

Hybrids between *Festuca rubra* L. *sensu lato* and *Vulpia membranacea* (L.) Dum.

C. A. STACE and R. COTTON

Department of Botany, University of Manchester

ABSTRACT

It is shown that at least two sand-dune cytodesmes (hexaploid and octoploid) of *Festuca rubra* L. *sensu lato* occur in Britain, and that both of them hybridise with *Vulpia membranacea* (L.) Dum. (tetraploid). The morphological characteristics of the two cytodesmes of *F. rubra sensu lato* in Britain are examined, and evidence is produced supporting the idea that the octoploids are morphologically distinct and identifiable with *F. juncifolia* St Amans (*F. arenaria* Osbeck, *sec.* Kjellqvist). The two hybrids are described under the new genus-hybrid \times **Festulpia** Melderis ex Stace & Cotton as \times **F. hubbardii** Stace & Cotton (*F. rubra* L. *sensu stricto* \times *V. membranacea* (L.) Dum.; pentaploid) and \times **F. melderisii** Stace & Cotton (*F. juncifolia* St Amans \times *V. membranacea* (L.) Dum.; hexaploid).

INTRODUCTION

FESTUCA RUBRA L. *SENSU LATO*

Hackel (1882), in his authoritative monograph on European fescues, placed the whole of the *F. rubra* aggregate in one species, *F. rubra* L., which he divided into 6 subspecies. 4 of these need not concern us further; the other two were subsp. *eu-rubra* and subsp. *dumetorum* (L.) Hackel. Subsp. *dumetorum* was not further subdivided; synonyms placed under it included *F. juncifolia* St Amans, *F. sabulicola* Duf. and *F. arenaria* Gren. & Godr., *non* Osbeck. Subsp. *eu-rubra* was divided into 7 varieties, including var. *genuina* and var. *fallax* (Thuill.) Hackel, the former of which was further separated into 7 subvarieties. One of these was subvar. *arenaria* (Osbeck) Hackel, whose synonyms included *F. dumetorum* Rafn, *non* L., *F. arenaria* Osbeck, *non* Gren. & Godr., and ? *F. oraria* Dum. Hackel separated subsp. *eu-rubra* (*F. rubra*) from subsp. *dumetorum* (*F. juncifolia*) mainly by the leaf tips, which are obtuse in the former but sharply acute in the latter, and in the mode of branching, which is mixed intravaginal and extravaginal in the former but wholly extravaginal in the latter. In addition the abaxial sclerenchyma of the lower leaf-blades, whose anatomy he explored in some detail, forms a continuous band in subsp. *dumetorum*, whereas it forms a series of discrete bundles (each underlying a vascular bundle) in 6 of the 7 varieties of subsp. *eu-rubra*; in the seventh variety (var. *oelandica* Hackel), it is again in a continuous band. Hackel did not consistently give measurements, but it is clear from his descriptions that several variants of subsp. *eu-rubra* have longer lemmas and spikelets than subsp. *dumetorum*. A number of other minor distinguishing features of the leaves and spikelets were also given, but Hackel did admit the existence of some intermediate plants.

Howarth (1924) applied Hackel's classification to the British fescues and made a number of relatively minor changes to it. In particular he raised the rank of

most of Hackel's taxa. Thus subsp. *eu-rubra* became *F. rubra* and subsp. *dumetorum* became *F. juncifolia* (the Linnaean *F. dumetorum* being considered to belong to *F. rubra*); subsp. *eu-rubra* var. *genuina* and var. *fallax* became *F. rubra* subsp. *genuina* (= subsp. *duriuscula* Syme = subsp. *rubra*) and *F. rubra* subsp. *fallax* (Thuill.) Howarth (= subsp. *commutata* Gaudin); and most of the sub-varieties of var. *genuina* became varieties of subsp. *genuina*. Like Hackel, Howarth was uncertain of the application of the name *F. oraria* and placed it as a 'large-glumed form' of *F. rubra* var. *arenaria* (Osbeck) Fr. It is clear from remarks made by Howarth on various herbarium sheets that he came to believe that *F. oraria* was intermediate between *F. rubra* var. *arenaria* and *F. juncifolia*, and he variously referred to it as an 'intermediate' or as a 'hybrid?'. All of the characters Howarth (1924) provided to distinguish *F. rubra* from *F. juncifolia* were culled from Hackel (1882), and the two authors also agreed that the sizes of the lemmas and spikelets of *F. juncifolia* fall well within the range shown by *F. rubra*; indeed they are somewhat smaller than those they gave for var. *arenaria*. It is only in some of the more recent British works (e.g. Hubbard 1954, 1968) that the lemma-length of the two species is said to differ markedly; according to Hubbard the lemma of *F. rubra* subsp. *rubra* (i.e. including var. *arenaria*) is 'mostly 5–6 mm long' and that of *F. juncifolia* 7–10 mm long.

Kjellqvist (1961, 1964) made further studies on the two sand-dune taxa, *F. juncifolia* and *F. rubra* subsp. *rubra* var. *arenaria*, and came to three important conclusions. In the first place he claimed that the leaf-blade sclerenchyma is not a taxonomically reliable character; it varies greatly in amount and its distribution is very much influenced by the environment. However, he did not actually show that the sclerenchyma could be either in a continuous band or in discrete bundles in one plant simply according to environmental conditions. Secondly, he concluded that *F. arenaria* Osbeck and *F. juncifolia* are synonymous; at the specific level *arenaria* is the earlier epithet, but at the subspecific and varietal levels the reverse is true. Thirdly, *F. juncifolia* (*F. arenaria*) is consistently octoploid ($2n = 56$), while *F. rubra* is hexaploid ($2n = 42$). Thus, according to Kjellqvist, even if one admits a variant within *F. rubra* which occurs on sand-dunes and resembles the plant usually called *F. juncifolia*, it cannot be called var. *arenaria* (Osbeck) auct., and it cannot be distinguished from *F. juncifolia* on the basis of sclerenchyma characters. Kjellqvist stated that the lemmas of *F. juncifolia* (*F. arenaria*) are 6–8 mm long. The specimens of *F. juncifolia* studied by Kjellqvist came from coastal localities ranging from Skåne, Sweden, to Santander, Spain, including one (with $2n = 56$) from Tentsmuir, Fife.

Gregor (1954) found that, in Britain, wild *F. rubra* is usually hexaploid but that octoploids occur in some extremely dry habitats such as sand-dunes and dry heathland. He mentioned that maritime octoploids closely resemble *F. juncifolia*, but as far as we have been able to tell he did not actually report that *F. juncifolia* was octoploid, as Kjellqvist (1964) suggested he did.

Wilde-Duyfjes (1964) considered *F. rubra sensu stricto* and *F. juncifolia* (*F. rubra* subsp. *juncifolia* (St Amans) R. Litard., incl. *F. arenaria*) as two subspecies of *F. rubra*, and separated them on leaf-sclerenchyma and the shape of the leaf-blade in transverse section. Freijsen & van Heusden (1965) found only plants with discontinuous leaf-sclerenchyma on the island of Terschelling, Netherlands. Freijsen & Heeres (1972) found plants with both sorts of sclerenchyma on the island of Voorne, Netherlands, but preferred to follow Kjellqvist in considering them environmentally-induced variants of one taxon. Wilde-

Duyfjes (1973) later agreed with Freijsen & Heeres; the key he provided to separate *F. rubra* subsp. *rubra* and subsp. *arenaria* is identical with that he earlier (1964) gave to separate subsp. *rubra* from subsp. *juncifolia*.

Willis & King (1968) reported a flat-leaved, rhizomatous, sand-dune variant from Braunton Burrows, N. Devon, which they referred to *F. rubra* (as var. *planifolia* auct. = var. *multiflora* Wallr.) because of its blunt leaf-apices, discontinuous leaf-sclerenchyma, almost glabrous lemmas, and intravaginal branches. It has long lemmas but is a hexaploid ($2n = 42$).

Extensive studies have been made by Huon (1970) on the Atlantic coast of France, using Hackel's original classification but substituting the name subsp. *juncifolia* for subsp. *dumetorum*. Huon confirmed Kjellqvist's reports of $2n = 42$ for *F. rubra* (incl. var. *arenaria*) and $2n = 56$ for *F. juncifolia*, although some abnormal numbers ($2n = 35, 44, 86$) were found in certain populations of the former, and he also agreed with Kjellqvist's conclusion that *F. juncifolia* may have either interrupted or continuous sclerenchyma. Huon continued to recognise a hexaploid dune variant (subvar. *arenaria*) of *F. rubra* as distinct from *F. juncifolia*. The former was said to be characteristic of fixed dunes and the latter of mobile dunes.

Auquier (1971) disagreed with Kjellqvist's conclusion that *F. juncifolia* and *F. arenaria* are synonymous, although he did not carry out cytological studies and, like Kjellqvist, found that the leaf-sclerenchyma was not a reliable discriminant. He also found that several of the minor characters which had been used previously to separate the taxa were too variable to be relied upon. Nevertheless he recognised *F. juncifolia* and *F. rubra* subsp. *arenaria* (Osbeck) Richt. as specifically distinct, separated mainly by their glume-lengths, but with a number of more minor diagnostic characters as well. Auquier included *F. oraria* in *F. juncifolia*.

Within *F. rubra sensu lato* there are numerous reliable chromosome counts in the literature ranging from diploid ($2n = 14$) to decaploid ($2n = 70$), but all sand-dune variants appear to be either hexaploid or octoploid. Skalínska *et alii* (1971) found both hexaploid and octoploid populations of inland *F. rubra sensu stricto* in Poland, and caryopses collected from some of the plants proved to be heptaploid ($2n = 49$), evidently the result of cross-pollination. Kjellqvist (1964) was able to synthesise heptaploid hybrids between *F. rubra* and *F. juncifolia* (*F. arenaria*), but he found none in the wild. It is clear that, whereas all *F. juncifolia* which has been cytologically investigated has been found to be octoploid, plants of *F. rubra* (normally hexaploid) are also sometimes octoploid.

VULPIA MEMBRANACEA (L.) DUM.

Fortunately there are fewer problems concerning the taxonomy of *Vulpia membranacea*. Several reports of chromosome numbers of this species have been made, the most frequent being $2n = 28$ (tetraploid). Roux (1960) found this number in populations on the Mediterranean coast of France, on the Atlantic coast of France as far north as Brittany, and on the Portuguese coast near Porto. He pointed out that diploid counts ($2n = 14$) had been obtained by Litardière (1950) from further south in Portugal (Beira), and that Maude (1940) had reported $2n = 42$ (hexaploid) in a British plant. In a footnote he mentioned a diploid count of his own made on a plant from the Rhône valley, and more recently Fernandes & Queirós (1969) have reported a diploid ($2n = 14$) from near Porto.

V. longiseta (Brot.) Hackel, a species largely confined to Portugal, Spain and France, is very similar to *V. membranacea* and has frequently been confused with the latter. It is a diploid ($2n = 14$) according to Litardière (1950), who counted Portuguese specimens.

FESTUCA × *VULPIA*

Putative hybrids between *Festuca rubra* and *Vulpia membranacea* were first reported by Melderis (1955), who based his note on specimens collected on 7th June 1954 by J. F. and P. C. Hall and B. Welch at Freshfield, S. Lancs. (BM), and on 21st June 1954 by M. McC. Webster at Sandwich Bay, E. Kent (BM). In the previous year, however, C. E. Hubbard had found two plants of this hybrid at Vazon, Guernsey, on 17th June 1953 (K), and much earlier specimens were later detected by both Hubbard and Melderis among folders of various species of *Festuca* and *Vulpia* at BM and K. For instance the hybrid was collected near L'Ancrese, Guernsey, in 1928, and at Portland, Dorset, in 1918, and there are some inadequately localised specimens probably from Wales and Dorset dating from around 1800. Since 1954 the hybrid has been found in many localities on the south and west coasts of England and Wales from E. Kent to S. Lancs., and in the Channel Isles. Willis (1967) reported somewhat more fully on the hybrids at Berrow, N. Somerset.

Melderis (1957) identified specimens collected on 9th June 1956 by J. F. and P. C. Hall from Dawlish Warren, S. Devon (BM) as *F. rubra* var. *arenaria* × *V. membranacea*, on the basis of their hairy lemmas. Plants known as *F. rubra* var. *arenaria* usually have conspicuously hairy lemmas, whereas the lemmas of var. *rubra* (and of *V. membranacea*) are nearly glabrous. Similar hybrids were collected on 15th June 1958 by E. B. Bangerter, J. F. Hall and J. E. Lousley at Clymping, W. Sussex, along with other hybrids having more or less glabrous lemmas (both BM). The Clymping locality is the same as that called Littlehampton Golf-Course in Table 1.

Hybrids between *F. rubra* and both *V. myuros* (L.) C. C. Gmel. and *V. bromoides* (L.) S. F. Gray have also been reported from Britain but will not be dealt with in this paper.

AIMS, MATERIALS AND METHODS

The results reported here have been obtained during a cytotaxonomic survey of the genus *Vulpia* in connexion with studies of its relationships with other annual Festuceae and with *Festuca*. The main aim of this paper is to describe the hybrids between *F. rubra sensu lato* and *V. membranacea*, and therefore we have considered here the characteristics and taxonomy of the parents only so far as is necessary for this purpose.

Samples of *V. membranacea* have been obtained from most parts of its total world range. We have in cultivation specimens of the intergeneric hybrids from W. Sussex (2 localities), N. Devon, N. Somerset, Glamorgan, Merioneth and S. Lancs., and of sand-dune variants of *F. rubra sensu lato* from all these localities and several other areas of Britain and France. In addition we have consulted the herbaria at BM, K and MANCH.

Chromosome preparations were made from root-tips obtained from either rhizomes (in *Festuca* and the hybrids) or caryopses (in *Festuca* and *Vulpia*). Root-tips were pre-treated with saturated aqueous gammexane for 4 hours at 15°C, and stained by the Feulgen method.

Experimental hybridizations were carried out on inflorescences which were emasculated one or two days before the first anthers would have dehisced, which in *V. membranacea* is well before the inflorescence is properly exerted from the uppermost leaf-sheath. The stamens were removed from the lowest floret in each spikelet and the rest of the florets (as well as any spikelets not at a suitable stage) wholly excised. Each emasculated inflorescence was enclosed in a pollen-proof bag. The emasculated florets were pollinated individually as the stigmas ripened and became exerted over the course of the next three days.

In the remainder of this paper we have used the names *F. rubra*, *F. rubra* var. *arenaria* and *F. juncifolia* to cover the plants as they are recognised in the current British Floras (e.g. Hubbard 1968). *F. rubra sensu lato* refers to *F. rubra* as recognised by Hackel (1882) but excluding *F. heterophylla* Lam. *F. juncifolia* is thus used to cover large sand-dune plants with long rhizomes, with stems borne singly (i.e. without intravaginal branches), and with stiff, inrolled leaves with well-developed (sometimes continuous) abaxial sclerenchyma.

RESULTS AND DISCUSSION

CHROMOSOME NUMBERS

The chromosome numbers of *V. membranacea*, *V. longiseta*, *F. rubra sensu lato* and the *Festuca* × *Vulpia* hybrids which have been found in the present study are summarised in Table 1.

TABLE 1. CHROMOSOME NUMBERS OF *FESTUCA RUBRA SENSU LATO*, *VULPIA MEMBRANACEA*, *V. LONGISETA* AND HYBRIDS

<i>Festuca rubra sensu lato</i>	
Braunton Burrows, N. Devon, v.c. 4	2n = 42
Near Berrow Church, N. Somerset, v.c. 6	2n = 42
Dunes by Littlehampton Golf-Course, W. Sussex, v.c. 13	2n = 42
Dunes by Littlehampton Golf-Course, W. Sussex, v.c. 13	2n = 56
Sandy shingle at Greatstone, E. Kent, v.c. 15 (ex K)	2n = 56
Dunes near Burnham Overy, W. Norfolk, v.c. 28 (ex K)	2n = 56
Dunes near Thornham, W. Norfolk, v.c. 28 (ex K)	2n = 56
Llangennith Burrows, Gower, Glamorgan, v.c. 41	2n = 42
Old railway at Barmouth Junction, Merioneth, v.c. 48	2n = 42
Harlech Dunes, Merioneth, v.c. 48	2n = 42
Harlech Dunes, Merioneth, v.c. 48	2n = 42
Ainsdale Dunes, S. Lancs., v.c. 59	2n = 42
Dunes at Montrose, Forfar, v.c. 90	2n = 56
Among muddy sand and shingle, Whitehills, Banff, v.c. 94	2n = 42
Dunes, Berck, Pas de Calais, France	2n = 56
Dunes, Le Touquet, Pas de Calais, France	2n = 56
Dunes, Ambleteuse, Pas de Calais, France	2n = 56
<i>Vulpia membranacea</i>	
Perran Beach, Perranporth, W. Cornwall, v.c. 1	2n = 28
Crantock, W. Cornwall, v.c. 1	2n = 28
Dawlish Warren, S. Devon, v.c. 3	2n = 28
Braunton Burrows, N. Devon, v.c. 4	2n = 28
Near Berrow Church, N. Somerset, v.c. 6	2n = 28
Dunes at East Head, West Wittering, W. Sussex, v.c. 13	2n = 28
Dunes by Littlehampton Golf-Course, W. Sussex, v.c. 13	2n = 28

TABLE 1 continued.

<i>Vulpia membranacea</i> continued.)	
Sandwich Bay, E. Kent, v.c. 15	2n = 28
Threecliff Bay, Gower, Glamorgan, v.c. 41	2n = 28
Llangennith Burrows, Gower, Glamorgan, v.c. 41	2n = 28
Harlech Dunes, Merioneth, v.c. 48	2n = 28
By Abersoch Golf-Course, Caernarvon, v.c. 49	2n = 28
Formby Dunes, S. Lancs., v.c. 59	2n = 28
Ainsdale Dunes, S. Lancs., v.c. 59	2n = 28
North of Kilmuckridge, Wexford, v.c. H12	2n = 28
Wexford Harbour, Wexford, v.c. H12	2n = 28
Ballyteige Burrows, Wexford, v.c. H12	2n = 28
Near Mizen Head, Wicklow, v.c. H20	2n = 28
L'Anresse Common, Guernsey	2n = 28
St. Ouen's Bay, Jersey	2n = 28
Corse (1 source)	2n = 28
Cyprus (1 source) (ex K)	2n = 28
France (3 sources)	2n = 28
Greece (1 source)	2n = 28
Italy (2 sources)	2n = 28
Jugoslavia (1 source)	2n = 28
Kriti (1 source)	2n = 28
Libya (1 source) (ex K)	2n = 28
Sicilia (3 sources)	2n = 28
Cultivated origin (3 sources)	2n = 28
<i>Vulpia longiseta</i>	
Spain (2 sources)	2n = 14
Cultivated origin (3 sources)	2n = 14
<i>Festuca rubra sensu lato</i> × <i>Vulpia membranacea</i>	
Braunton Burrows, N. Devon, v.c. 4	2n = 35
Near Berrow Church, N. Somerset, v.c. 6	2n = 35
Dunes by Littlehampton Golf-Course, W. Sussex, v.c. 13	2n = 35
Dunes by Littlehampton Golf-Course, W. Sussex, v.c. 13	2n = 42
Dunes at East Head, West Wittering, W. Sussex, v.c. 13	2n = 35
Llangennith Burrows, Gower, Glamorgan, v.c. 41	2n = 35
Harlech Dunes, Merioneth, v.c. 48	2n = 35
Ainsdale Dunes, S. Lancs., v.c. 59	2n = 35

In all cases (14 localities in Britain, 4 in Ireland, 2 in the Channel Isles, and several in Corse, Cyprus, France, Greece, Italy, Jugoslavia, Kriti, Libya and Sicilia) the tetraploid count ($2n = 28$) was obtained for *V. membranacea*. This is the same as most of Roux's French counts, but differs from most of the Portuguese counts and from Maude's single British count.

The 5 counts of *V. longiseta* are all diploid ($2n = 14$).

With the evidence at his disposal, Roux (1950) suggested that *V. membranacea* exhibited a polyploid series, with diploids in southern Portugal, tetraploids further north as far as Brittany, and hexaploids in the British Isles. Although the suggestion was reasonable at the time we now believe it to be incorrect. The single hexaploid count (Maude 1940) was said to refer to wild British material, but it was not further localised and no voucher specimen has been traced. There is thus no evidence to show that it referred to other than an abnormal plant in a tetraploid population, or even to an abnormal cell. Maude provided a figure of the karyotype, which suggests that her technique was not at fault, and she

acknowledged the taxonomic help of C. E. Hubbard which rules out a mistaken identification, although perhaps not a faulty clerical system. At any rate, our survey has covered almost all parts of the range of the species in the British Isles and has shown that the great majority of populations, if not all, are tetraploid.

We believe that the diploid counts in the literature all refer to *V. longiseta*. Of the authors that have reported *V. membranacea* with $2n = 14$, only Litardière (1950) counted *V. longiseta* as well, and in some cases the localities given for the specimens of *V. membranacea* (e.g. Orange in the Rhône valley by Roux (1950)) are areas from which we have seen only *V. longiseta*. One of our own diploid counts of *V. longiseta* from south-western Spain was of a plant sent to us as *V. membranacea*. Thus we consider that there is no good evidence that there are other than tetraploid populations of *V. membranacea*, although it is, of course, impossible to prove that no diploids or hexaploids exist.

Both hexaploid ($2n = 42$) and octoploid ($2n = 56$) chromosome numbers were found in the material of *F. rubra sensu lato*, in agreement with the results of Kjellqvist and Huon.

The hybrid *Festuca* × *Vulpia* was pentaploid ($2n = 35$) in all 7 British localities sampled, but in one of them (Littlehampton, W. Sussex) a hexaploid ($2n = 42$) was also present. This is comparable with the unpublished results of M. D. Hooper (1971 *in litt.*) who, in 1961, found pentaploid and hexaploid hybrids among collections from Sandwich Bay, E. Kent, although he found only pentaploids at Littlehampton. The presence of both pentaploid and hexaploid hybrids at Littlehampton coincides with the presence there of hexaploid and octoploid cytodesmes of *F. rubra sensu lato*, and it is likely that the latter two also occur at Sandwich (whence *F. juncifolia* has often been reported).

TAXONOMY OF *FESTUCA RUBRA SENSU LATO*

Specimens of *F. rubra sensu lato* from the localities listed in Table 1, as well as the herbarium specimens in **MANCH** (many of which had been earlier studied by W. O. Howarth) and in **herb. Stace**, were examined particularly with respect to those characters previously used to separate *F. rubra* from its var. *arenaria* and from *F. juncifolia*. In **MANCH** there are 5 sheets determined by Howarth as *F. juncifolia*: from Carnoustie, Forfar; Pettycur, Fife; Skegness, N. Lincs.; Caister, E. Norfolk; and St Aubins, Jersey.

Leaf Anatomy. Only 3 specimens in **MANCH** have truly continuous abaxial leaf-sclerenchyma. These are the E. Norfolk specimen mentioned above; a specimen collected by G. C. Druce from Skegness, N. Lincs., in 1909, and labelled by him *F. dumetorum* (but not annotated by Howarth); and a specimen collected by G. C. Brown from Walton-on-Naze, N. Essex, in 1930, and named by Howarth *F. rubra* var. *barbata* (Hackel) Howarth. The Burnham Overy specimen listed in Table 1 (ex **K**, Hubbard 28767) also has continuous leaf-sclerenchyma. In addition 6 specimens in **herb. Stace** collected by C.A.S. from Dovercourt, N. Essex (1957, 1962); Ambleteuse, Pas de Calais, France (1959, 1959, 1973); and Le Touquet, Pas de Calais, France (1973), also have this feature. All other specimens examined, including the four other specimens determined by Howarth as *F. juncifolia*, have discontinuous leaf-sclerenchyma. Although there is variation in the degree of the continuity of the sclerenchyma bundles, we rarely found difficulty in classifying leaves as having continuous or discontinuous sclerenchyma, so long as the middle parts of the blades of the lowest culm-leaves

(often brown at flowering time) were examined. The degree of continuity of the sclerenchyma decreases higher up the culm and towards the apex of each leaf-blade, and the uppermost leaf may have discontinuous sclerenchyma even on culms where the lower leaves have a continuous abaxial band. It is of interest that a specimen in MANCH of *F. rubra* var. *oelandica*, which exhibits the distinctive habit of this variety and was collected on Öland, Sweden, has leaves with discontinuous sclerenchyma, exactly as illustrated by Kjellqvist (1961), even though Hackel claimed that it was the only variety of *F. rubra* subsp. *rubra* to possess continuous leaf-sclerenchyma.

It is clear that Howarth did not cut leaf sections to examine the sclerenchyma before he determined herbarium material of *F. juncifolia*, although he stated (Howarth 1924) that 'the characters of the glumes, etc. often leave one undecided, but the unfailing test is to be found in the transverse section of the radical leaf'. The presence of continuous leaf-sclerenchyma is clearly not absolutely correlated with the other characters which Hackel and Howarth used to distinguish *F. juncifolia*. Indeed, both these authors noted the occurrence of occasional specimens of *F. juncifolia* with discontinuous leaf-sclerenchyma.

The presence of bundles of adaxial sclerenchyma in the apices of the ribs of the upper leaf-surface has also been used to characterise *F. juncifolia*, but variants of *F. rubra* with this feature are quite common (e.g. the material of var. *multiflora* studied by Willis & King (1968)). Auquier (1971) concluded that various other previously used leaf characters, such as the size of the lumen of the fibres, were too variable to be of much diagnostic value.

According to Hackel and Howarth, in *F. rubra* there are 5–7 vascular bundles ('*nervi*') in the leaf-blade while in *F. juncifolia* there are 7–11. Moreover the upper leaf-surface is raised into 3–7 ribs ('*costae*') in *F. rubra* but 5—many in *F. juncifolia*. The greater number of vascular bundles than ribs is due to the presence of one or two vascular bundles in the non-ribbed marginal zones of the leaf-blade. We have not investigated these characters in detail because of the overlaps admitted by the above authors; in the material of both *F. rubra* and *F. juncifolia* that we have examined, leaves with 7 vascular bundles and 5 ribs are by far the commonest. Willis & King (1968) reported the same number in *F. rubra* var. *arenaria* but their material of var. *multiflora* possessed 10 vascular bundles and about 8 ribs. The drawings given by Auquier (1971) show no interspecific differences in these two characters.

We have not been able to confirm the abaxial epidermal differences between *F. rubra* and *F. juncifolia* which were described by Huon (1970) and Auquier (1971). In our material the long-cells of *F. rubra* are often no longer than those of *F. juncifolia*, and *F. rubra* often possesses no more short-cells containing silica-bodies than does *F. juncifolia*.

Leaf Morphology. The acuteness of the leaf-apex was said by Hackel and Howarth to distinguish *F. rubra* from *F. juncifolia*, but we have been quite unable to make any use whatsoever of this character. The leaves of lax-leaved, typical *F. rubra* are often just as acute as those of any plants of *F. juncifolia*. The leaf-blades of plants which have been determined as *F. juncifolia* are certainly very stiff and often rather sharp ('*pungens*') at the apex, but this appears to be a measure of the consistent inrolling of the leaf and of the amount of sclerenchyma, especially at the margins, rather than of the acuteness of the apex, and is very difficult to measure objectively.

Hackel and some later authors have claimed that the leaves of *F. rubra* are V-shaped or strongly keeled in transverse section, while those of *F. juncifolia* are inrolled and thus suborbicular in transverse section ('*complicata*', '*junceae*'). Although the leaves of *F. juncifolia* collected from sand-dunes are invariably inrolled, as noted above, this is often not true of the same material grown on in the glass-house, as has also been pointed out by Kjellqvist (1961). Moreover flat-leaved variants of both *F. rubra* and *F. juncifolia* have been described, and the enormous range in leaf-shape of *F. rubra* covers the range of *F. juncifolia*. It seems probable that the inrolled leaves of sand-dune plants is at least partly environmentally controlled (cf. *Agropyron maritimum* (Koch & Ziz) Jans. & Wacht., a parallel variant of *A. repens* (L.) Beauv.) and is unlikely to be of taxonomic significance.

Branching Pattern. The mode of branching (intravaginal or extravaginal) of the stems is less easily observed than in living specimens, and in old than in young plants. Both sorts of branches arise at lower stem-nodes in the axils of leaf-sheaths; where they form a very acute angle with the main stem and are retained within its leaf-sheath for some distance they are termed intravaginal, and where they diverge widely and break through the leaf-sheath at its base (cf. branches of *Equisetum* stems) they are termed extravaginal. Thus intravaginal branches always give rise to a tufted growth-habit. Extravaginal branches, which bear scale-leaves at their bases, may grow horizontally for some distance, giving a loose, rhizomatous habit, or may almost immediately grow upwards to produce a tufted growth-habit. According to Hackel and Howarth, all plants of *F. rubra sensu lato* possess extravaginal branches, and in *F. juncifolia* they are long and creeping and are not accompanied by intravaginal branches, so that the plants are extensively rhizomatous with the aerial stems borne singly. *F. rubra* always possesses intravaginal branches, so that even in extensively rhizomatous plants some of the aerial stems are borne in tufts.

From our observations in Britain and France, the non-tufted, rhizomatous growth-habit is certainly typical of the larger, stiffer-leaved, sand-dune variants of *F. rubra sensu lato* which are often identified as *F. juncifolia*, but the inadequacy of herbarium material has prevented us from making detailed or quantitative observations of a wide range of material.

We have grown plants from seed of all our specimens of known chromosome number; in seedlings with up to about a dozen lateral branches the difference between intravaginal and extravaginal branches is very conspicuous. Only 8 of our specimens, all the octoploids, possess extravaginal branches alone, but in the others the proportion of intravaginal and extravaginal branches varies considerably.

The drawings given by Hubbard (1968) of *F. rubra* subsp. *rubra* and *F. juncifolia* are good representatives of the tufted and non-tufted growth-habits (both rhizomatous) distinguished by Hackel. But at the end of the description of the former taxon Hubbard mentioned var. *arenaria*, with 'scattered shoots', and under *F. juncifolia* he said that *F. rubra* var. *arenaria* and *F. juncifolia* have 'a similar loose form of growth'. Huon (1970) and Auquier (1971) made little use of this character in their diagnoses of *F. juncifolia*.

Spikelet Pubescence. A strong pubescence of the spikelets has often been used as a diagnostic character of both *F. juncifolia* and *F. rubra* var. *arenaria*. Although it is true that these taxa usually have densely and conspicuously pubescent

lemmas, while in typical *F. rubra* the lemmas are usually glabrous or very shortly pubescent, there are glabrous variants of otherwise typical *F. juncifolia* (f. *glabrata* (Lebel) Auquier) and of *F. rubra* var. *arenaria* (f. *glabrispicula* St Yves & R. Litard.). Thus no reliance can be placed on this character.

Lemma-length. Hubbard (1968) claimed there was a good difference in the lemma-lengths of *F. rubra* ('mostly 5–6 mm') and *F. juncifolia* (7–10 mm), although this was denied by Hackel, Howarth and Kjellqvist. In fact lemmas of 6–7 mm, said by Hubbard not to be found in either species, were given as the typical range for *F. juncifolia* by Hackel and Howarth, while Kjellqvist gave 6–8 mm. Our results (Fig. 1) do not agree entirely with any of the above.

All of the known hexaploids in our sample have distinctly shorter lemmas (5.0–6.0 mm) than the 8 octoploids (6.7–8.9 mm), although Willis & King's (1968) hexaploid material of var. *multiflora* has lemmas falling in the latter range (7.0 and 7.2 mm in two different samples). The lemma-lengths of our octoploids show reasonable agreement with those ranges of plants with continuous leaf sclerenchyma (6.5–7.8 mm), of plants in MANCH identified by Howarth as *F. juncifolia* (6.8–8.3 mm), and of Kjellqvist's octoploid plants (6–8 mm) which he identified as *F. arenaria* (*F. juncifolia*). It should be noted that the lemma-lengths given by Howarth (1924) for *F. juncifolia* (6–7 mm) were copied from Hackel (1882), and do not agree with the measurements of the specimens that Howarth actually identified as this species. The lemma-lengths given by Hubbard (1968) for *F. juncifolia* (7–10 mm) extend higher than those of any plants we have observed. On the other hand the lemma-lengths of our hexaploids are precisely those given by Hubbard for *F. rubra* subsp. *rubra*, and fall well within the range (4.4–6.3 mm) shown by the bulk of our plants identifiable with that taxon. Huon (1970) and Auquier (1971) used spikelet-length rather than lemma-length as a measure of the larger floral parts of *F. juncifolia*.

Of the specimens with lemmas exceeding 6 mm, those in MANCH had been previously identified (mostly by Howarth) as *F. juncifolia* or as *F. rubra* vars. *junceae* (Hackel) Richt., *arenaria* (Osbeck) Fr., *barbata* (Hackel) Howarth, *grandiflora* (Hackel) Howarth, and *planifolia* auct. Some of them, despite their long lemmas, do not resemble *F. juncifolia* as they have intravaginal branches, and they often have a tufted growth-habit and originate from areas (especially Lancashire) whence *F. juncifolia* has not been recorded. Thus all the plants which appear to be identifiable with *F. juncifolia* on the basis of growth-habit and leaf-sclerenchyma have lemmas over 6.0 (in fact at least 6.5) mm long, but some plants undoubtedly referable to *F. rubra* share this character.

We have not been able to confirm the slight differences in the shape of the lemmas of *F. rubra* and *F. juncifolia* given by Hackel and Howarth, nor the different lengths of the lemma-awns similarly claimed. In our experience the range of variation of *F. rubra* in both these characters includes that of *F. juncifolia*.

Anther-length and caryopsis-length. According to Hubbard (1968) the anthers of *F. rubra* are 2–3 mm long whereas those of *F. juncifolia* are 4–5 mm long. Unfortunately almost all our material is too advanced to enable us to investigate this character but Kjellqvist (1964) stated that the anthers of *F. juncifolia* are 'about 3 mm long'. There is no difference in the length of the caryopses; in our material it is 2.5–3.5 mm in both taxa.

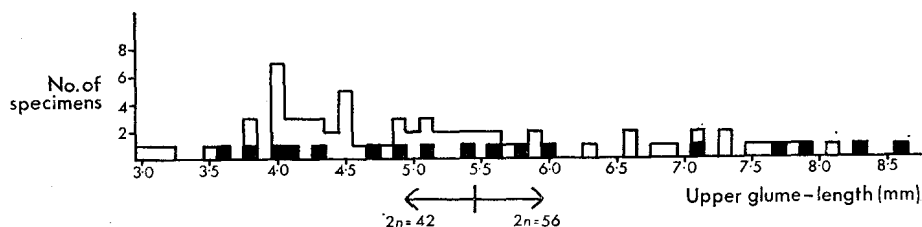
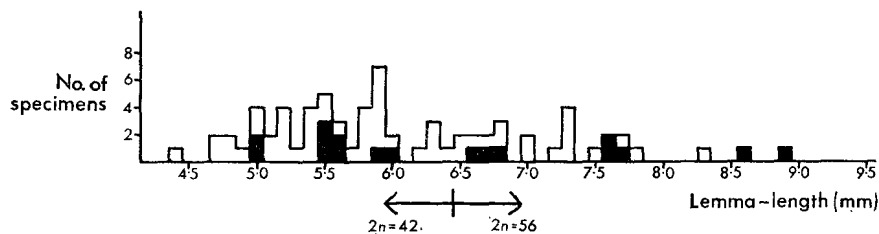


FIGURE 1. Histogram showing lemma-length of specimens of *F. rubra sensu lato*. Lengths are means of 10 lowest lemmas per specimen, and exclude awns. Black areas indicate plants of known chromosome number.

FIGURE 2. Histogram showing upper glume-length of specimens of *F. rubra sensu lato*. Lengths are means of 10 upper glumes per specimen, and include awns if present. Black areas indicate plants of known chromosome number.

Glume-ratio and -length. Hackel (1882) and Howarth (1924) claimed that the glumes of *F. rubra* are unequal and those of *F. juncifolia* subequal, but we have detected no such differences. Auquier (1971) used the ratio of the lengths of the upper glume and the second lemma.

Fig. 2 shows the upper glume-lengths of all the specimens we have examined in detail. In *F. rubra sensu lato* the glumes bear scarcely any or no awn; in cases where an awn is distinguishable it is included in the glume-length. The glumes of plants with long lemmas are distinctly longer than those with short lemmas. Hubbard (1968) gave measurements of the upper and lower glumes of *F. rubra* subsp. *rubra* as 3.5–5.0 and 2.0–3.5 mm, and of *F. juncifolia* as 8–10 and 6–8 mm. This leaves wide disjunctions at 5–8 and 3.5–6.0 mm, which in fact are quite close to the actual measurements given by Kjellqvist (1964) and Auquier (1971) for *F. juncifolia*. Our own results (Table 2) for the bulk of the *F. rubra* specimens agree closely with those of Hubbard; those for *F. juncifolia* are not very close to those of either Hubbard or Kjellqvist (4–7 and 3–5 mm), but are similar to those of Auquier (6.1–7.9 and 4.6–6.3 mm). We have found no specimens with glumes of the length of those at the upper part of the size-ranges given by Hubbard for *F. juncifolia* (indeed, only 3 of our plants fall within Hubbard's ranges). Willis & King's measurements for *F. rubra* (4.0–5.6 and 2.7–3.9 mm) agree with ours; their material of var. *multiflora* had glumes averaging 5.3 and 4.2 mm, and 6.0 and 4.9 mm, in two separate samples.

As with the cases of the lemmas, the plants with longer upper glumes (5.5 mm and more) include all those referable to *F. juncifolia* but also a number which are undoubtedly *F. rubra*. Clearly the pattern of variation of the glume-lengths parallels that of the lemma-lengths.

RECOGNITION AND VARIATION OF *FESTUCA RUBRA SENSU LATO* × *VULPIA MEMBRANACEA*

The intergeneric hybrids are easily distinguished, with practice, and their apparent rarity before about 1954 may be attributable to grazing by rabbits (Willis 1967). The hybrids are more or less rhizomatous perennials which flower freely but which are highly, if not entirely, sterile. In many respects they resemble plants of *F. rubra* with particularly long-awned lemmas and somewhat more distinctly one-sided inflorescences. In fact in vegetative characters they more closely resemble *F. rubra* but in floral characters they are more or less intermediate. No doubt because of the variable nature of *F. rubra sensu lato* the range of variation of the hybrids is considerable, and neither the descriptions by Melderis (1955, 1957) nor that by Willis (1967) adequately cover it.

The variously tufted or creeping growth-habit of *F. rubra sensu lato* with varying proportions of intravaginal and extravaginal branches, is in contrast with the tufted, annual growth-habit of *V. membranacea*, where the branches are all intravaginal. The hybrids bear both intravaginal and extravaginal branches, but in all the material we have seen the latter are by far the commoner, and in the hexaploid from Littlehampton (perhaps as well as in some others) are the only sort. Some plants are densely tufted, while others are noticeably creeping with the aerial stems borne singly, but the hybrids are never as extensively creeping as most sand-dune variants of *F. rubra sensu lato*. The growth-habit is at least partly environmentally determined; a densely tufted hybrid collected at Harlech has become conspicuously creeping in cultivation.

In seedlings of artificial hybrids, the lower leaf-sheaths are the characteristic deep vinous colour of those of *F. rubra*, in marked contrast to the pale green leaf-sheaths of *V. membranacea*, and this characteristic is retained to some degree in the mature state, as noted by Melderis (1955) and Willis (1967). The lower leaf-sheaths of *F. rubra* are frequently pubescent; those of hybrids involving such variants are also pubescent. The leaf-sheaths of the hybrid are at first tubular to within a few mm of the top, as in *F. rubra*, which contrasts with the situation in *V. membranacea*.

The leaf anatomy of *V. membranacea* resembles that of *F. rubra* except that the vascular bundles form a far less prominent ridge on the lower epidermis and there is much less sclerenchyma. Sclerenchyma is present in small bundles below the midrib and often the larger lateral veins, in a bundle at each leaf-margin, and sometimes in a rudimentary state at the apex of each adaxial rib. The leaf is thus far less rigid than that of *F. rubra*. It is often inrolled, but never conspicuously keeled at the midrib. The leaf of the hybrids is intermediate in all these characters; in particular the sclerenchyma is usually present below all the vascular bundles but it is never as well developed as in *F. rubra* and the midrib is keeled to a slight degree. There are scarcely any differences between the epidermis of *F. rubra* and that of *V. membranacea*. The hybrids are clearly intermediate between their parents in the length of the two glumes, lemmas and lemma-awns (Table 2). The ranges of lemma-lengths given by Willis (1967) obviously cover all the lemmas in a spikelet, but we feel it desirable to include only the lowest lemma on each side of the spikelet (i.e. the first and second lemmas), as the higher ones are considerably reduced in size, especially in *V. membranacea*. In Table 2 the ranges are those of mean lengths (ten measurements per plant), not of individual measurements, except in the case of the hexaploid hybrid of which we have only one collection. In the case of the *Festuca* species and the hybrids, the glume-

TABLE 2. FLORAL MEASUREMENTS OF *FESTUCA RUBRA*,
F. JUNCIFOLIA, *VULPIA MEMBRANACEA* AND HYBRIDS

	Mean length in mm (10 measurements per plant)			
	Lower Glume	Upper Glume	Lemma	Lemma-awn
<i>F. rubra</i>	2.2-4.1	3.0-5.8 (-7.3)	4.4-7.0 (-7.7)	0.1-3.3
<i>F. juncifolia</i>	4.2-6.7	5.5-8.6	6.5-8.9	0.1-2.1
Hybrid (pentaploid)	2.4-4.4	5.2-8.0	6.0-9.5	2.0-5.5
Hybrid (hexaploid)	3.5-7.2	8.0-11.5	9.5-10.5	3.5-5.0
<i>V. membranacea</i>	0.2-2.6	12.8-32.0 (10.7-19.3 excluding awn)	10.7-18.3	8.0-25.2

lengths include any awn which may be distinguishable; in the length of the awn on the upper glume the hybrids are much closer to their *Festuca* parent (awns up to *c* 0.5 mm in *F. rubra sensu lato*; up to *c* 1.5 mm in the hybrids). Perhaps the most reliable diagnostic character is the glume ratio: less than 1/10 in *V. membranacea*; approximately 1/2 in hybrids; and about 2/3 to 4/5 in *F. rubra sensu lato*.

The hexaploid hybrid from Littlehampton differs from all the pentaploids in its longer upper glumes, lemmas and (to a lesser extent) lower glumes. The hexaploid apparently has only extravaginal branches (although *V. membranacea* has only intravaginal ones), but several of the pentaploids have extremely few intravaginal branches and the use of this character as a discriminant between the hybrid cytodesmes is very risky. The pubescence of the lemmas of the hybrids varies to a considerable degree, obviously according to that of the *Festuca* parent, but we do not feel that it is a reliable guide to the chromosome number. The Littlehampton hexaploid is only slightly pubescent, and some of the pentaploids are equally so. Thus we cannot be certain of the parentage of the plants with pubescent lemmas from Clymping, W. Sussex, and Dawlish, S. Devon, identified by Melderis as *F. rubra* var. *arenaria* × *V. membranacea*. *F. juncifolia* has been recorded from Dawlish, along with *F. rubra*, and both hybrids could occur there, but the lengths of the lemmas and glumes of the Dawlish hybrid are within the range (though at the upper end) of our pentaploids. The Clymping locality is apparently the same as our Littlehampton Golf-Course site, where *F. rubra*, *F. juncifolia* and pentaploid and hexaploid hybrids occur; but Bangerter, Hall and Lousley's hybrids with pubescent spikelets have lemmas no longer than those of the glabrous hybrids they collected at the same time, or than our pentaploid hybrids from the same place. Clearly, until we have more cytologically verified *F. juncifolia* × *V. membranacea*, we cannot be sure of the range of variation of the hexaploid hybrids.

Pentaploid hybrids are found in a range of habitats from sparse grassland on fixed dunes to open, mobile dunes. At Littlehampton the hexaploid occurs in open, mobile dunes, but is mixed with pentaploids and all three parental species.

Simple tests of the fertility of the hybrids have given largely negative results; stainable pollen is often 0% and we have never observed it above 3%. The an-

thers and stigmas are well exerted (more so than in *V. membranacea*). The anthers are intermediate in size between those of the parents (1.5–2.0 mm long) and are dehiscent. We have not succeeded in germinating any caryopses but Willis (1967) said they were less than 1% fertile. He obtained some F₂ seedlings which were accidentally lost (Willis 1973 *in litt.*).

Our studies of pollen-mother-cell meiosis in plants from several localities suggest that there might be a considerable amount of homology between the chromosomes of the two parent species. There are generally 10–14 bivalents plus 7–15 univalents, which agrees well with M. D. Hooper's observations on 2 pentaploid hybrids from Littlehampton, in which he observed up to 14 bivalents (Hooper 1971 *in litt.*). If all pairing is heterogenetic in cells with 14 bivalents, all the 14 chromosomes from *V. membranacea* must be pairing with 14 of the 21 from *F. rubra*, which would suggest that *F. rubra* contains both the genomes of *V. membranacea*. If, however, *F. rubra* and/or *V. membranacea* are autopolyploids (normally behaving as diploids), some of the pairing in the hybrid is likely to be homogenetic. Clearly, more positive conclusions must await further meiotic analyses. In many cases it is difficult to be certain whether many of the chromosome bodies observed are univalents or bivalents, because most of the bivalents possess chiasmata in one arm only and which become very fully terminalised. Generally only 2 or 3 of the bivalents are ring-bivalents (with 1 or more chiasmata in both arms), which suggests a relatively loose homology since most of the chromosomes have two fairly long arms and in the parent species most form ring-bivalents.

EXPERIMENTAL HYBRIDIZATION

The crosses were carried out in 1972 using a cultivated (tetraploid) source of *V. membranacea* and a wild hexaploid strain of *F. rubra* subsp. *rubra* growing on a grassy bank in Manchester. 75 pollinations were carried out using *F. rubra* as the female parent; 1 caryopsis was obtained but it did not germinate. 139 pollinations were carried out using *V. membranacea* as the female parent; 63 caryopses were obtained of which 3 proved to be selfed *V. membranacea* but 60 have produced vigorous hybrid plants, which commenced flowering in April 1974. There is no doubt that these are F₁ hybrids because they much more closely resemble *F. rubra* (the male parent) than *V. membranacea*. In particular, the lower leaf-sheaths are a deep vinous colour and conspicuously pubescent, and extravaginal branches have been formed. Moreover the chromosome number of the few plants that have been counted is the expected pentaploid $2n = 35$.

Since the anthers of *F. rubra* are far further exerted and are far larger than those of *V. membranacea* and must therefore contribute far more aerial pollen, it might be expected that most natural hybrids are formed from female *V. membranacea*. Our experimental results, albeit based on only one strain of each species, suggest that the cross in that direction is in any case far more likely to succeed. Plants of *F. rubra* which were emasculated in the usual way but pollinated with pollen from the same species produced viable caryopses.

CONCLUSIONS

Plants traditionally known as *F. juncifolia* have been separated in the past from *F. rubra* by means of a wide range of characters; in the case of several of these characters the precise values which have been said to discriminate between the

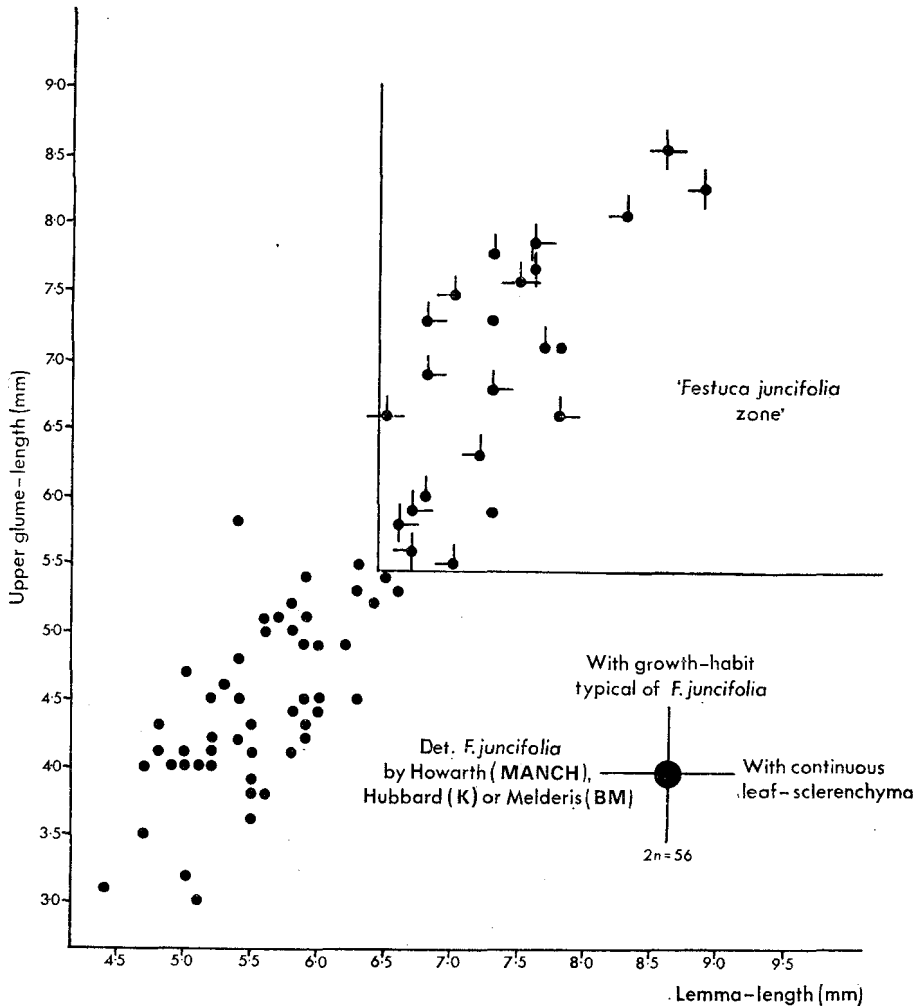


FIGURE 3. Scatter diagram of upper glume-length against lemma-length of specimens of *F. rubra sensu lato*. The primary data are taken from Figs. 1 and 2. Specimens previously determined as *F. juncifolia* are indicated. Also shown are extra characteristics supposed to distinguish *F. juncifolia* from *F. rubra*.

species have varied from author to author, and there has been considerable argument as to whether some characters are of any value at all. Nevertheless it is clear that one can define a taxon identifiable with *F. juncifolia* by means of a combination of the following characteristics: long upper and lower glumes and lemmas; rigid, inrolled leaf-blades with well-developed and sometimes continuous abaxial sclerenchyma; extensively creeping extravaginal but no intravaginal branches; and an octoploid chromosome number ($2n = 56$). According to our results the lower glumes are 4.2–6.7 mm, the upper glumes 5.5–8.6 mm, and the lemmas 6.5–8.9 mm. We consider the different results of some workers to be due to an erroneous concept of *F. juncifolia*, or to different (perhaps sometimes imprecise) methods of measuring these lengths, but in other cases the differences are no doubt due to different population samples.

Fig. 3 is a scatter diagram of lemma-length against upper glume-length and upon which lines have been drawn at the lowest limits for *F. juncifolia* with respect to these two characters. It can be seen that the '*F. juncifolia*-zone' contains all the plants with no intravaginal branches and with stiffly erect, inrolled leaves, all those which Howarth, Hubbard or Melderis have determined as *F. juncifolia*, all those with continuous leaf-sclerenchyma, and our 8 octoploid plants. All the plants outside this 'zone' possess intravaginal as well as extravaginal branches, and they include all our known hexaploids. There are, however, 3 plants within the '*F. juncifolia*-zone' which have intravaginal branches and lax leaves. Moreover some plants outside the 'zone' have upper glumes 5.5 mm or slightly more, or lemmas 6.5 mm or slightly more (but not, by definition of the 'zone', both). Although in our plants the octoploids and the hexaploids are separated in different 'zones', there are other plants which break down this distinction. For instance there are well-documented literature records of octoploids from Britain (Gregor 1954) and Poland (Skaltinska *et alii* 1971) which fall into the morphological range of *F. rubra*, and we ourselves have in cultivation an octoploid *F. rubra* collected from an improved roadside verge near Lesmagahow, Lanark, v.c.77. Willis & King's (1968) hexaploid plants of *F. rubra* var. *multiflora* fall into our '*F. juncifolia*-zone' according to one of their samples, but not according to the other. The three plants in the 'zone' which possess only the two primary characters of *F. juncifolia* may well also be hexaploids. They came from New Romney, E. Kent, v.c.15 (Druce, 1903, MANCH); sea coast near Cleveland, N. E. Yorks., v.c.62 (Hardy, 1854, MANCH); and near Blackpool, W. Lancs., v.c.60 (Searle, 1882, MANCH). They are all labelled *F. rubra* var. *junceae* (Hackel) Richt.

We have seen specimens agreeing with the above concept of *F. juncifolia* from many sand-dune localities in eastern, southern and south-western Britain, from E. Kent, v.c.15, northwards to Dornoch, E. Sutherland, v.c.107, and westwards to Gower, Glamorgan, v.c.41, and the Channel Isles, but they appear distinctly less common in south-western than in south-eastern Britain. On the Continent they occur on the Atlantic coast from Santander, Spain, northwards to at least Holland and perhaps to Scandinavia and the Baltic Sea coasts. They apparently always occupy unstable, sandy habitats, usually with *Ammophila arenaria* (L.) Link.

Thus none of the characters used to distinguish *F. juncifolia*, apart from the general growth-habit, can be used alone as an absolute criterion, and there is obviously a good case for considering *F. juncifolia* conspecific with *F. rubra* (cf. Hackel 1882, Huon 1970). On the other hand it is possible to identify *F. juncifolia* by a combination of growth-habit, chromosome number and the lengths of various floral parts, and the taxon so defined does possess a well-defined geographical and ecological distribution pattern. The exact degree of constancy in *F. juncifolia* of characters such as chromosome number and branching pattern is yet to be defined, but until it is shown that the frequency of anomalies makes identification of *F. juncifolia* uncertain we consider that it is better maintained as a distinct species. The further investigation of this question is obviously a topic of high priority.

We believe the difference of opinion between Kjellqvist (1964) and Auquier (1971) to be largely a question of the application of the name *F. arenaria* Osbeck. As far as we are aware neither author considered typical *F. rubra* to be a characteristic plant of sand-dunes. Both authors recognised two common taxa on

sand-dunes: a smaller plant (*F. rubra*) and a larger plant (*F. juncifolia*). According to Auquier the type specimen of *F. arenaria* Osbeck represents the smaller sand-dune taxon (= *F. rubra* var. *arenaria* (Osbeck) Fr.), but according to Kjellqvist it represents the larger one (*F. juncifolia*) and is the earlier name for it. There is no doubt that the two authors were referring to the same *F. arenaria*, for Kjellqvist (1964) selected and provided a drawing of the lectotype (S), which Auquier (1971) accepted and illustrated by a photograph. The drawing and the photograph are clearly of the same specimen. We have not seen the lectotype and thus cannot express a firm opinion, but the figures do appear to show intravaginal branches, which would support Auquier's conclusion. Until the situation is finally resolved we intend to use the name *F. juncifolia* St Amans (*F. arenaria* Osbeck, *sec.* Kjellqvist) for the larger plant, and *F. rubra* var. *arenaria* (Osbeck) Fr. for the smaller one, although the distinctive habitat and geographical distribution of the latter is perhaps evidence that it should be given subspecific status (*F. rubra* subsp. *arenaria* (Osbeck) Richt.). Should Kjellqvist be correct, the smaller plant could be known as *F. rubra* var. *arenaria* Fr., without the citation of Osbeck's name, as has been done by Hubbard (1968).

There is a problem in that Hackel (1882) and Howarth (1924) both described *F. rubra* var. *arenaria* as having large spikelets, but they did not give measurements of glumes or lemmas. Fortunately the specimen chosen by Howarth to represent var. *arenaria* in his Plate 28 is still at MANCH, although it is not annotated by him. It possesses intravaginal branches and has lemmas *c.* 5.4 mm long, and is clearly *F. rubra* rather than *F. juncifolia*. Thus the large spikelets referred to by Howarth are large in relation to those of much *F. rubra* var. *rubra*, but not as large as in *F. juncifolia*.

On a visit to Littlehampton, W. Sussex, in July, 1972, by A. Melderis and C.A.S., two morphologically distinct sand-dune variants of *F. rubra sensu lato* were detected, and their hexaploid and octoploid chromosome counts were correctly predicted from a knowledge of the available literature. In Fig. 3 the octoploid is the one with lemmas 7.7 mm and upper glumes 7.1 mm long; the hexaploid is the one with lemmas 5.5 mm and upper glumes 4.3 mm long. Two variants of *Festuca* × *Vulpia* hybrids were also distinguishable in the same locality and they were fairly obviously the crosses between hexaploid or octoploid *F. rubra sensu lato* on the one hand and *V. membranacea* on the other. The chromosome numbers of *V. membranacea* (tetraploid) and the hybrids (pentaploid and hexaploid) confirmed this view. M. D. Hooper (1971 *in litt.*) found only pentaploid hybrids at Littlehampton but both pentaploids and hexaploids at Sandwich, E. Kent. These plants are no longer available. Since *F. juncifolia* has often been recorded from Sandwich, Hooper's findings are completely in accordance with our expectations, but in 1971 we searched the extensive dunes at Sandwich without discovering any hybrid plants.

Hybrids between *F. rubra sensu stricto* and *V. membranacea* are to be expected throughout the whole range of the latter in Europe, for wherever it occurs *F. rubra* must surely occur nearby. In Britain hybrids are already known from all the main areas where *V. membranacea* occurs, but they have not been detected in south-eastern Ireland, where *V. membranacea* is locally common, and there is only one unconfirmed record from the Continent: from Suances, Santander, Spain (Patzke 1970). We feel the absence of records of hybrids from France is largely due to their not having been sought there.

F. juncifolia × *V. membranacea* must similarly be expected on the Atlantic

coasts of the Continent, and from other localities in southern England and Wales. However, *V. membranacea* does not occur over most of the range of *F. juncifolia* in eastern England and Scotland, while *F. juncifolia* is absent from those parts of south-eastern Ireland, central and northern Wales, and north-western England where *V. membranacea* occurs.

Hybrids between *F. rubra* and *V. longiseta* should also be sought in south-western Europe.

The morphological distinction between the pentaploid and hexaploid hybrids is narrow and may well disappear with the discovery of further hexaploids. In particular, hybrids involving *F. juncifolia* would be very difficult to distinguish from those involving large-glumed variants of *F. rubra*, especially if the latter prove to be octoploid. As far as we are aware there are no chromosome counts of most of the large-glumed varieties of *F. rubra* (vars. *junceae*, *barbata* and *grandiflora*), but Willis & King (1968) found their example of var. *multiflora* to be hexaploid. Huon (1970) reported that vars. *littoralis* Meyer and *pruinosa* (Hackel) Howarth are hexaploid, and our hexaploid *F. rubra* from Banff is also referable to var. *pruinosa*, but both these varieties are short-glumed and in Fig. 3 would fall well outside the '*F. juncifolia*-zone'.

Arguments both for and against the naming of hybrids have been vigorously made and there is no clear consensus. In the Gramineae, hybrids have in the past usually received binomials and there is scarcely a naturally occurring intergeneric hybrid combination without a valid hybrid-genus name. Hence, in naming these two *Festuca* × *Vulpia* hybrids, we are not only following our own preferences but also traditional practice. Moreover we are delighted to be able to associate these two plants with two of our leading agrostologists, C. E. Hubbard and A. Melderis.

DESCRIPTIONS OF NEW HYBRIDS

× ***Festulpia* Melderis ex Stace & Cotton, hybr. nom. nov.** (= *Festuca* L. × *Vulpia* C. C. Gmel.)

The name × *Festulpia* had already been suggested to us by A. Melderis (1972 pers. comm., BM *in sched.*).

× ***Festulpia hubbardii* Stace & Cotton, hybr. nov.**

Hybrida inter *Festuca rubra* L. *sensu stricto* et *Vulpia membranacea* (L.) Dum.

Gramen perenne rhizomatibus extravaginalibus et intravaginalibus, culmi 15–40 cm alti, ± erecti, laeves, glabri, caespitosi vel dispersi. Foliorum vaginae integrae, tubulosae, mox demum fissae, basilares rubrae, pilosae; laminae carinatae, conduplicatae, saepe demum convolutae, glabrae, laeves; ligulae breves, usque ad 0.3 mm longae.

Panicula 3.5–8.5 cm longa, erecta vel paulo nutans, effusa vel ± contracta, dimidio supero simplex, dimidio infero ramulis brevibus 2–3-spiculatis, vagina summa distans; rhachis scabra, angularis.

Spiculae 8.5–12.0 (15.5) mm longae (aristis exclusis), 4–6-florae, pedicellis 1.5–3.5 mm longis, gracilibus, leviter scabris, ad apicem incrassatis. Glumae binae, persistentes, inaequales: inferior 2.4–4.4 mm longa, superiore circa dimidio brevior, 1-nervia, acuminata; superior 5.2–8.0 mm longa (arista inclusa), 3-nervia, brevi-aristata ad 1.5 mm longa. Lemma 6.0–9.5 mm longum (arista exclusa), non persistens, lanceolatum, obscure 5-nervium, leviter scabrum, glabrum vel paulo pubescens, in aristam tenuem 2.0–5.5 mm longam sensim

acuminatum. Stamina 3; antherae 1.5–2.0 mm longae, per anthesin exclusae; pollinis grana sterilia, inchoata. Caryopsis nulla. Chromosomatum numerus $2n = 35$.

HOLOTYPUS: Channel Isles: Guernsey: Vazon, on consolidated sand with *F. rubra* and *V. membranacea*. 17 June 1953. C. E. Hubbard 13609 (K)

× *Festulpia melderisii* Stace & Cotton, **hybr.nov.**

Hybrida inter *Festuca juncifolia* St Amans et *Vulpia membranacea* (L.) Dum.

Hybridae × *Festulpia hubbardii* Stace & Cotton (*Festuca rubra* L. *sensu stricto* × *Vulpia membranacea* (L.) Dum.) similis, sed culmis robustioribus, dispersioribus, panícula usque ad 11.5 cm longa. gluma inferiore 3.5–7.2 mm longa, gluma superiore 8.0–11.5 mm longa, (arista inclusa), lemmate 9.5–11.5 mm longo (arista exclusa), paulo vel dense pubescenti differt.

Pollinis grana sterilia; caryopsis nulla. Chromosomatum numerus $2n = 42$.

HOLOTYPUS: England: W. Sussex: Littlehampton, on mobile sand-dunes by the golf-course, with *F. rubra*, *F. juncifolia* and *V. membranacea*. 17 July 1972. A. Melderis & C. A. Stace (BM)

ACKNOWLEDGMENTS

We are grateful to many people for supplying information and specimens; to the curators of the herbaria at the British Museum (Natural History), Royal Botanic Gardens, Kew, and the Manchester Museum for permission to consult their collections; and to the authorities at Kew for permission to remove caryopses for chromosome counts. In particular we wish to thank Dr A. Melderis for numerous discussions and helpful comments; M. D. Hooper, for supplying us with the results of his chromosome studies and giving us permission to publish them; Professor A. J. Willis, for helpful comments and suggestions; A. Newton, for correcting our Latin descriptions; and Mrs J. Burrow, for making most of the chromosome counts of *F. rubra sensu lato* and for other technical assistance. The research was carried out while R.C. was receiving an S.R.C. studentship.

REFERENCES

- AUQUIER, P. (1971). Le problème de *Festuca rubra* L. subsp. *arenaria* (Osb.) Richt. et de ses relations avec *F. juncifolia* St-Amans. *Lejeunia*, **57**.
- FERNANDES, A. & QUEIRÓS, M. (1969). Contribution à la connaissance cytotoxonomique des Spermatophyta du Portugal. *Bolm Soc. broteriana*, Sér. 2, **43**: 3–140.
- FREIJSEN, A. H. J. & HEERES, E. (1972). Welke soort rood zwenkgras (*Festuca rubra* s.l.) komt voor in de jonge kustduinen van Voorne en die van overig Nederland? *Gorteria*, **6**: 57–61.
- FREIJSEN, A. H. J. & HEUSDEN, H. T. A. VAN (1965). *Festuca rubra* L. op Terschelling. *Gorteria*, **2**: 154–158.
- GREGOR, J. W. (1954). Herbage plants and geneecology. *Ann. Rep. Scott. Pl. Breed. Stn*, **1954**: 23–26.
- HACKEL, E. (1882). *Monographia festucarum europaeorum*. Kassel & Berlin.
- HOWARTH, W. O. (1924). On the occurrence and distribution of *Festuca rubra*, Hack. in Great Britain. *J. Linn. Soc., Bot.*, **46**: 313–331.
- HUBBARD, C. E. (1954). *Grasses*. Harmondsworth.
- HUBBARD, C. E. (1968). *Grasses*, 2nd ed. Harmondsworth.
- HUON, A. (1970). Les fêtuques de l'ouest de la France. Recherches de biosystématique et de biogéographie. *Bot. Rhedonica*, Sér. A, **9**.

- KJELLQVIST, E. (1961). Studies in *Festuca rubra* L., 1. Influence of environment. *Bot. Notiser*, **114**: 403–408.
- KJELLQVIST, E. (1964). *Festuca arenaria* Osb. – a misinterpreted species. *Bot. Notiser*, **117**: 389–396.
- LITARDIÈRE, R. DE (1950). Nombres chromosomiques de diverses Graminées. *Bolm Soc. broteriana*, Sér. 2, **24**: 79–87.
- MAUDE, P. F. (1940). Chromosome numbers in some British plants. *New Phytol.*, **39**: 17–32.
- MELDERIS, A. (1955). A hybrid between *Festuca rubra* and *Vulpia membranacea*. *Proc. bot. Soc. Br. Isl.*, **1**: 390–391.
- MELDERIS, A. (1957). *Festuca rubra* var. *arenaria* × *Vulpia membranacea*. *Proc. bot. Soc. Br. Isl.*, **2**: 243.
- PATZKE, E. (1970). Untersuchungen über Wurzelfluoreszenz von Schingelarten Gliederung der Verwandtschaftsgruppe *Festuca* Linné. *Senckenb. biol.*, **51**: 255–276.
- ROUX, J. (1960). À propos de *Vulpia fasciculata* (Forsk.) Fritsch. (= *V. uniglumis* Dumort. = *V. membranacea* Link). *Naturalia monspel.*, Sér. bot., **10**: 105–107.
- SKALÍNSKA, M., JANKUN, A. & WCISŁO, H. (1971). Studies in chromosome numbers of Polish angiosperms, eighth contribution. *Acta biol. cracov.*, *Bot.*, **14**: 55–102.
- WILDE-DUYFJES, B. E. E. DE (1964). *Festuca ovina* L., *s.l.* en *Festuca rubra* L., *s.l.* in Nederland. *Gorteria*, **2**: 40–48.
- WILDE-DUYFJES, B. E. E. DE (1973). Over de twee ondersoorten van *Festuca rubra* L. in Nederland. *Gorteria*, **6**: 128–131.
- WILLIS, A. J. (1967). The genus *Vulpia* in Britain. *Proc. bot. Soc. Br. Isl.*, **6**: 386–388.
- WILLIS, A. J. & KING, S. M. (1968). A broad-leaved variety of *Festuca rubra* L. *Proc. bot. Soc. Br. Isl.*, **7**: 143–149.

(Accepted November 1973)