THE "RAISON D'ÊTRE" OF PYRROLIZIDINE ALKALOIDS IN Cynoglossum officinale: DETERRENT EFFECTS AGAINST GENERALIST HERBIVORES

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Abstract—In this study we tested whether pyrrolizidine alkaloids (PAs) of Cynoglossum officinale serve as antifeedants against herbivores. Total PA N-oxide extracts of the leaves significantly deterred feeding by generalist herbivores. Specialist herbivores did not discriminate between food with high and low PA levels. Three PAs from C. officinale, heliosupine, echinatine, and 3'-acetylechinatine, equally deterred feeding by the polyphagous larvae of Spodoptera exigua. Although the plants mainly contain PAs in their N-oxide form, reduced PAs deterred feeding by S. exigua more efficiently than PA N-oxides. On rosette plants, the monophagous weevil Mogulones cruciger significantly consumed more of the youngest leaves, which had the highest PA level and the highest nitrogen percentage. Larvae of Ethmia bipunctella, which are oligophagous within the Boraginaceae, did not discriminate between leaves. All generalist herbivores tested significantly avoided the youngest leaves with the highest PA levels. In the field, the oldest leaves also were relatively more damaged by herbivores than the youngest leaves. It is hypothesized that the skewed distribution of PAs over the leaves of rosette plants reflects optimal defense distribution within the plant.

Key Words—Cynoglossum officinale, Boraginaceae, pyrrolizidine alkaloids, chemical defense, specialist herbivores, generalist herbivores, Ethmia bipunctella, Mogulones (Ceutorhynchus) cruciger, Spodoptera exigua, Helix aspersa, Frankiniella occidentalis, Locusta migratoria, Lyriomyza trifolii.

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INTRODUCTION

Like philosophers who search for the meaning of life, chemical ecologists look for the "raison d'être" of secondary plant substances (Fraenkel, 1959) or, more specifically, alkaloids (Wink, 1993). Pyrrolizidine alkaloids (PAs) are mainly found in the Asteraceae and the Boraginaceae (Hartmann, 1991). Although the toxicity of PAs to vertebrates has been well documented (Greimer, 1900; Mattocks, 1986; Anonymous, 1989; Wink, 1993), their role as defenses against insect herbivores is less clear. It is often assumed "intuitively" (Wink, 1993) that PAs protect the plant against insect herbivores as well, although evidence for this assumption is sparse (Hartmann, 1991) and even contradictory (see Bentley et al., 1984).

Plants containing PAs still can suffer considerable herbivore damage. In the first place, the plants can be damaged by specialist herbivores that have adapted to PAs (Prins and Nell, 1990; Van der Meijden et al., 1991). Secondly, the total PA content may not be related to herbivory, because the different types of PAs in the plant are not equally deterrent (Bentley et al., 1984; Dreyer et al., 1985; Speiser et al., 1992). Thirdly, some plant parts contain less PAs than others (Hartmann and Zimmer, 1986; Hartmann et al., 1989; Van Dam et al., 1994).

In order to generate a hypothesis on the role of PAs in the feeding behavior of herbivores on the whole plant, we have to consider both the plant’s and the herbivore’s point of view. Young leaves are more valuable for the plant than old leaves, because they have the highest photosynthetic rates and the longest life expectancy (Harper, 1989). Meanwhile, young leaves are more attractive for herbivores (Hodkinson and Hughes, 1982; Soldaat and van der Meijden, 1990) because they contain higher nitrogen and water percentages (Mooney and Gulmon, 1982). According to optimal plant defense theory, the young leaves should thus be protected best (Zangerl and Bazzaz, 1992). Based on theories of coevolution of plants and herbivores (Ehrlich and Raven, 1964), it can be expected that specialist herbivores will not be deterred by high chemical defense levels in the youngest leaves, while generalists will (Cates, 1980).

In this paper we test whether PAs of rosette plants of Cynoglossum officinale L. (Boraginaceae) act as defenses against herbivores. PA levels differ significantly between leaves on the same rosette plant; the youngest leaves have 50-190 times higher PA concentrations than the oldest leaves (Van Dam et al., 1994). C. officinale contains several PAs, such as echinatine, 3'-acetylenechinatine, heliosupine, trachelanthamine, and viridiflorine (De Jong et al., 1990; Hartmann and Witte, 1994; Van Dam et al., 1995), which are mainly present in the N-oxide form (Sykulska, 1962; Van Dam et al., 1995).

C. officinale is a host plant for a range of herbivores (De Jong et al., 1990). Nevertheless, herbivory on C. officinale is usually less than 10% of the leaf