A seed chalcid (*Eurytoma squamosa* Bugbee) parasitizes buckbrush (*Ceanothus fendleri* Gray) seeds in a ponderosa pine forest of Arizona

David W. Huffman

*Northern Arizona University, Flagstaff*

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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 dehiscing 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.
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.


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 chalcid 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*.
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
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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