HERBIVORY INDUCES SYSTEMIC PRODUCTION OF PLANT VOLATILES THAT ATTRACT PREDATORS OF THE HERBIVORE: EXTRACTION OF ENDOGENOUS ELICITOR

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Abstract—It was previously shown that in response to infestation by spider mites (Tetranychus urticae), lima bean plants produce a volatile herbivore-induced synergone that attracts phytoseiid mites (Phytoseiulus persimilis) that are predators of the spider mites. The production of predator-attracting infochemicals was established to occur systemically throughout the spider mite-infested plant. Here we describe the extraction of a water-soluble endogenous elicitor from spider mite-infested lima bean leaves. This elicitor was shown to be transported out of infested leaves and was collected in water in which the petiole of the infested leaf was placed. When the petioles of uninfested lima bean leaves were placed in water in which infested leaves had been present for the previous seven days, these uninfested lima bean leaves became highly attractive to predatory mites in an olfactometer when an appropriate control of uninfested lima bean leaves was offered as alternative. The strength of this effect was dependent on the number of spider mites infesting the elicitor-producing leaves. Higher numbers of spider mites resulted in an elicitor solution with a stronger effect. In addition, spider mite density was important. The elicitor obtained from one leaf with 50 spider mites had a stronger effect on the attractiveness of uninfested leaves than the elicitor obtained from three leaves with 17 spider mites each. This suggests that the stress intensity imposed on a plant is an important determinant of the elicitor quantity. While the elicitor has a strong effect on the attractiveness of uninfested leaves, spider mite-infested leaves are still much more attractive to predatory mites than elicitor-exposed leaves. The data are discussed in the context of systemic

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effects in plant defense and the biosynthesis of herbivore-induced terpenoids in plants.


**INTRODUCTION**

One of the defense options of plants is to promote the effectiveness of natural enemies of herbivores (Price et al., 1980). This may be accomplished by attracting the enemies of the herbivores by volatile infochemicals whose production in the plant is induced by herbivory (Dicke and Sabelis, 1988a; Dicke et al., 1990a; Turlings et al., 1990b; Vet and Dicke 1992); these infochemicals were termed herbivore-induced synomones (Vet and Dicke, 1992). Upon infestation by two-spotted spider mites (*Tetranychus urticae*), lima bean plants and cucumber plants emit large amounts of a blend of volatile chemicals that attract the predatory mite *Phytoseiulus persimilis*, which can exterminate *T. urticae* populations (Dicke and Sabelis, 1988a; Dicke et al., 1990a,b). Similarly, corn plants that are infested by beet armyworm larvae (*Spodoptera exigua*) emit a blend of volatiles that attract the parasitic wasp *Cotesia marginiventris* (Turlings et al., 1990b, 1991). The plant has an active role in this process, and the chemicals that are emitted upon herbivory are either not emitted upon artificial damage or only in minute quantities (Dicke et al., 1990a,b; Turlings et al., 1990b, 1991). Moreover, the herbivore-induced synomones seem to be rather specific: the natural enemies discriminate between different plant-herbivore combinations (Sabelis and Van de Baan, 1983; Dicke, 1988; Dicke and Groeneveld, 1986; Sabelis and Dicke, 1985; Turlings et al., 1990a) and chemical differences between blends emitted by different plant-herbivore combinations have also been recorded (Dicke et al., 1990b; Takabayashi et al., 1991b).

The active role of the plant in the production of these volatile infochemicals has been inferred from two observations: the plant has a more pronounced influence on the composition of the chemical blend than the herbivore (Takabayashi et al., 1991b) and, more importantly, the production of volatile infochemicals that attract natural enemies of herbivores is not restricted to the infested plant parts but occurs systemically throughout the plant [Dicke et al., 1990b; Turlings and Tumlinson, 1992; note that Nadel and Van Alphen (1987) provide a similar conclusion but that their data are not convincing because they did not control for adsorption of infochemicals from the infested leaves onto the uninfested leaves of the same plant].

For several plant-herbivore and plant-pathogen interactions infestation-