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Effects of Fire, Browsers and Gallers on New Jersey Tea (Ceanothus herbaceous) Growth and Reproduction

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Abstract.—Woody plant species in grassland ecosystems can be subjected to damage from fire and multiple herbivore species, but interactions between fire and herbivory can modify their separate impacts on woody plant life histories. We studied how galling (by *Periploca ceanothiella,* Lepidoptera: Cosmopterigidae), deer browsing (*Odocoilius virginianus*) and fire affected the growth and reproduction of the woody shrub *Ceanothus herbaceous* (Rhamnaceae) on a burned and an unburned site at Konza Prairie Research Natural Area in eastern Kansas. Fire was the major influence on *C. herbaceous* growth, causing plants to produce long unbranched vegetative ramets from protected belowground meristems, while unburned plants were heavily branched and bore shorter shoots and numerous inflorescences. Unburned plants experienced higher gall frequencies, more galls on their longest shoots, but similar deer browsing compared to burned plants. Ramets with herbivore damage had more branches and inflorescences than undamaged ramets, especially where both herbivores were present. *Ceanothus herbaceous'* flexible life history responses suggest tolerance of multiple forms of damage.

Introduction

Fire and herbivory exert pervasive influences on the composition and productivity of many ecosystems, including the tallgrass prairies of North America. One major effect of fire is suppression of woody plants in favor of grasses and forbs (Bragg and Hulbert, 1976). Fire typically suppresses woody species by destroying aboveground biomass and meristems, which alters subsequent plant growth, architecture, reproductive capacity and competitive interactions (Glenn-Lewin *et al.,* 1990; Yeaton and Bond, 1991; Matlack *et al.,* 1993). In addition, fire modifies abiotic parameters important to plant growth, including temperature, light and resource availability (Old, 1969; Hulbert, 1988; Niesenbaum, 1992; Turner *et al.,* 1997).

Herbivory has many of the same influences on woody plants as fire including biomass removal, meristem death and reduced growth, reproduction and competitive ability (Fay and Hartnett, 1991; Erasmus *et al.,* 1992; Brown, 1994). The severity of herbivore impacts on plants depends on the timing, intensity and type of damage inflicted, and a plant's postdamage growth and physiological responses (Watson and Casper, 1984; Rosenthal and Kotanen, 1994; Fay *et al.,* 1996). Herbivore impacts may be compounded when plants are damaged by several herbivore species (Willis *et al.,* 1993).

Fire can strongly affect the extent to which herbivore damage actually occurs. For example, fire affects which herbivore species are present (Warren *et al.,* 1987). Some herbivore species tend to be killed in fires because their phenologies or life histories render them unable to escape. Other species mainly experience indirect effects such as postfire

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changes in host plant quality and abundance (Stein *et al.,* 1992) or abiotic conditions (Hulbert, 1988). These direct and indirect effects of fires can affect herbivore abundances (Warren *et al.,* 1987) and within-plant herbivore distributions (Rosenthal and Kotanen, 1994). As a result, the net impact on woody plant life histories of a fire/herbivore damage regime can be difficult to predict.

New Jersey Tea (*Ceanothus herbaceous:* Rhamnaceae) is found primarily on prairies and open woodlands throughout the midwest and south, and locally in the eastern United States (Bartgis *et al.,* 1997). It is an abundant shrub in Flint Hills tallgrass prairies (Gibson and Hulbert, 1987), where it persists despite regular damage from fire and herbivores. Fire damage typically occurs during spring prescribed burns, which are often conducted to reduce woody species populations. In addition, two herbivores commonly damage *C. herbaceous*; a stem-galling moth (*Periploca ceanothiella,* Lepidoptera: Cosmopterigidae) whose abundance is directly influenced by spring fires (PAF and D.C. Hartnett, pers. observ.), and a browsing mammal, white-tailed deer (*Odocoileus virginianus*). The abundance of *C. herbaceous* despite consistent pressure from fire and multiple herbivores suggests that this species possesses effective tolerance mechanisms. To examine damage tolerance in *C. herbaceous,* we conducted field studies of plant growth characteristics in burned, galled and browsed plants in natural populations. We focused on these specific questions: (1) how does fire affect the incidence of galling and browsing, and within-plant gall distributions? (2) how do fire, galling and browsing affect plant growth form and reproduction?

METHODS

Study site description.—*Ceanothus herbaceous* populations were studied at the Konza Prairie Research Natural Area, a 3487 ha tallgrass prairie in the northern part of the Kansas Flint Hills. Konza is divided into replicate watershed-sized experimental units assigned to factorial combinations of grazing (by cattle or bison) and burning (at 1, 2, 4, 10 or 20-yr intervals; *see* http://climate.konza.ksu.edu for detailed site map and descriptions). Konza's topography is steeply dissected, with each watershed containing shallow-soiled uplands, steep rocky slopes and deep-soiled lowlands. The overall vegetation consists of a matrix of dominant warm-season grasses (primarily *Andropogon gerardii, Sorghastrum nutans, Panicum virgatum* and *Schizachyrium scoparium*), numerous forbs and several woody species (Freeman and Hulbert, 1985; Van Cleve and Martin, 1991). Plant community composition at a specific location depends strongly on its particular fire/grazing regime and topographic position (Gibson and Hulbert, 1987; Hartnett and Fay, 1998).

Natural history.—*Ceanothus herbaceous* grows abundantly on watershed slopes at Konza (average cover ≅ 12% on LTER vegetation transects) regardless of fire frequency. *Ceanothus herbaceous* plants (*i.e.,* genets) consist of multiple ramets originating from belowground meristems. During the first year of growth, each ramet is generally unbranched, usually 20–25 cm tall, and bears numerous lateral meristems. In subsequent growing seasons, ramets become branched due to new shoots arising from the previous crop of lateral meristems. After several years, each ramet supports many shoots and can reach over 50-cm tall. Spring fires periodically reset plant growth form by killing all accumulated growth. This is followed by the rapid development of a new set of unbranched ramets. Ramets produce leaves in mid-to-late March, flower during April and May and set fruits by mid-June (Great Plains Flora Assoc., 1986).

Periploca ceanothiella is an abundant stem galler on *Ceanothus herbaceous.* Beyond basic taxonomic information (Cosens, 1908; Hodges, 1978) the species is unstudied. Galls form in July and contain one larva which feeds and overwinters in the gall, emerging the following March. Galls persist on the plant after larval emergence (PAF and HLT pers. observ.), allowing quantification of past galling history of plants. Morphologically, *P. ceanothiella* galls develop through a combination of inhibited internode elongation and lateral swelling. Galls are elliptical and retain the lateral buds from each node involved in the gall. Gall formation often prevents further terminal growth, and lateral shoots may arise from the gall's lateral buds.

White-tail deer browse *Ceanothus herbaceous* primarily during fall and winter, removing the terminal meristem from varying numbers of shoots per ramet. The amount of tissue lost to browsing cannot be determined after-the-fact, but the loss of the terminal meristem may alter *C. herbaceous* growth by increasing lateral branching at the expense of additional terminal growth. This is a common effect of herbivores in other woody plant species (Whitham and Mopper, 1985).

Field studies.—We conducted field studies during June and July 1995 in two ungrazed watersheds with similar soil type and topography. One watershed has been burned every April since 1988 (Konza designation K1A, 100 ha), and the adjacent watershed (K20A, 90 ha) has been burned approximately once every 20 yr, and was last burned in 1991. These watersheds are typical of burned and unburned Konza watersheds in overall species composition, soils and presence of *C. herbaceous* and its herbivores.

To assess *Ceanothus herbaceous* herbivory rates, growth characteristics and reproduction, we counted the numbers of herbivore damaged shoots, intact shoots and inflorescences on each ramet on plants in both watersheds. Plants were selected by marking four randomly-oriented transects per watershed, and then selecting the first ten plants per transect ($n = 40$ plants per watershed, except $n = 25$ plants for browsing data in K20A). For each plant we noted the numbers of inflorescences and undamaged, galled, or browsed shoots on each ramet. Herbivory was expressed as the percentage of ramets per plant galled or browsed.

Data analysis.—We used a randomization procedure (Manly, 1991) to analyze burning effects on herbivory rates and plant growth and reproduction responses. This procedure was chosen because standard analysis of variance techniques are considered inappropriate when samples are not statistically independent (Hurlbert, 1984), as could be the case with one watershed per burn treatment. Briefly, the randomization procedure generates an expected frequency distribution of treatment sum of squares for the null hypothesis of no treatment effect by repeatedly ($n = 5000$) assigning plants at random to two treatment groups and calculating sums of squares. The significance level of the test is the proportion of expected sums of squares that are less than the experimentally-observed sums of squares (Adams and Anthony, 1996).

To measure herbivore impacts on plant growth and reproduction, we compiled numbers of shoots and inflorescences per ramet by herbivory type (browsed, galled or both), and analyzed these responses using one way analysis of variance. This analysis was conducted on the unburned watershed only, due to low numbers of galls and inflorescences on the annually burned watershed.

To assess the effects of fire on the distribution of *Periploca ceanothiella* galls within *Ceanothus herbaceous,* we compiled shoot length frequency distributions for galled and undamaged shoots in each watershed. These frequency distributions were based on intact shoot lengths, measured directly for undamaged shoots and estimated for galled shoots (Fay and Samenus, 1993). Intact lengths of galled shoots (*i.e.,* their length had they not been galled) were estimated using bud count-shoot length regressions based on 200 randomly chosen shoots per watershed (for unburned plants length $= 0.95*\text{buds} + 5.69$, $R^2 = 0.71$, $P < 0.001$; for burned plants length $= 0.99*\text{buds} - 2.32$, $R^2 = 0.71$, $P < 0.001$). For analysis, shoot lengths were grouped in 20 cm intervals, and the frequencies of estimated galled shoot lengths were compared to the total distributions with chi-square tests.

TABLE 1.—Shoot, ramet and inflorescence production and incidence of *O. virginianus* browsing and *P. ceanothiella* galls on annually burned and unburned *C. herbaceous* plants. All values are mean ±SE. For all variables but browsing, 4999 of the randomly generated sums of squares were less than the observed, yielding P-values of 0.0002

	Annually burned	Unburned	P value
Ramets per plant	29.83 ± 3.44	7.63 ± 0.81	0.0002
Shoots per ramet	1.15 ± 0.04	37.77 ± 4.00	0.0002
Shoot length (cm)	32.84 ± 0.34	16.96 ± 0.41	0.0002
Inflorescences per plant	0.08 ± 0.08	29.38 ± 4.56	0.0002
% of ramets browsed	78.1 ± 4.5	79.7 ± 5.4	0.96
% of ramets galled	3.5 ± 1.2	71.7 ± 4.3	0.0002

RESULTS

Influence of fire.—Annually-burned *Ceanothus herbaceous* plants produced many new ramets from belowground buds (Table 1). The new ramets were generally unbranched (*i.e.,* composed of a single shoot), twice the length of the shoots produced on unburned ramets and bore no inflorescences. In contrast, unburned plants supported fewer ramets, but each ramet produced many shoots and inflorescences, resulting in a highly branched growth form.

Influence of herbivory.—Galls rarely formed on ramets of burned plants but were found on nearly 75% of ramets in unburned plants (Table 1). In contrast, deer browsing occurred on nearly 80% of ramets in both burned and unburned plants. Galls were equally likely to occur on all shoot lengths in burned plants, but in unburned plants long shoots (>40 cm) were nearly twice as likely to be galled as shorter shoots (Table 2).

Herbivory had the opposite effects of fire on *Ceanothus herbaceous* growth (Fig. 1). Damaged ramets produced more shoots and inflorescences than undamaged ramets. Ramets with damage from one herbivore showed increases in shoot and inflorescence numbers over undamaged ramets. Ramets damaged by both herbivores produced at least double the shoots and inflorescences of ramets damaged by a single herbivore.

TABLE 2.—Relationship between shoot length and galling rate for *P. ceanothiella* galls on burned and unburned *C. herbaceous* plants

Shoot length (cm)	# shoots	# galled (%)	# expected	χ^2
Annually burned plants				
<20	37	21 (56.7)	18.54	0.33
20–40	292	147 (50.3)	147.08	0.00
>40	80	38 (47.5)	40.38	0.14
Total	409	206 (50.4)		0.47 ns
Unburned plants				
<20	291	141 (48.4)	146.27	0.19
20–40	86	39 (45.3)	43.24	0.42
>40	29	24 (82.7)	14.48	6.26
Total	406	204 (50.2)		6.87*

* $P < 0.05$, df = 2

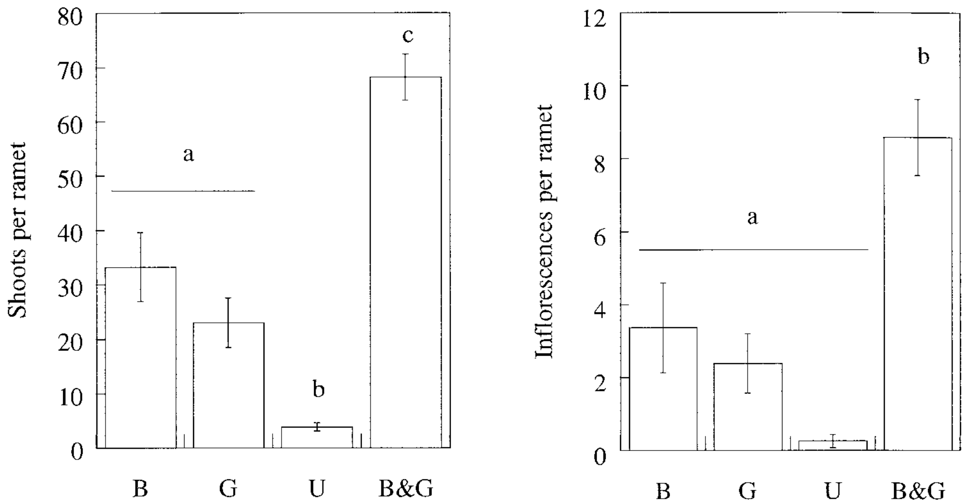

FIG. 1.—Effects of *P. ceanothiella* galls and *O. virginianus* browsing on shoot and inflorescence production of unburned *C. herbaceous* ramets. All values are mean ± SE. B = browsed, G = galled, U = undamaged, B&G = browsed and galled. Treatments with the same letters above columns are not significantly different. a) Shoots per ramet ($F = 35.7$, $P < 0.001$). b) Inflorescences per ramet ($F = 12.14$, $P < 0.001$)

DISCUSSION

Fire markedly altered the growth of *Ceanothus herbaceous*. Immediately following a fire many long, vigorous, asexual ramets arose from protected basal buds. In contrast, the established ramets of unburned plants were highly branched, and new growth consisted of many shorter shoots and inflorescences. Vigorous asexual regrowth is typical of shrubs in fire-prone habitats (Stein *et al.,* 1992; Romo *et al.,* 1993), which often regenerate from protected belowground parts (Paige, 1992). Despite this vigorous postfire regrowth, cover of *C. herbaceous* is low immediately after fire (Gibson and Hulbert, 1987; Gibson, 1988) and increases in the years following fire as ramets become increasingly branched.

By not producing inflorescences, annually burned *Ceanothus herbaceous* allocates resources primarily to vegetative growth. This allocation pattern has short- and long-term benefits. Immediately after fire, vegetative regrowth would help *C. herbaceous* acquire space in the highly competitive tallgrass prairie plant canopy (Collins and Gibson, 1990). Where fires recur annually, strong vegetative growth may also help prevent local extinction of *C. herbaceous* populations because suppressed flowering could lead to low seedling recruitment due to few seeds in the seed bank (Whelan, 1995). Where fire is less frequent, seed production may be maximized in later growing seasons by early investment in vegetative growth, since there is usually a strong correlation between plant size and sexual reproductive effort (Samson and Werk, 1986; Hartnett, 1990).

Fire reduced the frequency of *Periploca ceanothiella* galls but had no effect on deer browsing rates. Low gall frequencies on the burned watershed were most likely due to mortality of *P. ceanothiella* larvae in the spring fire. High mortality of larvae in galls during spring burns has been documented in other gallers of tallgrass prairie plants (Fay and Samenus, 1993). There was apparently little postfire immigration of *P. ceanothiella* adults into the burned watershed, even though potentially suitable shoots were available for galling and an abundant source of migrants was close by in the unburned watershed. We expected higher deer browsing rates on the burned watershed since postfire growth is often more nutritious and succulent than older plant tissue (Stein *et al.,* 1992). However, since deer browse *Ceanothus herbaceous* primarily during fall and winter, plant quality differences between burned and unburned watersheds may have been diminished.

Fire changed the within-plant distribution of shoot lengths and *Periploca ceanothiella* galls. Long shoots were less abundant and more frequently galled in the unburned watershed compared to the burned watershed. High gall frequencies on long shoots has been reported for other galling insects on woody plant species (Price *et al.,* 1987). Fire thus appeared to affect the potential for galls to damage *Ceanothus herbaceous* in two ways. Unburned plants experienced both higher overall gall frequencies as well as disproportionate damage to long shoots, which have the greatest potential for future growth.

Herbivore impacts on *Ceanothus herbaceous* were less severe than fire impacts. Whereas fire killed all aboveground tissues, both herbivores left live shoots and meristems from which *C. herbaceous* could continue to grow and flower. Galled and browsed ramets showed similar increases in branching. Even though their feeding styles differed, both herbivores caused damage that inhibited apical dominance, thus promoting similar lateral branching responses. However, browsing might be more harmful to *C. herbaceous* in the long term than galling because browsing removes part of *C. herbaceous*' reserve meristem population and removes more biomass than galling.

We summarize the net impacts of the fire/herbivore damage regime on *Ceanothus herbaceous* with a working hypothesis. *Ceanothus herbaceous* had a flexible, mainly fire-governed, life-history. Fire puts *C. herbaceous* in a vegetative unbranched state, and annual burning will maintain this state. With two or more years between fires, *C. herbaceous* becomes branched and allocation to sexual reproduction increases. Herbivory speeds the progression of branching and inflorescence production, but fire can mitigate herbivore impacts by reducing populations of one of *C. herbaceous*' common herbivores.

The flexible life history responses shown by *Ceanothus herbaceous* in response to fire and herbivores suggests tolerance of both forms of damage (Rosenthal and Kotanen, 1994), with fire tolerance conveyed by protected belowground meristems and herbivory tolerance conveyed by aboveground lateral meristems. Woody plants inhabiting fire-dominated ecosystems such as grasslands may commonly be subject to damage from fire and multiple herbivores. The response of *C. herbaceous* to fire and multiple herbivores suggests an important life history pattern by which woody plants can persist in such systems.

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