

Session 3

Origins and Evolutionary Effects

ORIGINS AND EVOLUTIONARY EFFECTS OF INVASIVE WEEDS

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ABSTRACT

Many regions of the world have floras that contain a high proportion of introduced species. Some introduced plants become aggressive weeds in their new surroundings and succeed in rapidly invading particular habitats and replacing indigenous species. This can lead to loss of biodiversity. Occasionally, however, an invading weed may hybridize with a native species or another alien plant and this can create evolutionary novelty leading sometimes to the origin of new species. Molecular techniques can be used to determine the ecological and evolutionary origins of invasive weeds and also the evolutionary events that may follow interspecific hybridization with other plants. Case studies of two invasive *Senecio* species in Britain and also *Rhododendron ponticum* are described to illustrate the power of molecular analysis in resolving the origins and evolutionary effects of such weeds.

INTRODUCTION

Many local and regional floras throughout the world now contain a large proportion of introduced species (Mooney & Drake, 1986; Heywood, 1989). In the British Isles, for example, approximately 45 per cent of the 2834 species that comprise the flora are judged to be alien (Stace, 1991). Most of these species have been introduced intentionally or accidentally by man and have subsequently become naturalized in the wild. Some introduced plants can develop into aggressive weeds in their new surroundings, and succeed in invading particular habitats and replacing indigenous species. This is a destructive process causing loss of biodiversity. Occasionally, however, invading weeds may interact with native or other introduced species in ways that can lead to episodes of rapid evolution and the creation of new biodiversity (Abbott, 1992).

From a number of different perspectives, invasive weeds have been regarded as model systems for the study of plant evolution. Frequently they are studied to monitor the type and amount of genetic change that occurs in species during and following the colonization of new distant localities (Barrett, 1982, 1992). More specifically, their study has provided considerable insight into the evolution of plant breeding systems (Barrett, 1992) and, to a lesser extent, the evolution of plant life histories (Thebaud and Abbott, 1995). Little is known about physiological changes that accompany a plant species invasion, but clearly opportunities are offered for the study of how easily or difficult such evolutionary change might take place. Finally, cases of hybridization between two or more introduced species or between an alien and native species offer excellent opportunities for the study of plant evolution following interspecific hybridization (Abbott, 1992).

A starting point in the evolutionary study of an invasive weed is to ascertain its origins. Here, it is important to determine both its ecological origin (i.e. the place from where it was introduced) and its evolutionary origin (i.e. the way in which the species first originated). Information on both types of origin is of considerable importance if a comprehensive

appreciation is required of evolutionary changes that might promote and/or accompany the rapid spread of an invading species. Although the primary reason for obtaining this information is normally to satisfy intellectual curiosity in regard to the evolutionary process, such information may also be of practical value, enabling pest and disease organisms to be collected from source and ancestral material for use in the biological control of an invasive weed. The latter could be of importance in situations where the genotype of the host plant determines resistance, and only those pests and pathogens that occur in source populations of the introduced material have the ability to overcome such resistance.

The aims of this paper are twofold. First, to show how it may be possible to determine accurately the ecological and evolutionary origins of invasive weeds. Second, to show how interspecific hybridization between an invasive and native species can have significant evolutionary consequences that may, on occasion, result in the evolution of new plant taxa. For both, we shall confine our attention to examples drawn from the British flora.

ECOLOGICAL AND EVOLUTIONARY ORIGINS OF INVASIVE WEEDS

Considerable documentation is available on many of the most troublesome invasive weeds that are found in Britain (e.g. Salisbury, 1961). Such documentation frequently provides information on the geographical sources of plants that were introduced intentionally to the British Isles, and which subsequently have become invasive weeds. In contrast, the ecological origins of invasive weeds introduced accidentally are less well known. Moreover, it is seldom recorded whether plants introduced intentionally or by accident, are derived from a single locality or from throughout the species native range. As regards the evolutionary origins of British invasive weeds, very little detailed evidence is yet available. In what follows, we present the results of recent work on three British invasive weeds - *Senecio squalidus*, *Senecio viscosus* and *Rhododendron ponticum* (Fig. 1) - in which the specific aim of the research was to establish their evolutionary and/or ecological origins.

Senecio squalidus (Compositae)

Senecio squalidus, commonly known in Britain as Oxford ragwort, is a diploid ($2n=20$), self-incompatible, short lived perennial plant which was introduced to the Oxford Botanic Garden sometime during the latter part of the 17th century (Kent, 1956; Druce, 1927). It was first reported to have escaped from the garden in 1794 (Druce, 1927) and has since spread rapidly as a ruderal throughout many parts of England and Wales, and into Ireland and Scotland (Abbott, 1992). Historical records indicate that the material raised in the Oxford Botanic Garden was introduced from Sicily, from the slopes of Mount Etna (Kent 1956; Druce, 1927). It remains unclear, however, whether Mount Etna material was the only source of plants that became established in Britain or whether there have been further introductions from throughout the species natural distribution in central and southern Europe and north Africa (Alexander, 1979). A further point of confusion has emerged from work by Crisp (1972) who reported that *S. squalidus* does not in fact occur on Mount Etna and that the British form of *S. squalidus* is most likely to have originated as a hybrid derivative of *S. chrysanthemifolius* and *S. aethnensis*, both of which are found in Sicily and which form hybrid swarms at 1200 +/- 200m altitude on Mount Etna.

To clarify the ecological and evolutionary origins of *S. squalidus* found in the British Isles, surveys of chloroplast DNA (cpDNA) and isozyme variation have been conducted in British and mainland European material of the species, and also in material of the two closely related species found on Mount Etna, *S. chrysanthemifolius* and *S. aethnensis*. The aim of these surveys was to resolve genetic markers in British material that are diagnostic of the ancestral material from which the British material was derived. Chloroplast DNA exhibits uniparental inheritance and is, therefore, not subject to genetic recombination. Consequently, it is expected that a considerable amount of historical information will be preserved in the

(a)



(b)



(c)



(d)



Fig. 1. (a) *Senecio squalidus* (Oxford ragwort); (b) *Senecio viscosus* (Sticky groundsel); (c) *Rhododendron ponticum*; (d) *R. ponticum* invading pine woods at Blea Tarn, Lake District, U.K.

cpDNA sequence of an individual. The molecule is highly conserved and so only limited amounts of intraspecific cpDNA variation are normally recorded in plants (Soltis *et al.*, 1992). However, this variation can be of considerable value in reconstructing and tracing past ecological and evolutionary events within a particular species.

The survey of restriction site variation of cpDNA (Abbott *et al.*, 1995) resolved three different cpDNA haplotypes - A, B and C - in the material examined. Haplotypes A and B were distinguished by a single restriction site mutation, while haplotype C was distinguished from haplotype A by the presence of an insertion of approximately 330 bp, and three site mutations. All three cpDNA haplotypes occurred in *S. squalidus* (Table 1; Fig. 2). Haplotype A was found in material of the species sampled from north Italy, Romania and Bulgaria. The B haplotype occurred in material from central Italy and in all samples from the British Isles and north France, while haplotype C was restricted to populations from south east Europe i.e. south Bulgaria and Greece. Based on this evidence, it is feasible that British *S. squalidus* was derived from material introduced from central Italy rather than Sicily, although there is no documentary historical evidence to support this hypothesis. The survey of cpDNA variation, however, also revealed that the B haplotype was present in *S. chrysanthemifolius* and *S. aethnensis* populations from Mount Etna, Sicily, and also in the hybrid swarms formed between these two species (Table 1; Fig. 2). Thus the cpDNA data do not rule out the hypothesis of Crisp (1972) that the British form of *S. squalidus* is in fact a hybrid derivative of *S. aethnensis* and *S. chrysanthemifolius*.

Table 1. Number of individuals per chloroplast (cpDNA) haplotype in *Senecio squalidus*, *S. aethnensis*, *S. chrysanthemifolius* and *S. aethnensis* x *S. chrysanthemifolius*.

Taxon	Location	No. Populations	cpDNA haplotype		
			A	B	C
<i>Senecio squalidus</i>	Bulgaria	4	2	-	9
	Greece	3	-	-	3
	Italy (mainland)	4	3	1	-
	Romania	4	4	-	-
<i>S. squalidus</i>	British Isles & France	21	-	22	-
<i>S. aethnensis</i>	Sicily, Italy	3	1	4	-
<i>S. chrysanthemifolius</i>	Sicily, Italy	7	-	11	-
<i>S. aet.</i> x <i>S. chrys.</i>	Sicily, Italy	4	2	5	-

N.B. Populations of *S. squalidus* from France are derived from material introduced from the British Isles (Lousley, 1956).

Further evidence to support a Sicilian, hybrid origin of British *S. squalidus* emerged from the results of the survey of isozyme variation. At a locus (*Acp-2*) encoding the enzyme acid phosphatase, one allele (*Acp-2b*) which occurred at high frequency in British *S. squalidus* and also in the Sicilian species *S. aethnensis* and *S. chrysanthemifolius*, was not present in populations of *S. squalidus* sampled from elsewhere in Europe including central Italy (Table 2). Of particular interest was the finding that the frequency of the *Acp-2b* allele in the hybrid swarms between *S. chrysanthemifolius* and *S. aethnensis* on Mount Etna was identical to that in the pooled British population of *S. squalidus*.

Taken overall, the results of the cpDNA and isozyme surveys of variation provide strong support for a single introduction of hybrid material from Mt Etna from which the British form of *Senecio squalidus* is derived.

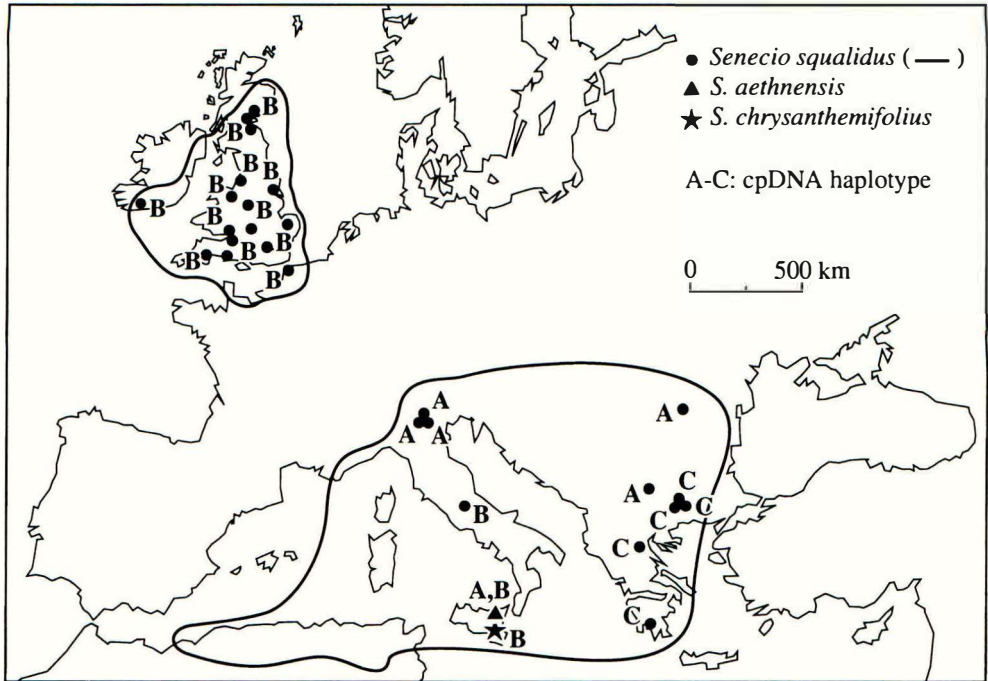


Fig 2. Distribution of chloroplast DNA haplotypes A, B and C in *Senecio squalidus*, *S. aethnensis* and *S. chrysanthemifolius* in Europe

Table 2. Allele frequencies at the *Acp-2* locus in *Senecio squalidus*, *S. aethnensis*, *S. chrysanthemifolius* and *S. aethnensis* x *S. chrysanthemifolius*. Values are pooled over populations within a country.

Taxon	Location	No. Populations	Total Sample Size	Acp-2	
				a	b
<i>Senecio squalidus</i>	Bulgaria	3	81	1.00	-
	Greece	1	30	1.00	-
	Italy (mainland)	9	230	1.00	-
	Romania	3	64	1.00	-
<i>S. squalidus</i>	British Isles	9	219	0.19	0.81
<i>S. aethnensis</i>	Sicily, Italy	3	65	0.66	0.34
<i>S. chrysanthemifolius</i>	Sicily, Italy	3	116	-	1.00
<i>S. aet.</i> x <i>S. chrys.</i>	Sicily, Italy	3	85	0.19	0.81

N.B. Three of the populations of *S. squalidus* from mainland Italy were from the region where the B cpDNA haplotype was present in populations (see Table 1).

Senecio viscosus (Compositae)

Senecio viscosus, commonly known as sticky groundsel due to its covering of viscid hairs, was first recorded in Britain in 1666 and has spread rapidly in the last 80 years (Salisbury, 1961). There are no records concerning its date of introduction to the British Isles, so it is assumed that it was introduced from Europe sometime during the early part of the 17th