Tritrophic interactions between aphids (Aphis jacobaeae Schrank), ant species, Tyria jacobaeae L., and Senecio jacobaea L. lead to maintenance of genetic variation in pyrrolizidine alkaloid concentration*

Klaas Vrieling, Wouter Smit, and Ed van der Meijden

Department of Population Biology, Research Group Ecology of Plants and Herbivores, University of Leiden, P. O. Box 9516, 2300 RA Leiden, The Netherlands

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Summary. We hypothesize that the tritrophic interaction between ants, the aphid Aphis jacobaeae, the moth Tyria jacobaeae, and the plant Senecio jacobaea can explain the genetic variation observed in pyrrolizidine alkaloid concentration in natural populations of S. jacobaea. The ant Lasius niger effectively defends S. jacobaea plants infested with A. jacobaeae against larvae of T. jacobaeae. Plants with aphids and ants have a lower pyrrolizidine alkaloid concentration than plants without aphids and ants. When these data are fitted to an existing theoretical model for temporal variation in fitness it is shown that varying herbivore pressure by T. jacobaeae in interaction with ants defending aphid-infested plants with a low pyrrolizidine alkaloid concentration can lead to a stable polymorphism in pyrrolizidine alkaloid concentration. Costs of the production and maintenance of pyrrolizidine alkaloids are not accounted for in the model.

Key words: Senecio jacobaea – Tritrophic interactions – Genetic variation – Pyrrolizidine alkaloids – Herbivory

There is substantial individual variation in the concentration of secondary plant products in natural populations (Coley 1983; van der Meijden et al. 1984; Berenbaum et al. 1986; Hartmann and Zimmer 1986; Cates and Redak 1989; Von Borstel et al. 1989). It has been demonstrated for several of these compounds that this variation is partially genetically based (Hanover et al. 1966; Berenbaum et al. 1986; Östrem 1987). One popular theory explains the maintenance of this variation by the operation of two opposing selective forces, namely: (1) benefits to the plant, because the secondary compound acts as a chemical defence against herbivores and (2) costs associated with the production and/or maintenance of this

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Offprint requests to: K. Vrieling
tion in herbivore pressure by *T. jacobaeae* explain the genetic variation in Pa concentration?

**Material and methods**

*Senecio jacobaea* is an abundant monocarpic perennial plant in the dunes of Northwestern Europe. Populations of *S. jacobaea* are frequently completely defoliated by larvae of the moth *Tyria jacobaeae* (Dempster and Lakhanli 1979; van der Meijden 1979; Myers 1980; Crawley and Gillman 1989). *T. jacobaeae* is univoltine and virtually monophagous on *S. jacobaea*. The main period of herbivory lasts 6 weeks with a peak in June. *S. jacobaea* plants contain at least seven Pa's (Fig. 1) (Aplin et al. 1968; Segall 1978; Segall and Krick 1979; Pieters et al. 1989) which act as a chemical defence (Hartmann et al. 1988; van der Meijden 1973, 1979; Segall 1977; Myers 1980; van der Meijden et al. 1984). Although Pa's are probably transported within the plant as N-oxides (Hartmann et al. 1988; van der Meijden 1979; G.J. de Bruin pers. comm.). The monophagous aphid *Aphis jacobaeae* is tended by ants (Heie 1986). Ants and aphids are present in the field when the larvae of *T. jacobaeae* start to feed. Circa 2% of plants were infested with *A. jacobaeae* (and nearly always tended by ants) during the study period. In some populations of *S. jacobaea*, however, infestation by *A. jacobaeae* reached 50–70%.

**Effect of ants on larvae of *T. jacobaeae***

In 1989 a single fourth- or fifth- (final) instar larva of *T. jacobaeae* was placed on the flowerheads of ten nearest-neighbour pairs of flowering plants with and without *A. jacobaeae* and *L. niger* in a natural population. The presence or absence of the larvae on the plant was then recorded 15 rain later. Fresh larvae were used in each trial.

**Host-plant selection by *A. jacobaeae***

*Field experiment I.* In 1987, 13 flowering plants with *A. jacobaeae* and the ants *L. alienius* or *L. niger* were harvested in a population near Wassenaar (The Netherlands). In each case the nearest flowering plant without aphids and ants was also collected. Because large plants have a higher probability of being attacked by herbivores height of plants was measured. Plant material, separated into leaves, stem and flowers, was dried for 3 days at 50°C. The leaf material from each plant was analysed for total Pa concentration.

Gas liquid chromatography (GLC) analysis

All GLC analyses were performed on a Packard 433 gaschromatograph equipped with a 25-m fused silica column 0.32 mm ID.