The vegetation associated with *Spiranthes romanzoffiana* Cham. (Orchidaceae), Irish Lady's-tresses, on the Isle of Coll, Inner Hebrides

S. A. HENDERSON

Dept. of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

ABSTRACT

This paper details some environmental preferences of the scarce orchid *Spiranthes romanzoffiana* Cham. on the Isle of Coll in the Inner Hebrides. Samples were categorised into four site types that form a continuum rather than a series of discrete habitat types. High cover of *Carex panicea* L., and to a lesser extent *Molinia caerulea* (L.) Moench and *Juncus articulatus* L., occurs throughout. The habitat sappear to be influenced by varying degrees of high water and low nutrient availability, as suggested by the disparate species. There is no apparent difference between former and present habitat of the orchid on the island, but few conclusions can be made from vegetation description alone. As it stands, the habitat as defined in this study is not uncommon, and it may be that other factors, such as seed sterility or availability of mycorrhizal associate, are limiting the species distribution.

KEYWORDS: Habitat preference, vegetation analysis.

INTRODUCTION

Spiranthes romanzoffiana Cham. (Orchidaceae), Irish Lady's-tresses, is one of the few British natives with an amphi-Atlantic distribution, found widespread in North America and limited to the Western fringes of Europe (Preston & Hill (1997) included it under their "boreal-montane element"). Indeed, within Europe it is almost entirely confined to the west of Scotland and southwestern, western and Northern Ireland. Other species that share a similar "asymmetrical" amphi-Atlantic distribution include *Potamogeton epihydrus* Raf., *Najas flexilis* (Willd.) Rostkov. & W. Schmidt and *Eriocaulon aquaticum* (Hill) Druce.

Although not discovered until 1810 in Ireland (Hackney 1992), it is widely accepted that *S. romanzoffiana* is native (e.g. Heslop-Harrison 1953; Löve & Löve 1958; Stace 1997). Theories explaining the amphi-Atlantic distribution include migration across a former land connection between Europe and North America (Dahl 1963; Hulten 1963) followed by a contraction in the European distribution during glaciation with survival in or near the present localities (see Coxon & Waldren 1995), or long distance dispersal (Heslop-Harrison 1953; Perring 1965). One of the outstanding features of North American elements in the British flora is that they are all aquatic, marsh or lake margin plants, suggesting a similarity in propagule dispersal. While controversy persists over the explanation for the uneven distribution of *S. romanzoffiana*, its similarity in geography to other species and the difficulty in accounting for seed transport to such relatively remote and more or less natural habitats by human means, are justifications of its native status (see Webb 1985).

The main populations of *S. romanzoffiana* occur round the Galway-Mayo lakes area and Lough Neagh in Ireland, and on Colonsay, Coll and the Outer Hebrides of Scotland, and it has one outlying post in South Devon, discovered in 1957 (Anon. 1958). Stewart, Pearman & Preston (1994) categorise the species as Scarce, found in only eighteen 10-km squares in Britain. As the only widely recognised orchid species of Britain not to be found elsewhere in Europe, and with a stronghold in Scotland, Scottish Natural Heritage has designated *S. romanzoffiana* a priority species for conservation. None of the Scottish localities recorded before 1981 now show the orchid, although several new sites have since been discovered (UK Biodiversity Group 1999). While little is known of the natural fluctuations of the populations, these results have increased concern over the orchid's status in the British Isles.

S. romanzoffiana coexists with an agricultural system based on extensive grazing. The orchid is supposedly sensitive to subtle changes in the type, timing and intensity of grazing (e.g. Summerhayes 1951; Ferreira 1978; Horsman 1994). Traditionally, pastoral agriculture in the Hebrides entails cattle grazing from September to May followed by a short period allowing for plant growth and a subsequent harvest for hay. The land management is conducive to both survival and fecundity of *S. romanzoffiana*, the two factors that determine population status. Cattle grazing enables survival by keeping more competitive tussock-forming species low while the period free from grazing coincides with the orchid's flowering period, thus ensuring fecundity. In Coll, a general trend in agricultural intensification is confounded by the heavy conservation priority placed on the corncrake, *Crex crex*, a bird which has now disappeared from most other parts of Britain (Stroud 1992). By encouraging "corncrake friendly" extensification of grazing on some nesting areas, the RSPB has forced intensification in other areas. Ironically, the conservation measure may pose a threat to populations of *S. romanzoffiana*.

In North America typical habitats are moist: in bogs, marshes, meadows, salt flats, muskegs, thickets, on sandy-gravelly beaches, but also occasionally on dry woods and dry open hillsides (Luer 1975; Correll 1978; Case 1987; Smreciu & Currah 1989; Homoya 1993). Typically a northern species, in the more southern parts of its range in America it is a mountain plant where it occurs up to 3000 m asl and flowers until October (Correll 1978). In the British Isles, however, it occurs within a narrower range of habitats, suggesting that here the populations are ecologically as well as geographically marginal.

In Ireland it grows in damp meadows, close to rivers and lake-shores and in cut-over bogs (Praeger 1934; Harron 1986; Hackney 1992). In Britain, the orchid is similarly described as occurring on low-lying sites that are at least periodically irrigated and sometimes inundated (Scottish Natural Heritage 1995). Horsman (1994) described Spiranthes romanzoffiana as having a distinct habitat of *Molinia caerulea* carpet on old cattle-grazed lazy-beds. The habitats of S. romanzoffiana have been surveyed on Coll, Colonsay (Scottish Natural Heritage 1995; Gulliver 1996) and Loch Sheil (Martin & Milnes 1993) using the National Vegetation Classification (NVC) system (Rodwell 1991). All fall into the categories for mire, wet heath and rush pasture (Table 1). Collectively, and on a national scale, these communities are not infrequent. However, as NVC categories are based on the means of nation-wide data, they fail to describe the particular idiosyncrasies of an actual plant community (see Legg 1992). Multivariate ordination and classification techniques are preferable for the level of detail required in the study of rarities. For example Prober & Austin (1991) used the ordination technique of correspondence analysis to compare floristically sites where a rare species occurred with similar sites where it does not. Bowles et al. (1993), Ratcliffe, Birks & Birks (1993), Vazquez & Norman (1995) and Read & Tweedie (1996) all used numerical classification techniques to characterise the habitats of rare species.

In order to investigate the floristic component of *S. romanzoffiana*'s habitat, a multivariate analytical approach was used, with data from samples taken at two spatial scales. The two-scale

TABLE 1. NATIONAL VEGETATION CLASSIFICATION COMMUNITIES AND SUB COMMUNITIES IN WHICH SPIRANTHES ROMANZOFFIANA HAS BEEN FOUND

Code	e NVC Community and sub-community (Rodwell 1991)	
M25	Molinia caerulea-Potentilla erecta mire	
M25 a	Erica tetralix sub-community	
M25 b	Anthoxanthum odoratum sub-community	
M23	Juncus effusus-Galium palustre rush pasture	
M23 a	Juncus acutiflorus sub-community	
M23 b	Juncus effusus sub-community	
M15a M10	<i>Scirpus caespitosus-Erica tetralix</i> wet heath <i>Carex panicea</i> sub-community <i>Carex dioica-Pinguicula vulgaris</i> mire	
M6	Carex echinata-Sphagnum recurvum/auriculatum mire	
M6d	Juncus acutiflorus sub-community	

SPIRANTHES ROMANZOFFIANA ON COLL

approach enables a distinction to be made between the habitat preferences at the scale of the individual plant and those of the typical mire community; habitat description is scale-dependent due to spatial heterogeneity. Further, the identification of associated single species at a small scale may facilitate fine-grained ecological insights into the nature of the rare species' requirements. The study was carried out on the Isle of Coll, in the Inner Hebrides, where the majority of the Scottish *S. romanzoffiana* populations are found, and where there is a relatively long history of recorded individuals (Ferreira 1978; Horsman 1990, unpublished; Scottish Natural Heritage 1995).

METHODS

FIELD SURVEY

All 107 sites (numbering 16 locations, although these do not necessarily form discrete populations) with accurate records of the orchid were visited, including two new sites found in 1996. Grid references, sketch maps (Ferreira 1978) and photographs (Horsman 1990, unpublished; Scottish Natural Heritage 1995) were used to relocate individuals or sites with previously recorded individuals which were, in 1996, apparently absent. The locations were also thoroughly searched for any unrecorded individuals. 1×1 m quadrats ("meso-scale samples") were placed around the orchid(s), including only visually homogenous areas of vegetation. The equivalent area was taken where the homogenous vegetation did not fit to a 1 m^2 . Similarly, for those samples not containing S. romanzoffiana, the quadrat was placed around the site of the absent orchid (this was made possible by having relatively detailed and accurate records). Within each sample the number of individuals of S. romanzoffiana and the abundance of all species were recorded using the Domin scale. Percentage bare ground was also estimated. 10×10 cm quadrats ("micro-scale samples") were then placed around each individual of S. romanzoffiana found and presence/absence of all species was recorded. This area was thought small enough to investigate the more specific requirements of the individual orchid but large enough to incorporate other associated species. Plant nomenclature follows Stace (1997) for vascular plants and Watson (1981) for bryophytes.

ANALYSIS

Ordination was used to summarise the sample data collected at both scales. Analysis of data used detrended correspondence analysis (DCA) (Hill 1979a; Hill & Gauch 1980), a modification of correspondence analysis (ter Braak 1987). Two-way indicator species analysis (TWINSPAN) (Hill 1979b; Gauch & Whittaker 1981) was used to classify the meso-scale samples. The computer packages CANOCO (ter Braak 1988) and CANODRAW (ter Braak 1992) were used for DCA analysis and ordination plots and VESPAN (Malloch 1995) for TWINSPAN analysis, raw data tables and descriptive statistics.

RESULTS

MESO-SCALE SITE TYPES

Spiranthes romanzoffiana was present in 54 of the 107 meso-scale sites, (distributed over 11 of the 16 locations) and was absent in 53 of the sites (in 8 locations). In total 93 species were found. *Carex panicea* and *Molinia caerulea* were constant occurring in 94% and 86% of samples respectively, and 11 other species were frequent, occurring in 50% or more of samples: *Juncus articulatus, Carex nigra, Hydrocotyle vulgaris, Nardus stricta, Ranunculus flammula, Holcus lanatus, Anagallis tenella, Succisa pratensis, Anthoxanthum odoratum, Carex echinata and Eriophorum angustifolium.*

The indicator species at divisions 1 and 2 of TWINSPAN are shown in Fig. 1. The first division distinguishes samples containing *Erica tetralix* from samples with *Holcus lanatus*, *Galium palustre*, *Ranunculus flammula* and *Ranunculus acris*. The characteristics of each of the four final groups of division 2 are summarised in Table 2.

The sample ordination by DCA with the TWINSPAN groups superimposed (Fig. 2) shows that

Species present in 80% or more samples	Species present in 50%-80% samples
Site typ	e A1
Spiranthes roman	nzoffiana (70)
Carex nigra (100) Hydrocotyle vulgaris (100) Ranunculus flammula (100) Carex panicea (95) Juncus articulatus (95) Galium palustre (90) Caltha palustris (80)	Equisetum fluviatile (75) Carex echinata (70) Filipendula ulmaria (70) Holcus lanatus (70) Potentilla palustris (70) Mentha aquatica (65) Calliergon cuspidatum (65)
Eriophorum angustifolium (80)	Leontodon autumnalis (55) Myosotis laxa (55) Senecio aquatica (55) Anthoxanthum odoratum (50) Pedicularis palustre (50)
Site typ Spiranthes roman	e A2 nzoffiana (49)
Carex panicea (97) Molinia caerulea (95) Juncus articulatus (92) Holcus lanatus (89) Nardus stricta (81)	Hydrocotyle vulgaris (78) Ranunculus flammula (78) Carex nigra (76) Ranunculus acris (76) Anthoxanthum odoratum (73) Succisa pratensis (70) Trifolium repens (62) Potentilla erecta (58) Agrostis canina (51) Carex echinata (51)
Site typ	e B1
Carex panicea (100) Molinia caerulea (95)	Nardus stricta (77) Anagallis tenella (75) Juncus articulatus (66) Carex nigra (61) Potentilla erecta (57) Succisa pratensis (57) Agrostis canina (55) Hydrocotyle vulgaris (55) Carex echinata (53) Eriophorum angustifolium (53) (note, Erica tetralix 39)
Site typ Spiranthes roman	e B2 nzoffiana (11)
Erica tetralix (100) Molinia caerulea (100) Carex hostiana (89) Schoenus nigricans (89)	Anagallis tenella (67) Carex panicea (67) Selaginella selaginoides (56) Scorpidium scorpioides (56) (note Drosera rotundifolia, Myrica gale and Narthecium ossifragum at 44)

TABLE 2. MOST FREQUENT SPECIES AT DIVISION TWO OF TWINSPAN. PERCENTAGE FREQUENCY IN $1{\rm M}^2$ SAMPLES IS DENOTED IN PARENTHESES

Those species characteristically present in high abundance are shown in bold. While subjective, this aids interpretation.



FIGURE 1. Indicator species of the TWINSPAN hierarchy for the first two divisions. The number of samples in each category is shown in parentheses.



FIGURE 2. Sample ordination plot for the first two axes of Detrended Correspondence Analysis (DCA) of meso-scale habitat data for *Spiranthes romanzoffiana*. TWINSPAN-defined groups are superimposed.

the TWINSPAN-defined site types are not readily separated, either at the first or the second divisions. The first four axes extracted in DCA explain only 22.8% of the total variation in species data, and the first two axes of the ordination (which are used in the ordination plot) explain only 17% of floristic variation between samples. There is thus a large proportion of variation that is not explained by the ordination plot.

The sample ordination plot shown with *S. romanzoffiana* presence/absence data superimposed (Fig. 3), shows for each group an ellipse within which, on average, 68% of the individuals will lie. Considerable overlap is shown which indicates little pattern of differentiation between current and former sites. The full set of samples were consequently analysed as potentially suitable.

MICRO-SCALE SITE TYPES

A total of 81 micro-scale samples were taken, all of which contained at least one individual of *S. romanzoffiana*. A total of 68 species were recorded and the mean per sample was 9 (standard error 0.29). Sample ordination by DCA showed that species composition reflects that of the larger scale though inevitably fewer species are present. The proportion of samples within which the 13 most constant species were present is shown in Table 3. *Carex panicea* was the most associated

Species	% constancy
[Spiranthes romanzoffiana	
Carex panicea	84
Molinia caerulea	63
Carex nigra	44
Hydrocotyle vulgaris	43
Anagallis tenella	38
Nardus stricta	35
Eriophorum angustifolium	27
Ranunculus flammula	27
Carex echinata	26
Trifolium repens	23
Holcus lanatus	21
Carex hostiana	20
Juncus articulatus	20

TABLE 3. THE 13 MOST ASSOCIATED SPECIES WITH SPIRANTHES ROMANZOFFIANA
AT THE MICRO-SCALE, AS MEASURED BY THE PERCENTAGE OF THE 10 CM ²
SAMPLES WITHIN WHICH THEY WERE PRESENT

species at the micro-scale occurring in 84% of the samples, *Molinia caerulea* occurred in only 63% of the samples. No other species was present in more than 50% of samples. *Juncus articulatus*, a species occurring with *S. romanzoffiana* in 76% of the meso-scale samples, is present in only 20% of the samples at the micro-scale.

DISCUSSION

SAMPLING CRITIQUE

The accessibility of all the sites relocated opens to question the extent to which the orchid occurs in relatively inaccessible areas. Known sites tend to occur close to roads - perhaps a sampling artifact (as it is assumed that not all individuals in the population will have been recorded, perhaps the unrecorded individuals grow in less accessible areas), indeed "road map recording" is a well known phenomenon. Alternatively, the distribution may reflect true habitat preference for the marginal land between dune and moor, generally known in the Western Isles as the "blackland" (Hambrey 1986). The transitional zone between lime-rich and acid soils is not only important for many species of plant but also tends to provide the most suitable terrain for roads.

Sampling was biased towards flowering spikes; vegetative individuals were normally only found when searched for thoroughly in a small site where an individual was known to occur, or in short open turf. Bias was additionally encountered by the relative ease of spotting plants (both vegetative and flowering) in short vegetation. Sites within taller vegetation may thus be underrepresented. It is difficult to determine whether an individual is truly absent from a former site or whether it has just been missed. The difficulty in distinguishing absences which are a result of poor sampling from those which are genuine is a serious problem in the study of rarity in general (McArdle & Gaston 1993: Gaston 1994) and accentuated here by the potential for *S. romanzoffiana* to lie dormant underground (Gulliver *et al.* 2000). Finally, there is sample bias towards those locations that have a longer history of recorded individuals; at the two new sites, absences cannot be recorded for the obvious reason that there is no comparative data from previous years.

THE HABITATS OF SPIRANTHES ROMANZOFFIANA

Horsman (1994) described *Spiranthes romanzoffiana* in Scotland as having a distinct habitat of *Molinia caerulea* carpet on old lazy beds grazed by cattle. *M. caerulea* is also listed as the closest associate in 17 Scottish sites surveyed in 1995 (Scottish Natural Heritage 1995). The present



FIGURE 3. Ordination plot for all meso-scale samples for the first two axes of Detrended Correspondence Analysis (DCA), with presence or absence of *Spiranthes romanzoffiana* in each sample superimposed. 68% confidence ellipses are shown.

author, in agreement with Gulliver's study on Colonsay (1996), found only one site on an old lazy bed. Further, despite it being *in general* abundant, and the second most associated species with the orchid at the micro-scale, it was found that in a number of samples, typically those of Site Type A1 (the habitat in which *S. romanzoffiana* was most frequent (Table 2)), *M. caerulea* was not abundant or even present. All the NVC habitats previously described for the orchid include *M. caerulea* as a typical species at intermediate to high frequency and abundance. However, to compare the results directly to equivalent NVC categories would be inappropriate without considering the effects of scale and pattern within the vegetation. NVC demands larger samples ($2 \times 2m$ or over) and treats minute mosaics as a single vegetation type (Rodwell 1991). The resulting NVC classification is therefore at a coarser grain than that presented here, which describes the floristics immediately surrounding the orchid. It would be similarly misleading to convert the present data into NVC classes.

All site types have an abundance and constancy of the generally low-growing *Carex panicea* and an abundance and frequency of *Hydrocotyle vulgaris*, *Ranunculus flammula* and/or *Anagallis tenella*. The species are characteristic of unshaded, soligenous mire on peaty, mildly acidic soils where growth of potential dominants is suppressed by low fertility and grazing pressure (Grime, Hodgson & Hunt 1990). While the soil characteristics were not analysed, grazing was evident in all sites. In these aspects, the habitats are similar.

However, TWINSPAN and ordination by DCA indicate differential abundances of the dominants and distributions of more minor species between the four species groups. The habitats are distinguished by these lesser species which have quite different ecological preferences and may reflect differences in water and nutrient levels.

Site-type A1 contains a species component tolerant of a degree of waterlogging and typical of neutral/mildly acid conditions (Grime, Hodgson & Hunt 1990): *Caltha palustris, Potentilla palustris* and *Equisetum fluviatile* define the habitat and are largely restricted to it. Other wetland species present in these sites and less abundant or absent in others include *Mentha aquatica, Myosotis laxa, Filipendula ulmaria, Senecio aquaticus* and *Iris pseudacorus. Carex nigra*, present and abundant in all samples within this site type, has a wide habitat tolerance but is usually found in mires with some degree of water movement or mineral enrichment (Jermy, Chater & David 1982). *Hydrocotyle vulgaris* is constant, and is a wetland species suggested to have an inability to exploit sites which are waterlogged all year (Grime, Hodgson & Hunt 1990), while *Ranunculus flammula*, also a constant, is adapted to both submergence and desiccation (Cook & Johnson

1968). The evidence suggests that A1 is composed of sites that are periodically flooded. Indeed, samples of this type are primarily found around a periodically flooded pasture and a flat, poorly drained area beside a lochán.

A1 grades into site-type A2, a drier, slightly more acidic habitat, as indicated by the significant contribution to cover of some graminoids less tolerant of inundation such as *Nardus stricta*, *Molinia caerulea* and *Holcus lanatus*, but one which still contains an element of species of A1 in the wetter samples, such as *Galium palustre*, *Senecio aquaticus* and *Filipendula ulmaria*. *Nardus stricta*, the TWINSPAN indicator species which distinguishes the habitat from A1, is a grass that is characteristic of free-draining, acid soils (Grime, Hodgson & Hunt 1990). Species found almost exclusively in this habitat, such as *Cynosurus cristatus*, a species susceptible to both drought and waterlogging (Grime, Hodgson & Hunt 1990) and *Achillea ptarmica*, again suggest a habitat that is moist but not waterlogged. Site type A2 thus appears to be of a wet, slightly acid graminoid and herb-rich turf.

Site type A2 (and to a lesser extent A1) grades into site type B1. Species that are common to both habitats A2 and B1 but not the others include frequent species such as Succisa pratensis, Potentilla erecta, Carex echinata as well as less abundant species such as Plantago maritima, P. lanceolata, Carex dioica and Euphrasia scottica. B1, however, contains elements typical of wet acid heath (Grime, Hodgson & Hunt 1990; Rodwell 1991; Stace 1997), primarily shown by the presence of the indicator species at division one, *Erica tetralix*, but also the other woody shrubs Calluna vulgaris and, occasionally, Salix repens and Myrica gale. The low cover and presence of these species in the samples indicates a habitat where their dominance is restricted to some extent. Further, the abundance of these subshrubs is sufficiently low to allow a relatively high cover and constancy of the creeping species Anagallis tenella, and the low-growing Drosera spp., typical of unshaded and wet, nitrogen-poor sites of heaths and bogs (Stace 1997). The wet, acidic conditions of the site type are further suggested by the presence of Sphagnum auriculatum and, more frequently, S. recurvum. Eleocharis quinqueflora, characteristic of damp, peaty places and wet flushes in the west of Scotland (Phillips 1994), also appears in this habitat. It seems therefore that these habitats may comprise flush vegetation within more enclosed communities where competition from low-growing shrubs would otherwise suppress the orchid.

The constancy of *Erica tetralix* and presence of species such as *Myrica gale*, *Pinguicula vulgaris*, *Selaginella selaginoides*, *Drosera* spp., and *Narthecium ossifragum* render site type B2 similar to B1; the habitat still appears to be a flush in wet, nutrient-poor heath. However, B2 is distinguished from B1 by the presence of the tuft-forming *Schoenus nigricans*, occurring in all samples but one, and also the bryophyte *Scorpidium scorpioides*. The combined presence of these species suggests a habitat of wet flushes where the water content is fairly base-rich (see Phillips 1994; Sparling 1968; Watson 1981). Such base and cation enrichment may result from flushed shell-sand or directly from the bedrock (Rodwell 1991).

Carex panicea is the species most associated with *S. romanzoffiana* at both the large and small scale. *C. panicea* is characteristically a wetland species, relatively low-growing, with a pH range from 4-7.5 (Grime, Hodgson & Hunt 1991); in vitro seed germination experiments have revealed that *S. romanzoffiana* prefers a soil pH from 4.7-5 (Arditti 1992). *C. panicea* is widespread throughout the British Isles, occurring in all British vice-counties, and has a capacity to exploit such diverse habitats as soligenous mire and limestone grassland (Grime, Hodgson & Hunt 1991) as well as dwarf-shrub heaths (Jermy, Chater & David 1982). The occurrence of *C. panicea* in a wide range of vegetation types outside those described here make it an unsuitable indicator species for potential *S. romanzoffiana* habitat. Associated species are therefore not necessarily good indicator species. However, the results suggest that, on Coll at least, habitats without *C. panicea* are unlikely to support *S. romanzoffiana*.

The low association of *Juncus articulatus* with *S. romanzoffiana* at the micro-scale, despite the presence of the rush in 76% of the samples at the meso-scale, may reflect an ecological preference of the orchid. Grime, Hodgson & Hunt (1990) claim that *J. articulatus* is morphologically variable (ranging in height from 20 mm to 600 mm), often depending on the level of grazing. It is possible that *S. romanzoffiana* cannot grow in the shade that the tall-growing rush provides, but can survive when *J. articulatus* is relatively short. Alternatively, the tufted nature of the rush may make survival and growth of the orchid amongst its stems difficult.

CONCLUSIONS

Overall vegetation description alone cannot provide a comprehensive summary of all habitat variables. The structure of vegetation may be one of the most important conditions determining habitat suitability and may be altered in a relatively short time by grazing. A period of inertia before species composition responds would then render floristic measurements inadequate. This may explain the apparent similarity in the current study of former and present habitats of *S. romanzoffiana*. Vegetation description also fails to account for environmental variables that affect only one species, in particular the requirement for orchid mycorrhizal infection before germination (Wells 1981). It would therefore be interesting to examine the presence of the specific symbiotic fungus in the soil in suitable and potentially suitable habitats for *S. romanzoffiana*.

There are other reasons why an individual may appear absent from a potentially suitable site. Dormant individuals will be recorded as absent unless destructive methods are used (hardly an option for a scheduled species!). The related orchid *S. spiralis* can lie dormant for at least a year before flowering (Wells 1967) and *S. romanzoffiana* has been documented to subsist for five years underground before producing above-ground growth (Gulliver *et al.* 2000). The role of stochastic events is also important; the processes of population extinction and colonisation may cause suitable sites to become unoccupied, at least temporarily. For this reason, all habitats in which *S. romanzoffiana* was known to occur, however infrequently, were included in the range of vegetation types designated suitable.

These results provide a more accurate depiction of the immediate habitat of *S. romanzoffiana* than do the NVC descriptions (Rodwell 1991). They demonstrate the orchid's ecological affinity to *C. panicea* and avoidance of tussock-forming species at the micro-scale. They also show that the orchid does not apparently have an affinity to *M. caerulea*, at least not at the spatial scale examined here. However, the plant associations recognised in this study are not uncommon. Gaston (1994) recognised two broad ranges of factors causing limited ranges and/or low abundances: environmental limitations and colonisation abilities. The results here suggest that factors other than the environment may be limiting the distribution of *S. romanzoffiana*. There is evidence that the species is reproductively limited where it is found in the British Isles; Heslop-Harrison (1953) found that, while it was an active colonist of cut-away bogs around Lough Neagh, there were few years when it set seed. While flowering spikes are produced, it appears that Scottish populations may produce fertile seed rarely (Gulliver 1997; Gulliver *et al.* 2000) and may even reproduce entirely vegetatively (Horsman 1994; UK Biodiversity Group 1999). Whether or not this accounts for the limited distribution of *S. romanzoffiana* are therefore required.

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