Introduction

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This special issue of phytochemistry reviews is in the honour of Eddy van der Meijden on the occasion of his retirement. He is one of the leading researchers in the field of evolutionary ecology of plant defence. Being trained as an animal ecologist he soon was aware of the fact that the population dynamics of herbivorous insects can only be understood in relation to food quantity and quality. He tried to understand food quality of the cinnabar moth, *Tyria jacobaeae*, as a compromise between nutritional requirements and the levels of plant defence. He also advocated the idea that in order to explain the evolution of plant defence systems one should not only focus on the enemies that are found on the plant but one should focus especially on potential enemies that are not found on the plant because these are the ones that are most likely to be affected by the plant's defence system. With this in mind van der Meijden and his co-workers studied the effects of pyrrolizidine alkaloids (Pas) on generalist and specialist herbivores within the framework of evolutionary ecology. Van der Meijden emphasized that the evolution of plant defence could only be understood when studied in relationship to the allocation patterns and life-history

characteristics of an individual. One of his classic papers is on regrowth and defence as alternative strategies in the struggle against herbivores. The fitness effects of secondary metabolites are determined by on one hand the benefits in terms of increased growth and reproduction and on the other hand the costs to produce them. For a long period it remained unclear whether or not there were costs associated with the production of alkaloids. At least the production costs were minute and hard to show. This lead van der Meijden to hypothesize that the costs were largely ecological. Alkaloids have a negative effect on generalist herbivores that are not adapted to the plant and attract specialist herbivores that use the alkaloids to recognize their host plant. The optimal alkaloid concentration is then determined by the relative herbivore pressure by specialist and generalist herbivores. This concept was later applied to explain the shift from quantitative to qualitative defence in invasive plants that lack the pressure of specialist herbivores. Van der Meijden cooperated with experts in the field of plant chemistry such as Thomas Hartman. Hartman's finding, that alkaloids are produced in the roots and that diversification takes place in the shoots, helped to explain how alkaloid concentrations depend on environmental conditions. Starting from Hartman's description of chemotypes of *Senecio jacobaea*, van der Meijden and his team studied the distribution of Pas both at the level of individual plants, populations and on a geographical scale and in a phylogenetic context, trying to describe and explain

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the bewildering diversity of Pas within the genus *Senecio s.l.*

The effects of alkaloid on insect herbivores were tested using chemotypes and experiments with artificial diets. It was shown that structurally related alkaloids differ in their effects on herbivores and that herbivores are differentially affected by the same alkaloid. Strong indications were found that different alkaloids have synergistic effects. The study of the effects of individual alkaloids or combinations was hampered by the availability of the relevant pure alkaloids. To overcome this problem a system was set-up by crossing *Senecio jacobaea* and *Senecio aquaticus*. The F1's were again crossed to produce an F2 generation. The parental species, the F1 and the F2 generation are all kept in tissue culture such that they can be reproduced endlessly. In the F2 generation one expects independent segregation of

characteristics such that with multivariate regression analyses the effects of individual Pas and their interactions can be studied. With this system the effects of alkaloids on a variety of herbivores are now being tested. In addition this system was used to evaluate the importance of hybridization events for the evolution of alkaloid diversity. His latest research on alkaloids is on their role in the oviposition of *T. jacobaea*. In total Eddy van der Meijden published over 70 peer reviewed papers on *Senecio* and many of his former PhD students now hold prestigious positions, among which three full professorships and one extra ordinary professorship.

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