

## Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds

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**Summary.** Seasonal patterns of insect damage to reproductive tissue of the legume *Baptisia australis* were studied for three years in native tallgrass prairie. Contrasting seasonal patterns of damage were associated with the major species of insect consumers. The moth *Grapholitha tristegana* (Olethreutidae) and the weevil *Tychius sordidus* (Curculionidae), which together infested 80–100% of developing fruits (pods), consistently damaged more seeds on average in early than in late maturing pods. But while late opening flowers were less subject to attack from moths and weevils, they were more subject to attack from chewing insects, particularly blister beetles (*Epicauta fabricii*, Meloidae), which destroyed >80% of all flowers and developing young pods (including moth and weevil larval inhabitants). The blister beetles arrived late in the flowering season and fed particularly on young reproductive tissue, allowing larger, older pods that had developed from early opening flowers to escape destruction. The relative abundances and impacts of blister beetles, moths, and weevils varied from year to year. Adding to the uncertainty of reproductive success of the host plant were the large and variable amounts of damage to immature buds inflicted by insects (including the blister beetles and weevil adults) and late killing frosts. Thus, timing of flowering is critical to success in seed production for *B. australis*. The heavy impacts of insects and weather can result in a very narrow window in time (which shifts from year to year) during which *B. australis* can flower with any success. The opposing pressures exerted by insects and weather on floral reproductive success may act in concert with other features of the plant's biology to foster the maintenance of considerable diversity in flowering times among individuals in local populations of *B. australis*.

**Key words:** Flowering time – Grassland – Herbivory – Phenology – Seed predation

Consequently, there has been great interest in how such animals respond to the phenological patterns of flowering and fruiting in host plant populations, and how such responses affect the reproductive success of individual plants (e.g., Janzen 1969; Smith 1970; Schemske 1977; Thompson and Willson 1979; Zimmerman 1980a; Augspurger 1981; Manasse and Howe 1983; Rathcke 1983; Benkman et al. 1984; Rathcke and Lacey 1985).

Insect consumers of reproductive tissue often destroy large percentages of many plant species' potential seed crops (e.g., Janzen 1971; Breedlove and Ehrlich 1972). This damage can limit plant recruitment (Louda 1982a, b). Janzen (1969) emphasized the potential for plant escape from insect seed predators in space and time as well as through chemical defense. The potential for plant escape in time (phenological escape *sensu* Kinsman and Platt 1984) has been studied extensively by comparing seed production and predation among years (e.g., Mattson 1971; Beattie et al. 1973; DeSteven 1983; Solbreck and Sillen-Tullberg 1986a, b). Patterns of seed production and predation over the course of single flowering/fruiting seasons (i.e., within years) have received much less attention (but see Dolinger et al. 1973; Zimmerman 1980b; Augspurger 1981; DeSteven 1981; Kinsman and Platt 1984; Bertness et al. 1987).

We studied a legume, *Baptisia australis* (L.), and its insect associates in native tallgrass prairie to examine the relationship between flowering time and predation intensity. Populations of this plant species, in common with populations of many other angiosperms, exhibit an extended flowering season that is largely due to individual variation in timing of initiation of flowering. Also, as in many other tallgrass prairie plants (e.g., Platt et al. 1974; Evans 1983; Kinsman and Platt 1984), members of the genus *Baptisia* sustain heavy damage to reproductive tissue from insect consumers (Johnson 1977; Haddock and Chaplin 1982). If insect consumers are denied access to reproductive tissue, the seed production of *B. australis* can increase by fifty fold (Meierhoff 1984). In the present study, we ask: (1) what are the seasonal patterns of damage to *B. australis* inflicted by each of the several major insect species attacking the plant?, and (2) how consistent from year to year are the intensities of damage inflicted by these insects? After addressing these questions, we speculate briefly on the potential role of flower and seed predation in the evolution and maintenance of present-day flowering patterns in local populations of the host plant.

The reproductive success of many plants is complexly intertwined with the behavior of animals that act as pollinators, dispersal agents, and consumers of reproductive tissue.

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### *The plant and its insect associates*

The study was conducted at Konza Prairie Research Natural Area, a preserve of The Nature Conservancy, operated by the Division of Biology at Kansas State University. This 3500 ha tract of native tallgrass prairie lies 10 km south of Manhattan, Kansas, USA, and is dominated by the grasses *Andropogon gerardii* Vitman, *A. scoparius* Michx., *Sorghastrum nutans* (L.), and *Panicum virgatum* (L.) (Freeman and Hulbert 1985). Populations of *Baptisia australis* consist of individuals scattered amongst the prairie flora. In presettlement tallgrass prairie, recurrent fire may have influenced plant-insect interactions (e.g., Hulbert 1973; Evans 1984); we therefore studied *B. australis* at both burned and unburned sites on Konza Prairie.

*Baptisia australis* is a long-lived perennial that blooms in early spring. A single plant bears 5–75 flowers on each of one to several inflorescences. Inflorescences remain in flower for one to two weeks while individual flowers persist for only a few days. Flowers are insect- (especially bumblebee-) pollinated. We do not know whether self-pollination occurs, but Haddock and Chaplin (1982) reported little capacity for self-pollination in two other species of *Baptisia*. After pollination, ovaries swell into large green inflated pods containing 30–50 seeds. Several weeks later, the pods gradually blacken, harden, and split open to disperse seed.

On Konza Prairie, three insect species in particular consume large quantities of reproductive tissue of *B. australis* (Johnson 1977; E.W. Evans unpublished work). The buds, flowers, and young pods are eaten by adult blister beetles, *Epicauta fabricii* (LeConte), Meloidae (the larvae are soil-dwelling predators), and the developing seeds are eaten by the larval moth *Grapholitha tristegana* (Clemens) (Olethreutidae) and the larval weevil *Tychius sordidus* LeConte (Curculionidae) (hereafter these insects are referred to simply as the blister beetle, the moth, and the weevil). Typically, a single moth larva (occasionally two) develops in a pod while several (as many as six) weevil larvae may share a pod. Larvae of the two species frequently occur together in pods. The larvae consume most (and often all) of the developing seeds. The weevil and the moth appear to be host-specific on *Baptisia* spp. in tallgrass prairie (Bertwell 1972; Clarke 1971; Frost 1945; Heinrich 1926). The weevil, moth, and blister beetle also attack *B. bracteata* (= *leucophaea*) Muhl., which also occurs abundantly on Konza Prairie and flowers concurrently with *B. australis*. Haddock and Chaplin (1982) record the weevil, moth, and blister beetle as inflicting heavy damage to *Baptisia* (*B. bracteata*) in Missouri.

Because insect consumers destroy so much of the reproductive tissue of *B. australis*, their feeding activities impinge strongly on one another. In particular, blister beetles act both as competitors and as predators in co-exploiting *B. australis* pods with moths and weevils. As pods are consumed by beetles, so too are the insect inhabitants of those pods; as flowers are destroyed, so too are the opportunities for oviposition by other insects in the pods that otherwise would have developed. Thus the feeding activities of blister beetles can have major impact on reproduction and survivorship of moths and weevils.

### Methods

Our focus was on the fates of individual *B. australis* flowers opening at different dates throughout the flowering season.

To establish seasonal trends for such fates, we monitored individual flowers by repeatedly visiting marked plants on Konza Prairie during the flowering seasons of 1984 and 1986. We supplemented these efforts by examining the contents of *B. australis* pods collected just prior to seed dispersal in 1983.

In 1984, marked plants of *B. australis* at four study sites (separated from each other by at least one km) were studied from the initiation of flowering until seed dispersal. In 1986, a new set of plants was studied similarly at each of the four sites. Two of the sites, denoted B1 and B2, were burned in 1984 and again in 1986, while the other two sites, U1 and U2, were unburned and had not been burned for over ten years.

A representative sample of plants (and flowers opening at different times in the season) was selected at each site in 1984 and 1986 by marking 40–60 haphazardly chosen individuals a few days before flowering for the population as a whole began. This ensured inclusion of individuals at various stages of stem and bud development. We also included particularly late maturing plants (and late opening flowers) by marking an additional 15–25 plants two weeks later (i.e., about halfway through the population flowering season). When marked, these plants had opened few if any flowers. In 1984, a single inflorescence on each plant was studied; in 1986, all inflorescences on each plant were studied. In both years, individual sites were visited at intervals of several (generally 2–3) days. Each newly opened flower was identified (by placing a small tag on every second or third flower pedicel) and thereafter checked on subsequent visits to the site to ascertain its eventual fate. Flower buds that never opened were not marked.

Before marking/checking flowers, we censused plants for adult insects. In 1984 and 1986, the same 35 and 50–75 plants, respectively, were checked carefully (and non-destructively) for insects at each visit to a site. These censuses established the seasonal abundance of adult blister beetles and weevils at each site (few of the nocturnally active adult moths were encountered in our daytime censuses). After flowering had finished and the adult beetles had disappeared from plants, censuses were conducted weekly in 1986 until July when we collected all marked inflorescences just before seed dispersal (when damage to seeds from insects infesting pods was essentially completed). In 1984, plant censuses were conducted only during the flowering season. In early July, pods were collected at sites B2 and U2 (in a futile attempt to assess percent seed fill in infested pods). Pods at B1 and U1 were collected three weeks later, just before seed dispersal.

Pods were dissected in the laboratory. Each pod was scored as intact and free from insect infestation or infested by moth and/or weevil larvae. In most cases, the insects had exited from pods, although occasionally, pupating moths and full grown moth and weevil larvae were found. Previous infestation by moth larvae was revealed by frass and silk and by pupal chambers. In pods infested by weevils alone, the weevils' characteristic frass was apparent on the inner pod walls and on partially consumed seeds. This frass was generally hard to detect when moth larvae had also been present. Therefore, to estimate the percentage of all pods (moth infested and moth-free) infested by weevils, it was assumed that roughly equal percentages of pods with and without moth larvae harbored weevil larvae. The overall level of weevil infestation was calculated as equalling

**Table 1.** Dates corresponding to early and late flowering periods at individual sites in 1984 and 1986 (e.g.,  $\leq$  May 24: flower opened on or before May 24)

Site	1984		1986	
	Early	Late	Early	Late
U1	$\leq$ May 24	$\geq$ May 29	$\leq$ May 5	$\geq$ May 9
U2	$\leq$ May 25	$\geq$ May 29	$\leq$ May 4	$\geq$ May 8
B1	$\leq$ May 25	$\geq$ May 30	$\leq$ May 9	$\geq$ May 14
B2	$\leq$ May 25	$\geq$ May 30	$\leq$ May 9	$\geq$ May 13

the percentage of moth-free pods that harbored weevil larvae. The number of seeds that were filled could only be determined for pods free of insects (the larvae destroyed many seeds entirely), but the number of large, filled seeds that escaped damage from insects was recorded for all pods. Because pods at B2 and U2 in 1984 were collected before moth and weevil larvae had completed development, this number of seeds escaping predispersal damage could not be determined for these pods.

In 1983, *B. australis* was not studied until just prior to seed dispersal in July, at which time a sample of mature pods was collected. Racemes bearing 2–3 dozen pods were sampled along a 2.5 km transect through an unburned portion of Konza Prairie (last burned more than ten years previously) by collecting the nearest suitable inflorescence at each of 50 stations at 50 m intervals. The 50 inflorescences thus collected were returned to the lab where the contents of pods were recorded as described above.

**Data analyses.** Because very few flowers developed into mature pods in 1984 and 1986, we analysed seasonal patterns in pod fates by pooling pods into two categories: those developing from flowers opening early or late in the flowering season (Table 1). Because flowers on a plant that overlapped in when they were open may not have had independent fates, we further pooled pods to calculate for each plant the average fate of its early or late maturing pods. Small sample sizes were an unfortunate but unavoidable result of this conservative approach.

We do not know the opening date of flowers producing the pods collected in 1983. We have therefore compared relatively early vs. late maturing pods for this year by examining the average fates of the bottom ten vs. the top ten pods on each of fifty inflorescences collected (flowering patterns in 1984 and 1986 suggest that the two groups of pods in 1983 developed from flowers opening roughly one week apart).

The potential exists for a confounding of effects of season and position on an inflorescence (upper vs. lower flowers) in our analyses of 1983 pod contents. We therefore tested for a position effect per se using 1984 and 1986 data. We compared fates of the lowermost and uppermost flowers from large clusters of flowers opening together on a given day on a given inflorescence ( $n=278$  pairs; flowers per cluster: 5–31, median=9). We found no significant difference in percentages of lower vs. upper pods that escaped insects entirely or that were infested either by moths or by weevils. We therefore conclude that no confounding effect of flower position is reflected in our analyses of bottom (=early) vs. top (=late) pods for 1983 inflorescences.

## Results

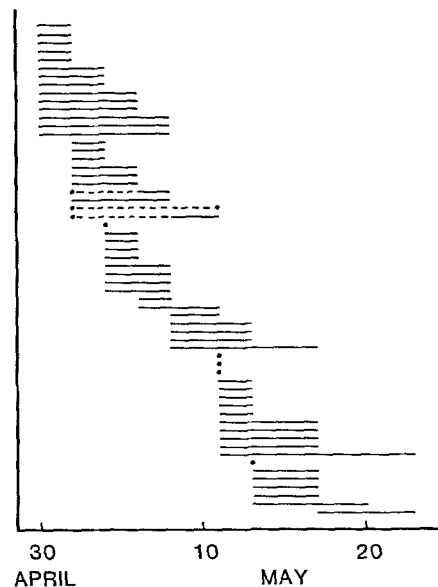
### Flowering times

At any given site in both 1984 and 1986, the flowering period of *B. australis* populations lasted 3–4 weeks. Flowering began in mid-May at all four sites in 1984, approximately at the long-term median date of flower initiation for this species in northeast Kansas (Hulbert 1963). Flowering began two to three weeks earlier (in late April-early May) during the unusually warm spring of 1986.

Burning did not markedly alter the flowering season. Sites B1 and B2 were burned on 19 April in 1984, well before initiation of aboveground growth of *B. australis*. There was little difference in initiation of growth in early May and subsequent flowering at these burned sites vs. the two unburned sites. Sites B1 and B2 were burned 9 April in 1986, just as *B. australis* was initiating aboveground growth. Consequently, flowering activity was initiated several days later at burned vs. unburned sites, as burned individuals had to resprout after the fire. Individual plants of *B. australis* typically flowered over a period of 5–10 days. Thus the extended flowering period of local populations derived largely from asynchrony in initiation of flowering among individual plants (Fig. 1).

### Overview of flower fates

Most flowers, or the young pods that developed from them, were destroyed by chewing insects, especially blister beetles, and produced no seeds in 1984 and 1986 (Table 2). Of those relatively few surviving pods, 96.1% (1984) and 87.6% (1986) were infested with moths and weevils, and consequently succeeded in producing at most only a few mature seeds. In contrast, the few flowers whose pods were



**Fig. 1.** Flowering periods of 60 individual plants of *B. australis* at site U1 in 1986. Plants are arranged in order of initiation of flowering. Solid lines connect consecutive census dates on which flowering was recorded while dotted lines connect census dates with flowering punctuated by at least one census date without flowering. Single points are shown for plants with flowering periods spanning only a single census

**Table 2.** The percentages of flowers yielding large mature pods at individual sites in 1984 and 1986 ( $N$ =number of flowers marked)

Site	1984		1986	
	%	( $N$ )	%	( $N$ )
U1	20.3	(1954)	13.4	(1547)
U2	19.5	(1911)	18.0	(1736)
B1	13.0	(1771)	8.4	(1307)
B2	17.9	(2116)	16.8	(2239)
All	17.8	(7752)	14.7	(6829)

neither consumed by blister beetles nor infested by moths and weevils ultimately yielded on average 24 mature seeds.

Populations of *B. australis* at both burned and unburned sites experienced uniformly low success. Strong, contrasting seasonal patterns of damage were associated with moths and weevils vs. blister beetles. The former insects particularly infested pods maturing from early flowers, while the latter insects particularly consumed late flowers and the young pods that developed from these late flowers. Details are given below by examining first the likelihood that a flower developed into a mature pod (escape from blister beetles),

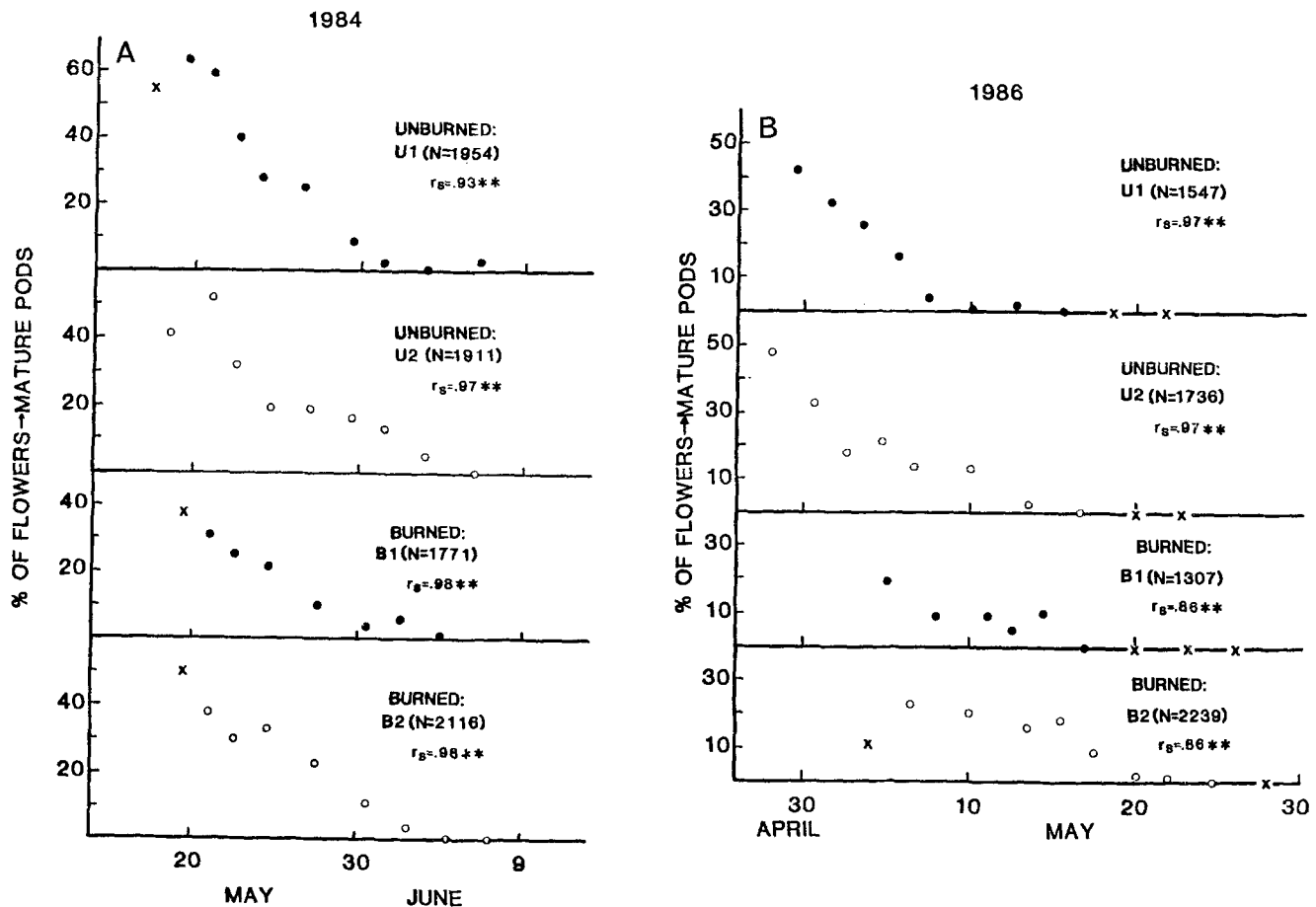
and secondly, the likelihood that seeds inside such a mature pod had not been damaged (escape from moths and weevils).

#### *Pod maturation: the impact of blister beetles*

Our regular censuses revealed that almost all ovaries began swelling into pods within a few days after flowers opened. As evidenced by chewed remains at later censuses, however, the vast majority of flowers and developing pods were destroyed by chewing insects. In both 1984 and 1986, a consistent seasonal pattern was apparent in the probability of flowers and young pods escaping these insects. At each site in both years, a steep seasonal decline occurred in the percentage of flowers opening on a given date that subsequently survived to mature into large pods (Fig. 2).

Adults of the blister beetle in particular were observed in large numbers feeding on flowers and developing pods. Destruction of tagged reproductive tissue by chewing insects generally coincided with the presence of these beetles at our sites. Thus we conclude that these beetles were primarily responsible for most failures of flowers to mature into large pods.

The seasonal patterns of damage by the blister beetles reflected their arrival time and subsequent feeding patterns. They were largely absent from the plants during the early



**Fig. 2. A, B.** The percentages of flowers developing into mature pods at each site in 1984 (A) and 1986 (B), plotted as a function of flowering date. Percentages are plotted for all marked flowers at a site opening between censuses (midpoints of intervals between censuses are plotted along the x axis against corresponding percentages along the y axis). Percentages based on a sample of less than 50 flowers are marked with an x.  $N$ =total number of flowers marked at each site;  $r_s$ =Spearman Rank correlation coefficient for percentage vs. flowering date (two-tailed test:  $**P < 0.01$ )

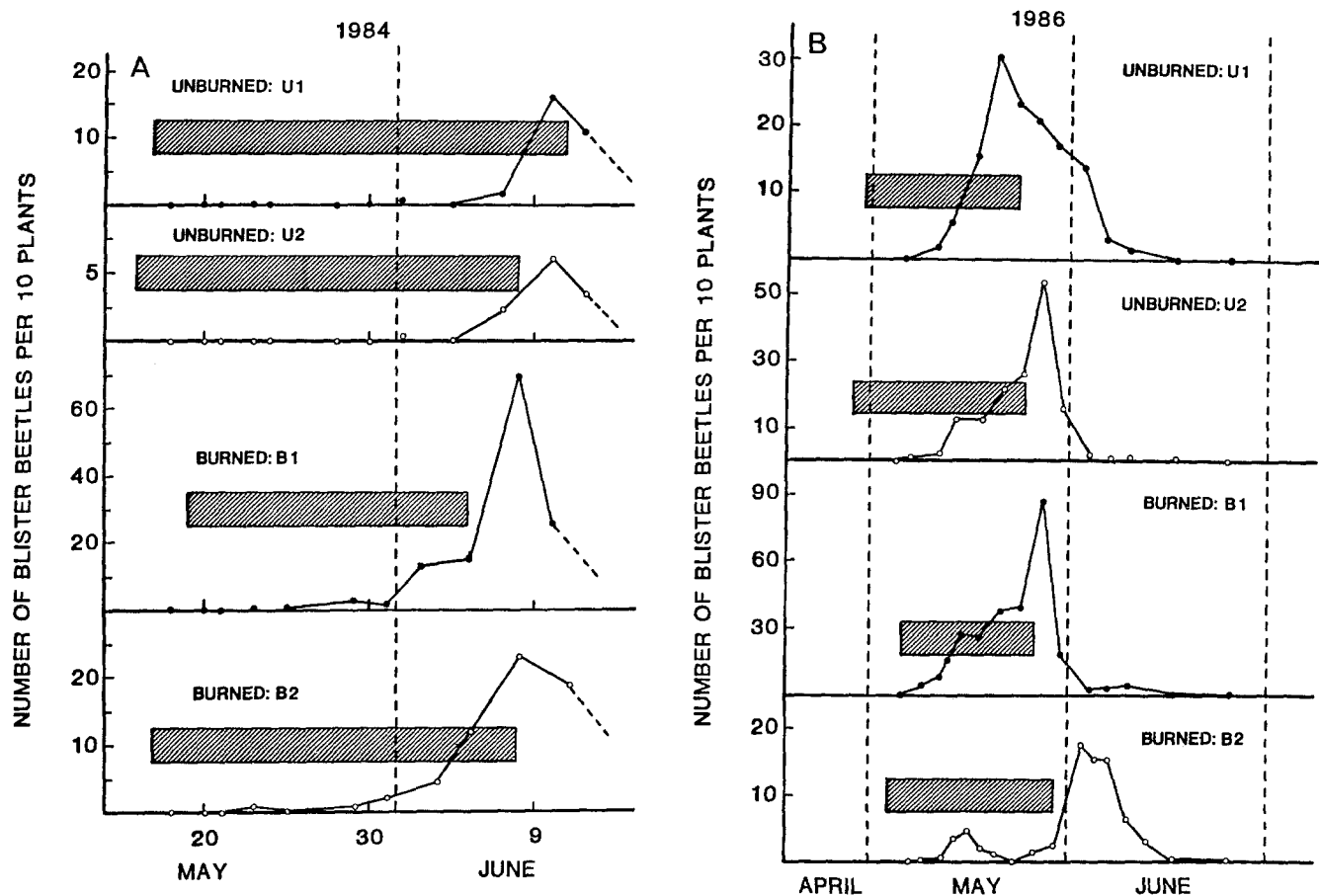


Fig. 3A, B. The number of blister beetles per ten plants at each site in censuses of *B. australis* in 1984 (A) and 1986 (B). Shaded rectangles indicate the flowering period of the local plant population. Last quantitative censuses of beetles were made June 10–12 in 1984; as indicated by dotted lines, few beetles were encountered thereafter in brief visits to study sites

flowering season, but thereafter built up to large numbers, only to drop rapidly in number soon after flowering of *B. australis* had finished (Fig. 3). Their sudden disappearance from the plants (and the prairie) coincided with their equally sudden appearance in large numbers in alfalfa fields (S. Blodgett unpublished work), suggesting mass migration (see also Alcock and Hadley 1987).

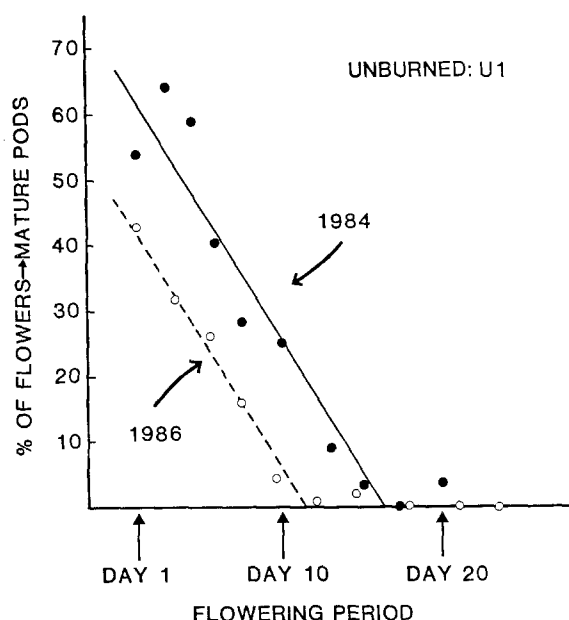
When they first arrived, the beetles first fed voraciously on buds, flowers, and young developing pods. In contrast, they fed relatively little on larger, more mature pods. After destroying virtually all the young reproductive tissue, the beetles switched to feeding primarily on leaves, and again generally left larger pods untouched. Pods that were large enough to escape damage had developed from flowers opening early in the season, well before arrival of the beetles, as is reflected in Fig. 2.

In general the beetles arrived at host populations earlier and in greater numbers in 1986 than in 1984 (Fig. 3). This resulted in a decrease in the overall percentage of flowers that produced mature pods in 1986 vs. 1984 (Table 2;  $\chi^2 = 24.61$ ,  $P < 0.001$ ). The difference between years in successful pod production is particularly striking for site U1 (Fig. 4). At any given point in the flowering season, the percentage of flowers that ultimately resulted in mature pods was markedly higher in 1984 when beetles arrived relatively later and in fewer numbers.

#### Pod infestation: the impact of moths and weevils

**Overall levels of damage.** As revealed by those few pods that blister beetles did not consume, most developing pods were attacked by the moth and the weevil in each year of the study (Table 3). The percentage of pods escaping entirely from insect infestation was always low, ranging from 0 to 35%. Levels of infestation of both moth and weevil varied considerably among sites and years, and there was no obvious correlation between the two species. Moth infestation was particularly heavy in 1984 (84% of pods at all sites combined) and relatively light (30%) at unburned sites in 1986, while weevil infestation was unusually light (13%) in 1983. The generally heavy damage inflicted by insects resulted in few seeds surviving to disperse from mature pods; numbers of seeds escaping predispersal damage from insects averaged 0.29 to 11.90 per pod at any given site (Table 3).

**Seasonal patterns: seed production per pod.** In general, more seeds escaped damage by moths and weevils in late than in early maturing pods. In 1983, for example, 147% as many seeds survived the predispersal period in late than in early maturing pods (Table 4). Similar results occurred in 1984 and 1986 in each of the four cases where contents of early and late maturing pods could be compared mean-



**Fig. 4.** The percentages of flowers developing into mature pods at site U1 in 1984 and 1986. Percentages are those given in Fig. 2; they are plotted here as occurring at successive days in the flowering season where "Day 1" is the first day that flowers opened in 1984 (17 May) and 1986 (29 April). Solid and dotted lines are plotted from simple linear regressions for results from Day 1 to Day 18 (1984) and Day 12 (1986):  $y = 46.1 - 4.0x$  (1984) and  $y = 66.4 - 4.1x$  (1986). Slopes of the regressions are not significantly different ( $P > 0.50$ ) but elevations are ( $P < 0.01$ ) (two-tailed  $t$  tests, Zar 1974:228 ff)

**Table 3.** Fates of mature pods, 1983–86: mean number ( $\pm$  two standard errors) of filled seeds per pod escaping predispersal damage by insects, and the percentages of pods escaping insect infestation (NUL) or infested by moth (LEP) and/or weevil (WV) larvae.  $N$  = number of pods

Year	Site	$N$	no Seeds/Pod		% Pods		
			$\bar{x}$	( $\pm 2$ SE)	NUL	LEP	WV
1983	–	1000	11.90	(0.76)	35.1	58.6	12.8
1984	U1	396	0.29	(0.17)	0	89.1	100.0
	U2	373	–	–	2.4	90.2	73.0
	B1	230	3.33	(0.93)	2.6	94.8	50.0
	B2	379	–	–	10.3	65.7	70.0
1986	U1	208	1.63	(0.67)	3.8	32.2	86.5
	U2	312	6.38	(1.12)	20.5	29.8	66.7
	B1	110	1.43	(0.89)	2.7	58.2	69.6
	B2	376	5.42	(0.91)	13.3	55.1	60.9

ingfully (Table 4; too few plants with late maturing pods were available for comparison at B1 in 1984 and 1986). While the difference between early and late pods at individual sites is significant only in 1983 (when sample sizes were largest), the two-tailed probability that more seeds would survive in late pods than in early pods in all five cases for 1983–1986 is 0.0625 (binomial distribution,  $p = q = 0.50$ ).

We assessed three general factors that might account (alone or together) for the seasonal increase in seed produc-

**Table 4.** The mean number of filled seeds per pod ( $\pm$  two standard errors) that escaped intact from moth and weevil damage for all pods maturing early or late in the season

Year	Site	no Seeds/Pods				
		Early		Late		$P^b$
		$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	
1983	–	9.64	(1.74, 50)	14.16	(2.14, 50)	$< 0.001$
1984	UL	0.20	(0.40, 24)	2.50	(2.60, 11)	NS
	B1	2.74	(1.86, 17)	5.65	(11.30, 2)	–
1986	U1	1.38	(1.05, 29)	5.34	(2.64, 8)	NS
	U2	4.32	(2.00, 33)	7.67	(5.61, 8)	NS
	B1	2.53	(2.84, 18)	0	(–, 3)	–
	B2	3.10	(1.54, 29)	5.41	(2.88, 27)	NS

<sup>a</sup>  $N$ : Number of plants

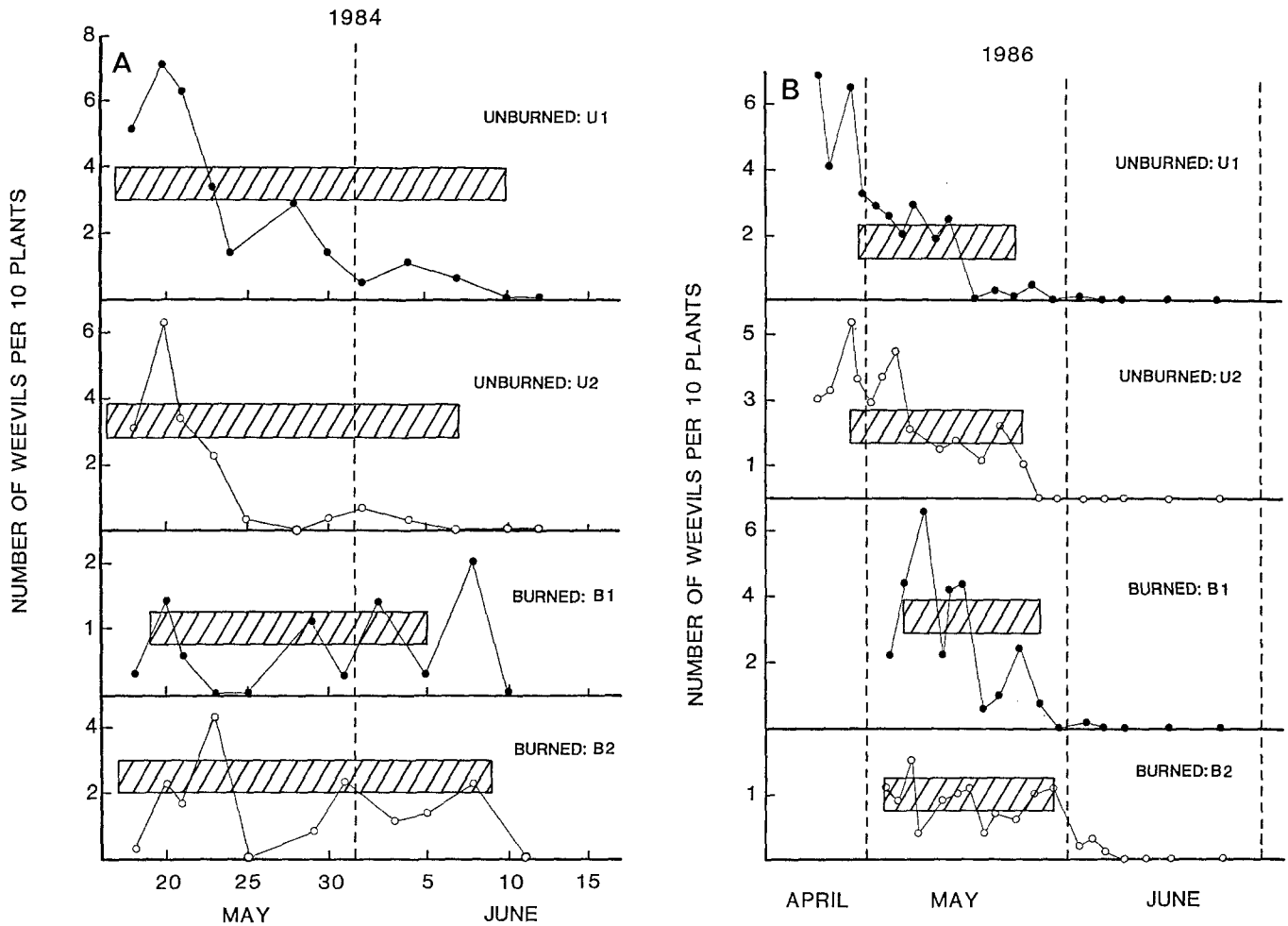
<sup>b</sup>  $P$ : Probability levels for paired  $t$  test (1983) and Wilcoxon Rank Sum Test (1984 and 1986)

tion: in comparison with early maturing pods, late maturing pods might have (1) filled greater number of seeds (e.g., because of greater pollination success), (2) more frequently escaped insect infestation (e.g., because fewer ovipositing adult insects were present), and/or (3) sustained damage to fewer seeds when pods were infested (e.g., because on average fewer larval insects matured in individual pods).

**Seeds filled per pod.** Sufficient numbers of mature pods that had escaped insect infestation were collected in 1983 (Table 3) to compare the number of filled seeds between early and late maturing pods (too few such pods were collected in 1984 and 1986 to make similar statistical comparisons). Late maturing pods actually filled fewer (85% as many) seeds than did early maturing pods ( $\bar{x} \pm 2$  s.e.:  $26.8 \pm 3.6$  (early) vs.  $22.8 \pm 2.9$  (late),  $P < 0.05$  for two-tailed paired  $t$ -test of means of individual racemes;  $N = 34$  racemes). Thus the greater number of seeds surviving the pre-dispersal period in late than in early maturing pods in 1983 (Table 4) was not the result of late maturing pods simply filling more seeds.

**Percentage of pods attacked.** A significantly greater percentage of late than of early maturing pods escaped insect infestation in 1983 (Table 5). The same pattern occurred in 1986 at individual sites (omitting site B1, as above), but no significant differences were detected between early and late pods (high variances and low sample sizes weakened the statistical analysis) (Table 5). In 1984, when overall insect attack was particularly high (Table 2), early and late pods did not differ in their success in escaping insect infestation (Table 5). Analyses for moths alone revealed significantly lower levels of infestation in late than in early pods in 1983 and 1986 (but only at burned sites). A significantly lower level of weevil infestation in late than in early pods was found in 1986 only, at unburned sites. Censuses of weevil adults revealed, however, that the number of weevils on plants often dropped dramatically as the season progressed (Fig. 5).

**Seed fates in infested pods.** Not all seeds in infested pods were consumed by moth and weevil larvae; an overall aver-



**Fig. 5A, B.** The numbers of adult weevils per ten plants at each site in censuses of *B. australis* in 1984 (A) and 1986 (B). Shaded rectangles indicate the flowering period of the local plant population

**Table 5.** The mean percentage of pods per plant ( $\pm$  two standard errors) that escaped infestation by moths and weevils, for pods maturing early or late in the season

Year	Site	% Pods Escaping				$P^b$
		Early		Late		
		$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	
1983	—	22.4	(3.8, 50)	47.8	(4.4, 50)	<0.01
1984	U1	0	(-, 24)	0	(-, 11)	—
	U2	1.6	(3.3, 25)	0	(-, 15)	NS
	B1	3.8	(4.9, 17)	5.0	(10.0, 2)	—
	B2	11.9	(7.8, 28)	1.6	(3.3, 8)	NS
1986	U1	1.3	(1.5, 29)	8.8	(12.8, 8)	NS
	U2	8.6	(5.2, 33)	28.1	(23.8, 8)	NS
	B1	6.9	(11.3, 18)	0	(-, 3)	—
	B2	4.3	(3.4, 29)	13.0	(10.8, 27)	NS

<sup>a</sup>  $N$ : Number of plants

<sup>b</sup>  $P$ : Probability level for two-tailed Wilcoxon matched pairs test (1983) or Wilcoxon rank sum test (1984, 1986)

age of 3–4 seeds per infested pod survived intact in 1983–86 (Table 6). In all three years, more seeds escaped insect damage in late than in early maturing infested pods (Table 6; Wilcoxon Matched Rank test for 7 comparisons, 1983–86:  $P < 0.05$ ). This general pattern was reflected in pods infested

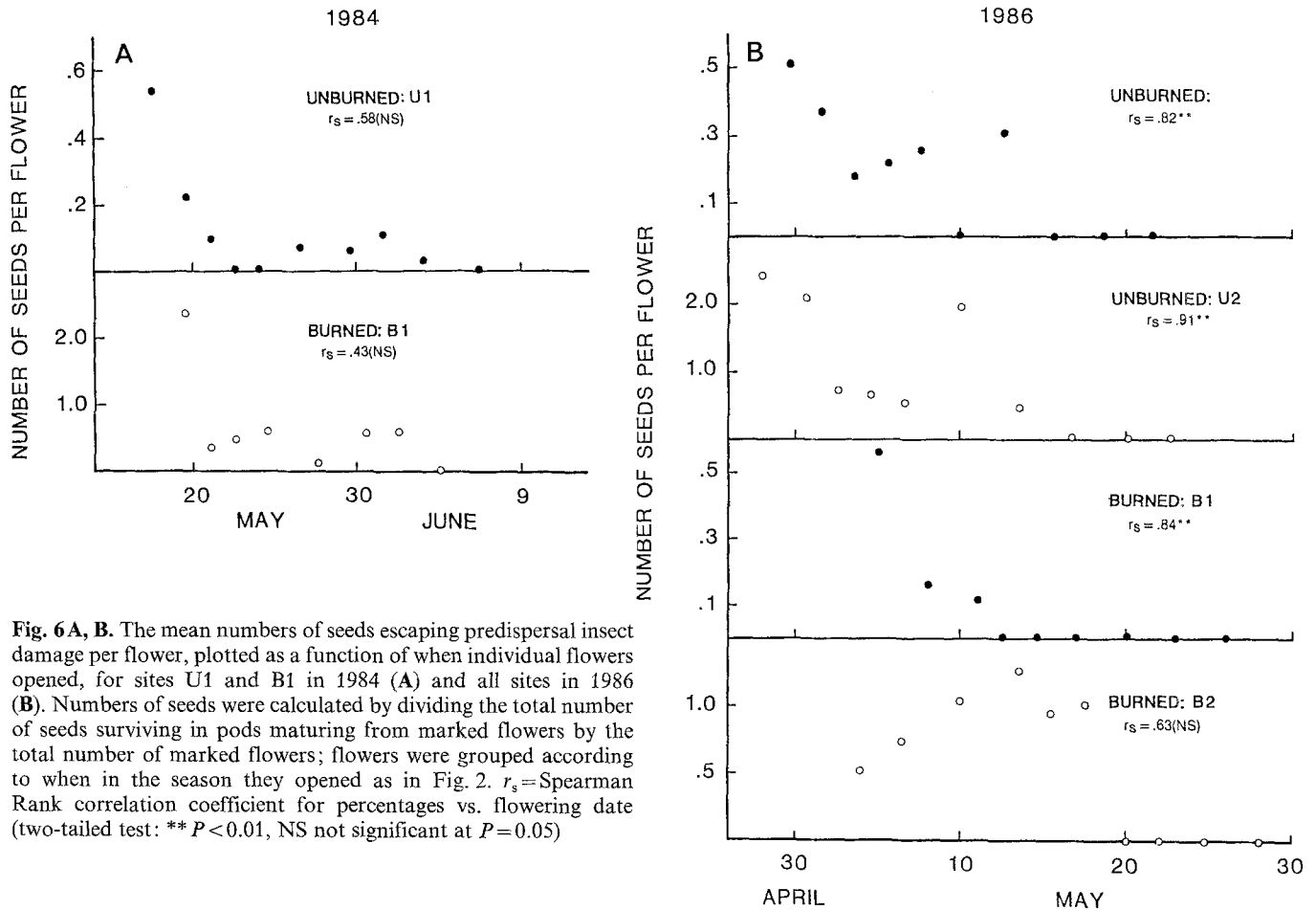
**Table 6.** The mean number of filled seeds per pod ( $\pm$  two standard errors) that escaped from moth and weevil damage, for only those pods (maturing early or late in the season) that were infested by these insects

Year	Site	no Seeds/Pod				$P^b$
		Early		Late		
		$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	$\bar{x}$	( $\pm 2$ S.E., $N^a$ )	
1983	—	5.05	(1.21, 47)	7.33	(1.66, 47)	<0.05
1984	U1	0.19	(0.14, 310)	1.22	(1.24, 32)	<0.03
	B1	1.99	(0.78, 168)	9.90	(4.15, 20)	<0.001
1986	U1	2.85	(0.80, 196)	6.00	(3.82, 22)	<0.06
	U2	0.94	(0.52, 143)	4.14	(4.54, 14)	NS
	B1	0.90	(0.78, 41)	0	(-, 18)	<0.05
	B2	3.06	(0.98, 110)	4.38	(1.46, 93)	NS

<sup>a</sup>  $N$  Number of plants in 1983 (i.e.,  $\bar{x}$  was calculated from pod means for individual plants), and number of pods in 1984 and 1986

<sup>b</sup>  $P$ : Probability level for two-tailed Wilcoxon matched pairs test (1983) or Wilcoxon rank sum test (1984, 1986)

with moth larvae in particular (Wilcoxon Matched Rank test, 7 comparisons:  $P < 0.05$ ). In pods infested with weevils alone, however, more seeds escaped in early than in late maturing pods in 1983–86 (Wilcoxon Matched Ranks test, 6 comparisons:  $P < 0.05$ ).



**Fig. 6A, B.** The mean numbers of seeds escaping predispersal insect damage per flower, plotted as a function of when individual flowers opened, for sites U1 and B1 in 1984 (A) and all sites in 1986 (B). Numbers of seeds were calculated by dividing the total number of seeds surviving in pods maturing from marked flowers by the total number of marked flowers; flowers were grouped according to when in the season they opened as in Fig. 2.  $r_s$  = Spearman Rank correlation coefficient for percentages vs. flowering date (two-tailed test: \*\*  $P < 0.01$ , NS not significant at  $P = 0.05$ )

#### Successful seed production per flower

Calculation of the number of seeds surviving the predispersal period per marked flower integrates the detrimental effects both of blister beetles and of moths and weevils. This number of seeds was generally highest for early opening flowers in 1984 and 1986 (Fig. 6), reflecting the especially heavy damage inflicted by blister beetles late in the season. An exception occurred at site B2 in 1986, where blister beetles arrived late (Fig. 2). Seed production at B2 in 1986 was highest for flowers opening in mid-season; seed production was less depressed in these flowers than it was in flowers opening earlier (which were heavily attacked by moths and weevils) or late (which were heavily attacked by blister beetles).

## Discussion

#### Seasonal patterns of flowering success

The timing of flowering had major consequences for the seed production of individual flowers of *B. australis*: most seeds were destroyed by insects, and these insects did not destroy the same proportion of seeds throughout the flowering season. The negative impact of moths and weevils on seed production was greatest for early opening flowers, while the impact of blister beetles was greatest on late opening flowers. In any given year, the relative success of early and late opening flowers therefore depended on the relative

impacts of moths and weevils vs. blister beetles. In 1986, for example, blister beetles were numerous and the number of seeds per flower maturing and surviving the predispersal period generally declined as the season progressed. We did not census blister beetles in 1983. They apparently were not abundant, however, as *B. australis* succeeded in producing unusually large numbers of mature pods. Haddock and Chaplin (1982) also note year-to-year variation in the number of blister beetles infesting *Baptisia* spp. In years when blister beetle populations are low but moth and weevil populations are high, the seasonal trend for floral reproductive success may be reversed, and later opening flowers may disperse relatively more seeds.

The variable climate of the tallgrass prairie probably underlies these shifting seasonal patterns of success of *B. australis* seeds in avoiding destruction by insects. Yearly variation in weather leads to large fluctuations in grasshopper densities in the tallgrass prairie (Smith 1954, E.W. Evans *pers. obs.*) and this may contribute to yearly variations in numbers of the blister beetles which as larvae prey on grasshopper eggs (Selander and Mathieu 1969). Furthermore, yearly variation in weather can alter the synchrony between emergence of adult blister beetles and *B. australis* flowering activity, leading to differences in beetle impact such as those observed at U1 in the more typical spring of 1984 and the warm spring of 1986. Because blister beetles consume insect inhabitants along with developing pods, the varying impact of blister beetles in turn may profoundly affect the population dynamics of the moth and weevil,



thus complexly affecting in turn the degree of damage inflicted on *B. australis* by these insects. Consideration of the biology of these species enhances understanding of their seasonal patterns of attack.

#### *Habits and impacts of flower and pod feeders*

**Blister beetles.** Upon emergence from the soil, the adult blister beetles immediately colonized *B. australis* and *B. bracteata*, ignoring adjacent vegetation also in flower. We found blister beetles feeding on only one other species in the prairie, *Schrankia nuttallii* (Leguminosae), and only after they had consumed essentially all locally available reproductive tissue of *B. australis*. The blister beetles characteristically arrived late in the flowering season of *B. australis* and preferentially fed on young reproductive tissue. It is unclear why the beetles generally did not consume older pods that had matured from early opening flowers. Because they did not, however, the situation is analogous to other predator-prey interactions in which the prey can escape predation by growing sufficiently large (size refuge) during periods of reduced predator activity (e.g., Connell 1975; Evans 1982).

The arrival of blister beetles late in the flowering season for *B. australis* may be linked to the insects' social habits. The blister beetles' synchronous emergence and strong tendency to aggregate results in rapid depletion of local food resources. The beetles may therefore benefit from emerging and colonizing *B. australis* when greatest quantities of young developing pods as well as flowers are available, i.e., late in the flowering season. An earlier arrival would force the beetles to consume relatively more buds (which generally would not be replaced by the plant) and fewer flowers and young pods; buds provide relatively small quantities of nutrients.

**Moths and weevils.** Collectively our results and observations suggest that adult weevils and moths were generally present and poised for oviposition as flowering began in *B. australis* populations. Greater numbers of seeds escaped destruction in later maturing pods, perhaps because the number of weevil and moth females surviving and ovipositing declined with time. The feeding activities of blister beetles may in part foster these seasonal patterns of adult moth and weevil activity. The feeding behavior of blister beetles is a major cause of moth and weevil larval mortality along with floral/young pod destruction. By causing least destruction to early flowers and developing pods, blister beetles correspondingly cause least mortality to moth and weevil larvae inhabiting such pods. The blister beetles may thus generate selective pressure for moth and weevil females to be present early in the season when oviposition provides the greatest chances for moth and weevil larvae to mature.

#### *Other factors affecting seed production*

**Pollination.** Our limited information does not suggest that seasonal variation in pollination success was as marked as seasonal variation in damage from insects to reproductive tissue. Thus we observed throughout the season that essentially every flower escaping consumption by insects initiated a pod (see also Haddock and Chaplin 1982). Pods maturing late in 1983 had only a few less filled seeds than pods maturing early (because the degree of seed fill may reflect pollination success and/or resource limitation, these results must

be interpreted with caution). These observations suggest that pollination success did not vary markedly over the flowering season (of course, we have no information on seasonal variation in the quality of pollen delivered).

**Bud damage: frost and insects.** We assessed the fate of reproductive tissue once it reached the open flower stage. A large fraction of potential flowers, however, never opened because the buds were destroyed by insects and weather. For example, a heavy frost on 22–23 April 1986 destroyed many developing buds on early emerging shoots of *B. australis*. Frozen tips of exposed inflorescences and often entire inflorescences bearing several dozen buds blackened, shriveled and died from frost damage. Insects observed feeding on buds included adult weevils, blister beetles, stinkbugs (*Euschistus* spp., Pentatomidae), and unidentified grasshopper nymphs (Tettigoniidae) and Lepidopteran larvae. While we cannot estimate the percentages of buds destroyed by these various agents, we estimate conservatively (from counts of bud scars on inflorescences bearing marked flowers and pods) that at least 32% (B1), 42% (B2), 52% (U1), and 40% (U2), of buds in 1986 failed to open as flowers.

We are unable also to compare probabilities of survival to flowering of buds developing at different times over the season. Such probabilities, however, very likely also shift in relative magnitude from year to year. Frost is common in northeast Kansas through early May, inflicting greatest but variable damage to early maturing individuals and buds. Weevil adults also do most damage to buds early in the season; as flowering commences, they largely abandon buds for open flowers. Blister beetles, in contrast, are most damaging to late maturing buds. Thus seasonal patterns of survival of buds as well as of flowers and seeds may vary among years as destructive agents with contrasting seasonal occurrences vary in their relative impacts. The combined effects of weather and insects can constrain severely when, in any given spring, *B. australis* can flower successfully. In 1986, for example, the combination of heavy frost damage to early maturing inflorescences and heavy damage from blister beetles to later opening flowers resulted in a very narrow window in time during which *B. australis* could flower with much success.

#### *Evolutionary implications for flowering time*

Although we have not focused on the seed production of individual plants, it is of interest nevertheless to speculate briefly on the evolutionary implications of the seasonal patterns of floral success that we have documented. The sheer magnitude of damage inflicted upon reproductive tissues of *B. australis* by insects creates the potential for these insects to influence significantly the flowering patterns of the plant. In the absence of moths and weevils, selection might favor earlier flowering by *B. australis* followed in turn by earlier emergence of blister beetles (until other pressures, e.g., frost damage (see Breedlove and Ehrlich 1968) or reduced pollination, had sufficient impact to stabilize flowering time). Ultimately this would shrink as well as shift the flowering season of the plant population as a whole while subjecting a greater fraction of flowers to damage from blister beetles. But exploitation by moths and weevils, shaped as it may be by adaptive response to blister beetle activity, often poses counterbalancing selection for later flowering.

The combined impact of the opposing seed mortality pressures exerted by blister beetles vs. frost, moths and weevils might select for an extended period of flowering by individual plants (such bet-hedging individuals would minimize the variance in annual seed production; see e.g. Gillespie 1977; Boyce and Perrins 1987). Alternatively (e.g., if such extended flowering is opposed by other factors), these variable pressures might favor early flowering individuals in one year but late flowering individuals in another, depending upon their relative impacts (e.g., see Primack 1980). While individuals of *B. australis* do exhibit an extended period of flowering, most of an individual's flowering is concentrated in a brief burst lasting only a few days. This suggests that the flowering patterns of individuals are heavily influenced by other factors (e.g., pollinator attraction) in addition to the activities of the insect consumers considered here.

On the other hand, local populations of *B. australis* exhibit considerable variation in when individual plants flower. Some of this variation may be environmental in origin (e.g., Jackson 1966). The initiation of flowering, however, has also been shown to have a strong genetic component in many species (e.g., Murfet 1977; Carey 1983), and may well have such in *B. australis* as well. If so, then the variable, opposing pressures imposed by blister beetles and moths and weevils, by favoring in different years individuals flowering early or late, may join with other factors in acting to maintain variation in flowering time in local populations of *B. australis*.

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