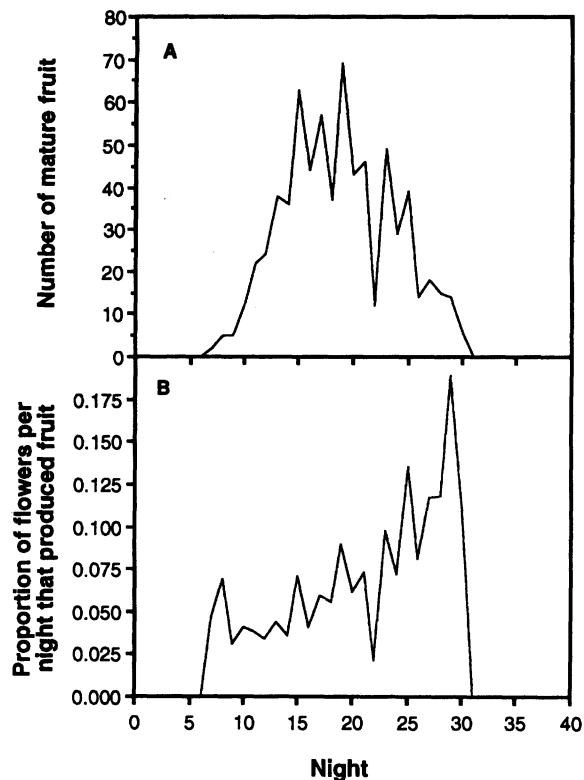


Fig. 3. Nightly pattern of fruit production on 38 *Y. elata* inflorescences during the study.

flowers from the natural population,  $F_{1,6}=0.417$ ,  $P=0.54$ ).

### Temporal patterns of fruit production

The inflorescences we studied produced 11786 flowers and 699 mature fruits. The number of fruits that were produced each night was correlated with the number of flowers open that night in the population ( $N=30$ ;  $r=0.85$ ;  $P=0.0001$ ). However, there was one night (night 22) when fruit set was unusually low (Fig. 3A; see below). The proportion of flowers producing mature fruits per night, increased during the flowering period ( $N=24$ ;  $r=0.74$ ;  $P<0.0001$  – Fig. 3B), but this increase was not correlated with the number of flowers that were open ( $N=30$ ;  $r=0.04$ ;  $P=0.85$ ).

Table 2. Results of hand pollination of all flowers on four inflorescences of *Y. elata*.

Characteristic	$\bar{x} \pm SD$	(Extremes)
Duration of flowering (nights)	9.3 $\pm$ 0.93	(8–10)
Number of flowers/inflorescence	153.0 $\pm$ 31.6	(117–194)
Number of mature fruit/inflorescence	12.5 $\pm$ 9.3	(5–26)
Proportion of flowers producing mature fruit	7.9 $\pm$ 4.5%	(3.3–13.4%)

Table 3. Number of flowers and fruit (in parentheses) produced each night by 38 *Y. elata* inflorescences pollinated naturally, and four

Plant no.	Night of study															
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
20	13	25	<u>33(2)</u>	<u>41(5)</u>	<u>47(2)</u>	<u>65(1)</u>	<u>87(8)</u>	<u>93(7)</u>	<u>83(11)</u>	<u>66(1)</u>	64	59	30	11	4	
49	3	5	8	11	<u>15(2)</u>	<u>23(10)</u>	<u>20(1)</u>	20	14	<u>17(1)</u>	4	5	0	1		
2			2	4	11	18	<u>16(1)</u>	<u>15(2)</u>	<u>16(1)</u>	<u>21(6)</u>	16	11	7	7		
34				1	19	47	63	86	116	128	<u>96(3)</u>	<u>128(3)</u>	<u>107(3)</u>	<u>77(2)</u>	<u>98(17)</u>	
37				7	20	41	70	54	58	97	<u>51(1)</u>	<u>55(2)</u>	<u>56(6)</u>	<u>32(7)</u>	13	
47				2	2	13	<u>19(2)</u>	10	25	21	16	14	4	3		
51				6	<u>27(1)</u>	<u>33(1)</u>	<u>48(1)</u>	64	70	73	<u>64(7)</u>	<u>82(2)</u>	<u>50(17)</u>	<u>38(5)</u>	<u>62(11)</u>	
5					4	5	30	38	13	40	<u>19(5)</u>	<u>19(1)</u>	24	7	<u>9(1)</u>	
6					5	2	14	22	<u>16(1)</u>	<u>24(3)</u>	<u>15(3)</u>	14	<u>9(3)</u>	<u>10(1)</u>	4	
10					3	13	<u>39(1)</u>	38	38	61	<u>50(11)</u>	<u>42(11)</u>	<u>23(6)</u>	<u>37(4)</u>	20	
23					5	20	51	49	28	25	39	<u>45(2)</u>	<u>17(3)</u>	5	1	
40					3	8	35	<u>19(1)</u>	<u>33(2)</u>	<u>23(11)</u>	20	12	16	10	7	
12						1	4	9	28	30	22	<u>16(1)</u>	<u>9(1)</u>	<u>19(1)</u>	<u>29(9)</u>	
18							1	<u>7(1)</u>	<u>4(2)</u>	<u>2(1)</u>	<u>18(2)</u>	<u>17(1)</u>	9	8	2	
21								2	<u>14(3)</u>	20	30	<u>26(1)</u>	<u>33(4)</u>	<u>47(3)</u>	<u>24(1)</u>	
35							2	<u>21(4)</u>	<u>24(4)</u>	<u>35(6)</u>	29	24	28	13	9	
4								3	21	63	64	52	88	86	50	
16								3	<u>12(3)</u>	<u>17(1)</u>	<u>10(1)</u>	<u>12(1)</u>	16	4	5	
29									2	3	23	<u>36(1)</u>	<u>15(3)</u>	<u>21(4)</u>	<u>22(2)</u>	
38									9	24	<u>40(1)</u>	<u>39(4)</u>	<u>34(5)</u>	<u>40(3)</u>	<u>39(1)</u>	
43									11	<u>25(1)</u>	<u>33(4)</u>	<u>22(2)</u>	<u>22(2)</u>	<u>29(3)</u>	19	
45									8	15	26	38	30	<u>35(3)</u>	<u>15(4)</u>	
32										<u>13(4)</u>	<u>21(10)</u>	<u>25(3)</u>	<u>19(2)</u>	<u>27(3)</u>	<u>42</u>	
36										17	21	35	<u>64(15)</u>	<u>80(4)</u>	<u>62(2)</u>	
46											3	5	2	23	<u>11(5)</u>	
48											2	19	45	58	93	
50											4	6	17	20	15	
33												6	5	<u>39(2)</u>	46	
28													6	23	19	
9														19	15	
17														26	34	
22														4	9	
39														<u>25(4)</u>	<u>23(2)</u>	
22														3	<u>4(3)</u>	
30															<u>26(6)</u>	
44															7	
52																
24																
79*												<u>8(1)</u>	19	<u>49(5)</u>	<u>36(2)</u>	
78*															<u>18(4)</u>	
98*																
99*																

Inflorescences were not consistent in their timing of fruit production (Table 3). Some inflorescences produced mature fruit only from flowers opening in the first few days (e.g., plant no. 32), whereas other inflorescences produced mature fruits from flowers opening in the middle (e.g., plant no. 49), or at the end of their flowering period (e.g., plant no. 28). Even for inflorescences that flowered at similar times, fruit production was asynchronous (e.g., compare 12 with 18, and 4 with 16). The fruit production period of an inflorescence was usually 3–5 nights (Table 1), although there was considerable variation in this (e.g., compare plants 23 and 47 with plants 20 and 34). Many inflorescences (20 of 38) produced all of their fruit over a single contiguous period lasting 1–10 nights, or 8–77% of the total flowering duration of an inflorescence. We interpret these patterns

as a ‘window of fruit production’ during which time a significantly higher proportion of flowers produced mature fruit compared with the overall proportion of flowers producing fruits (t-test = 8.9, 37 d.f.,  $P < 0.0001$ ). However, nearly half of the inflorescences did not produce fruit over a single contiguous period. Seventeen of 38 inflorescences produced fruit over two periods, and one inflorescence (plant no. 33) produced fruit over four separate periods. Inflorescences with multiple windows of fruit production were not exceptional in size or fruit production compared with those that produced fruit during a single contiguous period. The duration of the window of fruit production was not correlated with the size of the floral display (i.e., larger inflorescences did not have longer periods of fruit production;  $r = 0.29$ ,  $P = 0.08$ ), and the timing of the window of fruit production

hand-pollinated inflorescences (asterisked). Nights when fruit were produced are underlined.

(night 1 = 14 May)

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
2														
87(19)	93(19)	74(4)	75(3)	44(1)	20	6	1							
0	1													
1														
24	21	9	4	0	1									
5	4													
4														
19	17	7	15	5	6									
3	7	1												
23	16	10	13	3										
6	1													
15	3													
5	1	1												
63(5)	60(1)	50(2)	43	32(2)	3									
2	3	0	1											
9	8	1	1											
25(3)	14	15(1)	14	6										
16(3)	12(2)	11	5											
22(3)	19(2)	17(1)	3(1)	1										
13	9	11	4	1										
38	31	26	21(1)	11	4	1								
6	2	2	2											
55	54	86(1)	38(16)	29(7)	1(1)	15(1)	17(3)	9	12(3)	4(2)	2			
21(1)	9(1)	10	5	6	1									
34	20(1)	24	20(3)	30	8	0	1							
30	29(1)	22	14(5)	10(2)	5(1)									
41	60(4)	46(1)	47(6)	27(2)	37(12)	20(4)	14							
35	24(9)	36(1)	41(5)	28(5)	34(6)	18(2)	8(1)	5	1	2(1)	1			
47(5)	60(5)	48(1)	32(6)	32(5)	35(6)	14(1)	17	5	3					
34(4)	20(1)	19	21(1)	24(1)	9	14	18	5	1					
2	16	11	7	6	10	13(1)	13(3)	2	7(2)	10	1			
4	2	1	9	13	6	3	2	9(1)	6(1)	1(1)	0		1(1)	
4	4	14	20	12	1(1)	15(1)	17(3)	9	12(3)	4(2)	2			
2	3	2	31	36	29	25(3)	27(5)	42(12)	27(8)	23(2)	15	8	3	1
	2	3	16(2)	48(4)	45(11)	23(2)	29(1)	42(2)	17	15	6	3		
8(4)	14(5)	16(5)	23	3										
9(2)	13(6)	19	19	21(2)	13	13	5(1)	4	1					
				5(1)	14	18(4)	16	15(1)	17(1)	28(1)	12	8	5	5
					5	18	23	21	34	23(3)	16	5(1)	2	4

was not correlated with the proportion of flowers open on an individual inflorescence (i.e., fruit were not necessarily produced during the period of maximum floral display; Table 3). There was no well-defined window of fruit production in the four hand-pollinated inflorescences (Table 3). Fruit production in these inflorescences was pulsed throughout the flowering period.

Inflorescences that produced fruit late in their individual flowering period, produced proportionately fewer fruits than inflorescences that produced fruit early in their flowering period, though this relationship was weak ( $N=38$ ;  $r=-0.35$ ;  $P=0.031$ ). Thus, a flower that opened late during the flowering period of an inflorescence was less likely to result in the development of a mature fruit.

Relative abundance of moths varied greatly during the flowering period (Fig. 4A), and was not correlated with

any environmental variables measured (e.g., temperature at 2100 hr -  $N=22$ ;  $r=0.13$ ;  $P=0.55$ ; wind speed at 2100 hr -  $N=22$ ;  $r=0.02$ ;  $P=0.95$ ). There was no significant correlation between the relative abundance of moths on a given night and the proportion of flowers producing fruit on that night ( $r=0.003$ ;  $P=0.81$ ). Similarly, there was no significant correlation between the proportion of flowers on an inflorescence that produced fruit and the estimated total number of moth-nights the inflorescence received ( $r=0.27$ ;  $P=0.11$ ).

None of the environmental variables measured (wind speed, ambient temperature, and rainfall) were correlated with the proportion of flowers producing mature fruit on a given night. However, on one night when wind speed was high (night 22; Fig. 4B), fruit production was low. The effect of this windy night on moth abundance is not

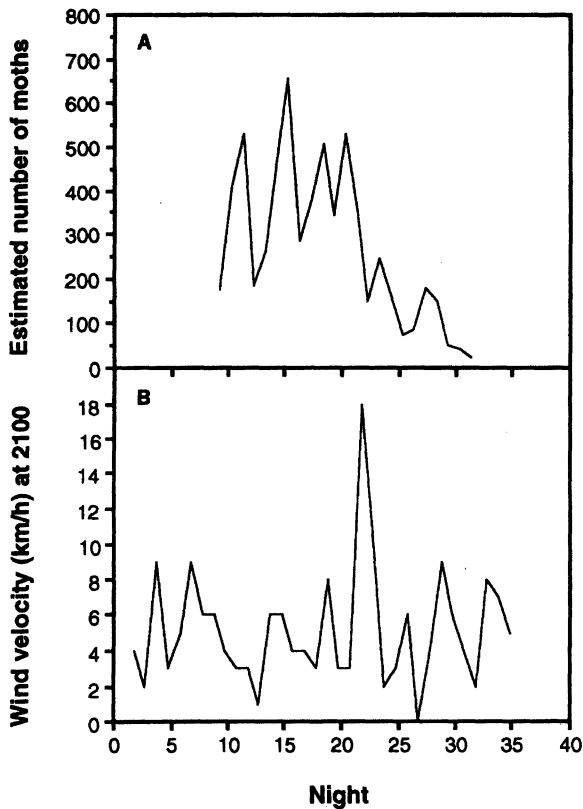


Fig. 4. Nightly pattern of yucca moth (*T. yuccasella*) abundance (A); and wind velocity (B) recorded 1 km from the study site at 2100 hr.

strong, presumably because we censused stationary moths in flowers, and not moth-flight activity.

## Discussion

### Fruit:flower ratios and fruit abortion

Ninety per cent of *Y. elata* flowers that were observed being oviposited into and pollinated by *T. yuccasella* subsequently aborted, mostly within a week of pollination. We believe that this result reflects accurately conditions in the natural population. Also, the proportion of flowers producing mature fruit was low and similar to that reported for other capsular species of *Yucca*: 9% in *Y. whipplei* (Udovic and Aker 1981), 1–11% in *Y. glauca* (Cruden et al. 1976, Kingsolver 1984, Fuller 1990), 4–7% in *Y. elata* (Schaffer and Schaffer 1979), and a range of values from 7–70% for nine other species of *Yucca* (Schaffer and Schaffer 1979). In addition, hand-pollination of all flowers on inflorescences did not significantly increase fruit set compared to inflorescences pollinated by *T. yuccasella*. Thus, low fruit:flower ratios and high rates of abortion of flowers and initiated fruit suggest that resources or energy availability limit fruit production in *Y. elata*. This result is consistent with the conclusions

from research on other species of *Yucca* (Udovic and Aker 1981, Kingsolver 1986, Fuller 1990).

Plants that have low fruit:flower ratios, and are apparently resource-limited, exhibit a number of patterns of fruit production (Stephenson 1981). Three of these patterns can be tested with the results of our study: (1) the first fruits initiated with compatible pollen monopolize resources and develop into mature fruits (Wyatt 1980); (2) fruits closer to the source of nutrients (i.e., at the proximal end of the inflorescence) are selectively matured (Wyatt 1982); and (3) fruits with more seeds are selectively matured (Janzen 1979, Lee and Bazzaz 1982, Bookman 1984, Stephenson and Winsor 1986).

Neither the first fruits initiated on an inflorescence, nor those at the bottom of the inflorescence (closer to the source of nutrients), necessarily developed into mature fruits in *Y. elata*. Flowers pollinated at the beginning of an inflorescence's flowering period did not necessarily develop into mature fruits (see results for hand-pollinated inflorescences). Instead, fruit maturation in the natural population seemed dependent on whether or not the flower opened within an apparently unpredictable 'window of production'. (This pattern was not as clear for the hand-pollinated inflorescences.) Second, mature fruit did not have a clumped spatial arrangement at the bottom of an inflorescence. The data for *Y. elata* does not support the first two hypotheses. These results appear to contrast with findings for *Y. whipplei* where flowers opening early (at the proximal end of the inflorescence) had a higher likelihood of becoming mature fruit than those opening later (at the distal end of the inflorescence – Aker and Udovic 1981). However, *Y. whipplei* flowers for longer than the moth flight period, so these spatial patterns of fruit production may also be the result of changes in moth abundance.

The third hypothesis suggests that to maximize seed production, individual *Y. elata* plants that have more initiated fruit than they can bring to maturity should selectively abscise fruits with potentially large numbers of yucca moth larvae that eat the seeds. Although our data do suggest that flowers with numerous ovipositions abort more frequently than those with fewer ovipositions, our sample sizes were too small to provide significant tests of the hypothesis. However, Fuller (1990) found that flowers of *Y. glauca* with large numbers of experimentally administered 'ovipositions' (>3) were more likely to abort than flowers with only one or two ovipositions. Of the three hypotheses examined, this is the only one that may explain some of the variation in fruit production in *Y. elata*, but needs further investigation.

### Temporal patterns of fruit production

Perhaps the most intriguing result from this study was the weak trend for a defined period or window of fruit production in most inflorescences, and the apparently unpredictable length and position of this window within an



inflorescence's flowering period. We could find no climatic, floristic or phenological variables that explained the variation in the timing or duration of the window of fruit production for an inflorescence. This result has not been recorded for other species of *Yucca*, yet it has implications for the mutualistic relationship between *Y. elata* and *T. yuccasella*. *Tegeticula yuccasella* have only a few days in which to deposit eggs in enough flowers to ensure that some larvae may survive. The larvae are totally reliant on the seeds produced by *Y. elata* to complete development. In contrast, *Y. elata* is iteroparous, reproduces by vegetative growth as well as sexually, and is reliant on *T. yuccasella* for seed production. Although a behavior that allowed a yucca moth to select flowers that have a higher probability of developing into mature fruit may be selectively advantageous for moths, it would result in high rates of seed predation. Our study found no predictable patterns of abortion or maturation of initiated fruit that would allow yucca moths to key-in on individual flowers, or periods when the probability of fruit maturation was higher than average. The only significant patterns found relating fruit production to phenology were that the probability of a flower developing into a fruit is higher at the beginning of an individual inflorescence's flowering period, and higher later in the flowering season. There is no evidence from other studies that female yucca moths are able to identify flowers that are more likely to develop into fruit, or inflorescences that have a higher frequency of fruit production (Powell 1984). Even if moths were able to choose flowers with a high probability of becoming mature fruit, selective abortion of fruits with large numbers of ovipositions or larvae could negate this advantage (Fuller 1990). Large numbers of larvae in a fruit may also be detrimental to *Tegeticula* because larval mortality increases with increasing numbers of larvae in a fruit (Kingsolver 1984). *Tegeticula maculata* on *Y. whipplei* appear to be able to detect if other moths have already oviposited in a flower, and often avoid ovipositing in such flowers (Aker and Udovic 1981). This ability may be widespread in other species and would allow moths to avoid hyper-ovipositing flowers.

If, as we suggest, moths cannot predict which flowers will become fruit, a risk-spreading strategy of laying one or two eggs in a number of different flowers is likely to be more successful than laying many eggs in one flower (Addicott et al. 1990, Fuller 1990). Our observations suggest that *T. yuccasella* usually lay a small number of eggs in each of a number of different flowers (James et al. 1993). We do not, however, understand why *Y. elata* tends to produce fruits during a discrete window rather than throughout the flowering period, or in a pattern consistent with one or more of the hypotheses examined above. Specific periods of moth activity at a single inflorescence may account for the window of fruit production, but our data are not detailed enough to test for this correlation. We also do not know if the patterns of fruit production for individual plants are consistent from one

flowering season to the next. A fruitful area of research in the future may be to examine year-to-year variations in the timing of the window of fruit production and the number of fruit produced by individual rosettes.

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