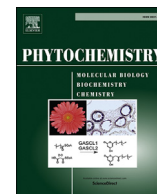




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The effect of structurally related metabolites on insect herbivores: A case study on pyrrolizidine alkaloids and western flower thrips

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ABSTRACT

Plant specialised metabolites (SMs) are very diverse in terms of both their number and chemical structures with more than 200,000 estimated compounds. This chemical diversity occurs not only among different groups of compounds but also within the groups themselves. In the context of plant-insect interactions, the chemical diversity within a class of structurally related metabolites is generally also related to their bioactivity. In this study, we tested firstly whether individual SMs within the group of pyrrolizidine alkaloids (PAs) differ in their effects on insect herbivores (western flower thrips, *Frankliniella occidentalis*). Secondly, we tested combinations of PA *N*-oxides to determine whether they are more active than their individual components. We also evaluated the bioactivity of six PA free bases and their corresponding *N*-oxides. At concentrations similar to that in plants, several PAs reduced thrip's survival but the effect also differed strongly among PAs. In general, PA free bases caused a lower survival than their corresponding *N*-oxides. Among the tested PA free bases, we found jacobine and retrorsine to be the most active against second instar larvae of thrips, followed by erucifoline and seneciophylline, while senecionine and monocrotaline did not exhibit significant dose-dependent effects on thrip's survival. In the case of PA *N*-oxides, we found that only senecionine *N*-oxide and jacobine *N*-oxide reduced thrip's survival, although the effect of senecionine *N*-oxide was weak. Combinations of PA *N*-oxides showed no synergistic effects. These findings indicate the differences observed in the effect of structurally related SMs on insect herbivores. It is of limited value to study the bioactivity of combined groups, such as PAs, without taking their composition into account.

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1. Introduction

Plant specialised metabolites (SMs) mediate many aspects of the interaction of plants with their environment (Pichersky and Lewinsohn, 2011) and they have an important role in defence against pathogens and herbivores (Johnson, 2011; Gols, 2014). One of the unique features of plant SMs is their high diversity, with more than 200,000 estimated compounds (Hartmann, 1996), and at least 1000 additional compounds are described each year (Seigler, 1998; Verpoorte, 1998). This chemical diversity is reflected by the wide variety of compounds, including such structurally different groups as glucosinolates, saponins, alkaloids, essential oils, flavonoids and organic acids among others (Scott et al., 2002; Mithofer and Boland, 2012). Moreover, within a group of structurally related metabolites it is possible to find large variation in chemical

features. For instance, at least 34 different glucosinolates have been identified in *Arabidopsis thaliana* (Kliebenstein et al., 2001) and more than 20 indole alkaloids in *Rauvolfia serpentina* (Sheludko et al., 2002).

This diversity of SMs in plants has led to a number of hypotheses regarding their origins. Ehrlich and Raven (1964) proposed an evolutionary scenario, the escape-and-radiate coevolution model, where plant lineages suffering herbivore pressure evolved new SMs releasing them from their erstwhile herbivores. This release leads to plant radiation and diversification. Later insect lineages adapt to the plants and also diversify.

The arms race hypothesis proposed that the diversity of plant SMs is the consequence of an ongoing evolutionary arms-race between plants and their specialist insect herbivores (Berenbaum and Feeny, 1981). Therefore, over time, plants evolved new toxic SMs and as corollary specialised herbivores adapted or became extinct. Becerra et al. (2009) showed that in the interaction between *Blepharida* beetles and the plant genus *Bursera*, new plant species

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eventually tend to be armed, not only with more SMs, but also with metabolites that could potentially prove to be challenging for herbivores to adapt to.

Firn and Jones (2000, 2003) proposed the screening hypothesis of plant metabolite diversity. They contended that while most plant metabolites have no function in plants, retaining this broad range of metabolites was useful as a reservoir of potential weapons to repel “new” herbivores. As an example, Firn and Jones (2003) argued that gibberellins are made by a pathway that evolved to generate and retain chemical diversity and that natural selection has still favoured enzymes that have a broad substrate tolerance. According to Firn and Jones (2000) this provides an explanation to the question of why plants produce so many gibberellins despite the majority of these possess very low biological activity. The screening hypothesis has generated a lot of opposition. Regarding the alleged inactivity of SMs, Berenbaum and Zangerl (1996) argued that the low activity detected in screening trials was simply the result of using inappropriate targets, suggesting that if the right ones were used, a very high level of biological activity would be found. Arnason et al. (2004) reported that most of 12 triterpenoids identified in *Rupti-liocarpon caracolito* increased larval mortality and significantly

reduced the growth of survivors, suggesting that screening for a rare effective defence molecule is not occurring in this species.

The multiple herbivores hypothesis states that the diversity of plant SMs may be maintained by the selection of different herbivores (Macel et al., 2005; Summers and Moore, 2011). For instance, Macel et al. (2005) found that senkirkinine was the most toxic PA for *F. occidentalis* while it was not at all toxic to *Myzus persicae*. Plants are attacked by multiple herbivores that respond differently to the different plant metabolites.

Finally, the diversity of plant SMs may also be explained by the synergism hypothesis, where a combination of related metabolites is more effective than the sum of the effects of the individual metabolites (see Arnason et al., 2004). If plant SMs act synergistically, an effective protection against herbivores can be achieved with a lower amount of each individual metabolite. However, while it is increasingly clear that interactions between plant SMs are important, only a few studies have demonstrated this in the context of plant-insect herbivore interaction. Synergistic effects were reported for two amides on several insects (Dyer et al., 2003; Richards et al., 2010; Whitehead and Bowers, 2014), for two potato glycoalkaloids on the snail *Helix aspersa* (Smith et al., 2001), and for two

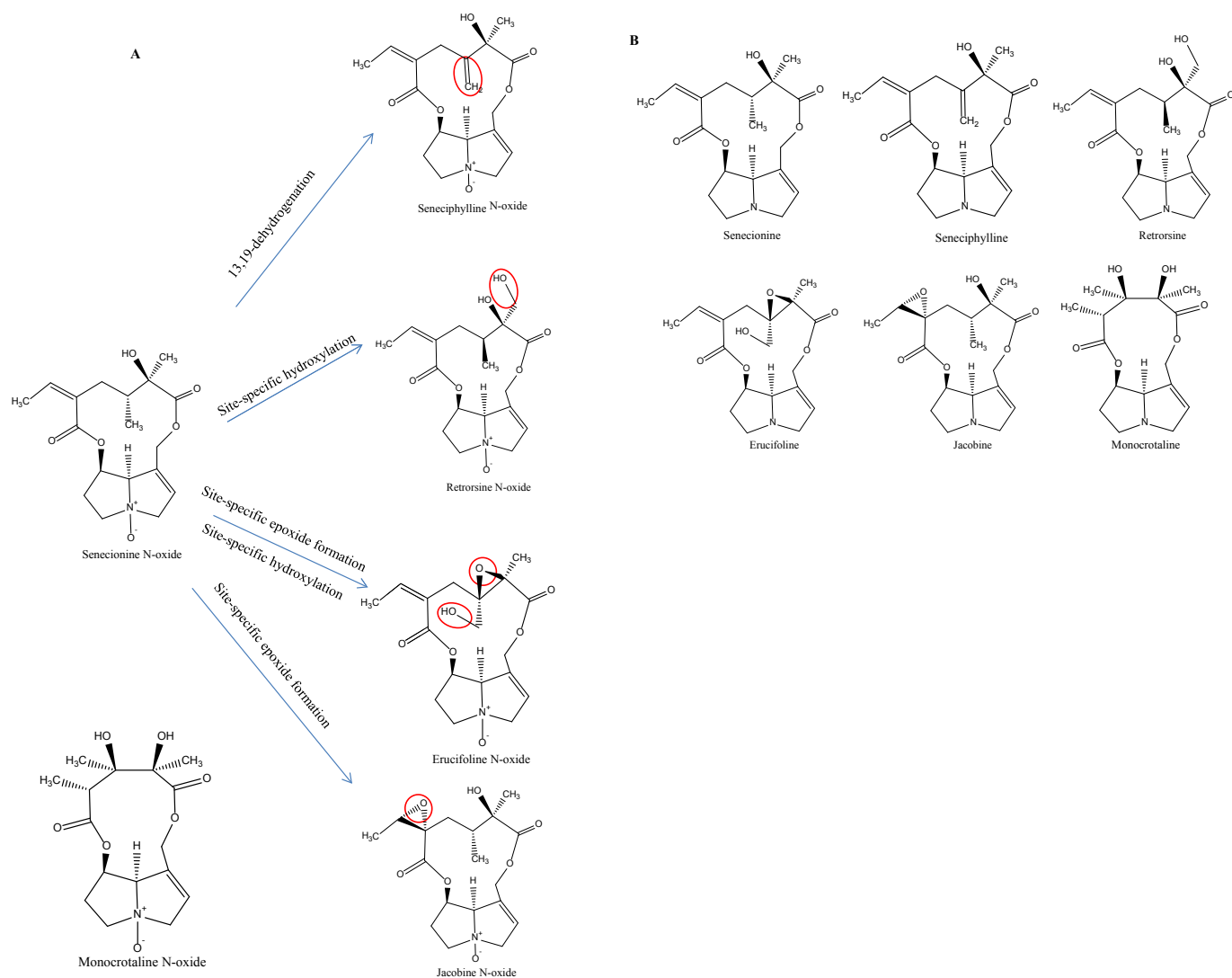


Fig. 1. Chemical structures of pyrrolizidine alkaloids (PAs) and a simplified biosynthetic pathway of PAs in *Jacobaea* species (after Hartmann et al., 1989). More specifically, senecionine N-oxide is biochemically modified in one step through 13, 19-dehydrogenation and epoxide formation to yield seneciphylline N-oxide, retrrorsine N-oxide and jacobine N-oxide respectively, as well as in two steps (i.e. epoxide formation and hydroxylation) to yield erucifoline N-oxide.

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