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FEEDING BEHAVIOR AND PERFORMANCE OF A RABBITBRUSH LEAF-BEETLE (*TRIRHABDA LEWISII*) FEEDING ON *CHRYSOTHAMNUS NAUSEOSUS* REGROWTH AFTER FIRE

Ann L. Herzig[1,2] and Cynthia Skema[1]

ABSTRACT.—Fire often positively affects the growth and nutrient content of plants regrowing after a burn. These changes have been associated with preferential feeding by herbivores in burned areas. In this study in southeastern Wyoming, *Chrysothamnus nauseosus* Pursh (rubber rabbitbrush) regrowing after a fire produced new shoots with a distinct growth form. Shoots were longer than those on unburned control sites and had longer leaves with longer internodes between leaves. We conducted feeding trials to detect whether *C. nauseosus* shoots regrowing after fire were nutritionally superior to shoots from unburned plants for the specialist leaf beetle, *Trirhabda lewisii* Crotch (Coleoptera: Chrysomelidae). We also measured C:N ratios and nitrogen and water contents of leaves from burned and unburned plants. *Trirhabda lewisii* adults preferred shoots from burned plants when given a choice. The beetles ate similar amounts of burned and unburned plants when fed only a single type. Females that were fed either burned or unburned plants did not differ in number of eggs laid. Chemical analyses revealed no significant differences in nitrogen or water content of leaves from burned versus unburned plants. Carbon-to-nitrogen ratio of burned plants was marginally lower compared with unburned plants. In contrast to previous studies, which suggest that herbivore attraction to burned areas leads to enhanced performance, our study shows that performance is not necessarily enhanced after fire.

Key words: Trirhabda lewisii, Chrysothamnus nauseosus, fire, herbivory, prescribed burn, leaf nutritional quality.

Fire is a catastrophic disturbance that causes changes in the physical environment and in community composition. In general, these changes can lead to enhanced productivity and vigorous plant growth (i.e., relatively rapid growth that results in larger-sized plant parts) following a fire (Hadley and Kieckhefer 1963, Daubenmire 1968, Old 1969, Christensen and Muller 1975, Lyon et al. 1978, Rundel and Parsons 1980, Boerner 1982, Knapp 1985, Romo et al. 1993, Whelan 1995, Throop and Fay 1999). Enhanced plant growth can have cascading effects in the community. Many studies have documented selective feeding by herbivores in previously burned areas (Daubenmire 1968). Herbivores that show this behavior are a large and varied group, including vertebrates such as elk (Leege 1968), cattle (Smith and Owensby 1972), sheep, deer, grouse (Miller and Watson 1973), waterfowl, muskrat (Smith and Kadlec 1985), and bison (Vinton et al. 1993); and insects, such as grasshoppers (Stein et al. 1992, Porter and Redak 1997), gall midges (Vieira et al. 1996), homopterans (Cancelado and Yonke 1970), hemipterans (Steinbauer et

al. 1998), and lepidopterans (Negron-Ortiz and Gorchov 2000). Researchers have suggested that the attractiveness of plant growth in burned areas is due to more succulent or more tender plant tissue (Leege 1968, Vieira et al. 1996), more accessible new growth (Miller and Watson 1973, Carlson et al. 1993), and an increase in nutritional value, particularly higher nitrogen levels (Smith and Owensby 1972, Miller and Watson 1973, Carlson et al. 1993, Negron-Ortiz and Gorchov 2000). Nitrogen and water are 2 key plant components affecting insect herbivore performance (Mattson and Scriber 1987). More vigorous plant growth, in general, is preferred by many insect herbivores and can enhance survival of insects that feed within plant tissue, such as leaf gallers (Price 1991).

In this investigation we observed *Chrysothamnus nauseosus* Pursh (Compositae), rubber rabbitbrush, producing shoots that had a strikingly different morphology following a prescribed burn in southeastern Wyoming. *Chrysothamnus nauseosus* is a deciduous shrub most commonly found in intermountain desert scrub; it is often associated with *Artemisia*

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tridentata Nutt., big sagebrush (Flora of North America Editorial Committee 1993). This low shrub flowers in a capitulum of yellow florets from August through October. *Chrysothamnus nauseosus* ranges from southern British Columbia to Saskatchewan and south to California, Texas, and New Mexico and is commonly found growing in disturbed areas, such as along roadsides and around prairie dog mounds (Britton 1970).

We investigated whether the distinctive, post-fire regrowth of *C. nauseosus* was nutritionally superior for a specialist rabbitbrush-feeding beetle, *Trirhabda lewisii* Crotch (Coleoptera: Chrysomelidae). *Trirhabda lewisii* specializes on *C. nauseosus* and *C. viscidiflorus* (Hogue 1970), with both larvae and adults feeding on foliage. *Trirhabda lewisii* is univoltine, overwintering in the egg stage. Larvae hatch in early spring (late May at our study sites) and begin feeding on newly expanding leaves. Larvae develop through 3 instars and then pupate in the upper layer of soil for about 2 weeks in early summer. Adults emerge in late June or early July, mate, feed, and, throughout the remainder of the summer, lay eggs in the soil at the base of the host plant. Adults die with the onset of cold weather in early autumn. Beetles in the genus *Trirhabda* are notorious for reaching tremendously high population levels at which they can cause complete defoliation and even death of their host plants (Hogue 1970). *Trirhabda* beetles disperse as young adults (Messina 1982, Herzig 1995). During this period, beetles could colonize a burned area to feed on resprouting foliage. Therefore, feeding trials in this study were conducted on adult beetles in July–August following the fire, at the time new adults started to appear in the field. We conducted feeding trials to determine whether fire resulted in foliage that was preferred by *T. lewisii*, whether beetles ate more foliage from burned or unburned plants to compensate for possible nutritional differences, and whether beetle fecundity increased when fed foliage from burned plants.

STUDY SITE

Our field site was along French Creek in the Sheep Mountain region of the Medicine Bow National Forest in southeastern Wyoming, 40 km southwest of Laramie at 2350 m elevation. *Chrysothamnus nauseosus* at the site grows in a band at the edge of the riparian zone, extending as far as 50 m up the adjacent hillside. The area we sampled covers approximately 2 ha. *Chrysothamnus nauseosus* is the dominant plant in this zone. Vegetation in this zone, a mix of grass and shrubs, is described as sagebrush steppe (Knight 1994). Fire and drought are common disturbances in sagebrush steppe ecosystems. Water is most available to plants in the spring, at the time of snowmelt, and becomes limiting by mid- to late summer (Knight 1994). *Chrysothamnus nauseosus* in this area typically initiates new growth in late May. The growing season generally ends in early October.

In March 1997 this area was the site of a prescribed burn that left a mosaic of burned and unburned areas. At our site a footpath that follows the creek and meanders through the zone of *C. nauseosus* separated burned and unburned sections. The other common shrub in the area, *A. tridentata,* was killed by the fire. *Chrysothamnus nauseous* shrubs were burned to the ground in the burned area, but by the next growing season, when we conducted our study, new sprouts were growing from the base of their charred stumps. The ground was blackened during the burn, but the fire was not so intense as to consume all plant litter. Some charred litter remained. In repeated surveys at our site early in the season, we found no *T. lewisii* larvae in the burned area.

METHODS

Plant Characteristics

Plant morphology was quantified to describe the long-leafed, elongated stems of *C. nauseosus* that had regenerated after the burn. We cut shoots at the base, where they intersected the stem, every other day (27 July–4 August) from a total of at least 50 different *C. nauseosus* plants, 25 burned and 25 unburned. We sampled discrete areas within our study area on each sampling occasion to ensure that we selected shoots from different plants each time. We sampled 1 or 2 shoots from each plant for a total of 100 shoots. Shoots of any one plant are presumably more similar than shoots from different plants. To control for this plant effect in our data, we took the most conservative approach we could by eliminating half of our sample. We could not eliminate the shoots that

we knew came from the same plants because these were not kept separate at the time of collection. We arranged the shoots in rank order for each of the 3 morphological measurements (leaf density, leaf length, shoot length) and eliminated every other shoot from our sample before analysis. In this way we reduced the sample size to reflect the minimum number of plants sampled and increased the variability in our sample by eliminating the most similar measurements. Leaf density was measured by counting all leaves on a shoot and dividing by the length of the shoot. Leaf length was estimated by categorizing leaves into length intervals to the nearest centimeter. We conducted *t* tests to compare shoot length, leaf density, and mean leaf length of previously burned and unburned plants.

To measure change in nutrient composition and water content of the foliage after the fire, we measured carbon, nitrogen, and water contents of the leaves from previously burned and unburned plants. On 29 July we haphazardly selected and cut 1 sprout from 10 burned and 10 unburned *C. nauseosus* plants. All leaves from each cutting were stripped from the stem by hand, weighed, and then freeze-dried until reaching a constant weight (approximately 24 hours). The proportion of water in the leaves was measured as the difference between wet and dry weights divided by wet weight. After freeze-drying, the leaves were pulverized using a mortar and pestle above a pool of liquid nitrogen, which cooled the leaves to brittleness so they could be pulverized effectively, maximizing homogeneity within each cutting sample. Carbon and nitrogen contents (percentage of dry weight) were measured using an elemental analyzer. A *t* test was conducted to test for differences in water content between the 2 treatments. Because nitrogen levels were expected to rise after fire, we conducted 1-tailed *t* tests to detect differences in nitrogen content and C:N ratio.

Beetle Feeding Trials

To measure differences in *T. lewisii* feeding behavior and fecundity on previously burned plants compared with unburned plants, we conducted 3 types of feeding trials: (1) preference trials to determine whether beetles, when given a choice, preferred shoots from previously burned or unburned plants, (2) compensation trials to see if beetles perceived 1 of the

2 plant types to be a lower-quality food and thus compensated by eating more of this plant type, and (3) fecundity trials to measure egg production of females fed the 2 plant types. All feeding trials were conducted in the laboratory using plant cuttings. To keep foliage as natural as possible, *C. nauseosus* cuttings for the experiments were clipped early in the morning and kept in water and shade while being transported immediately back to the lab. Beetles were given fresh cuttings every 48 hours, each day's cuttings having been clipped from areas of burned and unburned land adjacent to each other to minimize any effects of microhabitat. To avoid changes in plant chemistry that might have been induced by repeated clippings, each cutting was taken from a new, unclipped plant, a single cutting per plant. During the trials plant cuttings were kept in florist's water picks to help maintain turgor pressure and thus the structural integrity and quality of the food material.

Beetles were identified using the key in Hogue (1970). Beetles used in the feeding trials were collected from a population of *C. nauseosus* 1.5 km south of Woods Landing at an elevation of approximately 2320 m. This area, approximately 5 km from the site of the prescribed burn, had not been recently burned. We transported the beetles back to the lab in 9-dram plastic vials and placed them in 1-L, clear plastic containers with mesh lids for the experimental trials. They were maintained at 25°C under ambient light conditions. Beetles were placed in their experimental arenas on the same day they were collected from the field, except for those females used in preference trials; these were starved for 20–24 hours prior to testing.

To determine whether *T. lewisii* preferred leaves from previously burned or unburned plants, we conducted paired-choice tests (between 30 July and 7 August), replicated 15 times. A different, single *T. lewisii* female was used for each test and was housed with 2 sprouts, 1 of each plant type, for 48 hours. Paired sprouts contained approximately the same number of leaves. The approximate leaf area of the sprouts provided to the beetles was estimated prior to consumption by multiplying the length and width of each leaf and summing these values for all leaves on a stem. This is a valid estimate because the long, narrow leaves of *C. nauseosus* are approximately

rectangular in shape. Lengths and widths of the roughly rectangular-shaped bite marks were measured to obtain the approximate leaf area consumed. All measurements of leaves and bite marks were made using vernier calipers. Beetles were starved for 20–24 hours prior to their choice test. A 1-tailed, paired t test was conducted to measure differences between the amount of leaf area consumed of each sprout type.

To test whether beetles ate different amounts of *C. nauseosus* from burned or unburned plants to compensate for possible differences in nutritional quality, we placed 10 *T. lewisii* females in individual containers; 5 were fed sprouts from unburned plants and 5 were fed sprouts from previously burned plants for a period of 11 days (27 July to 6 August). Once the beetles had fed on the cuttings for 48 hours, old cuttings were removed and replaced with fresh sprouts. The amount of foliage consumed by the beetles was measured as in the preference experiment described above. We used the same beetle in the experiment over the entire 11 days to allow the beetle time to detect any potential nutritive differences and begin compensatory feeding. A t test evaluated the difference in leaf area consumed between treatment groups.

Our 3rd feeding trial analyzed the effect of the 2 plant types, burned and unburned, on the fecundity of *T. lewisii.* We measured egg production for females fed sprouts from the 2 plant types over a 13- to 19-day interval (21 July to 8 August). Plant cuttings were replaced and eggs were removed and counted every 48 hours. For each treatment 10 groups of 4 females and 1 male (included to ensure insemination) were placed in individual containers. Egg production of 5 of these foursomes for each treatment was measured over 13 days and the remaining 5 of each treatment over 17 days. To measure individual female's egg production, we placed 6 single females (each housed with 1 male) for each treatment in individual containers and measured their egg output over 19 days. To test for differences in egg output between burned and unburned treatments, t tests were conducted separately on single females and on groups of 4 females. The escape of an entire group of 4 beetles in the burned treatment on 5 August resulted in only 9 replicate foursomes for that treatment;

the unburned treatment had 10 replicates throughout the running time of the experiment.

RESULTS

Plant Change after Fire

Sprouts that regrew after the fire were very different in appearance from sprouts from unburned plants. Shoots were much longer on the previously burned plants than on the unburned plants (mean difference = 8.71 cm, t = 7.32, df = 48, P < 0.001; Fig. 1A). Leaf
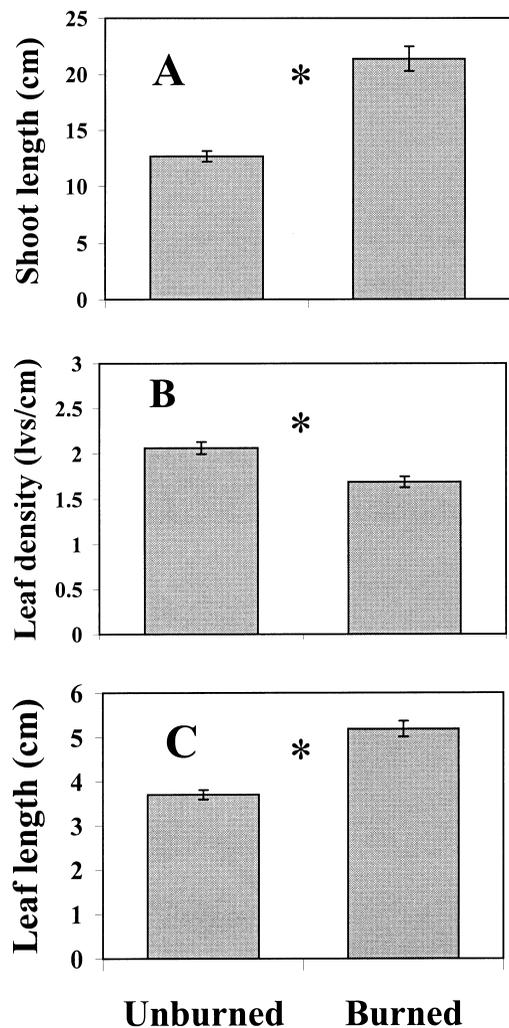
Figs. 1A–C. Shoot length (A), leaf density (B), and leaf length (C) comparisons between shoots of unburned *Chrysothamnus nauseosus* and shoots from plants that were burned the previous winter. Bars show the mean from 25 shoots ±1 $s_{\bar{x}}$; * indicates significant differences at P < 0.001.

TABLE 1. Mean carbon-to-nitrogen ratio, percent nitrogen, and percent water (±1 $s_{\bar{x}}$) in leaves of *Chrysothamnus nauseosus* sprouts from plants that were either previously burned or not affected by fire. $N = 10$ sprouts for each treatment. *P*-values for 1-tailed *t* tests are shown for C:N ratio and % N. *P*-value for 2-tailed *t* test is shown for % water.

Leaf measurement	Unburned	Burned	*t*	*P*
C:N ratio	19.2 (±0.6)	17.7 (±0.6)	1.74	0.055
% N	2.5 (±0.1)	2.6 (±0.1)	−1.09	0.15
% water	69.4 (±2.4)	67.3 (±1.1)	0.76	0.45

density was significantly lower on stems of burned *C. nauseosus* (mean difference = −0.37 leaves · cm⁻¹ stem, $t = -4.13$, df = 48, $P < 0.001$; Fig. 1B). Leaves from burned plants were significantly longer than those from unburned plants (mean difference = 1.49 cm, $t = 7.18$, df = 48, $P < 0.001$; Fig. 1C).

The carbon-to-nitrogen ratio of leaves from burned *C. nauseosus* was marginally lower than from unburned plants ($P = 0.055$; Table 1). Nitrogen and water contents of the leaves were not significantly different between burned and unburned plants (Table 1).

Beetle Feeding Trials

Trirhabda lewisii preferred leaves from burned *C. nauseosus* in the paired-choice tests (mean difference = 0.39 cm², $t = 1.96$, df = 14, $P = 0.04$; Fig. 2). In the compensation trials beetles ate similar amounts of sprouts from burned and unburned plants (mean difference = 0.07 cm², $t = 0.32$, df = 8, $P = 0.37$; Fig. 3). Females fed burned or unburned plants did not differ in the number of eggs laid (singletons: mean difference = 0.03 eggs, $t = 0.46$, df = 10, $P = 0.66$; foursomes: mean difference = 0.03 eggs, $t = 0.59$, df = 18, $P = 0.56$; Fig. 4).

DISCUSSION

Chrysothamnus nauseosus regrowth after fire was morphologically very different from that of unburned plants. The plants produced elongated shoots with longer leaves. A profusion of rapid vegetative growth with a distinctive morphology is commonly observed after a fire (Kituku et al. 1992, Stein et al. 1992, Romo et al. 1993, Vieira et al. 1996, Throop and Fay 1999, Radho-Toly et al. 2001). Surprisingly, despite a striking change in morphology after the burn, we found that *C. nauseosus* shoots from burned sites showed little difference in nitrogen and water content compared with shoots from unburned sites. We anticipated that nitrogen levels

in the foliage would increase after fire, because this increase has been reported previously in numerous studies (Daubenmire 1968, Rundel and Parsons 1980, Kituku et al. 1992, Radho-Toly et al. 2001). However, other studies have shown no change in foliar nitrogen levels or mixed results (Daubenmire 1968, Carlson et al. 1993, Knight 1994, Wambolt et al. 1996). The lack of a pronounced increase in nitrogen levels in this study could be due either to particularities in how *C. nauseosus* aquires nutrients or to the timing of our sample. Mature *C. nauseosus* plants are one of the most deeply rooted plants in shrub-dominated Great Basin communities; they do not take up summer rain, apparently lacking active roots at shallow depths and relying on moisture deeper in the soil (Donovan and Ehleringer 1994). This may limit their ability to take up nitrogen at the soil surface that may become available after a fire. In addition, in contrast to other Great Basin shrub species, *C. nauseosus* appears unable to exploit nitrogen when available in short-duration pulses (Bilbrough and Caldwell 1997) as would occur after a burn. Alternatively, we might have found no difference in nitrogen levels in our sample in early August because leaf composition had changed over the season. While increases in nitrogen levels in some plants can persist into the 2nd growing season after a fire (e.g., Rundel and Parsons 1980, Hobbs and Schimel 1984, Redman et al. 1993), other studies have shown that changes in leaf chemistry following fire can be of short duration, disappearing after a few months (Knapp 1985) or gradually declining with time since the burn (Anderson and Menges 1997).

Studies on other *Trirhabda* species have shown that the quality of host foliage can affect beetle behavior and performance. Host plant foliage with higher nitrogen content is preferred in the field by *T. geminata* (Wisdom 1985) and can increase egg output for *T.*
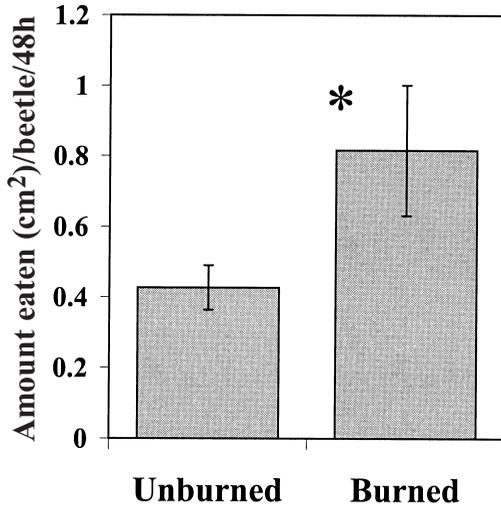
Fig. 2. Mean percentage of leaf material eaten from the total provided per beetle in 48 hours (±1 $s_{\bar{x}}$) when beetles were presented with a shoot from an unburned *C. nauseosus* and a shoot from a previously burned plant. $N = 15$ for each treatment; * indicates $P < 0.05$.
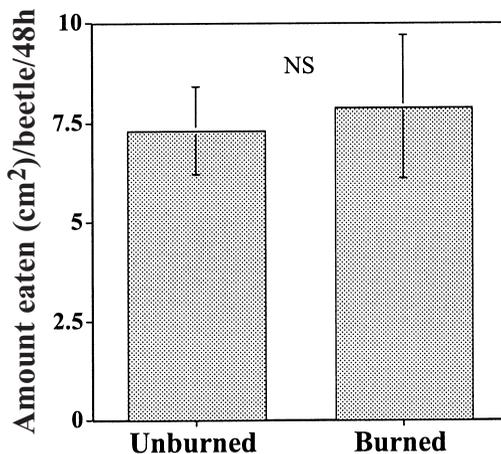

Fig. 4. Mean number of eggs laid per beetle per 48 hours (±1 $s_{\bar{x}}$). Open bars = beetles fed unburned shoots, solid bars = beetles fed shoots that had resprouted from burned plants. Measurements for singletons were averaged for 6 single females over 19 days. Measurements for foursomes were averaged from 2 groups of beetles: group 1 consisted of 5 sets of 4 females over 17 days, group 2 consisted of 5 sets of 4 females over 13 days. NS indicates $P > 0.05$.

Fig. 3. Mean amount of leaf material eaten in 48 hours per beetle (±1 $s_{\bar{x}}$) when beetles were presented with shoots from either previously burned or unburned *C. nauseosus*. $N = 5$ for each treatment; NS indicates $P > 0.05$.

canadensis (Brown and Weis 1995). The nitrogen content of foliage in these studies varied by 3.4% (Wisdom and Rodriguez 1983, Wisdom 1985) and 0.7% (Brown and Weis 1995), differences much greater than the mean difference of 0.1% found in *C. nauseosus* foliage from burned and unburned areas in this study.
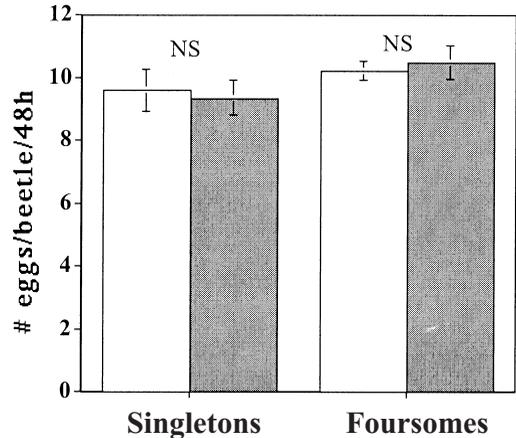
Johnson et al. (1985) found that *T. diducta* larvae and adults compensated for lower nitrogen levels in foliage by eating more, thus maintaining a constant daily intake of nitrogen. *Trirhabda bacharidis* adults prefer more tender leaves of their host plant (Krischik and Denno 1990).

There could be effects of fire on *T. lewisii* in the field that we were unable to measure in the lab. Differences in microhabitat or plant architecture can cause a preference by an herbivore for one plant population over another in natural conditions (Tabashnik and Slansky 1987). The texture of the landscape was more open after the fire, a condition that can promote faster development in insects (Cappuccino and Root 1992). More open stands where fire-susceptible plants have been killed, such as *A. tridentata* at our site, might be easier to find without neighboring plants masking the host odor, resulting in higher colonization rates on plants after a burn. Morrow et al. (1989) showed that *Trirhabda canadensis* adults move toward pure stands of their host plant over stands that contain a mixture of plant species. At our study site we did not observe large numbers of beetles colonizing the burned area.

Although numerous studies have shown that vigorous growth following a fire is attractive to some insect herbivores (Cancelado and Yonke 1970, Stein et al. 1992, Vieira et al. 1996, Porter and Redak 1997, Steinbauer et al. 1998, Negron-Ortiz and Gorchov 2000, Radho-Toly et al. 2001), studies that measure insect performance after a fire are rare and show mixed results. Vieira et al. (1996) found increased survival of gall midges in a burned site compared to an unburned site. In contrast, McCullough and Kulman (1991) found lower survival of jack pine budworm in burned versus clearcut sites. Rieske (2002) found no difference in relative growth rate or development time in gyspy moth larvae fed chestnut oak seedlings from burned and unburned areas despite slightly higher foliar nitrogen levels (0.17% higher) in seedlings from burned areas. Our study shows that despite a preference for the morphologically distinct foliage of burned plants, *T. lewisii* fecundity did not increase when fed these shoots. The effects of fire on herbivore performance may vary depending on the species and systems involved. Likewise, the effects of a fire on an ecosystem can vary depending on its severity and timing (Daubenmire 1968, Boerner 1980, Engle and Bidwell 2001). The prevailing dogma that herbivore attraction to plant regrowth in burned areas is due to changes in nutritional quality that lead to enhanced performance for the herbivore is not well supported.

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