Biol Invasions (2009) 11:1145–1158
DOI 10.1007/s10530-008-9382-3

ORIGINAL PAPER

Recent hybrid origin and invasion of the British Isles by a self-incompatible species, Oxford ragwort (*Senecio squalidus* L., Asteraceae)

**Richard J. Abbott · Adrian C. Brennan ·
Juliet K. James · David G. Forbes ·
Matthew J. Hegarty · Simon J. Hiscock**

Received: 13 June 2007 / Accepted: 7 December 2007 /

Abstract *Senecio squalidus* is a diploid hybrid species which originated in the British Isles following the introduction of material collected from a hybrid zone on Mount Etna, Sicily, approximately 300 years ago. Introduced hybrid material was cultivated in the Oxford Botanic Garden and gave rise to the stabilized diploid hybrid species, which later spread throughout much of the UK and into some parts of Ireland. Unusually for an invasive species, *S. squalidus* has a strong system of sporophytic self-incompatibility (SSI) that may have become modified as a result of its recent hybrid origin and spread. First, *S. squalidus* contains relatively few *S* alleles (between 2 and 6 *S* alleles within individual UK populations) compared to other species with SSI (estimates average ~17 *S* alleles per population). This most probably reflects the population bottleneck experienced by introduced hybrid material. Second, dominance relationships among *S. squalidus S* alleles are more extensive than those reported in other species with SSI. Third, although pseudo-self-compatibility occurs sporadically in *S. squalidus*, it is not widespread, indicating that SSI is maintained in the species despite potential mate availability restrictions imposed by low numbers of *S* alleles. Surveys of other forms of genetic diversity in *S. squalidus* show that allozyme variation is reduced relative to that within the progenitor species, but Randomly Amplified Polymorphic DNA variation is relatively high. Both types of genetic variation show little or no pattern of isolation-by-distance between populations in keeping with the recent range expansion of the species. During its spread in the British Isles, *S. squalidus* has hybridized with the native self-compatible (SC) tetraploid species, *S. vulgaris,* which has led to the origin of three new SC hybrid taxa: a radiate form of *S. vulgaris* (var. *hibernicus*), a tetrapoid hybrid species (*S. eboracensis*) and an allohexaploid (*S. cambrensis*).

Keywords Hybridization · Invasion · Pseudo self-compatibility · Self-incompatibility · *Senecio* · Speciation

Introduction

The invasion of land by plants and animals that are geographically removed from their native ranges is a common biological phenomenon that has occurred repeatedly since such organisms first became terrestrial. In recent years, much emphasis and interest has focused on invasions resulting from human activities following the accidental or intentional introduction of

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R. J. Abbott (✉) · A. C. Brennan · J. K. James ·
D. G. Forbes
Mitchell Building, School of Biology, University
of St Andrews, St Andrews, Fife KY16 9TH, UK
e-mail: rja@st-andrews.ac.uk

A. C. Brennan · M. J. Hegarty · S. J. Hiscock
School of Biological Science, University of Bristol,
Woodlands Road, Bristol BS8 1UG, UK

plants and animals to new sites. Some of these introductions have established successfully in their new surroundings, become invasive, and spread rapidly from points of introduction. Sometimes this has had an adverse effect on native components of the flora and fauna in the area invaded (Pimentel 2002; Gurevitch and Padilla 2004). On other occasions, the main effect has been to enrich the flora and fauna of a particular region (Sax and Gaines 2003; Walker 2007). The latter is particularly true in areas that were glaciated during the Pleistocene as illustrated by the flora of Britain and Ireland. According to Preston et al. (2002), just half the species that comprise this flora are native while the remainder is introduced, mainly within the past 500 years. Much of Britain and Ireland was covered by a thick ice-sheet as recently as 18,000 years ago, at the time of the Last Glacial Maximum, and thus virtually all of the current British and Irish Flora, apart from some arctic-alpine elements, is of relatively recent origin and the product of biological invasion. The same is likely to be true of floras in many other regions of the world that were subjected to glaciation during the last ice age (Brochmann et al. 2003).

Studying a species that recently invaded a new territory allows one potentially to reconstruct events leading to its successful establishment and spread, and the factors that were important in this process. If there is a sufficiently good historical record of when a species was first introduced and how it subsequently spread, it is possible to determine, for example, whether there was a lag phase between introduction and spread (as is often the case), the speed at which the species spread following establishment, and what effects it has had on other components of the local flora and fauna. There is also the possibility of a detailed analysis of the source of introduced material to determine its genetic composition, and evolutionary changes that occurred during establishment and spread across ecological gradients (Lee 2002; Rieseberg et al. 2007). Consequently, it is possible to determine if rapid evolutionary change occurred in the invasive populations and to reveal which particular traits promoted invasiveness. It is not surprising, therefore, that invasive species are increasingly used as models for the study of rapid evolutionary change (Lee 2002).

A particularly interesting finding in recent years has been the importance of hybridization in plant invasions. From a review of the literature, Ellstrand and Schierenbeck (2000) reported that invasiveness is frequently preceded by hybridization either between different varieties, races or subspecies of a species, or between different species. Provided that the hybrids are not sterile, it is expected that hybridization between genetically divergent stocks, followed by recombination and segregation, will generate a wide array of recombinant genotypes on which selection can act. These recombinant genotypes may provide the means for adaptation to changed conditions during establishment and also at later stages as material spreads widely from its initial site(s) of establishment (Lee 2002). The importance of hybridization will extend further if, during its invasive phase, the species hybridizes with other components of the introduced or native flora, and acquires genes through introgression that provide adaptations to local conditions (Milne and Abbott 2000; Abbott et al. 2003). Harlan and de Wet (1963) were first to promote this idea and termed such species ‘compilospecies’, from the Latin *compilo*, to plunder or to rob (see also Fuertes Aguilar et al. 1999). Additionally, hybridization involving an invasive species might lead to the origin of new hybrid taxa at the homoploid level (Rieseberg et al. 1991; Abbott 1992; Bleeker 2003) or via allopolyploidy following chromosome doubling (Abbott 1992; Ashton and Abbott 1992). On the other hand, outbreeding depression and/or gene swamping could be experienced by a native species that hybridizes with an invading species, leading possibly to its extinction and loss of native biodiversity (Bleeker et al. 2007).

It is often considered that successful establishment of an introduced species following long distance dispersal will be enhanced by uniparental reproduction, and this has been termed Baker’s Law (Baker 1955; Stebbins 1957). However, there are many exceptions to this rule (Lane and Lawrence 1993; Radford 1997; Sun and Ritland 1998) including species with self-incompatibility (SI) systems such as *Senecio squalidus* (Abbott and Forbes 1993; Hiscock 2000a, b). Until recently, there had been no detailed analysis of the population genetics of SI in an invasive species. However, this deficiency has been rectified recently by an analysis of the population genetics of SI in the Oxford ragwort, *Senecio squalidus* (Brennan et al. 2002, 2003a, b, 2006).

Senecio squalidus is a particularly interesting invasive species, in that it originated recently in the British Isles from hybrid material (Abbott et al. 2000;

James and Abbott 2005), it exhibits sporophytic SI (Hiscock 2000a, b), and it has hybridized with a native species to give rise to two new self-fertile hybrid species and one stabilized introgressant form of a native self-fertile taxon (Abbott et al. 2003; Abbott and Lowe 2004). In this paper, we review the evidence for these different phenomena and consider evolutionary changes that may have occurred in Oxford ragwort since its origin in the British Isles.

Oxford ragwort in the British Isles: introduction and spread

Oxford ragwort, *S. squalidus*, is a short-lived, perennial herb derived from material introduced to Britain from Mount Etna, Sicily, at the beginning of the eighteenth century (Harris 2002). A reconstruction of the history of this event suggests that plants were first grown at the Duchess of Beaufort's Garden at Badminton, before being cultivated at the Oxford Botanic Garden, sometime before 1719, where they have been in continuous cultivation ever since. Linnaeus described the species in 1753 from plants raised by him from seed sent from Oxford (Walker 1833; Harris 2002). In 1794, the species was reported growing on walls in the Oxford area (Sibthorp 1794) and was described as a garden escape. The subsequent spread of the species from Oxford was aided initially by exchange of seeds between botanic gardens, but in the late nineteenth century, following the establishment of the railway system in the British Isles, *S. squalidus* began spreading rapidly from Oxford via the railway network. Druce (1927) pointed out that railways provided the species with a substrate similar to the lava soils that it grows on in Sicily. More recently, the species has spread along motorway verges in Britain, and is now common on waste-ground especially in urban areas. The spread of the species in the British Isles was chronicled by Kent (1955, 1956, 1957, 1960, 1963, 1964a, b, c, 1966). Records show that it began to spread northwards in the late nineteenth century and reached different parts of northern England between the early to middle of the twentieth century (Fig. 1). The species became established in the wild in the Central Belt of Scotland during and after the mid-1950s (Kent 1955; 1966), and has continued to spread further north in Scotland and into Northern Ireland in recent years (Fig. 1).

Hybrid origin of *S. squalidus*

Druce (1927) and Kent (1956) described *S. squalidus* as introduced from Sicily, Italy. Crisp (1972) later proposed that the species originated in the British Isles from hybrids between the species *S. aethnensis* Jan. ex DC and *S. chrysanthemifolius* Poiret which grow at high and low altitudes, respectively, on Mount Etna in Sicily. Crisp (1972) advanced that following almost a century of cultivation in the Oxford Botanic Garden, stabilized derivatives of this introduced hybrid material escaped and spread rapidly to many parts of the British Isles. He concluded that "British *S. squalidus* is of hybrid origin…" and "…can be treated as a separate species… because it is both geographically isolated from the parental species, and it has evolved over…. many generations to a state where it is morphologically distinct from either of them, although still polymorphic and in general intermediate between them." The hypothesis that *S. squalidus* is a diploid hybrid derivative has since been tested by surveys of morphological and isozyme variation (Abbott et al. 2000, 2002), and more recently by a detailed survey of Randomly Amplified Polymorphic DNA (RAPD) and inter-simple sequence repeat (ISSR) variation (James and Abbott 2005) in *S. squalidus*, its two putative parents, and hybrid plants from Mount Etna.

In the wild, *Senecio aethnensis* produces large capitula and entire, glaucous leaves, while *S. chrysanthemifolius* has smaller capitula and highly dissected, non-glaucous leaves. These differences are retained in plants raised under 'common garden' conditions (Abbott et al. 2000). A principal component analysis of 32 morphological traits measured on plants raised from seed in a glasshouse (Abbott et al. 2000) showed that *S. squalidus* closely resembles plants derived from the hybrid zone on Mount Etna, and is morphologically intermediate to its putative parents. Interestingly, this morphological intermediacy is due to plants possessing a mix of traits that distinguish the two species, rather than possessing characters with means intermediate to those of the two parents. Two samples of *S. squalidus* were examined in the study—one from Oxford and the other from Edinburgh. The two samples differed in mean for only two characters—total floret number and disc floret number per capitulum. In Edinburgh material, there was no evidence for the mean of any

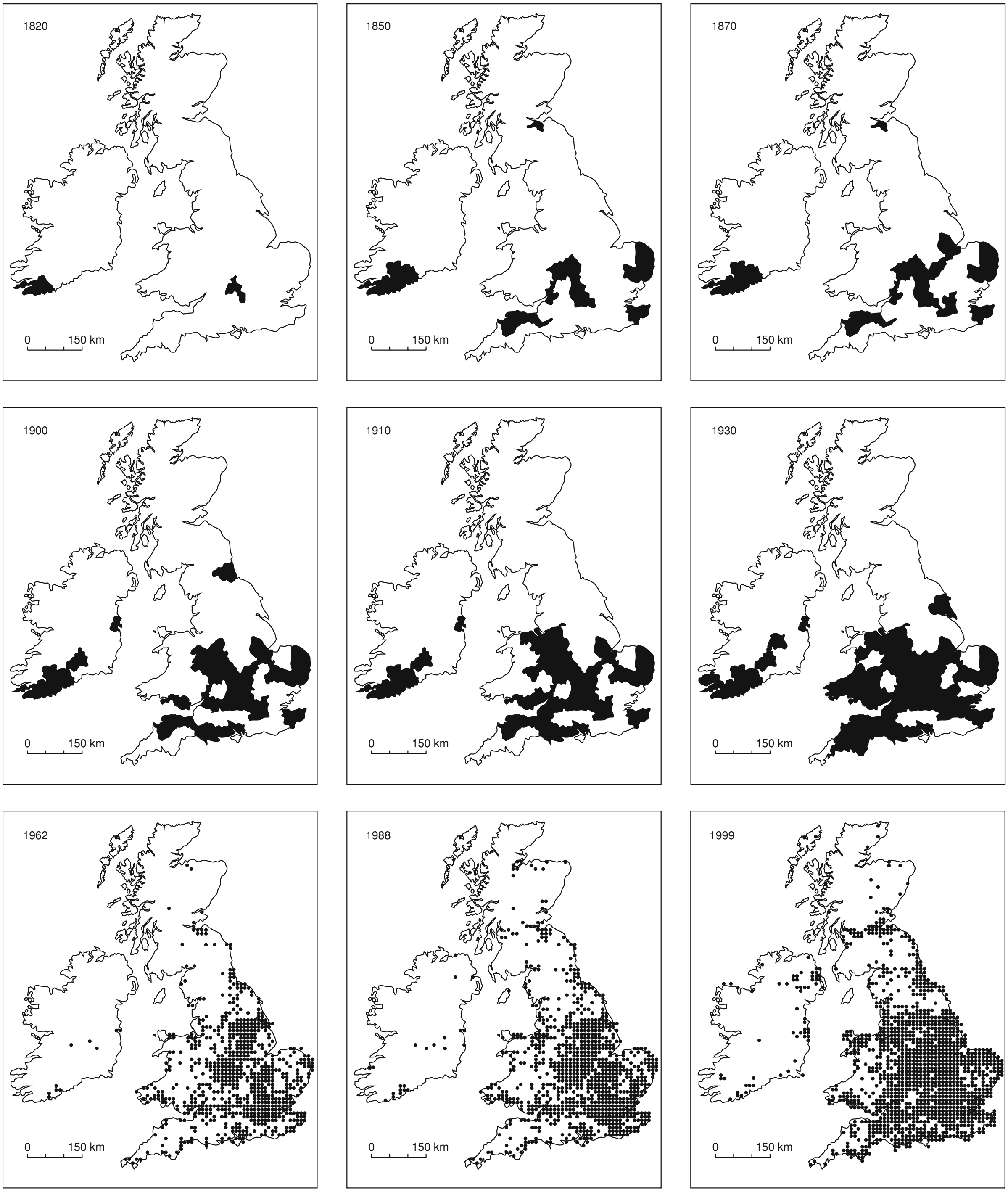
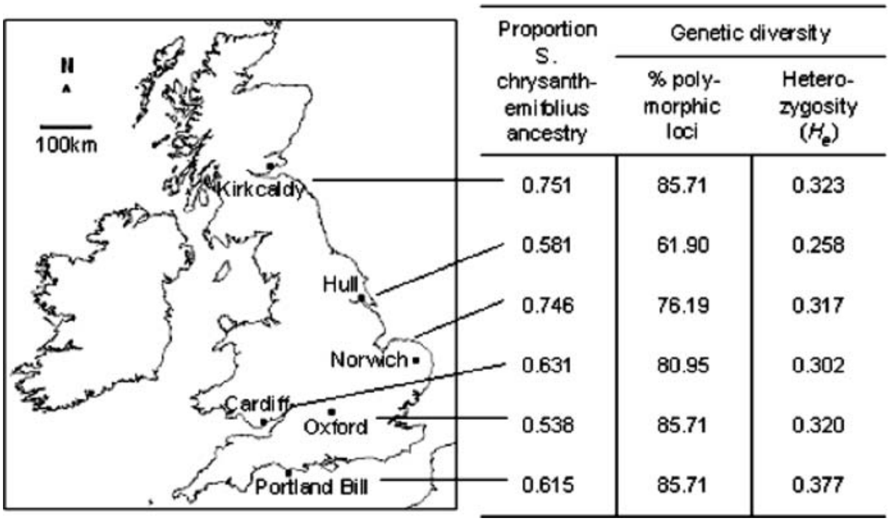


Fig. 1 The spread of *Senecio squalidus* in the British Isles from Oxford where it was first recorded in the wild in 1794. Maps for 1820–1930 are redrawn from Crisp (1972) and are based on the presence (*black*) or absence (*white*) of the species in Vice-Counties of the British Isles. Maps for 1962, 1988 and 1999 were obtained from the Biological Records Centre, Centre of Ecology and Hydrology, with each *black dot* representing at least one record of the species in a 10 km square of the National Grid

character measured being either significantly higher or lower than the means recorded for the same character in both putative parent species. Thus there was no evidence that transgressive segregation (Rieseberg et al. 1999) had generated morphological novelty in this material. In contrast, there was evidence of transgressive expression in morphology in Oxford material, but for only 3 of the 32 characters measured (one capitulum trait and two leaf characters). The fact that most morphological characters in *S. squalidus* do not appear to exhibit transgressive expression is interesting because transgressive segregation is reported to occur frequently in hybrid derivatives (Rieseberg et al. 1999), and has been suggested to be important in generating novel traits that could aid the adaptation of hybrids to new habitats from which parent species are excluded (Rieseberg et al. 2003; Lexer et al. 2003; Gross and Rieseberg 2005). Notwithstanding this, it is entirely possible that *S. squalidus* exhibits transgressive change in metabolic and physiological characters relative to its parents that have facilitated its colonization of Britain. This hypothesis is supported by studies of gene expression in *S. squalidus* using microarrays, which have revealed transgressive changes in the expression patterns of a number of metabolic genes relative to their expression in *S. chrysanthemifolius* and *S. aethnensis* (Hegarty et al. 2009).

Morphological analysis provides only an indication of whether a species is of hybrid origin. More substantial evidence requires molecular analysis (Rieseberg and Ellstrand 1993; Chapman and Abbott 2005). A survey of allozyme variation provided some initial molecular support for *S. squalidus* being of hybrid origin (Abbott et al. 2000, 2002) in that some British populations of *S. squalidus* were genetically similar to material collected from the hybrid zone between *S. aethnensis* and *S. chrysanthemifolius* on Mount Etna. In particular, at one allozyme locus (*Acp*2), *S. squalidus* and hybrids were both polymorphic for two alleles, one of which was fixed in *S. aethnensis*, while the other was fixed in *S. chrysanthemifolius*. Molecular confirmation that *S. squalidus* is of hybrid origin recently came from a survey of RAPD/ISSR variation (James and Abbott 2005). This showed that *S. squalidus* contained 11 of 13 RAPD/ISSR markers recorded at high frequency in *S. chrysanthemifolius*, but which were absent or occurred at low frequency in *S. aethnensis*, and 10 of 13 markers for which the reverse was true. Bayesian admixture analysis using the computer program STRUCTURE (Pritchard et al. 2000) showed that all individuals of *S. squalidus* surveyed (72 individuals from 6 populations) were of mixed ancestry with relatively high mean proportions of ancestry derived from both *S. chrysanthemifolius* and *S. aethnensis* (0.644 and 0.356, respectively). Populations varied significantly in mean *S. chrysanthemifolius* ancestry ranging from approximately 50–75% (Fig. 2). Although of hybrid origin, further analysis by principal coordinate analysis showed that each *S. squalidus* individual possessed a multilocus RAPD/ISSR phenotype clearly different from those possessed by nearly



Proportion S. chrysanth-emifolius ancestry	Genetic diversity	
	% poly-morphic loci	Hetero-zygosity (H_e)
0.751	85.71	0.323
0.581	61.90	0.258
0.746	76.19	0.317
0.631	80.95	0.302
0.538	85.71	0.320
0.615	85.71	0.377

Fig. 2 Mean proportion of *S. chrysanthemifolius* ancestry in six populations of *S. squalidus* in the British Isles (from James and Abbott 2005), and estimates of genetic diversity in these populations, based on a survey of RAPD/ISSR variation

all individuals screened from the hybrid zone on Mount Etna and that individuals clustered as a separate group. Moreover, all individuals of *S. squalidus* only possess the cpDNA haplotype that characterizes *S. chrysanthemifolius*, and never the one also found in *S. aethnensis*, whereas hybrids on Mount Etna may possess either one of these haplotypes. This is evidence, therefore, that *S. squalidus* has a unique genetic make-up, and should not simply be considered as an indistinguishable part of the hybrid swarm between *S. aethnensis* and *S. chrysanthemifolius* on Mount Etna that has been displaced to the British Isles. Crosses between *S. squalidus* and its parents usually produce vigorous and fertile F_1 and F_2 offspring under glasshouse conditions (R. J. Abbott, persernal observation). Consequently, there is little evidence of intrinsic postzygotic isolation between *S. squalidus* and its parent taxa under these conditions. However, it is hypothesized that reproductive isolation between the hybrid species and its parents is maintained by habitat isolation aided by spatial separation. Transplant studies are currently being conducted to test this hypothesis.

Population genetic structure

Allozyme variation

An examination of the population genetic structure of an invasive species may help to establish how the distribution of variation within and among populations has been affected by such factors as: (a) founder effects during the initial colonization phase; (b) range expansion; (c) genetic drift and gene flow; (d) mating system; and (e) selection on non-neutral variation.

A survey of allozyme variation for six enzymes representing eight loci within and among nine populations of *S. squalidus* in the British Isles showed that genetic diversity (measured in terms of mean number of alleles per locus, percentage of polymorphic loci, and gene diversity within populations (H_E) was lower in *S. squalidus* than in either of its parent species, *S. aethnensis* and *S. chrysanthemifolius,* or in hybrid populations from Mount Etna (Table 1; Abbott et al. 2000). This indicates that during the introduction of hybrid material to the British Isles and/or during the subsequent origin of *S. squalidus*, only a proportion of the genetic diversity present in Mount Etna material became incorporated into that now present in Britain. Seven out of the nine populations were at Hardy–Weinberg (H–W) genotype frequency equilibrium. Thus in most populations random mating can be assumed. Typical random mating within populations as measured by H–W equilibrium has been confirmed by an additional allozyme study investigating a different set of eleven populations for twelve loci (Brennan 2003a, b; Brennan et al. 2005). For both studies, significant genetic differentiation between populations was detected for allozyme variation based on F_{ST} estimates ($F_{ST} = 0.09$–0.385; significantly >0 at a 95% confidence level, Table 1). However, there is little obvious geographical pattern to population differentiation. The allozyme survey based on nine populations did not detect significant isolation-by-distance (Mantel's test; $R^2 = 0.11$, $P = 0.28$), while that based on eleven populations resolved a pattern of isolation-by distance but the correlation only explained a small proportion of the variation (Mantel's test; $R^2 = 0.19$, $P < 0.01$). It seems likely that population differences in allozyme variation are largely the product of founder effects and genetic drift occurring during and following the colonization of new sites, and that the recent range expansion of *S. squalidus* in the British Isles has prevented the accumulation of much isolation-by-distance between populations.

Table 1 Estimates of genetic diversity in *Senecio squalidus* based on surveys of variation over (a) 21 RAPD/ISSR loci, (b) eight allozyme loci (Abbott et al. 2000), and (c) 12 allozyme loci (Brennan 2003a, b)

Study	Number of populations	Mean number individuals per population	Mean % polymorphic loci per population	Mean H_E per population	PhiPT (a) or F_{ST} (b), (c)
(a)	6	12.0	79.37	0.316	0.210
(b)	9	24.9	20.83	0.063	0.385
(c)	11	17.3	41.67	0.156	0.091

RAPD/ISSR variation

The results of a survey of RAPD/ISSR variation conducted on 12 individuals from each of 6 populations of *S. squalidus* sampled from different parts of England, Wales and Scotland (Fig. 2) were used to demonstrate that *S. squalidus* is of hybrid origin (see above) and to examine its population structure (James and Abbott 2005). However, here we restrict population genetic analysis to 21 of the 26 loci previously examined. At these 21 loci a band was present in 1 or more *S. squalidus* individuals examined, whereas at the other 5 loci no band was recorded in any individual tested. Analysis shows that each of the 72 individuals examined possessed a unique RAPD/ISSR phenotype and that each population contained a relatively high level of genetic diversity (Fig. 2). Mean percentage of polymorphic loci and mean gene diversity within populations (H_E) were considerably greater than the same estimates of diversity based on allozyme variation (Table 1). An analysis of molecular variance (AMOVA) revealed that most RAPD variation across populations was due to differences between individuals within populations (79%), although variation between populations (21%) was significant. A Mantel test (Mantel 1967) showed that the correlation between pairwise genetic distances between populations (in terms of PhiPT) and geographical distances among populations, although higher than that recorded for allozyme variation (see above), was not significant ($R^2 = 0.320$, $P = 0.092$; Fig. 3). These results also suggest that genetic differences between populations result from founder effects and genetic drift and that the lack of an association between genetic and geographical distance between populations is most likely due to the recent rapid range expansion of *S. squalidus* in the British Isles (Fig. 4).

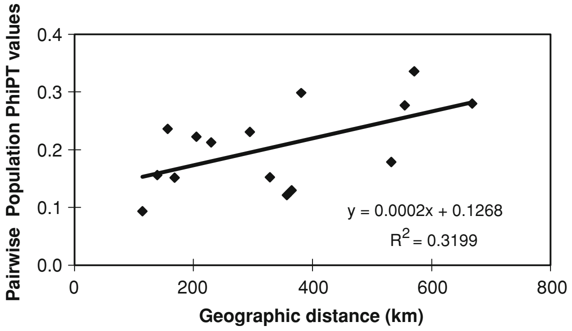
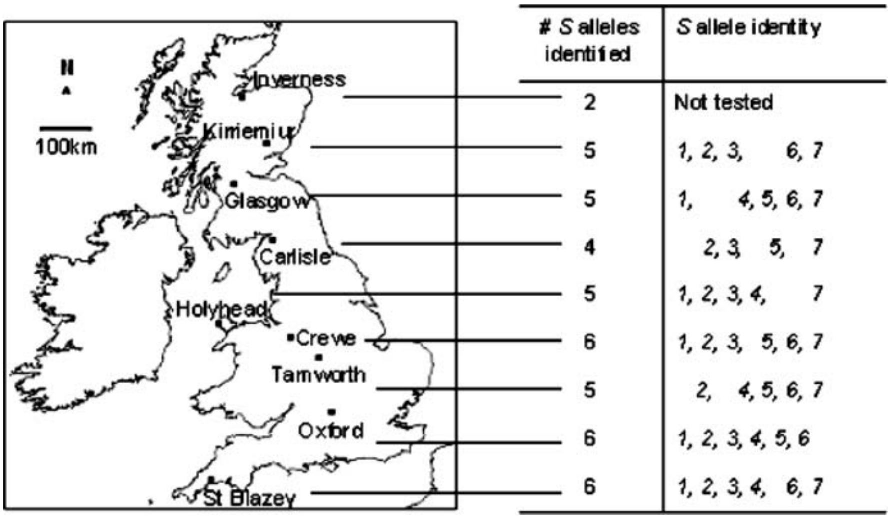


Fig. 4 A plot of pairwise genetic distance (based on PhiPT values) against pairwise geographic distance (km) between six populations of *S. squalidus* surveyed for RAPD/ISSR variation and described in Fig. 2. The slope of the regression line and R^2 value were calculated using a Mantel test with the software GenAlEx6 (Peakall and Smouse 2006)

Mating system

According to Baker's Law (Baker 1955), successful colonizing and invasive plants are usually self-fertile (self-compatible (SC)) (Stebbins 1957; Baker 1967). Studies of the mating system of *S. squalidus,* however, have shown that individuals exhibit strong SI across its

Fig. 3 The number, identity and distribution of self-incompatibility (*S*) alleles in *S. squalidus* (from Brennan et al. 2006)



# *S* alleles identified	*S* allele identity
2	Not tested
5	1, 2, 3, 6, 7
5	1, 4, 5, 6, 7
4	2, 3, 5, 7
5	1, 2, 3, 4, 7
6	1, 2, 3, 5, 6, 7
5	2, 4, 5, 6, 7
6	1, 2, 3, 4, 5, 6
6	1, 2, 3, 4, 6, 7

entire British range and, as in other species of Asteraceae, this SI is regulated sporophytically by a single polymorphic *S* locus (Abbott and Forbes 1993; Hiscock 2000a, b; Brennan et al. 2002, 2005, 2006). Baker's Law is clearly not 'set in stone' and there are other examples of SI species becoming successful colonists, (e.g., *Papaver rhoeas* (Lane and Lawrence 1993), *Senecio madagascariensis* (Radford 1997) and *Centaurea solstitialis* (Sun and Ritland 1998)), but the finding of strong SI in *S. squalidus* is intriguing, particularly in the light of the extreme population bottleneck that its ancestors must have experienced during its introduction and early colonization. Following a population bottleneck, allelic diversity at the *S* locus will be lowered and opportunities for mating (between individuals carrying different *S* alleles) correspondingly reduced (Hiscock 2000b; Brennan et al. 2002). Under such conditions, selection for reproductive assurance frequently leads to an erosion of the SI system and the evolution of self-compatibility (SC) (Reinartz and Les 1994; Cheptou et al. 2002; Nielsen et al. 2003). This has not happened in *S. squalidus* indicating that either the numbers of *S* alleles in British populations are sufficient to support effective mating and thereby maintain strong SI, or that other mating system characteristics (e.g., long flowering season, and generalist pollinators) can compensate for reduced allelic diversity at the *S* locus.

An extensive survey of the number and frequency of *S* alleles in populations of *S. squalidus* across the British Isles revealed that there are approximately seven *S* alleles in the entire British population (Brennan et al. 2006). Local populations maintain subsets of these 6–7 *S* alleles (mean 5.3), with the Oxford population maintaining a majority (6), in line with it being the center of introduction (Brennan et al. 2006; Fig. 3). These numbers of *S* alleles are very low when compared to population level estimates for other SI species which typically maintain ~10–43 *S* alleles (Lawrence 2000; Brennan et al. 2003b).

In species with SSI, such as *S. squalidus*, the incompatibility phenotype of the haploid pollen is controlled by the diploid genome of its parent plant, so pollen grains carry products of two *S* alleles as opposed to one (c.f. gametophytic SI). When *S* alleles are codominantly expressed, this increases the efficiency of kin recognition up to 50%, although this may also have the effect of further limiting the number of compatible mates in populations with few *S* alleles (Hiscock and McInnis 2003). However, with SSI, but not GSI, dominance relationships among *S* alleles are possible that mask recessive *S* allele phenotypes and introduce a degree of control over compatibility levels within populations independent of *S* allele number (Hiscock and Tabah 2003; Hiscock and McInnis 2003). Mate availability increases with greater levels of *S* allele dominance interactions with most improvement when there are few *S* alleles (Byers and Meagher 1992; Vekemans et al. 1998; Hiscock and Tabah 2003). Interestingly, populations of *S. squalidus* support these predictions, with few *S* alleles and high levels of dominance interactions. Comparisons between the limited number of population level studies of *S* allele dominance indicate that there is a negative correlation between *S* allele number and frequency of dominance (Brennan et al. 2003b). This suggests that the observed high frequency of dominance interactions among *S. squalidus* *S* alleles serves to optimize mate availability in these *S* allele-depleted populations and facilitates reproductive assurance during colonization (Brennan et al. 2006). Whether these high levels of dominance interactions represent a chance 'pre-adaptation' already present in the founding ancestors of *S. squalidus*, or whether dominance evolved among *S* alleles after the introduction event is being determined through studies of SI in populations of *S. squalidus'* relatives on Mount Etna (A. C. Brennan, S. J. Harris and S. J. Hiscock, in preparation).

Populations of *S. aethnensis*, *S. chrysanthemifolius* and their hybrids all maintain relatively large numbers of a diverse pool of *S* alleles, with estimates ranging from between 9 and 26 *S* alleles per population in line with 'typical' population *S* allele numbers for species with SSI (Lawrence 2000). The frequency of individuals exhibiting *S* allele dominance interactions in the Mount Etna populations appears relatively high, but lower than the frequency observed in British *S. squalidus* (A. C. Brennan, S. J. Harris and S. J. Hiscock, in preparation) supporting the hypothesis that the high frequencies of dominance interactions among *S* alleles in *S. squalidus* may be a relatively recent phenomenon that evolved as a consequence of establishment and invasiveness in Britain. The genetic basis of dominance among *S* alleles in *S. squalidus* is not known, but work on SSI in *Brassica* indicates that dominance is regulated epigenetically (Shiba et al. 2002) through reversible DNA methylation (Shiba et al. 2006). Epigenetic control of *S* allele dominance interactions clearly offers the potential for dominance levels to be highly responsive to selection. For now, we can only predict that dominance among *S* alleles in *Senecio* may have an epigenetic basis, because the molecular basis of SSI in *S. squalidus* is different to that found in *Brassica*, and is as yet unresolved (Hiscock et al. 2003; Hiscock and Tabah 2003; Tabah et al. 2004).

Despite strongly expressed SI in populations of *S. squalidus* across Britain, it is possible to identify a few individuals with 'leaky' SI that set small numbers of seeds after selfing within most populations (Brennan et al. 2005). This phenomenon has been observed in many SI species, especially in wild populations, and is usually referred to as 'pseudo-self-compatibility' (PSC), since while individuals are able to produce a few seeds after self-pollination, the number of seeds produced is far lower than that produced following a compatible cross-pollination (Levin 1996; Stephenson et al. 2000). PSC is a quantitative trait controlled by variable numbers of 'modifier loci' that modulate the strength of SI and which are unlinked to the *S* locus (Vogler et al. 1998; Stephenson et al. 2000; Vogler and Kalisz 2001).

In *S. squalidus,* 3.1% of all individuals sampled across the UK were classified as PSC (Brennan et al. 2005). These individuals produced 1–10 seeds (counted as the number of fruits or achenes) per capitulum after self-pollination, compared to 40–80 seeds per capitulum following a cross-pollination. It is likely that PSC has contributed to the success of *S. squalidus* as a colonist, by providing a basis for limited uniparental reproduction, because the frequency of PSC varies between populations (ranging from 0 to 8% of individuals), suggesting that PSC is sensitive to selection. When populations are small and mating opportunities are few (e.g., due to reduced *S* allele diversity), modifiers that weaken SI may be at a selective advantage because they deliver reproductive assurance, whereas in larger populations, modifiers which impart PSC may be at a selective disadvantage because they are associated with inbreeding depression; the latter has been shown in *Crepis sancta* (Cheptou et al. 2002). Indeed, an investigation into rates of selfing and associated inbreeding depression in *S. squalidus* revealed high levels of inbreeding depression associated with 'forced' selfing (induced by self-pollinating stigmas treated with dilute salt solution, Brennan et al. 2005) indicating that selfing through PSC carries a fitness cost upon which selection can act. The balance between the selective forces of inbreeding depression (maintaining SI) and reproductive assurance (favouring PSC) is likely to be critical in maintaining equilibrium between SI and PSC in *S. squalidus* populations. One could therefore predict that the frequency of PSC might be higher in pioneer populations experiencing metapopulation dynamics compared to more stable populations, but currently the empirical data are inconclusive (Brennan et al. 2005, 2006) because all UK populations so far studied appear to function as metapopulations (A. C. Brennan and S. J. Hiscock, unpublished). More ecological studies of PSC are therefore needed to test this hypothesis rigorously.

Expression of PSC in *S. squalidus* appears to be determined by at least three genetic loci and its strength can be affected by specific environmental factors, such as the presence of salt at the stigma surface (Tabah 2004; Brennan et al. 2005). Interestingly, regular exposure to salt is often a feature of many habitats of *S. squalidus*, particularly roadsides and to a lesser extent railway lines, suggesting that environmentally-induced PSC may also have contributed to the colonizing success of *S. squalidus* (Hiscock 2000b; Brennan et al. 2005).

Studies of mating system variation in natural populations of a wide range of outcrossing species, including *S. squalidus*, are now highlighting the fact that SI is not simply a qualitative trait (the *S* locus) because it can also be subject to variable levels of quantitative control through the action of modifiers (Vogler et al. 1998; Stephenson et al. 2000; Vogler and Kalisz 2001; Brennan et al. 2005). Species like *S. squalidus*, with a high degree of quantitative control over SI will have greater reproductive flexibility during population disturbances or metapopulation dynamics and may therefore make better colonists or become invasive. The extent to which the SI system of *S. squalidus* has been modified by its population history in the UK or was pre-adapted for colonizing success on account of its hybrid origin on Mount Etna will become clearer when studies of the SI mating system of its parental taxa and their hybrids on Mount Etna are complete. Evidence so far suggests that 'flexibility' within the mating system of *S. squalidus* in the form of variable levels of PSC and perhaps *S* allele dominance has probably contributed to its success as an invasive colonist.

Evolutionary change

Invasive species are increasingly recognized as suitable models for the study of rapid evolutionary change (Lee 2002; Rieseberg et al. 2007) and a number of studies have already shown that rapid evolution can take place when such species spread across ecological gradients (e.g., Weber and Schmid 1998; Huey et al. 2000). The fact that *S. squalidus* occurs in a climatic zone (temperate and oceanic) very different from that of its parents (Mediterranean) would suggest that significant evolutionary change might have occurred during the origin and early establishment of *S. squalidus,* aiding its adaptation to conditions in the British Isles and enhancing its ecological isolation from its parents. Moreover, further evolutionary change may have occurred as the species spread northwards from the warmer and drier climate in the south of the British Isles to the colder and moister climate in the north. Currently, there is no information on the nature and extent of possible adaptive divergence in *S. squalidus* in the British Isles. Clearly, an excellent opportunity is presented to obtain such information and to determine which characters and genes have been most influenced by selection. To this end, genomic screens and microarray analyses are currently being conducted in our laboratories to identify those parts of the genome, which may have been subjected to selection during the origin and subsequent establishment of *S. squalidus* in the British Isles. Others (John Pannell, University of Oxford, personal communication) are conducting reciprocal transplant experiments to establish if populations sampled from the south and north of the British Isles show local adaptation to environmental conditions at their respective locations.

Interspecific hybridization with native taxa and subsequent evolution

During its recent spread throughout a large part of the British Isles, *S. squalidus* has hybridized with the native species, *S. vulgaris* L. (Common Groundsel) (Marshall and Abbott 1980), and this has led to the origin of two new species, *S. cambrensis* Rosser and *S. eboracensis* Abbott & Lowe, and also the origin of a stabilized introgressant form of *S. vulgaris*, i.e., var *hibernicus* Syme. These events have been reviewed in detail elsewhere (Abbott and Lowe 1996, 2004; Abbott et al. 1998, 2005) and therefore will only be summarized briefly here.

Origin of *S. cambrensis*

Senecio cambrensis is the allohexaploid ($2n = 6x = 60$) of diploid *S. squalidus* ($2n = 2x = 20$) and tetraploid *S. vulgaris* ($2n = 4x = 40$), which originated in North Wales, in the early to mid-part of the twentieth century (Rosser 1955; Ashton and Abbott 1992). Isozyme and chloroplast DNA evidence shows that there were at least two independent origins of the species in the UK: at least one in North Wales, and another in Edinburgh, Scotland (Ashton and Abbott 1992; Harris and Ingram 1992). *Senecio cambrensis* is SC and reproduces mainly by self-fertilization (Ingram and Noltie 1995). It exhibits a metapopulation structure in the wild with subpopulations frequently becoming extinct and new ones establishing through colonization. The Edinburgh lineage, which was discovered in 1982 (Abbott et al. 1983), is now extinct in the wild (Abbott and Forbes 2002) due to sites being built on where it occurred, and a massive reduction in number of alternative potential sites for colonization from the early 1990s onwards (Abbott and Forbes 2002). The species remains present in north Wales (Ingram and Noltie 1995; Abbott and Lowe 2004) where its populations fluctuate greatly in size between years and locations (Ingram and Noltie 1995). However, there has been a notable decline in both number of populations and individuals per population in north Wales over the past 25 years (Abbott et al. 2007). This recent decline has occurred despite the fact that *S. cambrensis* contains high levels of genetic variability (Abbott et al. 2007) and also exhibits large-scale alterations in its gene expression relative to that of its parents and the triploid hybrid *S. X baxteri* (Hegarty et al. 2005, 2006). It might be expected that both of these factors would increase the ability of the species to adapt to conditions different from those experienced by its parents, and thus favor its maintenance (and possible spread) in the wild. However, its recent decline in north Wales is probably due to a marked loss of suitable sites for colonization and also to increased use of herbicide to control weed populations (Abbott et al. 2007).

Senecio eboracensis

Senecio eboracensis was first recorded in the British Isles in 1979 (Lowe and Abbott 2003). It is thought to have originated shortly before its discovery in York, England, as a tetraploid product of hybridization between *S. squalidus* and *S. vulgaris*. The hybrid status of *S. eboracensis* is evident from its intermediate morphology and its possession of an additive isozyme profile (Irwin and Abbott 1992). It is prezygotically isolated from both parent taxa due largely to its predominant self-fertilization in the wild (Lowe and Abbott 2004). However, its maintenance in the wild is currently in doubt. Following its discovery in York in 1979, populations of the species were maintained at two sites in the city until the late 1990s. Both of these sites have been built on in the last few years and also sprayed at regular intervals with herbicide, and since 2,000 *S. eboracensis* has not been found at either site or elsewhere in York.

Senecio vulgaris var. *hibernicus*

The inland radiate form of *S. vulgaris* (var. *hibernicus*) in the British Isles, originated following introgressive hybridization between the discoid form of *S. vulgaris* (var. *vulgaris*) and *S. squalidus* (Ingram et al. 1980; Abbott et al. 1992). The radiate form has flower heads (capitula) with ray florets, which are lacking in the discoid form. Presence/absence of ray florets is controlled by a single gene with var. *hibernicus* homozygous for the *ray* allele and var. *vulgaris* homozygous for the alternative allele (Trow 1912). There is molecular evidence that the *ray* allele was introgressed into *S. vulgaris* from *S. squalidus* to give rise to var. *hibernicus* (Abbott et al. 1992; Kim et al. 2008). The radiate variant was first recorded in 1832 in Oxford (Crisp 1972) and has subsequently been reported in many parts of the British Isles (Abbott et al. 1992; 2003). A number of factors are believed to have favoured its establishment, including greater seed production under some conditions (Oxford and Andrews 1977; Abbott 1985) and a difference in germination behavior (Abbott et al. 1998). However, pure stands of the variant are never found and an understanding of the factors that maintain populations that are polymorphic for both variants of *S. vulgaris,* and their heterozygote, remains elusive (Abbott et al. 1998). Marshall and Abbott (1982, 1984a) showed that the radiate morph exhibits a higher maternal outcrossing rate than the discoid morph, due to pistillate ray florets showing greater outcrossing than hermaphroditic disc florets (Marshall and Abbott 1984b), and also because radiate plants are more attractive to pollinators (Abbott and Irwin 1988).

Conclusions

Senecio squalidus is an excellent model for studying many aspects of the ecology, genetics, and evolution of an invasive diploid plant species. The species is known to have originated in the very recent past through diploid hybrid speciation, and then to have spread rapidly through a large part of the British Isles across an ecological gradient involving changes in temperature and rainfall. From the work conducted on this species, much has been learnt about its origin, its mating system (particularly in regard to the nature and population genetics of its SI system), its overall population genetic structure, and several important evolutionary events resulting from its hybridization with the native tetraploid species, *Senecio vulgaris*. However, much remains to be discovered in regard to why the species has been such a highly successful invasive plant. For example, it will be of interest to determine what genetic changes may have occurred during and following the origin of *S. squalidus* that adapted it to conditions in the British Isles and which in turn may have enabled it to spread widely thereafter. Currently, we are using a number of approaches, including genomic screens and microarray analysis, to isolate genes that may have been important in adapting *S. squalidus* to conditions in the British Isles. The isolation of such genes in this and other invasive plant species will lead to a greatly improved understanding of the genetic basis of invasiveness in plants.

Acknowledgments RJA and SJH are grateful to NERC for the award of several research grants and PhD studentships that allowed the work described in this paper to be conducted. We are also grateful for the comments of three reviewers on an earlier version of the manuscript.

References

Abbott RJ (1985) Maintenance of a polymorphism for outcrossing frequency in a predominantly selfing plant. In: Haeck J, Woldedorp J (eds) Structure and functioning of plant populations, 2. North-Holland Publishing, Amsterdam, pp 277–286

Abbott RJ (1992) Plant invasions, interspecific hybridization and the evolution of new plant taxa. Trends Ecol Evol 7:401–405

Abbott RJ, Forbes DG (1993) Outcrossing rate and self-incompatibility in the colonizing species *Senecio squalidus* L. Heredity 71:155–159

Abbott RJ, Forbes DG (2002) Extinction of the Edinburgh lineage of the allopolyploid neospecies *Senecio cambrensis* Rosser Asteraceae. Heredity 88:267-269

Abbott RJ, Irwin JA (1988) Pollinator movements and the polymorphism for outcrossing rate at the ray floret locus in groundsel, *Senecio vulgaris*. Heredity 60:295–299

Abbott RJ, Lowe AJ (1996) A review of hybridisation and evolution in British *Senecio*. In: Hind DJN, Beentje HJ (eds) Compositae: systematics. Royal Botanic Garden, London, pp 679–689

Abbott RJ, Lowe AJ (2004) Origins, establishment and evolution of new polyploid species: *Senecio cambrensis* and *S. eboracensis* in the British Isles. Biol J Linn Soc 82:467–474

Abbott RJ, Ingram R, Noltie HJ (1983) Discovery of *Senecio cambrensis* Rosser in Edinburgh. Watsonia 14:407–408

Abbott RJ, Ashton PA, Forbes DG (1992) Introgressive origin of the radiate groundsel, *Senecio vulgaris* L. var. *hibernicus* Syme: *Aat-3* evidence. Heredity 68:425–435

Abbott RJ, Bretagnolle FC, Thébaud C (1998) Evolution of a polymorphism for outcrossing rate in *Senecio vulgaris*: influence of germination behaviour. Evolution 52: 1593–1601

Abbott RJ, James JK, Irwin JA et al (2000) Hybrid origin of the Oxford ragwort, *Senecio squalidus* L. Watsonia 23: 123–138

Abbott RJ, James JK, Forbes DG et al (2002) Hybrid origin of the Oxford ragwort, *Senecio squalidus* L.: morphological and allozyme differences between *S. squalidus* and *S. rupestris* Waldst. and Kit. Watsonia 24:17–29

Abbott RJ, James JK, Milne RI et al (2003) Plant introductions, hybridization and gene flow. Philos Trans R Soc B 358:1123–1132

Abbott RJ, Ireland HE, Joseph L et al (2005) Recent plant speciation in Britain and Ireland: origins, establishment and evolution of four new hybrid species. Biol Environ Proc R Irish Acad 105B:173–183

Abbott RJ, Ireland HE, Rogers HJ (2007) Population decline despite high genetic diversity in the new allopolyploid species *Senecio cambrensis* (Asteraceae). Mol Ecol 16:1023–1033

Ashton PA, Abbott RJ (1992) Multiple origins and genetic diversity in the newly arisen allopolyploid species, *Senecio cambrensis* (Compositae). Heredity 68:25–32

Baker HG (1955) Self-compatibility and establishment after 'long-distance' dispersal. Evolution 9:347–348

Baker HG (1967) Support for Baker's Law – as a rule. Evolution 21:853–856

Bleeker W (2003) Hybridization and *Rorippa austriaca* (Brassicaceae) invasion in Germany. Mol Ecol 12:1831–1841

Bleeker W, Schmitz U, Ristow M (2007) Interspecific hybridization between native and alien plant species in Germany and its consequences for native biodiversity. Biol Conserv 137:248–253

Brennan AC (2003) The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae). D.Phil. dissertation, University of Oxford, UK

Brennan AC, Harris SA, Tabah DA et al (2002) The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae) I. *S* allele diversity in a natural population. Heredity 89:430–438

Brennan AC, Harris SA, Hiscock SJ (2003a) The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae) II. A spatial autocorrelation approach to determining mating behaviour in the presence of low *S* allele diversity. Heredity 91:502–509

Brennan AC, Harris SA, Hiscock SJ (2003b) The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae): avoidance of mating constraints imposed by low *S* allele number. Philos Trans R Soc Lond B 358:1047–1050

Brennan AC, Harris SA, Hiscock SJ (2005) Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. New Phytol 168:475–486

Brennan AC, Harris SA, Hiscock SJ (2006) The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae): *S* allele diversity across the British range. Evolution 60:213–224

Brochmann C, Gabrielsen TM, Nordal I et al (2003) Glacial survival or *tabula rasa*? The history of North Atlantic biota revisited. Taxon 52:417–450

Byers DL, Meagher TR (1992) Mate availability in small populations of plant-species with homomorphic sporophytic self-incompatibility. Heredity 69:353–359

Cheptou PO, Lepart J, Escarre J (2002) Mating system variation along a successional gradient in the allogamous and colonizing plant *Crepis sancta* (Asteraceae). J Evol Biol 15:753–762

Crisp P (1972) Cytotaxonomic studies in the Section *Annui* of *Senecio*. PhD dissertation, University of London, UK

Druce GC (1927) The flora of Oxfordshire, 2nd edn. Clarendon, Oxford

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? Proc Nat Acad Sci USA 97:7043–7050

Fuertes Aguilar J, Rosello JA, Nieto Feliner G (1999) Molecular evidence for the compilospecies model of reticulate evolution in *Armeria* (Plumbaginaceae). Syst Bot 48:735–754

Gross BL, Rieseberg LH (2005) The ecological genetics of homoploid hybrid speciation. J Hered 96:241–252

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470–474

Harlan JR, de Wet JMJ (1963) The compilospecies concept. Evolution 17:497–501

Harris SA (2002) Introduction of Oxford ragwort, *Senecio squalidus* L. (Asteraceae), to the United Kingdom. Watsonia 24:31–43

Harris SA, Ingram R (1992) Molecular systematics of the genus *Senecio* L. I. Hybridization in a British polyploid complex. Heredity 69:1–10

Hegarty MJ, Jones JM, Wilson ID et al (2005) Development of anonymous cDNA microarrays to study changes to the *Senecio* floral transcriptome during hybrid speciation. Mol Ecol 14:2493–2510

Hegarty MJ, Barker GL, Wilson ID et al (2006) Transcriptome shock after interspecific hybridization in *Senecio* is ameliorated by genome duplication. Curr Biol 16:1652–1659

Hegarty MJ, Barker GL, Brennan AC et al (2009) Extreme changes to gene expression associated with homoploid hybrid speciation. Mol Ecol (in press)

Hiscock SJ (2000a) Genetic control of self-incompatibility in *Senecio squalidus* L. (Asteraceae): a successful colonizing species. Heredity 85:10–19

Hiscock SJ (2000b) Self-incompatibility in *Senecio squalidus* L. (Asteraceae). Ann Bot 85(Supplement A):181–190

Hiscock SJ, McInnis SM (2003) Pollen recognition and rejection during the sporophytic self-incompatibility response—Brassica and beyond. Trends Plant Sci 8: 606–613

Hiscock SJ, Tabah DA (2003) The different mechanisms of sporophytic self-incompatibility. Philos Trans R Soc Lond B 358:1037–1045

Hiscock SJ, McInnis SM, Tabah DA et al (2003) Sporophytic self-incompatibility in *Senecio squalidus* (Asteraceae)—the search for *S*. J Exp Bot 54:169–174

Huey RB, Gilchrist GW, Carlson ML et al (2000) Rapid evolution of a geographic cline in size in an introduced fly. Science 287:308–309

Ingram R, Noltie HJ (1995) Biological Flora of the British Isles: *Senecio cambrensis* Rosser. J Ecol 83:537–546

Ingram R, Weir J, Abbott RJ (1980) New evidence for the hybrid origin of inland radiate groundsel, *S. vulgaris* L. var. *hibernicus* Syme. New Phytol 84:543–546

Irwin JA, Abbott RJ (1992) Morphometric and isozyme evidence for the hybrid origin of a new tetraploid radiate groundsel in York, England. Heredity 69:431–439

James JK, Abbott RJ (2005) Recent, allopatric, homoploid hybrid speciation: the origin of *Senecio squalidus* (Asteraceae) in the British Isles from a hybrid zone on Mount Etna, Sicily. Evolution 59:2533–2547

Kent DH (1955) Scottish records of *Senecio squalidus* L. Proc Bot Soc Br Isles 1:312–313

Kent DH (1956) *Senecio squalidus* L. in the British Isles. 1. Early records (to 1877). Proc Bot Soc Br Isles 2:115–118

Kent DH (1957) *Senecio squalidus* L. in the British Isles. 3. East Anglia. Trans. Norfolk Norwich Nat Soc 18:30–31

Kent DH (1960) *Senecio squalidus* L. in the British Isles. 2. The spread from Oxford. Proc Bot Soc Br Isles 4:375–379

Kent DH (1963) *Senecio squalidus* L. in the British Isles. 7. Wales. Nat Wales 8:175–178

Kent DH (1964a) *Senecio squalidus* L. in the British Isles. 4. Southern England (1940–). Proc Bot Soc Br Isles 5: 210–213

Kent DH (1964b) *Senecio squalidus* L. in the British Isles. 5. The Midlands (1940–). Proc Bot Soc Br Isles 5:214–216

Kent DH (1964c) Senecio squalidus L. in the British Isles. 6. Northern England (1940–). Proc Bot Soc Br Isles 5: 217–219

Kent DH (1966) *Senecio squalidus* L. in the British Isles. 4. The recent spread in Scotland. Glasgow Nat 18:407–408

Kim M, Cui M-L, Cubas P et al (2008) Regulatory genes control a key morphological and ecological trait transferred between species. Science (in press)

Lane MD, Lawrence MJ (1993) The population genetics of the self-incompatibility polymorphism in *Papaver rhoeas* VII. The number of S alleles in the species. Heredity 71:592–602

Lawrence MJ (2000) Population genetics of the homomorphic SI polymorphism in flowering plants. Ann Bot 85(Suppl. A):221–226

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386–391

Levin DA (1996) The evolutionary significance of pseudo-self-fertility. Am Nat 148:321–332

Lexer C, Welch ME, Raymond O et al (2003) The origin of ecological divergence in *Helianthus paradoxus* (Asteraceae): selection on transgressive characters in a novel hybrid habitat. Evolution 57:1989–2000

Lowe AJ, Abbott RJ (2003) A new British species of *Senecio* (Asteraceae), another hybrid derivative of *S. vulgaris* L. and *S. squalidus* L. Watsonia 24:375–388

Lowe AJ, Abbott RJ (2004) Reproductive isolation of a new hybrid species, *Senecio eboracensis* Abbott & Lowe. Heredity 92:386–395

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Marshall DF, Abbott RJ (1980) On the frequency of introgression of the radiate (T_r) allele from *Senecio squalidus* L. into *S. vulgaris* L. Heredity 45:133–135

Marshall DF, Abbott RJ (1982) Polymorphism for outcrossing frequency at the ray floret locus in *S. vulgaris* L. I. Evidence. Heredity 48:227–235

Marshall DF, Abbott RJ (1984a) Polymorphism for outcrossing frequency at the ray floret locus in *S. vulgaris* L. II. Confirmation. Heredity 52:331–336

Marshall DF, Abbott RJ (1984b) Polymorphism for outcrossing frequency at the ray floret locus in *S. vulgaris* L. III. Causes. Heredity 53:145–149

Milne RI, Abbott RJ (2000) Origin and evolution of invasive naturalised material of *Rhododendron ponticum* L. in the British Isles. Mol Ecol 9:541–556

Nielsen LR, Siegismund HR, Philipp M (2003) Partial self-incompatibility in the polyploid endemic species *Scalesia affinis* (Asteraceae) from the Galapagos: remnants of a self-incompatibility system? Bot J Linn Soc 142:93–101

Oxford GS, Andrews T (1977) Variation in characters affecting fitness between radiate and non-radiate morphs in natural populations of groundsel (*Senecio vulgaris* L.). Heredity 38:367–371

Peakall R, Smouse PE (2006) Genalex 6: genetic analysis in excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Pimentel D (ed) (2002) Biological invasions. CRC Press, Boca Raton

Preston CD, Pearman DA, Dines TD (2002) New Atlas of the British and Irish flora. Oxford University Press, Oxford

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Radford IJ (1997) Impact assessment for the biological control of *Senecio madagascariensis* Poir. (Fireweed). PhD dissertation, University of Sydney, Australia

Reinartz JA, Les DH (1994) Bottleneck-induced dissolution of self-incompatibility and breeding system consequences in *Aster furcatus* (Asteraceae). Am J Bot 81:446–455

Rieseberg LH, Ellstrand NC (1993) What can molecular and morphological markers tell us about plant hybridization? Crit Rev Plant Sci 12:213–241

Rieseberg LH, Beckstron-Sternberg SM, Liston A et al (1991) Phylogenetic and systematic inferences from chloroplast DNA and isozyme variation in *Helianthus* sect. *Helianthus* (Asteraceae). Syst Bot 16:50–76

Rieseberg LH, Archer MA, Wayne RK (1999) Transgressive segregation, adaptation and speciation. Heredity 83: 363–372

Rieseberg LH, Raymond O, Rosenthal DM et al (2003) Major ecological transitions in wild sunflowers facilitated by hybridization. Science 301:1211–1216

Rieseberg LH, Kim S-C, Randell RA et al (2007) Hybridization and the colonization of novel habitats by annual sunflowers. Genetica 129:149–165

Rosser EM (1955) A new British species of *Senecio*. Watsonia 3:228–232

Sax DF, Gaines SD (2003) Species diversity: from global decreases to local increases. Trends Ecol Evol 18: 561–566

Shiba H, Iwano M, Entani T et al (2002) The dominance of alleles controlling self-incompatibility in *Brassica* pollen at the RNA level. Plant Cell 14:491–504

Shiba H, Kakizaki T, Iwano M et al (2006) Dominance relationships between self-incompatiility alleles controlled by DNA methylation. Nat Genet 38:297–299

Sibthorp J (1794) Flora oxoniensis, exhibens plantas in agro oxoniensis sponte crescentes, secundum Systema Sexuale Distributas. Oxoni Typis Academicus, Oxford

Stebbins GL (1957) Self fetilization and population variability in higher plants. Am Nat 91:337–354

Stephenson AG, Good SV, Vogler DW (2000) Interrelationships among inbreeding depression, plasticity in the self-incompatibility system, and the breeding system of *Campanula rapunculoides* L. (Campanulaceae). Ann Bot 85(Supplement A):211–220

Sun M, Ritland K (1998) Mating system of yellow starthistle (*Centaurea solstitialis*), a successful colonizer in North America. Heredity 80:225–232

Tabah DA (2004) Studies of self-incompatibility in *Senecio squalidus* L. (Asteraceae). PhD dissertation, University of Bristol, UK

Tabah DA, McInnis SM, Hiscock SJ (2004) Members of the S-receptor kinase multigene family in *Senecio squalidus* L. (Asteraceae), a species with sporophytic self-incompatibility. Sex Plant Reprod 18:1–10

Trow AH (1912) On the inheritance of certain characters in the common groundsel—*Senecio vulgaris*—and its segregates. J Genet 2:239–276

Vekemans X, Schierup MH, Christiansen FB (1998) Mate availability and fecundity selection in multi-allelic self-incompatibility systems in plants. Evolution 52:19–29

Vogler DW, Kalisz S (2001) Sex among the flowers: the distribution of plant mating systems. Evolution 55:202–204

Vogler DW, Das C, Stephenson AG (1998) Phenotypic plasticity in the expression of self-incompatibility in *Campanula rapunculoides*. Heredity 81:546–555

Walker R (1833) Flora of Oxfordshire and its contiguous counties. Slatter, Oxford

Walker KJ (2007) The last 35 years: recent changes in the flora of the British Isles. Watsonia 26:291–302

Weber E, Schmid B (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. Am J Bot 85:1110–1121