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Effects of burning and burn season on the interaction between *Solidago altissima* and gallmaking insects

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Introduction

The complex interactions between plants and insects are commonly investigated on the Iowa prairie. Abiotic factors affect the success of host plants while insects adapt to take advantage of their hosts' relative success. While many plant-insect relationships fit this description, the close interaction between galling insects and their host plants makes them of particular interest. After a galling insect deposits its eggs into a host plant, the eggs release chemicals that induce the formation of a bulge in the stem. The larvae typically develop for a year inside the bulge before they emerge as adults. Because the reproductive success of galling insects is dependent on their ability to successfully use their host plant, the environmental factors that affect the abundance and size of their host plant indirectly affect the galling insects. Studying how environmental factors may link the size and density of a host plant to gall frequency and size creates an awareness of the intricate and multilayered relationships that characterize the Iowa prairie.

We chose to observe the relationship between the common prairie plant, *Solidago altissima* (Tall Goldenrod,) and its three gall makers, *Eurosta solidaginis* (Diptera: Tephritidae), *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechiidae) and *Rhopalomyia solidaginis* (Diptera: Cecidomyidea) in the seasonal burn treatments at the Conard Environmental Research Area (CERA). Round galls, spherical bulges found midway up a stem of Goldenrod, are created by the tephritid fly *E. solidaginis*. They are formed in the spring and must develop over-winter before the larvae pupate in the following spring. Less noticeable than the round galls, elliptical galls are created by the moth *G. gallaesolidaginis* and are found closer to the base of the Goldenrod stem. Adult *G. gallaesolidaginis* moths emerge to lay their own eggs in early autumn, and their galls will not form until the following spring. Unlike the ball and elliptical galls which usually contain one larva per gall, a rosette gall can house up to twelve (Abrahamson and Raman, 1995). Rosette galls are characterized by a rose-like cluster of small leaves appearing at the top of a stem of Goldenrod. Little is known about the lifecycle of the midge gall maker *R. solidaginis.*

In order to understand the relationship between *S. altissima* and the galls, we must understand what effects the environment has on the *S. altissima*. CERA is a reconstructed prairie, and like other reconstructed prairies, controlled burning is critical to its maintenance. Fire eliminates tree growth, favors grasses and forbs, and rids the ground surface of necromass which can block water and nutrients from reaching the soil (Howe 1995, Reichman 1987). Spring fires give late-flowering prairie plants such as *Solidago altissima* a competitive edge by the exposing soil to the sun without risking excessive dryness as the soil is already soaked from the melting snow. (Reichman 1987). However, spring fires significantly reduce the success of early-flowering forbs and grasses, especially fires in late spring. Early-flowering forb populations rarely completely recover from late spring burns, because by the following spring, aggressive late-flowerers such as *Andropogon gerardii* have already taken over space and resources (Copeland et al. 2002). In summer burns, the growth of typically dominating late-flowering grasses is slowed, giving the advantage of better access to sunlight to the shorter and less dominant species. This shift increases prairie species richness for at least the year after the summer burn (Copeland et al. 2002). As most growth and seed production has already occurred by the end of the summer, autumn burns seem to have little effect on prairie productivity, density, or diversity after the fire (Copeland et al. 2002). We isolated these seasonal differences by conducting our research on the seasonally burned experimental plots at CERA, and we suspected to see variation in *S. altissima* density and vigor consistent with what is known about the effects of seasonal burning.

Solidago altissima is a late flowering forb and consequently directs most nutrients into the production of inflorescences during the late summer and early fall months. This led us to expect greater *S. altissima* density on spring vs.

summer plots, because most of the plant's nutrients would still be safely stored below the soil during a fire. In contrast, fall burning should have the least affect on *S. altissima's* density as most nutrients of all prairie plants would have been recalled into root storage in preparation for the winter.

The seasons are also relevant to the cycles of the gall makers. Each species of gall maker has a unique reproductive cycle, and we suspected that the timing of the burns would affect the abundance and size of galls relative to their overlap with the insects' lifecycle. There is also evidence of preference among galling insects for certain heights of *S. altissima*. We hypothesized that if the differing burn treatments resulted in varying heights of *S. altissima*, galls might become more prevalent in plots with their preferred average *S. altissima* height and basal stem width.

Methods

We conducted our study at the Conard Environmental Research Area (CERA) near Kellogg, Iowa from mid October through late November. We studied the effects of seasonal burning on a tract that had been replanted with prairie grasses and forbs in 1987. The tract was divided into eighteen 10 x 20 meter plots, which were subdivided into six blocks which account for gradients in soil, topography, etc. across the tract that could alter the effects of burning treatments. Firebreaks are routinely mowed between the plots. Each plot was randomly assigned a spring, summer or fall burn treatment. Fall burn plots have been burned every fall since 1999 and spring burn plots have been burned every spring since 2000. Summer burn plots have been burned every other year since 2000, last in 2002 (Batterman et al., 2002). Plots can be burned only every other summer because there is not sufficient necromass after only one year to fuel a fire. We compared these seasonally burned plots with plots that have not been burned since 1997 (Batterman et al., 2002). The unburned plots are located across the road from the seasonally burned plots and are 10 x 10 meters. We randomly selected six out of ten of the unburned plots to study. In order to be able to test for a gradient in the unburned plots in our statistical analysis, we assigned each unburned plot to the block of the seasonally burned plot directly across the road.

We determined the density of *Solidago altissima* in the eighteen seasonally burned plots, as well as in the six unburned plots. We randomly selected two 1 x 20 meter transects of the burned plots and two 1 x 10 meter transects of the unburned plots and then counted the number of *S. altissima* stems in each transect. We estimated densities of elliptical, rosette and.

Table 1. ANOVA generated F and P values for effect of block and seasonal burn treatment over each variable. NS= not significant

VARIABLE	BLOCK	SEASONAL BURN TREATMENT
S. altissima density	F=5.57; P=0.010	NS
Density of Ball galls	NS	NS
Density of Elliptical galls	F=8.83; P=0.002	NS
Density of Rosette galls	NS	NS
% Ball galled	NS	NS
% Elliptical galled	F=2.74; P=0.082	NS
% Rosette galled	NS	NS
Ball galled height	NS	NS
Elliptical galled height	F=3.25; P=0.053	NS
Rosette galled height	NS	NS
Ungalled height	F=3.81; P=0.034	NS
Ball galled BSW	NS	NS
Elliptical galled BSW	NS	NS
Rosette galled BSW	NS	NS
Ungalled BSW	NS	NS
Ball gall width	NS	NS
Elliptical gall width	NS	NS
# of Rosette galls/plant	NS	NS

Table 2. ANOVA results for the effect of block and burn treatment on gall characteristics. Displayed are the means (± 1 SE) of *S. altissima* height (cm) * P < 0.05 and ** P < 0.09 (P values represent comparisons along treatment only, block effect was included)

	Burn Treatment				
***S. altissima* Height (cm)**	**Spring**	**Summer**	**Fall**	**Unburned**	**Average of all Burned**
Rosette	41.92 ± 6.48	56.44 ± 3.11	44.92 ± 2.23	68.33 ± 7.14*	47.76 ± 2.8*
Elliptical	69.09 ± 6.37	68.67 ± 5.73	67 ± 7.4	85.1 ± 7.73*	68.25 ± 3.55*
Ball	52.05 ± 6.99	66.17 ± 6.24	51.3 ± 10.6	81.5 ± 6.88*	58.4 ± 4.46*
Ungalled	50 ± 9.77	58.08 ± 5.95	55.5 ± 2.99	71.75 ± 5.81*	54.53 ± 3.79*

ball galls in each of our plots by flagging and counting each gall.

To study the characteristics of galled and ungalled *S. altissima*, we sampled two plants representative of each category of galls. We randomly selected two points within each plot and measured the heights and basal stem widths of the rosette galled plants, elliptically galled plants, ball galled plants and ungalled plants that were closest to each of the points. We also measured the widths of the elliptical and balls galls, and counted the number of rosette galls per stem

We used ANOVA to compare burn treatments for density of *S. altissima*, densities of each type of gall, and percentage of *S. altissima* galled by each of the three species of insect. We also looked at basal stem width and height of galled plants of each type vs. ungalled plants, as well as the size and number of the galls on each stem measured. These comparisons were made by comparing means by season and also between unburned plots and burned plots, regardless of season. We tested for significance for each variable by both treatment and block, to check for both the overall effects that treatments had on *S. altissima* and its galls, as well as a possible gradient in the plots. In addition to looking at how different burn treatments affect goldenrod and galls, we also looked at how the galls themselves affected *S. altissima* across all plots. We used ANOVA tests to compare mean height and basal stem width of ungalled *S. altissima* and galled *S. altissima* of each type combined from all burn treatments.

Results

Seasonal Burns

We discovered a significant block effect reflecting an increase from east to west in the height and density of *S. altissima* as well as in density of elliptical galls (Table 1). Density of goldenrod, percentage of stems galled, density of galls, height or basal width of stems, size of elliptical and ball galls, and number of rosette galls per plant showed no significant effect of seasonal burns (Table 1). However, the difference in basal stem width of elliptical and ungalled *S. altissima* was marginally insignificant by seasonal effect (F=3.6, p=.067); elliptically galled *S. altissima* tended to have larger basal stem widths than the ungalled *S. altissima*, and this difference was largest in summer burns (Figure 1).

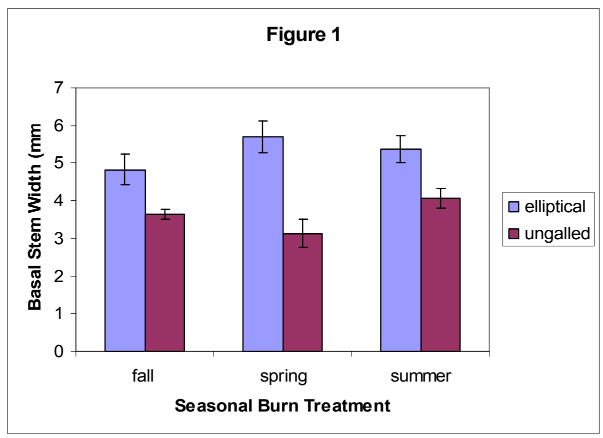

Figure 1. Mean basal stem width (± 1 SE) for elliptical and ungalled *S. altissima* plants in fall, spring, and summer burn treatments.

Burned and Unburned

To test for significant differences in the galling patterns of *S. altissima* between the burned and unburned treatments, we grouped the seasonally burned plots as one treatment and compared *S. altissima* height between the burned and unburned treatments (Table 2). Elliptically galled *S. altissima* on the burned plots were significantly smaller, 80% of the height of the plants on the unburned plots. *S. altissima* with rosette galls were significantly shorter (30%) on burned plots than on the unburned plots.

Likewise, the ungalled *S. altissima* were significantly taller (31%) on unburned plots than on burned plots and *S. altissima* with ball galls were significantly taller (49%) on the unburned plots. The average density of ball galls in the unburned plots was 3 times that found in the burned plots (Table 3, p=0.059). There were no significant differences between burned and unburned treatments in densities of elliptical or rosette galls (Table 3). There were also no significant differences in basal stem widths of galled or ungalled *S. altissima* between burned and unburned treatments, although rosette galled stems on average were 82% as thick on unburned plots as burned plots, a difference which was nearly significant (Table 4). The sizes of ball and elliptical galls and numbers of rosette galls as well as the percentages of *S. altissima* galled were not affected by burn treatment (Tables 5, 6).

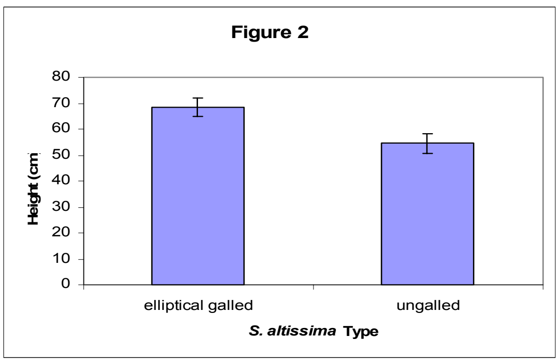

Figure 2. Mean height (± 1 SE) of elliptical and ungalled *S. altissima* from all treatments. t = 2.64, p = 0.012.

Comparative Gall Features

When using all treatments (both burned and unburned) as a pool, comparisons of other features of *S. altissima* reveal a number of significant differences between ungalled plants and those with elliptical galls. The average height of the elliptically galled *S. altissima* was 25% taller than the average height of the ungalled *S. altissima* (Fig. 2). We also found that the elliptically galled *S. altissima* had on average 44 % greater basal stem width than did the ungalled *S. altissima* (Fig. 3). There were no significant differences across seasonal burn treatments for the size of ungalled goldenrod and goldenrod with either ball or rosette galls (Table 1).

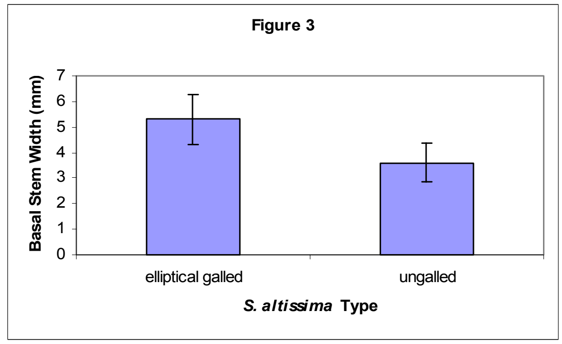

Fig. 3 Mean basal stem width (± 1 SE) of elliptical and ungalled *S. altissima* from all treatments. t = 5.78, p = 0.000.

Discussion

The significant block effect along the seasonal burn plots in the height and density of *S. altissima* and density of elliptically galled S. altissima reveals factors other than burning, such as soil moisture, pH or Nitrogen content, must have affected the abundance of *S. altissima*. While this gradient can be accounted for by comparing the burn treatments by block, it is important to consider that whatever factors cause the gradient may indirectly affect other aspects of the study as well.

Although we had expected that variation in

Table 3. ANOVA results for the effect of block and burn treatment on gall characteristics. Displayed are the means (± 1 SE) of each variable in the context of the Density (stems per m^2) * P < 0.05 and ** P < 0.09 (P values represent comparisons along treatment only, blocking effect was included)

	Burn Treatment				
Density (stems per m^2)	**Spring**	**Summer**	**Fall**	**Unburned**	**Average of all Burned**
S. altissima	3.54 ± 1.05	4.57 ± 1.12	4.712 ± 0.446	6.17 ± 2.93	4.274 ± 0.515
Rosette	0.1008 ± 0.0359	0.0875 ± 0.0276	0.274 ± 0.206	0.125 ± 0.0593	0.1542 ± 0.0692
Elliptical	0.0483 ± 0.0123	0.0642 ± 0.0245	0.0617 ± 0.0209	0.0967 ± 0.0387**	0.0581 ± 0.0109**
Ball	0.025 ± 0.00931	0.0175 ± 0.00382	0.02167 ± 0.00919	0.06 ± 0.0324**	0.02139 ± 0.00433**

Table 4: ANOVA results for the effect of block and burn treatment on gall characteristics. Displayed are the means (± 1 SE) of each group's basal-stem widths (mm). * $P < 0.05$ and ** $P < 0.09$ (P values represent comparisons along treatment only, block effect was included)

	Burn Treatment				
Basal Stem Widths (mm)	**Spring**	**Summer**	**Fall**	**Unburned**	**Average of all Burned**
Elliptically galled	5.7 ± 0.435	5.367 ± 0.349	4.833 ± 0.411	4.74 ± 0.274	5.3 ± 0.234
Ball galled	4.313 ± 0.826	4.625 ± 0.417	2.917 ± 0.862	5.01 ± 0.426	4.135 ± 0.337
Rosette galled	2.896 ± 0.230	4.033 ± 0.285	3.525 ± 0.360	4.242 ± 0.361**	3.485 ± 0.197**
Ungalled	3.133 ± 0.377	4.058 ± 0.259	3.642 ± 0.136	3.967 ± 0.348	3.611 ± 0.175

the density of *S. altissima* would be common, especially in the spring burned plots, we found that density of *S. altissima* was not significantly affected by the seasonal burn treatment it received. Howe (1995) proposes that it is difficult to compare the abundance of a species such as *S. altissima* among seasonal burn treatments, and instead it would be better to make comparisons by grouping species together. Studying the abundance of several prairie plants, including *S. altissima*, on spring burned, summer burned, and unburned plots, Howe found no significant difference in the density of *S. altissima* between treatments. However, he did find significant differences between the combined density of *S. altissima, Andropogon gerardii* and *Aster simplex*. Density was highest in spring burned, next highest in unburned, and lowest in summer burned, which corresponds with our hypothesis about *S. altissima* individually.

We found no significant differences in the height or basal stem width of ungalled *S. altissima* among seasonal burn treatments, which suggests that *S. altissima* is not affected by seasonal burns. This is an interesting result because it seems that *S. altissima* would be smallest on summer burned plots, as burning in the late stages of its growth would hinder development more than in the earlier spring stages (Copeland et al. 2002). Perhaps the effects of summer burning on *S. altissima* were minimized by the fact that the summer plots were last burned in the previous year. *S. altissima* was, however, affected by burning in general. The average height of the unburned plants was significantly taller than the average height of the burned plants. This makes sense as any kind of burning would tend to favor the fast growing grasses that aggressively compete for open space each spring.

There were also no significant differences in the densities of galled *S. altissima* between any of the treatments, nor were there significant differences in the percentages of galled *S. altissima* stems. Cronin and Abrahamson's study (2001) supports our results and found no correlation between density of *S. altissima* and density of *E. solidaginis* galls. A possible explanation for this lack of correlation is that *E. solidaginis* lacks the discriminatory power necessary to be very selective in choosing sites for egg deposition, and thus tend to form clusters of galls in the most convenient area of *S. altissima* they can find (Craig et al. 2000).

There are two possible explanations for the

Table 5. ANOVA results for the effect of burn treatment on gall characteristics. Displayed are the means (± 1 SE) of each group's Percentage of Galled *S. altissima* * $P < 0.05$ and ** $P < 0.09$ (P values represent comparisons along treatment only, blocking effect was included but not shown)

	Burn Treatment				
Percentage of Galled *S. altissima*	**Spring**	**Summer**	**Fall**	**Unburned**	**Average of all Burned**
Ball	0.696 ± 0.56	0.516 ± 0.157	0.459 ± 0.196	1.018 ± 0.203	0.5572 ± 0.0958
Elliptical	1.752 ± 0.479	1.146 ± 0.29	1.226 ± 0.358	2.122 ± 0.601	1.374 ± 0.218
Rosette	3.24 ± 1.15	2.155 ± 0.412	5.46 ± 4.09	3.22 ± 1.23	3.62 ± 1.38

Table 6. ANOVA results for the effect of block and burn treatment on gall characteristics. Displayed are the means (± 1 SE) of each variable for Gall width (mm) or number of rosette galls.

	Burn Treatment				
Gall Width (mm) and No. of Galls*	**Spring**	**Summer**	**Fall**	**Unburned**	**Average of all Burned**
Ball	14.138 ± 0.715	15.39 ± 1.03	12.4 ± 3.09	15.240 ± 0.660	14.315 ± 0.854
Rosette	1.75 ± 0.655	2.083 ± 0.688	2.417 ± 0.676	2.333 ± 0.654	2.083 ± 0.371
Elliptical	7.117 ± 0.481	9.71 ± 1.43	7.233 ± 0.575	8.86 ± 0.905	68.25 ± 33.55

nearly significant difference in density of the *G. gallaesolidaginis* galls between the burned and unburned plots. One explanation may simply be that the direct affects of fire lessen the chance of survival for the *G. gallaesolidaginis* eggs in the burned plots. In addition, it is possible that the young *G. gallaesolidaginis* adults are less mobile than *E. solidaginis* and have fewer options in their ultimate location. The second possibility is that *G. gallaesolidaginis* prefers to gall in unburned areas rather than burned areas. This is supported by our findings that *S. altissima* is taller in unburned plots than in burned plots. According to Cronin and Abrahamson (2001), there is evidence showing that gall makers, at least *E. solidaginis*, prefer to gall taller *S. altissima* stems. This preference may carry over to other types of gall makers, such as *G. gallaesolidaginis*.

The lack of significant variation between size of *S. altissima* and presence of galls suggests that gall makers do not have a strong preference for the height of the stem they choose to deposit their eggs in. As our study found that seasonal burning does not affect density, height, or basal stem width of *S. altissima,* there would not be an incentive for a gall maker to favor one seasonal plot over another when considering the size of the host plant. However, densities of both elliptical and ball galls were greater in unburned plots versus burned plots, and in all treatments the elliptically galled and ball galled *S. altissima* had greater average heights than ungalled *S. altissima*. While these density and height observations were only statistically significant in the burned vs. unburned comparisons, they suggest that both *E. solidaginis* and *G. gallaesolidaginis* might prefer to gall tall plants, although there is evidence suggesting that this preference is related to growth rate, not just height (Cronin and Abrahamson 2001, Craig et al. 2000).

Our study proved that burning, regardless of season, affects the average height of *S. altissima*. Overall the unburned *S. altissima* (both galled and ungalled) was taller than the *S. altissima* growing on the burned plots. However, we did not find any significant differences between seasonally burned plots even when the blocking effect was accounted for.

Although the focus of our experiment was to study how burning affects *S. altissima* and its galls, we also wanted to consider reasons why a gall maker might choose one particular stem over another. While the variables of height, basal stem width, and burn treatment that were tested in our study did not sufficiently answer this question, our results help to rule these factors out, thereby pointing future research to other promising directions. For instance, the gall makers might be acting in response to plant genotype, intraspecific competition, or presence of other herbivores. Even the age of the gall maker could be relevant (Cronin and Abrahamson 2001, Craig et al. 2000, Abrahamson and Weis 1997).

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Literature Cited

Ambrahamson, W.G., and K.D. Mc Crea. 1986. Nutrient and biomass allocation in *Solidago altissima*: effects of two stem gallmakers, fertilization, and ramet isolation. *Oecologia* 68:174-180.

Abrahamson, W.G. and A.E. Weis. 1997. Evolutionary Ecology across Three Trophic Levels; Goldenrod, Gallmakers and Natural Enemies. Princeton University Press: Princteon, NJ.
Batterman, S., Mueller, M. and D. Prignitz. 2002. Effects of spring and fall burns on C3 and C4 productivity. *Tillers* 3: 5-10.

Cappuccino, N. 1992. The Nature of Population Stability in *Eurosta solidaginis*, a Nonoutbreaking Herbivore of Goldenrod. *Ecology* 73: 1792-1801.

Copeland, T.E., W. Sluis and H.F. Howe. 2002. Fire Season and Dominance in an Illinois Tallgrass Prairie Restoration. *Restoration Ecology* 10:315-323.

Craig, T.P. et al. 2000. The influence of host plant variation and intraspecific competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis. Ecological Entomology* 25:7-18

Cronin, J.T. and W.G. Abrahamson. 2001 Goldenrod stem preference and performance: effects of multiple herbivores and plant genotypes. *Oecologia* 127:87-96.

Gagné, R.J. 1989. The Plant Feeding Gall Midges of North America. Cornell University Press; Ithaca, NY.

Howe, H.F. 1995. Succession and Fire Season In Experimental Prairie Plantings. *Ecology* 76:1917-1925.

Reichman, O.J. 1987. Konza Prairie. University Press of Kansas; Lawrence Kansas.

Raman, A. and W.G. Abrahamson. 1995. Morphometric relationships and energy allocation in the apical rosette galls of *Solidago altissima* (Asteraceae) included by *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae). *Environmental Entomology* 24:635-639

Weis, A.E. Just Lookin' for a Home. Sept 1998 *Natural History*.