Alopecurus × *plettkei* Mattfeld in Britain

P. J. O. TRIST

Glovers, High St, Balsham, Cambridgeshire CB1 6DJ

and

M. J. WILKINSON

Department of Botany, The University, Leicester LE1 7RH

ABSTRACT

The hybrid *Alopecurus* × *plettkei* Mattfeld (*Alopecurus bulbosus* Gouan × *A. geniculatus* L.) is reported new to Britain. Its variation, distribution, habitat and growth performance are discussed.

INTRODUCTION

Alopecurus × *plettkei* Mattfeld, the sterile hybrid between *A. bulbosus* Gouan and *A. geniculatus* L., is known from Belgium, Germany and the Netherlands (Hubbard 1975). It was first found in Britain by Brian Wurzell on 27 May 1977, and confirmed by C. A. Stace, from marshes west of Glynde Reach, near Lewes, E. Sussex, v.c. 14, GR 51/465.094. It has subsequently been found at several sites in S. Hants. (v.c. 11), W. Kent (v.c. 16) and E. Suffolk (v.c. 25). The following account describes the morphology, anatomy, phenology, cytology and ecology of the British populations.

DESCRIPTION OF *ALOPECURUS* × *PLETTKEI*

Perennial, erect and densely tufted or sometimes forming mats of decumbent spreading culms, compactly tufted or occasionally solitary, frequently branched from nodal growth, with some internodes arcuate. Culms (15–)18–77(–93) cm, weak, with (2–)4–13 nodes at uneven intervals, from 5–15 cm below the panicle, over the entire length of the culm; lowest internode 1–33 × 1–6(–7·5) mm, very swollen to slightly swollen, extremely variable in shape, with a smooth or ridged surface, sometimes with one or two slightly bulbous swellings but generally straight sided. Basal leaves (8–) 15–20 (–38) cm; culm leaves hairless, 1·5–15 cm × 0·7–3·3 mm, finely pointed, flat or infolded, minutely scabrid on margins and veins; sheaths smooth, the uppermost often inflated; ligule 1·8–4·5 mm, broadly obtuse, membranous.

Panicles 1·4–4·5 (–6·3) cm × 2·5–5 mm; dense, narrowly cylindrical, spike-like, bluntly pointed. Pedicels 0·4–1 mm. Spikelets oblong, 2·5–3 mm, flattened, 1-flowered, falling entirely at maturity. Glumes equal, 2·5–3 mm, free to the base, narrowly oblong, broadly obtuse, exceeding lemma by (0·05–)0·1–0·4(–0·5) mm, 3-veined with uneven-length hairs on the keel and margins. Lemma 2–3 mm, keeled, smooth, narrowly oblong, membranous, 4–veined, sometimes weakly hairy in distal quarter, awned on the back c. 1 mm from the base; awns 3–5·6 mm, protruding 1·0–2·8 (–3·5) mm beyond the glumes. Anthers 1–1·5 mm, indehiscent, containing imperfect pollen 0(–4)% stainable in Muntzing's aceto-carmine, 20–28 μm in diameter.

Leaves in section: adaxial and abaxial epidermises with cells of irregular size and shape, with small bulliform-cells on the adaxial surface between veins; small islets of sub-epidermal sclerenchyma usually occur in association with the veins.

Abaxial epidermis with solitary stomata 35–49 μm long, in continuous or semi-continuous rows,

47–95 μm apart in continuous rows; short-cells (other than stomata) (0–)1–4(–6) per 100 μm², 27–73% being hook-cells or prickles; long-cells (60–)100–220 μm.

Adaxial epidermis with fewer stomata than abaxial epidermis but with (2–)4–10 non-stomatal short-cells per 100 μm²; long-cells 90–380 μm long.

A comparison of *A.* × *plettkei* and its parental species is given in Table 1.

TABLE 1. A COMPARISON OF *A. BULBOSUS, A.* × *PLETTKEI* AND *A. GENICULATUS*

Character	*A. bulbosus*	*A.* × *plettkei*	*A. geniculatus*
Culm	erect	erect to spreading	spreading, geniculate
Culm length (cm)	11–29	(15–)18–77(–93)	15–38
No. of branches per culm	0	0–3(–7)	0–3(–5)
No. of nodes per culm	1–4(–5)	(2–)4–13	2–6(–8)
Rooting culm	absent	absent or present	absent or present
[a]Basal internode swelling (mm)	(1–)2–4·5(–6·0)	(0–)0·5–2·2	(–0·5–)0–1·0(–1·5)
Basal internode length (cm)	0·4–2	0·6–33	10–35
[b]'Twin' basal swollen internodes	present or absent	usually absent	absent
Cauline leaf width (mm)	0·5–3·5	0·7–4·5	0·7–5·0
Cauline leaf	infolded	usually flat	flat
Ligule (mm)	1·6–4·0	1·8–4·5	2·0–5·5
Panicle length (cm)	1·3–4·4(–5·4)	1·4–6·3	(2·0–)2·6–5·0
Spikelet length (mm)	2·5–3·3	2·5–3·0	2·0–3·0
Glumes	lanceolate, acute. Short hairs on keel and margins	lanceolate, acute to obtuse. Uneven long and short silky hairs on keel and margins	lanceolate, obtuse. Silky hairs on keel and shorter appressed hairs from middle to base of keel
Total awn length (mm)	(3·4–)4·0–5·3(–6·5)	(3·0–)4·5–5·5	3·0–4·5(–5·0)
Awns	exceeding glumes by 3–4 mm	exceeding glumes by 1·0–3·5 mm	exceeding glumes by 0·8–1·7 mm
Lemma	hairy at tip	hairs at tip present (often few) or absent	usually no hairs at tip
Anther length (mm)	1·2–2·2	1·0–1·5	0·8–1·7
Distance between glumes and lemmas (mm)	0·2–0·7(–0·9)	(0–)0·1–0·4(–0·5)	(0–)0·1–0·35(–0·55)
Chromosome no.	14, 21, 28	21	28

[a] Difference between basal internode width and stem width.
[b] Adjacent basal internodes swollen.

The hybrid is very variable morphologically and anatomically and cannot be reliably identified with any one character. Indeed, even pollen sterility can break down as a diagnostic character; specimens of both *A. bulbosus* and *A. geniculatus* have been recorded with highly sterile pollen (<1% stainable with Muntzing's aceto-carmine).

All hybrids were observed to contain at least some characteristics from both parents, although all were invariably much more similar to one parent than to the other. Whilst scatter diagrams can be used to show some degree of intermediacy (Fig. 1), overall intermediacy is best represented on a percentage hybrid index. Representatives of *A. bulbosus*, *A.* × *plettkei* and *A. geniculatus* were compared on a percentage hybrid index according to the scheme given in Appendix 1. A histogram constructed from the index (Fig. 2) shows that the individual plants fall into two relatively broad but distinct groups, corresponding to the index range of the two parental species. The score of the hybrids falls at the margins of the two parents and is in no case entirely intermediate between them. Hence, there are both '*A. geniculatus*-like' and '*A. bulbosus*-like' representatives of *A.* × *plettkei*, but apparently no nearly intermediate representatives.

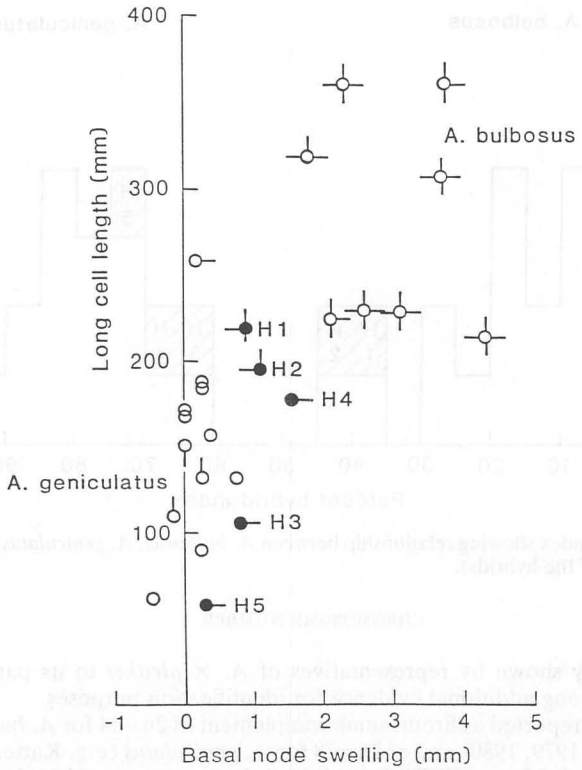

FIGURE 1. Scatter diagram showing specimens of *A. bulbosus*, *A. geniculatus* and some representatives of the hybrid between them, *A.* × *plettkei* (H1–5).

KEY

○ <25% of short-cells are prickles/hook-cells (abaxial surface)
○– >25% of short-cells are prickles/hook-cells (abaxial surface)
○ glumes obtuse
♀ glumes obtuse to acute
♀ glumes acute
○ leaves flat
–○ leaves mostly infolded
○ rooting nodes absent
♂ rooting nodes present
○ tetraploid or diploid
● triploid

Hybrid localities: H1, GR 63/505.074; H2, GR 50/514.994; H3, GR 41/362.144; H4, GR 51/465.094; H5, GR 40/170.918

The decumbent growth habit of the '*A. geniculatus*-like' hybrid makes it unlike either of its two parents. The panicle is often hidden under leaves or just turning up beyond the leaf-tips. The lengths of the stem, panicle, cauline and basal leaves and the widths of the panicle and cauline leaves are extremely variable. On open ground, decumbent stems readily develop from 4–5 nodes, producing branches which in total produce 15–50 leaves on a stem. This nodal branching is seen in *A. geniculatus* but with less leaf production. This hybrid is not a robust plant: its stems, unlike those of either parent, need support from surrounding vegetation.

Two features are significant for field recognition: the number of nodes and the number of leaves per culm, which both far exceed those of either of the parents.

The '*A. bulbosus*-like' hybrids are less distinctive in the field but may be identified by their intermediate internode swelling (0·5–2 mm), their variable glume-tip shape (obtuse to acute), their lemmas which are only weakly hairy in the distal third, their fairly erect culms, and their '*A. geniculatus*-like' awn length (3–4·4 mm).

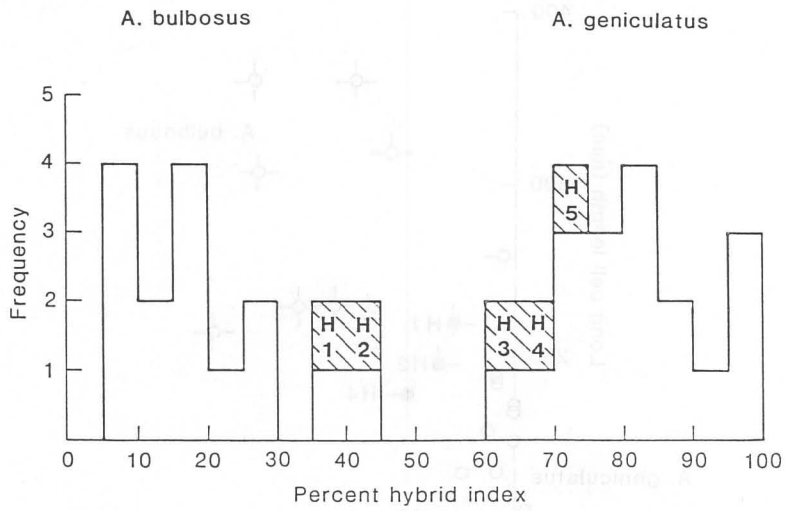

FIGURE 2. Percent hybrid index showing relationship between *A. bulbosus*, *A. geniculatus* and *A.* × *plettkei* (H) (see Fig. 1 for localities of the hybrids).

CHROMOSOME NUMBER

Given the close affinity shown by representatives of *A.* × *plettkei* to its parents, chromosome number can provide strong additional evidence for identification purposes.

Several authors have reported a chromosome complement of 2n=14 for *A. bulbosus* (e.g. Maude 1939; Sieber & Murray 1979, 1980) and of 2n=28 for *A. geniculatus* (e.g. Kattermann 1930; Sieber & Murray 1979). Sieber & Murray (1979) investigated chromosome numbers in *Alopecurus* species at several stations on the south coast of England. For *A. bulbosus* they recorded that, in addition to diploids, triploids and tetraploids were found growing together in a mixed population from Seasalter, E. Kent, v.c. 15. Of the eight plants studied three were diploid, three were triploid and two were tetraploid. The chromosome numbers were 2n=14, 21, and 28. In a subsequent work (Sieber & Murray 1980) it was concluded on the basis of pairing behaviour during meiosis that the triploid and tetraploid plants were autopolyploids.

The same authors (Sieber & Murray 1979) found 2n=28 in natural populations of *A. geniculatus* from Buxton, Derbys., v.c. 57. Their observations on the meiotic and mitotic behaviour of two tetraploid species of *Alopecurus* agree with those of Johnsson (1941) and support the suggestion that *A. pratensis* is an allotetraploid and *A. geniculatus* is an autotetraploid.

Dr P. E. Brandham of Kew has recently confirmed that material of *A.* × *plettkei* on the Stanpit South Marsh, Christchurch, S. Hants., v.c. 11, (Sept. 1985) is triploid (2n=21). We have also confirmed the following hybrids to be triploid: two specimens from Stanpit South Marsh, Christchurch, S. Hants, GR 40/170.918 and three specimens from Glynde Reach, nr. Lewes, E. Sussex, v.c. 14, GR 51/465.094. It is of some importance to remember that because specimens of *A. bulbosus* exist with chromosome numbers of 2n=21 and 2n=28, there may be specimens of *A.* × *plettkei* derived from such plants with chromosome numbers 2n=21–28. Therefore it is possible that there are tetraploid representatives of *A. bulbosus* and *A.* × *plettkei* as well as of *A. geniculatus*. Furthermore, although the possession of 21 chromosomes is strong additional evidence of hybrid status it is not a guarantee since triploid representatives of *A. bulbosus* also occur.

PHENOLOGY

In *A.* × *plettkei* the anthers are indehiscent and produce very little pollen; that produced is largely sterile. Presumably reproduction is almost entirely by vegetative means by growth from swollen

stem bases (particularly in the '*A. bulbosus*-like' hybrids) and by rooting at culm nodes (particularly in the '*A. geniculatus*-like' hybrids). In cultivation, the decumbent culms of the '*A. geniculatus*-like' hybrids will develop 4–5 nodes which are quick to root and produce leaves 10–35 cm long within two weeks. This is also seen in the wild, where propagation has taken place on bare ground.

In cultivation, the autumn leaf growth of the hybrids survives a fairly severe winter up to mid-February. This growth then withers and is quickly followed by spring growth with culms appearing before the end of April. Panicles break from the sheath throughout May but their progress is slow; stems with partial panicle exsertion of ± 2·5 cm in mid-May can take a further 15 days for the panicle to break fully to a length of 4·5–5·8 cm. At this stage the plants are light green in colour with a slightly glaucous sheath as in *A. bulbosus*. All flowering is completed before the end of June, when the leaves start to wither. By early July new growth is developing, as the panicles of previous growth are breaking up.

This hybrid is vigorous and responds to management by grazing and cutting by extending its growing season. At Glynde Reach, E. Sussex, in 1986 the marsh had been cut for hay in July and on 8th August there was fresh *A.* × *plettkei* growth with panicles only half exserted. At Nursling N.R., S. Hants., v.c. 11, in late July, in an area grazed by cattle earlier in the year, *A.* × *plettkei* had regrown, with decumbent culms up to 77 cm long and with a considerable bulk of basal leaves. To consider the hybrid's capacity for propagation, three basal internodes of 2 cm in length were put into autumn cultivation, with subsequent production of 93 culms. Single internodes autumn-planted will produce 4–13 tillers by February.

THE DISTRIBUTION OF *ALOPECURUS* × *PLETTKEI* IN BRITAIN

1. South Hampshire, v.c. 11: marshes subject to occasional tidal overflow. Lower Test Nature Reserve, Nursling, GR 41/368.145 and 41/362.144, *R. P. Bowman*, 1978 (**CGE**, **K**, **herb. R.P.B.**, **herb. P.J.O.T.**). The Furlongs, Redbridge, GR 41/364.137, *R.P. Bowman*, 1978 (**CGE**, **K**, **herb. R.P.B.**, **herb. P.J.O.T.**). Unprotected coastal marshes, Stanpit South Marsh, Christchurch, GR 40/170.918, *S. R. Davey*, 1980 (**CGE**, **herb. R.P.B.**, **herb. P.J.O.T.**, **herb. R.M. Walls**). Derelict marsh subject to tidal inflow, Keyhaven, GR 40/305.916, *R.P. Bowman*, 1986 (**herb. R.P.B.**).
2. East Sussex, v.c. 14: managed grazing marshes, south-east of Decoy Wood and adjacent to Glynde Reach, near Lewes, GR 51/465.094, *B. Wurzell*, 1977 (**CGE**, **LTR**, **herb. P.J.O.T.**, **herb. B.W.**). Disturbed river wall-berm, east bank of R. Cuckmere, near Exceat bridge, Seaford, GR 50/514.994, *Lady R. FitzGerald*, 1987 (**herb. P.J.O.T.**, **herb. R.F.**).
3. West Kent, v.c. 16: wet track in rough grazing, upland of marsh level, Higham marshes, Church Street, near Higham, east of Gravesend, GR 51/713.742, *Lady R. FitzGerald*, 1987 (**herb. P.J.O.T.**, **herb. R.F.**).
4. East Suffolk, v.c. 25: managed grazing marshes, Castle Farm, Burgh Castle, GR 63/473.058, *R. P. Libbey*, 1980 (**LTR**). Humberstone marshes, south of Breydon Water near Great Yarmouth, GR 63/505.074, *P.J.O. Trist*, 1982 (**herb. P.J.O.T.**).

Specimens collected from Lewes and from Burgh Castle resemble *A. bulbosus* more closely than *A. geniculatus*. Specimens collected from the remaining sites show a stronger resemblance to *A. geniculatus*.

ECOLOGY

The habitat of *Alopecurus* × *plettkei* is coastal marsh that is inadequately protected from tidal water owing to an absence or a breakdown in sea defences. These areas are occasionally shallowly flooded for a few hours at periods of high spring and autumn tides, when tidal water runs up the ditches and overflows on the land. A saline deposit is built up in the soil, more particularly in the marsh depressions and in the furrows on marshes that were at one time under cultivation.

A. × *plettkei* thrives in a soil texture of organic loam with additions of alluvium. It has a lower salt tolerance than *A. bulbosus* and a preference for an open position at or slightly above marsh level. It will colonise the bare margin of a depression, but not the depression itself, showing its preference for drainage, as opposed to *A. bulbosus* which will thrive in the water-logged bed of a depression. At

Stanpit South Marsh, Christchurch, where there are old grips, and rills in adjacent saltings, the hybrid colonises the margin and not the bed of grips that support *Salicornia* spp., an indication of a high salt level (too high for *A. bulbosus*).

At Keyhaven in a small 0·5 ha marsh, *A.* × *plettkei* has been found only in two small colonies at the back of the marsh, just above the general level, so that a tide lapping near the area would rapidly run off. Here *A. bulbosus* is widespread but thinly spaced among *Glaux maritima*, *Puccinellia maritima* and some *Aster tripolium* in a soil with 0·5% NaCl. During the warm months of the year it is likely that this percentage is higher and that *A. bulbosus* is here at its limit of salt tolerance. At The Furlongs, Redbridge, there is a similar demonstration of the difference in saline tolerance of *A. bulbosus* and *A.* × *plettkei*. The sward, subject to fairly frequent tidal over-spills, is almost entirely a simple mixture of *Puccinellia maritima* and *Agrostis stolonifera* with some *Aster tripolium*. Soil samples taken contained a range of 0·4–0·5% NaCl, but the presence of *Aster tripolium* suggested a higher percentage in June–July. *A. bulbosus* was thinly distributed and only occasionally small, weak plants of *A.* × *plettkei* were found on low elevations of old ditch spoil where drainage would be rapid following tides.

The marshes on the Lower Test N.R. at Nursling have probably never been disturbed. The surface levels are therefore uneven, with isolated areas of halophytes demonstrating saline deposits from occasional flooding. In an unimproved marsh, *Eleocharis uniglumis*, *Festuca rubra*, *F. arundinacea*, *Agrostis stolonifera* and *Trifolium fragiferum* are common associates, but, where *A. bulbosus* is present in lower levels, these plants are supplemented by *Glaux maritima*, *Juncus gerardii*, *Plantago maritima*, *Ranunculus sceleratus* and *Triglochin maritima*. *A.* × *plettkei* would be found in open areas of *Agrostis-Festuca* but not, or rarely, in the lower and wetter areas of *A. bulbosus* and its associates.

On the Lower Test N.R. the limits of variation of salt content of soil samples taken in August at 15 cm depth were 0·08–0·48% NaCl. This range will vary with the temperature of the season when samples are taken, and seasonal factors diluting sea water. Both at Redbridge by Southampton Water and at Stanpit South Marsh by Christchurch, for instance, there is a complicated double tide which increases salinity on the one hand, and an outflow of fresh-water from the R. Test, Avon and Stour which diminishes salinity on the other.

The hybrid was abundant on the site where it was first recorded in 1977 (Glynde Reach, v.c. 14) and occupied wet areas over a large part of G.R. 51/46.09. No *Alopecurus bulbosus* was present in 1977; it was last recorded near the river bank in 1962 by B. Wurzell, C. A. Stace and others on a London Natural History Society field day. The site would have been in the area of a now derelict ditch below the high bank containing the river. Over-spills of saline water no longer occur. Sometime prior to 1975, a tidal flap and pump were installed on The Reach at the point just above the A27 road, preventing land flooding. The former wet state of the hybrid site is still witnessed by small grips crossing the marsh and connecting to boundary ditches. The marsh is now dry with a diminishing amount of *Alopecurus* × *plettkei*. A soil sample taken in August 1986 at 15 cm from the bed of a grip, where only a few plants of the hybrid were seen, contained 0·01% NaCl. There was no plant indicative of salinity in the sward or in the river which rejoiced with *Nuphar lutea* on its surface.

A. × *plettkei* would not make a constituent of a grass-seed mixture. It produces long decumbent stems which are weak and lie over the ground and would therefore be smothered by tall marsh grasses such as *Festuca arundinacea*, *Agrostis stolonifera* and *Elymus repens*. The *A. geniculatus* parent of the hybrid is common on most coastal marshes, but its other parent, *A. bulbosus*, is still comparatively rare, in spite of the fact that it has been removed from the Red Data lists (Perring & Farrell 1983). This hybrid is able to continue to occur where *A. bulbosus* is extinct, as on the marshes by Glynde Reach, but from observations of this taxon in cultivation we consider its perennial life is limited.

IS *A.* × *PLETTKEI* A THREAT TO THE SURVIVAL OF *A. BULBOSUS*?

It has been suggested that the spreading growth of *A.* × *plettkei* may have a smothering affect on *A. bulbosus* and may pose a threat to its survival. This is unlikely. The growth period of the two taxa does not overlap. *A. bulbosus* is fully developed and flowering by the last week in May to the first

week in June, and, before the end of July, leaves and culms have died back when cattle-treading soon disperses the plant remains so that *A. bulbosus* is difficult to trace until the following year, except by exploration for the swollen stem bases (Trist 1981). *A.* × *plettkei* has an extended growing season and the plants which over-winter die back in July only to be immediately replaced by new growth which continues into September. Thus *A. bulbosus* has completed its growth in early summer while strong growth of the hybrid continues throughout July and August.

There is a significant difference in the habitat of the two taxa. The hybrid is seen on average mid-marsh level and not below, and preferably in a position of better drainage which is slightly above the average level. *A. bulbosus* prefers a reasonably constant moisture supply and has a tolerance to salinity of the order of 0·4–0·5% NaCl. It is found on the higher margin of saltings and often in the low areas and furrow depressions of marsh adjacent to tidal rivers, which gives an indication of tolerance or even preference for salinity. Although it can be cultivated for several years in the absence of salinity and a constant moisture supply, it eventually reverts to a poor state and dies. *A.* × *plettkei* behaves as a perennial but it is likely that it is short-lived.

ACKNOWLEDGMENTS

We would like to thank Dr R. Page, Conservation Officer of the Hampshire and Isle of Wight Naturalists Trust, for permission to study *A.* × *plettkei* on the Lower Test Nature Reserve. Thanks are also due to Marian Reed, R. M. Walls, Paul Bowman, and Rosemary FitzGerald for help in the field; Dr B. Davies (of M.A.F.E.) for arranging salt analyses; Dr P. Brandham of Kew for a hybrid chromosome count; and Mrs Sue Ogden for drawing the Figures. We are grateful for the help and advice of Professor C. A. Stace and C. D. Preston.

REFERENCES

HUBBARD, C. E. (1975). *Alopecurus* L., in STACE, C. A., ed. *Hybridization and the flora of the British Isles*, p. 585. London.

JOHNSSON, H. (1941). Cytological studies in the genus *Alopecurus*. *Acta Univ. Lund* **37**: 1–43.

KATTERMANN, G. (1930). Chromosomenuntersuchungen bei Gramineen. *Planta* **12**: 19–37.

MAUDE, P. F. (1939). The Merton Catalogue. A list of the chromosome numerals of species of British flowering plants. *New Phytol.* **38**: 1–31.

PERRING, F. H. & FARRELL, L. (1983). *British red data books: 1. Vascular plants*, 2nd ed., p. 81. Lincoln.

SIEBER, V. K. & MURRAY, B. G. (1979). The cytology of the genus *Alopecurus* (Gramineae). *Bot. J. Linn. Soc.* **79**: 343–355.

SIEBER, V. K. & MURRAY, B. G. (1980). Spontaneous polyploids in marginal populations of *Alopecurus bulbosus* Gouan (Poaceae). *Bot. J. Linn. Soc.* **81**: 293–300.

TRIST, P. J. O. (1981). The survival of *Alopecurus bulbosus* Gouan in former sea-flooded marshes in East Suffolk. *Watsonia* **13**: 313–316.

(*Accepted May 1988*)

APPENDIX: SCORING SCHEME FOR HYBRID INDEX

	A. bulbosus	Intermediate	*A. geniculatus*
Score	0	1	2
Vegetative characters			
No. of nodes per culm	3	3–4	4
No. of branches per culm	0	N/A[a]	1
Rooting nodes	absent	N/A	absent
Basal node swelling (mm)	(1–)2–4·5(–6·0)	(0–)0·5–2·2	(–0·5–)0–1·0(–1·5)
'Twin' basal swollen internodes	present	N/A	absent
Basal leaves infolded	mostly infolded	N/A	mostly flat
Stem	erect	fairly erect or spreading	spreading, geniculate
Flag-leaf width (mm)	1–2	2·01–3	>3
Lower culm-leaf width (mm)	1–2	2·01–3	>3
Reproductive characters			
Panicle length (cm)	2·0–2·5	2·51–4·4	>4·4
Panicle width (cm)	<3·5	3·5–4·5	>4·5
Glume sharpness	acute	acute to obtuse	obtuse
Awn length (mm)	>5	4–5	<4
Hairs at top of lemma	present	sparse	absent
Distance between glume tips & lemma tip (mm)	>0·4	0·25–0·4	<0·25
Pollen diameter (μm)	<29·4	29·4–33·0	>33·0
Abaxial epidermis			
% short-cells being hooks/prickles	0–20	21–37	>37
Short-cell frequency (per 0·11 mm^2)	0	1–2	>2
Mean long-cell length (μm)	>200	180–200	<180
Presence of rows of short-cells	absent	N/A	present
Distance between stomata in continuous rows (μm)	>90	70–90	<70
Stomatal length (μm)	<38	38–41	>41
Adaxial epidermis			
Mean long-cell length (μm)	>210	190–210	<190
Short-cell frequency (per 0·11 mm^2)	<3	3–4	>4
Prickles above nerves	present	N/A	absent

[a] N/A: not applicable