VOLATILE COMPOUNDS INDUCED BY HERBIVORY ACT AS AGGREGATION KAIROMONES FOR THE JAPANESE BEETLE (Popillia japonica NEWMAN)

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Abstract—The Japanese beetle is a polyphagous insect that typically aggregates on preferred host plants in the field. We studied the response of Japanese beetles to artificial damage, fresh feeding damage, and overnight feeding damage to test the hypothesis that beetles are attracted to feeding-induced volatiles. Crabapple leaves that had been damaged overnight by Japanese beetles or fall webworms attracted significantly more Japanese beetles than did undamaged leaves. Artificially damaged leaves or leaves freshly damaged by Japanese beetles, however, were not significantly more attractive than undamaged leaves. Leaves that had been damaged overnight by Japanese beetles or fall webworms produced a complex mixture of aliphatic compounds, phenylpropanoid-derived compounds, and terpenoids. In comparison, artificially damaged leaves or leaves with fresh Japanese beetle feeding damage generated a less complex blend of volatiles, mainly consisting of green-leaf odors. Feeding-induced odors may facilitate host location and/or mate finding by the Japanese beetle.

Key Words—Popillia japonica, Coleoptera, Scarabeidae, apple, Malus × domestica, attractant, induction, plant–insect interaction, semiochemical, terpene.
INTRODUCTION

Odors induced by arthropod herbivory on higher plants have recently been implicated as attractants of predators and parasitoids (Turlings et al., 1990). In the cases so far examined, volatiles were induced by arthropod feeding in a delayed manner, and the induced odors were typically a complex blend of aliphatics, terpenoids, and/or phenylpropanoid-derived compounds. The induced blends are often floral in character, which may increase the likelihood of predation on lepidopteran larvae in that many adult parasitic Hymenoptera are dependent on nectar for food (Leius, 1960).

Little is known, however, about the effects of these induced volatiles on the herbivores themselves. Still, evidence has been obtained for the additive or synergistic effects of host volatiles along with sex pheromones on insect aggregation. For example, female mountain pine beetles, *Dendroctonus ponderosae* Hopkins, convert the host-produced monoterpene α-pinene into trans-verbenol, which is an aggregation pheromone for this species. Verbenone, which is produced by microbial symbionts of *D. ponderosae*, serves as an anti-aggregation pheromone and terminates mass attacks on individual host trees (Borden, 1984; Hunt and Borden, 1990). In another example, fruit volatiles released by feeding of the green June beetle, *Cotinis nitida* L., were shown to be highly attractive to other green June beetles (Domek and Johnson, 1988). To our knowledge, however, no studies have examined feeding-induced volatile compounds from the leaves of woody angiosperms and their effect on aggregation of herbivorous insects.

The adult Japanese beetle (*Popillia japonica* Newman: Scarabaeidae) is a highly polyphagous insect that feeds upon nearly 300 plant species in 130 families (Fleming, 1972). Since its accidental introduction into New Jersey about 80 years ago, the beetle has become one of the most destructive pests of shade trees, fruit and vegetable crops, and ornamental plantings in the eastern United States. One of the more curious aspects of this insect's behavior is its tendency to congregate on individual hosts, often nearly defoliating them, while other suitable hosts in the vicinity often suffer only minimal damage (Van Leeuwen et al., 1928; Fleming, 1972). Males of this species are strongly attracted to the female sex pheromone, (Z)-5-(1-decenyl)-dihydro-2-(3H)-furanone (Tumlinson et al., 1977), but this alone cannot explain the aggregative behavior because females are normally mated on the ground at emergence, and mated females do not attract males at long range (Ladd, 1970). This has led to speculation of an aggregation pheromone (Adler and Jacobson, 1971; Iwabuchi and Takahasi, 1983).

We speculated that volatile compounds induced by feeding on leaves could act as aggregation kairomones for the Japanese beetle. The present study using