Ecology (1975) **56**: pp. 1435–1440

EFFECTS OF INSECT SEED PREDATORS ON *ASTRAGALUS CIBARIUS* AND *ASTRAGALUS UTAHENSIS* (LEGUMINOSAE)[1,2]

THOMAS W. GREEN[3] AND IVAN G. PALMBALD
Department of Biology and The Ecology Center, Utah State University,
Logan, Utah 84322 USA

Abstract. The genus *Astragalus* (Leguminosae) is noted for a wide diversity of compounds toxic to animals and for varied fruit morphology. Seed predation by insects was measured in mixed populations of *Astragalus cibarius* (browse milkvetch or locoweed), a toxic species with glabrous fruits, and *Astragalus utahensis* (Utah milkvetch), a nontoxic species with pubescent fruits. The study was conducted for 3 yr in areas where both species were sympatric, allowing direct comparison of insect faunas. The major seed predator on both species was a seed beetle (*Acanthoscelides fraterculus*, Coleoptera: Bruchidae) which destroyed 74% of the *A. cibarius* seeds and 60% of the *A. utahensis* seeds examined. Additional *A. cibarius* seed destruction, principally the result of predation by a seed chalcid wasp (*Bruchophagus mexicanus*, Hymenoptera: Eurytomidae), averaged 25%.

Differential predation on the two plant species may be due to differences in phenology, seed and pod energy content, internal pod temperature, chemicals in the pods, and pod morphology. As *A. cibarius* and *A. utahensis* individuals apparently compete for a number of resources when they occur sympatrically, the differential predation rate probably influences the population dynamics of both species. Selection pressure by seed-eating insects may account for much of the chemical and morphological diversity exhibited by the genus *Astragalus* at the present time.

Key words: Acanthoscelides; Astragalus; *Bruchidae*; *coevolution*; *Leguminosae*; *plant-insect interactions*; *seed beetles*; *seed predation.*

INTRODUCTION

The genus *Astragalus* (Leguminosae) contains over 1,500 species worldwide, 180 of which are located in the intermountain region of the western United States (Barneby 1964, Holmgren and Reveal 1966). The genus exhibits greater variations in fruit morphology than any other angiosperm genus (Barneby 1964). Variable pod characteristics in intermountain species include size, outline, thickness of pericarp, texture, color, number of locules, pubescence, and composition. The genus is also chemically diverse with some species highly toxic because of selenium accumulation (Trelease and Trelease 1937, Rosenfeld and Beath 1964); some contain organic poisons which disturb the central nervous system and cause locoism (Kingsbury 1964); others contain high concentrations of nitrosugars (Williams and Binns 1967, Williams and Norris 1969, Williams et al. 1969); and still other species are apparently quite palatable. The study of predispersal seed predators on *Astragalus* (Johnson 1970, Green 1973, Center and Johnson 1974) presents an opportunity to understand coadapted strategies to such morphological and chemical diversity.

We selected two herbaceous perennial species, *Astragalus cibarius* Sheld. (browse milkvetch or locoweed) and *Astragalus utahensis* (Torr.) T. and G. (Utah milkvetch or pink ladyslipper) which are common on dry slopes in northern Utah. The two species often occur in mixed populations, allowing direct comparison of their seed eating faunas. The mature fruits of *A. cibarius* are thick, tough, and leathery while those of *A. utahensis* are thin and relatively fragile. In external morphology, the pods are dissimilar; the pods of *A. cibarius* are glabrous, while the densely pubescent pods of *A. utahensis* resemble balls of cotton (Fig. 1). *Astragalus cibarius* contains toxic chemicals based on 3-nitropropanoic acid (Stermitz et al. 1972). There are no known toxic organic chemicals in *A. utahensis* (M. Coburn Williams, *personal communication*), nor is the species a selenium accumulator.

In this study we attempted to quantify predispersal seed predation by various insect species. In addition we examined plant adaptations (such as resource allocation, internal pod temperatures, pod morphology, and potential reproductive capacity) that may be the result of selection pressure by seed predators and how these adaptations affect such predation. The potential role of seed predators on the population dynamics of *A. cibarius* and *A. utahensis* as they compete in mixed stands was also investigated.

---

[1] Manuscript received 16 September 1974; accepted 1 August 1975.

[2] Utah Agricultural Experiment Station Paper Number 1942.

[3] Present address: Environmental Statement Project, Argonne National Laboratory, Argonne, Illinois 60439 USA.

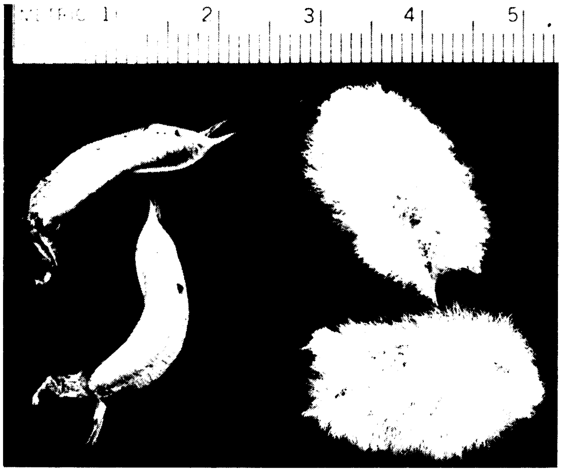

FIG. 1. External pod morphology of *A. cibarius* (left) and *A. utahensis* (right).

METHODS

The study was conducted during 1970–1972 in north-central Utah. Three sites were selected that provided large mixed populations of *A. cibarius* and *A. utahensis*: Logan Canyon (LC), Dry Canyon (DC), and Green Canyon (GC). The sites were within 7 km of each other on the western slope of the Wasatch Mountains at elevations ranging from 1,500 m (GC) to 1,585 m (LC). Each site was visited at least weekly during the growing season during all 3 yr.

Damage preventing complete development in immature pods by seed predators, which would not be included in subsequent pod collections, was examined by following five tagged racemes on 20 plants of each species at the LC site. Insect species that were seed predators on immature pods and seeds were identified and the type of damage caused by each species was determined by field observation. Seed predation in fully developed pods was determined by taking pod collections each year at pod maturity but prior to seed dispersal. Each sample consisted of at least 100 pods collected from at least 10 plants. In 1971, additional small collections of early- and late-maturing pods were gathered each year from 20 tagged plants of each species at the LC site. The entire pod crop was gathered each year from 20 tagged plants of each species at the LC site to see if predation polymorphisms existed. Half of these samples were subdivided by location on the plant (distance from soil surface and distance from edge of plant) to determine if predation was correlated with pod location. Potential seed production per pod (P_s) for each sample was established by counting funicles in 20 pods taken at random, and calculating the mean. Mean percent predation ($\overline{X}_s$) was calculated for each sample using the relationship

$$\overline{X}_s = [P_s N_s - (V + A)]/P_s N_s \cdot 100 \qquad (1)$$

where N_s was the number of pods in the sample, V was the number of undamaged seeds, and A was the number of unsuccessful ovules and aborted seeds, not due to insect damage. Tetrazolium tests indicated that insect-damaged seeds were not viable. Where possible, $\overline{X}_s$ was subdivided by type of damage, and the damage was attributed to a particular insect species or feeding type by isolating pods and seeds in gelatin capsules and observing feeding and emergence behavior.

Resource allocations were measured by cutting off five adult plants of each species at ground level at 10-day intervals during the 1972 season. The plants were divided into four categories: (1) leaves and stems, (2) buds and flowers, (3) pods, and (4) seeds. Roots could not be successfully collected because of the rocky soil. After ovendrying to constant weight, the percent dry weight per category was determined for each collection date and species. Energy values of seeds, pods, and pubescence, when present, were determined by oxygen bomb calorimetry. Field measurements of the internal temperatures of live pods were obtained with copper-constantan thermocouples; ambient air temperatures were obtained simultaneously with shielded thermocouples.

We determined the potential reproductive capacity (PRC) of both species, using the relationship (P_s − A) multiplied by the mean number of pods (N) produced each year on plants used in the experiments described above. The number of seeds dispersed, or actual reproductive capacity (ARC), was derived using the relationship

$$\text{ARC} = \text{PRC}[(100 - E)/100][(100 - \overline{X})/100] \quad (2)$$

where E was the percentage of immature pods that failed to complete development as a result of seed predators and $\overline{X}$ was the mean percent predation on seeds from mature pods in all samples for the species.

RESULTS

Lycaenid butterfly larvae preyed upon both species of *Astragalus* in all 3 yr. These caterpillars chewed a hole through the pericarp of the developing pod and fed on the immature seeds within the pod. Although the larvae seldom removed all the seeds, neither the pod nor the seeds matured when damaged. A larva generally destroyed all the fruits of one raceme before moving to another raceme on the same plant. Larvae of the orange-margined blue (*Plebejus melissa* Edw.) destroyed 10% of the tagged

TABLE 1. Percentage of seed crop destroyed by seed chalcids and beetles in *A. cibarius* and *A. utahensis*. No. pods is total in all samples. Figures for chalcid damage probably include some destruction caused by Hemipterans

	A. cibarius				*A. utahensis*	
Year	No. pods	% chalcid destruction ($\bar{x} \pm 1$ SD)	% beetle destruction ($\bar{x} \pm 1$ SD)	Total % destruction ($\bar{x}$)	No. pods	% beetle destruction ($\bar{x} \pm 1$ SD)
1970	1,402	23.4 ± 6.7	65.6 ± 8.8	88.9	1,130	60.5 ± 5.24
1971	1,765	13.3 ± 5.5	80.4 ± 7.2	93.7	1,746	58.0 ± 8.1
1972	1,276	18.9 ± 0.9	75.1 ± 3.5	94.0	1,937	62.7 ± 2.3
$\bar{x}$ all 3 years		18.6	73.7	92.9		60.4

A. utahensis racemes in 1971 and 18% in 1972. Together, the larvae of the silvery blue (*Glaucopsyche lygdamus* Dbldy.) and the gray hairstreak (*Strymon melinus* Hubner) accounted for pod losses in *A. cibarius* of 9% in 1971 and 11% in 1972.

Stink bugs (*Chlorochora uhleri* Stal. and *C. ligata* Say) were most often found on *A. cibarius* while the coreid bug (*Tollius setosus* Van Duzee) apparently preferred *A. utahensis*. These hemipterans puncture the pod and an individual seed testa with their beaks, apparently inject a digestive secretion, and then suck up the internal contents of the seed. Field observation and subsequent examinations of seeds within the pod indicated that a single seed was consumed in 30–45 min. Precise differentiation of *A. cibarius* seed destruction by hemipterans *versus* seed chalcids was not possible, therefore the chalcid-caused damage figures listed below and in Table 1 include destruction by hemipterans. This error is not great because *Astragalus utahensis* seed destruction by hemipterans averaged 2% during the study. However, the effect of these hemipterans may be underestimated as one or more species may be the vector of the fungus *Cladosporium* sp. (Deuteromycetes) which will kill all seeds within a pod (Stephenson and Russell 1974). Losses due to this fungus ranged from 4% of *A. cibarius* pods in 1970 to a high of 13% in one 1972 sample. The mean occurrence of *Cladosporium* sp. of all samples and years was 5% for *A. cibarius* and < 2% for *A. utahensis* pods.

The seed chalcid wasp (*Bruchophagus mexicanus* Ashmead) was found in all *A. cibarius* pod collections but was absent from all collections of *A. utahensis*. Females oviposited directly on developing seeds by inserting their ovipositors through the pericarp of immature pods. A developing larva consumed all but the testa of a single seed. There were apparently two generations per year; the last generation overwintered inside the seeds. Seed destruction by chalcids averaged 19% (Table 1).

Larvae of seed beetles (*Acanthoscelides fraterculus* Horn) and seed weevils (*Tychius soltaui* Casey) were found in pods of both plant species. The damage caused by the two species could not be distinguished, but *A. fraterculus* outnumbered *T. soltaui* in the collections by about 100–1 and was assumed to be the major seed predator. Oviposition by seed beetles was never observed. Six eggs were found on *A. cibarius* pods—four on the outside and two inside. Five eggs were found in the pubescence of *A. utahensis* pods, but none were observed directly on or inside the pods. Mean seed destruction by beetles was 74% in *A. cibarius* and 60% in *A. utahensis* (Table 1). Although *Astragalus cibarius* and *A. utahensis* are new host plant records for *A. fraterculus* (C. D. Johnson, *personal communication*), the life history of *A. fraterculus* in both *Astragalus* species is similar to that described by Johnson (1970) and Center and Johnson (1974).

There was no correlation between amount of seed destruction and pod location on the plant ($p > 0.05$, *t*-test). Three of the 20 tagged *A. cibarius* plants had significantly less predation in each of the years they were examined ($p > 0.05$, Duncan's New Multiple Range Test), indicating that predation resistance polymorphisms may exist. None of the tagged *A. utahensis* plants had a significant difference in predation. Predation rates also varied with the time of pod development; late-maturing pods experienced greater predation (Table 2).

The distribution of aboveground dry weight among various plant parts is shown for both species in Fig. 2. The decline in percent dry weight in the pod and seed categories in July is due to dispersal. Weights and energy values of seeds, pods, and pubescence are given in Table 3. While caloric content may not accurately reflect the cost of a structure in terms of energy expenditure by the plant, comparisons between similar structures, such as seed-seed or pericarp-pericarp are probably reasonable. Comparisons between pericarp and pubescence can only be estimated until the efficiency of the different metabolic pathways is determined.

Internal temperatures (± 1 SD) of *A. cibarius* pods averaged 28.5° ± 0.6°C, while those of *A. utahensis* averaged 31.8° ± 0.4°C, when ambient air temperature was 26.3° ± 0.1°C.

The potential reproductive capacity and the actual seed rain at the soil surface (seeds that escape insect

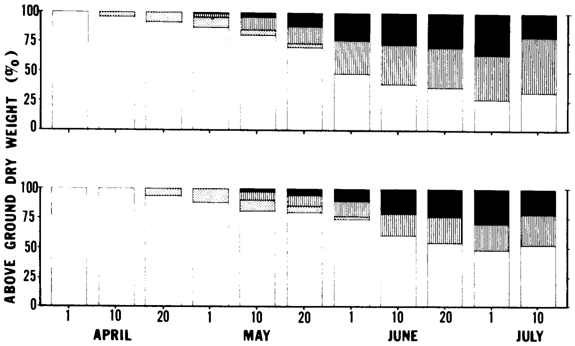

FIG. 2. Distribution of aboveground dry weight in *A. cibarius* (top) and *A. utahensis* (bottom) divided into leaves and stems (open), buds and flowers (dots), pods (lines), and seeds (solid).

predators or predator-borne diseases) for both species are shown in Fig. 3. We intend these figures to serve simply as generalities indicating the impact of predispersal seed predators. At this point more refined statistics (which would include variations in pod production, seed set, predator population levels, etc., as a function of climate, plant age, and reproductive output in the previous season) are not available.

DISCUSSION

Several of the adaptations observed in *A. cibarius* and *A. utahensis* may be at least partially due to selection pressure by insect seed predators. Both species flower, disperse seed, and die back earlier in the growing season than any other associated species (Green and Bohart 1975). This phenology could be a response to the increased predation on late-maturing pods resulting from both increased consumption by individual larvae and more larvae per pod. A similar situation has been postulated for a *Lupinus amplus* Greene population in Colorado (Breedlove and Ehrlich 1968). Lower predation pressure on *A. utahensis* may be partially responsible for the species initiating flowering ≈ 10 days after *A. cibarius*. Whatever the reason, the advanced phenology of *A. cibarius* is probably maintained by strong selective pressures, since late frosts (like the one in 1972 which killed over half the *A. cibarius* flowers) are frequent in the region.

TABLE 2. Percent total seed destruction on *A. cibarius* and *A. utahensis* at the LC site in 1971 in relation to time of pod collection. No. pods is total in all samples collected on this date. All pods were fully mature, but had not dehisced at the time of collection

Collection date	Pods (N)	$\bar{x}$ Beetles/pod	$\bar{x}$ % destruction
A. cibarius			
18 June	37	2.2	44
29 June	1,265	2.5	93
16 July	29	2.7	99
A. utahensis			
18 June	42	1.0	27
29 June	1,481	1.0	58
16 July	61	1.3	73

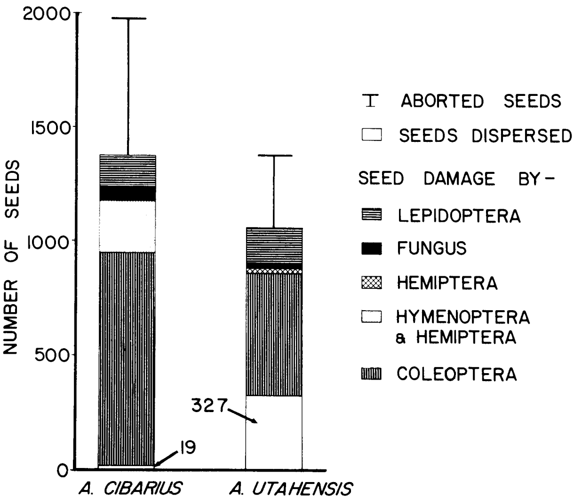

FIG. 3. Potential number of seeds produced by average *A. cibarius* and *A. utahensis* adult plants. Bars indicate fate of seeds. Numbers indicate actual seeds dispersed by an average plant.

Chemical defense mechanisms directed against herbivores (including seed predators) are apparently common in many plant groups (e.g., Applebaum 1964, Ehrlich and Raven 1965, Fraenkel 1969, Janzen 1969, 1971, Feeny 1970, Erickson and Feeny 1974). The presence of organic nitro-compounds based on 3-nitropropanoic acid in *A. cibarius* may be a chemical adaptation to predators. These compounds are chemically similar to those of closely related *Astragalus miser* Dougl. ex Hook., which are highly toxic to ruminants (Stermitz et al. 1972) and may also be toxic to some insects. Whatever the original purpose for the compound, it is presently ineffective in preventing seed predation by *B. mexicanus* and *A. fraterculus*. The latter appears capable of handling a wide variety of toxic substances as it also feeds on *Astragalus bisulcatus* (Hook) A. Gray, which has selenium concentrations in the seeds as high as 1,400 ppm (Trelease and Trelease 1937). The differential predation rates observed in *A. cibarius* may indicate that new defensive mechanisms are currently evolving.

Resource partitioning strategies are different in the two species, with *A. cibarius* allocating 20% more of its aboveground weight to reproduction. The difference is mainly the result of increased numbers of pods per plant and seeds per pod and may be a partial move toward predator satiation (Janzen 1969).

TABLE 3. Mean weights (in milligrams) and energy values in kilojoules) of *A. cibarius* and *A. utahensis* seeds and fruits. $\bar{x}$ energy values based on two runs in O_2 bomb calorimeter

	N	*A. cibarius*	*A. utahensis*
Seeds			
Weight ($\bar{x} \pm 1$ SD)	50	5.6 ± 0.8	3.9 ± 0.3
Energy content ($\bar{x}$)		18.83 (= 4.5 kcal)	19.25 (= 4.6 kcal)
Pods			
Weight ($\bar{x} \pm 1$ SD)	50	90.3 ± 13.2	88.4 ± 8.2 46.2 ± 8.3[a] 42.2 ± 8.1[b]
Energy content ($\bar{x}$)		17.15 (= 4.1 kcal)	17.99 (= 4.3 kcal)[a] 16.32 (= 3.9 kcal)[b]

[a] Pod pericarp only.

[b] Pod pubescence only.

The pubescence on *A. utahensis* pods has a direct effect on seed predation. The dense mat of hairs prohibits seed chalcids from penetrating the pod pericarp with their ovipositors, accounting for the absence of these insects in *A. utahensis* seeds. The pubescence also prevents beetles from depositing eggs within the pod or even directly on the pericarp. Eggs must be laid on or within the pubescence, and the first instar larvae must not only penetrate the pod but negotiate the pubescence prior to penetration.

Menusan's studies (1934, 1935, 1936) of *Acanthoscelides obtectus* Say, a species closely related to *A. fraterculus*, indicate that temperature directly affects oviposition and larval development. The higher temperature regime within *A. utahensis* pods may speed up *A. fraterculus* larval development resulting in increased seed consumption by an individual larva. Once inside *A. utahensis* pods, bruchid larvae have the advantage of being free of the parasite *Bracon bruchivorus* Mues., since the pubescence apparently prevents oviposition by this species. We made several unsuccessful attempts to remove the pubescence from immature *A. utahensis* pods, but the manipulated fruits failed to mature.

The cost of producing a fruit (in terms of caloric content) is about equal for both species. Apparently, *A. cibarius* budgets energy solely into thick-walled pods while *A. utahensis* divides the budget about equally between thin-walled pods and pubescence. The net effect is a greater efficiency in the latter in terms of energy expenditure per seed that escapes predation.

Studies by Palmbald (1968*a*, *b*) and Harper and his coworkers (Harper 1960, 1965, 1967, Sager and Harper 1960, Harper et al. 1965, Cavers and Harper 1967, Harper and White 1971) indicate that plant abundance in a given area is strongly influenced by the seed rain at the soil surface and the availability of safe-sites. Given a limited number of safe-sites, the greater the number of seeds surviving to reach the soil surface the higher the probability that one or more seeds will occupy a safe-site. Since seed weight, germination requirements, seed longevity and seedling parameters are similar for both species (Green 1973) their niche breadths in relation to safe-sites probably have considerable overlap. Therefore the higher seed production by *A. cibarius* may give the species an advantage when competing with *A. utahensis* for safe-sites in the absence of predation. When observed levels of predation are included, the advantage is reversed in favor of *A. utahensis*. Although admittedly overly simplistic, such observations indicate that seed predation, especially at the differential rates observed, may heavily influence the population dynamics of the two species and may have provided intensive selection pressures during their evolutionary histories.

Plant species are islands in evolutionary time, defended by various barriers preventing feeding by insect species (Janzen 1968). In view of the fact that seed characteristics such as size, weight, shape, composition of the testa, and endosperm dormancy and longevity are usually subject to strict environmental controls (e.g., Palmbald 1968*b*, Harper et al. 1970, Baker 1972), it is more likely that barriers against seed predators would be centered in the fruits because they are probably subject to less stringent environmental selection pressures. The parent stock for the group that includes *A. fraterculus* apparently penetrated *Astragalus* barriers, and subsequent coevolution has led to speciation in both groups (Johnson 1970). Ancestral *Astragalus* species probably did not have pubescent pods (Barneby 1964), but as seed predators began to exert sufficient selection pressure, a variety of new defensive barriers were selected for, which may contribute to the diversity in pod morphology exhibited by *Astragalus* at the present time.

ACKNOWLEDGMENTS

The following entomologists kindly identified insect specimens: C. D. Johnson (Bruchidae), R. E. Warner (Curculionidae), P. M. Marsh (Braconidae), C. M. Yoshimoto (Eurytomidae), G. E. Bohart (Lepidoptera), D. J. E. Brown (Hemiptera). A. H. Holmgren verified the plant identifications, and R. P. Price identified the fungi.

Our thanks to B. B. Green, J. A. MacMahon, M. C. Williams, C. D. Johnson, D. H. Janzen, T. H. Hsiao, and members of the University of Houston Population Biology Group and Argonne National Laboratory Environmental Statement Project for their comments on the manuscript at various stages of development.

This study is part of a dissertation submitted in partial fulfillment of the requirements of the degree of Doctor of Philosophy at Utah State University. The work was supported in part by a predoctoral NDEA Title IV Fellowship, a Sigma XI Grant-in-Aid of Research and a postdoctoral research fellowship with the University of Houston Coastal Research Center to the senior author.

LITERATURE CITED

Applebaum, S. W. 1964. Physiological aspects of host specificity in the *Bruchidae*. I. General considerations of developmental compatibility. J. Insect Physiol. **10**:783–788.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology **53**: 997–1010.

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Mem. N. Y. Bot. Gard. **13**. 1188 p.

Breedlove, D. E., and P. R. Ehrlich. 1968. Plant-herbivore coevolution: Lupines and lycaenids. Science **162**:671–672.

Cavers, P. B., and J. L. Harper. 1967. Studies in the dynamics of plant populations. I. The fate of seeds and transplants introduced into various habitats. J. Ecol. **55**:59–71.

Center, T. D., and C. D. Johnson. 1974. Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts. Ecology **55**:1096–1103.

Ehrlich, P. R., and P. H. Raven. 1965. Butterflies and plants: A study in coevolution. Evolution **18**:586–608.

Erickson, J. M., and P. Feeny. 1974. Sinigrin: A chemical barrier to the black swallowtail butterfly, *Papilio polyxenes*. Ecology **55**:103–111.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565–581.

Fraenkel, G. S. 1969. Evaluation of our thoughts on secondary plant substances. Entomol. Exp. Appl. **12**:473–486.

Green, T. W. 1973. Factors affecting the ecology of *Astragalus cibarius* and *Astragalus utahensis* with emphasis on the role of insects. Ph.D. Dissertation. Utah State Univ., Logan. 121 p.

Green, T. W., and G. E. Bohart. 1975. The pollination ecology of *Astragalus cibarius* and *Astragalus utahensis*. Am. J. Bot. **62**:379–386.

Harper, J. L. 1960. Factors controlling plant numbers, p. 119–132. *In* J. L. Harper [ed.] The biology of weeds. British Ecological Society, Oxford.

———. 1965. Establishment, aggression, and cohabitation in weedy species, p. 243–386. *In* H. G. Baker and G. L. Stebbins [ed.] The genetics of colonizing species. Academic Press, New York.

———. 1967. A Darwinian approach to plant ecology. J. Ecol. **55**:247–270.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The sizes and shapes of seeds. Annu. Rev. Ecol. Syst. **1**:327–352.

Harper, J. L., and J. White. 1971. The dynamics of plant populations, p. 41–63. *In* P. J. den Boer and G. R. Grodwell [ed.] Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol. **53**:273–286.

Holmgren, A. H., and J. L. Reveal. 1966. Checklist of the vascular plants of the intermountain region. U.S. For. Serv. Res. Pap. INT-32. 160 p.

Janzen, D. H. 1968. Host plants as islands in evolutionary and contemporary time. Am. Nat. **102**: 592–595.

———. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution **23**:1–27.

———. 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. **2**:465–492.

Johnson, C. D. 1970. Biosystematics of the Arizona, California, and Oregon species of the seed beetle genus *Acanthoscelides* Schilsky (Coleoptera: Bruchidae). Univ. Calif. Publ. Entomol. **59**:1–116.

Kingsbury, J. M. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Inc., Englewood Cliffs, N.J. 626 p.

Menusan, H., Jr. 1934. Effects of temperature and humidity on the life processes of the bean weevil, *Bruchus obtectus* Say. Ann. Entomol. Soc. Am. **27**: 515–526.

———. 1935. Effect of constant light, temperature and humidity on the rate and total oviposition of the bean weevil *Bruchus obtectus* Say. J. Econ. Entomol. **28**:448–453.

———. 1936. The influence of constant temperature and humidity on the rate of growth and relative size of the bean weevil, *Bruchus obtectus* Say. Ann. Entomol. Soc. Am. **29**:279–288.

Palmblad, I. G. 1968*a*. Comparative response of closely related species to reduced competition I. *Senecio sylvaticus* and *S. viscosis*. Can. J. Bot. **46**: 225–228.

———. 1968*b*. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology **49**:26–34.

Rosenfeld, I., and O. A. Beath. 1964. Selenium. Academic Press, New York. 411 p.

Sagar, G. R., and J. L. Harper. 1960. Factors affecting the germination and early establishment of Plantains (*Plantago lanceolata, P. media* and *P. major*), p. 236–245. *In* J. L. Harper [ed.] The biology of weeds. Blackwell Scientific Publications, Oxford.

Stephenson, L. W., and T. E. Russell. 1974. The association of *Aspergillus flavus* with Hemipterous and other insects infesting cotton bracts and foliage. Phytopathology **64**:1502–1506.

Stermitz, F. R., W. T. Lowry, F. A. Norris, F. A. Buckeridge, and M. C. Williams. 1972. Aliphatic nitro compounds from *Astragalus* species. Phytochemistry **11**:1117–1124.

Trelease, S. F., and H. M. Trelease. 1937. Toxicity to insects and mammals of foods containing selenium. Am. J. Bot. **24**:448–451.

Williams, M. C., and W. Binns. 1967. Toxicity of *Astragalus miser* Dougl. var. *oblongifolius* (Rydb.) Cronq. Weeds **15**:359–362.

Williams, M. C., and F. A. Norris. 1969. Distribution of misertoxin in varieties of *Astragalus miser* Dougl. ex Hook. Weed Sci. **17**:236–238.

Williams, M. C., K. R. Van Kampen, and F. A. Norris. 1969. Timber milkvetch poisoning in chickens, rabbits and cattle. Am. J. Vet. Res. **30**:2185–2190.