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A SEED CHALCID (*EURYTOMA SQUAMOSA* BUGBEE) PARASITIZES BUCKBRUSH (*CEANOTHUS FENDLERI* GRAY) SEEDS IN A PONDEROSA PINE FOREST OF ARIZONA

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ABSTRACT.—Predispersal seed parasitism rates were quantified for buckbrush (*Ceanothus fendleri* Gray) in 3 Arizona ponderosa pine (*Pinus ponderosa* Laws.) forest units that had been thinned for ecological restoration objectives. The chalcidoid wasp *Eurytoma squamosa* Bugbee (Eurytomidae) was responsible for 35% of total seed loss in a single year. These findings represent an expansion of the known range and host list for *E. squamosa* and increase our understanding of factors that may constrain regeneration of *C. fendleri* in Southwest ponderosa pine forests.

Key words: predispersal seed predation, range expansion, Hymenoptera, *Eurytoma squamosa*, *Ceanothus fendleri*, ecological restoration, plant-insect interactions, parasitism.

In ponderosa pine (*Pinus ponderosa* Laws.) forests of the Southwest, ecological restoration treatments have been initiated that include thinning dense stands of young trees and applying low-intensity fire (Covington and Moore 1994, Covington et al. 1997, Moore et al. 1999). Although reestablishment of ecological function is theorized to flow from overstory structural manipulation and the reintroduction of surface fire, ecological interactions, particularly between arthropods and understory plant hosts, have been minimally researched.

In 1999 I began a study to examine various factors affecting regeneration of *Ceanothus fendleri* Gray in areas undergoing ecological restoration treatments. *Ceanothus fendleri* is a shrub common in the understory of ponderosa pine forests in the Southwest. It is a preferred browse of mule deer (*Odocoileus hemionus hemionus* Rafinesque; Urness et al. 1975), a nitrogen fixer (Story 1974), and a provider of structural heterogeneity in predominantly grassy and herbaceous understory communities. Resprouting of *C. fendleri* after disturbances such as fire is common (Pearson et al. 1972, Ffolliott et al. 1977, Vose and White 1991). Its seeds are forcibly ejected from dehiscent capsules and likely remain in forest floor seed banks for years until stimulated by heat from fire to germinate (Kearney and Peebles 1951, Reed 1974, Krishnan 1989). Large ungulate use of understory forage can increase

after forest thinning (Patton 1974), and herbivory on *C. fendleri* can be intense and constrain flower and fruit production (Huffman and Moore in preparation). Other factors that likely affect *C. fendleri* regeneration and vary with forest condition include seed predation and parasitism.

Prior to this study, rates of seed parasitism and predation had not been reported for *C. fendleri*, although nearly complete predispersal consumption of seed crops by invertebrates has been reported for overstory ponderosa pine (Blake et al. 1985). The objectives of my research were to (1) collect preliminary data on predispersal seed parasitism for *Ceanothus fendleri* in areas thinned for ecological restoration objectives and (2) identify common insect species infesting *C. fendleri* seeds. Information concerning processes that affect ovule and seed fate can help resource managers predict rates of ecological recovery in communities undergoing restoration treatments.

METHODS

The study was conducted from 1999 to 2000 on the Fort Valley Experimental Forest (latitude 35°16'N, longitude 111°41'W) in Coconino County approximately 10 km northwest of Flagstaff, Arizona. The site is approximately 2300 m above mean sea level and has flat to gently rolling topography with slopes

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generally less than 20%. Annual precipitation averages 52 cm, of which approximately half falls as snow in late winter. Soils are moderately well drained and classified as Brolliar stony clay loam (Meurisse 1971) developed from tertiary basalt parent material.

Overstory vegetation is nearly pure ponderosa pine with scattered occurrence of Gambel oak (*Quercus gambelii* Nutt.). Common understory species include bunchgrasses *Festuca arizonica* Vasey, *Muhlenbergia montana* (Nutt.) A.S. Hitchc., *Elymus elymoides* (Raf.) Swezey, and *Blepharoneuron tricholepis* (Torr.) Nash; forbs *Lupinus* spp., *Erigeron* spp., *Eriogonum* spp., *Achillea millifolium* L., and *Antennaria* spp.; and woody shrubs *Ceanothus fendleri* and *Rosa woodsii* Lindl.

Large mammalian herbivores present on the site are mule deer and elk (*Cervus elaphus* Linnaeus). Livestock were excluded from the study site.

Overstory trees were thinned in February 1999, which reduced tree density in three 15-ha experimental forest restoration units to approximately 111–120 trees per hectare. In May 1999, I established 60 plots (4 m² in size) centered on *Ceanothus fendleri* shrubs in each of the 3 restoration units (180 shrub plots total). *Ceanothus fendleri* plants on these plots produced no fruit in 1999. Therefore, I collected seeds from *C. fendleri* shrubs growing on microsites adjacent to the restoration units and monitored parasite emergence from these seeds until June 2001. Adult parasites emerging were captured and immediately preserved in 70% isopropyl alcohol. Specimens were sent to Dr. Robert Zuparko at the California Academy of Science (CAS), San Francisco, California, USA, and to the USDA Systematic Entomology Laboratory (SEL; specimens identified by E. Eric Grissell, Research Entomologist), Bethesda, Maryland, USA, for identification.

Fruit developed on 11 total *C. fendleri* plots in July 2000. To capture seeds as fruits dehisced, I installed seed traps constructed from bridal veil material (mesh size <2 mm) tied around fruiting stems. Twenty-three traps were installed on 1 to 5 stems per plot and each enclosed 1 to 14 fruits.

Seeds collected from traps were separated from plant debris and counted in the laboratory. Seeds were classified as “developed” or “undeveloped.” Developed seeds were approximately 2 mm in diameter, had smooth, full

seed coats, and were glossy brown in appearance (Fig. 1a). In contrast, undeveloped seeds were typically smaller than 2 mm and flattened; additionally, they had wrinkled, yellowish seed coats (Fig. 1b). Seeds were examined under a dissecting scope (10–20X) for parasite emergence holes or other signs of infestation and then dissected to determine embryo condition and presence of parasite larvae/pupae.

RESULTS

Parasite specimens collected as they emerged from 1999 seeds were all from a single chalcidoid wasp species, *Eurytoma squamosa* Bugbee (Eurytomidae; Figs. 1c–d). Although emergence was not specifically studied, I observed adult wasps emerging up to 20 months after the 1999 seed collection.

A total of 144 seeds were recovered in 2000 from traps installed on *C. fendleri* fruiting stems. Each trap yielded 1 to 24 seeds. Fifty percent of the seeds captured were undeveloped (Table 1), and in these seeds no parasite larvae or signs of infestation were found.

Parasitism was responsible for 35% of the total seed loss and 71% of the loss of developed seeds (Table 1). No clear trends were observed for rate of parasitism and number of seeds per trap or seeds per plot. Parasite emergence holes in developed seeds were approximately 0.5 mm in diameter (Fig. 1e). Embryonic tissue of seeds with emergence holes was completely consumed, leaving the seeds hollow. Seeds housing parasite larvae showed no external signs of infestation. Emergence hole appearance (i.e., size and shape) was consistent between seeds trapped in 2000 and those collected in 1999. Likewise, characteristics of larvae within dissected seeds of both collections were consistent. We found no evidence of other parasitic species associated with *C. fendleri* seeds.

The majority of developed seeds that had not been parasitized were filled with apparently healthy embryos (Fig. 1f, Table 1). However, approximately 3% of these showed no signs of parasitism but were hollow nonetheless.

DISCUSSION

These results represent an expansion of the known range and host list for *Eurytoma squamosa*. Prior to this study, this wasp species was not known to occur in Arizona or on *Ceanothus*

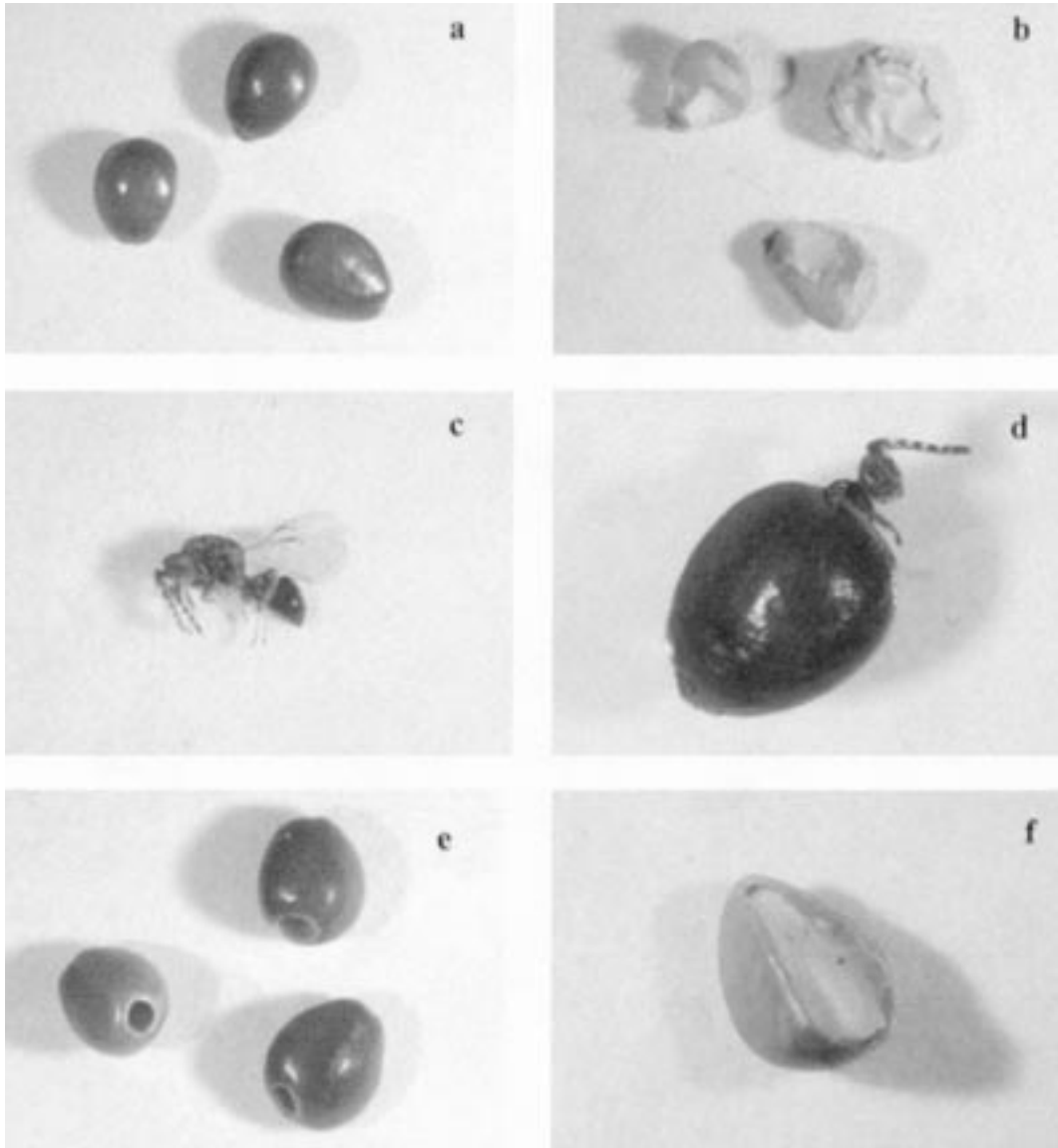


Fig. 1. Images (10–20X) showing (a) normally developed seeds of *Ceanothus fendleri*, (b) undeveloped seeds, (c) adult parasite *Eurytoma squamosa*, (d) emerging seed parasite, (e) characteristic emergence holes made by seed parasite, and (f) cross-section of developed seed with healthy embryo.

fendleri. Occurrence of the species has been reported in Idaho, Washington, and California, USA (Bugbee 1967). In these states its hosts are other species of *Ceanothus* including *C. divaricatus*, *C. thyraiflorus*, *C. cordulatus*, *C. velutinus*, and *C. sanguineus*. For *C. sanguineus* in Idaho, *E. squamosa* and 2 other phytophagous insects were responsible for an

average loss of 9–27% of total seeds in fruits over a 3-year period (Furniss et al. 1978). Another *Eurytoma* species (*E. greggii* Bugbee) has been reported to infest >80% of the seeds of *Ceanothus greggii* Gray in chaparral ecosystems of Arizona (Bugbee 1971). Seed chalcids are well-known parasites of seeds of commercial tree species such as ponderosa pine in

TABLE 1. Fate of seeds collected from *Ceanothus fendleri* plants in ponderosa pine forests of northern Arizona.

Seeds	Developed					Total
	Parasitized ^a		Filled	Hollow	Undeveloped	
	Emerged	Larval				
Number	37	14	19	2	72	144
Percentage of developed seeds	51.4	19.4	26.4	2.7	—	100
PERCENTAGE OF TOTAL	25.7	9.7	13.2	1.3	50	100

^aParasites (*Eurytoma squamosa*) either had emerged prior to seed collection or were found within seeds as larvae or pupae.

northern Arizona (e.g., Blake et al. 1985), but little research has quantified parasitism on understory plants.

With the data presented here, long-term effects of seed parasitism on *Ceanothus fendleri* regeneration are difficult to determine. Traits such as innate dormancy suggest that *C. fendleri* utilizes a seed bank strategy similar to congeneric species (Quick 1935, Reed 1974, Conard et al. 1985, Krishnan 1989). However, resprouting after disturbance is also common (Ffolliott et al. 1977, Vose and White 1991). Thus, although my data suggest that *E. squamosa* constrained replenishment of seeds in soil seed banks, temporal patterns of seed parasitism and the relative importance of sprouting versus seedling recruitment for *C. fendleri* persistence are not yet clear.

Presettlement characteristics of *C. fendleri*–*E. squamosa* interactions are not known. Plausibly, frequent surface fires common in ponderosa pine forests prior to Anglo and Hispanic settlement of northern Arizona (ca 1876; Fulé et al. 1997) could have functioned to control larval populations of *E. squamosa* in dispersed seeds. Fires heating *C. fendleri* seeds in soil seed banks may have caused wasp mortality while stimulating seed germination. Thus, future research could address questions related to fire or heat effects on parasite and seed survival and seed germination. Studies illuminating presettlement conditions with respect to plant–insect interactions could help ecologists and land managers expand their understanding of ecosystem dynamics and, in turn, make informed decisions concerning forest restoration and management.

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