

century. The species is a tetraploid ($2n=40$), self-compatible, winter annual plant that grows as a ruderal in open habitats with a high degree of disturbance.

Emig and Kadereit (1993) proposed that *S. viscosus* originated by differentiation from the tetraploid, self-incompatible species *Senecio nebrodensis*, which is restricted to several mountain ranges in Spain. To test this hypothesis, Kadereit *et al.*, (1995) undertook a survey of cpDNA and isozyme variation in material sampled from populations of both putative progenitor and derivative species. The survey of cpDNA restriction site variation revealed that the cpDNA of *S. viscosus* and *S. nebrodensis* could be distinguished from that of haplotype A found in *S. squalidus* (see above) due to the presence of a deletion of 45 bp and the loss of one restriction site. These two mutations also distinguished *S. viscosus* and *S. nebrodensis* from all other *Senecio* taxa whose cpDNA has so far been examined (Kadereit *et al.*, 1995), thus strengthening the hypothesis of a progenitor-derivative relationship between the two species. Further support for the derivation of *S. viscosus* from *S. nebrodensis* emerged from the survey of isozyme variation which showed that *S. viscosus* contained only a small subset of the alleles found in *S. nebrodensis* at enzyme coding loci (Kadereit *et al.*, 1995). This finding is in accordance with those of most previous studies of progenitor-derivative species pairs, which have shown that derivative species contain only a small sample of the genetic diversity present in progenitor species (Crawford, 1990). Because no new allozyme alleles were resolved in *S. viscosus*, Kadereit *et al.*, (1995) have proposed a relatively recent evolutionary origin of *S. viscosus* most probably in late glacial or postglacial times.

Rhododendron ponticum (Ericaceae)

As a native plant, *Rhododendron ponticum* has a distribution (Godwin, 1975) centred on the southern Black Sea and western Caucasus (var. *ponticum*), but with disjunct outlier populations in Lebanon (var. *brachycarpum*) and the south west part of the Iberian peninsula (var. *baeticum*). It is a plant of comparatively wet and humid areas, growing usually under the shelter of trees, on acidic soils and normally sloping terrain. The Iberian populations occupy three small areas, one in Spain and two in Portugal, occurring within 65 km of the coast. Fossil evidence (Godwin, 1975) from interglacial deposits indicates that the species once ranged across southern Europe, and also occurred in Ireland most probably as a member of the lusitanian floral assemblage, some of whose members still link Portuguese and Irish floras today. *R. ponticum* failed to reach Ireland during the current (Flandrian) interglacial until it was introduced recently by man. The species was clearly 'preadapted' to the climate of Ireland and Britain and now ranks amongst the most aggressive invasive aliens in the British Isles (Crawley, 1987).

R. ponticum was first introduced into Britain in 1763 (Loudon, 1844). This and most subsequent introductions are believed to have been of Iberian origin (Bean, 1970; Michalak, 1976); however, morphological differences between Iberian (var. *baeticum*) and Turkish (var. *ponticum*) material are insufficient for use in clearly determining the ecological origin of all *R. ponticum* plants in the British Isles. In an attempt to determine from where *R. ponticum* was introduced to Britain, we have initiated a survey of cpDNA restriction site variation in material of the species sampled from sites in Britain, Portugal and Turkey. An initial aim was to establish whether Portuguese and Turkish material possessed different cpDNA haplotypes. To this end, leaf material of one plant sampled from each of the two regions was subjected to a cpDNA restriction site analysis involving treatment of total genomic DNA with 22 restriction enzymes and 5 cpDNA probes (i.e. 110 enzyme-probe combinations). The 5 cpDNA probes used were drawn from a library of cloned *Lactuca sativa* cpDNA fragments and were composed either of single (C1, C7) or combined (C2/C3, C4/C5, C8/C9/C10/C11) fragments. In total, 10 of the 15 available fragments were used in the analysis, covering approximately 78% of the cpDNA genome. Different restriction fragment patterns were resolved for the cpDNA of the two samples analysed for 7 different enzyme digests probed with C2/C3, 3 enzyme digests probed with C1, and 2 enzyme digests probed with C4/C5.

The enzyme-probe combination *Bcl*I x C2/C3, which clearly differentiated the cpDNA haplotypes of Portuguese and Turkish material was used to screen 57 samples of *R. ponticum* collected from various parts of Britain (i.e. 13 samples from east Scotland, 30 from west Scotland, 4 from south and 7 from north England, and 3 from Wales). Of these British samples surveyed, 54 exhibited a restriction fragment pattern identical to the Portuguese type, while 3 showed a pattern that was slightly different. So far, no British sample has been found to exhibit the Turkish cpDNA pattern when treated with *Bcl*I x C2/C3. Although this study can only be regarded as preliminary, the results obtained provide strong support for the hypothesis that all material of *R. ponticum* in the British Isles is derived from the introduction of Iberian rather than Turkish material.

EVOLUTIONARY EFFECTS OF INVASIVE WEEDS

Evolutionary change following interspecific hybridization between two or more invasive weeds or between an invasive weed and a native species, has been the subject of several recent studies (see Abbott, 1992). These studies have confirmed that such hybridization can lead to: (i) the introgressive origin of new interspecific taxa, e.g. varieties, ecotypes and subspecies (Rieseberg *et al.*, 1990a; Abbott *et al.*, 1992); (ii) the origin of new fertile homoploid hybrid derivative species (Rieseberg *et al.*, 1990b; Arnold *et al.*, 1990b); (iii) the origin of new allopolyploid species (Soltis & Soltis, 1990; Raybould *et al.*, 1991; Ashton & Abbott, 1992). In this section we shall focus on a particular case study of recent evolution of several new taxa in the British flora i.e. that which has followed hybridization between the invasive diploid *Senecio squalidus* ($2n=20$) and the native tetraploid species, *S. vulgaris* ($2n=40$).

New introgressive taxa

In Britain, *S. squalidus* and *S. vulgaris* are often found growing together on open disturbed sites, especially in urban areas. Triploid hybrids (*S. x baxteri*, $2n=40$) are formed at low frequency in the wild (Marshall & Abbott, 1980), with *S. vulgaris* normally acting as the maternal parent (Abbott & Lowe, 1995). The triploid hybrid is highly sterile, but may backcross to *S. vulgaris*, and occasionally hybrid swarms form with genetic material introgressed from *S. squalidus* into *S. vulgaris*. Currently there is no evidence for introgression proceeding in the opposite direction. One known product of this introgression is the radiate variant of groundsel, *S. vulgaris* var. *hibernicus*, which differs from the common non-radiate groundsel, *S. vulgaris* var. *vulgaris*, in that it produces flower heads possessing an outer whorl of ray florets in addition to the disc florets produced by non-radiate groundsel. The difference in flower head type results from allelic variation for a single gene which controls presence/absence of ray florets. *S. vulgaris* var. *hibernicus* was first described in the British Isles in 1866 (Syme, 1875) from material which grew around Cork in Ireland. Crisp (1972) has since recorded a specimen of the same variant collected from Oxford in 1832. Both radiate and non-radiate forms of groundsel co-occur on urban sites in many parts of Britain, although the radiate variant is notably absent from the south-east (Stace, 1977) and large populations composed entirely of the radiate form have never been reported.

Evidence for the introgressive origin of *S. vulgaris* var. *hibernicus* is based on: (1) its parallel spread with *S. squalidus* in Britain over the past 160 years (Crisp, 1972); (2) the artificial synthesis of tetraploid plants bearing a close resemblance to var. *hibernicus* following backcrossing the triploid hybrid to var. *vulgaris* (Ingram *et al.*, 1980); (3) the occurrence of an allozyme marker allele (*Aat-3c*) at an intermediate frequency in var. *hibernicus*, which is absent from populations monomorphic for var. *vulgaris* but present at high frequency in *S. squalidus* (Abbott *et al.*, 1992). The *Aat-3* locus has been shown to segregate independently from the radiate locus, and thus there is good evidence that genes on more than one chromosome have been introgressed into *S. vulgaris* and have tended to remain associated in var. *hibernicus*. It is of interest that the presence of the radiate allele in *S. vulgaris* has

significantly boosted the outcrossing rate of the species, with the radiate variant exhibiting a much higher rate of outcrossing relative to the non-radiate variant (Marshall & Abbott, 1982, 1984a, 1984b).

In addition to leading to the origin of *S. vulgaris* var. *hibernicus*, introgressive hybridization between *S. vulgaris* and *S. squalidus* has resulted in the origin of a second tetraploid product which differs from var. *hibernicus* in several ways (Irwin & Abbott, 1992). This product which was discovered in York, England, in 1979, exhibits an intermediate morphological phenotype and an additive esterase banding pattern that combines the divergent esterase isozyme profiles of the parent species. In contrast, *S. vulgaris* var. *hibernicus* closely resembles var. *vulgaris* in morphology and esterase banding profile. The York variant, which has not been formally named, breeds true on selfing, shows a high level of seed fertility and is interfertile with *S. vulgaris*. Its phenotype has remained unchanged since it was first discovered in York which indicates that it is reproductively isolated from *S. vulgaris* in the field. It appears that the York variant, contains a much greater proportion of the *S. squalidus* genome than is present in var. *hibernicus*. It will be of interest to see whether this variant spreads to other parts of Britain over the coming years or remains restricted to locations in York.

New allopolyploid taxa

Hybridization between the invasive *S. squalidus* and the native *S. vulgaris* has also led to the origin in Britain within the last century of a new allopolyploid species, *S. cambrensis* (the Welsh groundsel, $2n=60$), following doubling of the chromosome number of the triploid hybrid (Ashton & Abbott, 1992; Ingram & Noltie, 1995). This newly evolved species was first discovered in 1948 from near Wrexham, north Wales. It is now commonly found as a ruderal in and around Wrexham, and has been reported subsequently from the Colwyn Bay area, north Wales, in 1966, from Ludlow, England, between 1972 and 1980, and from Edinburgh in 1982 (Ingram & Noltie, 1995).

When *S. cambrensis* was first discovered in Edinburgh, there seemed two possible ways by which the species had become established there. First, the species could have arrived following long distance dispersal of seed from north Wales: alternatively the species may have originated in Edinburgh via an independent origin. The question was raised, therefore, as to whether there had been a single origin of the Welsh groundsel in Britain followed by dispersal to other sites or whether there had been two or more origins of the species in Britain. Surveys of isozyme and cpDNA variation were conducted in *S. cambrensis* and its two parent species in an attempt to answer this question. It was established that at two enzyme encoding loci (*Acp-2* and *α Est-1*) material of *S. cambrensis* from north Wales exhibited a different enzyme phenotype from that exhibited by material from Edinburgh (Table 3). These differences were in accordance with the enzyme phenotypes exhibited by the parent species at the two locations and reflected separate origins of *S. cambrensis* in north Wales and Edinburgh (Ashton & Abbott, 1992). Evidence for at least two independent origins of *S. cambrensis* in Britain also emerged from a comparison of the cpDNA haplotypes of Welsh and Scottish *S. cambrensis* (Harris & Ingram, 1992; Lowe & Abbott, 1995). It was shown that whereas Edinburgh material possessed the A cpDNA haplotype, material of the Welsh groundsel from north Wales contained the C haplotype, (N.E. haplotype designations are the same as were described earlier for *S. squalidus*). It was clear from this that Edinburgh and Welsh plants of *S. cambrensis* are derived from different maternal parents.

The possession of the A haplotype by Edinburgh *S. cambrensis* is easily explained as this haplotype is common in non-radiate *S. vulgaris* (Lowe & Abbott, 1995), which is assumed to have acted as the maternal parent of *S. cambrensis*. More surprising, is the possession of the C haplotype by the Welsh form of *S. cambrensis*. Surveys of cpDNA variation have so far failed to detect the presence of the C cpDNA haplotype in British material of *S. vulgaris* var.

vulgaris (or in British *S. squalidus*) although the haplotype has been found in one accession of radiate groundsel, *S. vulgaris* var. *hibernicus*, (Lowe & Abbott, 1995). It is assumed, therefore, that the C haplotype is present in *S. vulgaris*, but at low frequency in the British population of the species.

Table 3. Frequencies of electrophoretic phenotypes resolved for *Acp-2* and α *Est-1* in populations of *Senecio cambrensis* and its parent species *S. vulgaris* and *S. squalidus* sampled from north Wales and Edinburgh.

Location/Taxon	n	<i>Acp-2</i>			α <i>Est-1</i>		
		a	ab	b	a	ab	b
N. Wales							
<i>S. vulgaris</i>	337	1.0	-	-	0.81	0.01	0.18
<i>S. squalidus</i>	101	0.27	0.39	0.34	-	-	-
<i>S. cambrensis</i>	163	1.0	-	-	1.00	-	-
Edinburgh							
<i>S. vulgaris</i>	98	1.0	-	-	0.82	0.02	0.16
<i>S. squalidus</i>	44	-	-	1.0	-	-	-
<i>S. cambrensis</i>	28	-	1.0	-	-	-	1.00

N.B. Material from N. Wales was sampled from Wrexham and Mochdre (Colwyn Bay). A null *Acp-2* phenotype recorded at very low frequency in *S. squalidus* in N. Wales is omitted from the values calculated.

From the results of the analyses that have been conducted on *S. cambrensis*, it is apparent that this new species is a recent product of hybridization between *S. squalidus* and *S. vulgaris* and that its establishment and spread in Britain has been aided by at least two independent origins of the species following invasion of the British Isles by *S. squalidus*.

CONCLUSION

It is now possible to determine with reasonable accuracy the ecological and/or evolutionary origins of invasive weeds and any evolutionary consequences that arise from interspecific hybridization between such weeds or between an invasive weed and a native species. This ability rests on the availability of suitable genetic markers in the material under investigation. In our studies of British *Senecio* species and *Rhododendron ponticum*, isozyme and cpDNA markers proved to be of particular value in reconstructing past evolutionary and ecological events. With continuing advances in DNA technology a much wider range of genetic markers will become available for this type of research. Restriction analysis of ribosomal DNA or amplified fragments of the cpDNA genome have been employed by others in reconstructing past evolutionary and ecological events involving invading species (Soltis & Soltis 1990; Rieseberg *et al.*, 1990a, 1990b; Rieseberg, 1991; Arnold *et al.*, 1990a, 1991; Dorado *et al.*, 1992; Harris & Ingram, 1992; Ferris *et al.*, 1993), while yet others have used RAPDs for the same purpose (Arnold, *et al.*, 1991; Arnold, 1993; Rieseberg *et al.*, 1995; Bailey *et al.*, 1995). The advantage of using genetic markers in this type of research is obvious. Morphometric and crossing evidence etc. is of value in advancing particular hypotheses relating to the evolutionary and ecological history of an organism, but only the direct examination of the genetic material can confirm that such hypotheses are correct (Avice, 1994).

In this paper we have focussed on only one case study of the evolutionary consequences of hybridization between an invasive weed and a native plant. It is clear from other work, however, that such consequences are not uncommon. Recent studies by Rieseberg *et al.*,

(1990ab, 1995) on North American sunflowers (*Helianthus* spp.) and Arnold *et al.*, (1990ab, 1991) on North American irises (*Iris* spp.), have demonstrated that introgression and the origin of new hybrid diploid species has occurred in these groups following the invasion of new territory by a weedy species and hybridization with another species. Similarly, the origin of new allopolyploid species as a result of such hybridization is well known in *Tragopogon* (Soltis & Soltis, 1990) in North America and in *Spartina* (Gray *et al.*, 1991) in the British Isles. It is likely that other examples of such evolution will come to light following further studies. In the British flora there are many other recorded cases of interspecific hybridization involving invasive plants. For example, *S. viscosus* and *R. ponticum*, in addition to *S. squalidus*, are known to hybridize with related species in Britain (Crisp & Jones, 1978; Abbott & Lowe, 1995; unpublished) and in the case of *S. viscosus* an allohexaploid has been produced after treating the hybrid with *S. squalidus* with colchicine (Crisp & Jones, 1978). Similarly, recent work by Bailey *et al.* (1995) on the Japanese knotweed (*Fallopia japonica*), which is regarded by Crawley (1987) as one of the 'top twenty' invasive aliens in Britain, has shown that in the British Isles the most common form of the species, var. *japonica*, is always male sterile and produces viable seed only via interspecific hybridization with the related introduced species *F. sachalinensis* and *F. baldschuanica* (Russian vine). Hybrids between *F. japonica* var. *japonica* (2n=88) and *F. sachalinensis* (2n=44) are hexaploid (2n=66) and highly sterile, although small amounts of fertile pollen are produced by these hybrids and backcrossing to both parental taxa is expected to occur in the wild (Bailey *et al.*, 1995). Whether hybridization between these two species will lead to the evolutionary consequences that have followed other cases of hybridization involving invasive species, awaits to be determined. What we know from these other examples, however, is that the potential is present for such evolution to occur.

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