SUITABILITY OF A NON-HOST PALO VERDE FOR DEVELOPMENT OF *STATOR LIMBATUS* (HORN) (COLEOPTERA; BRUCHIDAE) LARVAE

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Abstract.—In the southwestern United States, there are five species of palo verdes (*Cercidium* and *Parkinsonia* sp.; Fabaceae). *Stator limbatus* (Horn), a seed beetle, has been reared from four of these: *Cercidium floridum* (Benth.), *C. microphyllum* (Torr.) Rose & Johnst., *Parkinsonia aculeata* Linnaeus, and *P. macra* (Johnst.). However, despite extensive collections in North and Central America, *S. limbatus* has never been reared from *P. texana* (A. Gray) S. Watson. We tested the suitability of *P. texana* as a host for a Texas population of *S. limbatus*. Survivorship of *S. limbatus* on *P. texana* was high relative to the other palo verde species (except for *C. microphyllum*, on which survivorship was also high). Development time and body weight of emerging adults on *P. texana* were each approximately intermediate between those on *C. floridum* and *P. aculeata* (on which beetles developed slowly and emerged small) and *C. microphyllum* (on which beetles developed rapidly and became large adults). These data indicate that *P. texana* is a suitable host for *S. limbatus* and that, relative to other species of palo verde (except *C. microphyllum*), *P. texana* is a high-quality host. However, our study examines only the suitability of these palo verdes as hosts for *S. limbatus* in a controlled laboratory experiment. We discuss other hypotheses that may explain why *P. texana* is not used by *S. limbatus* in nature.

Key Words.—*Cercidium*, diet breadth, Fabaceae, host range, *Parkinsonia*

Most herbivorous insects feed on few of the plant taxa available to them (Fox & Morrow 1981). It is often observed, however, that herbivores develop very well, or even better, on plants they will not oviposit or feed upon than on plants they regularly use (Dethier 1954, Waldbauer 1962). *Stator limbatus* (Horn) (Coleoptera: Bruchidae) is a generalist seed beetle that uses >50 host plants in its large geographic range (from northern South America to the southwestern United States; Johnson & Kingsolver 1976, Johnson et al. 1989). In the southwestern United States, there are five species of palo verdes (Isley 1975), and *S. limbatus* has been reared from four of these: *Cercidium floridum* (Benth.), *C. microphyllum* (Torr.) Rose & Johnst. *Parkinsonia aculeata* Linnaeus, and *P. macra* (Johnst.) (Johnson & Kingsolver 1976, Nilsson & Johnson 1993). However, despite extensive collections in North and Central America, *S. limbatus* has never been collected on or reared from *Parkinsonia texana* (A. Gray) S. Watson (Nilsson & Johnson 1993, C. W. Fox, unpublished observation), although other insects, such as *Mimosestes amicus* (Horn) (Coleoptera: Bruchidae) have been reared from both *P. texana* and other palo verde species (Nilsson & Johnson 1993). Here, we test the suitability of *P. texana* as a host for a Texas population of *S. limbatus*. We find that *P. texana* is indeed a suitable host for *S. limbatus*. We speculate on numerous hypotheses to explain the failure of *S. limbatus* to use *P. texana* as a host plant, and also speculate whether, despite an inability to collect *S. limbatus* on this plant, *P. texana* is actually a host for this beetle.

MATERIALS AND METHODS

Stator limbatus for these experiments were collected from >50 *Acacia greggii* A. Gray (Fabaceae: Mimosoideae) plants along a ≈30 km stretch of Hwy 90, just south of Van Horn, Texas. Beetles were collected by picking mature pods from *A. greggii*. These pods were transferred to the lab, and seeds containing beetles were separated from uninfested seeds. We estimate that the laboratory population was initiated with >200 field collected individuals. Before initiating the laboratory experiments, beetles were reared in the lab for one generation at 27° C, 24 h light, on *A. greggii*.

Virgin female *S. limbatus,* collected from isolated seeds <24 h after emergence, were weighed and paired with a virgin male (also <24 h post-emergence). Each pair was confined in a 30 mm plastic dish with 12 seeds of one of the following species; *C. floridum, C. microphyllum, P. aculeata, P. texana,* or *A. greggii*. Although *A. greggii* is not a palo verde (and is even in a different subfamily of the Fabaceae), it was included here so that these data can be compared with previous and future projects (e.g. Siemens & Johnson 1990; Siemens et al. 1991, 1992; Fox et al. 1994, 1995).

Dishes were checked at 24 h intervals, and seeds bearing eggs were transferred to clean dishes, until a female had laid an egg on each of >10 seeds. All eggs were reared to adult at densities of one beetle per seed (additional eggs were scraped from each seed), 27° C, constant light. Development time, body weight, and survivorship were recorded for all offspring. Development time was estimated as the time between egg-laying and adult emergence, and thus includes embryonic, larval, and pupal development time. Emerging adults were weighed individually on an electronic balance within 24 h of adult emergence.

RESULTS AND DISCUSSION

As in other experiments examining *S. limbatus* life history (Siemens & Johnson 1990; Siemens et al. 1991, 1992; Fox et al. 1994, 1995), survivorship on *A. greggii* was very high relative to survivorship on the palo verde species (Table 1). Survivorship on *P. texana,* which has not been documented as a host for this beetle, was also high compared to the other palo verdes (except for *C. microphyllum,* on which survivorship was also high); beetles reared on *C. floridum* and *P. aculeata* had much lower survivorship than beetles reared on *P. texana.* This is a surprising result because *C. floridum* is heavily attacked by *S. limbatus* in southern California and Arizona (Mitchell 1977, Siemens & Johnson 1990), and females regularly lay eggs on *P. aculeata* in California (where it has escaped from cultivation), Arizona (where it is likely native in Yuma Co. and escaped from cultivation elsewhere) and in Texas (where it is native throughout most of the state; Isley 1975), but *S. limbatus* has never been reared from *P. texana.*

As previously demonstrated for *C. floridum* (Siemens et al. 1993; Fox et al. 1994, 1995), most of the mortality on each palo verde species occurred as larvae penetrated the seed coat (except for mortality on *C. microphyllum*; Table 1). For example, although egg-to-adult survivorship on *P. aculeata* was only 4.6 ± 6.9%, survivorship of larvae that successfully penetrated the seed coat was 77.3 ± 34.4%. Extractions from the seed coat applied to other host species suggest that mortality on *C. floridum* is due largely to allelochemicals in the seed coat (Siemens et al. 1992). The high mortality of larvae entering *P. aculeata* and *P. texana,* relative

Table 1. Survivorship of *Stator limbatus* reared on five host plants. Males and females are lumped because dead larvae could not be sexed. Values sharing the same letter (within columns) are not statistically different (Mann-Whitney *U*-tests).

Host species	n	Survivorship		
		Egg–adult	Entering seed	Within seed
Acacia greggii	28	0.93 ± 0.14a	0.99 ± 0.03a	0.94 ± 0.14a
Cercidium floridum	31	0.25 ± 0.21	0.35 ± 0.23	0.67 ± 0.31b
Cercidium microphyllum	29	0.89 ± 0.18a	0.99 ± 0.03a	0.89 ± 0.18a
Parkinsonia aculeata	31	0.05 ± 0.07	0.06 ± 0.09	0.77 ± 0.34ab
Parkinsonia texana	32	0.70 ± 0.28	0.75 ± 0.28	0.93 ± 0.11a

to mortality within these seeds and mortality entering other seed species, suggests that *P. aculeata* and *P. texana* have similar seed defense mechanisms to those of *C. floridum*, although those of *P. texana* are clearly less effective at preventing damage to seeds than the defenses of *C. floridum* and *P. aculeata*.

The observed patterns of development time and body weight (Table 2) of emerging beetles closely resembled those for survivorship: *C. floridum* and *P. aculeata* were generally poor hosts for *S. limbatus*, while *A. greggii* and *C. microphyllum* were generally good hosts for *S. limbatus*. Development time and body weight on *P. texana* were each approximately intermediate between those on the poor and good hosts.

Our data thus indicate that *P. texana* is a suitable host for *S. limbatus*, and that, relative to other species of palo verde, including *C. floridum*, which is heavily attacked by *S. limbatus* in Arizona, *P. texana* is a high-quality host. Nonetheless, there is no evidence that this host is used by *S. limbatus* in nature (Johnson & Kingsolver 1976, Nilsson & Johnson 1993). However, our study examines only the suitability of these palo verdes as hosts for *S. limbatus* in a controlled laboratory experiment. It is often observed that many herbivores develop very well in the laboratory on plants that they will not use in nature (Dethier 1954; Waldbauer 1962; Wiklund 1974, 1975, 1982; Hsiao 1982; Thompson 1988), suggesting that the selective environment influencing diet breadth evolution includes nu-

Table 2. Development time and body weight of *Stator limbatus* reared on five host plants. The low sample sizes on *Parkinsonia aculeata* reflect very high mortality on this host, and thus few emerging adults. Values sharing the same letter, with sexes, are not statistically different from each other (Mann-Whitney *U*-tests).

Host species	Sex	n	Development time (days)	Body weight (mg)
Acacia greggii	f	28	28.5 ± 0.3a	3.13 ± 0.04a
	m	27	28.8 ± 0.3a	3.45 ± 0.07a
Cercidium floridum	f	18	36.3 ± 0.7b	2.74 ± 0.08b
	m	17	36.9 ± 0.6b	3.03 ± 0.14b
Cercidium microphyllum	f	27	29.8 ± 0.3c	3.64 ± 0.05c
	m	29	29.8 ± 0.3c	3.80 ± 0.06c
Parkinsonia aculeata	f	7	36.0 ± 1.3b	2.74 ± 0.20a,b,d
	m	3	36.7 ± 2.2b	3.00 ± 0.32a,b,d
Parkinsonia texana	f	30	31.0 ± 0.3d	3.00 ± 0.06d
	m	27	31.1 ± 0.3d	3.09 ± 0.07b,d

Table 3. The mean size of seeds of *Acacia greggii* and the four palo verde species used in this experiment (± 1 SE).

Host species	n	Seed weight (mg)
Acacia greggii	150	187 ± 5
Cercidium floridum	300	229 ± 2
Cercidium microphyllum	201	156 ± 2
Parkinsonia aculeata	150	99 ± 2
Parkinsonia texana	100	84 ± 1

merous factors other than host suitability. Hypotheses proposed to explain this imperfect relationship between host use and host suitability variously implicate predators and parasitoids (Lawton & McNeill 1979, Bernays & Graham 1988), plant apparency (Feeny 1976, Rhoades & Cates 1976), phenology (Tahvanainen 1983), abundance (Wiklund 1982), or reliability (predictability) (Futuyma 1976, Cates 1981), and the interaction between plant chemistry and the neuro-physi-ological capabilities of insects (Ehrlich & Raven 1964, Smiley 1978, Jermy 1984, Fox & Lalonde 1993). Currently, there is insufficient data available to reject any of the above hypotheses as explanations for *S. limbatus*'s failure to use *P. texana*.

The small size of *P. texana* seeds relative to the other palo verde species (Table 3) does not likely prevent *S. limbatus* from using this host. Although survivorship was lower and surviving adults were slightly smaller when reared on *P. texana* than when reared on either *A. greggii* or *C. microphyllum* (Table 2), beetles reared on *P. texana* survived better and were of similar size to beetles reared on *C. floridum*. Also, *Mimosestes amicus* (Horn), a seed beetle that is substantially larger than *S. limbatus* throughout most of its distribution (*M. amicus* biomass >2 × *S. limbatus* biomass), successfully uses *P. texana* in nature (Nilsson & Johnson 1993), although surviving *M. amicus* adults reared from *P. texana* are generally much smaller than those reared from other hosts.

Possibly, beetles may ignore *P. texana* in favor of *Acacia berlanderii* Bentham, which is interspersed with *P. texana* throughout southern Texas and is heavily attacked by *S. limbatus*. *Acacia berlanderii* is closely related to *A. greggii*, and thus survivorship on seeds of this host is likely high, such that it is a physiologically more suitable host than *P. texana*. However, *A. berlanderii* pods dehisce early in the year relative to *P. texana*, such that its seeds are not available after July, whereas *P. texana* is available into late autumn. Our data suggest that *S. limbatus* should use *P. texana* when *A. berlanderii* is not available. However, in field collections we have found *S. limbatus* eggs on *A. berlanderii* seeds, but not on *P. texana* seeds, even when the two species are within meters of each other (C. W. Fox, personal observation).

Predation and parasitism may significantly influence the patterns of host use by *S. limbatus*. For example, the parasitoid *Uscana semifumipennis* Girault (Hymenoptera: Trichogrammatidae) attacks eggs of *S. limbatus* on *C. floridum* in Arizona (Siemens & Johnson 1992). Rates of parasitism may be affected by host plant species, such that eggs laid on *P. texana* may have lower success than eggs laid on alternative hosts due to parasitism of eggs and larvae, selecting for females that avoid *P. texana*. However, mortality due to parasitism is density-dependant on *C. floridum* (Siemens & Johnson 1992). If mortality due to parasitism on hosts

in southern Texas is also density-dependant, then *P. texana* would represent an ecological escape from parasitoids (and possibly predators) because other *S. limbatus* are not currently using it.

Alternatively, we must acknowledge that, although *S. limbatus* has not yet been collected from *P. texana,* this shrub may actually be a host for *S. limbatus* and that more extensive collections may detect its use of this plant. However, even if *S. limbatus* uses *P. texana,* the frequency of use is clearly very low; *S. limbatus* is easily collected on *Acacia* species in southern Texas but, despite extensive collections, has not been collected from *P. texana.* The above hypotheses proposed to explain the absence of *S. limbatus* on *P. texana* need also be considered to explain the low frequency of use of this host, if indeed future surveys should detect *S. limbatus* on *P. texana.*

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