TOXICITY OF LINEAR FURANOCOUMARINS TO
Spodoptera exigua: EVIDENCE FOR ANTAGONISTIC INTERACTIONS

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Abstract—The linear furanocoumarins psoralen, bergapten, and xanthotoxin were tested for toxicity to the beet armyworm Spodoptera exigua (Hübner) under short ultraviolet (UVB) radiation. Increased dietary concentrations of each furanocoumarin significantly decreased insect larval weight, extended generation time, and induced higher mortality. Xanthotoxin was the most toxic, followed by psoralen and bergapten. Combining psoralen with bergapten, xanthotoxin, or both resulted in significantly antagonistic effects on insect mortality. The combination of bergapten and xanthotoxin, however, produced additive effects. The implications of these observations for S. exigua resistance in the wild plant accession of Apium prostratum and the enigma the findings represent for plant–insect relationships are discussed.

Key Words—Spodoptera exigua, Lepidoptera, Noctuidae, psoralen, 5-methoxypsoralen, 8-methoxypsoralen, furanocoumarins, antagonistic toxicity, plant–insect interactions, Apium prostratum.

INTRODUCTION

The linear furanocoumarins are plant secondary compounds that have been isolated from members in a number of plant families including Rutaceae, Apiaceae, Compositae, Leguminosae, Moraceae, Pittosporaceae, Solanaceae, and Thy-
meaceae (Scott et al., 1976; Murray et al., 1982). These compounds are photosensitizers (Igali et al., 1970; Zangerl and Berenbaum, 1987) and have shown toxicity against a broad spectrum of animals (Berenbaum, 1978; Berenbaum and Neal, 1985; Trumble et al., 1991). Because of this toxicity, it has been suggested that the linear furanocoumarins can play an important role in plant–herbivore interactions (Berenbaum, 1978; Berenbaum and Feeny, 1981; Trumble et al., 1991).

The major linear furanocoumarins isolated from *Apium* species are psoralen, bergapten (5-methoxypsoralen), and xanthotoxin (8-methoxypsoralen) (Trumble et al., 1990). These compounds were toxic to the beet armyworm *Spodoptera exigua* (Hübner) when combined in artificial diet (psoralen 15 μg/ml diet + bergapten 38 μg/ml diet + xanthotoxin 82 μg/ml diet) during assays exposed to 350 μW/cm² UVB radiation (Trumble et al., 1991). Diawara et al. (1992) reported higher concentrations of these furanocoumarins in the *S. exigua*-resistant wild *Apium prostratum* ssp. *prostratum* than the susceptible celery *A. graveolens*. However, *A. prostratum* resistance was primarily non-preference based, and additional studies designed to test furanocoumarin-free plant extracts for insect preference suggested that the resistance was not only furanocoumarin-induced. Subsequent studies found no significant correlation between *S. exigua* resistance in celery breeding lines and linear furanocoumarin concentrations (Diawara et al., 1993). Therefore, the potential role of these linear furanocoumarins in the *A. prostratum–S. exigua* relationship is not clearly defined. We initiated this study to compare three linear furanocoumarins (psoralen, bergapten, and xanthotoxin) for toxicity against *S. exigua* and to determine the additive, synergistic, or antagonistic effect of their combinations. Information on the relative toxicity of these different linear furanocoumarins to herbivores, when ingested alone or in combination, will improve our understanding of the role of these compounds in plant–herbivore interactions.

**METHODS AND MATERIALS**

The three linear furanocoumarins psoralen, bergapten, and xanthotoxin were obtained from Aldrich Chemical Company (Milwaukee, Wisconsin). *S. exigua* larvae were from a colony less than 1 year old maintained on artificial diet (Shorey and Hale, 1965) at 27 ± 2°C and 16:8 hr light–dark photoperiod. Activity of the three linear furanocoumarins against *S. exigua* was determined in a two-phase experiment conducted between April 1991 and May 1992.

**Experiment I: Toxicity of Individual Furanocoumarins.** Seven concentrations of each of the three linear furanocoumarins were tested: 0 (control), 62.5, 125, 250, 375, 500, and 750 μg/g diet. This range, which was chosen following pilot studies of toxicity, includes the total concentration range of 0 to 406