

PLANT AND PREDATOR EFFECTS ON INTERPLANT MOVEMENT BY THE GLASSY-WINGED SHARPSHOOTER

Project Leaders:

Christine Armer and Sharon Strauss
Ecology and Evolution
University of California
Davis, CA 95616

Cooperator:

David Morgan
California Dept. of Food and Agriculture
Mount Rubidoux Field Station
Riverside, CA 92501

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ABSTRACT

Adult GWSS in caged habitats were monitored hourly to determine the effects of plant species availability and predator presence on intra- and inter-plant movement, as these factors are directly related to the acquisition and spread of Pierce's Disease. GWSS were placed in caged habitats with either a monoculture of beans or polyculture of bean, sunflower, and tree tobacco, and either with or without spiders, in a 2x2 factorial design. Origin of the GWSS (field-caught or laboratory-reared) was also included as a third factor in the multi-factor MANOVA to determine the importance of each treatment on GWSS feeding, resting, and intra- and inter-plant movement. Approximately 85-90% of the day was spent feeding or resting on plants. Only 0.5-1.5% of the observations recorded flying GWSS, and another 1-2% found GWSS walking between plants. More insects moved between plants in the mixed-plant cages than in the bean-only cages, suggesting the GWSS are able to detect the presence of other species of plants in the vicinity. This increase in interplant movement would probably correspond to an increase in Pierce's disease transmission. Field-collected insects spent less time feeding and more time resting on plants than did laboratory-reared insects. Both sets of insects spent more time feeding in bean-only cages than in mixed-plant cages. Beans may not have provided optimal nutrients, and GWSS may have moved to other plants to supplement nutrient intake. GWSS fed on sunflower and tobacco readily, although preferences have not yet been calculated. No predator-mediated spread of Pierce's Disease is expected to occur, as the presence, activity levels, and predation by spiders had no effect on GWSS behavior. Further analysis of feeding times and movement between plant species may clarify the relative importance of toxin dilution (nicotine from tree tobacco) and nutrient balancing from bean and sunflower plants.

INTRODUCTION

The glassy-winged sharpshooter (GWSS) *Homalodisca coagulata* Say, is primarily of economic importance because it vectors the Pierce's disease-causing bacterium, *Xylella fastidiosa* (Blua et al. 1999). The insect feeds on hundreds of species of plants (Adlerz 1980; Hoddle et al. 2003), many of which harbor asymptomatic populations of *X. fastidiosa* (Purcell and Hopkins 1996). Every time a GWSS moves to a new plant to feed, the chances of acquiring and transmitting Pierce's Disease increase. Therefore, the factors causing GWSS to move between plants are directly related to the spread of Pierce's disease.

Generalist herbivores such as the GWSS may move to new plants to balance nutrients, to avoid intra- or inter-specific competition, to dilute plant defensive toxins, or to avoid predation. GWSS feeds primarily, if not exclusively, on the xylem, where nutrients are very dilute (Andersen et al. 2003). The nutritional requirements of GWSS have been determined (Andersen et al. 1992; Brodbeck et al. 1996), and only cowpea and soybean have been found to reliably sustain GWSS throughout a complete generation (D.J.W. Morgan, pers. comm.; Brodbeck et al. 1999). However, why GWSS move between plants, especially when a nutritionally adequate host such as bean is available, is unknown. Interspecific competition is rarely a concern for GWSS, as few other organisms feed on the xylem on the host plants on which GWSS can feed. Intraspecific competition may occur, as GWSS move off plants when present in very high densities (Armer, pers. obs.), but these densities will not occur frequently when biological control is in place. Plant defensive compounds are not common in the xylem (Raven 1983), but alkaloids and quinones are present in certain plant families and may be more prevalent than scientists have previously expected. For example, solanaceous plants carry defensive compounds from synthesis sites in the roots to the leaves via the xylem. Tree tobacco is one such solanaceous plant, which contains nicotine in the xylem. Finally, predators may affect herbivore behavior, as some herbivores can detect and respond to the presence of predators by halting feeding or altering host plant selection (Schmitz et al. 1997; Schmitz and Suttle, 2001). Alternately, an herbivore that moves frequently between plants to optimize feeding may be more apparent to visual predators.

OBJECTIVE

Determine the effect of plant species variety and predators on GWSS interplant movement.

RESULTS

Caged habitats of 0.56m² contained 6 plants in soil. Plants and predators were set up in a 2x2 factorial design, with either a monoculture (all bean plants) or polyculture (2 bean, 2 sunflower, and 2 tree tobacco plants) and with or without spiders. Sixteen adult GWSS were placed in each cage and their location and behavior were monitored every hour throughout as daylight was available, for 10-14 hours. The behaviors are shown on the x-axis of Figure 1. The percent of adult GWSS in a cage performing each activity was averaged over all hours observed. The data were compared by a 3-factor MANOVA (SAS

v.8) for differences due to the plant availability (beans-only or mixed plants), spiders (presence or absence), and whether the GWSS were field-collected as adults or lab-reared. Adults that had been reared from birth only on bean plants in laboratory colonies were used in 27 cages, and GWSS that had been captured in the wild as adults were used in 9 cages. One behavior was omitted from the analysis to allow independence of the observations (see Cisneros and Rosenheim 1998).

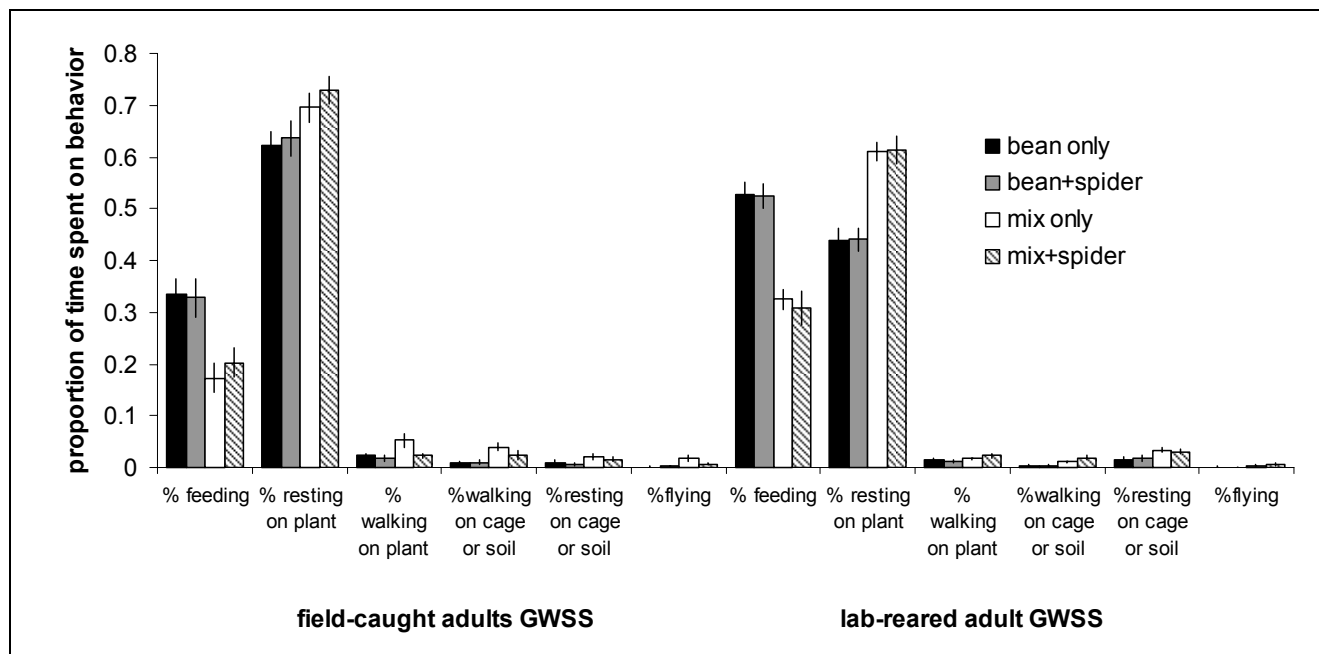


Figure 1. Behaviors performed by caged GWSS adults observed during daylight hours. The average time spent by individuals in each cage on each behavior is shown; error bars indicate standard error.

GWSS spent nearly all of their time either feeding or resting on plants (Figure 1). About 2-5% of the time was devoted to walking on a plant, 1-5% to walking on the cage or soil, 2-5% to resting on the cage or soil, and 0-2% to flying. Plant treatment (bean-only or mixed species) affected all behaviors ($F=13.87$, $df=5,132$, $P<0.0001$). Individuals on beans spent more time feeding and less time resting than insects did on plants in mixed-species cages. Field-caught insects varied significantly from laboratory-reared individuals in their behaviors ($F=16.20$, $df=5, 132$, $P<0.0001$), feeding less and resting more than laboratory insects. However, both groups of insects showed similar time budgets. Both spent less time feeding on beans than on mixed plants. However, lab-reared insects spent less time resting than feeding on beans, and field-reared insects rested more than feeding on beans. This interaction between plant treatment and insect origin (field-caught vs. lab-reared) was significant ($F=2.58$, $df=5,132$, $P=0.029$). Both plant treatment and insect origin significantly affected all insect behaviors at the $p=0.01$ level or greater.

Interplant movement, either by walking or by flying, was higher in the mixed-species cages. GWSS also spent more time resting on the cage or on the soil in the mixed-plant treatment cages, although such a small amount of time was spent in this behavior that it was probably not biologically significant. However, the increase in movement between plants in the mixed cages, although small, is significant in that such behavior increases the GWSS' opportunities to acquire and transmit Pierce's disease.

The three plant species were selected because one provided a host on which GWSS can complete multiple generations (bean), one was an alternate host favored in the field (sunflower), and the final plant contains potentially toxic nicotine in the xylem (tree tobacco), and so may be preferentially avoided. All three plant species were used as host for feeding, but the amount of time spent feeding on each species has not yet been calculated. Both the time spent feeding, and the frequency of leaving each species of plant, will indicate the GWSS' preference for the 3 species.

The presence of spiders did not affect GWSS behaviors ($F=1.08$, $df=5, 132$, $P=0.376$). There were no interactions between spiders and plant species or origin of GWSS. Spiders used in the experiments were field-collected, and the species changed as the season progressed. Predation activity also varied within species, perhaps due to hunger levels of each individual. The presence of spiders did not affect GWSS, but wide variation in spider activity level might hide predation effects. We therefore examined spider activity levels (% of observations in which the spider moved), based on intra- and inter-plant movements, to correlate predation pressure to GWSS movement and feeding behavior. GWSS did not show a behavioral response to spider activity levels (spider activity not correlated to GWSS time spent feeding, moving on the same plant, resting on the plant, moving on the soil or cage, flying) in either plant treatment, nor was the number of GWSS eaten related to spider activity (all non-significant in direct regressions). The spiders were equally active in the two plant treatments,

moving an estimated $28 \pm 3\%$ (mean \pm SE) of the observation period in both treatments. Spiders in the bean treatment caught and fed on 0.22 ± 0.07 GWSS per day, whereas those in the mixed-plant treatment fed on 0.33 ± 0.09 GWSS. All GWSS were sexed after observation, and data were examined for possible behavioral differences. However, there were no differences between the sexes in terms of their behavior (MANOVA with sex and plant-spider treatment as the factors; $F=1.29$, $df=5,276$, $p=0.27$).

CONCLUSIONS

The availability of multiple plant species increased GWSS interplant movement, and feeding times were reduced in these cages, suggesting GWSS 1) can detect the presence of other host species in the vicinity, probably through olfaction, and 2) that diet-mixing helps GWSS obtain needed nutrients more rapidly. However, the increased movement between plants also may correspond to an increased acquisition and spread of the bacterium that causes Pierce's Disease. The effects of potentially toxic plants, such as tree tobacco, are not currently understood on GWSS interplant movement. Further data analysis should help clarify the insects' response. Spiders did not affect GWSS feeding and intra- and inter-plant behavior in the observations described here. Thus, these (and possibly other arthropod) predators should not affect the GWSS' acquisition and spread of Pierce's Disease.

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