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## PATTERNS OF FAUNAL SUCCESSION IN *AGAVE PALMERI*

GWENDOLYN L. WARING AND ROBERT L. SMITH

**ABSTRACT**—A survey of arthropods associated with nonblooming and blooming *Agave palmeri* Engelmann revealed that distinct herbivore groups colonize four habitats within the plant in a successional pattern. The leaves of nonblooming *A. palmeri* were colonized by seven species of leaf feeders. Upon blooming, leaves dried up as their energy stores were shunted to the plants' large inflorescence, and leaves became free of herbivores. A possible breakdown of defensive compounds in the bole of the plant was correlated with blooming. Sixteen species of herbivores and detritivores colonized the boles of blooming plants. The stalk of *A. palmeri* was colonized by four stem boring insects and the inflorescence by other species of herbivores. There was little spatial overlap between species colonizing different portions of the plant. The physiological and morphological complexities of *A. palmeri* appear to be the mechanisms influencing the diversity and structure of its associated herbivore community. All animals reported to be associated with *A. palmeri* are listed.

Succession occurs at many levels within biological communities. At the community level, species of plants and animals are replaced as a community moves through seral stages. Within a community, succession takes place as groups of herbivores replace one another on a host plant. As a host plant undergoes its ontogeny, a succession of habitats is provided for herbivores. Martin (1966) found successional patterns in the herbivore fauna associated with red pine. His study revealed that herbivore species composition changed dramatically as trees mature. Waloff (1968) also found successional patterns among herbivores colonizing Scotch broom and that age was an important determinant of herbivore community structure. These studies demonstrate that successional replacement of herbivores takes place on individual host plants.

In community-wide succession, changes in plant species predictably alter the composition of herbivore species (e.g., Chevin, 1966). However, the mechanisms behind changes in the herbivore community of a single plant species represent a more subtle and neglected aspect of community ecology (Connell and Slatyer, 1977). For example, why does aging in red pines result in a dramatic displacement of one herbivore group by another? Waloff (1968) investigated the factors driving insect succession on Scotch broom and found that lepidopteran, chrysomelid, and curculionid stem miners colonized only green stems, while stem-mining scolytids colonized only dead stems. When the chrysomelid beetle, *Phytodecta*, was forced to mine and breed in old stems rather than young preferred stems, its fecundity was significantly reduced (Waloff, 1968). The differences between young and old stems as resources were not elucidated by Waloff (1968). Apparently, herbivore community succession on a single plant species is the result of changing properties of host plant tissues, but few of these changes are understood for any plant species.

*Agave palmeri* Engelmann is well suited to the study of insect succession with an emphasis on changes in the host and in the composition of

herbivores that use it. This agave is a succulent perennial that grows vegetatively for 8 to 25 years (Gentry, 1972) and then produces a large inflorescence, reproduces sexually, and dies ("big bang" or semelparous reproduction, see Ricklefs, 1973). The leaves and bole of *A. palmeri* are moist and starchy, the stalk is woody, and the inflorescence produces large fleshy fruits. While the plant is structurally complex, not all of its resources are simultaneously available to herbivores. During the plant's vegetative growth phase, it accumulates a store of carbohydrates in the leaves and bole of its rosette. When the plant reproduces, the succulent leaves lose over half of their water and carbohydrates to the stalk and inflorescence causing a considerable change in resource quality for herbivores (Nobel, 1977). The rosettes of many agave species have been found to contain high concentrations of saponins, which are transferred from the rosette to the developing inflorescence as the plant blooms (Dawidar and Favez, 1961) as may be the case for *A. palmeri*. Saponins are toxic for many herbivores (Applebaum and Birk, 1979) and may function to protect agaves from herbivores.

The purposes of this study were to survey the herbivore community associated with *A. palmeri* in its vegetative and reproductive stages and to document the bases for changes in community structure. Additionally, a complete list of the organisms reported to be associated with *A. palmeri* has been compiled from the literature.

**MATERIALS AND METHODS**—Five *A. palmeri* populations located on rocky rolling hills within 165 km of Tucson, Arizona, were examined in this study. Site 1 was located in the western foothills of the Huachuca Mountains at an elevation of 1,690 m, about 100 km southeast of Tucson. Forty-seven *A. palmeri* (six blooming) were examined. Site 2 was located along state Highway 83, ca. 100 km south of Tucson at an elevation of 1,400 m. Twenty-nine plants (nine blooming) were examined. Site 3 was also located along Highway 83, 50 km south of Tucson. Fifty-four plants (28 blooming) were examined. Site 4 was located ca. 30 km north of Tucson on the Santa Catalina Highway at an elevation of 1,540 m. Nine plants (three blooming) were examined. Site 5 was located in the eastern foothills of the Santa Rita Mountains, ca. 120 km southwest of Tucson, at an elevation of 1,700 m. Sixteen plants (10 blooming) were examined.

Nonblooming and blooming plants in all populations were sampled in July and August of 1980. Sampling took place between 1400 h and 1800 h. Plant leaves, boles, and stalks of inflorescences were considered discrete habitats. The flower portion of the inflorescence was not sampled to avoid damaging developing flowers and seeds. Data taken included location of all arthropods on the plants and estimates of their relative densities using density classes as follows: rare (<5 individuals), occasional (>5<15), and common (>15). The University of Arizona Entomology Department's collection and staff as well as the relevant literature were consulted to identify specimens. The data collected from all populations were pooled for statistical purposes and to provide an overall qualitative description of the animal species found to be associated with the different plant life history stages. Jaccard's coefficient of community similarity (Southwood, 1966) was used to compare similarity of species groups occurring in the leaves, boles, and inflorescences of the plants. A computer literature search produced references on animals previously reported to be associated with *A. palmeri*.

**RESULTS**—Forty-two species of arthropods and evidence of vertebrate herbivory were collected from 155 nonblooming and blooming agaves in this study. Seven herbivore species were collected from the leaves, 16 from rotting boles, and 4 from the flower stalks (Table 1). There was no spatial overlap in species of herbivores between habitats as measured by Jaccard's coefficient (values for all habitat comparisons equalled zero).

TABLE 1—The arthropod fauna collected and reported from *Agave palmeri* and the density status of each.

Arthropod fauna	Density class <sup>1</sup>
<b>Herbivores in and on leaves</b>	
<i>Hymenarcys crassa</i> Uhler (Hemiptera: Pentatomidae)	1
<i>Prionosoma podopioides</i> Uhler (Hemiptera: Pentatomidae)	2
<i>Acanthocephala</i> sp. (Hemiptera: Coreidae)	2
<i>Agathymus</i> sp. (Lepidoptera: Megathymidae)	3
<i>Acmaeodera</i> sp. (Coleoptera: Buprestidae)	1
Tettingoniidae, Acrididae (Orthoptera)	2
unknown pentatomid (Hemiptera)	2
<b>Predators on leaves</b>	
Salticidae, Lycosidae (Araneida)	1
Scorpionida	1
<b>Herbivores and detritivores in boles</b>	
<i>Scyphophorus acupunctatus</i> Gyll. (Coleoptera: Curculionidae)	3
<i>Sphenophorus phoeniciensis</i> Chitt. (Coleoptera: Curculionidae)	1
<i>Metoponium candidum</i> Casey (Coleoptera: Tenebrionidae)	1
<i>Metoponium</i> Casey	1
<i>Ulosonia marginata</i> LeConte (Coleoptera: Tenebrionidae)	1
<i>Carpophilus humeralis</i> (Fab.) (Coleoptera: Nitidulidae)	1
<i>Carpophilus dimidiatus</i> (Fab.)	1
<i>Ataemoides hirsutus</i> Horn (Coleoptera: Scarabeidae)	1
<i>Ataenius</i> sp.	1
<i>Cotinus</i> sp. (Coleoptera: Scarabeidae)	1
<i>Hermetia comstockii</i> Williston (Diptera: Stratiomyiidae)	3
<i>Volucella haagi</i> Jaennicke (Diptera: Syrphidae)	3
<i>Drosophila buskii</i> (Diptera: Drosophilidae)	1
<i>Drosophila</i> sp.	1
<i>Spongovostox apicedentatus</i> (Caud.) (Dermaptera: Labiidae)	2
<i>Euborella annulipes</i> (Lucas) (Dermaptera: Labiduridae)	2
<b>Predators and parasitoids in and on boles</b>	
<i>Dinocheirus arizonensis</i> (Pseudoscorpionida: Chernetidae)	1
<i>Parachelifer hubbardi</i> (Pseudoscorpionida: Cheliferidae)	1
<i>Hololepta yucateca</i> Marseul (Coleoptera: Histeridae)	2
<i>Pelosoma capillotum</i> LeConte (Coleoptera: Hydrophilidae)	1
<i>Polistes</i> sp. (Hymenoptera: Vespidae)	1
<i>Iphiaulax</i> sp. (Hymenoptera: Braconidae)	1
Cleridae	1
<b>Herbivores in stalks</b>	
<i>Peltophorus seminiveus</i> (LeConte) (Coleoptera: Curculionidae)	3
<i>Tragidion armatum armatum</i> LeConte (Coleoptera: Cerambycidae)	1
<i>Valenus inornatus</i> Casey (Coleoptera: Cerambycidae)	1
<i>Xylocopa</i> sp. (Hymenoptera: Xylocopidae)	1
<b>Predators in stalks</b>	
<i>Enoclerus zonatus</i> (Klug) (Coleoptera: Cleridae) (Powell, 1975)	1
<b>Herbivores in inflorescence<sup>2</sup></b>	
<i>Peltophorus adustus</i> Casey (Coleoptera: Curculionidae)	1
(Cicero, pers. comm.)	
Coreidae (Hemiptera) (Gentry, 1972)	1
microlepidopterans (Lepidoptera) (S. Sutherland, pers. comm.)	
<b>Additional species collected from agave with habits unknown</b>	
<i>Omalodes grossus</i> Marseul (Coleoptera: Histeridae)	1
<i>Carcinops gilensis</i> LeConte (Coleoptera: Histeridae)	1
<i>Geomysparinus</i> sp. (Coleoptera: Histeridae)	1
<i>Scymaenus</i> sp. (Coleoptera: Scymaenidae)	1
<i>Bitoma</i> sp. (Coleoptera: Colydiidae)	1
numerous species of staphylinids (Coleoptera: Staphylinidae)	2

<sup>1</sup> 1 = rare, <5 collected; 2 = occasional, >5<15 collected; 3 = common, >15 collected.<sup>2</sup> See text for additional associations.

The developmental changes which occur during the life history of *A. palmeri* lead to the creation or degradation of the leaves, bole, and stalk as habitats, and it is these changes which lead to the successional faunal patterns we observed (Table 2). In addition, leaf-feeding species in particular seem to be temporally as well as spatially separated from other herbivore groups, as no leaf-feeding species were found on blooming plants.

*Agave Leaf Fauna*—Three of the seven herbivore species collected from *A. palmeri* leaves were sucking insects in the order Hemiptera (Table 1). A pentatomid, *Hymenarcys crassa* Uhler, was once seen copulating on *A. palmeri* leaves. *Prionosoma podopoides* Uhler (Pentatomidae) and *Acanthocephala* sp. (Coreidae) were occasionally found on leaves. These hemipterans were typically found on flat, exposed leaf blades. Leaf-mining *Agathymus* sp. larvae (Lepidoptera: Megathymidae) were common in all agave populations examined except on site 4. Up to four mines per leaf caused no obvious negative effects such as wilting or chlorosis of the leaves. According to Roever (1964), larvae of *Agathymus* sp. suffered heavy mortality when agaves secreted a clear acidic exudate in response to wounding (see also Waring and Smith, 1986). Adult buprestids, *Acmaeodera* sp. (Coleoptera), were found rarely at the bases of the leaves, as were various acridids and tettigoniids (Orthoptera). The orthopterans fed near the leaf bases and left long scraping marks. Predators of arthropods on the leaves included spiders (Salticidae and Lycosidae) occasionally and scorpions rarely. They were found near the bases of the leaves. Herbivores were not found on leaves of plants which had bloomed.

*Agave Bole Fauna*—When the agave produced its flower stalk, the bole of the plant was quickly colonized by a large variety of arthropods (Table 1). Agave boles were colonized initially by an agave weevil, *Scyphophorus acupunctatus* Gyllenhal (Curculionidae). The adult weevil bored into the bole to oviposit, at the same time infecting the plant with micro-organisms that decompose agave tissue. The weevil larvae feed within the bole and also spread microbes (Waring and Smith, 1986).

Following colonization by *S. acupunctatus*, the bole was rapidly colonized by other herbivores as well as detritivores, predators, and parasites, giving rise to a diverse ephemeral arthropod community (Table 1). The bole tissues decompose rapidly in the presence of the mining herbivores. Although *S. acupunctatus* was the only insect consistently found in rotting agave boles, flies (larvae of the stratiomyiid *Hermetia comstockii* Williston and the syrphid *Volucella haagi* Jaenicke) were very common. One fly species or the other was usually present in large numbers, although they rarely co-occurred. In numbers and biomass, their larvae were more abundant in advanced rots than those of *S. acupunctatus*. In one rotten bole, 509 *H. comstockii* larvae were found, and, in another, 878 *V. haagi* larvae were found; no more than 100 weevil larvae were ever collected from a single rotting bole. Although larvae of both fly species occurred in close proximity to *S. acupunctatus* in the boles, no antagonistic interactions were observed between them. Adult *V. haagi* have been collected from various Arizona crops (Butler and Werner, 1957), but it is not known that larvae of this species occur in agricultural ecosystems. No data are available on

TABLE 2—Some actual and possible changes in morphology and physiology of *Agave palmeri* coincident with herbivore colonization.

Life history stage	Morphological/physiological development response	Herbivore
1. Vegetative growth phase	Carbohydrate and water concentrations in the leaves.	Leaf-feeding
2. Reproduction	A. Carbohydrate and water concentrations drop by over 50% in leaves.	Leaf-feeding discontinued
	B. Saponins shunted from the bole.	Bole is colonized and rotted.
	C. Inflorescence stalk.	Stalk-boring insects colonize.
	D. Flower production.	Pollination and herbivory of flowers and fruits.

alternative hosts for *H. comstockii*. Adult *H. comstockii* is an excellent mimic of *Polistes* sp. (wasps; James, 1960); fly and wasp were commonly seen on and near rotting agaves.

Two earwig species, *Spongovostox apicedentatus* (Caud.) and *Euborellia annulipes* (Lucas), were common in rots. They are described as scavengers by Borror et al. (1976) and Langston and Powell (1975). However, according to Jackson (1964), both species eat insects in captivity. *Spongovostox apicedentatus* has been collected from rotting cacti, including *Cereus* sp., *Echinocactus* sp., and *Opuntia* sp., as well as the liliaceous *Yucca whipplei* Torr. *Euborellia annulipes* has been found in garden plants and stored foods (Langston and Powell, 1975). The coincident presence of most instars of these species suggests that they have multiple generations in a single agave rot.

Other herbivore and detritivore species were found only rarely (Table 1). Three species of tenebrionid beetles collected are considered to be generalist feeders occupying habitats such as rotting wood and decaying vegetable matter (Glen et al., 1943). Nitidulid beetles, *Carpophilus humeralis* (Fab.) and *Carpophilus dimidiatus* (Fab.), have been collected from stored grains, ripe nuts, and fruits (Connell, 1975). A weevil, *Sphenophorus phoeniciensis* Chitt. (Curculionidae), has been collected from other monocots including grasses (Vaurie, 1951). The scarab beetles (Scarabaeidae) are also considered to be generalists. Many species of staphylinid beetles (Staphylinidae) in a variety of sizes were collected. When more than one staphylinid species was collected from a given plant, they usually differed in length by 1 mm or more. None of these were identified. Larvae of *Drosophila buskii* Coquillett were reared from agave rots and are known to colonize other plant rots as well (W. Heed, pers. comm.).

Ten species of predators and parasitoids of arthropods on and in the boles were collected. *Hololepta yucateca* Marseul, recorded as a predator of *S. acupunctatus* (Woodruff and Pierce, 1973), was found in most rots. It has also been collected from *Cereus* sp., *Echinocactus virescens* Nuttall, *Opuntia occidentalis* Engelm. and Bigel., and *Ferocactus* sp. and from fruits and compost, where it preys on other arthropods. The braconid, *Iphiaulax* sp., was reared from *S. acupunctatus*, six adult *Iphiaulax* emerged from a single

pupa. This wasp species was seen flying about rotting agaves. The pseudoscorpions (Arachnida: Pseudoscorpionida) *Parachelifer hubbardi* (Banks) and *Dinocheirus arizonensis* (Banks) are known to be predators of dipteran larvae including *Drosophila* sp. and have been collected from various species of cacti (D. Zeh, pers. comm.). Other predaceous species (Table 1): included *Polistes* sp. (Vespidae), a hydrophilid beetle, *Pelosoma capillotum* LeConte, and an unidentified clerid beetle (Cleridae).

The following beetles of unknown habits were collected (rarely) from rots (Table 1): the histerids *Omalodes grossus* Marseul, *Carcinops gilensis* Leconte, and *Geomysaprinus* sp. (Histeridae), the scydmaenid *Scydmaenus* sp. (Scydmaenidae) and *Bitoma* sp. (Colydiidae). We assume that the histerids are predators of larvae occurring in rots (Borror et al., 1976).

*Agave Flower Stalk Fauna*—Four species of stem-boring insects were collected from the woody *A. palmeri* stalks (Table 1). The weevil (Curculionidae), *Peltophorus seminiveus* (Leconte), was common in all five agave populations studied. Adults were found copulating on the leaves of the rosette, and larvae were reared from agave stalks. Their association with agaves was first reported by Kissinger (1964). *Scyphophorus acupunctatus* and *P. seminiveus* adults were found in close proximity on agave leaves. When disturbed, *P. seminiveus* moved very quickly while *S. acupunctatus* was extremely sluggish. *Peltophorus seminiveus* larvae were never reared from the boles, indicating no niche overlap for larvae of the two weevil species.

The hymenopteran stem nester *Xylocopa* sp. (Xylocopidae) was collected rarely from stalks. Occupied stalks typically had a row of chambers, each of which contained pollen and pupa or larva. An adult xylocopid was observed defending a developing agave stalk whose flowers were almost ready to bloom. Other xylocopids attempting to land on the stalk were attacked by the defender. The extent to which this territorial behavior may influence pollen resource utilization and pollination is not known.

Stem-boring beetles *Tragidion armatum armatum* LeConte and *Valenus inornatus* Casey (Cerambycidae) were found along with *P. seminiveus* in *A. palmeri* stalks at one collection site. Linsley (1962) reported *T. armatum* from yucca and agave stalks, and Dillon (1956) reported *V. inornatus* from yucca stalks. Adults of *T. armatum* have also been seen feeding on the fruits of *A. utahensis* Engelm. (L. Stevens, pers. comm.).

A predaceous clerid (Cleridae) *Enoclerus zonatus* (Klug) has been reared from stalks of *A. palmeri* (Powell, 1975). Powell (1975) also reared *E. zonatus* adults from the fruits of *Yucca schottii* Engelm. and *Nolina microcarpa* Wats.

*Agave Inflorescence Fauna*—Most of the information presented on this group of species has been derived from the literature and personal communications (Table 1). *Agave palmeri* is alleged to be dependent on nectar feeding bats (*Leptonycteris sanborni* Hoffmeister and other species in that genus) for pollination (Howell and Roth, 1981). It is also visited by sphinx moths (Sphingidae) and solitary nectar-feeding bats (*Choeronyctis mexicana* Tschudi) which may serve as pollinators (Howell and Roth, 1981). Coreids (Hemiptera) feed on agave fruits in the inflorescence and

rodents rapidly collect seeds from the ground (Gentry, 1972; Nobel, 1977; Howell and Roth, 1981). A weevil that breeds and mines in agave seed pods, *Peltophorus adustus* Casey (J. Cicero, pers. comm.), was rarely collected. Several species of microlepidopterans have been observed in seed pods (S. Sutherland, pers. comm.), and bighorn sheep (*Ovis canadensis* Merriam) and deer (*Odocoileus* sp.) are known to forage on the green stalks and inflorescence (Gentry, 1972). At site 1, inflorescences were removed from over 50% of blooming plants by vertebrate herbivores, illustrating how important herbivory by vertebrates can be to this plant.

In summary, 32 of 45 species (70%) were observed only rarely, that is, only five or fewer individuals per species were collected during the study. Conversely, five species (11%) were commonly encountered (Table 1). These patterns indicate that many of these species are generalists (or accidentals) while a much smaller number of herbivores are consistently associated with and dependent on this plant species.

**DISCUSSION**—A succession of herbivore groups colonize *A. palmeri* as it passes from one developmental stage to another. Leaves, boles, stalks, and inflorescences represent discrete habitats and each is utilized by a distinct faunal assemblage (Table 2). The leaves of vegetatively growing agaves were fed upon by seven herbivore species until blooming commenced. Upon blooming, water and energy reserves of the leaves are shunted to the inflorescence, and the leaves as resources literally dry up (Nobel, 1977). Consequently, no leaf herbivores were found after blooming began. While the physiological changes in the agave bole that permit colonization are not known, they are clearly correlated with flowering. Waring and Smith (1986) determined that wild, nonblooming *A. palmeri* were never successfully colonized by *S. acupunctatus*, although the weevils did land on many nonblooming plants and apparently evaluated them by tasting leaf tissue. Only after blooming is *A. palmeri* colonized by the weevil. The basis for this may involve a change in allocation of chemical defense; specifically, saponins may be translocated from the rosette to the inflorescence during the plant's reproduction as found by Dawidar and Fayez (1961) for some agave species. The bole is apparently unavailable as a resource to herbivores until blooming commences by which time the leaf fauna has abandoned the plant because of leaf desiccation.

The agave bole was by far the richest habitat in the plant, as evidenced by the great diversity and biomass of arthropods it supported. Colonization of the bole by many of these species appears to depend on the presence of weevil larvae as well as changes in plant physiology and thus represents a successional process in itself. Weevil larvae were adept at rapidly boring through dense plant tissue thereby spreading microorganisms and plant tissue necrosis as they mined (Waring and Smith, 1986).

The stalk and flowers of the inflorescence also appear to be discrete habitats, although a thorough survey of the floral fauna has not been conducted. The two habitats may be sufficiently distinct that a shift in specialization from one to the other permitted a speciation event, in the case of the congeners *Peltophorus adustus* (a fruit feeder) and *P. seminiveus* (a



stalk borer). The stalk was colonized only by insects capable of boring through dense fibrous tissue.

We found over 40 animal species, including 27 herbivores, to be associated with *A. palmeri* through its life history. This is a large list for an architecturally simple plant. Many of these associations are perhaps inconsequential evolutionarily, while others have probably affected many of the life history traits which *A. palmeri* exhibits.

This survey suggests that the plants' structural and physiological ontogeny influences the composition and diversity of its herbivores and their colonization patterns. Lawton and Price (1979), Moran (1980), and others have found that the architectural complexity of a host plant contributes significantly to the number of species of herbivores it can support. *Agave palmeri* offers herbivores at least four distinct habitats (leaves, bole, stalk, and inflorescence), and each of these is colonized by a distinct group of herbivores. Physiological changes within the plant, including transfer of resources and defense compounds, may represent mechanisms which adaptively influence both the diversity of herbivores present at any time and the overall diversity of herbivores associated with *A. palmeri*. Future studies of this system might well be designed to reveal the physiological changes these plants undergo as they develop in an effort to account for changes in their herbivore community structure.

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