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Research and Development

Final Project Report

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Project title	A review of the potential effects of seed sowing for habitat re-creation on the conservation of intraspecific biodiversity		
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Executive summary (maximum 2 sides A4)

1. Since the 1960s non-local and non-native genotypes, including agricultural forage varieties of British native species, have increasingly been used to restore and re-create habitats for conservation, amenity and landscape purposes. This has led to growing concern that such introductions will have a number of negative impacts on native genetic plant biodiversity (see Box 1 below).
2. **Although these concerns have led to recommendations for the use of local provenance material in habitat re-creation knowledge of the actual or likely impacts (which could be beneficial, benign or detrimental) on the native genetic diversity are not well understood.**
3. **In this review we assess the potential impacts of seed sowing on local populations on 151 native species frequently used to re-create lowland habitats of wildlife value in the UK. More specifically we assess which species are most frequently sown; how variable semi-natural populations of these species are in the UK; how the introduction of non-local genotypes might affect these patterns of variation; the extent to which such changes will be beneficial, benign or detrimental to the conservation of genetic resources; and which traits are important in determining variation. Finally, we suggest a number of recommendations for seed sowing and future research needs.**
4. Although a small number of native plant species (mainly grasses and legumes) have a very long history of agricultural use, the sowing of wildflowers for habitat re-creation began in the 1960s and has increased dramatically in recent decades due to increased sowing within agri-environment schemes.

Between 1990 and 2003 the annual supply of native provenance seed, largely for habitat re-creation, was in the region of 20-30 tonnes per annum (in comparison to 20,000 tonnes of agricultural seed)[1]. 60 native wildflower species covered by this review accounted for three-quarters of this seed, the most important (in terms of sales volume) being *Leucanthemum vulgare, Prunella vulgaris, Galium verum, Ranunculus acris, Calluna vulgaris* and *Sanguisorba minor*.

5. The introduction of non-native genotypes from the continental Europe, which was widely recognised as a threat to native biodiversity in the 1980s, has largely ceased. However, the majority of ‘native’ genotypes currently being used for habitat re-creation have either been selectively bred for agricultural use (i.e. forage grasses and legumes), or are native genotypes which originate from a small number of semi-natural populations which are seldom close to the recipient site or from the same habitat type.

6. The restricted number of donor sites and habitat types used for seed harvesting and the unconscious selection of certain genotypes during multiplication suggests that commercial wildflower material will only carry a very small proportion of the genetic diversity available in native populations. As has been shown in a small number of studies, re-introduced populations are therefore likely to be founded from a few individuals (founder effects) and have a narrow genetic base. Although the consequences are difficult to predict and may be genotype dependent recent research suggests that such populations are likely to have reduced fitness due to increased relatedness or poor adaptation within the population (inbreeding depression).

Box 1. Summary of the main threats associated with the introduction of non-local/non-native genotypes

Main threat	Probability (impact = Risk1	Level of know-ledge2	Comment/examples
On-site effects: risks to newly established populations and other organisms			
1. Founder effects	2 (1 = 2	2	Only applies to small, newly establishe populations
2. Inbreeding depression	2 (1 = 2	2	Only applies to small, newly establishe populations
3. Changes to plant-invertebrate interactions			
- pollinators	2? (1? = ?	1	Long term implications poorly understo (e.g. Lotus corniculatus, Trifolium pratense)
- herbivores	2? (1? = ?	1	Long term implications poorly understo (e.g. Lotus corniculatus, Trifolium repens, Dauscus carota, Leucanthemum vulgare, Silene latifolia)
Off-site effects: risks to existing semi-natural populations			
4. Disrupt native patterns of genetic variation	3 (2? = 6?	2	High risk for species with a long history of agricultural use (e.g. Loli

			perenne, Trifolium repens); medium ris for species widely sown for habitat re-creation (e.g. Centurea nigra, Leucanthemum vulgare, Galium verum, Sanguisorba minor).
5. Genetic swamping	3 (3? = 9?	2	Native species widely sown for habitat re-creation (e.g. Centurea nigra, Leucanthemum vulgare, Galium verum, Sanguisorba minor).
6. Heterosis	3 (1 = 3	3	Outcrossing species only; initially positive, but may be followed by outbreeding depression (e.g. Succisa pratensis)
7. Outbreeding depression	2 (3 = 6	3	Mixed mating, outcrossing species (e.g Papaver rhoeas)
8. Outbreeding depression & heterosis	2 (3 = 6	3	Mixed mating, outcrossing species only (e.g. Silene latifolia, Agrostemma githago)

Notes: 1 Probability/impact scores: 1, low; 2, moderate; 3, high; ?, some degree of uncertainty. 2 Level of knowledge: 1, theoretical risk, no evidence; 2, thoeretical risk, backed by limited actual data, results often contradictory; 3, actual risk, backed by several studies but further research required.

7. Physiological and phenological differences between local and non-local genotypes may have potentially damaging effects on species in the same or higher trophic levels. For example, variations in plant defences, which occur in response to differences in the intensity of herbivory across a species range, have been shown to affect herbivory in a few legume species. Equivalent differences in phenological traits (e.g. flowering time, pollen and nectar production and quality) between native and agricultural genotypes are well known but potential impacts on native pollinators and mutualists are as yet poorly understood.

8. Human-mediated gene-flow has been shown to have caused significant disruptions to patterns of genetic diversity in populations of species which have been widely and repeatedly sown for agriculture in the past (e.g. *Lolium perenne*). In contrast, the risks of disruption are likely to be much lower for other native species where the scale of introduction, as a result of habitat re-creation, has been comparatively minor.

9. Although genetic swamping, either due to a numerical or fitness advantage of the introduced genotype or as a result of hybridisation, is potentially one of the most significant threats to native genetic variation, the findings of recent studies are contradictory making it difficult to generalise about the potential outcomes of genetic exchange following habitat re-creation. However, they do suggest that local genotypes may perform better under semi-natural conditions and that their fitness will decline with increasing ecological or geographic distance during introduction. These local advantages may be ruled out where conditions at the recipient site are extreme (e.g. highly disturbed, fertile agricultural soils). Under these conditions non-local genotypes may perform better without posing a significant threat to local genotypes which occur nearby (i.e. in nutrient-poor, semi-natural swards).

10. Hybridisation between genotypes may lead to fitness advantages as a result of hybrid vigour (heterosis) in the first generation (F1) although this has usually been followed by overall declines in fitness in the longer term (outbreeding depression) thereby potentially reducing the fitness of introgressed native populations following re-creation.

11. 60% (88) of the species included in this review show some degree of intraspecific[2] (e.g. morphological, ecotypic, cytological, clinal) variation. In contrast, very little is known about the genetic structure of selectively-neutral variation in populations of common wildflower species which are frequently used for habitat re-creation.

12. Life-history, breeding system and dispersal ability were found to be the important determinants of intraspecific variation in the species included in this review. A 'risk analysis' based on variation and traits (i.e. biologically determined) identified *Silene latifolia, Rumex acetosa, Deschampsia cespitosa, Gentianella amarella, Holcus lanatus* and *Caltha palustris* as species at greatest risk from introgression with non-local genotypes and *Silene latifolia, Rumex acetosa, S. dioica, Caltha palustris, Ranunculus acris* and *Calluna vulgaris* when information on seed supply was also included (i.e. commercially determined).

13. For species with a long history of agricultural use further human-mediated gene-flow as a result of habitat re-creation is unlikely to pose significant risks to native patterns of diversity. However, the use of 'native genotypes' should continue to be promoted for other wildflower species particularly where sowing occurs over large areas, where potential introgression with local genotypes is likely to take place (e.g. close to semi-natural grassland or for species where geneflow is likely to be significant) or for species which display clear phenotypic or genetic variation (e.g. ecotypes, cytotypes, subspecies, etc.).

14. The production of official guidelines for 'good practice' in seed sourcing and production are urgently required and should stress the importance of harvesting wild seed from a greater range of donor sites (both in terms of regions and habitats) in order widen the genetic base of 'native' wildflower seed supplied in the UK. One way of doing this would be to encourage the production of local stocks of species within regional 'seed zones'. In addition, sustainably harvested wild seed (e.g. as 'green hay') from a range of species-rich sites in the wider countryside (e.g. nature reserves, road verges, grassland remnants on farms) should be promoted as a more cost-effective and benign alternative to commercial seed. Defra should also seek to revise current seed regulations in order to ensure the legality of sowing of native provenance seed of 20 species requiring certification before their seed can be marketed in England (e.g. forage grasses and legumes) which are currently being widely used for habitat re-creation within agri-environment schemes.

15. Future research should address the extent to which species commonly used for habitat re-creation are genetically differentiated in semi-natural habitats using both genetic approaches and reciprocal transplant studies which assess the performance of different genotypes in a range of different environments. In addition there is urgent need to assess the impact of hybridisation and introgression on plant fitness. Other important questions include how commercial harvesting and production techniques have affected the genetic diversity of seed and plant stocks and the extent to which human-mediated gene-flow has disrupted natural patterns of genetic diversity. Finally, there is also a need to assess what implications these changes will have for biotic interactions and ecosystem function.

Contents

Reference for citation:

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A review of the potential effects of seed sowing for habitat re-creation on the conservation of intraspecific biodiversity.
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|Scientific report (maximum 20 sides A4)
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1. Introduction

Since the 1960s British native plant species have increasingly been used to restore and re-create habitats for conservation, amenity and landscape purposes. Sometimes these seeds or plants have been of 'local provenance', but such material has often not been available or affordable, and so seeds have often been harvested from non-local populations or imported from outside the UK (Bullock et al. 2003). In addition, traditional plant breeding has, over the past few hundred years, resulted in the selection and widespread use of agricultural and horticultural cultivars of many common native species, such as clovers and grasses. These varieties are much cheaper and more readily available than native seed or plant material and have therefore been used as a major component of wildflower mixtures. As a result, non-native, and more latterly non-local genotypes of common native species have been repeatedly introduced into environments containing wild relatives.

These introductions have led to growing concern over potential impacts on native patterns of genetic diversity both in the UK (Akeroyd 1994a; Akeroyd 1994b; Gilbert and Anderson 1998; Moore 2000; Jones 2001; Sackville Hamilton 2001), Europe (Mennema 1984), and North America (Millar and Libby 1991). These potential adverse impacts include:

1. **Disruptions to native patterns of genetic diversity;**
2. **Genetic swamping** of locally differentiated populations;
3. **Reduced fitness** as a result of **hybridisation** and **introgression**;
4. **Destabilisation of interactions with other species in the same or higher trophic levels.**

Although these concerns have led to recommendations for the use of local provenance material in habitat restoration schemes (e.g. King 1998; Flora Locale and Plantlife 2000; Flora Locale and English Nature 2003) there has been very little research to assess the extent to which non-local genotypes constitute a *real* and *significant* threat to native genetic diversity (Bullock and Hodder 1997). As a consequence, knowledge of the actual or likely impacts (which could be beneficial, benign or detrimental) on the native genetic diversity are not well understood (Biodiversity Research Working Group 2000; Wilkinson 2001).

Intraspecific genetic variation is a fundamental component of biodiversity (Convention Biological Diversity 1992) and, as a result, its conservation is now an explicit objective of conservation policy in the UK (Anon. 1995; Sackville Hamilton 2001). Furthermore, patterns of variation provide important information on the history of a species as well as a resource for future adaptive change. As a consequence, knowledge of the levels and distribution of genetic variation in natural populations is a prerequisite for an assessment of the potential impacts on native gene-pools as well as ecosystems more generally (Hamrick et al. 1991). In addition, it also demands a clearer understanding of the processes by which genetic changes take place and how these are influenced by ecological and biological life history traits. Furthermore, the scale of introduction is also likely to be important because this will define which species are likely to be most at risk from hybridisation and introgression and also the frequency at which such changes are likely to take place in response to factors such as climate change or eutrophication.

In order to assess the potential impacts of the sowing of non-local genotypes on local populations of native species used in habitat re-creation we address the following questions:

1. Which species are most frequently used for habitat re-creation?
2. How variable are native populations of these species?
3. How might the introduction of non-local genotypes affect this variation?

4. Will these effects be beneficial, benign or detrimental to the conservation of genetic resources?
5. Which ecological and biological traits make these effects more likely to occur?
6. What are the current gaps in knowledge and future research needs?

1.1 Species covered by this review

We focus on 151 British native species which are being increasingly used to recreate lowland habitats of wildlife value in the UK (Appendix 1). All are currently available from commercial suppliers and are either sold as seed or plant material (Table 1). Many are prescribed for sowing within agri-environment schemes and, as a result, have been covered by scientific studies on grassland re-creation (e.g. BD1433; Pywell et al. 2003). Trees and shrubs used for similar purposes are excluded from this review as their genetic conservation has been assessed in an earlier review (Ennos et al. 2000). A glossary of terms used (highlighted in bold in the main text) is also provided on page 28.

1.2 Definition of status

We distinguish between the following categories of ‘native’ and ‘introduced’ plants:

Native – a species which arrived in the UK without the intervention of humans having come from an area in which it is native or one which has arisen *de novo* in the UK.

- **Local provenance** – a native **genotype** originating from a population close to the introduction site, but not necessarily from the same habitat type. A subset of native.
- **Non-local provenance** – a native genotype originating from a population distant to the introduction site which may or may not be from the same habitat type. A subset of native.
- **Non-native/introduced** – a species which was brought to the UK by humans, either intentionally or unintentionally, even if native in the source, or one which has come to the UK without the intervention of humans but from an area where it is present as an introduction.

Throughout this review we therefore use the term **local/non-local genotypes** as subsets of native when referring to plants originating from seeds or plants introduced from populations within the UK and **non-native genotypes** for material introduced from populations elsewhere. Obviously, the definition of ‘close’ and ‘distant’ are critical and this point is discussed in the review.

2. Wildflower species and habitat re-creation in the UK

2.1 The use of wildflower species in the UK

2.1.2 Agriculture and amenity

Native legume species, such as clover, sanfoin and lucerne, have been used to provide fodder and as nitrogen fertilisers since at least the 1620s (Daniels and Sheail 1999). Although such species may have been unconsciously used for fodder before then, this marks the beginning of the commercial importation of ‘wildflower’ seed, and from then on these imported substitutes would have contained genetic varieties distinct from wild progenitors (Ambroseli 1997). For example, *Trifolium repens*, which is one of the most important fodder legumes of the temperate world (Hopkins et al. 1995), probably originated in Southern Spain around 1000 AD (Kj?rgaard 2003) and was subsequently transported throughout lowland Europe arriving in England, from the Netherlands, in 1620 (Fussel 1964). By the end of the seventeenth century it was being enthusiastically grown over much of lowland England and throughout the eighteenth and nineteenth was widely sown as a ‘break-crop’ in the production of both potatoes and corn, as well as for fodder in the production of beef and dairy products. Similarly, native grass species were also widely used for fodder in the past. As early as the 1600s grasslands were being systematically cultivated, fertilised and sown with grass seeds in order to improve their quality for livestock (Sheail 1986). This not only included hay but also the selective hand-collection of seeds of species such as *Alopecurus pratensis*, *Anthoxanthum odoratum* and *Festuca pratensis* which, by the 1790s, were being sold within mixtures tailored to different soil types (Curtis 1790). Following the crash in the price of corn in the 1880s large quantities of native grass seed were sown to create pasture (Sheail 1986) and this led to a dramatic increase in the demand for forage mixtures included species such as *Agrostis stolonifera, Cynosurus cristatus, Dactylis glomerata, Festuca ovina, Phleum pratense, Poa trivialis*, and *Trisetum flavescens* (de Laune 1882).

Much of this agricultural grass seed originated from native material sent for production to North America however, during the early part of the twentieth century this was replaced by more productive varieties bred at Welsh Plant Breeding Station in Aberystwyth. Plant breeders had long realised that the indigenous strains of grasses and clovers were far superior to the imported varieties, and as a result began to collect 'wild strains' for qualities such as growth rate and frost hardiness. The most promising individuals were selected for breeding programmes which led to the famous 'S' varieties of *Lolium perenne* including the legendary S23 which was to provide the bulk of the grass monocultures of the latter half of the twentieth century (Harvey 2001). As a result improved varieties of *Trifolium repens* and *Lolium perenne* began to replace coarser grasses, such as *Dactylis glomerata*, within forage mixtures (Figure 1; Bark 1984).

These improved varieties, which had originally been bred for their vigorous growth and upright habit, were completely unsuitable for amenity areas and sports pitches. As a result, plant breeders began to develop tougher, more wear-resistant 'turf grass' varieties of *Agrostis capillaris*, *Festuca rubra, Lolium perenne*, and *Poa pratensis* (Hubbard 1984). These were initially collected from heavily trampled or intensively mown habitats and the most persistent under close-mowing and heavy wear selected for commercial breeding. These are now mostly bred for use in intensively managed turf, though they can also be produced for less intensive maintenance or special conditions such as high salinity.

2.1.2 Habitat re-creation and restoration

The use of native wildflowers for habitat re-creation began in the late 1960s with expansion of the motorway network (Way 1976) and the creation of 'green spaces' intended for recreational and amenity activities within urban areas (Smart 1989). This was followed in the 1970s by increased demand for wildflower seed for landscaping of large areas of land contaminated by heavy industry (Bradshaw and Chadwick 1980) as well as sites used for landfill and mineral extraction which were unsuitable for agricultural use (Davis and Coppeard 1989). During the same period there was also increasing evidence to show that large areas of ancient grassland had been lost as a result of development and agricultural improvement. As a result there was increased research into potential techniques for restoring diverse grassland using wildflower seed. The results of this research were published as a series of practical guides for the collection, cleaning and sowing of seeds of native wildflower species (e.g. Wells et al. 1981, 1986, 1989) and these led to considerable interest, both in the public and private sector, into what later became known as habitat re-creation. Subsequently there has been an extraordinary increase in the use of native wildflower seed for a whole range of purposes including wildlife gardening, landscaping and more recently grassland re-creation under agri-environment scheme options (see Section 2.2.2). Much of this seed (and plant material) has been used to re-create habitats *de novo* on heavily disturbed sites although as well as repair habitats degraded by other uses such as agriculture (e.g. improved grasslands, moorland) or recreation (e.g. submontane heath, sand dunes). A summary of the main uses of wildflower seed in the UK is given in Section 2.3.4.

2.2 The supply of wildflower seed and plant material in the UK

At present there are limited data on the supply of seed of native British species included in this review. Exceptions include 20 agricultural and amenity grasses and legumes covered by the European Seeds Directive (66/401/EEC; Table 2), i.e. those requiring certification before seed can be marketed in England[3]. For these species Defra produce annual figures for the amount of seed sold by the by main seed suppliers in the UK (Table 2) and the amount of seed produced (Table 3). There are no equivalent figures for 'non-certified' native species so we contacted 19 commercial wildflower suppliers in order to a) assess how much seed of the 151 species included in this review are sold in an 'average year' and, b) the nature of their commercial production and supply including sourcing, harvesting, propagation and use. A summary of the information received is given in Section 2.3 and Appendix 3.

2.2.1 Supply of certified species

The European Seeds Directive requires that signatory countries carry out official tests to ensure that seed of agricultural and vegetable species (including 20 which occur as native species in the UK; Table 2) meet with certain quality standards before they are marketed. As a result seed under production is inspected by the National Institute of Agricultural Botany (NIAB) and seed tested for purity and viability before it can be marketed. NIAB collate these data and maintain a database (Eurosemstats) of annual seed production of varieties for the UK and 23 other European countries (Table 3; NIAB 2002).

As can be seen in Tables 2 and 3 *Lolium perenne* is by far the most important forage species in Europe with nearly 100,000 hectares under commercial seed production. The UK is the fourth largest producer with seed produced from around 8,000 ha, whereas Denmark and the Netherlands each produce around 38,000 and 20,000 ha respectively with an average yield of about 1 t ha^{-1}. For all other species, Britain is a minor producer: for example, for *Festuca rubra* Britain only produces seed from around 340 ha compared to 20,000 ha in Denmark. The figures given in Table 3 also indicate the likely origin of seed being imported into the UK. At present the main European producers are (in order of importance) Denmark, France, the Netherlands and Germany who all produce the bulk of the agricultural and amenity grasses (i.e. *Lolium perenne*, *Festuca rubra*, *Poa pratensis*, and *Dactylis glomerata*). Germany is also a major producer of *Arrhenatherum elatius*, *Festuca ovina*, *F. pratensis*, *Alopecurus pratensis* and *Trisetum flavescens* whereas the Czech Republic produces the greatest quantities of *Trifolium pratense* and a range of other species of lesser agricultural value (e.g. *Agrostis capillaris*, *A. gigantea*, *Cynosurus cristatus*, *Festuca pratensis*, *Onobrychis viciifolia*).

The second main source of information on the supply of certified species are the Seed Trader’s Statistics compiled annually by Defra in order to provide up-to-date information on the trade in agricultural seeds eligible for Seed Production Aid. Each year seed merchants are asked to provide information on the quantity of certified seed that has been imported, exported, maintained in stock or ‘delivered for use’ to UK customers (Table 2). These figures (Table 2) show that around 20,000 tonnes of seed (of the 20 native species covered by this review) are sold annually with roughly two thirds being imported (Figure 2). Not surprisingly *Lolium perenne* makes up over half of this amount (c.12,000 tonnes) whereas the majority of seed of *Festuca rubra* (3,000 tonnes), *Agrostis capillaris*, *Phelum pratense* and *Poa pratensis* is imported. With the exception of *Trifolium repens* very little legume seed is now sold in the UK.

2.2.2 Supply of uncertified species

There is currently no legislation governing the sale (or quality) of native wildflower species. As a consequence there is virtually no information on the production and supply of native-sourced material or assessments carried out into its purity, germination capacity or source, although producers are increasingly following unofficial ‘codes of practice’ which cover seed sourcing, harvesting and production techniques (Flora Locale and Plantlife 2000).

The first commercial mixtures for habitat re-creation were marketed in the 1970s as alternatives to agricultural mixtures used to re-sow pasture leys (Brown 1989). However, these were often unsatisfactory as seed of appropriate native species were not always available and as a result agricultural and foreign varieties were often used instead. In addition, non-native species such as *Cichorium intybus*, *Coronilla varia* and *Papaver somniferum* were also often included as they were relatively inexpensive and produced colourful displays (Wells 1987; Brown 1989). However, during the 1980s there was increased recognition of the need to produce seed of native grass and wildflower species and as a result a range of ‘native seed mixtures’, often modelled on target communities, were developed to suit specific soil conditions. In 1983 around three tonnes of these mixtures were being sold annually, containing about 15-20% seed of native species (Wells 1987). At the time this was sufficient to seed about 85 ha but three-quarters of the seed sold had been supplied as mixtures of less than 8 kg (enough to sow less than half an acre) with over half used by local authorities to create ‘wildlife’ habitats within urban areas. Although subsequent growth was constrained by seed availability demand for native seed expanded at a rate of between 20-50% per annum during the 1980s. As a consequence there was an increase in both the number of species available and commercial companies and by the late 1980s it was estimated that the market was in the region of 10 tonnes (1987-88), sufficient seed for up to 300 ha with a market value of £350,000 (Brown 1989). As in the early 1980s public authorities and landscapers accounted for about 80% of the seed sold whereas conservationist organisations accounted for less than 5% (by weight).

Although there is no information on changes in market supply during the 1990s the demand for seed for sowing on land entered into agri-environment schemes (e.g. Environmentally Sensitive Areas (ESAs) and Countryside Stewardship (CS)) suggests that there has been a dramatic growth in demand since then (Appendix 1). Twelve English ESAs now offer options to revert arable land to grassland (including five for arable fields margins; Table 4) and to date this has led to the recreation of around 18,000 ha of grassland (equivalent to 164 tonnes of seed), although the vast majority of this area is likely to have been sown with a 'basic ESA mixture' of six or seven certified agricultural grass species and varieties (e.g. *Agrostis capillaris*, *Cynosusrus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *F. rubra* subsp. *commutata*, *Phleum pratense* and *Poa pratensis*). In addition, around £217,000 worth of native seed has been purchased under grant aid (under GS/RS supplements) between 1998-2002 which is equivalent to around 1.2 tonnes at current market prices (at an average cost of £175 per kg).

Since 1990 native seed has also been sown options within CS (Table 4): in terms of the area of land entered into agreement Arable Reversion (R1) has been the most important option and requires the sowing of six grasses (from an approved list of 18). In addition, there are also supplements for the sowing of native seed (GS) and grassland management (GX), which includes native seed sowing, but has often been used for weed control (M. Stevenson, pers. comm.). In addition, there is currently (from 2002) a 'Pollen and Nectar Margin' option (WM2) which requires the sowing of more than four nectar-rich plants (usually legumes) and four non-competitive grasses (Appendix 1). There was a steady increase in the annual uptake of these options during the 1990s (Figure 3) particularly towards the end of the decade due to a dramatic increase in uptake of R1 and R3 (Table 5). This rise in uptake was largely a result of an increase in the budget for direct payments but also because falling wheat prices made R1 and R3 attractive options for arable farmers. At the same time therefore there was also increase in the native seed supplement. The total area sown under these options was in the region of 31,000 hectares (minus GX/RX), two-thirds of which was sown under arable reversion. Assuming a sowing rate of 35 t ha^{-1} approximately 1000 tonnes of seed would have been required to seed this area, of which around 50 tonnes is likely to have been of native origin (i.e. GS/RS).

2.3 Survey of commercial seed suppliers

The 19 companies contacted for this review are all 'recommended' native seed suppliers (e.g. by Defra, Plantlife, Flora Locale) and probably represent around three-quarters of the total native seed supply market in the UK (Appendix 2). Each supplier was asked to provide information on a) the nature of their business, and b) the approximate quantities of seed or plant material supplied in an 'average year' for each of the 151 species covered by this review (Appendix 1). Full details of the survey are given in Appendix 3. All 19 companies provided responses to a) and 14 also provided information on the supply of individual species.

2.3.1 Seed/plant suppliers

Twelve of the companies contacted sell both plant material and seed whereas seven specialise in seed and one in plant material alone. Of these seven just import or buy-in and sell seed whereas 12 are both retailers and growers. The majority of these retailer-growers tend to be the smaller, specialist growers who 'multiply' wild-harvested seed (directly or supplied by another grower) and then sell on to other wholesalers such as the larger seed merchants, or in some cases other small, specialist growers. Indeed all but one of the companies 'buy-in' some seed which for the smaller companies usually includes agricultural grasses and legumes which typically comprise the bulk by weight of the 'native' wildflower seed mixtures. Most are relatively small companies with nine selling less than 10 tonnes of seed annually and seven less than 100,000 plants per year, although two of these companies expect to supply more than 500,000 plants annually (Figure 4). In contrast, the seven retailers primarily supply agricultural varieties and a small amount of native seed sourced from the smaller specialist growers.

2.3.2 Current market size

The 14 companies who supplied information on individual species supply sell around 71 tonnes of seed of the 151 native species covered by this review in an average year; although it is not clear to what extent forage varieties of native grasses contribute to this overall total, and just over 5 million plug plants. This suggests that the overall market for wildflower seed has increased markedly in the last decade from around 10 tonnes in the late 1980s (Brown 1989) to, as a conservative estimate, at least 20-30 tonnes per annum from 2000 onwards. Indeed this increase was reflected in the responses of many companies: in terms of overall trends in sales, 15 companies (79%) considered that their sales had increased over the last decade, ten of which (53%) estimated by more than 50% (Appendix 3).

2.3.3 Source and harvesting

All 19 companies claim to sell at least some native seed (or plants) originally sourced from semi-natural populations in the UK, although these make up less than 10% of the sales of the five largest companies who 'buy-in' native seed from smaller, specialist suppliers. In contrast, native seeds make up over 90% of total sales for seven of the specialist suppliers, the vast majority of which is produced by multiplying seed from plants grown from an original collection. Eleven (58%) companies also sell seed (usually of certified grasses and legumes) which has been imported into the country, usually via a British seed merchant (83%), the vast majority of this seed apparently coming from other European countries (9 responses; 100%), North America (6 responses; 67%) and Australia/New Zealand (7 responses; 78%). However, for eight (72%) of these companies this seed only makes up a small proportion of total sales (< 50%).

Sixteen (84%) of the companies sell native seed which has been harvested from cultivated plants originating from seed collected from semi-natural habitats. In addition, eight companies (42%) sell mixtures which have been harvested directly from semi-natural sites such as SSSI meadows. Fourteen companies actually carry out the harvesting of wild populations themselves with over half (57%) sourcing from more than 10 donor sites. Of the 11 companies who produce their own seed through multiplication five supplement their seed samples with wild seed every two years or less, whereas four revisit 'wild sites' once every five years to ensure that native wild-flower stock is never grown on for more than five generations. The majority of these companies (69%) collect this seed by hand in order to target individual species.

2.3.4 Uses

The responses of the seed suppliers suggest that the majority of native seed is being used for agri-environment schemes, habitat re-creation, amenity and landscaping projects (Figure 5). In addition, a small proportion of seed is also being used by gardeners, and public bodies involved in landscaping industrial works and civil engineering schemes. Minor uses include game cover, pictorial packets, other seed companies, and experimentation.

2.3.5 Supply of individual species

The 61 most frequently sold species covered by this review are listed in Table 6. These account for over 75% of the total production (79% and 75% respectively). Overall *Leucanthemum vulgare*, *Galium verum*, *Sanguisorba minor*; *Prunella vulgaris*, *Ranunculus acris*, *Calluna vulgaris* are the most important both in terms of seed and plant material sold. The approximate figures for seed and plants sold for the most important species are summarised in Table 7.

2.3.5.1 Seed

Over 1 tonne of seed is sold annually for the 32 species listed in Table 6. This list is dominated by three groups of species: grasses (*Agrostis capillaris, Anthoxanthum odoratum, Cynosurus cristatus, Dactylis glomerata, Festuca ovina, F. pratensis, F. rubra, Poa pratensis*), arable weeds (e.g. *Agrostemma githago, Anthemis arvensis, Centaurea cyanus, Chrysanthemum segetum*) and wildflower herbs which are extremely popular in habitat re-creation schemes (e.g. *Agrimonia eupatoria*, *Leucanthemum vulgare*, *Centuarea nigra*, *Galium verum*, *Sanguisorba minor*).

2.3.5.2 Plug plants

Over 100,000 plug plants are sold annually for the 23 species listed in Table 6. Once again these are dominated by herbs which are popular in grassland re-creation schemes (e.g. *Achillea millefolium*, *Leucanthemum vulgare*, *Galium verum*, *Prunella vulgaris, Ranunculus acris*) some of which are difficult to raise from seed (e.g. *Calluna vulgaris*, *Filipendula ulmaria Hyacinthloides non-scripta*, *Primula vulgaris*, *P.*

veris, Succisa pratensis), as well species of wet habitats which are frequently used in wetland re-creation (e.g. *Iris pseudacorus*, *Lychnis flos-cuculi, Lythrum salicaria*).

3. Plant genetics and conservation: basic concepts

3.1 Genetic basis of biodiversity

A **gene** is a sequence of **nucleotides** that carries the code for a specific protein, and is found at a particular segment of **DNA** known as a **locus**. Different sequences are referred to as **alleles** and one measure of genetic diversity is the variety of alleles per locus found in a group of individuals (allelic diversity). This variety is ultimately created by **mutation** at each generation and provides the resource enabling adaptive evolution to environmental change. The **genotype** is the combination of alleles at a locus in an individual which may be **heterozygous** (different) or **homozygous** (the same) for those alleles and genetic diversity *within* a population may be estimated as the degree of heterozygosity. When *comparing* populations the genetic distance may be estimated as the difference between allele frequencies usually based on many **loci** or simply the number of shared alleles (Beaumont et al. 1998).

However, many DNA sequences are non-coding; therefore, diversity in this genetic material does not translate to protein diversity. Likewise, not all protein diversity leads to **phenotypic** diversity and not all phenotypic diversity is **adaptive**. Variation may be therefore be **selectively neutral**, having no *detectable* effect on the phenotype, or **adaptive** and affect traits which influence reproductive fitness. The environment varies over time and space and adaptive diversity within and between populations is very important in ensuring that some individuals are adapted to each combination of environmental conditions. However, the distinction between these two categories may not be absolute and changes in environmental conditions may cause a previously neutral mutation to affect the performance of an individual. For instance, a gene for drought tolerance may be selectively neutral until changes in the environment, such as climate change, cause it to become adaptive.

3.2 Assessing genetic diversity

Genetic diversity can be measured using an array of quantitative and molecular methods. The earliest estimates of intraspecific genetic diversity were made using **common garden studies** (Turesson 1922b) and this methodology is currently used to determine whether observed differences have a genetic basis (Dyer and Rice 1997; Knapp and Rice 1998). However, such studies do not differentiate between **neutral** and **adaptive** variation although reciprocal transplants (i.e. whereby individuals are moved between populations) can be used to detect a 'home site advantage' thereby indicating whether genetic diversity results from **genetic drift** or **natural selection** (Joshi et al. 2001; Montalvo and Ellstrand 2000). In contrast, artificial selection experiments, which use controlled crosses between plants from different populations followed by planting out in a uniform environment, are useful for detecting possible consequences of intraspecific hybridisation such as **outbreeding depression** or **heterosis** (Montalvo and Ellstrand 2001).

Studies of genetic diversity were revolutionised by the appearance of molecular methodologies in the 1960s. The first molecular technique developed plant studies was **allozyme electrophoresis** although it is now known that this method substantially underestimates genetic diversity. As a consequence it is currently being replaced by more complicated methods that assess DNA directly (Table 8; Frankham et al. 2002). The vast majority of genetic variation currently detected by these molecular tools is selectively **neutral**. However, diversity found in **isozyme** studies may not always be neutral (Prentice et al. 2000) and better understanding of **adaptive diversity** may emerge from molecular techniques in the future (Hedrick 2001). Nevertheless, data from molecular studies of neutral markers can provide information on **genetic structure**, breeding systems and **gene flow** (Gray 2002) all of which affect genetic processes important in restoration such as **founder effects**, **genetic swamping** and population genetic divergence that might indicate local adaptation thereby indicating vulnerability to **outbreeding**

depression (see Section 3.4; Hufford and Mazer 2003). However, studies of population divergence should be interpreted with caution as molecular and morphological methods may give disparate results (Knapp and Rice 1998).

3.3 Genetic processes

The genetic diversity in a population is not static and the aim of restoration should be to conserve a dynamic system with a range of processes of change rather than to fix arbitrary levels of genetic diversity. Extensive research has shown that natural selection acts powerfully to shape the spatial pattern of genetic diversity (Gray 2002) leading to adaptive evolution of local populations (Section 3.4) through retention of advantageous alleles. Such processes are continuous as environmental conditions change and mutations arise. However, exchange of genetic material may also occur *between* populations of a plant species by **gene flow**. Although it varies greatly both between and within species this process is now known to occur at significant distances and at evolutionarily significant rates (Ellstrand 2003). **Gene flow**, which occurs through pollen and seed dispersal, has a major impact on the distribution of selectively neutral genetic diversity and even at very low rates maintains connectivity between populations (Gray 2002). Under conditions of high gene flow there may be no genetic differentiation between populations and they are described as **panmictic**. Where there are environmental differences between populations, however, selection can maintain adaptive diversity even in the presence of substantial gene flow.

Variation is lost from within populations through genetic drift which is the random sampling and loss of alleles (especially those which are rare) at each sexual generation. The loss of alleles and heterozygosity leads to a reduction in genetic diversity and hence a reduction in the capacity of the population to respond to environmental change. Because of its random nature it also increases between-population diversity with its importance inversely related to population size. The population size required to prevent the erosion of genetic diversity should be based on the size of the effectively breeding population (N_e) which is likely to be smaller than the census number (N) (Gray 2002).

Where new populations arise from a few plants the population may have low genetic diversity and hence a loss of evolutionary potential (Knapp and Connor 1999). Non-adaptive inter-population variation may also arise due to this **founder effect**, such as variation found among populations of the silver beech *Nothofagus menziessii* (Haase 1993). If isolated populations are small the production of offspring from related individuals may lead to a reduction in reproductive **fitness** known as **inbreeding depression**. This increases the chances of homozygosity at a locus potentially leading to the expression of deleterious **recessive alleles** which have been previously masked by dominant alleles. The effects are cumulative, so that the period of isolation is important and there is strong evidence that **inbreeding** adversely affects many taxa (Charlesworth and Charlesworth 1987; Thornhill 1993) including plants (Husband and Schemske 1996; Briggs and Walters 1997; Carr and Dudash 2003).

Conversely crossing of genetically differentiated populations may result in reduced fitness through outbreeding depression. Evidence for this phenomenon has been published for many plant species (Waser (1993). There are two main mechanisms involved in outbreeding depression: **genetic dilution** and **hybrid breakdown** (Hufford and Mazer 2003). Genetic dilution may result when individuals from different locally-adapted populations are crossed and the combinations of alleles in the offspring are less suited to the recipient environment (Fenster and Galloway 2000; Montalvo and Ellstrand 2001). **Hybrid breakdown** occurs when crosses between populations result in the disruption of coadapted gene complexes such that the required combination of alleles is no longer present (Templeton 1986). Such effects may not occur until the second generation (F2) or subsequent generations and if coadapted gene complexes are involved outbreeding depression may occur even when individuals are derived from populations with the same environmental conditions (Frankham et al. 2002; Hufford and Mazer 2003).

Intraspecific hybridisation may not always reduce reproductive fitness. Where differences between populations have arisen through genetic drift hybridisation frequently leads to **heterosis**, that is hybrid vigour in the first generation (F1) (Hauser and Siegismund 2000; Luijten et al. 2002). Mechanisms of heterosis include the masking of deleterious **recessive alleles** and **epistasis** which is the formation of novel multilocus genotypes with a favourable fitness effect on the phenotype (Hufford and Mazer 2003). In F1 hybrids there may often be an advantage to intermediate genetic crossing distance such that excessive closeness would risk inbreeding depression and excessive distance might cause outbreeding depression (Waser and Price 1994; Waser et al. 2000). A review by Waser (1993) lists empirical data for 15 angiosperm species which appear to perform better with intermediate crossing distances and this suggests that there may be an 'optimal outcrossing distance' for many plant species (Price and Waser 1979; Barrett and Kohn 1991). However, recent research has indicated that heterosis in the F1 may often be followed by outbreeding depression in later generations (Keller et al. 2000) with the implication that introgression of maladaptive genes into plant populations could potentially reduce the fitness of native populations following restoration (Section 4.3.4).

Introgression of genes may also have the potential to cause **genetic swamping** of locally evolved populations, following the introduction of variants with a fitness advantage (Rhymer and Simberloff 1996). However, the effects of swamping following intraspecific hybridisation have yet to be demonstrated as this would require a molecular assay before and after a translocation (Hufford and Mazer 2003). However, genetic swamping has been observed in **congeners**. Enhanced pollen production and dispersal of F1 hybrids from congeneric cord grasses in California (the native *Spartina foliosa* and introduced *S. alterniflora*) threatens the native species (Daehler et al. 1999; Anttila et al. 2000). Genetic swamping may also occur without introgression, where the introduced genotype holds either a numerical or fitness advantage over the **endemic** taxa (Hufford and Mazer 2003). Examples include St. Johns Wort *Hypericum perforatum* introduced from Australia that grew taller than native European variants (Pritchard 1960) and a Eurasian variant of the common reed *Phragmites australis* which has caused a loss of genetic diversity by swamping North American variants (Saltonstall 2002, 2003). This process of initially undetected increase in a foreign genotype has been described as a 'cryptic invasion' (Hufford and Mazer 2003).

It is difficult to predict the outcome of genetic exchange following ecological restoration, however it is likely that a successful widespread genotype may pose a threat to an isolated endemic, and that the period of isolation and distance of separation of populations will influence the effect of mixing. Greater isolation might lead to more severe outbreeding depression or alternatively greater heterosis (hybrid vigour) (Fenster and Dudash 1994; Gray 2002).

3.4 Ecotypes and local adaptation

Selection for genes conferring advantage in local conditions may lead to intraspecific variation and the evolution of **ecotypes** or local races (Turesson 1922a, 1922b; Briggs and Walters 1997). It may be difficult to demonstrate local adaptation in short term experiments because conditions arising in infrequent events may be required to select for superior fitness in the individuals of local origin (Jones and Hayes 1999). However, ecotypes have been described for hundreds of species (see Section 4.2), and extreme variants may be found in extreme habitats, such as plants with tolerance to heavy metal ions (Smith and Bradshaw 1979). In fact genetic population differentiation has been demonstrated in relation to most habitat variables the most important being climate, altitude, soil type, soil moisture, salinity, herbivory, and plant competition and density (Gray 1996a, 1996b, 2002). The boundaries between ecotypes may be abrupt, or where environmental gradients exist a continuum or cline of intraspecific variants may occur (Briggs and Walters 1997).

Joshi et al. (2001) used reciprocal transplant experiments, involving eight field sites across Europe, to reveal ecotypic variation in the common forage plants *Trifolium pratense, Dactylis glomerata* and *Plantago lanceolata*. Measurements of almost all traits, including survival, and size of vegetative and reproductive parts, indicated a home-site advantage for all three species. However, note that the sites in this study were separated by very large geographic distances, and it is important to note that geographic distance between recipient and donor sites in restoration is often less important than similarity of habitat type (Gray 2002). For instance, Barratt et al. (1999) indicated the importance of intraspecific variation in the response of wet grassland species collected from wet and dry sites to different water level regimes.

3.5 Life history traits and effects on genetic diversity

Molecular studies on seed plants have shown that species with certain life history traits tend to have different levels of genetic diversity. Hamrick and Godt (1997) combined data from many studies to show that about 25% of the genetic variation among species of plants could be explained by life history traits. The traits with the greatest effect were breeding system, seed dispersal mechanism, life form, geographic range and taxonomic status (i.e. gymnosperm, dicotyledon or monocotyledon). Plants with light, wind dispersed seed or good pollen dispersal are likely to show less genetic diversity between populations than those with heavier seeds. Narrowly distributed and endemic plant species (within the same breeding system) generally had lower genetic diversity than more widely distributed species. Finally, genetic variation between populations was strongly influenced by life form with annuals in particular having higher levels of variation than perennials. Breeding system was also found to be important with the lowest within species genetic diversity and highest between populations divergence found in endemic selfing species (Hamrick and Godt 1997).

In higher plants breeding systems may be asexual (e.g. clonal or **apomictic**) or one of a spectrum from mixed mating to entirely outbreeding. In some species outcrossing may be ensured by systems such as self-incompatibility, widespread in angiosperms (Waser 1993), or separation of the sexes. Incompatibility systems also help to restrict inbreeding between close relatives (Briggs and Walters 1997). Sexual or outbreeding species have lower genetic diversity *among* populations than selfing or mixed mating species regardless of other traits (Hamrick and Godt 1997). However, mutation and **recombination** will ensure that sexual species will have much higher genetic diversity *within* populations than asexual 'species' because they carry a **genetic load** of maladaptive characters. In contrast, clonal plants produce identical, locally adapted progeny.

Asexual reproduction in plants may take place through vegetative apomixis by means of structures such as bulbils, rhizomes or stolons. In insect-pollinated species this mode of reproduction may confer the ability to survive at the margins of the geographic range where pollinators are rare or absent (or populations very small; e.g. *Saxifraga cernua* in Scotland). It is also common in weedy species which are able to colonise new habitats rapidly and from low initial numbers in the absence of pollinators and/or sexual partners. It is possible for variants to arise through somatic mutation (i.e. mutation in non-reproductive cells) but it is unknown whether this has any significance for population genetics (Briggs and Walters 1997). Alternatively plants such as the common dandelion *Taraxacum officinale* may set seed in the absence of sexual fusion in a process known as **agamospermy**.

The breeding system may also affect the susceptibility of a plant species to outbreeding depression (Fenster and Dudash 1994). Many plants vulnerable to outbreeding depression are 'at least partially self-fertilising' (e.g. *Chamaecrista fasciculata, Ipomopsis aggregata, Lotus scoparius* and *Delphinium nuttallianum*; Edmands and Timmerman 2003). Simulation modelling by Edmands and Timmerman (2003) suggests that the effects of outbreeding depression will be more persistent in selfing species. However, breeding system alone does not reliably predict whether outbreeding depression will occur (Barrett and Kohn 1991). Breeding system may also influence the risk of inbreeding depression. Study of an invasive population of smooth cord grass (*Spartina alterniflora*) yielded a significant negative correlation between the overall magnitude of inbreeding depression and self-fertility rate among maternal plants, presumably because the selfing plants carried a relatively low genetic load (Daehler 1999).

3.6 Seed sampling strategies for restoration

In a restoration schemes it is important to determine the correct balance between short-term requirements for local adaptation and longer term evolutionary capacity. A solution to this dilemma is to guide sampling for restoration by the degree and extent of disturbance (Lesica and Allendorf 1999). Where the disturbance prior to restoration is low and the habitat shows little alteration, plants of local provenance and/or from matching habitats are preferred. Plants of local origin are also recommended in large schemes in order to minimise possible impacts on the existing gene pool. This approach is likely to be suitable in the restoration of grassland which may have been fertilised but otherwise has had little disturbance. However, acquisition of local seed may be difficult in practice due to real or perceived risk of damage to limited seed resources or invertebrate species in existing reserves (Stevenson et al. 1994). It may also be very difficult to mechanically harvest adequate seed of some species such as *Lotus corniculatus* (Stevenson and Ward 1993) and collection by hand may be extremely time consuming.

Genotypic mixtures (seeds obtained from a number of genetically differentiated sites)

are advised in large sites with high disturbance (e.g. quarries). Such mixtures can provide the potential for natural selective processes to take place. These mixtures may also be appropriate in restoration of arable land where the soil is highly disturbed. Specially selected cultivars may be a good choice in small contaminated areas as certain varieties have been bred for tolerance to potentially toxic conditions such as heavy metals. However, this approach should be avoided in larger areas due to potential problems from gene flow from the cultivars (Lesica and Allendorf 1999; Gray 2002). Recommendations for sampling strategies for restoration has been proposed by Millar and Libby (1991) and Knapp and Rice (1994) that both emphasise the importance of matching the sampling policy to the genetic structure and variability of the species and the heterogeneity of the environment (Gray 2002). Specific advice for avoidance of potentially deleterious genetic shifts following 'bulking up' of seed include growing in a matching environment for a minimum of generations, using multiple harvest times and isolating from gene flow (Knapp and Rice 1994). None of these strategies are currently employed in the UK by the wildflower seed industry.

Another strategy involves the delineation of seed zones where it is assumed that translocation can be carried out without detrimental genetic effects. Such zones were first described for commercially grown conifers (Kitzmiller 1990), and a similar system of seed zones is being developed for all native tree and shrub species in the UK (Ennos et al. 2000). This approach is also likely to have more general applicability in restoration ecology (Hufford and Mazer 2003). More recently Jones (2003) proposed a 'Restoration Gene Pool' concept which decouples the issues of genetic identity (number of shared alleles) and genetic adaptation. It assigns plants to one of four gene pools in terms of their genetic correspondence to a target population. He stresses that maximising genetic identity between target and donor sites will not necessarily maximise genetic adaptation to a site particularly if the site has been altered.

4. The potential impacts of introduced genotypes

With the expansion of creative conservation during the 1980s, and particularly the use of wildflower mixtures to create species-rich grasslands, it soon became apparent that many non-native cultivars made up a significant proportion of the seed being sown in restoration schemes. As early as the 1960s botanists had noted the appearance of robust alien subspecies of *Anthyllis vulneraria* (subsp. *polyphylla*) from central and eastern Europe on newly sown roadside verges (Akeroyd 1991) and by the 1980s there were numerous records of introduced *A. vulneraria* subsp. *carpatica* var. *pseudovulneraria* from the Alps (Figure 6a; Akeroyd 1991, 1994a, 1994b). At the same time there was increasing evidence that agricultural varieties of species such as *Lotus corniculatus* (var. *sativus*), *Onobychis viciifolia*, *Sanguisorba minor* (subsp. *muricata*), and *Trifolium pratense* (var. *sativum*) were being introduced within conservation seed mixtures, as well as distinctive variants of common meadow species such as *Achillea millefolium* and *Centaurea nigra* (Akeroyd 1992, 1994b). These introductions led to a campaign dedicated to ensuring that only native plants of British, preferably local, origin were introduced (e.g. King 1998; Flora Locale and Plantlife 2000). The main focus of this campaign was the potentially harmful impacts that these non-native genotypes might have on native plants and animals (Gray 2002).

This section outlines the main potential impacts that are relevant to seed sowing for restoration. The impacts are grouped into those that might jeopardise the establishment of viable populations after restoration, and those with possible effects on existing natural or semi-natural populations. The impacts are illustrated where possible using the species that are included in this review. Current understanding of the processes involved and how these relate to life-history traits are reviewed in Section 3.

4.1 Alteration of native patterns of genetic diversity

Theoretically human-mediated gene-flow is likely to have altered native patterns of genetic diversity in some agriculturally and horticulturally important species which have experienced massive amounts of gene-flow through the sowing of selected cultivars and crops (e.g. forage grasses and legumes, crops, ornamental trees and shrubs).

Example:

1. *Lolium perenne*: In a study of 27 populations in unimproved pastures in the UK, Warren et al. (1998) found that populations from adjacent regions were genetically less similar than populations separated by greater differences. A possible explanation was long-scale gene-flow as a result of agricultural usage, with material being widely sown in regions distant from where they were originally sampled (Kent). In addition, the greater similarity of populations within rather than between regions was probably due to the extensive gene-flow within regions either because the species was extremely abundant or because of the regional preferences of farmers in selecting varieties. As the populations were all from unimproved pastures this also implied that there had been significant gene-flow from adjacent improved pastures apparently without disrupting the semi-natural communities in which it was found to grow.

The lack of other studies on this issue presumably reflects the complexity and cost of large-scale surveys of selectively neutral variation in widespread taxa. This is in contrast to tree species in Europe (Ennos et al. 2000) and rare and localised species in the UK (Tew et al. 1997; Section 5.5).

4.2 Risks to the establishment of new populations

4.2.1 Founder effects

A population founded from a few individuals (e.g. in habitat re-creation) may only carry part of the genetic diversity available in source populations. This could result from seed collection from limited sources (Hufford and Mazer 2003) or from poor germination or seedling survival after restoration sowing. This can result in non-adaptive genetic differentiation from other populations and low genetic diversity, which may limit the ability of the population to survive and adapt to future environmental or ecological changes. Low genetic diversity also increases the risk of the population suffering from deleterious effects of inbreeding depression such as genetic drift.

Examples:

1. *Zostera marina*: An investigation into restored eelgrass populations in Southern California indicated significantly lower genetic diversity in a restored population compared to natural populations. Furthermore, fitness consequences were suggested by lower production of reproductive shoots and reduced germination rates in the restored population (Williams and Davis 1996).
2. *Argyroxiphium sandwicense*: Re-introduction of the endangered plant *Argyroxiphium sandwicense* on Mauna Kea, Hawaii, resulted in a severe genetic bottleneck. A sample of around 1500 plants was found to be descended from only two or three founders (Friar et al. 2000).

4.2.2 Inbreeding depression

Inbreeding depression is the reduction in fitness due to breeding between individuals related by descent. Examples in the literature refer to small, isolated populations, and experimental work, but could apply to restoration work if seed collection was from limited, closely related sources.

Examples:

1. *Succisa pratensis*: In a study of 17 Dutch populations of *Succisa pratensis* Vergeer et al. (2003) showed that plants from smaller populations with high inbreeding coefficients had reduced reproductive fitness. They produced fewer seeds, with lower germination rates, and higher seedling mortality. Deleterious effects of relatedness were also demonstrated in re-introduced populations that had increased mortality, reduced biomass and lower seed weight and production (Vergeer et al. In press).
2. *Arnica montana*: In a field experiment in the Netherlands involving five populations of this self-incompatible, rosette forming perennial, significant inbreeding effects were demonstrated. These included reduced seedling size and growth rate. In the same experiment, only plants that were not inbred were able to survive in the field (Luijten et al. 2002).
3. *Silene latifolia*: Evidence is also available for inbreeding effects on host-pathogen relationships although the outcome may be influenced by the genotype of the parent plants. Working with eight plant populations from different parts of the Netherlands, Ouborg et al. (2000) found significant effects of inbreeding on the resistance of *Silene latifolia* (*S. alba*) to the anther-smut fungus *Microbotryum*

violaceum, a host-sterilising pathogen. However, their results were highly variable showing that inbreeding may increase or decrease resistance. They concluded that '…the net effect of inbreeding on field resistance is genotype dependent' such that the '…outcome of the dynamic host–pathogen interaction is unpredictable at the local population level'.

3. Impacts on existing populations

4.3.1 Genetic swamping

Genetic swamping can occur in the absence of hybridisation because of either a numerical or fitness advantage of introduced plants or alternatively from introgression of introduced genes through hybridisation with local populations. When the relative contribution of gametes from a poorly adapted non-local source is low, genes from the non-local individuals, as well as their hybrids, might readily be removed from the population through natural selection without much consequence to population fitness. Indeed, local selection will continue to ensure that genes of adaptive significance survive any bouts of introgression with non-natives (Gray 2002). However, if large numbers of non-local, and often poorly-adapted, organisms are introduced (as is the case of many crop species) the potential exists for the swamping of locally, well-adapted genes. In this scenario there is erosion, or complete loss of the locally adapted genes and, therefore, a reduction in the overall fitness of hybrids. Inevitably this loss of variation may restrict a species ability to evolve and adapt to changing environmental conditions. In the case of habitat recreation locally evolved populations close to restoration sites may become vulnerable to genetic swamping following the introduction of variants with a fitness advantage.

Examples:

1. *Lotus corniculatus*: Using morphometric data Jones (1990) identified agricultural cultivars of *Lotus corniculatus* on roadside verges in the UK. Seed from these plants was lighter than from local plants, but when introduced to a new verge, it showed equal recruitment, and higher post-seedling growth rate and survival compared with seed from local plants. He also found evidence for in situ hybridisation between native plants and cultivars on road verges (Bonnemaison and Jones 1984) and at one site the gradual replacement of the local varieties by hybrids.
2. *Phagmites communis* (*australis*): Chambers et al. (1999) and Saltonstall (2002, 2003) used molecular analysis to detect the cryptic invasion of Eurasian *Phagmites communis* in coastal wetlands (containing native *Phragmites* genotypes) of North America. This species expands primarily through vegetative growth; hence the range expansion may be explained by competitive advantage of the aggressive strain, rather than as the result of intraspecific hybridisation.
3. *Spartina foliosa* and *S. alterniflora*: Hybridisation by two closely related species may also lead to genetic swamping. This has been documented in the Californian cord-grass *Spartina foliosa* which is threatened by hybridisation with the introduced *S. alterniflora*. The F1 hybrids were highly vigorous with enhanced pollen production and dispersal (Anttila et al. 2000).

In contrast to fears from 'genetic swamping' a number of studies have shown that local genotypes may outperform non-local genotypes from distant sites (both in terms of geographic and ecological distance) because they have a 'home site' advantage – i.e. they are better adapted to local conditions (e.g. climate, soils, etc.):

4. **Joshi et al.** (2001) investigated the performance of *Trifolium pratense*, *Dactylis glomerata* and *Plantago lanceolata* in relation to genetic diversity and local adaptation at a continental scale using reciprocal transplants at eight sites across Europe. The overall performance of the species was generally highest for plants replanted at their home site and declined with transplant distance.
5. *Lotus corniculatus* (Bird's-foot trefoil): Smith et al. (submitted) studied the effect of geographical and ecological distance on the establishment and performance of *Lotus corniculatus* planted on treated and untreated clay quarry soils in Dorset. Plants were sampled from a range of sites within 15 regions, each site consisting of plants from a habitat equivalent to the 'home site' (i.e. calcareous) and non-calcareous habitats (i.e. different to the home site). Local plants were found to have a 'home site' advantage in terms of survival on the treated plots only and there was a significant negative correlation between survival and geographic distance. Surprisingly, however, there was also a significant positive correlation between ecological distance and plant size and fecundity on the untreated plots; plants from more ecologically distant populations (i.e. non-calcareous) were larger and more fecund. This

was interpreted as a result of local adaptation: small chalk grassland plants were adapted to growth in a harsh environment (e.g. nutrient-poor, drought tolerant) which was very similar to conditions on the untreated plots.

6. *Centaurea nigra* (Knapweed): In a study of the effects of water-level on the germination and growth of wet grassland species Barratt et al. (1999) showed that both reproductive effort and biomass allocation for a wetland grassland ecotype of *C. nigra* was greater at the higher water-levels than a dry grassland ecotype, emphasising the importance of selecting the appropriate variants for restoration.
7. **Jones and Hayes** (1999) studied the effects of provenance (local vs. non-local) on the establishment of several wildflower species (*Achillea millefolium, Centuarea nigra, Plantago lanceolata, Prunella vulgaris, Stachys officinalis*) sown into established swards each receiving different management regimes. After two years the local provenances of *A. millefolium*, *P. vulgaris* and *S. officinalis* all had survived markedly better than the non-local genotypes. In contrast, the other two species showed no clear differences in plant numbers but both flowering and seeding were significantly better in non-local provenances of *P. lanceolata* and *P. vulgaris*. As with *Lotus corniculatus* the variability of these results may reflect the short-term nature of this study. Indeed, the importance of local adaptation may not become apparent or fully tested for many years, or until ‘rare’ events or infrequent or extreme conditions to show superior fitness (survival) for local provenances.
8. **Keller and Kollman** (1999a) examined the germination response of European provenances of seven species (*Centurea cyanus*, *Cichorium intybus*, *Daucus carota*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Papaver rhoeas*, *Silene latifolia* (*alba*)) along a W-E climatic gradient in Europe in a laboratory trial and a common garden study in Switzerland. In the laboratory trial English samples had distinct germination responses (less responsive to temperature) which were thought to be a result of different climatic properties of the winter and spring, which either require different germination triggers or earlier germination. In contrast delayed germination in a common garden experiment may have been due to a requirement for greater soil moisture. *C. intybus*, *D. carota*, *L. vulgare* and *S. latifolia* (but not *C. cyanus*) from distant provenances (England and Hungary) all performed less well than those from closer to the field site presumably because of a lack of adaptation to Swiss field conditions. Overall variability in provenances was lowest in *C. cyanus*, intermediate in *D. carota* and *L. vulgare*, and highest in *S. latifolia*. Although species-specific these results suggest that non-native genotypes are likely to suffer from poor establishment during habitat recreation, with the exception of arable weeds, such as *C. cyanus*, which are likely to have over-riding adaptation to agricultural management rather than climate.

4.3.2 Heterosis

Crossing between genetically differentiated populations may lead to significant changes in the fitness of offspring. Where differences between populations have arisen through genetic drift, then mixing of genotypes following restoration could result in heterosis i.e. hybrid vigour in the F1. In some circumstances this may increase the fitness of hybrid offspring by masking deleterious recessive alleles (Section 3.3) although recent research (Keller et al. 2000) suggests that heterosis may be followed by outbreeding depression in later generations thereby potentially reducing the fitness of native populations following restoration (Section 4.4.2).

Examples:

1. *Succisa pratensis*: Crosses between *S. pratensis* from isolated populations in the Netherlands led to changes in some characters. For instance, inter-population hybrids produced more and heavier seeds than plants from large single populations. Plants from the inter-population crosses also showed higher flowering capacity than those from small or large populations (Vergeer et al. in press). The authors conclude that genetic reinforcement of small threatened populations might be successful if source populations are carefully chosen. However, it is important to note that this experiment was conducted in an artificial environment and selective pressures in the field could lead to different outcomes. The study was also only continued to the first generation, so is possible that advantages could be lost in later generations (see Section 3.3).
2. *Arnica montana*: In the same field experiment described above Luijten et al. (2002) also reported heterosis in *Arnica montana*. This was demonstrated by an increase in seed production, seedling size and probability of flowering for the inter-population progeny. However, data were only available up to the first generation.

3. *Sarracenia flava*: *S. flava* is an insectivorous plant restricted to four sites in Virginia, USA. Sheridan and Karowe (2000) tested for effects of intra-site outcrossing, and inter-site outcrossing on offspring quantity (total seed number and total seed mass) and offspring quality (average seed mass, germination, and growth) up to the first generation. Relative to offspring from intra-site crosses, offspring from inter-site crosses were significantly larger after five years of growth. The authors conclude that restoration efforts for Virginia *S. flava* will be most successful when plants from multiple sites are used. As above effects in subsequent generations were not studied.

4.3.3 Outbreeding depression

Crossing genetically differentiated populations may also result in reduced fitness either through dilution of locally adapted genotypes or through hybrid breakdown (epistasis; Section 3.3). As stated above F1 hybrids are heterozygous at the locally-adapted loci and therefore there is a 50% 'dilution' of each differently adapted genome. As a result subsequent F2 hybrids may perform worse than the parental genotype in the native environment of both parents.

Examples:

1. *Papaver rhoeas*: Keller et al. (2000) compared the growth of intraspecific hybrids of *P. rhoeas* in a field experiment involving parent plants from wild populations in Switzerland and commercial varieties from Switzerland, Germany, England and Hungary. Comparing above–ground biomass, survival and seed mass, they found a clear tendency towards outbreeding depression due to hybrid breakdown (epistasis) expressed as reduced biomass and survival in the F2 crosses.
2. *Lotus scoparius*: Montalvo and Ellstrand (2001) evaluated the potential for outbreeding depression by hybridizing individuals from six different populations of the sub-shrub *L. scoparius*. In the greenhouse, the success of crosses (seeds/flower (seedlings/seed) decreased with increasing genetic distance (based on allozyme data) between populations revealing outbreeding depression. From this, and from further evidence indicating a loss of local adaptation, the authors conclude that '…mixing genetically differentiated seed sources of *Lotus scoparius* may significantly lower the fitness of augmented or restored populations'.

4.3.4 Heterosis followed by outbreeding depression

Heterosis in the first F1 may often be followed by outbreeding depression in later generations (Keller et al. 2000). After initial hybrid vigour recombination in subsequent generations may lead to disruption of coadapted gene complexes.

Examples:

1. *Silene latifolia* and *Agrostemma githago*: In the same field experiment described above for *Papaver rhoeas* Keller et al. (2000) compared interpopulation crosses of *S. latifolia* and *A. githago* with controls (plants mated with other plants of the same stock). Inter-population crosses of both species tended to show increased fitness (above-ground biomass and seed mass) in the F1 and reduced fitness in the F2. Germination tests with *S. latifolia* revealed no differences in viability between any of the crosses.
2. *Chamaecrista fasciculata*: Crosses of plants from populations between 100 m to 2000 km apart were carried out throughout the range of this North American plant. F1 crosses showed superiority over the parents but the F3 hybrids suffered a loss of fitness compared to the F1 hybrids. The drop off in fitness of the F3 reflected both the loss of heterozygosity and the disruption of coadapted gene complexes. The F3 performance, however, was still often equal to that of the parents, suggesting that heterosis can outweigh the loss of coadaptation except for the longest-distance crosses. Interestingly, in a subset of environments the F3 performance of long-distance (1000 km) inter-population crosses was less than that of both parents and indicated outbreeding depression without any heterosis in the F1. Also the degree of F1 heterosis and F3 outbreeding depression varied between site and year, however, indicating an important role for the environment in the expression of these effects (Fenster and Galloway 2000).

4.4 Effects on species in the same or other trophic levels

It is possible that the introduction of non-native genotypes may have damaging impacts on species in the same or higher trophic levels, such as natural enemies (e.g. vertebrate and invertebrate herbivores, fungal pathogens, and bacterial and viral diseases) and mutualists important for plant growth and reproduction (e.g. pollinators, seed dispersers, nitrogen-fixing bacteria, and mycorrhizae). For example, there is some evidence to suggest that plant provenance may affect the food choice and growth of associated herbivores where there are known to be intraspecific physiological differences in plant defences such as the production of cyanide compounds. This may confer a competitive advantage on non-native genotypes and result in changes to plant-invertebrate interactions with unforeseen ecological consequences. In addition, differences in phenology or food resource quality (e.g. pollen and nectar) between different genotypes may have adverse effects on invertebrate assemblages following re-creation. However, the impacts of non-local genotypes on natural enemies and mutualists are at present poorly understood and the examples below only suggest possible impacts.

Examples:

1. *Lotus corniculatus*: cyanogenesis has been shown to confer a fitness advantage in *L. corniculatus* by discouraging herbivory (Compton et al. 1983; Compton and Jones 1985) with some slugs and snails feeding preferentially on acyanogenic forms (Jones et al. 1978). However, Smith et al. (submitted) found that cyanogenesis was not correlated with survival, production or predation of *L. corniculatus* collected from 15 different regions and planted on a restoration site in Dorset despite the fact that plants from the study region (Dorset) had a higher proportion of cyanoganic plants.
2. *Trifolium repens*: Daday (1954a) reported intraspecific variation in herbivory on *T. pratense* in relation to the distribution of cyanogenesis, with decreasing frequencies from western and Mediterranean origins to those from northern and eastern Europe. This adaptation was interpreted as increased selection pressures for plants to develop defence mechanisms against herbivores such as slugs in cooler, milder climates (e.g. in the UK), where slugs are assumed to be more abundant.
3. **Keller et al.** (1999b) studied herbivory on juvenile plants of *Cichorium intybus*, *Daucus carota*, *Leucanthemum vulgare* and *Silene latifolia* of different European origins exposed to grazing by two slug species (*Deroceras reticulatum* and *Arion lusitanicus*). These confirmed the results of Daday (1954a) in that plants of more eastern provenances were more palatable whereas English plants suffered low herbivory as a result of defences generated by intense selection pressures from high population levels of slugs associated with mild winters. In a separate experiment they also showed that for *Silene latifolia* non-local plants (non-Swiss) were more susceptible to rust fungal pathogen.
4. *Trifolium pratense* and *Lotus corniculatus*: Comparisons between the flowering of native and agricultural genotypes sown on six arable field margins in southern England has shown that there are distinct differences in phenology with agricultural genotypes flowering either much later (*T. pratense*) or much earlier (*L. corniculatus*) than native genotypes (Meek et al. 2004).

5. Intraspecific variation in the British flora

Some British species show a remarkable degree of intraspecific variation due to phenotypic plasticity and genetic variation across the range (Huenneke 1991) with differences occurring across a range of scales from 100s of kilometres to just a few metres (Bradshaw 1984). The degree of variation largely depends on the interplay between natural selection (the tendency to enhance differences) and gene-flow (tending to reduce differences) but because of their largely sedentary nature gene-flow is often outweighed by selection (Bradshaw 1972). As a result, patterns of differentiation tend to follow patterns in the environment very closely (Linhart and Grant 1996) with most genetic diversity lying along the axis of environmental and more specifically habitat variability (Gray 1996b). The study of these adaptations, and the mechanisms which bring them about, is called **genecology** (Heslop-Harrison 1964), a term first used by the Swedish botanist Göte Turesson (1923) who studied distinctive variants of many common European species in the 1920s (Section 5.2). Since these early studies differentiation has been shown to vary in an abrupt or gradual manner as well as occurring at smaller and smaller scales. Intraspecific variation therefore appears to be more complex than the first thought and for many species the patterns have defied taxonomic recognition (Briggs and Walters 1997). Given these caveats, four main ‘types’ of variation have been traditionally recognised: morphological, ecotypic, clinal, and cytological.

5.1 Morphological variation

Morphological variation (**polymorphism**) provide the most basic evidence for intraspecific 'types' and are found in numerous plant characters (e.g. hairiness, flower colour, etc.). Although for some species such variation has been shown to be adaptive the vast majority is likely to be of little evolutionary, physiological or ecological significance (Valentine 1975). On the other hand underlying genetic differentiation may be cryptic (in terms of structure) and therefore important adaptive variation may be underestimated for some species if measured by morphological characters alone.

Although the treatment of intraspecific variation has differed greatly in the past plant taxonomists now recognise five hierarchical, intraspecific **ranks**: subspecies, variety, subvariety, form, and subform (Heslop-Harrison 1964; Stace 1989). At present about one-third of common British species possess well defined subspecies, some of which have morphologically distinct forms which have been recognised at the varietal level (e.g. *Anthyllis vulneraria* subsp. *vulneraria* vars *langei* and *coccinea*). Many of these intraspecific taxa date from the nineteenth and early twentieth centuries and arose from the efforts of botanists to fit observed variation into a conventional taxonomic framework (Akeroyd 1997). English botanists, from the seventeenth century onwards, were particularly interested in intraspecific variation and were not only interested in naming species but also in seeing if extreme characters, such as dwarfing, were retained under cultivation (Allen 1966; Valentine 1979). This trend reached a peak in the late nineteenth and early twentieth century and culminated in the inclusion of 2400 'varieties' in the *British Plant List* published in 1928 (Druce 1928). Since then there has been a decline in the use of these intraspecific taxa (Chater 2003), largely because of the poor treatment of named variants in standard floras and checklists since the Second World War (Allen 1966, 1987), although there has been a resurgence of interest in recent years (e.g. Allen 1987; Sell and Murrell 1996; Rich and Jermy 1998; Cowell 1999).

5.1.1 Morphological variation in species included in this review

Fifty-one species included in this review have named intraspecific taxa recognised in recent taxonomic works (Table 9; Appendix 4). The most variable species, with three or more native subspecies are *Anthyllis vulneraria*, *Cerastium fontanum*, *Deschampsia cespitosa*, *Festuca ovina*, *F. rubra*, and *Rhinanthus minor* all of which are represented by generalist taxa which occur throughout the range of the species and a number of ecologically restricted subspecies. For example, *Rhinanthus minor* is divided into six subspecies only one of which (subsp. *minor*) is common and widespread. In contrast subsp. *stenophyllus* is restricted to damp grasslands (e.g. fens, flood meadows, dune slacks, etc.) particularly in the north and west, subsp. *calcareus* to calcareous soils in the south, and subspp. *lintonii*, subsp. *monticola* and subsp. *borealis* to montane habitats in the north and west (Stace 1997).

As can be seen from Table 9 there are also a number of species for which there is taxonomic uncertainty over the validity of intraspecific taxa. A good example is *Pilosella officinarum* for which seven subspecies have been recognised in the past (Rich and Jermy 1998). Although these are easily separated on morphology few are geographically or ecologically separable and are therefore thought to be nothing more than varieties (Stace 1997). Taxonomic variation within the **agamospermous** *Poa pratensis* aggregate has also posed many difficulties for British botanists, with three closely related taxa being recorded in the British Isles. These are now treated separately as *Poa pratensis* s.s., *P. humilis* and *P. angustifolia* but the two former species are still poorly understood and may represent complex patterns of ecotypic variation which has developed as a result of inbreeding.

5.2 Ecotypic variation

As described in Section 3.3 many species possess **ecotypes** which represent 'local races' adapted to a particular ecological niche but fully interfertile with other ecotypes in the same species (Stace 1976, 1989). Often these distinct ecotypes, which have been described in hundreds of species, represent discontinuous genetic variation correlated with specific habitat types. However, recent research suggests that many are **clinal** occurring along environmental gradients, or occur as races within a graded 'patchwork' of habitats where differentiation can occur over very short distances (Bradshaw 1959; Gray et al. 1979).

As early as the eighteenth century botanists were aware that many species showed marked variation between populations such as dwarfing in very dry or exposed conditions or the production of succulent leaves in maritime habitats affected by salt (e.g. Bonnier 1895; Kerner 1895). In 1901 Ludwig (1901) coined the term 'local race' to account for these distinct morphological types but it was not until the 1920s that their significance was fully appreciated largely as a result of the work of the Swedish botanist Göte Turesson (1922a, 1922b, 1923, 1925, 1930) who, by growing samples of several variants of a species in a **common garden**, was able to demonstrate the heritability of certain traits. His approach was to collect living plants of many common species from a variety of natural habitats in southern Sweden (and latterly from sites all over Europe) and grow them in experimental gardens. Distinctive variants of plants from different habitats could therefore be grown side by side with normal plants from inland localities under comparable conditions. In some cases the distinctiveness of the variants was lost in cultivation, but usually they were retained even in the absence of shading, exposure etc., suggesting that for some species variation was genetically fixed (Heslop-Harrison 1964). A good example of Turesson's work is *Hieracium umbellatum* in Sweden, for which he found races specific to particular habitats including woodland, sandy fields, dunes and cliff-tops. Turesson called these local races **ecotypes** and described ecotypes for more than 50 European species including 19 included in this review (Table 10). Ecotypes can be related to climate (**climatic ecotypes**), soil conditions (**edaphic ecotypes**) and management (**biotic ecotypes**). Those described for species included in this review are given in Table 11 (see Appendix 5 for further details).

5.2.1 Climatic ecotypes

Some of the most famous experiments on climatic ecotypes were carried out during the 1940s and 1950s by Clausen, Keck and Hiesey in North America. In a large programme of reciprocal transplant experiments they studied the effects of climate on a range of species collected along a 200-mile transect across Central California ranging from a Mediterranean climate in the west to an alpine climate in the east (Clausen et al. 1940; Clausen and Hiesey 1958). Transplants were grown in three separate gardens at a range of altitudes and performance measured in relation to extremes of temperature and growing season. Most famously four climatic ecotypes of *Potentilla glandulosa* were identified using a range of morphological characters and latterly a number of physiological traits (Hiesey and Milner 1965). Most importantly, however, they also discovered that the subspecies were made up of two or more individual ecotypes, although these were not considered to be distinct taxonomic entities (Clausen and Hiesey 1958; Elkington 1986). In similar series of experiments Clausen and colleagues also showed that the North American population of *Achillea millefolium* s.l. (including *A. lanulosa* and *A. borealis*) and *Zauschernia californica* were made up of a series of parallel ecological races, each consisting of several genetically distinct populations.

5.2.2 Edaphic ecotypes

Where edaphic conditions such as pH, mineral nutrients, or other physical features are extreme they generate selection pressures which can produce localised patterns of variation. As a result edaphic ecotypes can be differentiated from surrounding populations (often within a few metres) by their ability to grow and survive in soils with a surplus or a deficiency of a particular element. Some of the most striking examples are found on serpentine soils which support an impoverished flora of specialised plants which can tolerate high concentrations of nickel, magnesium, and chromium and low concentrations of calcium and phosphorous. The earliest experiments on serpentine 'races' were carried out by Kruckeberg (1951, 1954, 1967) who showed that some of the 'classic' climatic ecotypes described by Grant and Clausen (e.g. *Gilia capitata* subsp. *capitata*; *Achillea borealis* subsp. *californica*) possessed local populations specifically adapted to serpentine soils. Other classic edaphic ecotypes are those adapted to growth on contaminated soils on lead mines and other mineral workings (Bradshaw 1952). The evolution of heavy metal tolerance has been known to be a powerful selective force for several decades (Antonovics et al. 1971) and was subsequently found to be ubiquitous in mine populations of some grasses but entirely absent from populations growing just a few metres away in adjacent pastures (e.g. Antonovics and Bradshaw 1970). Tolerance to high levels of metal contaminants (e.g. lead, copper, zinc, arsenate, lead) has been reported in a number of grasses included in this review including *Agrostis capillaris*, *A. stolonifera*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Deschampsia cespitosa*, *Holcus lanatus* and *Festuca ovina* (see Appendix 5 for details). Similarly, tolerance to high levels of pollutants such as sulphur dioxide (*Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus*, *Lolium perenne*), lead in car exhaust fumes (*Plantago lanceolata*) and de-icing salt (*Anthoxanthum odoratum*) have also been reported for some species.

The regular application of fertilisers can change soil properties and therefore plant growing conditions and selection pressures. Tolerance of, or dependence on high fertiliser levels has been shown to occur in *Anthoxanthum odoratum* (Davies and Snaydon 1973a, 1973b, 1974;

Snaydon and Davies 1982). Furthermore, 'natural' variations in soil nutrients and conditions has also been shown to lead to substantial genetic differentiation (Linhart and Grant 1996). For example, Bradshaw (1959, 1960) found morphological and physiological differences in relation to local environmental variation in populations of *Agrostis capillaris* collected from 33 sites in central Wales. As an out-breeding and wind-pollinated species such differences suggest a mosaic of reproductively isolated populations each closely adapted to its own environment, accompanied by a similar pattern of physiological adaptation (Bradshaw 1960). Similar findings have been found in a range of other species (Table 11). Similarly, plants growing on cliffs, dunes, and other coastal habitats are exposed to such extremes of light, wind, salt deposition, and wave action. As a result adaptations to maritime exposure or salt-spray have been reported in a wide range of common species including *Agrostis stolonifera*, *Festuca rubra*, *Filipendula ulmaria*, *Leontodon autumnalis*, *Lotus corniculatus, Lythrum salicaria*, *Silene dioica*.

5.2.3 Biotic ecotypes

Biotic influences such as mowing or grazing can obviously exert strong selection pressures on grassland species. As a result the evolution of prostrate life forms that can flower and set seed very close to the ground has been documented for a number of British lawn weeds such as *Poa annua*, *Bellis perennis*, *Plantago lanceolata*, *P. major* and *Prunella vulgaris* (Warwick and Briggs 1979). In addition, grazed ecotypes have been recorded for *Dactylis glomerata* (Stapledon 1928), *Poa pratensis*, and *Trifolium repens* (Kemp 1937) whereas Bradshaw (1963) and Walters (1970) have described dwarf variants of *Alchemilla*, the origin of which is likely to have been selection in response to grazing by sheep. In addition, the experiments of van Tienderen and van der Toorn (1991a, 1991b) on *Plantago lanceolata* provides an excellent example of local adaptation in relation to contrasting habitat management. Selection under different management was shown to have favoured co-adapted traits, life-history strategies, and reproductive tactics such as erect, tall, earlier-flowering ecotypes in hay-meadows, and short-leaved, decumbent, light-seeded variants in grazed sites.

Competition for resources such as light, water, nutrients, space, pollinators, etc. may also have adaptive significance which leads to localised differentiation. Different kinds of interspecific competition have been investigated in *Trifolium repens*, which in competition with common meadow grasses showed differentiation in response to long-term associations with these species (Turkington and Aarssen 1984; Turkington 1989). Shading can also exert a biotic influence, but its primary impact is the physical reduction of available light. For example in *Plantago lanceolata* there exist genetically differentiated sun and shade populations (Teramura and Strain 1979) whereas morphological and survival differences have been found for *Anthoxanthum odoratum* (Grant and Antonovics 1978).

5.3 Clinal variation

Ecotypes often occur within an overall gradient of variation correlated with gradual changes in habitat conditions (Heslop-Harrison 1964). Such gradients are known as **clines** (Huxley 1938) and, when linked with ecological conditions, **ecoclines**. The earliest work on clinal variation was carried out by Gregor (1930, 1938, 1946) who studied variation in *Plantago maritima* along an environmental gradient from a muddy salt-marsh to a cliff-top. Each plant was scored for a series of characters and the results showed that there was a well marked gradient in these characters as the habitat changed from one end of the series to the other (Valentine 1978). Gregor (1944) therefore used the term **ecocline** to describe where these patterns mirrored ecological gradients and **topocline** where they were correlated with regional changes in climate. Clinal variation has subsequently been described for a number of British species (Table 11), probably the most famous example being seed polymorphism in populations of *Spergula arvensis* (New 1978). In Britain plants with non-papillate seeds are more common in the south and east whereas plants with rough seeds are more common at low latitudes or at higher altitudes (New 1958). Plants with rough seeds are known to have lower germination rates at higher temperatures suggesting that they are better adapted to germinate in warmer, drier conditions (New and Herriott 1981). Other well studied examples include physiological clines for cyanide production in *Trifolium repens* (Daday 1954a, 1954b, 1965) and *Lotus corniculatus* (Jones 1970, 1977), seed and pollen morphology and flavone-glycosylation gene frequencies in *Silene latifolia* (Mastenbroeck et al. 1984; Prentice et al. 1984; Prentice 1986) and flower colour variants in *Lotus corniculatus* (Crawford and Jones 1986).

5.4 Cytological variation

By the 1960s it was apparent that species possessed groups of individuals which differed in terms of their **cytology** (i.e. the number of chromosomes). In general, the number of **chromosomes** in each cell of a species is constant, except for simple multiples of that number. Usually this information is provided in the form of the diploid number (*2n*) when the count is based on **mitosis** in **sporophytic** tissue and the haploid number (*n*) when based on **mitosis** in the **gametophytic** tissue. Often closely related species (e.g. within the same genus) or populations within a species differ in chromosome number, the most frequent variations being based upon the phenomenon of **polyploidy** (Stace 1989). In a diploid species the number of chromosomes (x) is represented by $x = n$, but in a polyploid species n is a multiple of x (three or more). Hence for the genus *Festuca*, which has a gametophytic **base-number** of 7, a diploid species will be $2n$ = 14 (or $n = 2x = 14$) whereas for polyploids $2n$ = 28, 42, 56, and 70 (commonly referred to as **tetraploids**, **hexaploids**, **octoploids** and **decaploids)**. Groups of organisms in which there is a range of chromosome numbers representing different degrees of polyploidy (ploidy level) are known as a **polyploid series** or **polyploid complexes** where relationships to morphological characters are uncertain.

Polyploid series or complexes have proved to be one of the richest sources of cytological data of value to taxonomists and have frequently been used to determine the specific and subspecific limits of separate taxa. Although chromosome numbers can not be used to redefine genera or species alone, there are many good examples in the British flora where a range of morphological divergence has been associated with differences in ploidy level (e.g. ferns). However, as with ecotypic variation there are probably many more cases where there is very little correlation between morphology and ploidy level. This is often referred to as cryptic or semi-cryptic polyploidy.

5.4.1 Cytological variation in British wildflower species

Thirty-five species included in this review are cytologically variable in the UK with distinct polypoid series or complexes (Table 12; Elkington 1984). However, only a handful of these species have distinct cytotypes that have been recognised at the subspecific level. One of the best studied examples is *Galium palustre* which has three cytotypes in the British Isles (Clapham 1949), all three of which are morphologically and ecologically distinct (Stace 1997). A more complex pattern of variation occurs in *Deschampsia cespitosa.* Currently three subspecific taxa are recognised; subsp. *cespitosa*, which occurs as a diploid (2n = 26) in the south and a diploid, triploid or tetraploid (2n = 39, 52) in the north, subsp. *parviflora*, a diploid of shaded habitats, and subsp. *alpina*, a triploid or near tetraploid (2n = 34-56) in mountains in the north (Sell and Murrell 1996) although there is still much debate, in particular, over the taxonomy of the upland tetraploid taxa (Rich and Jermy 1998).

There are also a number of cryptic polyploids included in Table 12 where the delimitation of subspecies is extremely problematical as ploidy levels are not represented by completely distinctive sets of morphological characters. For example, there are two cytotypes of *Hippocrepis comosa* in Britain; a diploid race (2n = 14) confined to ungrazed harder limestones in the south and west of England and Derbyshire, and a much more widespread tetraploid race (2n = 28) which occurs throughout the range of the species (Fearn 1972). In addition, many other species included in Table 12 have two ploidy levels (e.g. *Campanula rotundifolia*, *Lathyrus pratensis*) although the extent to which these species are ecologically, morphologically or geographically differentiated is still poorly understood.

5.5 Genetic variation

As described in Section 3 two fundamentally different approaches have been used to measure genetic variation in plants. The most common technique has been to measure **genetic marker variation** (using molecular methods such as isozyme and DNA markers) which may be **selectively-neutral**. In contrast, the second approach has been to directly measure **quantitative genetic variation** in traits which are likely to effect fitness of individuals. This form of variation is termed **adaptive genetic variation** and is best detected by measuring differences in phenotype and performance between populations, families or clones when these are growing under common environmental conditions.

One of the crucial differences between these two approaches is that selectively-neutral variation is only measured at single loci which, if monomorphic, suggest that a species or population have low diversity. However, quantitative variation in certain adaptive traits are often controlled by mutations on a range of different loci and therefore indirect measures will often give a misleading (lower) estimate of genetic diversity (Ennos et al. 1997). Such indirect measures of adaptive variation are summarised in the sections above.

Despite these caveats selectively-neutral variation can provide important information on genetic variation which can be potentially used to guide decisions concerning conservation and, in the context of this review, the introduction of non-local genotypes during habitat recreation (Tew et al. 1997). However, with the exception of a few rare and threatened species and agricultural grasses very little research has been carried out on the genetic structure of populations of widespread or common species in the UK. Recent work on a number of rare species has shown a diverse range of genetic variation. For example, a near complete absence of genetic variation has been found in species spreading predominantly by vegetative means at the edge of their range such as *Chamemelum nobile* and *Cirsium dissectum* (Kay and John 1997) and self-compatible species in small, isolated populations such as *Gastridium ventricosum* (Gray 1997) and *Primula scotica* (Glover and Abbott 1995; although see Ennos et al. 1997). In contrast, some autogamous species with poor powers of dispersal have been shown to possess 'stepped patterns' of variation with some population differentiation (e.g. *Ononis recclinata*; Kay and John 1997), whereas partial or complete outbreeders with small populations have been shown to have interrupted clines and stochastic variation (e.g. *Mibora minima*, Kay and John 1997; *Agrostis curtisii*, Gray 1997).

6. Assessing the potential impacts of introduced genotypes

6.1 Assessing risk

In order to assess which British species are at greatest risk from the introduction of non-native or non-local genotypes we combine information on the three most important factors which are most likely to determine the degree of risk: a) the scale of introduction, in terms of the overall supply and use of seed and plant material, b) life-history traits known to determine the partitioning genetic diversity, and c) the degree of intraspecific variation displayed by the species included in the review. This 'risk assessment' is based on the assumption that species displaying the greatest amount of variation will have greater population differentiation and therefore will be most susceptible to disruptions to native patterns of variation arising from introduction and introgression.

Details on the scale of introduction were taken directly from the responses of the seed suppliers contacted from this review (Section 2.3.5) with each species being assigned an overall score based on the supply of both seed and plant material (Appendix 6; see Table 6 for summary). The life history traits included in the analysis were those previously shown to be important in partitioning genetic diversity (Table 15), each of the eight attributes being divided into three categories (high, medium, low) based on its potential to explain genotypic variation (Section 3.5). For example, outbreeding species with effective dispersal abilities (e.g. wind) are known to be more genetically variable than inbreeders with unspecialised dispersal strategies. Therefore attributes promoting outbreeding (e.g. wind pollination, sexual versus vegetative reproduction, crossing, long flowering period) and effective dispersal (e.g. small seeds, wind/water dispersal, wide habitat breadth) scored highly and vice versa. Short-lived species also scored highly as their potential to cross with or be out competed by introduced genotypes may be much greater than for long-lived species which might survive long lived species. These assumptions were based on the findings of earlier studies (e.g. Hamrick and Godt 1991) and are summarised in Table 15. Finally, information on known intraspecific variation was taken from the studies described in Section 4 and divided into morphological, ecotypic and cytological (as in Tables 9-12). Once again each species was assigned to one of three categories as described in Table 14 in relation to the degree of variation displayed (as we have no direct measures of genetic variation these variables are used as a surrogate).

In particular we were interested in the extent to which life history variables and evidence for genetic variation were related. More specifically:

1. Do species show clustering in life history variables (as scored in relation to the hypotheses about the causes of differences in intraspecific variation)?
2. Do any life history variables explain species differences in the amount of intraspecific variation (and thus indicating important processes)?

6.1.1 Do species show clustering in life history variables?

To investigate 1) above we initially carried out a Principal Components Analysis (PCA) of the eight traits of the 151 species included in the review. The results of the first two axes are given in Figure 7 which shows that there is very little clustering between the species suggesting that the life history traits varies relatively independently. As a result it was not possible to select a group of species (with a specific combination of traits) which are potentially more likely to show more intraspecific variation, and therefore more susceptibility to the introduction of non-local genotypes. This was verified by the low correlation among the eight life-history traits (Table 16): only 4 of the 28 trait combinations were significantly correlated (e.g. long-lived species or those with short flowering periods tend to wind-pollinated, annuals tend to reproduce by seed, species reproducing solely by seed tend to have heavier seeds).

2. How do life history variables relate to intraspecific variation?

There was significant correlation between the three measures of intraspecific variation (morphological, ecotypic, cytological; Table 17) and therefore the overall mean of the three variation scores (and re-scaled means for logistic regression) provide good representations of all three measures of variation used in the analyses presented here. In order to investigate the relationship between this variation (using the re-scaled mean) and the eight life-history traits we used ordinal logistic regression, with family and higher taxonomic status (dicotyledon or monocotyledon) also included in the analysis as factors. Using stepwise elimination of non-significant variables, life history (most important), breeding system and dispersal ability (least important) were found to account for the greatest amount of variation in the intraspecific variability within the species included (G = 14, $p = 0.003$; Table 18). All these effects were positive with family and higher taxonomic classification having no effect. This confirms the results of earlier studies that outbreeding species with effective seed dispersal strategies and short-life histories will tend to display greater intraspecific variation than those with other combinations of traits.

2. Species at greatest risk

In order to provide an overall assessment of the degree of risk posed by the introduction of non-local genotypes, we combined the scores for these three most important life-history traits determining the degree of intraspecific variation identified using logistic regression with scores for the commercial supply and known variation (Table 14). The individual and overall scores and rank of species in relation to risk are given in Appendix 6 and summarised for the most threatened 50 species in Table 20. For each species we calculated an overall score for 1) the degree of variation displayed (i.e. **variation score**; average score for the three types of variation given in Table 14: morphological, ecotypic, cytological); 2) the three most important life history traits in determining variation identified using logistic regression (i.e. **life history score**; average score for life history, breeding system and dispersal ability given in Table 15) and 3) the overall supply of species (i.e. **supply score**; as determined in Table 6). As life history and variation scores were correlated (Table 19) we calculated two different overall ‘risk’ scores. The first combines the life history and variation scores to provide a ‘risk score’ which is biologically determined and therefore independent of the amount of plant material being supplied in the UK. In contrast we also calculated a second risk score which included the supply score because this will obviously increase the ‘risk’ posed by introduction (i.e. biologically and commercially determined risk). The difference between these two scores is illustrated for the 50 most threatened species in Table 20. The ‘Diff rank’ column gives the differences between the ranks of the individual species under the separate analyses. Those with positive values are therefore considered to be a greater ‘risk’ when information on supply is taken into account whereas those with negative values are considered to be of lower risk because the degree of supply is much smaller.

The species listed in Table 20 are ranked in terms of overall (i.e. biologically and commercially determined) risk, because this is a more realistic reflection of the potential threats that introduced genotypes pose. Species considered to be high risk under both analyses include

Silene latifolia, *Rumex acetosa*, *Caltha palustris, Papaver rhoeas*, *Leontodon autumnalis*, *Agrostis stolonifera* and *Festuca ovina*. In addition, *Angelica sylvestris*, *Calluna vulgaris, Centaurea nigra, Galium verum, Leucanthemum vulgare, Prunella vulgaris, Ranunculus acris, Sanguisorba minor* and *Silene dioica* are all considered to be at high risk when commercial supply is taken into account. In contrast species considered to be at high risk from a biological point of view but much less so when supply are taken into account are *Campanula rotundifolia, Deschampsia cespitosa, Gentianella amarella, Holcus lanatus*, *Matricaria recutitta, Ranunculus bulbosus*, *Rumex acetosella*. This list also shows that although two of the most threatened species are outbreeding annuals (i.e. *Silene latifolia*, *Papaver rhoeas*) the majority of the most threatened species are well dispersed perennials with either inbreeding (e.g. *Ranunculus acris*), mixed mating (e.g. *Sanguisorba minor*) or outcrossing mating strategies (e.g. *Rumex acetosa*, *Silene dioica*, *Caltha palustris*, *Calluna vulgaris*).

The analysis above is largely based on the level of risk relating to species which exhibit high degrees of 'natural differentiation' amongst populations. Therefore such species face the obvious risks of declines in fitness (i.e. outbreeding depression) following the introduction of novel or distant genotypes which lead to the breakdown of coadpated gene complexes. In contrast, the risks posed by genetic swamping and introgression will not always depend on the degree of genetic differentiation but more on the ability for high geneflow. For some species therefore the degree of risk may be more a function of the breeding systems and pollen and seed dispersal. In recent years there has been increasing interest in the measurement and modelling of such gene-flow largely as a result of the potential risks posed by the release of genetically-modified (GM) crops and introgression with non-GM crops and wild relatives (Moyes and Dale 1999; Ramsay et al. 2000; Dale et al. 2002). As in the case of GM crops the amount of geneflow via pollen between different genotypes will be mediated by a number of factors: first, the physical distance of pollen movement between the different genotypes; second, the degree of outbreeding in the native population; third, the synchrony of flowering; and fourth, and the number of non-local genotypes introduced and persisting. Modelling of geneflow between *Brassica rapa* and *B. napus* provides an example of how such information can be used at the national scale in order to provide an assessment of the degree of risk posed by an introduced organism (Wilkinson et al. 2003). In crop plants geneflow can also occur via seed albeit at much lower frequency. For some crop species, seed is easily dispersed between fields either as a contaminant within the crop, on machinery, as volunteers or naturally (Moyes and Dale 1999). Similarly the dispersal of non-local genotypes may occur by a variety of means.

We suggest that the list of species given in Table 20 should be used to guide decisions concerning the sowing of non-local seed in the short term, although more detailed research is required to assess the potential risk of geneflow between local and non-local genotypes (see Section 8).

7. Conclusions and recommendations

1. General conclusions concerning seed supply and intraspecific variation

1. The production and supply of wildflower material

1. The introduction of the native wildflower species for habitat re-creation probably began shortly after 1960 but has increased exponentionally in recent decades (largely as a result of large-scale sowing within agri-environment schemes) and is likely to increase further over the coming years due proposed changes to agricultural policy.
2. Over the last decade the average annual supply of native provenance seed in the UK has been in the region of 20-30 tonnes as compared to 20,000 tonnes (per annum) of seed of agricultural cultivars of native species (mainly grasses).
3. The introduction of non-native genotypes sourced from Continental Europe, which was widely

recognised as a threat to native biodiversity in the 1980s, has largely ceased. However, the majority of native seed currently being sold for habitat re-creation is likely to be of non-local origin and/or from a different habitat from the recipient site (e.g. semi-natural meadows).

4. Around 60 common wildflower species (one-third of the species included in this review) account for over three quarters of the seed supplied for habitat re-creation in the UK, the most important being *Leucanthemum vulgare, Prunella vulgaris, Galium verum, Ranunculus acris, Calluna vulgaris* and *Sanguisorba minor* (Table 6).
5. The restricted number of donor sites and habitat types used for seed harvesting and the unconscious selection of certain genotypes during multiplication suggests that commercial wildflower material will only carry a very small proportion of the genetic diversity available in native populations (see Section 7.2).

7.1.2 Intraspecific variation in the British flora

1. Over the past eighty years genecological research has shown that intraspecific variation is a ubiquitous feature of flowering plant populations and occurs in response to powerful selection pressures such as climate, soils, herbivory, pest and pathogens, etc. (Briggs and Walters 1997).
2. Abiotic and biotic selection pressures have shaped the spatial pattern of genetic diversity in a wide range of common species leading to the adaptive evolution of local populations through the retention of advantageous alleles.
3. 88 species included in this review, which covers 10% of the British native flora, show some degree of intraspecific variation (e.g. morphological, ecotypic, cytological, and clinal).
4. Some of this variation has received formal taxonomic recognition but the vast majority is cryptic and has only been revealed as a result of genecological, and latterly more direct genetic approaches.
5. The adaptive significance of much of this variation is poorly understood and at present very little is known about the genetic structure of selectively-neutral variation in populations of common wildflower species which are frequently used for habitat re-creation.

7.2 Risks posed to native genotypes during restoration / re-creation

The potential risks posed by the introduction of non-native or non-local genotypes during restoration can be divided into those that occur on the re-creation site (i.e. those which effect the establishment of introduced populations or populations of native species on the re-creation sites as well as knock-on effects on organisms in the same or higher trophic levels) and those which are likely to have an effect on native populations outside the re-creation site. Therefore we summarise the main potential risks as follows:

On-site effects	Reduced likelihood of survival on the receptor site (through founder effects or inbreeding depression); Reduced value of the restored vegetation for other organisms.
Off-site effects	Disruption of native patterns of genetic diversity; Direct threats to genetic diversity of native populations (through genetic swamping outbreeding depression).

On-site effects are important to Defra and other organisations involved in habitat restoration because of the costs involved, the legality of the actions taken (with respect to the Seed Marketing Regulations) and the cost-effectiveness of policy mechanisms, such as options in Agri-environment schemes, for achieving broader biodiversity targets. In contrast, **off-site effects** are potentially more important as they may serve to impoverish the genetic diversity of native species that they are intended to bolster. However, the scientific evidence for these effects are variable, and in many cases there is still considerable debate as to the level of risk they pose. Indeed, a number of hypothesised risks have not been studied in any detail or are based on single studies, whereas for others there are a limited number of studies, but the results have proved contradictory. In contrast, several studies have shown that some risks are likely to be slight whereas only in a few cases are there sufficient data to prove an actual risk to populations of native species, although in most cases further research is required, particularly under field conditions and/or within a re-creation environment.

We therefore differentiate three levels of ‘risk’ in order to guide decisions relating to policy changes and future research work:

1. Theoretical risk, no or scant evidence;
2. Thoeretical risk, backed by limited actual data, results often contradictory;
3. Actual risk, backed by several studies but further research required.

Finally in this section, we assess the scope and magintiude of each of the potential risks and provide key recommendations for Defra and other organisations involved in habitat re-creation/restoration.

1. On-site effects: risks to newly established populations and other organisms

Theoretical risk, no or scant evidence

1. The restricted number of donor sites used for seed harvesting and the bias towards certain habitats means that commercial wildflower material will only carry a very small proportion of the ecotypic / genetic diversity available in native populations. Furthermore, this limited gene-pool may be further eroded as a result of propagation techniques used in commercial seed production (e.g. sourcing from a restricted number of donor sites, selection of specific variants, etc.).
2. The wider ecological consequences of changes to plant-invertebrate interactions during re-creation are poorly understood. For example, genotypic differences in insect food resource quality and phenology (e.g. pollen and nectar, leaf tissues) and the extent to which such differences are positive, negative or benign has yet to be investigated (see below).
3. Phenological differences between native and agricultural genotypes are well known although potential impacts on the feeding behaviour of native pollinators and mutualists has yet to be studied.

Thoeretical risk, backed by limited actual data, results often contradictory

4. As a small number of studies have shown re-introduced populations are likely to be founded from a few individuals (or genotypes) and therefore have a narrow genetic base.
5. The consequences are difficult to predict and may be genotype dependent, however, some populations have shown reduced fitness which may have occurred due to increased relatedness or poor adaptation within the population.
6. Non-local genotypes may have a number potentially damaging impacts on species in the same or higher trophic levels, such as natural pests and pathogens and mutaulists important for plant growth and reproduction. For example, physiological differences across a species’ range, such as those involved in plant defences, have been shown to affect herbivory. However, the results from re-creation studies have been equivocal stressing the need for further research.

2. On-site effects: recommendations

Hazard	Scope and magnitude of risk	Recommended action
Use of inappropriate / unsuitable ecotypes leading to reduced likelihood of survival on receptor site	This risk is likely to be high where species exhibit clear ecotypic variation (species listed in Table 11) The risk is unknown for other common native plants but is likely to be higher for those displaying strong regional phenotypic or genetic variation (species listed in Tables 9 and 12) and low for those with wide ecological tolerance	Ensure that known ecotypes (or ecotypic mixtures) are only sown on appropriate si (in terms of edpahic and hydrological regimes) Other plant species showing strong regio phenotypic or genetic variation should o be sown close to source populations (i.e. within a clearly defined regions or ‘see zones’) or in a suitable habitat Species not displaying clearly marked ecotypic or phenotypic variation may be in all situations. However, further rese is required to assess the genetic divers of widely sown native such as Leucanthem

		vulgare and Ranunculus acris which may possess ‘cryptic’ variation Further research required (see Sections 8 and 8.2)
Genetic uniformity of seed leading to reduced likelihood of survival on receptor site	This risk is likely to be especially high for 20 native species of agronomic value covered by the Seed Marketing regulations (species listed in Table 2) This risk is likely to be high for all other species if sourced from a narrow range of habitats and donor sites (species listed in Table 6) The risk is unknown for other common plants although it is likely to be low for those displaying little or no pnenotypic or genetic variation in native populations (NB: ‘cryptic’ variation may exist for some widespread species)	Seek to revise current seed legislation t promote the production and use of native seed of agronomic species Encourage commercial seed suppliers to maintain detailed records of seed sourcin production and supply Encourage suppliers to source seed from a greater range of donor sites (both in ter of regions and habitats) Promote the production of stocks of regio genotypes and specific habitat ecotypes o the most commonly sown species (listed in Table 6) Promote more benign alternatives to seed mixtures (e.g. ‘green hay’) harvested sustainably from nature reserves, road verges and grassland refugia on agricultu land Further research required (see Section 8.
Reduced value for other organisms	This risk is largely unknown for most species but is likely to be especially high where genotypic differences in insect food resource quality and phenology have been shown to occur (e.g. legumes)	Further research required (see Section 8.

7.2.2 Off-site effects on established populations of native genotypes

1. Disruptions to native patterns of genetic diversity

Thoeretical risk, backed by limited actual data, **results often contradictory**

1. Although there have been a number of studies on genetic variation within populations of rare and declining species few studies have focussed on widespread species typically used for habitat re-creation.
2. Human-mediated gene-flow has been shown to have disrupted patterns of genetic diversity in *Lolium perenne*. Although not proven, this is also likely to be the case for around 20 other native species (see Table 2) which have been widely and repeatedly sown for agriculture over the past 50 years. The impact of human-mediated gene-flow on non-agricultural species is largely unknown. However, the scale of introduction has been comparatively minor during the same period and therefore the risk of ‘genetic swamping’ by non-local genotypes **may have** been slight.

7.2.2 .2 Genetic swamping versus ‘home site’ advantage

Thoeretical risk, backed by limited actual data, **results often contradictory**

‘Genetic swamping’, i.e. the loss of local adaptation, either due to a numerical or fitness advantage or as a result of hybridisation is seen as one of the main threats to native patterns of genetic variation. However, the results of recent research are contradictory: in some cases non-local genotypes out-performed locals (e.g. on disturbed, fertile re-creation sites), whereas in others local genotypes had a ‘home site’ advantage over genotypes from distant sources. These findings make it difficult to generalise about the potential outcomes of genetic exchange following habitat re-creation and strees the need for further research on a range of different species in different re-creation environments.

1. With a few exceptions (e.g. *Lotus corniculatus*, *Lolium perenne*) there is no evidence that a local gene-pool has been ‘swamped’ because of gene-exchange (hybridisation/introgression) or interspecific competition (numeric advantage) with a non-local genotype. However, ‘cryptic’ introgression is likely to

have occurred in some species (e.g. *Lotus corniculatus* in the UK, *Phragmites australis* in North America) and is only likely to be ‘discovered’ following detailed genetic studies.

2. Some non-local genotypes have been shown to have superior fitness under highly disturbed and fertile conditions, such as re-creation sites. The ability of these genotypes to persist within less-fertile, more competitive semi-natural swards has yet to be fully investigated although it is likely that swamping may occur where these non-local genotypes are repeatedly introduced on a large scale into areas adjacent to small or isolated populations of native genotypes.

3. Plant fitness

Actual risk, backed by several studies but further research required

1. Crossing between local and non-local genotypes has been shown to effect plant fitness (heterosis versus outbreeding depression).
2. Crossing may lead to fitness advantages as a result of hybrid vigour (heterosis), although in the longer term these have usually been followed by a reduction in plant fitness as a result of outbreeding depression. These findings were based on laboratory studies using annual species and therefore further research is required to test a wider range of species, particularly perennials associated with species-rich grassland, ideally in the greenhouse **and** under selection pressures in the field.

4. Off-site effects: recommendations

Hazard	Scope and magnitude of risk	Recommended action
Disruption of native patterns of genetic diversity	The risk is likely to be especially high with rare species or species with clear ecotypic variation The risk is low with the 20 agronomic species which have been widely sown in the past The risk is unknown for other common native plants, but is likely to be higher for outbreeding species with short-life-spans and effective dispersal abilities	Rare or nationally scarce plants should be sown unless sourced from local populations 20 agronomic species may be sown in all situations (although see on-site effects) although agricultural cultivars should be replaced by native sourced material once this becomes available (NB: this would require changes to the seed marketing regulations and associated actions as proposed in 7.2.1.1 above) Plant species showing strong regional phenotypic or genetic differentiation sho not be sown unless sourced locally or fro an appropriate habitat Promote the use of locally harvested seed (e.g. green hay) rather than commercial mixtures for use adjacent to sensitive si such as nature reserves and grassland refugia in the wider countryside Further research is required (see Section 8.1)
Genetic swamping / outbreeding depression	Risk higher when large quantities of seed are sown close to existing small populations of native species The risk is unknown for other common plants but likely to be higher for outbreeding species where gene flow by dispersal of either pollen or seed is high and/or species have short generation times	Phenotypically variable species with the potential for high geneflow (those specie with high biological risk scores in Table 20) should not be sown close to existing semi-natural grasslands NB: exceptions mi include agronomic species for which large-scale geneflow is already likely to have already taken place as a result of agricultural use (e.g. Festuca rubra, Poa pratensis) Consider reducing sowing rates for these wildflowers species in all other situatio As an alternative promote the use of loca harvested seed and mixtures (e.g. green h for use adjacent to semi-natural grasslan Further research required (see Section 8.

8. Further research

In this final section five key research questions for plant genetic conservation are outlined in order of priority from high to low. In addition, we suggest how such studies could be carried out as well as species and community types urgently in need of further investigation. These build on earlier attempts to define research needs for genetic conservation in the UK (e.g. Jones and Everett 1999; Biodiversity Research Working Group 2000).

8.1 How genetically diverse are populations of native species?

Ultimately the potential impact of introduced genes will depend on the degree of genetic differentiation between local and non-local populations, as well as aspects of life history, the nature of the recipient site, etc. However, with the exception of a few trees and agricultural grasses most genetic studies have focussed on very localised species with ancient, restricted distributions or those showing alarming declines. Therefore there is an urgent need to evaluate local genetic differentiation within a range plants commonly used for habitat re-creation (e.g. those in Table 21). For these species priorities for research should be to:

1. Identify variation in relation to population, region, habitat, and degree of improvement (i.e. improved, semi-improved and semi-natural populations), etc.;
2. Assess how human-mediated geneflow via agricultural introduction has altered patterns of genetic diversity in the past;
3. Separate studies to assess neutral (structure) and adaptive variation.

Using standardised sampling and analytical methods such studies should include large-scale surveys of selectively neutral variation (using microsatellites etc.) within and between populations over both large geographic (regional) and ecological (habitat) distances. Trait comparisons between pairs of species (e.g. inbreeding vs. cross, annual vs. perennial) would provide powerful generality especially where species-pairs were phylogenetically constrained (i.e. from the same family or genus). A possible list of ‘model-pairs’ in large families are given in Table 21.

8.2 How do different genotypes perform in a common environment?

The potential impacts on within-species genetic diversity should also be addressed by reciprocal transplant and common garden studies which assess the performance of different genotypes in different environments. These will provide and assessment of adaptive variation within widespread species, and therefore highlight where variation might be lost (or enhanced) through gene-flow and introgression with non-local genotypes. Key questions to be addressed by such experiments include the following:

1. Do local genotypes perform better in both semi-natural and re-creation environments?
2. Are non-local genotypes more invasive and competitive within highly disturbed (i.e. re-created) environments?
3. Which measures of performance are likely to be of most selective importance within re-created environments (e.g. growth, reproductive ability, dispersal ability, etc.)?
4. Can introduced genotypes ‘rescue’ poorly adapted or inbred populations?

Ideally such studies should compare native genotypes collected from a range of semi-natural habitats and regions in the UK, with non-native genotypes from other European companies, agricultural cultivars, and plants from populations with a history of agricultural improvement (e.g. semi-improved pastures). Performance should be tested in relation to a range of selection pressures likely to be important in habitat re-creation as well as biotic factors such as management and herbivory. Ideally experiments should assess performance under controlled conditions and in the field. Furthermore, manipulative experiments would allow adaptive variation to be measured under a greater range of conditions for specific selection pressures (e.g. herbivory).

8.3 What are the impacts of hybridisation and introgression on plant fitness?

For 'model' species where hybridisation and introgression with non-local genotypes is likely to occur crossing experiments should be carried out in order to assess the effects on the fitness of hybrid offspring. Such studies should focus on:

1. The effects of genetic crossing distance on plant fitness.
2. The extent of inbreeding depression in local populations.
3. The extent to which hybrid vigour in the first generation (heterosis) is followed by reduced fitness in subsequent generations (outbreeding depression).
4. The extent to which introgression leads to genetic 'swamping' of locally adapted populations.

Studies to investigate the first two research questions could be undertaken in parallel with surveys of selectively neutral variation described above (i.e. using the same species and provenances) and ideally would be carried out under both controlled (e.g. laboratory, greenhouse) and field conditions. In contrast, assessments of genetic 'swamping' would require a molecular assay before and after the introduction of local and non-local genotypes either into a novel re-creation environment or laboratory mesocosm (e.g. similar to the one reported in Booth and Grime 2003).

8.4 How does genetic provenance affect biotic interactions and ecosystem function?

Modification of the gene-pool of a particular species may have consequences for other species and assemblages. Although these changes may have obvious advantages (e.g. enemy release, increased competitive ability) or disadvantages (e.g. poor defences against local pests and pathogens, lack of mutualists, etc.) for plant fitness the potential effects on key mutualists, pests and pathogens and ecosystem function are at present very poorly understood. As a result studies on the following are urgently required:

1. The feeding behaviour of herbivores (e.g. caterpillars, slugs) on genotypes from different provenances;
2. The performance of generalist and specialist herbivores on genotypes from different provenances;
3. The behaviour of pollinators on genotypes from different provenances;
4. Differences in the quality of food resources (e.g. pollen and nectar, plant tissues) provided by different genotypes;
5. The incidence of pests and pathogens on genotypes from different provenances.

8.5 What are the effects of commercial harvesting and production on genetic diversity?

Undoubtedly the methods used to collect and propagate plants for commercial sale can cause significant genetic changes which may have an effect during habitat re-creation. For example, commercial cultivation is likely to have exerted strong selection pressures on stocks by favouring larger, earlier flowering genotypes with high seed production. Furthermore, the commercial 'wildflower gene-pool' is likely to be extremely restricted and dominated by genotypes from particular regions (e.g. south east England) or favoured habitats, such as hay-meadows, which have been traditionally been utilised due to cost and practicality. In some cases such practices may pose a greater threat to native genetic diversity than the introduction of non-native genotypes. As a result there are a number of important research questions we need to be addressed:

1. What is the historic scale of seed sowing of species of agricultural value?
2. How has seed harvesting (in particular the distribution and nature of donor sites) affected the genetic diversity of commercial plant material?
3. How genetically diverse are commercial stocks of native wildflower species?
4. Have commercial production techniques led to the selection for specific traits (e.g. greater seed production, earlier flowering, etc.)?
5. How does seed production affect the genetic diversity within commercial plant stocks?
6. What is the maximum generation that a crop can be harvested before shifts in genetic variation

are likely to take place?

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Glossary

Sources for definitions in the glossary include (Barrett and Kohn 1991; Briggs and Walters 1984; Ennos et al. 2000; Frankham et al. 2002; Hufford and Mazer 2003):

Adaptive variation – genetically determined variation in the **phenotype** (morphology and performance) upon which natural selection operates.
AFLP (Amplified Fragment Length Polymorphism) **-** is very similar to **RAPDs** but has more repeatable results.
Agamospermy – the production of seeds by asexual means (agamospermous).
Allele - alternative forms of a gene at a particular locus. **Diploid** organisms have two alleles for each gene. If the alleles are the same (or indistinguishable) on both chromosomes the individual is a **homozygote**; if the alleles differ then the individual is a **heterozygote**.
Allozyme – protein variant that can be visualised by staining and **electrophoresis**.
Allozyme electrophoresis - measures the genetic variation for a particular protein locus. Only about 30% of genetic diversity is detected by this method.
Aneuploid – individuals having one or more whole chromosomes of the normal complement absent or in addition to that complement.
Apomixis – replacement of sexual by various forms of asexual reproduction.
Archaeophyte – a plant that was introduced by man, intentionally or unintentionally, and became naturalised there between the start of the Neolithic period (c.4000 BC) and AD 1500 (Preston et al. In press).
Base-number – the gametophytic chromosome-number of the diploid species.
Chromosome – a DNA-histone protein thread usually associated with RNA in the nucleus of the cell. They always occur in pairs which associate in a particular way at meiosis. Each species tends to have a characteristic number which is usually multiples of the base-number for a genus, the gametophytic chromosome number of the diploid species.
Cline – spatial variation in measurable characters found in a population or series of populations of a species.
Clone – a group or lineage of individuals derived vegetatively from a single plant.
Coadapted gene complexes – combinations of genes at multiple loci that interact to confer higher fitness relative to other genotypes.
Common garden studies – cultivation trials in a uniform environment of a range of varieties from a range of different environment to determine whether observed population differences are genetically based.
Congenor – a species belonging to the same genus (i.e. congeneric).
Cultivar – a distinct **taxa** created by artificial crossing or selection which is clearly distinct from other taxa within a species (e.g. cultivars, ecotypes, subspecies, etc.), as well as being uniform and stable in

its characteristics thereby retaining its characteristics upon propagation.

Cytotypes – populations or intraspecific taxa differing in chromosome number (or chromosome morphology).

DNA Sequencing - is the most direct measure of genetic diversity. Relatively time consuming; it is primarily used in taxonomy.

Ecocline – a cline apparently correlated with an observable ecological gradient.

Ecotype – distinct genotypes (or populations) of a species capable of interbreeding with other genotypes of the same species but which differ in their tolerance of certain environmental conditions such as salinity, fertility, climate etc.

Electrophoresis – polarized gel through which one runs proteins or DNA. The material then separates by weight or polarity and allows one to distinguish genetic variants.

Endemic – a population or species confined to a single area, region or country.

Epistasis – Interactions among gene loci in their effects on the phenotype.

F1 – the first generation of hybrid offspring (subsequent generations are referred to as F2, F3, etc.).

Fitness – the number of fertile offspring surviving to reproductive age.

Founder effect – loss of genetic diversity due to establishment of a population from one or a few individuals.

Gametophyte – the haploid gamete-producing phase of the life cycle of plants.

Genotype – genetic information within an individual. It interacts with the environment to produce the phenotype.

Genetic dilution – reduction in fitness of hybrids relative to parents caused by expression of only one half of locally adapted genotypes. Sometimes referred to as 'extrinsic' outbreeding depression.

Genetic drift – change in the frequency of alleles from one generation to the next as a consequence of chance sampling events.

Gene flow - the transfer of genes between populations by pollen or seed.

Genetic load – the load of deleterious alleles in a population.

Gene pool – the sum of all the genotypes within a particular population or region.

Genetic structure – the spatial arrangement of genetic variation within and between populations.

Genetic swamping – rapid increase in the frequency of an introduced genotype that might lead to the replacement of local genotypes; caused by numerical or fitness advantage.

Heterosis - fitness advantage in the first hybrid (**F1**) generation.

Heterozygote – an individual carrying two different alleles for a gene (**heterozygous**).

Homozygote – an individual with two copies of the same alleles for a gene (**homozygous**).

Hybridisation - interbreeding of individuals from genetically distinct populations including mating between species, subspecies and even populations that, although not taxonomically distinct, differ genetically (Rhymer and Simberloff 1996).

Hybrid breakdown – reduction in fitness of hybrids in relation to parents caused by disruption of co-adapted gene complexes, also known as 'intrinsic' outbreeding depression. This occurs in the F2 or later generations.

Inbreeding depression – reduction in fitness due to breeding between individuals related by descent.

Intraspecific variation – variation within a species often expressed taxonomically as subspecies, varieties and forms. Synonymous with infraspecific variation.

Introduced – transferred artificially from another country or region. Synonyms include non-native, exotic, alien.

Introgression – where hybrids backcross to one or more parental populations.

Isozymes - enzyme variants with the same functional role.

Locus – from the Latin for 'place'. A segment of DNA at a particular place on a particular chromosome.

Microsatellites (Simple Sequence Repeats (SSR) or Short Tandem Repeats (STR)) - are tandem repeats of very short DNA segments (1-5 bases) typically showing a high degree of polymorphism. They are defined using unique conserved sequences (Primers) which must be developed for each species (closely related species may be used but detection of diversity may be reduced).

Minisatellites or Variable Number Tandem Repeats (VNTR)) - use highly variable tandem repeat sequences (10-100 bases) isolated with restriction enzymes from the entire genome. Individuals in outbreeding populations (apart from clones) usually have unique DNA fingerprints but individual loci are not normally identifiable.

Mitosis – the nuclear division of somatic plant tissue in which the nucleus divides to produce two identical sets of chromosomes.

Mutation – any heritable change in the DNA sequence.

Native – a species which arrived in a specific area without the intervention of man having come from an area in which it is native or having arisen *de novo* in that area (synonymous with 'local', 'indigenous', endemic', etc.).

Natural Selection - a process resulting in the survival of those individuals from a population of animals or plants that are best adapted to the prevailing environmental conditions. The survivors tend to produce more offspring than those less well adapted, so that the composition of the population is changed.

Neophyte – a species first introduced by man after 1500, or was present before 1500 as a casual and is naturalised now only because it was re-introduced subsequently.

Nucleotide - the building blocks of DNA (and RNA). DNA nucleotides comprise a nitrogenous base, a deoxyribose sugar and a phosphate group.

Outbreeding depression – reduction in mean population fitness resulting from hybridisation between two genetically distinct individuals.

Panmictic – random mating leading to no genetic differentiation.

Phenotype – the observed characteristics of an individual (e.g. morphological, anatomical and physiological) produced by the interaction between the **genotype** and the environment.

Polymorphism – the occurrence of two or more distinct genetic variants of a species in a habitat.

Polyploidy - Polyploids are commonly referred to as tetraploids, hexaploids, octoploids and decaploids respectively. Groups of organisms in which there is a range of chromosome numbers representing different degrees of polyploidy (ploidy level) are known as a **polyploid series** or **polyploid complexes** where relationships to morphological characters are uncertain.

Ranks – intraspecific divisions of a species (i.e. subspecies, variety, subvariety, form, subform).

RAPDs (Rapid Amplified Polymorphic DNA) - assay many loci by amplifying random primer sequences (as opposed to specific in microsatellites) using Polymerase Chain Reactions (PCR). Repeatable results may be difficult to obtain.

RFLP (Restriction Fragment Length Polymorphism) - tracks variation in moderately variable known genes but requires known probes and reveals less variability than microsatellites, so it is being replaced other methods.

Recessive - an **allele** that is not expressed in the **heterozygous** condition.

Recombination - Exchange of gene segments by crossing over at chiasmata during meiosis (cell division during production of gametes in sexual reproduction).

Seed zones – geographical regions within which individuals of a species may be transferred with detrimental effects on population mean fitness.

Selectively neutral variation – genetic variation that has no apparent effect on phenotype or reproductive fitness under current environmental conditions.

SNPs (Single Nucleotide Polymorphism) are detected by sequencing (determination of the order of nucleotides in a DNA molecule) or using DNA chips.

Sporophyte – the diploid spore-producing stage of the life-cycle of plants arising from the fertilisation of the haploid gametes.

SSCP (Single Strand Conformational Polymorphisms) - use Polymerase Chain Reactions (PCR) to detect diversity of mitochondrial and some nuclear DNA.

Subspecies – a population of several biotypes forming a more or less distinct regional facies of a species (e.g. ecotype, geographical race).

Topocline – a cline following a geographical gradient.

Variety – a population of one or several biotypes, forming a more a less distinct local facies of a species.

References

Akeroyd, J. R. (1991). *Anthyllis vulneraria* L. subsp. *polyphylla* (DC.) Nyman, an alien kidney-vetch in Britain. *Watsonia* **18**: 401-403.

Akeroyd, J. R. (1992). A remarkable alien flora on the Gog Magog Hills. *Nature in Cambridgeshire* **34**: 35-42.

Akeroyd, J. R. (1994a). Some problems with introduced plants. *The Common Ground of Wild and Cultivated Plants.* A. Perry and R. Gwynn Ellis. Cardiff, National Museum of Wales**:** 31-40.

Akeroyd, J. R. (1994b). *Seeds of Destruction? Non-native Wildflower Seed and British Floral Biodiversity*. London, Plantlife.

Akeroyd, J. R. (1997). Intraspecific variation in European coastal plant species. *Ecosystems of the World 2C. Dry Coastal Ecosystems. General Aspects*. E. van der Maarel. Oxford, Elsevier**:** 145-162.

Al-Hiyaly, S. A. K., T. McNeilly, et al. (1993). The effect of zinc contamination from electricity pylons: genetic constraints on selection for zinc tolerance. *Heredity* **70**: 22-32.

Allen, D. E. (1966). A list of intraspecific taxa of British phanerogams tested in cultivation. *Watsonia* **6**: 205-215.

Allen, D. E. (1987). Presidential address, 1986. Part two: Work on intraspecific variation. *Watsonia* **16**: 241-247.

Ambroseli, M. (1997). *The Wild and the Sown. Botany and Agriculture 1350-1850.* Cambridge, Cambridge University Press.

Anon. (1995). *Biodiveristy: the UK Action Plan*. London, HMSO.

Antonovics, J. and A. D. Bradshaw (1970). Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* **25**: 349-362.

Antonovics, J., A. D. Bradshaw, et al. (1971). Heavy metal tolerance in plants. *Advances in Ecological Research* **71**: 1-85.

Anttila, C. K., R. A. King, et al. (2000). Reciprocal hybrid formation of *Spartina* in San Francisco Bay. *Molecular Ecology* **9**: 765-770.

Aston, J. L. and A. D. Bradshaw (1966). Evolution in closely adjacent plant populations. II. *Agostis stolonifera* in maritime habitats. *Heredity* **21**: 649-664.

Azayloo, M. and J. N. B. Bell (1981). Studies on the tolerance to sulphur dioxide of grass populations in polluted areas. I. Identification of tolerant populations. *New Phytologist* **88**: 203-222.

Baker, H. G. (1948). The ecotypes of *Melandrium dioicum* (L. emend.) Coss. and Gren. *New Phytologist* **47**: 131-145.

Bark, N. S. (1984). Trends in grass seed sales and usage. *The Ley Today.*

Barratt, D. R., K. J. Walker, et al. (1999). Variation in the responses of intraspecific variants of wet grassland species to manipulated water levels. *Watsonia* **22**: 317-328.

Barrett, S. C. H. and J. R. Kohn (1991). Genetic and evolutionary consequences of small population size in plants: implications for conservation. *Genetics and Conservation of Rare Plants.* D. A. Falk and K. E. Holsinger. Oxford, University Press: 3-30.

Beaumont, M., K. Ibrahim, et al. (1998). Measuring genetic distance. *Molecular Tools for Screening Biodiversity*. A. Karp, P. Isaac and D. Ingram. London, Chapman and Hall**:** 315-325.

Beckstead, J. and I. M. Parker (2003). Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens? *Ecology* **84**: 2824-2831.

Blossey, B. and J. Kamil (1996). What determines the increased competitive ability of non-indigeonous plants? *Proceedings of the 9th International Symposium on Biological Control of Weeds.* V. Moran and J. Hoffman. Stellenbosch, South Africa, University of Cape Town**:** 3-9.

Blossey, B. and R. Nötzold (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* **83**: 887-889.

Böcher, T. W. (1949). Racial divergences in *Prunella vulgaris* in relation to habitat and climate. *New Phytologist* **45**: 285-314.

Bonnemaison, F., Jones, D.A. (1984). Variation in alien *Lotus corniculatus* L. 1. Morphological differences between alien and native British plants. *Heredity* **56**: 129-138.

Bonnier, G. (1895). Recherches experimnetales sur l'adaptation des plantes au climat Alpin. *Annales des Sciences NAturelles (Botanique)* **20**: 217-360.

Booth, R. E. and P. Grime (2003). Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* **91**: 721-730.

Bradshaw, A. D. (1952). Populations of *Agrostis tenuis* resistant to lead and zinc poisoning. *Nature* **169**: 1098.

Bradshaw, A. D. (1959). Population differentiation in *Agrostis tenuis* Sobth. I. Morphological differentiation. *New Phytologist* **59**: 208-227.

Bradshaw, A. D. (1960). Popuation differenation in *Agrostis tenuis* Sibth. III. Populations in varied environments. *Heredity* **59**: 92-103.

Bradshaw, A. D. (1972). Some of the evolutionary consequences of being a plant. *Evolutionary Biology* **5**: 25-47.

Bradshaw, A. D. (1984). Ecological significance of genetic variation between populations. *Perspectives on Plant Population Ecology*. R. Dirzo and J. Sarukhan. Sunderland, Mass., Sinauer**:** 213-228.

Bradshaw, A. D. and M. J. Chadwick (1980). *The Restoration of Land*. Oxford, Blackwell Scientific Publications.

Bradshaw, M. E. (1963). Studies on *Alchemilla filicaulis* Bus., senu lato and *A. minima* Walters. Introduction and I. Morphological variation in *A. filicaulis*, sensu lato. *Watsonia* **5**: 304-320.

Briggs, D. and S. M. Walters (1997). *Plant Variation and Evolution*. Third Edition. Cambridge, Cambridge University Press.

Brown, R. (1989). Wild flower seed mixtures: supply and demand in the horticultural industry. *Biological Habitat Reconstruction*. G. P. Buckley. London, Bellhaven**:** 201-220.

Biodiversity Research Working Group (2000). *Setting the Agenda for Biodiversity Research: Introductions, Translocations and Genetic Conservation.* London, DETR.

Bullock, J. B., V. Brown, et al. (2003). Genetic provenance of seed mixtures for habitat restoration. *British Ecological Society Bulletin* **34**: 14-17.

Bullock, J. B. and K. H. Hodder (1997). Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology and Evolution* **12**: 68-69.

Butler, D. (1994). Bid to protect wolves from genetic pollution. *Nature* **370**: 497.

Carr, D. E. and M. R. Dudash (2003). Recent approaches into the genetic basis of inbreeding depression in plants. *Philosophical Transactions of the Royal Society of London Series B* **358**: 1071-1084.

Convention Biological Diversity (1992). *Convention on Biological Diversity*. http://www.biodiv.org./convention/.

Chambers, R., L. Meyerson, et al. (1999). Expansion of *Phagmites australis* into tidal wetlands of North America. *Aquatic Botany* **64**: 261-273.

Charlesworth, D. and B. Charlesworth (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**: 237-68.

Chater, A. O. (2003). The treatment of infraspecific taxa in local floras. *Watsonia* **24**: 281-286.

Clapham, A. R. (1949). Taxonomic problems in *Galium* and *Juncus*. *British Flowering Plants and Modern Systematic Methods*. A. J. Wilmott. London, Botanical Society of the British Isles**:** 72-74.

Clausen, J. and W. M. Hiesey (1958). Experimental studies on the nature of the species. IV. Genetic structure of ecological races. *Carnegie Institution of Washington Publication* **615**: 1-312.

Clausen, J., D. D. Keck, et al. (1940). Experimental studies on the nature of species. I. The effect of varied environments on the western North American plants. *Carnegie Institution of Washington Publication* **520**: 1-452.

Clement, E. J. and M. C. Foster (1994). *Alien Plants of the British Isles*. London, Botanical Society of the British Isles.

Coles, S. M. (1971). The *Ranunculus acris* L. complex in Europe. *Watsonia* **8**: 237-261.

Compton, S. G., S. G. Beesley, et al. (1983). On the polymorphism of cyanogenesis in *Lotus corniculatus* L. IX. Selective herbivory in natural populations at Porthdafarch, Anglesey. *Heredity* **51**: 537-548.

Compton, S. G. and D. A. Jones (1985). An investigation of the responses of herbivores to cyanogensis in *Lotus corniculatus* L. *Biological Journal of the Linnean Society* **22**: 21-38.

Coombe, D. E. (1961). *Trifolium occidentale*, a new species related to *T. repens*. *Watsonia* **5**: 68-87.

Coombe, D. E. (1973). The prostrate junipers of Gew Graze. *The Lizard* **5**: 7-12.

Coulaud, J. and T. McNeilly (1992). Zinc tolerance in populations of *Deschampsia cespitosa* (Graminae) beneath electricity pylons. *Plant Systematics and Evolution* **179**: 175-185.

Cowell, D. (1999). *Infraspecific Flora of the British Isles. Checklist of Taxa: Crassulaceae, Euphorbiaceae, and Fabaceae.* Cardiff, National Museum of Wales.

Crawford, T. J. and D. A. Jones (1986). Variation in the colour of the keel petals in *Lotus corniculatus* L., 2. Clines in Yorkshire and adjacent counties. *Watsonia* **16**: 15-19.

Curtis, W. (1790). *Practical Observations on the British Grasses Best Adapted to the Laying Down, or Improving of Meadows and Pastures*. London.

Cussans, J. and A. Morton (1990). The distribution of the subspecies of *Arrhenatherum elatius*. *BSBI News* **55**: 18-19.

Daday, H. (1954a). Gene frequencies in wild populations of *Trifolium repens*. II. Distribution by altitude. *Heredity* **8**: 377-384.

Daday, H. (1954b). Gene frequencies in wild populations of *Trifolium repens*. I. Distribution by latitude. *Heredity* **8**: 61-78.

Daday, H. (1965). Gene frequencies in wild populations of *Trifolium repens*. IV. Mechanisms of natural selection. *Heredity* **20**: 355-366.

Daehler, C. C. (1999). Inbreeding depression in smooth cordgrass (*Spartina alterniflora*, Poaceae) invading San Francisco Bay. *American Journal of Botany* **86**: 131-139.

Daehler, C. C., C. K. Anttila, et al. (1999). Evolution of a new ecotype of *Spartina alterniflora* (Poaceae) in San Francisco Bay, California, USA. *American Journal of Botany* **86**: 543-546.

Dale, P. J., Clarke, B. and Fontes, E.M.G. (2002). Potential for the environmental impact of transgenic crops. *Nature Biotechnology* **20**: 567-574.

Daniels, R. A. and J. Sheail (1999). Genetic pollution: concepts, concerns and transgenic crops. *Gene Flow and Agriculture. Relevance for Transgenic Crops*. British Crop Protection Council.

Davies, M. S. and R. W. Snaydon (1973a). Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment. I. Response to calcium. *Journal of Applied Ecology* **10**: 33-45.

Davies, M. S. and R. W. Snaydon (1973b). Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment. II. Response to aluminium. *Journal of Applied Ecology* **10**: 47-55.

Davies, M. S. and R. W. Snaydon (1974). Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment. III. Response to phosphate. *Journal of Applied Ecology* **11**: 699-708.

Davis, B. N. K. and R. P. Coppeard (1989). Soil conditions and grassland establishment for amenity and wildlife on a restored landfill site. *Biological Habitat Reconstruction.* G. P. Buckley. London, Bellhaven**:** 221-234.

de Laune, F. (1882). On laying down land to permanent grass. *Journal of the Royal Agricultural Society* **43**: 229-264.

Dixon, J. M. (2001). On the status of *Koeleria* Pers. (Poaceae) in Britain. *Watsonia* **23**: 377-390.

Donneaux, A. (1981). Contribution a l'etude cytotaxonomique gu genre *Galium* L. s.l. (Rubiaceae) en Belgique et dans les regionsvioines. *Lejeunia* **103**: 1-74.

Druce, G. C. (1928). *British Plant List.* Second edition. Arbroath, T. Buncle & Co.

Ducousso, A., D. Petit, et al. (1990). Genetic variation within and between populations of a perennial grass *Arrhenatherum elatius*. *Heredity* **65**: 178-188.

Dyer, A. R. and K. J. Rice (1997). Evidence of spatial genetic structure in a California bunchgrass population. *Oecologia* **112**: 333-339.

Edmands, S. and C. C. Timmerman (2003). Modeling factors affecting the severity of outbreeding depression. *Conservation Biology* **17**: 883-892.

Elkington, T. T. (1984). Cytogenetic variation in the British flora: origins and significance. *New Phytologist* **98**: 101-118.

Elkington, T. T. (1986). Patterns of variation in wild plants in relation to selection pressures and infraspecific categories. *Infraspecific Classification of Wild and Cultivated Plants.* B. T. Styles. Oxford, Oxford University Press**:** 33-52.

Ellstrand, N. C. (2003). Current knowledge of gene flow in plants: implications for transgene flow. *Philosophical Transactions of the Royal Society of London Series B* **358**: 1163-1170.

Ennos, R., N. R. Cowie, et al. (1997). Which measures of genetic variation are relevant in plant conservation? A case study of *Primula scotica*. *The Role of Genetics in Conserving Small Populations*. T. E. Tew, T. J. Crawford, J. W. Spencer et al. Peterborough, JNCC**:** 77-86.

Ennos, R., R. Worrell, et al. (2000). *Genetic Variation and Conservation of British Native Trees and Shrubs: Current Knowledge and Policy Implications*. Edinburgh, Forestry Commission.

Fearn, G. M. (1972). The distribution of chromosome races of *Hippocrepis comosa* L. and their phytogeographical significance. *New Phytologist* **71**: 1221-1225.

Fenster, C. B. and M. R. Dudash (1994). Genetic considerations for plant population restoration and conservation. *Restoration of Endangered Species: Conceptual Issues, Planning, and Implementation.* M. L. Bowles and C. J. Whelan. Cambridge, University Press**:** 34-62.

Fenster, C. B. and L. F. Galloway (2000). Inbreeding and outbreeding depression in natural populations of *Chamaecrista fasciculata* (Fabaceae). *Conservation Biology* **14**: 1406-1412.

Fenster, C. B., X. Vekemans, et al. (2003). Quantifying gene flow from spatial genetic structure data in a metapopulation of *Chamaecrista fasciculata* (Leguminosae). *Evolution* **57**: 995-1007.

Flora Locale and English Nature (2003). *Methods of Collecting Wild Seed from Native Grasslands.* Newbury, FloraLocale.

Flora Locale and Plantlife (2000). *Planting with Wildlife in Mind. Guidance on the Supply and Use of Native Flora for Projects in the Town or Countryside*. Newbury, Flora Locale.

Frankham, R., J. D. Ballou, et al. (2002). *Introduction to Conservation Genetics*. Cambridge, Cambridge, University Press.

Friar, E. A., T. Ladoux, et al. (2000). Microsatellite analysis of a population crash and bottleneck in the Mauna Kea silversword, *Argyroxiphium sandwicense* ssp. *sandwicense* (Asteraceae), and its implications for reintroduction. *Molecular Ecology* **9**: 2027-2034.

Fussel, G. E. (1964). The grasses and grassland cultivation of Britain. *Journal of the British Grassland Society* **19**: 49-54.

Gilbert, O. L. and P. Anderson (1998). *Habitat Re-creation and Repair*. Oxford, Oxford University Press.

Glover, J. G. and R. J. Abbott (1995). Low genetic diversity in the Scottish endemic *Primula scotica* Hook. *New Phytologist* **129**: 147-153.

Goodman, P. J. (1969). Intraspecific variation in mineral nutrition of plants from different habitats. *Ecological Aspects of Mineral Nutrition in Plants*. I. H. Rorison. Oxford, Oxford University Press: 239-253.

Grant, M. C. and J. Antonovics (1978). Biology of ecologically marginal populations of *Anthoxanthum odoratum*. I. Phenetics and dynamics. *Evolution* **32**: 822-838.

Grant, V. (1950). Genetic and taxonomic studies in *Gilia*. I. *Gilia capitata*. *El Aliso* **2**: 239-316.

Grant, V. (1952). Genetic and taxonomic studies in *Gilia*. II. *Gilia capitata abrotanifolia*. *El Aliso* **2**: 361-373.

Grant, V. (1954). Genetic and taxonomic studies in *Gilia.* III. *Gilia achilleaefolia*. *El Aliso* **3**: 1-18.

Gray, A., R. J. Parsell, et al. (1979). The genetic structure of plant populations in relation to the development of saltmarshes. *Ecological Processes in Coastal Environments.* R. L. Jeffries and A. J. Davy. Oxford, Blackwell: 43-64.

Gray, A. J. (1996a). The genetic basis of conservation biology. *Conservation Biology.* I. F. Spellerberg. Harlow, UK, Longman: 107-122.

Gray, A. J. (1996b) Genetic diversity and its conservation in natural populations of plants. *Biodiversity Letters* **3**: 71-80.

Gray, A. J. (1997). Genecology, the genetic system and the conservation genetics of uncommon British grasses. *The Role of Genetics in Conserving Small Populations*. T. E. Tew, T. J. Crawford, J. W. Spenceret al. Peterborough, JNCC: 56-64.

Gray, A. J. (2002). The evolutionary context: a species perspective. *Handbook of Ecological Restoration. Volume 1: Principles of Restoration*. M. R. Perrow and A. J. Davy. Cambridge, University Press: 66-80.

Gregor, J. W. (1930). Experiments on the genetics of wild populations. *Plantago maritima*. *Journal of Genetics* **22**: 15-25.

Gregor, J. W. (1938). Experimental taxonomy. II. Initial population differentiation in *Plantago maritima* L. of Britiain. *New Phytologist* **37**: 15-49.

Gregor, J. W. (1944). The ecotype. *Biological Reviews* **19**: 20-30.

Gregor, J. W. (1946). Ecotypic differentiation. *New Phytologist* **45**: 254-270.

Gregor, J. W. and F. W. Sansome (1927). Experiments on the genetics of wild populaitons. Part I. Grasses. *Journal of Genetics* **17**: 349-364.

Gregor, J. W. and P. J. Watson (1954). Some observations and reflections concerning patterns of intraspecific differentiation. *New Phytologist* **53**: 291-300.

Gregor, J. W. and P. J. Watson (1961). Ecotypic differentiation. *Evolution* **15**: 166-173.

Haase, P. (1993). Genetic variation, gene flow and the founder effect in pioneer populations of *Nothofagus menziesii* (Fagaceae) South Island, New Zealand. *Journal of Biogeography* **20**: 79-85.

Hamrick, J. L. and M. J. W. Godt (1997). Effects of life history traits on genetic diversity in plant species. *Plant Life Histories. Ecology, Phylogeny and Evolution*. J. Silvertown, M. Franco and J. L. Harper. Cambridge, Cambridge University Press: 102-118.

Hamrick, J. L., M. J. W. Godt, et al. (1991). Correlations between species traits and allozyme diversity: implications for conservation biology. *Genetics and the Conservation of Rare Plants.* F. A. Falk and K. E. Holsinger. Oxford, Oxford University Press: 75-86.

Harbred, D. J. (1961). The case for extensive rather than intensive sampling in genecological studies. *New Phytologist* **60**: 325-338.

Harvey, G. (2001). *The Forgiveness of Nature. The Story of Grass*. London, Johnathon Cape.

Hauser, T. P. and H. R. Siegismund (2000). Inbreeding and outbreeding effects on pollen fitness and zygote survival in *Silene nutans* (Caryophyllaceae). *Journal of Evolutionary Biology* **13**: 446-454.

Hedrick, P. W. (2001). Conservation genetics: where are we now? *Trends in Ecology & Evolution* **16**: 629-636.

Heslop-Harrison, J. (1964). Forty years of genecology. *Advances in Ecological Research* **2**: 159-247.

Hiesey, W. M. and H. W. Milner (1965). Physiology of ecological races and species. *Annual Review of Plant Physiology* **16**: 203-216.

Hopkins, A., D. A. Davies, et al. (1995). White clover - its present role and future prospects in British grassland farming. *Journal of the Royal Agricultural Society of England* **156**: 11-23.

Hubbard, C. E. (1984). *Grasses. A Guide to their Structure, Identification, Uses and Distribution in the British Isles.* London, Penguin.

Huenneke, L. F. (1991). Ecological implications of genetic variation in plant populations. *Genetics and the Conservation of Rare Plants*. F. A. Falk and K. E. Holsinger. Oxford, Oxford University Press: 31-44.

Hufford, K. M. and S. J. Mazer (2003). Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology & Evolution* **18**: 147-155.

Husband, B. C. and D. Schemske (1996). Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* **50**: 54-70.

Hutchinson, T. C. (1967). Ecotype differentiation in *Teucrium scorodonia* with respect to susceptibility to lime-induced chlorosis and to shade factors. *New Phytologist* **66**: 439-453.

Hutchinson, T. C. (1968). A physiological study of *Teucrium scorodonia* ecotypes which differ in their susceptibility to lime-induced chlorosis and iron-deficiency chlorosis. *Plant and Soil* **28**: 81-105.

Huxley, J. S. (1938). Clines: an auxillary taxonomic principle. *Nature* **142**: 219-220.

Jain, S. K. and A. D. Bradshaw (1966). Evolutionary divergence among adjacent plant populations. I. Evidence and its theoretical analysis. *Heredity* **21**: 407-441.

Jakobs, G., E. Weber, et al. (2004). Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions* **10**: 11-19.

Jones, A. (1990). Alien varieties of *Lotus corniculatus* L. on new roadside verges. Unpublished PhD thesis, University of Hull.

Jones, A. (2001). We plough the fields, but what do we scatter? A look at the science and practice of grassland restoration. *British Wildlife* **12**: 229-235.

Jones, A. and S. Everett (1999). *UK Native Flora. Research Needs in Relation to Genetic Conservation, Translocations and the Introduction of Exotic, Artificially Selected or Modified Varieties. A Synthesis of Prioritised Research Requirements.* Newbury, Flora Locale.

Jones, A. T. and M. J. Hayes (1999). Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. *Biological Conservation* **87**: 381-390.

Jones, D. A. (1970). On the polymorphism of cyanogenesis in *Lotus corniculatus* L. III. Some aspects of selection. *Heredity* **25**: 633-641.

Jones, D. A. (1977). On the polymorphism of cyanogenesis in *Lotus corniculatus* L. VII. The distribution of the cyanogenic form in western Europe. *Heredity* **39**: 27-44.

Jones, D. A., R. J. Keymer, et al. (1978). Cyanogenesis in plants and animal feeding. *Biochemical Aspects of Plant and Animal Coevolution*. J. Harborne. London, Academic Press: 21-34.

Jones, T. A. (2003). The restoration gene pool concept: Beyond the native versus non-native debate. *Restoration Ecology* **11**: 281-290.

Joshi, J., B. Schmid, et al. (2001). Local adaptation enhances performance of common plant species. *Ecology Letters* **4**: 536-544.

Kay, Q. A. N. and R. John (1997). Patterns of genetic variation in relation to the conservation of rare and declining plant species. *The Role of Genetics in Conserving Small Populations.* T. E. Tew, T. J. Crawford, J. W. Spencer et al. Peterborough, JNCC: 41-55.

Kay, Q. A. N. (2001). Past, present ... and future? Conservation practice and the conservation genetics of plant populations. *Transactions of the Suffolk Naturalist's Society* **37**: 37-47.

Keane, R. M. and M. J. Crawley (2002). Exotic plant invasions and the eneny-release hypothesis.

Trends in Ecology & Evolution **17**: 164-170.

Keller, M. and J. Kollmann (1999a). Effects of seed provenance on germination of herbs for agricultural compensation sites. *Agriculture Ecosystems & Environment* **72**: 87-99.

Keller, M., J. Kollmann, et al. (1999b). Palatability of weeds from different European origins to the slugs *Deroceras reticulatum* Müller and *Arion lusitanicus* Mabille. *Acta Oecologica* **20**: 109-118.

Keller, M., J. Kollmann, et al. (2000). Genetic introgression from distant provenances reduces fitness in local weed populations. *Journal of Applied Ecology* **37**: 647-659.

Kemp, W. B. (1937). Natural selection within plant species. *Journal of Heredity* **28**: 329-333.

Kerner, v. M. A. (1895). *The Natural History of Plants. Volume 2.* London, Blackie & Son.

Kiang, Y. T. (1982). Local differentiation of *Anthoxanthum odoratum* L. populations on roadsides. *American Midland Naturalist* **107**: 340-350.

Kik, C. (1989). Ecological genetics of salt resistance in the clonal perennial *Agrostis stolonifera*. *New Phytologist* **133**: 453-458.

King, M. (1998). Conserving British varieties of wildflower species. *Grassland Management in the 'Environmentally Sensitive Areas'.* R. D. Sheldrick, British Grassland Society. Occasional Symposium no. 38: 249-250.

Kitzmiller, J. H. (1990). Managing genetic diversity in a tree improvement program. *Forest Ecology and Management* **35**: 131-149.

Kj?rgaard, T. (2003). A plant that changed the world: the rise and fall of clover 100-2000. *Landscape Research* **28**: 41-49.

Knapp, E. E. and P. Connor (1999). Genetic consequences of a single-founder population bottleneck in *Trifolium amoenum* (Fabacae). *American Journal of Botany* **86**: 124-130.

Knapp, E. E. and K. J. Rice (1994). Starting from seed: genetic issues in using native grasses for restoration. *Restoration and Management Notes* **12**: 40-45.

Knapp, E. E. and K. J. Rice (1998). Comparison of isozymes and quantitative traits for evaluating patterns of genetic variation in purple needlegrass (Nassella pulchra). *Conservation Biology* **12**: 1031-1041.

Kruckeberg, A. R. (1951). Intraspecific variability in the response of certain native species to serpentine soil. *American Journal of Botany* **38**: 408-419.

Kruckeberg, A. R. (1954). The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* **35**: 267-274.

Kruckeberg, A. R. (1967). Ecotypic response to ultramafic soils by some plant species of north western United States. *Brittonia* **19**: 133-151.

Larsen, K. (1954). Cytotaxonomical studies in *Lotus*. I. *Lotus corniculatus*. *Botanique Tidsskr* **51**: 205-211.

Larsen, K. (1958). Cytological and experimental studies on the genus *Erodium* with special reference to the collective species *E. cicutarium* (L.) L'Her. *K. Dan. Vidensk. Selsk. Biol. Meddel.* **23**: 1-25.

Lawrence, W. E. (1945). Some ecotypic relations of *Deschampsia cespitosa*. *American Journal of Botany* **32**: 298-314.

Lesica, P. and F. W. Allendorf (1999). Ecological genetics and the restoration of plant communities: Mix or match? *Restoration Ecology* **7**: 42-50.

Linhart, Y. B. and M. C. Grant (1996). Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* **27**: 237-277.

Lousley, J. E. (1968). *Rumex hibernicus* Rech. fil. *Proceedings of the Botanical Society of the British Isles* **7**: 25.

Ludwig, F. (1901). Uber variationsstatistiche probleme und materialen. *Biometrika* **1**: 11-29.

Luijten, S. H., M. Kery, et al. (2002). Demographic consequences of inbreeding and outbreeding in *Arnica montana*: a field experiment. *Journal of Ecology* **90**: 593-603.

Lumaret, R. (1984). The role of polyploidy in the adaptive significance of polymorphism at the GOT I locus in the *Dactylis glomerata* complex. *Heredity* **52**: 153-169.

Marsden-Jones, E. M. and W. B. Turrill (1933). Studies in variation in *Anthylllis vulneraria*. *Journal of Genetics* **27**: 261-275.

Mastenbroeck, O., H. C. Prentice, et al. (1984). Corresponding patterns of geographic variation among populations of *Silene latifolia* (=*S. alba =S. pratensis*) (Caryophyllaceae). *Plant Systematics and Evolution* **145**: 227-242.

McKell, C. M., E. R. Perrier, et al. (1960). Responses of two subspecies of orchard grass (*Dactylis glomerata* subsp. *lusitanica* and *judaica*) to increasing soil moisture stress. *Ecology* **41**: 772-778.

McNeilly, T. (1968). Evolution in closely adjacent plant populations. III. *Agrostis tenuis* in a small copper mine. *Heredity* **23**: 99-108.

Meek, W.R., C. Carvell, et al. (2004). *The Buzz Project: technical report 2004*. Report to the Farmed Environment Company Ltd. CEH, Monks Wood.

Meharg, P. A., Q. J. Cumbes, et al. (1993). Pre-adaption of Yorkshire Fog *Holcus lanatus* L. (Poaceae) to arsenate tolerance. *Evolution* **47**: 313-316.

Mennema, J. (1984). The end of plant geography in the Netherlands. *Norrlinia* **2**: 99-106.

Millar, C. I. and W. J. Libby (1991). Strategies for conserving clinal, ecotypic and disjunct population diversity in widespread species. *Genetics and Conservation of Rare Species*. D. A. Falk and K. E. Holsinger. New York, Oxford University Press**:** 149-170.

Montalvo, A. M. and N. C. Ellstrand (2000). Transplantation of the subshrub *Lotus scoparius*: testing the home-site advantage hypothesis. *Conservation Biology* **14**: 1034-1045.

Montalvo, A. M. and N. C. Ellstrand (2001). Nonlocal transplantation and outbreeding depression in the subshrub *Lotus scoparius (*Fabaceae). *American Journal of Botany* **88**(2): 258-269.

Moore, P. D. (2000). Seeds of doubt. *Nature* **407**: 683-685.

Moyes, C.L. and Dale, P.J. (1999). *Organic farming and gene transfer from genetically modified crops.* MAFF Research Project OF0157. John Innes Research Centre, Norwich.

Nehou, J. (1961). Recherches sur la taxonomie du genre *Daucus* (Umbelliferes) en Bretagne. *Bulletin Societie Scientifique Bretagne* **36**: 81-107.

New, J. K. (1958). A population study of *Spergula arvensis.* I. Two clines and their significance. *Annals of Botany* **22**: 457-477.

New, J. K. (1978). Change and stability of clines in *Spergula arvensis* L. (corn spurrey) after 20 years. *Watsonia* **12**: 137-143.

New, J. K. and J. C. Herriott (1981). Moisture for germination as a factor affecting the distribution of seedcoat morphs of *Spergula arvensis* L. *Watsonia* **13**: 323-324.

NIAB (2002). *Eurosemstats. Seed Certification Statistics for Europe*. Cambridge, National Institute of Agricultural Botany (NIAB).

Ouborg, N. J., A. Biere, et al. (2000). Inbreeding effects on resistance and transmission-related traits in the Silene-Microbotryum pathosystem. *Ecology* **81**: 520-531.

Perring, F. H. and P. D. Sell (1968). *Critical Supplement to the Atlas of the British flora*. London, Thomas Nelson & Sons.

Platenkamp, G. A. W. and R. G. Shaw (1992). Environmental and genetic constraints on adaptive population differentiation in *Anthoxanthum odoratum*. *Evolution* **46**: 341-352.

Prentice, H. C. (1986). Climate and clinal variation in seed morphology of the white campion, *Silene latifolia* (Caryophyllaceae). *Biological Journal of the Linnean Society* **27**: 179-189.

Prentice, H. C., M. Lonn, et al. (2000). Changes in allozyme frequencies in *Festuca ovina* populations after a 9-year nutrient/water experiment. *Journal of Ecology* **88**(2): 331-347.

Prentice, H. C., O. Mastenbroeck, et al. (1984). Geographic variation in the pollen of *Silene latifolia* (*S. alba, S. pratensis*): a quantative morphological analysis of population data. *Canadian Journal of Botany* **62**: 1259-1267.

Preston, C. D., D. A. Pearman, et al. (2002). *The New Atlas of the British and Irish flora*. Oxford, Oxford University Press.

Preston, C. D., D. A. Pearman, et al. (In press). Archaeophytes in Britain. *Biological Journal of the Linnean Society*.

Price, M. V. and N. M. Waser (1979). Pollen dispersal and optimal outbreeding in *Delphinium nelsonii*. *Nature* **277**: 294-298.

Pritchard, T. (1960). Race formation in weedy species with special reference to *Euphorbia cyparissias* L. and *Hypericum perforatum* L. *The Biology of Weeds*. J. Harper. Oxford, Blackwell**:** 61-66.

Pywell, R. F., J. M. Bullock, et al. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* **40**: 65-77.

Ramsay, G., Thompson, C. and Squire, G. (2000). *Quantifying landscape-scale gene flow in oilseed rape*. Defra Project RG0216. Scottish Crop Research Insitute, Dundee.

Rhymer, J. M. and D. Simberloff (1996). Extinction by hybridisation and introgression. *Annual Review of Ecology and Systematics* **27**: 83-109.

Rich, T. C. G. (2001). What is *Anthyllis vulneraria* L. subsp. *corbierei* (Salmon & Travis) Cullen (Fabaceae)? *Watsonia* **23**: 469-480.

Rich, T. C. G. and A. C. Jermy (1998). *Plant Crib 1998.* London, Botanical Society of the British Isles.

Richards, A. J. (1973). An upland race of *Potentilla erecta* L. (Räusch). in the British Isles. *Watsonia* **9**: 301-317.

Rilstone, F. (1938). *Anagallis arvensis* L. var. *carnea* Schrank. *Journal of Botany* **76**: 85.

Rozema, J., -. D. Rozema, E, et al. (1978). Population differentiation within *Festuca rubra* L. with regard to soil salinity and soil water. *Oecologia* **34**: 329-341.

Sackville Hamilton, N. R. (2001). Is local provenance important in habitat creation? A reply. *Journal of Applied Ecology* **38**: 1374-1376.

Saltonstall, K. (2002). Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 2445-2449.

Saltonstall, K. (2003). Microsatellite variation within and among North American lineages of *Phragmites australis*. *Molecular Ecology* **12**: 1689-1702.

Sell, P. D. and G. Murrell (1996). *Flora of Great Britian and Ireland. Volume 5. Butomaceae-Orchidaceae.* Cambridge, Cambridge University Press.

Sheail, J. (1986). Grassland management and the early development of British ecology. *British Journal of Historical Studies* **19**: 283-299.

Sheridan, P. M. and D. N. Karowe (2000). Inbreeding, outbreeding, and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. *American Journal of Botany* **87**: 1628-1633.

Smart, J. (1989). Common-sense approaches to the construction of species-rich vegetation in urban areas. *Biological Habitat Reconstruction*. G. P. Buckley. London, Belhaven**:** 115-128.

Smith, B., A. Diaz, et al. (Submitted). The effect of provenance on plant establishment in a restoration environment. *Biological Conservation*.

Smith, D. C., E. L. Nielsen, et al. (1946). Variation in ecotypes of *Poa pratensis*. *Botanical gazette* **108**: 143-166.

Smith, R. A. S. and A. Bradshaw (1979). The use of metal-tolerant plants populations for the reclamation of metalliferous wastes. *Journal of Applied Ecology* **16**: 595-612.

Snaydon, R. W. and A. D. Bradshaw (1961). Differential response to calcium within the species *Festuca ovina* L. *New Phytologist* **60**: 219-234.

Snaydon, R. W. and A. D. Bradshaw (1962). Differences between natural populations of *Trifolium repens* in response to mineral nutrients. I. Phosphate. *Journal of Experimental Botany* **13**: 422-434.

Snaydon, R. W. and A. D. Bradshaw (1969). Differences between natural populations of *Trifolium* *repens* in response to mineral nutrients. II. Calcium, magnesium and potassium. *Journal of Applied Ecology* **6**: 185-202.

Snaydon, R. W. and M. S. Davies (1982). Rapid divergence of plant populations in response to recent changes in soil conditions. *Evolution* **36**: 289-297.

Spence, D. H. N. (1970). Scottish serpentine vegetation. *Oikos* **21**: 22-31.

Stace, C. A. (1976). The study of infraspecific variation. *Current Advances in Plant Science* **8**: 513-523.

Stace, C. A. (1986). The present and future infraspecific classification of wild plants. *Infraspecific Classification of Wild and Cultivated plants*. B. T. Styles. Oxford, Oxford University Press**:** 9-20.

Stace, C. A. (1989). *Plant Taxonomy and Biosystematics*. Cambridge, Cambridge University Press.

Stace, C. A. (1997). *New Flora of the British Isles.* Second Edition. Cambridge, Cambridge University Press.

Stapledon, R. G. (1928). Cocksfoot grass (*Dactylis glomerata* L.): ecotypes in relation to the biotic factor. *Journal of Ecology* **16**: 72-104.

Stevenson, M., R. Snazell, et al. (1994). *M3 Bar End to Compton: Chalk Grassland Restoration Seed Collection.* Dorset, Institute of Terrestrial Ecology.

Stevenson, M. and L. Ward (1993). *M3 Bar End to Compton: Chalk Grassland Restoration, Seed collection and Pot Plant Production*. Dorset, Institute of Terrestrial Ecology.

Templeton, A. (1986). Coadaptation and outbreeding depression. *Conservation Biology: the Science of Scarcity and Diversity.* M. Soulé, Sinauer**:** 105-116.

Teramura, A. H. and B. R. Strain (1979). Localised population differences in photosynthetic response to temperature and irradiance in *Plantago lanceolata*. *Canadian Journal of Botany* **57**: 2559-2563.

Tew, T. E., T. J. Crawford, et al. (1997). *The Role of Genetics in Conserving Small Populations.* Peterborough, JNCC.

Thornhill, N. (1993). *The Natural History of Inbreeding and Outbreeding*. Chicago, University of Chicago Press.

Turesson, G. (1922a). The species and variety as ecological units. *Hereditas* **3**: 100-113.

Turesson, G. (1922b). The genotypical response of the plant species to the habitat. *Hereditas* **3**: 211-350.

Turesson, G. (1923). The scope and import of genecology. *Hereditas* **4**: 171-176.

Turesson, G. (1925). The plant species in relation to habitat and climate. *Hereditas* **6**: 147-236.

Turesson, G. (1930). The selective effect of climate upon the plant species. *Hereditas* **14**: 99-152.

Turkington, R. A. (1989). The growth, distribution, and neighbour relationships of *Trifolium repens* in a permanent pasture. V. The coevolution of competitors. *Journal of Ecology* **77**: 717-733.

Turkington, R. A. and L. W. Aarssen (1984). Local scale differentiation as a result of competitive interactions. *Perspectives in Plant Population Ecology*. R. Dirzo and J. Sarukhan. Sunderland Mass., Sinauer**:** 107-127.

Tutin, T. G., V. H. Heywood, et al. (1964-). *Flora Europaea, Volumes 1-5*. Cambridge, Cambridge University Press.

Valentine, D. H. (1975). The taxonomic treatment of polymorphic variation. *Watsonia* **10**: 385-390.

Valentine, D. H. (1978). Ecological criteria in plant taxonomy. *Essays in Plant Taxonomy*. H. E. Street. London, Academic Press**:** 1-18.

Valentine, D. H. (1979). Presidential address, 1978. Experimental work on the British flora. *Watsonia* **12**: 201-207.

Valentine, D. H. (1980). Ecotypic and polymorphic variation in *Centaurea scabiosa* L. *Watsonia* **13**: 103-109.

van Kleunen, M. and B. Schmid (2003). No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* **84**: 2816-2823.

van Tienderen, P. H. and J. van der Toorn (1991a). Genetic differentiation between populations of *Plantago lanceolata*. I. Local adpatation in three contrasting habitats. *Journal of Ecology* **79**: 27-42.

van Tienderen, P. H. and J. van der Toorn (1991b). Genetic differentiation between populations of *Plantago lanceolata*. II. Phenotypic selection in a transplant experiment in three contrasting habitats. *Journal of Ecology* **79**: 43-59.

Vergeer, P., R. Rengelink, et al. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91**: 18-26.

Vergeer, P., E. Sonderen, et al. (In press). Reintroduction strategies put to the test: outbreeding depression versus heterosis. *Conservation Biology*.

Walters, S. M. (1970). Dwarf variants of *Alchemilla* L. *Fragmenta Floristica et Geobotanica* **16**: 91-98.

Warren, J. M., A. F. Raybould, et al. (1998). Genetic structure in the perennial grasses *Lolium perenne* and *Agrostis curtisii*. *Heredity* **81**: 556-562.

Warwick, S. L. and I. Briggs (1979). The genecology of lawn weeds. III. Cultivation experiments with *Achillea millefolium* L., *Bellis perennis* L., *Plantago lanceolata* L., *Plantago major* L. and *Prunella vulgaris* L. collected from lawns and contrasting grassland habitats. *New Phytologist* **83**: 509-536.

Waser, N. and M. V. Price (1994). Crossing distance effects in *Delphinium nelsonii*: outbreeding and inbreeding depression in progeny fitness. *Evolution* **48**: 842-852.

Waser, N. M. (1993). Population structure, optimal outbreeding, and assortative mating in angiosperms. *Natural History of Inbreeding and Outbreeding.* N. Thornhill. Chicago, Illinois, University of Chicago Press.

Waser, N. M., M. V. Price, et al. (2000). Outbreeding depression varies among cohorts of *Ipomopsis aggregata* planted in nature. *Evolution* **54**(2): 485-491.

Way, J. M. (1976). *Grassed and Planted Areas by Motorways.* Monks Wood, Institute of Terrestrial Ecology.

Wells, T. C. E. (1987). The establishment of floral grasslands. *Acta Horticulturae* **195**: 59-69.

Wells, T. C. E., S. Bell, et al. (1981). *Creating Attractive Grasslands Using Native Plant Species*. Peterborough, NCC.

Wells, T. C. E., A. Frost, et al. (1986). *Wild Flower Grasslands from Crop-grown Seed and Hay-bales*. Peterborough, Nature Conservancy Council.

Wells, T. C. E., R. Cox, et al. (1989). *The Establishment and Management of Wildflower Meadows*. Peterborough, NCC.

Wilkins, D. A. (1960). The measurement and genetical analysis of lead tolerance in *Fesuca ovina*. *Scottish Plant Breeding Station Report 1960*: 85-98.

Wilkinson, D. M. (2001). Is local provenance important in habitat creation? *Journal of Applied Ecology* **38**: 1371-1373.

Wilkinson, M. J., L. J. Elliott, et al. (2003). Hybridisation between *Brassica napus* and *B. rapa* on a national scale in the United Kingdom. *Science* **302**: 457-459.

Williams, S. L. and C. A. Davis (1996). Population genetic analyses of transplanted eelgrass *Zostera marina* beds reveal reduced genetic diversity in southern California. *Restoration Ecology* **4**(2): 163-180.

Wilson, G. B. and J. N. B. Bell (1986). Studies on the tolerance to sulphur dioxide of grass populations in polluted areas. IV. The spatial relationship between tolerance and a point source of pollution. *New Phytologist* **102**: 563-574.

Winfield, M. and J. Parker (1998). *A Molecular Analysis of Gentianella in Britain*. London, Plantlife.

Winfield, M. and J. Parker (2000). *A Molecular Analysis of Gentianella in Britain*. London, Plantlife.

Wu, L. and J. Antonovics (1976). Experimnetal genetics of *Plantago lanceolata*. II. Lead tolerance in *P. lanceolata* and *Cynodon dactylon* from a roadside. *Ecology* **37**: 205-208.

Wu, L., A. D. Bradshaw, et al. (1975). The potential for evolution of heavy metal tolerance in plants. III. The rapid evolution of copper tolerance in *Agrostis stolonifera* L. *Heredity* **34**: 165-187.

Figures

Figure 1. Change in the supply of seed of the main forage legumes and grasses since the 1960s. Figures for 1961 and 1984 are from Bark (1984) and 2002 from the Seed Trader's Returns (see Table 2 for details).

Figure 2. Changes in the production, imports and sale of seed of British native species requiring certification before marketing in England. Figures are from the annual Seed Trader's returns produced by the Defra PVS (see Table 2 for details).

Figure 3. The total area of land under various seed sowing options in the Countryside Stewardship Scheme for England (see Table 5 for detailed breakdown by CSS option). The total area minus the GX supplement is given as this option is usually used for weed control. Data supplied from the following sources: 1991-1995 Countryside Agency database; 1996-1998 GSMS snapshot data; 1998-2000 Live AESIS reports. CMD, Defra 2003.

Figure 4. The amount of plant material (seeds and plants) sold by the 19 main wildflower companies included in this review per annum (see Appendix 3 for details).

Figure 5. The main uses of plant material sold by the 19 companies included in this review (see Appendix 3 for details).

Figure 6. Examples of introduced subspecies of native species which have been widely sown in grassland seed mixtures in the UK (red squares, historic and recent introductions; blue squares, native): a) *Anthyllis vulneraria* subsp. *carpatica*; b) *Festuca rubra* subsp. *commutata* (treated as if native but many of the records undoubtedly refer to introductions) and c) *Medicago sativa* subsp. *sativa*. Figures reproduced from the New Atlas of the British and Irish Flora (CD-Rom; Preston et al. 2002).

Figure 7. Principal components analysis of the eight traits (see Table 15) for the 151 species included in this review. Numbers refer to species.

[pic]

Figure 8. The relationship between possible sources of plants for a restoration and the degree and size of disturbance. Adapted from (Lesica & Allendorf 1999).

Tables

Table 1. The types of wildflower material used for habitat re-creation.

Type	Description	Main uses
Native seed	Seed of native British species (mainly herbs), originally sourced from wild populations in the UK and then grown on as stocks from which seeds are harvested. The vast majority of seed is supplied as individual species either in bulk or in pre-prepared amounts by smaller specialist suppliers.	Wildlife gardening; Small-scale habitat recreation projects; Experimental studies; Inclusion within mixtures for large-scale sowing (e.g. AE schemes)
Native seed mixtures	Pre-prepared mixtures of the above, but often including large amounts of agricultural grass and legume seed of non-native provenance. Often tailored to suit the soil type or desired target community (85:15% grass:herb ratio). Sold by both smaller specialist growers as well as large commercial seed houses.	Large-scale habitat re-creation (e.g AE schemes, etc.); Civil engineering projects (e.g. new roads, flood defences, mine-workings etc.); Amenity plantings (e.g. urban developments, landscaping, etc.).
Harvested mixtures	Mixtures cut as hay from species-rich grasslands (often conservation sites such as SSSIs). Often harvested under licence as contracts for specialist projects (e.g. High Weald). However, the number of donor sites is currently limited in number.	Specialised habitat re-creation/restoration projects (e. on SSSIs, etc.).
Native transplants	Usually pot-grown herbs, especially aquatic species, originally harvested (as seed) from wild populations in the UK. Usually supplied as plug-plants, rhizomes, etc. by smaller specialist growers.	Specialised habitat re-creation/restoration (e.g. new wetlands, etc.); Civil engineering (e.g. flood defenc bioremediation, etc.).
Agricultural cultivars and varieties	A small number of forage grasses and legumes, many of which are certified in Europe. Often sold in large quantities direct to farmers via large commercial seed houses, although often also supplied by smaller specialists growers of native seed. Largely imported varieties bred in other European countries (e.g. Denmark, Holland).	Mainly used for reseeding pastures b also used for ‘bulking-up’ wildflowe mixtures for large-scale habitat re-creation (e.g. AE schemes, etc.).
Amenity cultivars and varieties	A small number of ‘turfgrass’ varieties bred specifically for hard-wearing qualities. Often bought direct from large commercial seed houses although also supplied by smaller specialist growers of native seed. The majority of seed is imported from Europe and New Zealand.	Mainly use as ‘turf’ for sports pitches, lawns, parks, golf courses, etc; Landscaping of contaminated or waste ground; ‘Bulking-up’ wildflower mixtures for large-scale habitat re-creation (e.g AE schemes, etc.).

Table 2. The supply (tonnes) of seed of native species requiring certification before marketing in England. Figures are averages per annum for the period 1993-2002 and are ranked by amount delivered. ‘Delivered for use’ is the amount of seed sold by the main seed traders excluding exports and seed maintained in stock. Source: Seed Trader’s Annual Returns (available at http://www.defra.gov.uk.).

	Home grown	Imported	Delivered for use		Home grown	Imported	Delive for us
(a) Agricultural grasses				Poa trivialis	0	14	13
Lolium perenne	7678	5229	11938	Agrostis stolonifera	0	17	12
Festuca rubra	307	2824	2959	Agrostis canina	0	4	2
Festuca rubra subsp. commutata	8	979	990				
Phelum pratense	127	542	694	(b) Forage legumes			
Agrostis capillaris	0.2	409	390	Trifolium repens	21	573	468
Poa pratensis agg.	0.3	327	308	Trifolium pratense	8	90	87
Festuca ovina (inc. F. brevipila)	4	136	140	Medicago x varia (sativa)	0.2	34	33
Dactylis glomerata	120	37	109	Trifolium hybridum	0	12	12
Festuca pratensis	10	54	62	Medicago lupulina	0	3	3
Festuca arundinacea	9	29	19	Onobrychis viciifolia	0	2	2
Phelum bertolonii	2	7	16	Trifolium incarnatum	0	0.5	0.4

Table 3. European production[1] (hectares) of species requiring certification before marketing in England in 1998 (listed in order of total production). Source: Eurosemstats (NIAB 1998).

	Denmark	France	Nether	Germany	Czech Rep.
Countryside Stewardship	Arable reversion to grassland	R1	280	20,640	Sow 6 grasses provenance
	Six-metre arable margin	R3	533	6,170	Natural regene
	Two-metre arable margin	R4	400	2,634	Sow a grass ma
	Native seed supplement	GS/RS	250	1,511	Supplement to
	Grassland supplement	GX/RX	40	15,605	Supplement to sowing
	Pollen and nectar margin	WM2	510	N/D2	>4 nectar-rich
Environmentally Sensitive Areas					
Avon Valley	Arable reversion to grass	2A	300	102	Species from a appropriate
	Arable buffer strip	2B	425	6	Establish a 5- provenance
Breckland	Arable reversion to grass	4CA	500	45	Native/local s
	Arable reversion to grass	4CW	300	11	Native/local s
Broads	Arable reversion to grass	4A	260	1,133	None
	Arable grass margin	4B	500	108	Establish a gr
Clun	Arable reversion to grass	3A	255	215	Species from a appropriate
Cotswolds	Arable reversion to grass	2	290	2,613	As above
Essex Coast	Arable reversion to grass	3	275	582	As above
North Kent Marshes	Arable reversion to grass	2	275	1,720	As above
	Arable buffer strip	BSS	400	139	Establish a 6-
South Downs	Arable reversion to chalk grass	3A	330	1,347	Where practica
	Arable reversion to grass	3B	240	5,993	None
South Wessex Downs	Downland turf creation	2A	330	934	Species from a appropriate
	Arable reversion to grass	2B	230	306	As above
Suffolk River Valleys	Arable reversion to grass	3	290	977	As above
Test Valley	Arable reversion to grass	2A	300	188	As above
	Arable buffer strip	2B	425	13	Establish a 5- provenance
Upper Thames Tributaries	Arable reversion to grass	3A	310	1,324	As above
	Arable reversion to wet grass	3B	330	47	As above
	Arable reversion to wet grass	3BR	435	324	As above
	Arable margin	3C	400	210	Establish a 5-

Notes: [1] Data for CSS agreements are from the Defra AESIS Database and should not be quoted in external documentation (see Table 5). ESA data were correct as of October 2001 and were taken from Ecoscope (2003) which is available at www.defra.gov.uk/erdp/schemes/esas/esasmonitor.htm. [2] WM2 was only made available to farmers in 2002 and therefore no figures on uptake are yet available.

Table 5. The annual uptake (hectares) of Countryside Stewardship options which require the sowing of native wildflower species[1].

	Native seed supplement (GS/RS)	Grassland supplement[2] (GX/RX)	Arable reversion (R1)	Six-metre margin (R3)	Two-metre margin (R4)	Total	Total (minus GX/RX)
1991		9	1440			1450	1441
1992		141	2687	3	2	2832	2691
1993	4	1350	2562	42	6	3963	2613
1994	0	1068	1189	65	45	2367	1299
1995	0	332	473	38	555	1399	1067
1996	2	1473	851	184	152	2662	1189
1997	8	1584	1051	576	401	3619	2036
1998	7	2483	1522	986	635	5633	3150
1999	492	2928	2681	1028	332	7461	4533
2000	998	4237	6188	3248	508	15179	10941
2001	463	nd	7800	nd	nd	-	-
2002	381	nd	9357	nd	nd	-	-
Total 1991-2000	1511	15605	20644	6170	2634	46565	30960
Seed (tonnes)[3]	53	-	723	216	92	-	1084

Notes: [1] Data supplied from the following sources: 1991-1995 Countryside Agency database; 1996-1998 GSMS snapshot data; 1998-2002 Live AESIS reports (not all data was available at the time of writing for 2001 and 2002. Source: CMD, Defra 2003.

[2] The majority of payments for GX/RX were used for weed control although some were used for the purchase of native seed or hay.

[3] Calculated at a sowing rate of 35 kg/ha.

Table 6. Summary of the amount of plant material sold by 15 of the suppliers included in the review. Codes for species are as follows: seeds - 1 = < 500 kg; 2 = 500-1,000 kg; 3 = > 1,000 kg; plants - 1 = < 10,000 plants; 2 = 10-100,000 plants; 3 = > 100,000 plants.

Species	Seed (Kg)	No. plants	Overall score	Species	Seed (Kg)	No. plants	Over scor
Leucanthemum vulgare	3	3	6	Geum rivale	2	2	4
Prunella vulgaris	3	3	6	Alisma plantago-aquatica	2	2	4
Galium verum	3	3	6	Leontodon autumnalis	2	2	4
Ranunculus acris	3	3	6	Rumex acetosa	2	2	4
Calluna vulgaris	3	3	6	Anthyllis vulneraria	2	2	4
Sanguisorba minor	3	3	6	Filipendula vulgaris	2	2	4
				Stachys sylvatica	2	2	4
Primula vulgaris	2	3	5	Hippocrepis comosa	2	2	4
Filipendula ulmaria	2	3	5	Papaver rhoeas	2	2	4
Silene dioica	2	3	5	Briza media	2	2	4
Succisa pratensis	2	3	5	Alliaria petiolata	3	1	4
Centaurea nigra	3	2	5	Anthoxanthum odoratum	3	1	4
Silene latifolia	3	2	5	Cynosurus cristatus	3	1	4
Agrimonia eupatoria	3	2	5	Festuca rubra	3	1	4
Allium ursinum	3	2	5	Alopecurus pratensis	3	1	4
Angelica sylvestris	3	2	5	Phleum bertolonii	3	1	4
				Agrostis stolonifera	3	1	4
Primula veris	1	3	4	Festuca arundinacea	3	1	4
Hyacinthoides non-scripta	1	3	4	Blackstonia perfoliata	3	1	4
Lychnis flos-cuculi	1	3	4	Arctium minus	3	1	4
Achillea millefolium	1	3	4	Anthemis arvensis	3	1	4
Knautia arvensis	1	3	4	Festuca ovina	3	1	4
Geranium pratense	1	3	4	Dactylis glomerata	3	1	4
Digitalis purpurea	1	3	4	Chrysanthemum segetum	3	1	4
Iris pseudacorus	1	3	4	Agrostemma githago	3	1	4
Cardamine pratensis	1	3	4	Centaurea cyanus	3	1	4
Lythrum salicaria	1	3	4	Phleum pratense	3	1	4
Caltha palustris	1	3	4	Agrostis capillaris	3	1	4
Hypochaeris radicata	1	3	4	Festuca pratensis	3	1	4
Hypericum perforatum	1	3	4	Poa pratensis	3	1	4
Malva moschata	2	2	4	Lolium perenne	3	1	4
Plantago lanceolata	2	2	4				

Table 7. Summary of the amount of plant material sold for individual species included in this review. Only species for which more than 1 tonne or 100,000 plants are sold in an average year are shown.

Species sold as seed (>1,000 kg)	Total (kg)	Species sold as plants (>100,000)	Total
Cynosurus cristatus	3100	Primula vulgaris	355500
Anthemis arvensis	2105	Leucanthemum vulgare	310500
Festuca ovina	2100	Primula veris	310500
Festuca rubra	2060	Hyacinthoides non-scripta	210000
Agrostis capillaris	1700	Lychnis flos-cuculi	170500
Agrimonia eupatoria	1665	Prunella vulgaris	166000
Anthoxanthum odoratum	1650	Filipendula ulmaria	125500
Leucanthemum vulgare	1615	Silene dioica	125500
Poa pratensis	1605	Achillea millefolium	125500
Dactylis glomerata	1600	Knautia arvensis	125500
Festuca pratensis	1560	Geranium pratense	125500
Lolium perenne	1550	Digitalis purpurea	125500
Festuca arundinacea	1550	Galium verum	121000
Blackstonia perfoliata	1505	Ranunculus acris	121000
Centaurea nigra	1200	Iris pseudacorus	116500
Galium verum	1200	Cardamine pratensis	116000
Sanguisorba minor	1165	Succisa pratensis	112000
Chrysanthemum segetum	1160	Lythrum salicaria	112000
Alopecurus pratensis	1155	Caltha palustris	111500
Phleum bertolonii	1150	Hypochaeris radicata	111000
Prunella vulgaris	1110	Calluna vulgaris	110000
Ranunculus acris	1110	Sanguisorba minor	107000
Agrostemma githago	1105	Hypericum perforatum	107000
Centaurea cyanus	1105		
Phleum pratense	1105		
Agrostis stolonifera	1100		
Angelica sylvestris	1065		
Alliaria petiolata	1065		
Silene latifolia	1060		
Arctium minus	1060		
Allium ursinum	1020		
Calluna vulgaris	1010		

Table 8. Tools for assessing genetic diversity (after Frankham et al. 2002). All markers other than allozymes are for DNA. Definitions of method acronyms are given in the glossary.

Method	Relative Cost	Development time*	Marker type**
Allozyme / Isozyme electrophoresis	Low	None	Co-dominant
Nuclear microsatellites	Moderate	Considerable	Co-dominant
Chloroplast microsatellites	Moderate	Considerable	All expressed
Mitochondrial markers	Moderate	Considerable	All expressed
DNA fingerprints	Moderate	Low	Dominant
RAPD	Low-moderate	Low	Dominant
AFLP	Moderate-high	Low	Dominant
RFLP	Moderate	Low	Co-dominant
SNP	Moderate-high	Considerable	Co-dominant
SSCP	Moderate	Moderate	Co-dominant
DNA sequencing	High	Low	Co-dominant

* Time required to develop the technique for a species.

**Molecular markers exhibiting *co-dominant* gene action are preferable, as all genotypes are distinguished. In co-dominant methods, if the plant is heterozygous at a locus, both alleles will be detected. Dominant methods only detect the dominant allele. All alleles are expressed by chloroplast and mitochondrial markers because organelle DNA exists as single copies; and hence there is no dominance.

Table 9. Species included in the review with native intraspecific taxa recognised in recent taxonomic works (e.g. Sell & Murell 1996; Stace 1997; Rich & Jermy 1998). The number of intraspecific taxa included in Druce (1928) and *Flora Europaea* (Tutin et al. 1964-) and those introduced into the UK (see Appendix 4 for further details).

	Intraspecific taxa				Intraspecific taxa		
	Subsp.	Vars	Druce	Intro	Europe		Subsp.
Achillea millefolium							1
Bellis perennis							Phenology
Caltha palustris							
Campanula rotundifolia						1	
Dactylis glomerata				Small panicle			
Festuca rubra			1				
Filipendula ulmaria		Dwarf				1	
Filipendula vulgaris							1
Galium verum							
Lythrum salicaria		Dwarf					
Leontodon autumnalis	1	Succulent lvs			1		
Lycnhis flos-cuculi							Stature
Primula vulgaris							1
Rumex acetosella							
Ranunculus acris					1		
Rumex acetosa					1		
Rumex acetosella	Prostrate						
Silene dioica		Succulent lvs			1	1	
Succisa pratensis						1	

Table 11. Species included in the review with known ecotypes (climatic, edpahic, biotic) or displaying clinal variation in various morphological characters. See Appendix 5 for further details on individual species.

Species	Climatic	Edaphic[1]	Biotic	Clinal
Achillea millefolium	1	1c		1
Agrostis capillaris	1	1c,m,n		
Agrostis stolonifera		1m,s		
Anagallis arvensis		1c		
Anthoxanthum odoratum		1f,s	1	1
Anthyllis vulneraria		1c		
Arrhenatherum elatius		1m		
Bellis perennis	1		1	
Campanula rotundifolia	1			
Centaurea scabiosa		1c		
Cerastium fontanum		1c,k,n		
Dactylis glomerata	1	1c,b,m	1	1
Daucus carota	1			
Deschampsia cespitosa	1	1m		
Erodium cicutarium		1c		
Festuca ovina		1m,n		
Festuca rubra		1c,m,n,s		
Filipendula ulmaria	1	1c		
Filipendula vulgaris	1			
Galium mollugo		1c		
Galium verum		1c		
Geum rivale	1			
Holcus lanatus		1m,p		1
Hypochaeris radicata		1c		
Leontodon autumnalis	1	1c,n		
Lolium perenne		1c,n,p		
Lotus corniculatus		1c		1
Lychnis flos-cuculi	1			
Lythrum salicaria		1c		
Plantago lanceolata		1m,n	1	
Poa pratensis		1c	1	
Poa trivialis		1n		
Prunella vulgaris	1	1c,k	1	
Ranunculus acris	1			1
Ranunculus bulbosus		1c		
Rumex acetosa	1	1c,k		
Rumex acetosella		1k,n		
Scutellaria galericulata		1c		
Serratula tinctoria		1c		
Silene dioica	1	1c		
Silene latifolia				1
Stachys officinalis		1c		
Stachys sylvatica		1c		
Succisa pratensis	1	1c		
Teucrium scorodonia		1n		
Trifolium pratense		1c		
Trifolium repens		1c,n	1	1
Vicia cracca		1c		
Total	17	40	7	8

Notes:

[1] Codes for edaphic ecotypes are as follows: b, soil moisture; c, coastal; f, fertilisers; k, serpentine ; m, heavy metals; n, variation in soil ; p, pollution; s, salinity.

Table 12. Species included in the review which are cytologically varable in the UK with chromosome numbers given in most recent floras (Sell & Murrell 1996-; Stace 1997)

Species	2n =	Species	2n =
Agrostis stolonifera†	28, 30, 32, 35, 42, 44, 46	Knautia arvensis	16, 20, 40
Bromopsis erecta	42, 56	Koeleria macrantha†	14, 28 (+0-6), 42, 70
Bromus commutatus	14, 28, 56	Lathyrus pratensis	14, 28
Caltha palustris†	48, 52, 54, 56, 64, 72, c.80	Leucanthemum vulgare	18, 36
Campanula rotundifolia†	68, 102	Medicago sativa†	16, 32
Cardamine pratensis†	30, 56-58, c.64, 72 (16-96)	Myosotis arvensis†	36, 48, 52
Carex flacca	76, 90	Phleum pratense	21, 35, 36, 42, 49, 56, 63, 84
Centaurea nigra†	22, 44	Pilosella officinarum	18, 27, 36, 45, 54
Cerastium fontanum†	72, 108, 144	Poa nemoralis	28-33, 42, 56
Dactylis glomerata	14, 28	Poa pratensis†	42, 50-78, 91, 98
Deschampsia cespitosa†	26, 39?, 52, 34-56	Rumex acetosella†	28, 42
Deschampsia flexuosa	26, 28, 56	Sanguisorba officinalis	28, 56
Festuca ovina†	14, 28	Saxifraga granulata	c.32, 48
Festuca rubra†	42, 56, 70	Scutellaria galericulata	30, 32
Galium palustre†	24, 48, 96 (144)	Teucrium scorodonia	32, 34
Hippocrepis comosa	14, 28	Trisetum flavescens	14, 28
Hordeum secalinum	14, 28	Valeriana officinalis†	28, 56, 70
Hyacinthoides non-scripta	16, 24		

Notes:

Species where there is a marked correlation between morphological characters and cytology are given in **bold**.

† Species for which intraspecific taxa have been recognised in recent taxonomic works.

In addition, aneuploid variation in chromosome numbers occurs in *Agrostis gigantea*, *Filipendula ulmaria*, *F. vulgaris*, *Rumex acetosa* and *Thymus polytrichus*.

Table 13. Details of species included in the review with known introductions of non-native genotypes into Britain (details from Clements & Foster 1994; Stace 1997).

Species	Recognised taxa	Details of introductions
Achillea millefolium	-	Robust variants frequently sown in seed mixtures
Alopecurus pratensis	-	Many agricultural cultivars have been introduced
Anagallis arvensis	Subsp. foemina	Subsp. foemina has occasionally been introduced from S Europ in seed mixtures
Anthyllis vulneraria	Subsp. carpatica; subsp. polyphylla	Subsp. carpatica (NW and Central Europe) and subsp. polyphyl (E. Europe, Turkey, Caucasus) are both persistent grass or agricultural seed aliens which are sometimes abundant on grassy banks in widely scattered localities
Dactylis glomerata	Subsp. aschersoniana; subsp. hispanica	Agricultural cultivars and ornamentals have become established
Daucus carota	Subsp. sativus	A casual of waste places originating from market gardens.
Festuca arundinacea	-	Many agricultural cultivars have been introduced
Festuca rubra	Subsp. commutata; subsp. megastachys	Subsp. commutata is an important component of grass mixtures and is frequently sown on roadsides, lawns and amenity plantings. The status and use of subsp. megastachys is unknown.
Leucanthemum vulgare	-	Frequently sown in grass mixtures
Lotus corniculatus	Var. sativus	A forage variety which is frequently sown in wildflower mixtures
Medicago sativa	Subsp. sativa	An established escape from cultivation throughout most of th British Isles, widely naturalised in grassy places, especial in the south and east; introduced with grass seed on roadsides. Hybrids with native subsp. falcata (subsp. varia) have been frequently recorded in East Anglia
Onobrychis viciifolia	-	Robust agricultural cultivars are frequently sown
Pastinaca sativa	Var. hortensis	Cultivated and sometimes escapes
Phleum pratense	-	Many agricultural cultivars have been introduced
Poa pratensis	-	Many agricultural cultivars have been introduced
Poa trivialis	-	Many agricultural cultivars have been introduced
Rumex acetosa	-	Rare alien, introduced with wildflower seed
Sanguisorba minor	Subsp. muricata	A persistent escape from cultivation, and frequently sown in seed mixtures (S. Europe)
Tragopogon pratensis	Subsp. pratensis; subsp. orientalis	Rare introductions from C & E Europe
Trifolium dubium	-	Many agricultural cultivars have been introduced
Trifolium pratense	e.g. vars. americanum and sativum	A number of agricultural cultivars have been introduced
Trisetum flavescens	Subsp. purpurascens	Has been introduced in seed mixtures from Eastern Europe
Vicia sativa	Subsp. segetalis; subsp. sativa	Established escapes from cultivation and bird-seed aliens. Both are fodder varieties which have become widely naturalis following sowing

Table 14. Three measures of intraspecific variation used in order to analyse potential risks from the use of non-native genotypes

	Low	Medium	High
(1) Morphological	No intraspecific taxa	2-3 intraspecific taxa	>3 intraspecific taxa
(2) Ecotypic	None reported	Few reported cases	Many reported cases
(3) Cytological	Single cytotype	Few (<3) cytotypes or aneuploid	Many ploidy levels (>3 cytotypes)

Table 15. Life history measures which are theoretically linked to genotypic variation (Hamrick & Godt 1997) in the species included in this review. (1)-(7) were derived from the ECOFLORA and ECPE databases and (8) from Preston et al. (2002).

	Suggested resulting genetic variation (score in brackets)		
	Low (1)	Medium (2)	High (3)
(1) Dispersal ability	Unspecialised, explosive	Animals	Wind or water
(2) Breeding system	Apomictic/viviparous/self	Mixed mating	Cross (inc. normally crossing
(3) Phenology	Short (<3 months)	Medium (3-5 months)	Long (>5 months)
(4) Reproduction	Vegetative	Vegetative and seed	Seed
(5) Pollen vector	Self	Insect	Wind
(6) Life history (generation time)	Long-lived perennial	Biennial, paucennial	Annual
(7) Seed weight	>5 mg	1-5 mg	<1 mg
(8) Habitat breadth	Narrow	Intermediate	Wide

Table 16. Correlations between the eight life history traits (numbers in bold $p < 0.05$).

	(1) Dispersal ability	(2) Breeding system	(3) Phenology	(4) Reprod.	(5) Pollen vector	(6) Life history	(7) Seed weight
(2) Breeding system	-0.065	-					
(3) Phenology	0.148	0.003	-				
(4) Reproduction	-0.031	0.032	0.045	-			
(5) Pollen vector	-0.143	-0.154	-0.314	-0.120	-		
(6) Life history	0.046	-0.086	0.141	0.371	-0.280	-	
(7) Seed weight	0.135	-0.116	0.032	-0.264	0.144	-0.133	-
(8) Habitat breadth	-0.117	-0.021	0.017	-0.043	0.147	-0.015	0.104

Table 17. Correlations between the measures of variation (numbers in bold $p < 0.05$).

	(1) Morphological	(2) Ecotypic	(3) Cytological	(4) Mean
(2) Ecotypic	0.320	-		
(3) Cytological	0.311	0.121	-	
(4) Mean	0.770	0.700	0.649	-
(5) Re-scaled mean	0.772	0.692	0.659	0.999

Notes: ‘Mean’ is the mean of the scores for the three variables combined and the ‘re-scaled mean’ is these means re-scaled to integer values between 1 and 7 suitable for use in logistic regression.

Table 18. Relationship between the overall measures of variation and the eight life history traits using logistic regression.

Predictor	Coef	Z	P	Odds ratio	95% CI	
					Lower	Upper
(1) Dispersal ability	0.2962	1.76	0.048	1.34	0.97	1.87
(2) Breeding system	0.5132	2.28	0.023	1.67	1.07	2.60
(6) Life history	0.6292	2.69	0.007	1.88	1.19	2.97

Notes:

Log-likelihood = -210.290. Test that all slopes are zero: G = 14.037, DF = 3, P-Value = 0.003.

Table 19. Correlations between the scores for variation, life history, supply and overall measure (numbers in bold $p < 0.05$).

	Variation score	Life history score	Supply score	Variation an life history score
Life history score	-0.566	-		
Supply score	-0.203	-0.324	-	
Variation and life history score	0.485	0.446	-0.564	-
Variation, life history and supply score	0.248	0.135	0.513	0.413

Table 20. Assessment of risk based on the scores for intraspecific variation, life history traits and supply of plant material in the UK given in Table 15. Species ranked on level of ‘biological risk’.

Species	Scores			Risk	
	Variation1	Life history2	Supply3	Biological4	Commercial5
Silene latifolia	1.7	3	2.5	4.7	7.2
Rumex acetosa	2.3	2.3	2	4.6	6.7
Deschampsia cespitosa	2.7	1.7	1.5	4.4	5.8
Gentianella amarella	1.7	2.7	1	4.4	5.3
Caltha palustris	2	2.3	2	4.3	6.3
Holcus lanatus	2	2.3	1	4.3	5.3
Silene dioica	1.7	2.3	2.5	4.0	6.5
Papaver rhoeas	1	3	2	4.0	6
Leontodon autumnalis	2	2	2	4.0	6
Agrostis stolonifera	3	1	2	4.0	6
Festuca ovina	2.3	1.7	2	4.0	6
Campanula rotundifolia	2	2	1.5	4.0	5.5
Anthyllis vulneraria	2	1.7	2	3.7	5.7
Plantago lanceolata	1.7	2	2	3.7	5.7
Blackstonia perfoliata	1	2.7	2	3.7	5.7
Chrysanthemum segetum	1	2.7	2	3.7	5.7
Festuca rubra	2.7	1	2	3.7	5.7
Ranunculus bulbosus	1.7	2	1.5	3.7	5.2
Rumex acetosella	2	1.7	1.5	3.7	5.2
Matricaria recutita	1	2.7	1.5	3.7	5.2
Lychnis flos-cuculi	1.3	2.3	2	3.6	5.7
Lythrum salicaria	1.3	2.3	2	3.6	5.7
Achillea millefolium	1.3	2.3	2	3.6	5.7
Arctium minus	1.3	2.3	2	3.6	5.7
Vicia sativa	1.3	2.3	1.5	3.6	5.2
Daucus carota	1.3	2.3	1.5	3.6	5.2
Leontodon hispidus	1.3	2.3	1.5	3.6	5.2
Carex flacca	1.3	2.3	1.5	3.6	5.2
Ranunculus acris	1.7	1.7	3	3.4	6.3
Centaurea nigra	1.7	1.7	2.5	3.4	5.8
Geum rivale	1.7	1.7	2	3.4	5.3
Anthoxanthum odoratum	1.7	1.7	2	3.4	5.3
Calluna vulgaris	1	2.3	3	3.3	6.3
Angelica sylvestris	1	2.3	2.5	3.3	5.8
Anthemis arvensis	1	2.3	2	3.3	5.3
Poa pratensis	2.3	1	2	3.3	5.3
Iris pseudacorus	1	2.3	2	3.3	5.3
Cardamine pratensis	2	1.3	2	3.3	5.3
Knautia arvensis	1.3	2	2	3.3	5.3
Hypochaeris radicata	1.3	2	2	3.3	5.3
Sanguisorba minor	1	2	3	3.0	6
Prunella vulgaris	1.7	1.3	3	3.0	6
Galium verum	1.7	1.3	3	3.0	6

Table 20. Continued

Species	Scores			Risk	
	Variation1	Life history2	Supply3	Biological4	Commercial5
Leucanthemum vulgare	1.7	1.3	3	3.0	6
Primula vulgaris	1	2	2.5	3.0	5.5
Filipendula ulmaria	1.7	1.3	2.5	3.0	5.5
Succisa pratensis	1.3	1.7	2.5	3.0	5.5
Agrimonia eupatoria	1	1.7	2.5	2.7	5.2
Allium ursinum	1	1.7	2.5	2.7	5.2

Notes:
[1] Average score for variation variables (Table 14); [2] Average score for life-history variables (only breeding system, life history and dispersal ability included; Table 15); [3] Average supply score; [4] biologically determined risk is the sum of 1 and 2; [5] commercially determined risk is the sum of 1-3.

Table 21. Potential ‘model-pairs’ of species for surveys of selectively neutral and adaptive genetic variation. Species in bold were amongst the 50 most threatened species identified by the analyses outlines in Section 6 (see Table 18).

	Model-pair		Model-pair	
Family	Annual-inbreeding/mixed mating	Perennial-outbreeding	Perennial-inbreeding/mixed mating	Annual-outbreeding
Ranunculaceae	Adonis annua	Caltha palustris Ranunculus bulbosus	Ranunculus acris	Ranunculus arvensis
Caryophyllaceae	Agrostemma githago Silene noctiflora	Lychnis flos-cuculi Silene dioica	Cerastium fontanum	Silene latifol
Fabaceae	Medicago lupulina Trifolium dubium Vicia sativa	Anthyllis vulneraria Lathyrus pratensis Lotus corniculatus Trifolium pratense Vicia cracca	Medicago sativa	
Apiaceae	Pastinaca sativa	Angelica sylvestris Pimpinella saxifrage	Silaum silaus	Daucus carota
Rosaceae		Potentilla erecta	Agrimonia eupatoria Filipendula ulmaria Geum rivale Sanguisorba minor	
Rubiaceae		Galium mollugo	Galium verum	
Scrophulariaceae	Rhinanthus minor	Veronica chamaedrys	Digitalis purpurea	
Dipsacaceae		Succisa pratensis	Knautia arvensis	
Asteraceae	Centaurea cyanus Chrysanthemum segetum	Achillea millefolium Centaurea nigra Hypochaeris radicata Leontodon hispidus	Leontodon autumnalis Leucanthemum vulgare	Anthemis arven
Lamiaceae		Clinopodium vulgare Lycopus europaeus Origanum vulgare Teucrium scorodonia	Prunella vulgraris Scutellaria galericulata Thymus polytrichus	
Poaceae	Bromus commutatus	Anthoxanthum odoratum	Agrostis stolonifera	

		Festuca ovina Holcus lanatus		Deschampsia cespitosa Festuca rubra Lolium perenne Poa pratensis

Appendices

Appendix 1. Summary information on species included in this review.

Appendix 2. Plant suppliers who provided information on seed and plant supply for this review.

Appendix 3. The results of the survey of 19 commercial seed and plant suppliers (* = missing responses).

Appendix 4. Summary of intraspecific taxa recorded for species included in this review.

Appendix 5. Summary of studies on ecotypic and clinal variation within native species included in this review.

Appendix 6. Summary of scores for variation, history traits and commercial supply with overall assessment of risk from the introduction of non-local genotypes. See text for details.

Appendix 1

Summary information on species included in this review

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|                      |
|                      |Recommended seed mixtures for agri-environment scheme options (% composition; A
|                      |additional species)1
|                      |
|                      |
|                      |Basic
|                      |
|                      |Basic
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|                      |Basic
|                      |
|                      |Basic
|                      |
|                      |Basic
|                      |
|                      |Basic
|                                                                  |
|                                                                  |Basic
|                                                                  |
|Agrifactors                                                       |Rowland Davies
|British Flora                                                     |Glyn Onione
|British Seed Houses                                               |Jon Chippendale
|British Wild Flower Plants                                        |Linda Laxton
|Cotswold Seeds                                                    |Ian Wilkinson
|DLF-Perryfields1                                                  |Jeremy Hindle
|Emorsgate Seeds                                                   |Richard Brown
|Flower Farms                                                      |Bob Anderson
|Growing Wild                                                      |James Johnson
|Herbiseed                                                         |Steve Morton
|Heritage Seeds                                                    |Gerard Russell
|John Chambers                                                     |John Chambers
|MAS Seed Specialists                                              |Tim Evans
|Mike Handyside Wildflowers                                        |Mike Handyside
|Naturescape                                                       |Mark Scarborough
|Really Wildflowers (HV Horticulture Ltd)                          |Rob Flowers/Graham Dixie
|Scott’s Wildflowers                                               |Ted Scott
|The English Wildflower company                                    |John Schumacher
|YSJ Seeds                                                         |Yvonne Saunders
|                                                                  |
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Notes: [1] Includes Pope & Chapman, Johnsons, Cebeco and Oliver Brothers.

Appendix 3

The results of the survey of 19 commercial seed and plant suppliers (* = missing responses)

Questions	Number of responses	%
1. What is the nature of your business?	19	100
Retailer/wholesaler	7	39
Retailer/wholesaler and grower	12	67
Number of companies selling seed	18	95
Number of companies selling plants	12	63
Number selling both seed and plants	12	63
Number selling seed alone	7	37
Number selling plants alone	1	5
2. How much seed/plant material do you sell in an average year?		
Seed	17*	100
< 1 t	6	35
1-10 t	3	18
11-100 t	5	29
101-500 t	1	6
>500 t	2	12
Plants	12	100
1000-10000	2	17
10000-100000	5	42
100000-500000	3	25
>500000	2	17
3. How have your plant sales changed in the last decade?	19	100
Decreased	0	0
Remained stable	4	21
Increase up to 50%	5	26
Increase by more than 50%	10	53
4. Do you buy-in seed from a commercial supplier?	19	100
Yes	18	95
No	1	5
4a. If yes, what proportion do these make up of total sales?	18	100
<10%	4	22
10-50%	8	44
50-90%	2	11
>90%	4	22

Appendix 3 continued.

Questions	Number of responses	%
5. Would you be willing to name your main supplier(s)?	18	100
Yes	16	84
No	4	16
Main supplier:		
Advanta	1	6
Barrenbrug (DSV)	2	13
BSH	3	19
British Flora	1	6
DLF-Perryfields	7	44
Emorsgate	9	56
Flower Farms	1	6
Growing Wild	2	13
Herbiseed	2	13
John Chambers	1	6
Naturescape	3	19
Powerseeds	2	13
Scotia Seeds	1	6
YSJ	3	19
6. Do you sell seed / plants sourced from semi-natural populations?	19	100
Yes	19	100
No	0	0
6a. If yes, what proportion do these make up of total sales?	17*	100
<10%	5	26
10-50%	2	11
50-90%	3	16
>90%	7	37
7. What is the origin of these plants?	17*	100
Direct harvesting	8	42
Seed bulked from an original collection	16	84
Other suppliers	6	32
Other	0	0
8. Do you harvest seed from semi-natural populations?	19	100
Yes	14	74
No	5	26

Appendix 3 continued.

Questions	Number of responses	%
8a. If yes, how many sites do you harvest from?	14	100
1	1	7
2-5	3	21
6-10	2	14
>10	8	57
9. Is this seed used to bulk-up plants from which further seed can be harvested?	14	100
Yes	11	79
No	3	21
9a. If yes, how often do you return to donor sites to restock seed samples?	10*	100
Annually	2	20
Every 2 years	3	20
1 in 5 years	4	40
1 in 10 years	0	0
Never	1	10
10. What proportion of the site do you harvest from?	13*	100
< half (target individual species)	9	69
More than half	0	0
Whole site	2	15
Depends on contractor/species	2	15
11. Do you sell seed imported plants from outside the UK?	19	100
Yes	11	58
No	8	42
11a. If yes, what proportion do these make up of total sales?	11	100
<10%	4	36
10-50%	4	36
50-90%	3	27
>90%	0	0
12. Do you know the origin of this seed?	10*	100
Yes	9	90
No	1	10
12a. If yes, what proportion comes from the following continents?	9	100
Europe	9	100
North America	6	67
Australia/New Zealand	7	78

Asia	1	11
Other	0	0

Appendix 3 continued.

Questions	Number of responses	%
13. Who supplies your imported seed?	11	100
British seed merchants	10	83
Foreign seed merchants	3	25
British growers	1	8
Local collectors	1	8
14. Do you know what the seed is being used for?	19	100
Yes	18	95
No	1	5
Agricultural mixtures (inc AE mixtures)	18	100
Habitat restoration schemes	15	83
Amenity/landscaping	14	78
Roadworkd/building	9	50
Gardening	6	33
Mineral extraction/landfill	5	28
Private individuals/retail	5	28
Other seed companies	2	11
Landscaping/civil engineering	1	6
Experiments	1	6
Game cover	1	6
Golf courses	1	6
Pictorial packet seed	1	6
15. Do you offer any of the following services?	19	100
Local seed harvesting	11	58
Regionally matched seed mixtures	14	74
Advice on site/species suitability	18	95

Appendix 4

Summary of intraspecific taxa recorded for species included in this review

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Achillea millefolium	Native	54	1	0	2	2	?	Polymorphic but few intraspec
Achillea ptarmica	Native	18	1	0	1	1	0	
Adonis annua	Archaeo	32	1	0	1	2	0	
Agrimonia eupatoria	Native	28	1	0	1	3	0	
Agrostemma githago	Archaeo	48	1	0	4	1	0	
Agrostis canina	Native	14	1	0	9	1	0	Formerly included in Agrostis
Agrostis capillaris	Native	28	1	0	6	1	0	Ecotypes from contaminated so
Agrostis gigantea	Archaeo	42 + 0-4	1	0	1	2	0	
Agrostis stolonifera	Native	28, 30, 32, 25, 42, 44, 46	1	5	8	?	0	Very variable although it doe British varieties (var. marin stolonifera, var. palustris)
Alisma plantago-aquatica	Native	14	1	0	4	1	0	
Alliaria petiolata	Native	42	1	0	?	1	0	
Allium ursinum	Native	14	1	0	1	2	0	
Alopecurus pratensis	Native	28	1	0	2	2	?	Very variable as many strains till the 1950s (Sell & Murrel
Anagallis arvensis	Native & archaeo	40	1	0	3?	1?	1?	In Europe this species is ver flowered plants are replaced al. 1964).
Angelica sylvestris	Native	22	1	0	2	1	0	
Anthemis arvensis	Archaeo	18	1	0	1	4	0	
Anthoxanthum odoratum	Native	20	1	0	3	?	0	A very variable grass in heig 1996). A component of grass m and has declined under improv

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Calluna vulgaris	Native	16	1	0	4	1	0	
Caltha palustris	Native	48, 52, 54, 56, 64, 72, c.80	1	1	5	5?	0	An extremely variable species the specific and subspecific vary independently of chromos been described from upland ar with var. palustre although i
Campanula glomerata	Native	30	1	0	1	7	0	Widely grown in gardens and s 2002).
Campanula rotundifolia	Native	68, 102	2?	0	5	4?	0	An extremely variable species appear continuous and there i al. 1964). Tetraploids and he the Scandinavian C. giesekiar also been reported (Preston e
Campanula trachelium	Native	34	1	0	2	2	0	
Cardamine pratensis	Native	30, 56-58, c.64, 72 (16-96)	3?	0	4	7	0	Morphologically and cytologic subdivide satisfactorily. Pos (Stace 1997).
Carex flacca	Native	76, 90	1	0	6	2	0	
Centaurea cyanus	Archaeo	24	1	0	1	1	0	
Centaurea nigra	Native	22, 44	2?	0	5	3	0	Subsp. nemoralis has been rep has been treated as a separat considered to be conspecific
Centaurea scabiosa	Native	20	1	1?	4	2?	0	Plants with entire basal leav populations in Wales and Scot (Valentine 1980).
Cerastium fontanum	Native	72, 108, 144	3	1	9	6?	0	The commonest subsp. vulgare chromosome number and there i (Rich & Jermy 1998). Subsp. h is much more common in the no confined to serpentine soils
Chrysanthemum segetum	Archaeo	18	1	0	1	1	0	
Cirsium acaule	Native	34	1	0	1	3	0	Var. caulescens has been reco growth-form.
Clinopodium vulgare	Native	20	1	0	1	2	0	
Conopodium majus	Native	22	1	0	1	1	0	

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Cynosurus cristatus	Native	14	1	0	1	1	0	Cynosurus cristatus was a fre 1940s, and is still used in a poor soils (Preston et al. 20
Dactylis glomerata	Native	14, 28	1	0	4	10	2?	Many variants are recognised distinguishable other than by robust plants of artificial h These include subsp. ascherso naturalised in woods in south which has been reocrded from agricultural cultivars, usual station at Aberystwyth (Sell Denmark and it is often a rel (Preston et al. 2002).
Anthyllis vulneraria	Native & alien	12	3	2	6	25	2	Three native subspecies occur subsp. lapponica) although th recently been questioned (Ric (langei, coccinea) are curren represented in our area by va Britain as early as 1895 (Gue plantings. In contrast subsp. 2002).
Arctium minus	Native	36	2?	0	3	1	0	There is no consensus on the workers treating A. nemerosum subsp. of A. minus. All taxa clearly defined (Tutin et al.
Arrhenatherum elatius	Native	28	2	1	2	2	0	Subsp. bulbosum is a troubles also occurs in semi-natural h 1990).
Bellis perennis	Native	18	1	0	1	2?	0	
Blackstonia perfoliata	Native	40	1	0	1	4	0	
Brachypodium sylvaticum	Native	18	1	0	2	2	0	
Briza media	Native	14	1	0	2	2	0	
Bromopsis erecta	Native	42, 56	1	0	1	4	0	
Bromus commutatus	Native	14, 28, 56	1	0	3	2	0	Very variable and possibly be (Stace 1997).
Daucus carota	Native & alien	18	2	0	3	12	1	Subsp. gummifer occurs on the of calcareous soils inland. M seperate the subspecies becom Sell 1968). Subsp. sativus is garden areas and fens; Rich & garden origin (Stace 1997).
Deschampsia cespitosa	Native	26, 39?, 52, 34-56	3	0	6	7	0	Subsp. cespitosa is represent and a diploid, triploid or te in the north. Subsp. parviflo and shady borders in the lowl tetraploid (2n = 34-56) and c & Murrell 1996; Stace 1997).

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Deschampsia flexuosa	Native	26, 28, 56	1	0	2	1	0	
Digitalis purpurea	Native	56	1	0	3	3	0	A very complex polytopic spec each with several local varia
Dipsacus fullonum	Native?	18	1	0	1	1	0	
Erodium cicutarium	Native	40	2?	0	5	3	0	An extremely variable species Only three can be recognised In the UK E. cicutarium s.l. and E. lebelii (Rich & Jermy latter species. It is current al. 2002).
Eupatorium cannabinum	Native	20	1	0	2	2	0	
Euphrasia nemorosa	Native	44	1	0	?		0	Euphrasia nemorosa is the com our eyebrights, becoming more in the north. However, it for introgressed populations can difficult (Preston et al. 200
Festuca arundinacea	Native	42	1?	0	2	5	?	Very variable and represented (Sell & Murrell 1996) but the and frequent naturalisation (
Festuca ovina	Native	14, 28	3	2	4	0	0	Subsp. ovina (2n = 14) and su well drained, usually acid so on calcareous or serpentine s the widespread taxon whereas the west of the British Isles
Festuca pratensis	Native	14	1	0	4	0	0	Often sown for fodder and has and waste ground. The native may only occur in N. & W. Bri may be decreasing due to the popularity in grass mixtures
Festuca rubra	Native & alien	42, 56, 70	5	0	9	7	2	This very variable species is occur in the UK (Tutin et al. the range of the species, sub 42), whereas subsp. juncea (2 confined to caostal and subsp 70) are confined to mountains Non-native subsp. commutata (constituent of grass-seed mix grasslands and garden lawns a 2002). Subsp. megastachys (2n in 1966 (Shetland) and is unc
Filipendula ulmaria	Native	14, 16	1	0	2	3	0	
Filipendula vulgaris	Native	14, 15	1	0	1	1	0	It is grown in gardens, somet
Galium mollugo	Native	44	2	0	4	1	0	Two subspecies may occur in c their taxonomic status is unc album is treated as a subspec 1998). It is common in wild- roadsides.

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Galium palustre	Native	24, 48, 96 (144)	2	0	8	1?	0	Different chromosome races of subspecies (subsp. palustre, Stace 1997). They represent a constrictum (Rich & Jermy 199
Galium saxatile	Native	44	1	0	2	1	0	
Galium verum	Native	44	1	1	2	2?	0	Var. maritimum occurs in coas subspecies hybridise and form have to be classified (Tutin wild-flower seed mixtures (Pr
Gentianella amarella	Native	36	5?	0	2	2?	0	Recent research suggests that genetically similar and may r variants (Winfield & Parker 1 subspecies alongside subsp. s all recognised in Stace (1997
Geranium pratense	Native	28	1	0	2	1	0	Alien records for Geranium pr separating native and alien p difficult (Preston et al. 200
Geum rivale	Native	42	2?	0	2	1	0	Dwarf northern plants have be subspecific status as interme
Geum urbanum	Native	42	1	0	1	1	0	
Helianthemum nummularium	Native	20	1?	0	4	9?	?	Garden escapes may represent
Helictotrichon pratense	Native	126	2?	0	3	2?	0	Scottish plants with larger m separate taxon (Tutin et al.
Helictotrichon pubescens	Native	14	1	0	2	1	0	
Hippocrepis comosa	Native	14, 28	1	0	1	1?	0	En extremely variable species
Holcus lanatus	Native	14	1	1?	2	1	0	Stoloniferous var. soboliferu
Hordeum secalinum	Native	14, 28	1	0	1	1	0	
Hyacinthoides non-scripta	Native	16, 24	1	0	2	1	0	Freely hybridises with the no (Stace 1997).
Hypericum hirsutum	Native	18	1	0	1	1	0	
Hypericum humifusum	Native	16	1	0	2	1	0	
Hypericum perforatum	Native	32	1?	0	3	1?	0	Very variable in leaf shape (
Hypericum tetrapterum	Native	16	1	0	2	1	0	
Hypochaeris radicata	Native	8	1	0	4	1	0	
Iris pseudacorus	Native	34	1	0	3	1	0	
Knautia arvensis	Native	16, 20, 40	1	0	3	1?	0	A very polymorphic taxon. Mar Alps (Tutin et al. 1964).

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Koeleria macrantha	Native	14, 28 (+0-6), 42, 70	2?	2	1	1?	0	A very polymorphic taxon whic referable to Koeleria glauca, in the UK (Dixon 2001). Howev macrantha and subsp. glauca w
Lathyrus pratensis	Native	14, 28	1?	0	4	?	0	A very polymorphic taxon poss et al. 1964) although there c chromosome number and morphol
Leontodon autumnalis	Native	12	2?	1	4	2	0	A very polymorphic taxon. It from tall, hairy plants on mo virtually glabrous plants in
Leontodon hispidus	Native	14	1	1	2	6	0	A very polymorphic taxon. Var 1997).
Leucanthemum vulgare	Native	18, 36	1	0	3	15?	?	A very polymorphic taxon or s large number of taxa many of 1964). Throughout much of its activities, frequently being
Linum catharticum	Native	16	1	0	2	1	0	
Lolium perenne	Native	14	1	?	9	1	0	Lolium perenne has been culti cultivars developed by plant sown agricultural grasses (Pr forms and varieties have been cultivation (Sell & Murrell 1
Lotus corniculatus	Native	24	1?	1	5	4?	1	Very variable and it may even the native distribution of ma forage crops (Tutin et al. 19 commonly sown within seed mix
Lotus pedunculatus	Native	12	1	0	3	1	0	
Lychnis flos-cuculi	Native	24	1	1	1	2	0	A dwarf form (var. congesta), Caithness, Sutherland and She cultivation (Preston et al. 2
Lycopus europaeus	Native	22	1	0	4	3?	0	Very variable in Europe with
Lythrum salicaria	Native	60	1	0	2	1	0	
Malva moschata	Native	42	1	0	4	1	0	It may be increasingly introd escapes (Preston et al. 2002)
Malva sylvestris	Archaeo	42	1	0	4	?	0	Very variable with a number c maintained on a continental s
Matricaria recutita	Archaeo	18	1	0	?	1	0	Probably only native in S.E.
Medicago lupulina	Native	16	1	0	5	1	0	
Medicago sativa	Native & neophyte	16, 32	2	0	1	5	2?	Three subspecies occur: subsp this forms hybrids (subsp. va These arise either spontaneou sativa subsp. sativa was firs Britain in the 17th century a more frequently grown in a pe especially on dry sandy soils however, are very persistent 'Grimm' Lucerne (subsp. varia

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Myosotis arvensis	Archaeo	36, 48, 52	1	1	3	2	0	Very variable the habit deper 1964).Var. sylvestris is a la
Oenanthe fistulosa	Native	22	1	0	2	1	0	
Onobrychis viciifolia	Native	28	1	0	1	1	1?	Robust alien variants are fou chalk and less often on other sown roadsides (Preston et al
Origanum vulgare	Native	30	1	0	4	1?	0	Extremely variable although v populations (Tutin et al. 196
Papaver rhoeas	Archaeo	14	1	0	13	1	0	Grown in gardens (Shirley Pop
Pastinaca sativa	Native	22	1	2	2	4	1	Var. hortensis is cultivated roadsides (Stace 1997). It ma (Preston et al. 2002).
Phleum bertolonii	Native	14	1	0	1	0	0	It is possible that British P (P. serotinum) (Stace 1997). Robust agricultural strains a their differing chromosome nu
Phleum pratense	Native	21, 35, 36, 42, 49, 56, 63, 70, 84	1	0	10	2	?	Much seed sown as leys comes
Pilosella officinarum	Native	18, 27, 36, 45, 54	7?	0	7?	8	0	Seven subspecies are recognis are more or less connected by discrete geographically and e varieties.
Pimpinella saxifraga	Native	40	1?	0	4	1?	0	Very variable particularly ir In Europe variation has recei 1964).
Plantago lanceolata	Native	12	1	0	10	1?	0	Extremely variable although m be clinal. Formal recognitior genetically and phenotypicall
Plantago media	Native	24	1	0	3	1?	0	Serpentine ecotypes occur (Tu
Poa nemoralis	Native	28-33, 42, 56	1	0	10	1	0	It was occasionally sown in w while in some areas it may ha or soil (Preston et al. 2002) Britain (Stace 1997).
Poa pratensis	Native	42, 50-78, 91, 98	1	0	10	4?	?	Four agamospermous species ha include Poa. angustifolia and in British floras. Overall me largely apomictic. As a conse and the four European taxa ma pratensis in the broadest ser one occasion as a result of h followed by an increase in ch system. Intercrossing is prob predominantly agamospermous b species (Tutin et al. 1964). has many strains, although Br humilis as distinct (Sell & M constituent of commercial see amenity and wild-flower grass

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Poa trivialis	Native	14	1	0	9	2	?	Formerly included in agricult still used in amenity and wil
Potentilla erecta	Native	28	2	0	3	1	0	Subsp. strictissima is a robu 1973).
Primula veris	Native	22	1	0	1	4	0	Becoming more frequent on roa wild-flower mixtures (Preston
Primula vulgaris	Native	22	1	0	2	3	0	
Prunella vulgaris	Native	28	1	0	4	1	0	
Pulicaria dysenterica	Native	18	1	0	3	1	0	
Ranunculus acris	Native	14	1	3	10	4	0	Vars pumillus and villosus ar Stace 1997).
Ranunculus arvensis	Archaeo	32	1	0	2	1	0	
Ranunculus bulbosus	Native	16	2	1?	6?	3	0	Subsp. bulbifer is continuous does not merit subspecific st
Reseda lutea	Native	48	1	0	3	1	0	
Reseda luteola	Archaeo	26	1	0	2	1	0	
Rhinanthus minor	Native	22	6	0	3	4	0	Rhinanthus minor is very vari inter-fertile subspecies have whilst they show broad geogra races cannot be clearly assig minor and subsp. stenophyllus taxa and are probably the sow calcareous soils in the south confined to mountains in the
Rumex acetosa	Native	14 (female), 15 (male)	3	1?	1	4?	1	Subsp. acetosa is the widespr biformis are both coastal. Su 1998).
Rumex acetosella	Native	28, 42	2	1	7	4	0	Subsp. acetosella and subsp. are poorly known and many int
Sanguisorba minor	Native	28	1	0	1	6	1	Subsp. muricata, introduced i often grown in gardens and so calcareous soils. It was reco increasing (Preston et al. 20 subspecies.
Sanguisorba officinalis	Native	28, 56	1	0	1	1	0	
Saxifraga granulata	Native	c.32, 48	1	0	2	2	0	Very variable in both morphol populations include a double-
Scabiosa columbaria	Native	16	1	1?	2	3	0	Often dwarfed maritime forms
Scutellaria galericulata	Native	30, 32	1	0	4	1	0	
Serratula tinctoria	Native	22	1	0	5	?	0	An extremely variable species below the species level. Two et al. 1964).

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Silaum silaus	Native	22	1	0	1	1?	0	A linear-lobed leaf variant o
Silene dioica	Native	24	1	1?	3	1?	0	Dwarf mountain variants occur rank (Tutin et al. 1964; Stac
Silene latifolia	Archaeo	24	2	0	1	5?	0	
Silene noctiflora	Archaeo	24	1	0	1	1	0	
Stachys officinalis	Native	16	1	1	4	1	0	It is occasionally found in c dwarf var. nana (Preston et a
Stachys sylvatica	Native	64	1	0	3	1	0	
Succisa pratensis	Native	20	1	0	4	1	0	
Teucrium scorodonia	Native	32, 34	1	0	2	3	0	
Thalictrum flavum	Native	84	1	0	3	2	0	
Thymus polytrichus	Native	50-56	1	0	9	7?	0	Very variable. Flora Europaea variation although boundaries
Torilis japponica	Native	16	1	0	?	1	0	
Tragopogon pratensis	Native & neophyte	12	1	0	4	3	2	Subsp. minor is the only nati orientalis are both rare intr
Trifolium dubium	Native	32	1	0	3	1	?	
Trifolium hybridum	Neophyte	16	1	0	1	3	1?	Subsp. hybridum is cultivated (Stace 1997); it used to be m the wild by 1762. It is still (Preston et al. 2002).
Trifolium pratense	Native	14	1	1	6	5	1?	Extremely variable both in th specialised wild populations bring the numerous local taxa often sown into stubble as le mixtures (Preston et al. 200
Trifolium repens	Native	32	1	0	3	6	0	It is very widely sown as a roadsides, and many commercia
Trisetum flavescens	Native	14, 28	1	0	3	3	1	Subsp. purpurascens (2n = 14) Cambrideshire and is now know Murrell 1996) and in grasslan
Valeriana officinalis	Native	28, 56, 70	2	0	2	6?	0	Several taxa occur in Europe worked through (Tutin et al. = 28) occur on calcareous soi octoploid or rarely decaploid in damp grassland, marshes, f throughout the country.
Veronica chamaedrys	Native	32	1	0	5	2	0	
Vicia cracca	Native	28	1	0	3	1	0	

Appendix 4 continued.

Species	Status	2n	Subsp.	Vars	Druce	Europe	Non-native	Comment
Vicia sativa	Native & archaeo	12	1	0	8	6	2?	Subsp. nigra is the native su throughout the UK. Subsp. seg probably introduced as a fodd many ruderal habitats. Subsp. was formerly much grown for f casual. However, the acreage by 91% between 1891 and 1958, decreased accordingly. It is, gardeners.
Viola hirta	Native	20	1	1?	10	1	0	Subsp. calcarea is smaller bu

Appendix 5

Summary of studies on ecotypic and clinal variation within native species included in this review

Species	Climatic	Edaphic ecotype
Achillea millefolium	Turesson (1925, 1930)	Coastal forms (Akeroyd 1997)
Agrostis capillaris	Differential growth over 800m alt (Bradshaw 1960)	Different soil types including coastal ecotypes (Bradshaw 1959, 1960); heavy metal tolerance (Jain & Bradshaw 1966) including copper (McNeilly 1968) and zinc (Al-Hiyaly et al. 1993)
Agrostis stolonifera		Tolerance to heavy metals (Jain & Bradshaw 1966) including copper (Wu et al. 1975), salinity (Kik 1989) an a range of soil types including coastal ecotypes (Aston & Bradshaw 1966)
Anagallis arvensis		Coastal variety (Rilstone 1938)
Anthoxanthum odoratum		Adaptation to applications of fertilisers (Davies & Snaydon 1973a,b, 1974), de-icing salt (Kiang (1982) and heavy metals (Platenkamp Shaw 1992)
Anthyllis vulneraria		Coastal forms (Mardsden-Jones & Turrill 1933; Akeroyd 1997)
Arrhenatherum elatius		Heavy-metal tolerance (Ducousso et al. 1990)
Bellis perennis	Differences in phenology (Turesson 1925, 1930)	
Campanula rotundifolia	Sub-alpine ecotypes (Turesson 1925, 1930)	
Centaurea scabiosa		Coastal ecotpye (Valentine 1978, 1980)
Cerastium fontanum		Coastal forms (Akeroyd 1997), serpentine ecotypes (Spence 1970) an soil conditions along amoisture gradient in a Agrostis-Festuca grassland (Harberd 1961)
Dactylis glomerata	Different growth rates (Lawrence 1945)	Maritime ecotypes (Gregor & Sansome 1927; Valentine 1978; Akeroyd 1997); tolerance to variation in soil moisture (McKell et al. (1960); SO2 (Azayloo & Bell 1981), and some heav metals (Bradshaw 1984)

Appendix 5 continued

Species	Climatic	Edaphic ecotype
Daucus carota	Different growth forms at coast from inland (Nehou 1961)	
Deschampsia cespitosa	Different growth rates etc. at different altitudes (Lawrence 1945)	Tolerance to zinc (Coulaud & McNeill 1992)
Erodium cicutarium		Coastal ecotypes (Larsen 1958)
Festuca ovina		Tolerance of lead (Wilkins 1960) and variations in soil nutrients (Snaydo & Bradshaw 1971)
Festuca rubra		Coastal ecotypes (Turesson 1925, 1930; Hannon & Bradshaw 1968), tolerance to salinity (Rozema et al. 1978), SO2 (Azayloo & Bell 1981), heavy metals (Bradshaw 1984) and variations in soil conditions along grassland moisture gradient (Harbred 1961)
Filipendula ulmaria	Sub-alpine ecotypes (Turesson 1925, 1930)	Dwarf coastal ecotype (Turesson 1925 1930)
Filipendula vulgaris	Climatic ecotypes (Turesson 1925, 1930)	
Galium mollugo		Coastal ecotype (Donneaux 1981)
Galium verum		Coastal ecotype (Donneaux 1981)
Geum rivale	Montane ecotype (Tureson 1925, 1930; Valentine 1978)	
Holcus lanatus		Tolerance to SO2 (Azayloo & Bell 1981) and heavy metals (Bradshaw 1984) including arsenate (Meharg et al. 1993)
Hypochaeris radicata		Coastal ecotype (Akeroyd 1997)
Leontodon autumnalis	Montane ecotype (Tureson 1925, 1930)	Succulent coastal and dry soil ecotypes (Turesson 1925, 1930)
Lolium perenne		Coastal ecotypes (Gregor & Sansome 1927); variation in soil conditions (Gregor & Waton 1954) and nutrients (Goodman 1969); tolerance to SO2 (Azayloo & Bell 1981; Wilson & Bell 1986)
Lotus corniculatus		Coastal ecotypes with fleshy leaves (Larsen 1954; Akeroyd 1997)
Lychnis flos-cuculi	Montane ecotype (Turesson 1925, 1930)	

Appendix 5 continued

Species	Climatic	Edaphic ecotype
Lythrum salicaria		Dwarf coastal ecotype (Turesson 1925 1930)
Plantago lanceolata		Tolerance to variation in soil conditions (Gregor & Watson 1961) an lead in exhaust fumes (Wu & Antonovics 1976)
Poa pratensis sens.lat.		Coastal ecotype (Akeroyd 1997)
Poa trivialis		Variation in soilm conditions along moisture gradient (Harbred 1961)
Prunella vulgaris	Differences in life-history in relation to latitude (Turesson 1925, 1930; Böcher 1949)	Coastal (Akeroyd 1997) and serpentin ecotypes (Kruckeberg 1967)
Ranunculus acris	Alpine ecotype (Turesson 1925, 1930)	
Ranunculus bulbosus		Coastal ecotype (Akeroyd 1997)
Rumex acetosa	Alpine ecotype (Turesson 1925, 1930)	Coastal (Lousley 1968; Akeroyd 1997) and serpentine ecotypes (Spence 1970
Rumex acetosella		Serpentine (Kruckeberg 1967) and dry soil ecotypes (Turesson 1925, 1930)
Scutellaria galericulata		Coastal ecotype (Akeroyd 1997)
Serratula tinctoria		Coastal ecotype (Coombe 1973)
Silene dioica	Alpine and sub-alpine ecotypes (Turesson 1925, 1930)	Succulent leaved coastal ecotype (Turesson 1925, 1930; Baker 1948)
Silene latifolia		
Stachys officinalis		Coastal ecotype (Akeroyd 1997)
Stachys sylvatica		Coastal ecotype (Coombe 1973; Morton 1973)
Succisa pratensis	Sub-alpine ecotypes (Turesson 1925, 1930)	Coastal ecotype (Turesson 1925, 1930 Akeroyd 1997)
Teucrium scorodonia		Variation in soil nutrients (Hutchinson 1967, 1968)

Appendix 5 continued

Species	Climatic	Edaphic ecotype
Trifolium pratense		Coastal ecotype (Akeroyd 1997)
Trifolium repens		Coastal ecotype now treated as a separate species (T. occidentale; Coombe 1961). Ecotypes adapted to variations in soil nutrients (Snaydor & Bradshaw 1962)
Vicia cracca		Coastal ecotype (Akeroyd 1997)

Appendix 6

Summary of scores for variation, history traits and commercial supply with overall assessment of risk from the introduction of non-local genotypes (see text for details). Species listed in order of biological risk (life history and variation score).

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   Variation (see Table 14) Life history traits (see Table 15) Risk scores   Taxonomic status Family co
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[1] Of native species certified under the European Seeds Directive (66/401/EEC), the Fodder Plant Seed
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