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RESEARCH PROJECT

Evolution of mating systems in plants: the causes and consequences of inbreeding in *Aconitum lycocotonum* s.l.

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Summary

- 1 In this study we will be using a combination of molecular data, observations of flower visitors, and field experiments to test hypotheses concerning pollinator–flower coevolution, evolution of mating systems, and speciation in the *Aconitum lycocotonum* group.
- 2 *Aconitum lycocotonum* flowers have features that suggest a highly outcrossing mating system: they are morphologically specialized for bee pollination, and they have both temporal and spatial mechanisms for limiting self fertilization. However, contrary to the expectation of an outcrossing mating system, our preliminary investigations using protein markers indicate that there is very little genetic variation in at least some populations of this species.
- 3 The fact that so many features of the flower's pollination system suggest outcrossing mechanisms, whereas the genetic analyses suggest inbreeding, has led us to propose a secondary loss of outcrossing in this species.
- 4 Because there is variation in percentage polymorphic loci (0–27%), heterozygosity (0.003–0.08), and inbreeding coefficients ($F_{IS} = -0.086$ –0.66) among populations we have an unusual opportunity to test hypotheses concerning the ecological and evolutionary factors contributing to differences in the realized mating system.

Keywords: allozymes, bumble bees, coevolution, nectar robbers, outcrossing, pollination ecology

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Introduction

MATING SYSTEM EVOLUTION

Flowers often appear to be specialized for particular kinds of insect visitors. For example, moths often visit large, white, sweet smelling flowers that open at night, and bees often visit tubular blue flowers. These correlations between flower shape and/or color and

the attraction of specialized insects has lead to the description of numerous pollination syndromes such as the “moth” flower described above (Baker & Hurd 1968; Faegri & van der Pijl 1971). However, more careful ecological observations (reviewed in Waser *et al.* 1996) and the development of molecular markers,

which give us the ability to examine the actual genetic consequences of mating behaviour, have called into question many of the assumptions concerning the closeness of the coevolution between flowers and their pollinators.

Life history characteristics are known to have an influence on the extent and structure of genetic variation in plant populations. Species with large ranges, high fecundity, an outcrossing mode of reproduction, wind pollination, a long generation time, and from habitats representing later stages of succession have often more genetic variation than species with other combinations of life history traits (Hamrick *et al.* 1979; Hamrick 1989). Mating systems have the largest effect on genetic diversity. Outbreeding populations have a greater genetic diversity, with higher levels of heterozygosity and more polymorphic loci, and show less differentiation among, but more within populations than self-fertilized populations (Gottlieb 1981; Hamrick 1989).

NECTAR ROBBERY

One factor that may influence the reproductive success of flowers is nectar robbery. If plants experience high nectar robbery rates (which is true of *Aconitum*), and if true pollinators avoid robbed flowers, then there may be a selective advantage for self-fertilization even if inbreeding depression is present. Studies concerning the impact of nectar robbers on the reproductive success of the visited plant species suggest that nectar robbery may indeed have this kind of effect (Roubik *et al.* 1985). However, positive and neutral interactions are also possible (Heinrich & Raven 1972; McDade & Kinsman 1980). Neutral effects are most likely when the robber also acts as a pollinator (Rust 1979; Arizmendi *et al.* 1996).

The system *Aconitum* - *Bombus*

THE GENUS *ACONITUM*

The genus *Aconitum* (Ranunculaceae) includes about 400 species and is found throughout Eurasia and North America (excluding Arctic and tropical regions) with its center of distribution in East Asia (Hess *et al.* 1977). The genus is found in many habitats, but especially in mountainous regions. Most taxa in Europe show extreme morphological variability which has led to the description of numerous subspecies, varieties and forms, and resulted in unclear and often inconsistent systematics (Warncke 1964; Götz 1967; Seitz 1969; Hegi 1974; Hess *et al.* 1977; Tutin *et al.* 1993).

We are interested in *A. lycoctonum* s.l. (subgen. *Lycocionum*, ser. *Lycocionia*, Tamura & Lauener 1978) in Central and Southern Europe (Table 1). The *A. lycoctonum* group includes yellow flowering taxa of still uncertain taxonomic rank. We are focusing here primarily on ssp. *lycoctonum* and ssp. *ranunculifolium*, and hybrids between these two subspecies (nomenclature after Warncke 1964). The two subspecies are separated by the division of their leaves, and by their distributions; ssp. *lycoctonum* occurs in Central Europe, ssp. *ranunculifolium* occurs in Southern Europe, and their supposed hybrids primarily in the Alps. All species of the *A. lycoctonum* group in Europe are diploid with $2n = 16$. However, Seitz *et al.* (1972) reported a difference between the two subspecies in the morphology of the chromosomes. He found two pairs of chromosomes with satellites in *A. lycoctonum* ssp. *lycoctonum*, but none in *A. lycoctonum* ssp. *ranunculifolium*.

POLLINATION ECOLOGY OF *ACONITUM LYCOCTONUM*

The flowers of *Aconitum* have five perianth-segments and are zygomorphic, the posterior

Table 1. Taxonomy, distribution, and characteristics of the series *Lycocionia* (subgen. *Lycocionum*) in Europe. Taxonomy after Tamura & Lauener (1978) and Warncke (1964)

Species name	Distribution	Distinctive characters
A. Species we are studying both ecologically and systematically		
<i>A. ranunculifolium</i> (= <i>A. lycocionum</i> ssp. <i>ranunculifolium</i>)	Europe (Austria, Bulgaria, France, Italy, Romania, Spain, Switzerland, Yugoslavia)	Flowers yellow, leaves deeply divided
<i>A. vulparia</i> (= <i>A. lycocionum</i> ssp. <i>lycoctonum</i>)	Europe (Austria, Belgium, Czechoslovakia, France, Germany, Hungary, Italy, Netherlands, Poland, Romania, Switzerland, Yugoslavia); N. Africa	Flowers yellow, leaves shallowly divided
<i>A. pauciflorum</i> (part of <i>A. lycocionum</i> ssp. <i>lycoctonum</i>)	Europe (Austria, Yugoslavia)	Flowers yellow, leaves shallowly divided, glabrous
B. Additional species that we are only examining systematically		
<i>A. septentrionale</i> (= <i>A. lycocionum</i> ssp. <i>septentrionale</i>)	Europe (Norway, Finland, Sweden); USSR, Mongolia, China	Flowers violet
<i>A. moldavicum</i> (= <i>A. lycocionum</i> ssp. <i>carpathicum</i>)	Europe (Czechoslovakia, Hungary, Poland, Romania); USSR-Ukraine; China	Flowers blue

petal is helmet-shaped protecting the two characteristic nectaries. The stamens are numerous and there are usually three follicles. The flowers are usually protandrous (Hegi 1974), and the racemes open from the bottom to the top. This pattern, combined with protandry, leads to racemes with male flowers at the top, hermaphrodites in the middle, and female flowers at the bottom.

The flowers of *Aconitum* are visited by numerous insect species, including different bumble-bees which collect nectar and/or pollen (Erhardt 1996). Because of the characteristic nectaries, the mode of collecting nectar depends on the length of the proboscis of the bumble-bee. After Løken (1949; 1950) the bumble-bees observed on *Aconitum* can be classified in the following groups (terminology after Inouye 1980): (1) Primary nectar robbers: bumble-bees making holes in the helmet of the blossom to "steal" the nectar

(e.g. *Bombus mastrucatus* Gerstäcker, Hegi 1974); (2) Secondary nectar "robbers": bumble-bees using the holes made by others to "steal" the nectar; (3) Pollen collectors: these bumble-bees do not have to pass the stamens and pistils and thus they are not pollinators; and (4) Nectar collectors or pollen/nectar collectors: bumble-bees passing the stamens and pistils when collecting nectar; these are long-tongued bees, and they act as pollinators. At low elevations in Central Europe, *B. hortorum* collects nectar from *Aconitum*, whereas at higher elevations the pollinator is *Bombus gerstaeckeri* (Hegi 1911). *Bombus hortorum* occurs throughout Europe, except in Ireland (Rasmont 1983), and is found from low elevations to about 1500 m a.s.l., locally even higher (A. Scholl, pers. comm.). *Bombus gerstaeckeri* is an alpine bumble-bee, occurring in the Alps, Pyrenees and Balkans (Rasmont 1983).

The long-tongued bumble-bees pass the stamens and pistils when crawling into the flower to collect nectar. They generally work the plant systematically, first visiting the lower flowers in the raceme and then by and by the higher ones (Løken 1949; Hegi 1974; Erhardt 1996). This pollination mechanism should encourage outcrossing; spontaneous inbreeding might be almost entirely excluded if the flowers were completely protandrous. Thus it was supposed that the *Aconitum* species depend on *Bombus* spp. for pollination and that they are outcrossed. However, recent

crossing experiments with species in the *A. lycoctonum* group showed that self-pollination can occur (Erhardt 1996).

Research questions

- (1) What is the pattern of genetic variation and inferred mating systems across the range of *A. lycoctonum*?
- (2) What is the potential for *A. lycoctonum* to outcross and self, and what are the consequences of selfing, mating with relatives, and outcrossing on seed production and germination?

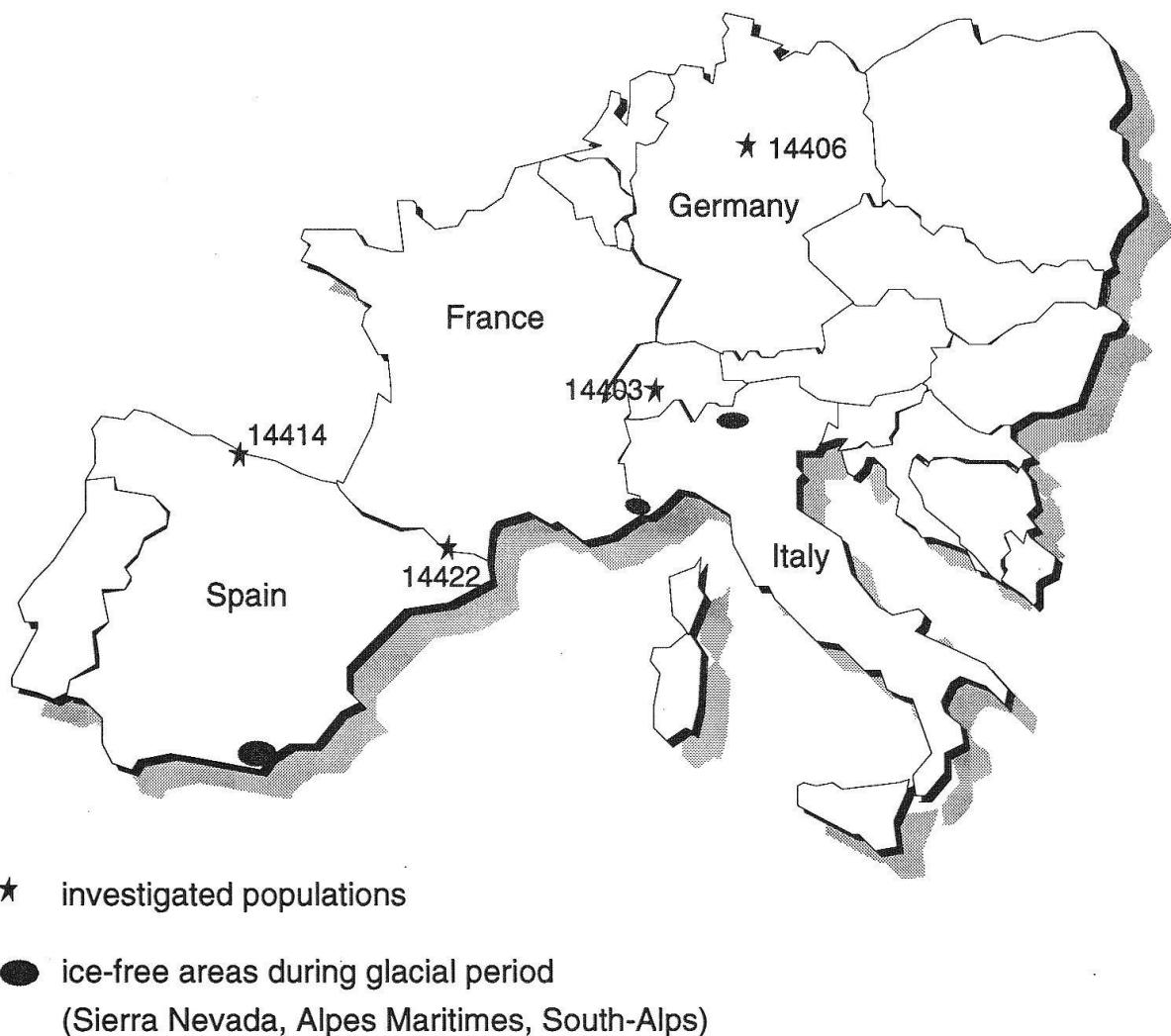


Fig. 1. Locations of the populations of *A. lycoctonum* under investigation in Central and Southern Europe.

Table 2. Genetic variation in four populations of *A. lycocotonum*. Population numbers correspond to the localities shown in Figure 1.

A, mean no. of alleles/locus; P, percent polymorphic* loci; H_{obs} , observed heterozygosity; F_{IS} , the inbreeding coefficient, which indicates the probability that an individual in a population is autozygous; based on Weir & Cockerman (1984) and calculated using the program FSTAT

Population	Mean sample size/locus	$A \pm SE$	P	$H_{obs} \pm SE$	F_{IS}
1. #14403	30.4	1.2 ± 0.1	0	0.003 ± 0.003	0.666
2. #14406	30.9	1.2 ± 0.1	18.2	0.038 ± 0.038	0.390
3. #14414	31.8	1.2 ± 0.1	9.1	0.026 ± 0.02	-0.086
4. #14422	29.0	1.5 ± 0.2	27.3	0.082 ± 0.046	0.124

*A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.

(3) Why are there such large differences in genetic variation among populations of *A. lycocotonum*?

Hypothesis 1: The observed levels of low genetic diversity are the result of an adaptive shift from an outcrossing mating system to a selfing mating system. We will test two potential mechanisms leading to selfing being advantageous: loss of pollinators and selection by nectar robbers.

Hypothesis 2: The observed patterns of genetic variation are largely the result of random processes and not selection. We will use genetic data and population size estimates to evaluate the roles of drift and founder effects.

(4) Are self-fertilization or hybridization contributing to the morphological diversity and confused systematics of the *A. lycocotonum* group?

Preliminary experiments and discussion

Allozymes continue to be the main source of genetic markers for analyzing breeding systems because they are co-dominant markers (Barrett & Harder 1996). We have collected 33 individuals from each of four Central and Southern European populations of *A. lycocotonum* (stars in Fig. 1). We have investigated these four populations for genetic variation.

We screened 24 enzymes, to yield nine enzymes and twelve loci that were reliably resolved. In Table 2 we present a summary of the genetic statistics for these populations.

The results of the preliminary investigations indicate extensive variation in the levels of genetic variation and realized mating system in populations of *A. lycocotonum* (Table 2). For example, the percent polymorphic loci ranges from 0 to 27%, and the inbreeding coefficient F_{IS} ranges from an excess of heterozygotes at -0.086 to highly homozygous and inbred at 0.66. The population with no polymorphic loci is almost certainly completely inbred as continuous selfing or mating among close relatives ultimately depletes the population of all heterozygosity, producing a totally homozygous inbred population with no polymorphic loci (Mitton 1993).

How does our data compare with other plant species? According to Godt *et al.* (1996) endemic species, which often occur in isolated habitats with associated small population sizes and founder effects have an expected heterozygosity of 0.076, whereas non-endemic short-lived herbaceous species have an expected heterozygosity of 0.103. Of the four populations surveyed our highest expected value was 0.091, which is close to the average for short-lived perennials, and the

lowest was 0.009, which is smaller than the typical endemic. The fact that there are some populations with multiple polymorphic loci and higher heterozygosity leads us to hypothesize that the homozygous populations are the result of either a shift in mating system towards more selfing as a result of ecological factors, or that there has been considerable mating among close relatives following one or more genetic bottlenecks.

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