Basal stem width, and herbivory differ in galled ramets versus ungalled ramets for *Solidago altissima*

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Introduction

Plants respond to herbivore damage in many ways. A wide range of studies show that herbivory generally has a negative impact on plants (Belsky 1986, Krischik and Denno 1983, Huffaker et al. 1984, Schowalter et al. 1986, Verkaar 1988). Yet some studies show that some herbivores do not cause significant damage to plants and even enhance plant growth (Inouye 1982, McNaughton et al. 1983, Wallace et al. 1985, Maschinski and Whitham 1989).

Insects have natural instinctive mechanisms by which they can tell if a plant will be a good host for the galls (Abrahamson and Weis, 1997). Galls are a tumor-like growth of plant tissue concentrating nutrition and providing shelter, caused by a chemical interaction between gallmaking insects and host plants. These galls then serve as a place for the growth and maturation of the offspring of the insects (Abrahamson and Weis 1987). Some studies suggest that galls adversely affect the growth of the individual (McCrea et al. 1985).

We studied *Solidago altissima* because a large body of knowledge already exists concerning its interactions with multiple enemies. Abrahamson and Weis (1997) document the relationship between *Solidago altissima* and gall makers. We can generalize to the entire forb population, using *Solidago* as a base of study.

We selected three prairie areas at the Conard Environmental Research Area (CERA) with different burn treatment histories. We examined *Solidago* across different burn treatments in order to minimize the differences in treatment history. We examined gall size, basal stem width, and herbivory on *Solidago altissima*. The purpose of this study is to understand the effects of how multiple enemies might interact.

Methods and Materials

We established 16 plots along the road in the northern area of CERA. Each plot was a ten by ten meter area. Five of the plots were from the fall burn treatment group, five from the spring burn treatment group, and six from the unburned treatment group. We constructed transects of ten meter length, measuring half a meter on either side of the transect to gather our data. On each transect, we measured every ramet of *Solidago altissima* that we encountered. In categorizing plants as galled versus not galled, we did not differentiate between ball-galls, elliptical galls, and rosette galls.

In each of the plots, we ran one 10 m by 1 m transect for our study of herbivory. From each ramet of *Solidago altissima* we took the sixth, seventh, and eighth leaf from the top of the ramet. We then divided this data according to whether or not the ramets had galls on them. Finally, we froze the leaves for later analysis. We thawed the samples for computer analysis on October 26 and 28. We used *NIH Image 1.61* to calculate the area of each leaf and its percent area lost to herbivory. However, we had to discard some leaves from various samples due to damage in the freezing / storing process. We conducted *t*-tests on this data.

To study basal stem width and gall width, we established two new transects within every plot. We measured every ramet of *Solidago altissima* at the base using an electronic caliper. For every ramet that had a gall, we measured the diameter of the gall with an electronic caliper. The basal stem width of galled and ungalled *Solidago altissima* were compared separately in the fall burn, spring burn, and unburned treatment areas using *t*-tests; a comparison based on the pooled sample was also performed. Additionally, we determined if there was a significant correlation between gall width and basal stem width by conducting regression analysis using *Excel*.

Results

Gall width - There was a significant difference in the fall burn treatment area (t = 6.31, df = 376, $P = 7.77 \times 10^{-10}$), with galled ramets being 30% narrower than ungalled ramets. However, within the spring burn and unburned treatment groups, there was no significant difference ($t_{unburned}$ = .257, $df_{unburned}$ = 94, $P_{unburned}$ = .80, $t_{tspring}$ = .977, df_{spring} = 116, P_{spring} = .33,). These differences can possibly be attributed to the small sample size in the spring burn and unburned areas (Table 1).

Table 1. Sample size for stem width analysis

N	Stems	Galls
Fall Burn	378	61
Unburned	96	8
Spring Burn	118	5

Despite the small sample sizes, the same patterns of stem width in galled versus ungalled ramets existed over all three burn types. Regardless of the burn treatment applied to the prairie, there was a significant difference (t = 5.87, df = 590, $P = 7.12 \times 10^{-9}$) between the width of ramets that were galled versus those that were ungalled, with stems of galled ramets being 25% narrower than ungalled ramets at the base (Figure 1). We did not find any relationship between gall width and basal stem width (F = 0.734) (Figure 2).

Herbivory - In no individual burn treatment was there a statistically significant difference in herbivory for ramets that were galled versus those where galls were not present. In the fall burn treatment, the difference was marginally significant (t=1.94, df=212, *P*=.053), with galled ramets suffering from almost twice the herbivory loss of ungalled ramets. In the unburned treatment area, the difference was clearly not significant (*t*=1.01, df=224, *P*=.316), while the spring burn data for percent vegetation loss was incalculable due to the fact that no galls were found (Table 2).

Table 2. Sample size for herbivory analysis

N	Total leaves	Total leaves from galled plants
Fall Burn	114	24
Unburne d	226	46
Spring Burn	31	0

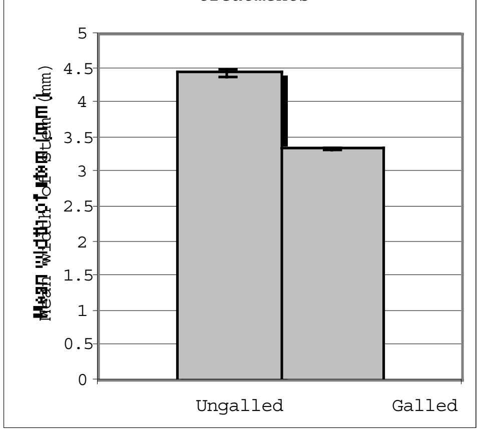


Figure 1 - Comparision of galled ungalled Solidago altissima across treatments

There was a significant difference in the percent vegetation loss due to insect predation across all burn treatments for ramets of *Solidago altissima* that were galled versus those where no galls were present (*t*=2.14, df=469, *P*=.033), with ungalled ramets suffering from 66% less herbivory than galled ramets.

Discussion

Galls affect resource distribution in *Solidago altissima* (Abrahamson and Weis 1997) and the results of our study suggest that in doing so they inhibit stem width growth. Additionally, our observation of higher percentages of herbivory on galled ramets of *Solidago altissima* leads us to believe that a relationship exists herbivory and gallmaker’s choice of host plant.

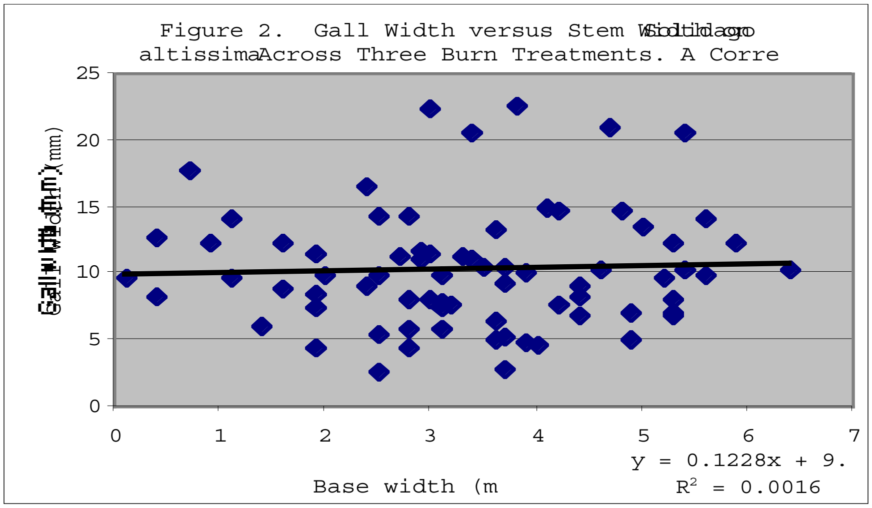


Figure 2. Gall Width versus Stem Width *Solidago altissima* Across Three Burn Treatments. A Corre

Stem width – We found that ramets with galls had narrower basal stems and suspect that this is due to the fact that galls block carbon translocation. McCrea, et al (1985) found that ball-galls on *S. altissima* block normal C translocation (nonmobilizing sink). Consequently, ramets that have ball galls exhibit slower stem growth than ramets without ball galls. We can theorize that this analysis holds for both elliptical and rosette galls. In addition to narrower basal stems, McCrea et al. (1985) found that ramets that are afflicted with galls exhibit lower biomass, propagules, and total production.

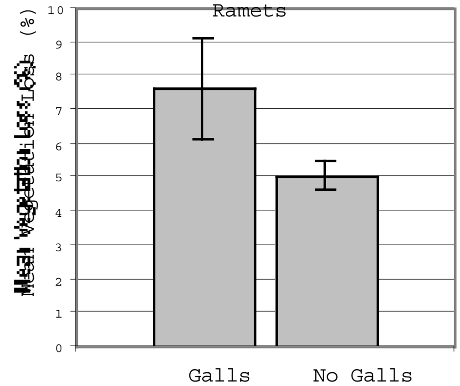
We did not find a significant relationship between the width of the gall and basal stem width (Figure 2). However, Abrahamson and Weis (1997) found that the size of the gall is closely related to the overall growth of the ramet, because larger galls block and intercept more resources than do smaller galls. Resources are translocated upward through the xylem vessels of the host plant's stem. Therefore, the process of translocation allocates resources away from the base of the stem. It is highly likely that this will result in narrower basal stems on galled plants than ungalled plants, which is as we observed. Meanwhile, organic nutrients produced in leaf cells through photosynthesis move down the stem, through the phloem (Agrios, 1988). These photosynthetic resources, however, are removed from "circulation" by the presence of a stem gall, and do not successfully travel through the base of the stem into the below-ground organs. Thus, the net flow of resources to, and through, the basal stem is reduced by the presence and activity of the gall; galls result in narrower stem growth (Figure 1).

Herbivory - Across all burn treatments, there was a significant difference in mean percentage herbivory (Figure 3). One explanation is that plants with galls attract more insect attack; an alternate hypothesis is that insects choose plants that are more susceptible to insect predation to serve as hosts. Abrahamson and Weis

(1997) proposed that many gall making adult insects choose plants as hosts that serve as a food source for their offspring. These insects select their host plants on the basis of tolerance and ability to repair and regrow damaged structures. They are attracted to plants that have high regrowth rates because these plants can more easily withstand attack by multiple enemies. When a plant is frequently exposed to multiple types of shock (fire, predation, etc.), it becomes more tolerant of such damage (Abrahamson and Weis 1997). Thus damage levels are a likely reflection of a plant's vigor and tolerance. Consequently, we theorize that high herbivory levels on galled plants might reflect the gallmaker's natural selection for plant tolerance.

The gallmaking insect chooses its host plant so that its offspring have the highest probability of surviving. We observed a higher percentage herbivory loss on galled ramets versus ungalled ramets. The insect has natural instinctive mechanisms by which it can tell if a plant will be a good host (Abrahamson and Weis, 1997). The gall concentrates resources from plant in order to ensure food for its developing offspring. One study found relatively high concentrations of nitrogen in gall tissues (Stinner and Abrahamson, 1997). Nitrogen availability to plants increases with herbivory, because of changes caused by plant physiological responses to the loss of vegetation (Holland and Detling, 1990). We speculated that it is possible that mechanisms exist by which a gallmaking insect chooses its host according to its

Figure 3. Mean Percent Vegeta Across Three Burn Types for S altissima in Galled versus U Ramets



susceptibility to herbivory loss. This could account for why there was a higher mean percentage loss in herbivory on galled ramets versus ungalled ramets.

Abrahamson and Weis (1997) suggest that there is a direct correlation between damage levels found on a plant and a plant's level of tolerance to sustain such damage. The ability of *Solidago altissima* to regrow damaged areas is a measure of its tolerance. Reproductive effort is greater in damaged than undamaged plants because they overcompensate for herbivore attack (Abrahamson and Weis, 1997). Despite increased reproductive effort, ramets with galls have narrower stem widths (McCrea, et al. 1985; Figure 1). Paige and Whitham (1987) suggest that plants benefit from herbivore attack, and Abrahamson and Weis (1997) conclude that at intermediate levels of damage expected fitness for a plant species peaks. The peak in expected fitness is beneficial to the gall because of the increased output of production, and we suspect that the narrower stem widths and higher herbivory levels that we observed are beneficial both to the gall and to the plant.

Questions raised – For future study, we suggest that this study be replicated including the categories of plant height, reproductive effort, propagules, biomass, and rhizomes. We also suggest that each data category be taken for the same individuals of *Solidago altissima*, so that data sets can be compared and analyze together, and not separately. Furthermore, we suggest that the data be separated by type of gall, in order to understand the different biological responses of *Solidago altissima* to varying types of galls.

The percent herbivory loss data leads us to ask questions about the gall makers' selection of host plants. We also wondered if it was a precursor to the presence of galls, or whether it was a result of the presence of galls. This question led us to ask about the tolerance of the plant itself and how that plays into the gall maker's preference. We propose uprooting both galled and ungalled individuals of *Solidago altissima* from the field and replanting them in a greenhouse, then performing various tests on the individuals to see how they respond. One such test would involve removing half of the leaves and afterwards measuring at timed intervals the recovery of the plant to that shock.

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