

Natural hybrids between *Festuca* and species of *Vulpia* section *Vulpia*

M. M. AINSCOUGH, C. M. BARKER and C. A. STACE

Department of Botany, The University, Leicester, LE1 7RH

ABSTRACT

The occurrences and characteristics of the intergeneric hybrids between *Festuca rubra* L. agg. and *Vulpia bromoides* (L.) S. F. Gray and *V. myuros* (L.) C. C. Gmelin (Poaceae) are detailed. The hybrid of *V. bromoides* has been found on five occasions in three localities in England, involving both *F. rubra* and *F. nigrescens* as the other parent. The hybrid of *V. myuros* has been found on five occasions in four localities in England and Wales, and once in Holland, also involving both *F. rubra* and *F. nigrescens* as the other parent. Studies of meiosis in the hybrids show that the chromosomes of *F. rubra* can exchange genetic material with those of both *V. bromoides* and *V. myuros*, although both hybrids are very highly sterile. The significance of these facts to the evolution of *F. rubra* agg. is discussed.

INTRODUCTION

THE GENUS *FESTUCA*

Festuca contains several hundred species, which were placed in six sections by Hackel (1882). One of these sections, *Ovinae* (= *Festuca*), consists largely of the *F. rubra* and *F. ovina* aggregates, and included eleven species in Hackel's classification. Resulting from the extensive taxonomic splitting which has taken place in the last 100 years within the above two aggregates, Markgraf-Dannenberg (1980) recognized 129 species (out of a total of 170 for the genus) that are referable to section *Festuca*. 91 of these fall into *F. ovina* sensu Hackel and 21 into *F. rubra* sensu Hackel.

14 of the latter 21 form our concept of the *F. rubra* aggregate. These are species 65 to 78 in *Flora Europaea* (Markgraf-Dannenberg 1980), which correspond to Hackel's *F. rubra* subsp. *eu-rubra*, *pyrenaica*, *dumetorum* and *nevadensis*. Five of Markgraf-Dannenberg's 14 species occur in Britain: *F. rubra* (with five subspecies: *rubra*, *litoralis* (G. F. W. Meyer) Auquier, *arenaria* (Osbeck) Syme, *pruinosa* (Hackel) Piper and *juncea* (Hackel) Soó), *F. richardsonii* Hooker, *F. juncifolia* St Amans, *F. diffusa* Dumort. and *F. nigrescens* Lam. All members of the *F. rubra* aggregate are perennials with extra-vaginal non-flowering shoots (often as rhizomes), and have leaf-sheaths which are closed to the mouth (hence lacking infolded thin margins). Chromosome number reports vary from diploid to decaploid ($2n = 14, 28, 42, 56, 70$); the hexaploids are by far the commonest and octoploids are the only other frequently occurring plants. Some taxa do exist at more than one ploidy level, but a number of reports of this phenomenon are based on misidentifications. All the taxa are chasmogamous and behave as outbreeding diploids; figures above 10% self-fertility are very exceptional (Auquier 1977; Barker & Stace 1982).

Taxa of the *F. rubra* aggregate are the only members of *Festuca* which have been found to hybridize with the genus *Vulpia*.

THE GENUS *VULPIA*

Vulpia consists of about 20 species, which are currently placed in five sections (Cotton & Stace 1977; Stace 1978, 1981). Species of section *Vulpia* differ markedly from all species of *Festuca* in their annual habit, cleistogamous florets with usually only one or two stamens, and usually markedly unequal glumes. In addition they have overlapping leaf-sheaths and only intravaginal innovations, and are fully self-fertile. Each species is characterized by a single chromosome number at the diploid (e.g. *V. bromoides* (L.) S. F. Gray), tetraploid (e.g. *V. ciliata* Dumort.) or hexaploid (e.g. *V. myuros* (L.) C. C. Gmelin) levels ($2n = 14, 28, 42$).

However, species of the other four sections approach *Festuca* more closely, but to varying degrees. Species of the western Mediterranean section *Loretia* (Duval-Jouve) Boiss. are highly self-incompatible diploids having chasmogamous florets with three large anthers, and one species (*V. sicula* (C. Presl) Link) is a perennial. In other respects (e.g. the markedly unequal glumes) *V. sicula* is easily separable from *Festuca*, but without such a combination of characters it is impossible to separate the two genera. However, their taxonomic distinctness or otherwise is not a matter for discussion here.

Species of the remaining three sections of *Vulpia* are intermediate between those of sections *Vulpia* and *Loretia* in several ways. Sections *Spirachne* (Hackel) Boiss. and *Apalochloa* (Dumort.) Stace each contain one diploid self-fertile annual species, exhibiting semi-chasmogamous and chasmogamous flowering respectively. Section *Monachne* Dumort. contains four semi-chasmogamous self-fertile annual species, all but *V. fasciculata* (Forsskål) Fritsch, which is tetraploid, being diploids.

INTERGENERIC HYBRIDS (\times *FESTULPIA* MELDERIS EX STACE & COTTON)

An extensive programme of crossing carried out by C. M. Barker (Barker & Stace 1982, 1984, in press) obtained the following intergeneric combinations (female parents first): *V. sicula* (diploid) \times hexaploid *F. rubra* agg.; hexaploid *F. rubra* agg. \times *V. sicula* (diploid); *V. sicula* (diploid) \times octoploid *F. rubra* agg.; *V. fasciculata* (tetraploid) \times hexaploid *F. rubra* agg.; and *V. myuros* (hexaploid) \times hexaploid *F. rubra* agg. Hence the *Vulpia* parents included species from three different sections (all of those used), both annuals and perennials, and all three ploidy levels. The *Festuca* parents included both ploidy levels used and six of the eight segregate taxa used: *F. rubra* subsp. *rubra*, *arenaria* and *pruinosa*, *F. nigrescens*, *F. diffusa* and *F. juncifolia*. Earlier, R. Cotton had synthesized the hybrid *V. fasciculata* \times *F. rubra* subsp. *rubra* with considerable success (Stace & Cotton 1974).

In Barker's experiments two of the 20 plants obtained of hexaploid *F. rubra* agg. \times *V. sicula* (diploid) (both involving the same plant of *F. nigrescens* as female parent) were unexpectedly heptaploid, presumably resulting from unreduced female gametes. These two plants exhibited about 60% pollen stainability, though no seed-set has been detected. All the other hybrids possessed the expected intermediate chromosome numbers and were highly sterile, with very rarely as high as 1% pollen stainability.

Morphologically the artificial hybrids were more or less intermediate between their parents in appearance and, in the cases involving *Vulpia myuros* and *V. fasciculata*, they closely resembled wild hybrids.

Wild hybrids are known between the *Festuca rubra* aggregate and three species of *Vulpia*: *V. fasciculata*, *V. bromoides* and *V. myuros*.

Many details of the natural intergeneric hybrids involving *V. fasciculata* (as *V. membranacea*

TABLE 1. DIAGNOSTIC MEASUREMENTS OF FOUR \times *FESTULPIA* COMBINATIONS AND THE 1961 COLLECTION FROM LITTLEHAMPTON

The ranges given for *F. rubra* \times *V. myuros* and *F. rubra* \times *V. bromoides* are derived from the wild collections detailed in Tables 4 and 2 respectively. Figures are ranges of means per inflorescence. Glume lengths include awns; lemma lengths exclude awns and refer to only the first and second lemmas of each spikelet; awn lengths refer to the longest in each spikelet.

	<i>F. rubra</i> \times <i>V. myuros</i>	<i>F. rubra</i> \times <i>V. bromoides</i>	Littlehampton hybrid 1961	<i>F. rubra</i> \times <i>V. fasciculata</i>	<i>F. juncifolia</i> \times <i>V. fasciculata</i>
Lower glume length (mm)	1.5-3.3	2.0-3.4	3.0-3.7	2.4-4.4	5.2-8.0
Upper glume length (mm)	3.2-5.0	3.4-5.9	6.2-7.4	3.5-7.2	8.0-11.5
Glume ratio	0.48-0.7	0.5-0.75	0.45-0.58	0.55-0.69	0.6-0.69
Lemma length (mm)	4.5-6.2	4.5-7.0	7.5-8.4	6.0-9.5	9.5-10.5
Awn length (mm)	3.0-6.0	3.2-6.0	5.7-7.2	2.0-5.5	3.5-5.0
Anther length (mm)	0.6-1.5	0.8-1.7	1.6-1.7	1.5-2.0	1.5-2.0

(L.) Dumort.) were given by Stace & Cotton (1974) and Willis (1975), and further data have been provided by Barker & Stace (1984, in press), and by Stace & Ainscough (1984) on the progeny of one of these hybrids. A summary of diagnostic measurements is provided in Table 1. The number of taxa of the *F. rubra* aggregate which have produced natural hybrids with *V. fasciculata* is uncertain, but both hexaploids and octoploids are involved, producing pentaploid and hexaploid hybrids respectively. On the basis of morphological characters Stace & Cotton (1974) deduced that the British hexaploid and octoploid *Festuca* taxa were *F. rubra* and *F. juncifolia* respectively, and they named the two hybrids × *Festulpia hubbardii* Stace & Cotton and × *F. melderisii* Stace & Cotton respectively. However, it is possible that the octoploid parent of × *F. melderisii* was actually *F. rubra* subsp. *arenaria*, which exists as both hexaploids and octoploids, and in fact the precise distinction between *F. rubra* subsp. *arenaria* and *F. juncifolia* is unclear. Which hexaploid taxa of *F. rubra* agg. are involved in the parentage of × *F. hubbardii* in Britain is also uncertain, but the restricted habitat (sand-dunes) involved suggests only *F. rubra* subsp. *rubra* and *arenaria*.

Pentaploid × *Festulpia hubbardii* occurs in many places on the coasts of southern Britain, from E. Kent to S. Lancashire, while hexaploid × *F. melderisii* has been confirmed from only two localities in south-eastern England (Fig. 1).

This paper presents data on natural hybrids between the *Festuca rubra* aggregate and the other two species of *Vulpia*: *V. bromoides* and *V. myuros*. Their known occurrences in the British Isles are shown in Fig. 1.

FESTUCA RUBRA AGG. × *VULPIA BROMOIDES*

OCCURRENCE

1. Coastal sand-dunes at Littlehampton, W. Sussex, 1961, A. Melderis (**BM**) (Melderis 1965), close to plants of both parents as well as of *V. fasciculata*, × *F. hubbardii* and × *F. melderisii*. *Festuca rubra* subsp. *rubra* and *arenaria* and *F. juncifolia* occur in the immediate vicinity. We have not traced a voucher specimen of the original collection, but a garden-grown specimen (coll. 1964) of the original plant is in **BM**. We have no doubt that it is *F. rubra* × *V. fasciculata*. Its measurements fall within the range of the latter hybrid and outside those of *F. rubra* × *V. bromoides* (Table 1). Most of the upper glumes have a distinct awn and the pedicels are distinctly dilated distally (both characters of the *V. fasciculata* hybrid but not of the *V. bromoides* hybrid). Searches for *F. rubra* × *V. bromoides* in the locality have not been successful.
2. Ten plants on fixed shingle at Shingle Street, E. Suffolk, 1969, P.J.O. Trist (**K**, det. C. E. Hubbard). The only other species of *Vulpia* in the area is *V. myuros*, whose hybrids with *F. rubra* are of different appearance. The hybrid has been sought there in several subsequent years by Trist, but was refound only in 1973 (two plants) and 1976 (one plant). A specimen collected on the last occasion is in cultivation at Leicester. All material of *F. rubra* near the hybrid at Shingle Street is subsp. *rubra*, though subsp. *litoralis* occurs within a few hundred metres.
3. On ballast by railway sidings, East Ella, Hull, S.E. Yorkshire, 1980, J.E.L. Spencer (**LTR**). It was growing with *Vulpia bromoides*, *V. myuros* and *Festuca nigrescens*, and was determined by C. A. Stace as probably *F. nigrescens* × *V. bromoides*. It has been searched for in subsequent years by Spencer, but without success.
4. One plant on cinders of a disused railway line at Leire, Leicestershire, 1983, C.A. Stace (**LTR**). This is being cultivated at Leicester. *Festuca rubra* subsp. *rubra* and *F. nigrescens* occur in close proximity, but *V. bromoides* is the only species of *Vulpia* in the area. The *Festuca* parent is probably *F. rubra* subsp. *rubra* as the hybrid has a limited rhizome development.

CHARACTERISTICS

Festuca rubra × *Vulpia bromoides* closely resembles × *F. hubbardii* in most characters. Vegetatively the characters of the *Festuca* parent are dominant: the plants are densely caespitose perennials with many non-flowering shoots, some of which are extravaginal in origin and in some plants form short rhizomes. The leaf-sheaths are closed almost to the mouth (not overlapping as in *Vulpia*), and are pubescent in those hybrids involving a pubescent *Festuca* parent (always glabrous

FESTUCA x VULPIA

- *F. rubra* x *V. fasciculata*
- *F. rubra* x *V. fasciculata*
and
F. juncifolia x *V. fasciculata*
- B *F. rubra* agg. x *V. bromoides*
- M *F. rubra* agg. x *V. myuros*

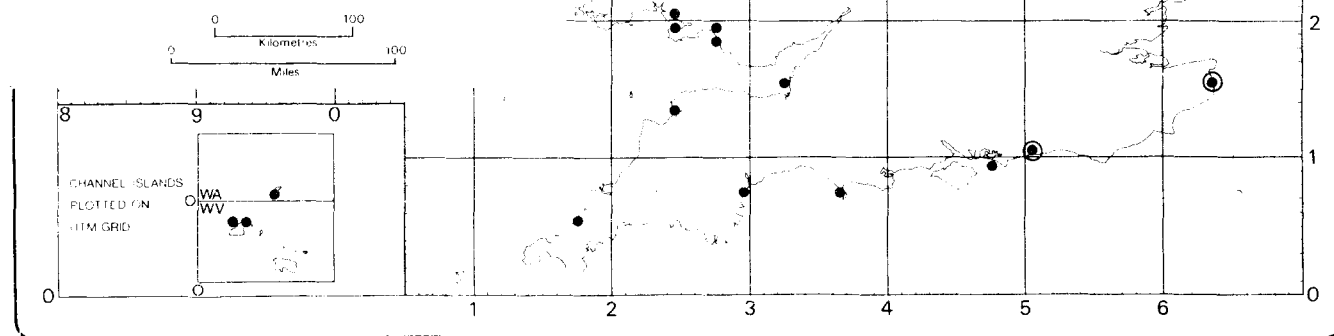


FIGURE 1. Distribution of four taxa of \times *Festulia* in the British Isles. For *F. juncifolia* \times *V. fasciculata*, only the two cytologically confirmed hybrids are shown. Records of pubescent hybrids in S. Devon (20/97) and Glam. (21/78) might refer to this hybrid or to *F. rubra* \times *V. fasciculata*, but in both places undoubted *F. rubra* \times *V. fasciculata* also occurs.

in *V. bromoides*). The leaf-blades are intermediate in anatomy and morphology, being more slender and with less sclerenchyma than in *F. rubra*. The floral characters are intermediate. The inflorescence is more one-sided than in *F. rubra*, and the awns are longer. The glume ratio is the same as in *V. bromoides*, i.e. lower than that in *F. rubra*. There are three stamens, as in *F. rubra*, but they are indehiscent and shorter than those of *F. rubra*, though longer than the usually single stamen of *V. bromoides*.

It is best distinguished from × *F. hubbardii* by its thin, not distally thickened, pedicels; by the spikelets usually having only one ovary-less floret at the apex, the lemmas of the other florets varying little in length; and by the awn-less, rather than distinctly awned, upper glumes. In × *F. hubbardii* there are usually two or three apical ovary-less florets, and the lemmas diminish markedly in length acropetally. In fact there is no *Vulpia fasciculata* (the parent of × *F. hubbardii*) in localities 2–4 above.

The characters of *F. rubra* × *V. bromoides* vary not only according to the characteristics of the *Festuca* parent, but also with environmental conditions. Living plants grown at Leicester have shown significant differences in some characteristics from year to year. An indication of the range of variation shown by this hybrid is given in Table 2.

Chromosome counts have been made of the E. Suffolk (1976) and Leics. (1983) plants; in both cases the surprising count of $2n = 42$ was obtained, whereas $2n = 28$ would have been expected. Stace & Ainscough (1984) have attempted to explain this anomaly on the basis that the two plants in question are actually backcrosses to *Festuca rubra*, not F_1 hybrids. Pollen stainability is less than 1% (0.1–0.7%) in all cases, and no seed-set has been observed.

Attempts to synthesize hybrids between *V. bromoides* and a range of taxa of *F. rubra* agg. have been unsuccessful.

CHROMOSOME BEHAVIOUR

Meiotic analyses were undertaken on the plants from E. Suffolk (collected 1976) and Leics. (Table 3). The former plant gave significantly different results in 1978 and 1984, the later ones agreeing very closely with results obtained from the Leics. plant in 1984. The 1984 results produced means of 16.0 and 14.38 bivalents per cell, of which 11.2 and 11.75 respectively were ring bivalents, amounting to a rather high degree of pairing. Multivalents were very rare or absent. The 1978 results showed a much lower pairing affinity, with a mean of only 7.8 bivalents and many more univalents, although there were more trivalents, quadrivalents and quinquevalents. More technical problems were encountered in 1978, and the results are less accurate than those of 1984, but the differences are so marked as to be undoubtedly real (note, for example, mean numbers of univalents of 20.3 and 9.7 respectively). Chiasma frequency (26–28 per cell in 1984) is high for a $2n = 42$ hybrid. Despite this, pollen grain stainability is very low and no seed-set has been observed.

TABLE 2. DIAGNOSTIC MEASUREMENTS OF FIVE WILD COLLECTIONS OF *FESTUCA RUBRA* AGG. × *VULPIA BROMOIDES*

Figures are ranges of means per inflorescence. Glume lengths include awns; lemma lengths exclude awns and refer to only the first and second lemmas of each spikelet; awn lengths refer to the longest in each spikelet. Dates indicate year of collection.

	Shingle Street				
	1969	1973	1976	Hull	Leire
Lower glume length (mm)	2.0–3.1	2.1–3.0	2.5–3.4	2.1–3.1	2.0–2.5
Upper glume length (mm)	3.9–5.8	4.0–4.6	4.5–5.9	3.4–5.2	3.5–4.4
Glume ratio	0.5–0.62	0.5–0.65	0.52–0.62	0.51–0.75	0.53–0.71
Lemma length (mm)	5.7–6.5	4.5–6.2	5.9–7.0	5.1–6.4	5.0–5.7
Awn length (mm)	5.0–6.0	3.6–5.4	3.2–5.0	3.4–5.1	3.7–5.3
Anther length (mm)	1.1–1.6	1.5–1.7	1.1–1.3	0.8–1.2	0.9–1.5

TABLE 3. MEIOTIC ANALYSES OF FIVE \times *FESTULPIA* HYBRIDS

Figures represent ranges and (in brackets) means. The term 'chromosome pairs' represents the number of bivalents plus a minimum number to take account of the multivalents. Dates represent year of observation.

Chromosome configurations	<i>F. rubra</i> \times <i>V. bromoides</i>			<i>F. rubra</i> \times <i>V. myuros</i>	<i>V. myuros</i> \times <i>V. diffusa</i>
	Shingle St 1978	Shingle St 1984	Leire 1984		
V	0-1 (0.1)	0	0	0	0
IV	0-4 (0.4)	0	0	0-2 (0.3)	0-1 (0.2)
III	0-3 (1.2)	0-1 (0.1)	0	0-1 (0.1)	0-1 (0.2)
II (total)	5-14(7.8)	13-19(16.0)	11-18(14.4)	9-18(13.6)	15-20(17.8)
II (ring)	—	8-18(11.2)	9-15(11.8)	4-16(9.2)	9-20(14.4)
II (chain)	—	1-8 (4.8)	1-5 (2.6)	0-9 (4.4)	0-8 (3.4)
I	12-27(20.3)	4-16(9.7)	6-20(13.3)	6-24(13.3)	2-12(5.4)
Chromosome pairs	7-14(10.0)	13-19(16.1)	11-18(14.4)	9-18(14.3)	15-20(18.2)
Chiasmata per cell	—	22-37(27.9)	20-32(26.1)	16-32(24.3)	26-40(33.2)

FESTUCA RUBRA AGG. \times *VULPIA MYUROS*

OCCURRENCE

1. On rubble by road just east of Mawddach Crescent, Arthog, Merioneth, 1957, *P.M. Benoit* (LTR, NMW); and on disused railway track 690 m south-east of this locality, 1970, *P.M. Benoit* (LTR). Searched for unsuccessfully in the area in other years. In both cases one plant appeared with *V. myuros* and *F. rubra* subsp. *rubra*, which are presumed to be the parents even though both hybrids show no rhizome development. Both are still (1984) grown in P. M. Benoit's garden in Barmouth, Merioneth.
2. On cinders in railway sidings immediately north of Stockport Station, S. Lancashire, 1974, *R. Cotton & C.A. Stace* (LTR). The only species of *Vulpia* present was *V. myuros*, and the commonest *Festuca* immediately adjacent was *F. nigrescens*; these are presumed to have been the parents.
3. On sandy shingle bank near sea at Snettisham, W. Norfolk, 1974, *R.P. Libbey* (LTR). A sample of this plant is in cultivation at Leicester. The commonest related plants in the immediate vicinity are *Festuca rubra* subsp. *litoralis* and *Vulpia myuros*, which are presumed to be the parents.
4. Between cobble-stones at old railway station, Woensdrecht, Noord Brabant, Netherlands, 1978, *E.J. Weeda* (L, LTR). This is the only confirmed example of \times *Festulpia* from outside Britain. It was determined originally as *F. rubra* agg. \times *V. bromoides* by C. A. Stace, but it is probable that *V. myuros* rather than *V. bromoides* was involved. It has not been refound. The only other relevant taxa found at the same site were *V. myuros* and *F. nigrescens*, which were the likely parents.
5. Two plants on disused railway line near Oswestry, Salop, 1983, *P.M. Benoit* (in litt.). *Festuca rubra* subsp. *rubra* and *Vulpia myuros* were the only possible parents in the area.

CHARACTERISTICS

This hybrid is extremely similar to the last in all characters, and may not be always distinguishable from it. However, all specimens seen lack any rhizome development. Unfortunately, whereas glume ratio is a very important character for separating *V. myuros* and *V. bromoides* (as well as *V. fasciculata*), the dominance of the subequal glumes of *F. rubra* produces a similar glume ratio in hybrids between *F. rubra* and all three species of *Vulpia*. The best character for distinguishing the *V. bromoides* and *V. myuros* hybrids is the inflorescence shape, which is very long and narrow in the latter, but shorter and often more spreading in the former. The lemmas are usually narrower and more gradually tapering in the *V. myuros* hybrid. Some characteristics of this hybrid are given in Table 4. Again, variation is probably an effect both of the different *Festuca* parent involved and

TABLE 4. DIAGNOSTIC MEASUREMENTS OF FIVE WILD COLLECTIONS AND ONE ARTIFICIAL HYBRID OF *FESTUCA RUBRA* AGG. × *VULPIA MYUROS*

Rubric as in Table 2.

	Arthog				Holland	<i>V. myuros</i> × <i>F. diffusa</i>
	1957	1970	Stockport	Snettisham		
Lower glume length (mm)	2.4-3.2	2.0-2.4	1.5-3.0	2.0-3.3	2.3-3.0	1.3-2.2
Upper glume length (mm)	3.7-4.7	4.0-4.6	3.2-4.5	4.0-5.0	3.9-4.4	3.2-4.3
Glume ratio	0.6-0.7	0.5-0.55	0.48-0.67	0.5-0.67	0.57-0.68	0.45-0.6
Lemma length (mm)	5.3-5.6	4.6-5.5	4.5-5.0	5.5-6.2	5.5-6.1	4.7-6.4
Awn length (mm)	3.6-4.3	3.2-4.2	3.5-4.5	3.0-6.0	3.6-4.4	4.0-4.9
Anther length (mm)	0.8-1.0	1.0-1.1	0.6-0.9	1.0-1.3	1.3-1.5	1.0-1.5

of environmental conditions. For example, the longer lemma length of the W. Norfolk hybrid compared with the S. Lancs. hybrid indicates that in the former case *F. rubra* subsp. *litoralis* (lemmas mostly 6.0-7.5 mm) was the likely parent whereas in the latter case *F. nigrescens* (lemmas mostly 5.0-6.5 mm) was involved. On the other hand the Dutch hybrid, probably involving *F. nigrescens*, has lemmas as long as those of the W. Norfolk hybrid. Of the two plants collected at Merioneth (1957 and 1970) one has glabrous and one pubescent leaf-sheaths.

The chromosome number of the W. Norfolk hybrid is, as expected, $2n = 42$. The pollen stainability is c. 0.4% and no seed-set has been observed.

Two plants of *Vulpia myuros* × *Festuca diffusa* were synthesized by Barker (1980), and measurements of the diagnostic features were presented by Barker & Stace (1984) (see also Table 4). In all cases the characteristics were very close to those of the wild hybrids (despite the very different *Festuca* parents involved). Pollen was 0% stainable.

CHROMOSOME BEHAVIOUR

Meiotic analysis of the W. Norfolk hybrid (Table 3) showed a slightly lower degree of pairing than the wild hybrids involving *Vulpia bromoides* showed in 1984. A mean of 13.6 bivalents, of which 9.2 were ring bivalents, and a mean chiasma frequency of 24.3 per cell, were obtained. In view of the markedly different results obtained in 1978 and 1984 for the E. Suffolk plant of *F. rubra* × *V. bromoides*, the differences between the *V. bromoides* and *V. myuros* hybrids are probably not significant.

For comparison the results of meiotic analysis of the artificial hybrid *Vulpia myuros* (female) × *Festuca diffusa* are given in Table 3. Pairing affinity in this hybrid is slightly higher than in any of the wild hybrids mentioned above, emphasizing the point that there are probably no significant differences between any of the data.

DISCUSSION

Wild hybrids occur in Britain and the Channel Isles in the following combinations: *Festuca rubra* × *Vulpia fasciculata*, *F. juncifolia* × *V. fasciculata*, *F. rubra* × *V. bromoides*, *F. nigrescens* × *V. bromoides*, *F. rubra* × *V. myuros* and *F. nigrescens* × *V. myuros*. Probably three subspecies (*rubra*, *arenaria* and *litoralis*) of *F. rubra* are involved. The three species of *Vulpia* represent three ploidy levels (diploid, tetraploid, hexaploid) and two sections of the genus (*Vulpia*, *Monachne*). Two ploidy levels of *Festuca* (hexaploid, octoploid) are involved. Because of the cleistogamous or semi-cleistogamous nature of the *Vulpia* parents, and the small amount of pollen that they produce, all the wild hybrids are probably formed by crosses of male *Festuca* with female *Vulpia*.

Artificial hybrids (Barker & Stace 1982) include a number of the above as well as crosses involving a third (self-incompatible, chasmogamous) section of *Vulpia* (*Loretia*). In the latter case reciprocal hybrids were raised, but in the crosses between *Festuca* and *Vulpia* sections *Vulpia* and *Monachne* hybrids were raised only when the *Vulpia* parent was used as female. Whether this is

due to the small amount of *Vulpia* pollen available for crosses, or to unilateral interspecific incompatibility, is unknown.

Elsewhere the only recorded occurrences of \times *Festulpia* are *F. nigrescens* \times *V. myuros* in Holland, detailed above, and the report by Patzke (1970) of *F. rubra* subvar. *microphylla* \times *V. membranacea* found in 1966 by Peter at Suances, Santander, Spain. According to the nomenclature of *Flora Europaea* the latter hybrid is presumably *F. nigrescens* subsp. *microphylla* (St Yves) Markgr.-Dannenb. \times *V. fasciculata*. We have not seen the specimen.

The relative rarity of *Festuca* \times *Vulpia* crosses in the wild is probably due largely to the cleistogamous or semi-cleistogamous and self-compatible floral biology of the *Vulpia* species in the British Isles, so that stigmas are rarely available to foreign pollen, together with the very small amounts of pollen (often none of it air-borne) produced by these species. The lack of records of hybrids between *F. rubra* and chasmogamous, self-incompatible species of *Vulpia* section *Loretia* in the Mediterranean region is less easily explained. However, both *F. rubra* and suitably experienced field-botanists are much less common there than in north-western Europe.

Festuca rubra \times *Vulpia fasciculata* occurs in most sand-dune areas of south-western Britain and the Channel Isles where *V. fasciculata* is common. We have never failed to find it in such places, although the same is not true of similar localities in East Anglia or Jersey. Hybrids involving *V. bromoides* and *V. myuros* are much less certain in occurrence. The much greater regularity of complete cleistogamy (compared with the normal semi-cleistogamy of *V. fasciculata*) in these two species might explain this. The S. Lancs. hybrid of *F. nigrescens* \times *V. myuros* was, in fact, found in a population of *V. myuros* exhibiting a high (and very unusual) degree of chasmogamy, with dehiscing anthers and receptive stigmas partially exposed.

In cultivation the hybrids appear not to be very long-lived (a few years only), and not all of them flower every year. These facts might contribute to the rarity of records in the wild. The E. Suffolk locality of *F. rubra* \times *V. bromoides* has yielded hybrids on three occasions (1969, 1973, 1976), but it is as likely that, in years when unsuccessful searches were made, the hybrids occurred there in the vegetative state as the locality is especially conducive to hybridization. Moreover the number of hybrids found dropped from ten to one over the eight-year period, and the hybrid found in 1976 (having $2n = 42$) was not an F_1 plant (Stace & Ainscough 1984).

Unfortunately it might not be possible to distinguish the hybrids involving *V. bromoides* from those involving *V. myuros* on all occasions. The best character is the inflorescence shape. Since the only two plants of *F. rubra* \times *V. bromoides* with a known chromosome number are hexaploids, it remains a possibility that they are *F. rubra* \times *V. myuros* hybrids. However, in both cases the inflorescence is very short, quite unlike the elongated panicles of known natural and artificial hybrids of *F. rubra* \times *V. myuros*, and in one case (Leics.) there is no *V. myuros* known in the vicinity.

Similarly, it is very difficult to distinguish hybrids involving *F. rubra* from those involving *F. nigrescens* (the same is also true of those involving *F. juncifolia*). If the hybrid is rhizomatous, obviously *F. rubra* (not *F. nigrescens*) is involved, but the known hybrids of *F. rubra* \times *V. myuros* from Merioneth and W. Norfolk are not rhizomatous.

Despite the relative rarity of hybridization, and the high degree of sterility of the hybrids, there remains a considerable degree of genomic homology between species of *Vulpia* and the *Festuca rubra* aggregate. In the hexaploid hybrids involving *V. bromoides* and *V. myuros* (Table 3) more than 14 bivalents were rather regularly observed, and there were often more than 14 ring-bivalents. Therefore both homogenetic (F-F and V-V) and heterogenetic (F-V) pairing, often with chiasmata in both chromosome arms, occurs. Similarly, in the hexaploid derivative of *F. rubra* \times *V. fasciculata* reported by Stace & Ainscough (1984), both homogenetic and heterogenetic pairing takes place. The same is also true of artificial hybrids between the diploid *V. sicula* and hexaploid *F. rubra* agg. (Barker & Stace in press). Hence there is genomic homology between *F. rubra* agg. and species of all three sections (*Loretia*, *Monachne*, *Vulpia*) of *Vulpia* investigated.

We interpret the main evolutionary trend in *Vulpia* as being away from a perennial, chasmogamous outbreeder (section *Loretia*) to an annual, cleistogamous inbreeder (section *Vulpia*), the former being derived from a *Festuca*-like ancestor similar in many respects to *F. rubra* agg. Whereas *F. rubra* agg. has developed into a declining polyploid complex, with very few (if any) diploid representatives still extant, *Vulpia* has retained a substantial number of diploids as well as developing tetraploidy and hexaploidy. The apparently 'closed' genetic system of *F. rubra*

agg. is, however, alleviated by the retention of its ability not only to hybridize with *Vulpia* but also for its chromosomes to exchange genetic material with those of *Vulpia*. Stace & Ainscough (1984) have demonstrated that this level of genomic homology can result in backcrossing and the introgression of *Vulpia* genes into *F. rubra*, which thus retains a partially 'open' genetic system normally out of the reach of a declining polyploid complex. This is a good illustration of the evolutionary importance of relatively rare hybridization events between superficially dissimilar taxa, even where the primary hybrids are highly sterile.

ACKNOWLEDGMENTS

We are grateful to P. M. Benoit, R. P. Libbey, G. Renaud-Nooy v.d. Kolff, J. E. L. Spencer and P. J. O. Trist for kindly sending us material and for supplying valuable information on sites, to Professor A. J. Willis and the Biological Records Centre for help with the records of *V. fasciculata* hybrids, and to D. Halsall for preparing Fig. 1.

REFERENCES

- AUQUIER, P. (1977). Biologie de la reproduction dans le genre *Festuca* L. (Poaceae), 1. Systèmes de pollinisation. *Bull. Soc. r. bot. Belg.*, **110**: 129–150.
- BARKER, C. M. (1980). Investigation into the relationships and ancestry of *Vulpia* and *Festuca*. Ph.D. thesis, University of Leicester.
- BARKER, C. M. & STACE, C. A. (1982). Hybridization in the genera *Vulpia* and *Festuca*: the production of artificial F₁ plants. *Nord. J. Bot.*, **2**: 435–444.
- BARKER, C. M. & STACE, C. A. (1984). Hybridization in the genera *Vulpia* and *Festuca* (Poaceae): the characteristics of artificial hybrids. *Nord. J. Bot.*, **4**: 289–302.
- BARKER, C. M. & STACE, C. A. (in press). Hybridization in the genera *Vulpia* and *Festuca*: meiotic behaviour of artificial hybrids. *Nord. J. Bot.*
- COTTON, R. & STACE, C. A. (1977). Morphological and anatomical variation of *Vulpia* (Gramineae). *Bot. Notiser*, **130**: 173–187.
- HACKEL, E. (1882). *Monographia Festucarum europaeorum*. Kassel.
- MARKGRAF-DANNENBERG, I. (1980). *Festuca*, in TUTIN, T. G. et al., eds. *Flora Europaea*, **5**: 125–154. Cambridge.
- MELDERIS, A. (1965). *Festuca rubra* × *Vulpia bromoides*, a new hybrid in Britain. *Proc. bot. Soc. Br. Isl.*, **6**: 172–173.
- PATZKE, E. (1970). Untersuchungen über Wurzel fluoreszenz von Schwingelarten zur Gliederung der Verwandtschaftsgruppe *Festuca* Linné. *Senkenberg. biol.*, **51**: 255–276.
- STACE, C. A. (1978). Changing concepts in the genus *Nardurus* Reichenb. (Gramineae). *Bot. J. Linn. Soc.*, **76**: 344–350.
- STACE, C. A. (1981). Generic and infrageneric nomenclature of annual Poaceae: Poaeae related to *Vulpia* and *Desmazeria*. *Nord. J. Bot.*, **1**: 17–26.
- STACE, C. A. & AINSCOUGH, M. M. (1984). Continuing addition to the gene-pool of the *Festuca rubra* aggregate (Poaceae: Poaeae). *Pl. Syst. Evol.*, **147**: 227–236.
- STACE, C. A. & COTTON, R. (1974). Hybrids between *Festuca rubra* L. sensu lato and *Vulpia membranacea* (L.) Dumort. *Watsonia*, **10**: 119–138.
- WILLIS, A. J. (1975). *Festuca* L. × *Vulpia* C. C. Gmel. = × *Festulpia* Melderis ex Stace & Cotton, in STACE, C. A., ed. *Hybridization and the flora of the British Isles*, pp. 552–554. London.

(Accepted March 1985)