POPULATION ECOLOGY

Gall Wasp (Hymenoptera: Cynipidae) Mortality in a Spring Tallgrass Prairie Fire

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ABSTRACT The life history of the cynipid gall wasp, *Antistrophus silphii* Gillette, leaves it vulnerable to mortality in spring fires in the habitat of its host plant, *Silphium integrifolium* var. *laeve* Torrey and Gray. This article examines the mortality of gall wasp larvae during a prescribed burn at the Konza Prairie Research Natural Area in the tallgrass prairie of northeast Kansas. The three goals of the study were to determine (1) if *A. silphii* galls are most frequently found on the tallest *S. integrifolium* shoots, (2) if there is a relationship between growing season gall height and overwinter lodging, and (3) if gall wasps can survive fire at the heights at which they are found after overwinter lodging. A 1988 survey found that galls were relatively rare on short shoots (<100 cm), were most abundant on middle-length shoots (100–140 cm), and occurred at random on long shoots (>140 cm), suggesting that gall wasps avoided short shoots but that gall placement did not maximize gall height. A 1992 survey found that growing season gall height was not related to overwinter lodging of galled shoots, indicating that any gall wasp shoot selection patterns affecting later gall height were disrupted by winter lodging. Gall wasps placed at post-overwinter lodging heights were unable to survive an experimental fire, but a few gall wasps survived when placed above the range of naturally-occurring gall heights. *A. silphii* and other species with similar life histories must re-establish after fire by immigration, with subsequent population levels affected by indirect effects of fire on host-plant quality.

KEY WORDS *Antistrophus silphii*, fire, mortality

FIRES ARE A NATURAL OCCURRENCE in the tallgrass prairie (Collins & Wallace 1990), where they help determine prairie plant community structure (Gibson & Hulbert 1987). Prescribed fires are a commonly used management tool in cattle ranching operations in the region. Fire has been a consistent presence in grasslands over their roughly 5-million year history on the North American continent (Anderson 1990), so there has been ample opportunity for fire to shape prairie plant–insect interactions.

Herbivorous insect species persist in tallgrass prairies despite periodic fires. However, fires affect insect population densities and community composition. Individual species are affected differently, depending on insect life history; the timing, frequency or intensity of the fire; and changes in the composition, structure, and quality of the vegetation (Evans 1984, Warren et al. 1987, Anderson et al. 1989). Soil insects and winged forms are often least affected by fire (Seastedt & Reddy 1991), but larval or sedentary forms living in parts of vegetation that are aboveground may be highly vulnerable.

Gall insects may be among the most vulnerable of grassland insects to the direct and indirect effects of fire. Many galling species spend much of their life cycle immobilized in galls that may afford little protection from an approaching fire. Gall insects often have univoltine life cycles that are tightly synchronized with the phenology of their host plant (Weis et al. 1988). A fire at the wrong time in the insect's life cycle could disrupt this synchrony and preclude reproduction until the next growing season. In addition to the direct effects of fire, gall insect reproductive success is often highly correlated with host- plant vigor (Craig et al. 1986, Price et al. 1987). Thus, if host-plant growth is reduced by fire, the survivorship or fecundity of the gall insects on that host could be reduced.

In this article, we examine the direct effects of a spring fire in a tallgrass prairie on a gall-insect's survivorship. The cynipid wasp, *Antistrophus silphii* Gillette, galls wholeleaf rosinweed, *Silphium integrifolium* var. *laeve* Torrey and Gray (Asteraceae). *A. silphii* forms a spherical gall on growing shoot tips. Galls range from 1 to 4 cm in diameter and contain up to 20 larvae. *A. silphii* is highly vulnerable to fire because it occupies the gall for a full year, from its initiation in early May until adult gall wasps emerge the following May. The greatest danger to these galls occurs during spring, when natural fires in tallgrass prairies are thought to be most frequent (Hulbert 1973) and when most ranchers and land managers in eastern Kansas tallgrass prairies conduct prescribed burns.

Because of *S. integrifolium's* growth form and the location of galls on the plant, *A. silphii* might avoid death in a fire by placing galls on more vigorous shoots. *S. integrifolium* shoots grow vertically from a woody rhizome, and galls remain at the tip of the shoot as it elongates. Although galls reduce shoot height an average of ≈20% (Fay & Hartnett 1991), galls on more vigorous shoots will be higher off the ground than on less vigorous shoots, potentially protecting them from passing fire. However, shoots are subject to overwinter lodging. Thus, the height of a gall going into a spring fire could be different from its original height during the growing season, negating any shoot selection behavior designed to maximize the height of a gall.

The three goals of the study were to determine: (1) if *A. silphii* galls are most frequently found on the tallest *S. integrifolium* shoots, (2) if there is a relationship between growing season gall height and overwinter lodging, and (3) if gall wasps can survive fire at the heights at which they are found after overwinter lodging.

This study was conducted in an annually burned old field at the Konza Prairie Research Natural Area, a 3,487-ha site near Manhattan in the Flint Hills region of northeastern Kansas (39°05′N, 96°35′W). An experimental regime of prescribed burning is conducted annually at Konza Prairie during April, before the vegetation becomes active. Insect galls are a frequently occurring but little-studied component of the tallgrass prairie fauna. To date, galls have been found on 40 plant species on Konza Prairie. Long-term population monitoring is finding that fire plays an important role in prairie gall-insect population dynamics. Gall-insect populations are depressed the year after a fire but steadily increase in succeeding years until they are lowered by a subsequent fire (D. C. Hartnett and P.A.F., unpublished data).

Materials and Methods

Shoot Length and Gall Distributions. During the 1988 growing season, the *S. integrifolium* shoot population was surveyed to determine whether or not galls are most frequently found on the tallest (=most vigorous) *S. integrifolium* shoots. Shoot height was measured after shoot elongation was complete (late July) on 1,062 randomly chosen shoots, 450 of which were galled, in 38 heavily galled plants. Ungalled shoot heights were measured directly, and the potential height of a galled shoot, had it remained ungalled, was estimated from the shoot's ground-level diameter. This parameter is a good estimator of growth potential because it is linearly related to shoot height in ungalled shoots (R^2 = 89%) and because shoot diameter is unaffected by the presence or absence of a gall (P.A.F., unpublished data). Shoot lengths were grouped at 20-cm intervals and presented as frequency distributions and as the percent of shoots galled.

For statistical analysis, shoot lengths were divided into three larger height groups: <100 cm, 100–140 cm, and >140 cm. The frequency distribution of galled shoot lengths was tested against the distribution of all shoot lengths in the population (galled + ungalled), using a χ^2 test.

Growing Season Gall Height Versus Overwinter Lodging. Gall heights after overwinter lodging were surveyed on 548 randomly chosen galled shoots in March and early April 1992. Lodging was characterized by the angle of the galled shoot with respect to the ground and by the gall's lodged height. Both ways of describing lodging were used because a short shoot and a long shoot lodged to the same angle could have considerably different gall heights. Lodging angle was calculated from stem length and the vertical distance from gall to ground.

Gall Height Versus Gall Wasp Survival. After the gall height versus lodging survey, a 20-ha field site where *S. integrifolium* is attacked by *A. silphii* was burned to see if gall wasps in galls at typical lodged heights could survive a spring fire. Galls (n = 160) containing soon-to-emerge gall wasps were collected from the site the day before it was burned and attached at four heights (0, 45, 90, and 135 cm off the ground) on each of 40 metal conduit posts. The posts were placed at 2-m intervals in a 4 by 10 post grid. Gall heights up to 90 cm were typical of lodged gall heights. Galls were placed at 135 cm to see if gall wasps could survive fire above the typical range of gall heights. An additional 20 galls were collected to serve as unburned controls. These galls were held outside with the experimental galls until the site was burned.

The site was burned at approximately 1130 h on 22 April 1992. The air temperature was 10.5°C, relative humidity was 38%, and wind speed was 4.4 m/s. Control and burned galls were returned to the lab immediately after the fire, and gall wasps were allowed to emerge under ambient laboratory conditions.

The temperatures experienced by galls during the fire were recorded using 15 temperature-indicating paints (Tempilaq, Omega Engineering, Stamford, CT) applied to ceramic tiles hung with each gall. Each paint melted to indicate a specific temperature between 38 and 550°C. This method has been successfully used in detailed studies of fire temperatures at Konza Prairie (Gibson et al. 1990) and provides a good estimate of the temperature profile at various heights off the ground.

This experiment was analyzed as a randomized complete-block design. The gall was the experimental unit, each metal post was consid-

Table 1. Frequencies of shoots galled by *A. silphii* and all (galled + ungalled) shoots in the *S. integrifolium* shoot population surveyed in 1988

Shoot length	All shoots	Galled shoots			
		Attack rate (%)	No. observed	No. expected	χ^2
<100 cm	314	21.02	66	133.05	33.7896
100–140 cm	526	55.14	290	222.88	20.2131
>140 cm	222	42.34	94	94.07	0.0001
Total	1,062	42.37	450		54.0028

These data are derived from Fig. 1, with shoot length grouped into three larger categories.

ered a block, and gall height was the treatment factor.

Results

Shoot Length and Gall Distributions. Overall, 42% of the surveyed shoots were galled (Table 1). Short shoots (<100 cm) were less frequently galled (21%), and middle length shoots (100–140 cm) were more frequently galled than expected (55%, χ^2 = 54.0028, P < 0.001, Table 1; Fig. 1). These two shoot-length categories accounted for almost all of the overall χ^2 for these distributions because longer shoots (>140 cm) were galled almost exactly as often as expected if they were attacked at random (42%, Table 1). This is also seen in the nearly exact match of the galled shoot length distribution with the expected distribution for shoots >140 cm (Fig. 1). These data suggest that gall wasps avoided short shoots, but that their oviposition behavior did not maximize gall height.

Growing Season Gall Height Versus Overwinter Lodging. There was no relationship between growing season gall height and winter lodging in galled shoots. Growing season gall height (Fig. 2) ranged from 40 to 120 cm. Although some unlodged galled shoots could be found, the majority of galled shoots lodged to some extent (Fig. 2), and 75% of the galls were found below 50 cm off the ground. There was no relationship between growing season gall height and lodged gall height or angle after lodging (Figs. 3 and 4). This indicates that any gall wasp shoot selection affecting later gall height was disrupted by winter lodging.

Spring Gall Height and Gall Wasp Fire Survivorship. Not all galls were recovered after the fire. Out of 40 galls at each height, 4 galls were lost at 0 cm, 36 at 45 cm, 26 at 90 cm, and 21 at 135 cm. Some lost galls could not be found and were probably incinerated, while others were found scattered on the ground but their height assignment could not be determined. Galls have been commonly found on the ground after fire during previous burns, and such galls contain no surviving gall wasps (P.A.F., unpublished data). Thus, zero was recorded for survivorship for all lost galls.

Temperatures during the fire were lowest at 0 cm and 135 cm, highest at 45 cm and intermediate at 90 cm ($F_{3,117}$ = 41.89, P < 0.0001, Fig. 5). The pattern of gall loss generally corresponded to this temperature profile. However, despite equal temperatures during the fire, more galls were recovered at 0 cm than at 135 cm because 0 cm galls were not scattered by the fire.

From the recovered galls, 4 gall wasps emerged from one gall at 135 cm. In comparison,

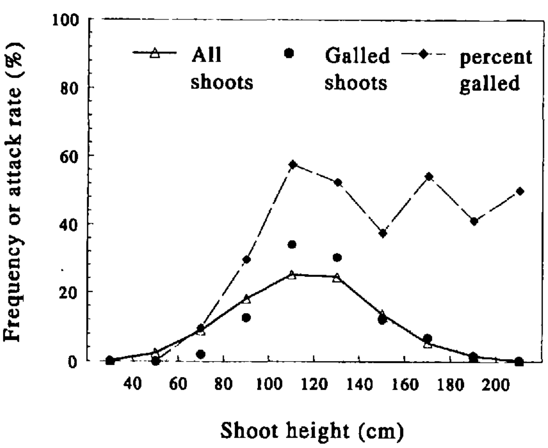

Fig. 1. Shoot height distributions and attack rates of *A. silphii* galls on *S. integrifolium* shoots in 1988. Plots show frequency distributions (%) for shoot heights from the galled shoot population (n = 450) and all (galled + ungalled) shoots (n = 1,062), and the attack rate (=percentage of shoots galled) for each shoot height.

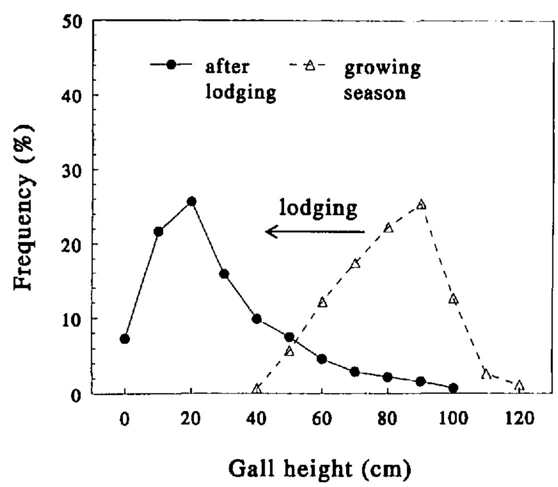

Fig. 2. Frequency distributions of growing season gall heights and gall heights after overwinter lodging. These dimensions are defined in the inset of Fig. 3. The height distribution after lodging was the range of heights in the natural gall population when the study site was burned.

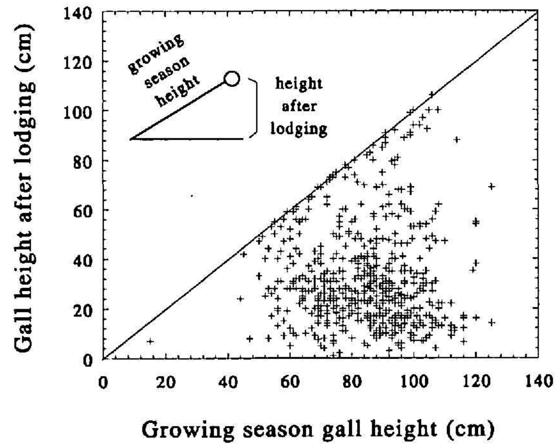

Fig. 3. Lodged gall height versus growing season gall height. The diagonal line indicates where lodged height = growing season gall height, i.e., unlodged shoots. $y = 0.04x + 29.94$, $R^2 = 0.0007$.

12.90 ± 1.32 wasps per gall emerged from the unburned control galls. These data show that there was virtually no chance for gall wasps to survive the fire except at heights greater than were observed in the gall population just before the fire occurred.

Discussion

A. silphii was unable to survive fire, except at heights above where galls were found in the population. A few galls, such as the large woody galls formed by some Coccoidea in Australian eucalypt forests, may be adaptations to tolerate fires (Koteja 1986). However, the spherical gall formed by *A. silphii* on *S. integrifolium* affords no such protection. Selection for the most vigorous shoots, a common feature in other gall insects (Whitham 1978, Craig et al. 1986, Price et al. 1987, Caouette & Price 1989), was not found

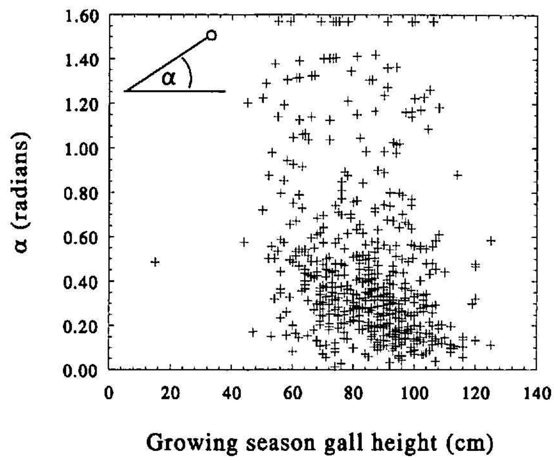

Fig. 4. Galled shoot angle with respect to horizontal versus growing season gall height.

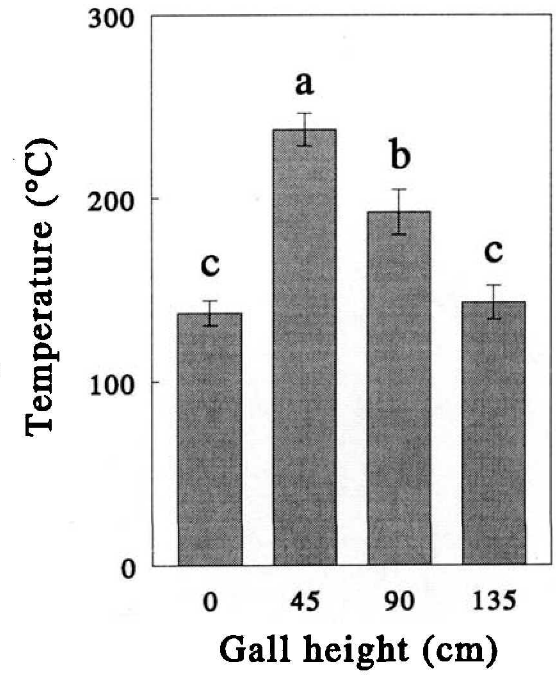

Fig. 5. Vertical temperature profile during the controlled fire. Means (±1 SE) with different letters are significantly different by the Student-Neuman-Keuls multiple separation procedure.

and would have been an ineffective means of increasing gall height because overwinter lodging disrupted any relationship between shoot vigor and later gall height.

The survivorship of a few gall wasps at 135 cm was surprising because the fire on this site was a headfire, a large, fast fire moving with the wind. Temperatures measured in the fire were typical of fire temperatures on similar sites at Konza Prairie reported by Gibson et al. (1990). Gall wasp survivorship would probably have been higher in a backfire, a much smaller, slower fire moving against the wind. Gibson et al. (1990) reported that temperatures in backfires were half that of headfires, so that under backfire conditions, galls high off the ground could be at an important advantage. However, it seems unlikely that fire intensity could selectively favor gall wasp preference for taller shoots because in addition to the problem of lodging, fire intensity is probably a random factor from year to year.

Gall wasp habitat selection based on factors other than shoot height might be a more effective means of avoiding fire mortality. When *S. integrifolium* grows in large, dense patches there tends to be little accumulation of fuel (standing dead grass, etc.), and there is often little or no fire in such patches. Galled shoots in which gall wasps have successfully emerged can be found in such patches after a fire (P.A.F., personal observation). Gall wasp preference for large host-plant patches would be selectively favored in populations subject to periodic fire.

Because fire can cause catastrophic gall wasp mortality, gall wasp immigration is a critical factor in local gall wasp population dynamics. The proximity of other *S. integrifolium* populations will determine the likelihood of new migrants finding a burned *S. integrifolium* population, and the frequency of fire will determine what immigration rate is necessary to re-establish gall wasp populations. *A. silphii* appears vulnerable to local extinction, especially in land managed with annual burning for cattle production or brush control. Other insects with similar life histories would be equally vulnerable.

This study did not address indirect consequences of fire, which also influences grassland plant–insect interactions. Preliminary results from an ongoing project on the population trends in gall insects over several years following fire (D. C. Hartnett & P.A.F., unpublished) show that gall populations are depressed in the growing season following a spring fire but that these populations increase in each following year. This pattern may be attributed to a mixture of direct mortality such as we have shown for *A. silphii*, and indirect effects. The effect of fire on the quality of *S. integrifolium* as a host plant is not known. Other authors suggest that fire changes microclimate, host-plant growth responses, and host-plant abundance for herbivorous insects (Evans 1988a, b, Bock & Bock 1991, Seastedt et al. 1991). For example, fire-induced changes in grasshopper communities documented by Evans (1984, 1988a, b) are at least partly attributable to changes in the relative abundance of grasses and forbs. For *A. silphii*, these indirect effects will assume increasing importance in gall wasp population recovery in future growing seasons, with fire and immigration effects being most important in determining gall wasp populations the year of a fire.

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