Observations on some critical Bromegrasses

P. M. SMITH

Department of Botany, University of Edinburgh

ABSTRACT

A group of critical bromegrasses (in *Bromus* L. section Bromus) is defined. Critical characters which may be used to distinguish the taxa are listed and illustrated. The status, variation and relationships of *B. grossus* Desf. ex Lam. & DC., *B. secalinus* L., *B. pseudosecalinus* P. M. Smith, *B. commutatus* Schrad., *B. racemosus* L. and *B. multiflorus* J. E. Smith *non* Weigel are examined, and a key is provided. It is suggested that *B. commutatus* and *B. racemosus* hybridise in Britain. An account of the known distribution of *B. pseudosecalinus* is given, with a map.

INTRODUCTION

The grasses in the annual section Bromus of the genus *Bromus* L. (Smith 1970, 1972) have for two centuries been regarded as a critical group. This paper attempts to identify the reasons for this with respect to species which are found in Britain. Species involved in the discussion, not all of which are native to Britain, are listed in Table 1 with their somatic chromosome numbers. The confusion of species in this section has been partly due to the difficulty of communicating certain of their subtle differences on the printed page. It is hoped that the key, the table of principle differences (Table 2) and the illustrations, provided below, will lessen this problem.

This account does not discuss the bromegrasses related to the *Bromus* hordeaceus aggregate, which were the subject of a previous paper (Smith 1968a). For reasons developed in the text, the present account concentrates on six taxa only, viz. *Bromus multiflorus*, *B. grossus*, *B. secalinus*, *B. pseudosecalinus*, *B. commutatus* and *B. racemosus*.

TABLE 1. CRITICAL SPECIES OF *BROMUS* SECTION BROMUS MENTIONED IN THE TEXT

| Name of species | Somatic chromosome number (2n) |
|--------------------------------|---|
| B. hordeaceus L. | 28 |
| B. lepidus Holmberg | 28 |
| B. racemosus L. | 28 |
| B. commutatus Schrad. | 28 |
| B. interruptus (Hack.) Druce | 28 |
| B. arvensis L. | 14 |
| B. secalinus L. | 28 |
| B. grossus Desf. ex Lam. & DC. | 28 |
| B. bromoideus (Lej.) Crép. | 28 |
| B. pseudosecalinus P. M. Smith | well its brie, bed nace 14 and a national a |
| B. sauarrosus L. | 14 |

P. M. SMITH

HISTORICAL ASPECTS

Linnaeus changed his concept of some of the species of Bromus several times (Smith 1968a) and when his specific names were uncritically taken up by botanists outside Sweden a number of mistaken typifications occurred. Linnaean binomials were applied not only to material of the wrong Linnaean species, but also to taxa unknown to Linnaeus himself. Gradually there arose a confused situation where the limits of no species were properly recognised, and where the synonymy grew more complex and intractable every year.

Some eighteenth century botanists appreciated the difficulty of ensuring the correct use of Linnaeus' binomials in other territories. One solution in critical genera was to lump all or most of the awkward species into a single taxon. Thus Hudson (1762) put them all into B. polymorphus Hudson.

Among the first efforts to clarify the taxonomy of these bromegrasses were those of Sir James Edward Smith. With the powerful advantage given by his personal acquisition of the Linnaean herbarium and library, he tried, not without some success, to correct the record, at least so far as the British flora was concerned. His Observations on the British species of Bromus (Smith 1798) marked a useful advance in our understanding of these very variable plants. Even though he included Brachypodium silvaticum (Huds.) Beauv. and B. pinnatum (L.) Beauv. in the genus, he decided that Linnaeus' Bromus giganteus should be transferred to Festuca.

In British material J. E. Smith was able to distinguish six species in the section Bromus, and he firmly discounted the idea that all were varieties of a single polymorphic species. These six species are listed below:

B. secalinus L.

B. racemosus L. B. multiflorus J. E. Smith non Weigel B. squarrosus L. B. hordeaceus L. (with var. nanus Weigel) B. arvensis L.

He satisfied himself that the Linnaean names he used were correctly applied. Since then, other studies of the Linnaean specimens (Munro 1861, Smith 1968a) have confirmed that these names applied to British material are compatible with Linnaeus' identifications of his own plants.

Not everyone was persuaded of the distinctness of these taxa. Bentham (1858) amalgamated B. arvensis, B. secalinus, B. hordeaceus and B. racemosus, together with a fifth species, B. commutatus Schrad., under B. arvensis. Such was Bentham's authority that this treatment was retained up to the last revised edition of his work.

Of J. E. Smith's six taxa, B. arvensis and B. squarrosus are now well understood and are known to occur only as casuals in Britain. The variation in *B. hordeaceus* L. has been discussed by Smith (1968a).

Holmberg (1924) used the texture of the glumes and lemmas to separate two groups of annual bromegrasses (Smith 1972). Of British species, B. hordeaceus, B. lepidus and B. interruptus fall into the group Molles, with thin, papery lemmas (Smith 1968a). Holmberg's second group, Coriacei, included species with thicker, hornier lemmas and glumes. The remaining three species from J. E. Smith's list, B. secalinus, B. racemosus and B. multiflorus, belong here.

Since the time of Linnaeus and J. E. Smith, other species with horny lemmas and glumes have been described, and all have at least a morphological affinity with northern and western European species included in Coriacei by Holmberg. Not all these species are well described or illustrated in the literature and not surprisingly they have often been poorly understood and confused by collectors. Seed proteins of all these species have now been studied serologically and found to be rather similar, with the exception of *B. pseudosecalinus* (Smith 1972). The list below is of the species with horny lemmas which are involved:

- B. bromoideus (Lej.) Crép.
- B. commutatus Schrad.
- B. grossus Desf. ex Lam. & DC.
- B. multiflorus J. E. Smith non Weigel

B. pseudosecalinus P. M. Smith B. racemosus L. B. secalinus L.

Bromus bromoideus is (or was, for it is probably extinct in the wild) an endemic of the Ardennes region of Belgium and France, where it contaminated fields of spelt (*Triticum spelta* L.). With improved seed-cleaning techniques and a decline in spelt cultivation, the weed species has declined in abundance and probably has now been lost. So closely is it related to *B. grossus* in terms of genetics, geographical distribution and morphology, that Tournay (1968) regarded it as a subspecies of that taxon. Nevertheless it is so easily identified by its unique marginal lemma tooth that it cannot be regarded as critical. For British botanists it can be of only academic interest.

The rest of the species are difficult to identify because of their variability and the subtlety of their diagnostic characters. Communication of accurate descriptions has been bedevilled by confusion of juvenile and depauperate states, and by the overweighting of trivial characters, e.g. spikelet indumentum. The six species can be arranged in three groups within which it is difficult to delimit and identify the constituent taxa. These three groups are discussed and illustrated below in terms of their similarities and differences and possible explanations of the variation observed. The principal distinguishing features of the five species which are here recognised are summarised in Table 2.

CLASSIFICATION AND BIOSYSTEMATICS

1. Bromus grossus Desf. ex Lam. & DC. B. multiflorus J. E. Smith non Weigel, and B. secalinus L.

Bromus grossus is a plant of spelt fields mainly in the Ardennes and has decreased in frequency with the decline of spelt as a crop (Cugnac & Camus 1936). It survives at least in Belgium (Tournay 1971 *in litt.*). Adaptations which it shows to life as a weed of cereal fields are similar to those more familiar to British botanists in the rye-brome, *B. secalinus*. These are chiefly the slow disarticulation of the spikelet and the large, longitudinally rolled or furrowed caryopsis which is enclosed by the inrolled lemma and mimics the size and shape of the grain of the cereal crop. The difficulty of separating weed and crop caryopses led to the wide distribution and abundance of *B. secalinus* and *B. grossus* in the recent past. Tournay (1968) meticulously studied the variation of these two taxa, and of their close relative *B. bromoideus*. The principal differences between the former two are incorporated in Table 2. They are completely interfertile (Cugnac & Camus 1936).

B. grossus is larger in all its parts than *B. secalinus*, but robust specimens of the latter have frequently been mistaken for *B. grossus*. On the basis of actual specimens, or measurements in the literature, Tournay (1968) concluded that

P. M. SMITH

TABLE 2. PRINCIPAL DISTINGUISHING FEATURES OF B. GROSSUS,B. SECALINUS, B. PSEUDOSECALINUS, B. COMMUTATUS ANDB. RACEMOSUS

| Character | Character-state | | | | | |
|---|-----------------------------------|-------------------------------|-----------------------------------|-----------------------------------|--|--|
| | B. grossus | B. secalinus | B. pseudo- secalinus | B. commutatus | B. racemosus | |
| Hairs on lower leaf-sheath | absent, rarely sparse | absent, rarely sparse | present | present | present | |
| Panicle-shape | spreading, later drooping | secund | erect, stiff | erect, later drooping | erect, narrow, sometimes drooping later | |
| Spikelet-length (mm) | 18-50 | 10-30 | 8-12 | 15-25 | 10-15 | |
| Spikelet-width (mm) | 9–13 | 5–9 | 2-4 | 4-6 | 3–5 | |
| Hairs on spikelet | present or absent | present or absent | absent | present or absent | absent | |
| Disarticulation of mature spikelet | slow | slow | slow | rapid | rapid | |
| Awns on glumes | always present | very rarely present | absent | absent | absent | |
| Lemma-length (mm) | 10-14 | 6.5-10 | 56 | 8-11 | 6.5-8 | |
| Shape of lemma in transverse section | ± terete | ± terete | ± terete | ± terete | somewhat compressed laterally | |
| Position of mature lemmas | divaricate | divaricate | divaricate | imbricate | imbricate | |
| Marginal angle of lemma | blunt | blunt, sometimes absent | blunt | blunt | absent | |
| Margins of mature lemma | rolled around caryopsis | rolled around caryopsis | rolled around caryopsis | free | free | |
| Lemma-apex | not cucullate | not cucullate | not cucullate | not cucullate | cucullate | |
| Anther-length (mm) | 2-3 | 1-2 | 1.25-1.75 | up to 1.5 | 1.5-3 | |
| Margins of mature caryopsis | inrolled | inrolled | inrolled | free | free | |
| Relative length of caryopsis | markedly shorter than lemma | equalling lemma | slightly shorter than lemma | slightly shorter than lemma | slightly shorter than lemma | |
| Thickness of mature caryopsis | thick | thick | thin | thin | thin | |
| Length of basal internode of rachilla (mm) | 1.5-2 | 0.75-1.5 | 0.5-0.75 | c 1.5 | 0.5-1 | |

B. grossus has been reliably recorded as an indigenous plant only in Belgium, France, Luxembourg, S. Germany, Switzerland, N. Italy, W. Austria and W. Czechoslovakia. In Britain the only apparently genuine record is from Wiltshire (Grose 1957). Many other reports of *B. grossus* are certainly errors for *B. secalinus*.

The appearance of these two species is illustrated in Figs. 1 & 2 and Plates 1 & 2.

Tournay (1968) commented on the uncertainty of identity of material, particularly from Britain, which is named *B. multiflorus* J. E. Smith. Although Smith (1798) cited Weigel as the source of this name, it is clear from his very full account of the plant that *B. multiflorus* Weigel (= *B. arvensis* L.) is *not* intended. Therefore he misapplied the name. Tournay considered it possible that some of

OBSERVATIONS ON SOME CRITICAL BROMEGRASSES

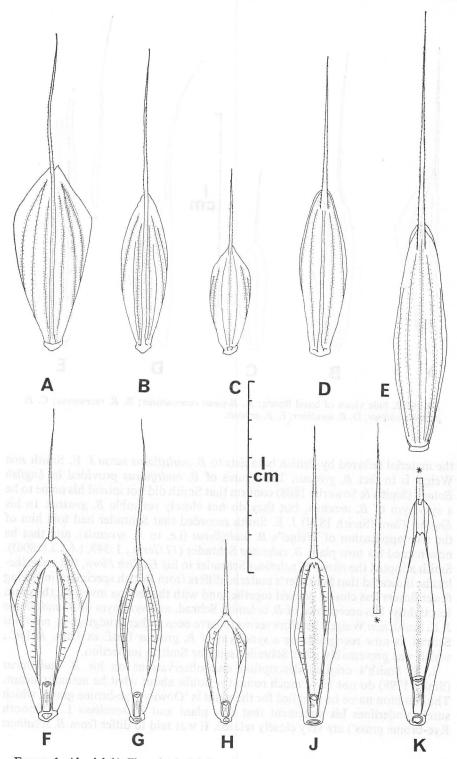


FIGURE 1. Abaxial (A-E) and adaxial (F-K) views of basal florets: A & F. Bromus commutatus; B & G. B. racemosus; C & H. B. pseudosecalinus; D & J. B. secalinus; E & K. B. grossus.

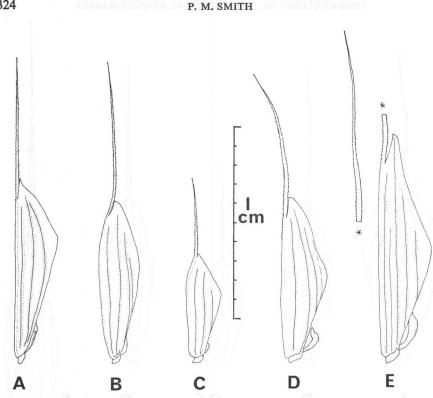


FIGURE 2. Side views of basal florets: A. Bromus commutatus; B. B. racemosus; C. B. pseudosecalinus; D. B. secalinus; E. B. grossus.

the material referred by British botanists to B. multiflorus sensu J. E. Smith non Weigel is in fact B. grossus. The figures of B. multiflorus provided in English Botany (Smith & Sowerby 1808) confirm that Smith did not intend his name to be a synonym of B. arvensis, but they do not closely resemble B. grossus. In his English Flora (Smith 1824) J. E. Smith recorded that Schrader had told him of the true application of Weigel's B. multiflorus (i.e. to B. arvensis), and that he now named his own plant B. velutinus Schrader (Fl.Germ., 1:349, t.6,f.3 (1806)). Smith adopted the name B. velutinus Schrader in his English Flora, but nevertheless he indicated that Schrader's material differs from British specimens in having fewer florets less closely packed together and with the lemma investing the grain less tightly. His acceptance of B. velutinus Schrad. as a synonym of B. multiflorus J. E. Smith non Weigel therefore seems to have been rather grudging. B. velutinus Schrad. is now recognised as a synonym of B. grossus Desf. ex Lam. & DC., which was presumably what Schrader sent for Smith's inspection.

J. E. Smith's original description and observations on his B. multiflorus (Smith 1798) do not leave much room for doubt about what he actually meant. The common name he supplied for the plant is 'Downy Rye-brome grass', which surely underlines his statement that this plant and B. secalinus L. ('Smooth Rye-brome grass') are very closely related. It was said to differ from B. secalinus

mainly in its larger number of florets, in its usually hairy spikelets, and in the fact that its florets are more imbricate at maturity.

Thus it seems clear from Smith's account that he sought to divide the material which we now refer to *B. secalinus* into two groups. In one the plants have a larger number of florets (12–16) and hairy spikelets; this is *B. multiflorus* J. E. Smith *non* Weigel. The other group is of grasses with fewer florets (9–12) and usually glabrous spikelets; this group he named *B. secalinus* L. Probably *B. multiflorus* J. E. Smith *non* Weigel therefore consists of robust specimens of *B. secalinus* which develop more florets in the spikelet owing mainly to their growth in richer soils. It is certainly true that specimens of *B. secalinus* with glabrous spikelets are much rarer in Britain than are those with hairy ones. It may therefore be anticipated that robust specimens, which are in any case more often noticed and collected, will usually have hairy spikelets.

Nowhere in his descriptions of his *B. multiflorus* did J. E. Smith comment on differences in the size of the glumes and lemmas, in the development of awns on the glumes, or in the shape of florets and spikelets, such as occur between *B. secalinus* and *B. grossus*. They are unlikely to have been overlooked by so careful a botanist as J. E. Smith. When eventually he saw a specimen of *B. grossus* (as *B. velutinus* Schrad.) he at once noticed how it differed from British material in having looser margins to the lemmas.

The name *B. multiflorus* J. E. Smith *non* Weigel persists in herbaria up to the present. I have examined plants so named from major British herbaria. In all cases the name has been applied to unusually robust or many-flowered variants of *B. secalinus*. Foreign specimens of *B. grossus* are occasionally found in these folders but I have found among them no plant originating in the British Isles which is not referable to *B. secalinus* or, in a few cases, to *B. commutatus*.

An examination of the plants of *Bromus* in the Smith herbarium, which is kept by the Linnean Society of London (LINN), shows that Smith's *B. multiflorus* (Sheet 133.5) is undoubtedly a variant of *B. secalinus* with unusually numerous florets in the spikelets. His herbarium contains no plants of *B. grossus* of British origin, but several European specimens which may have been sent to him by Schrader under the name *B. velutinus* Schrad. He altered his identifications of his own specimens of *B. multiflorus* to *B. velutinus* Schrad.

Taking all these considerations into account it seems safe to assume that *B. multiflorus* J. E. Smith *non* Weigel is not synonymous with *B. grossus* Desf. ex Lam. & DC., and that the latter plant has never been indigenous to the British Isles.

It has proved difficult to obtain living material of *B. grossus* for observation and experiment. I am grateful to Professor A. de Cugnac for supplying living material recently. Plate 1A is of a portion of a fruiting panicle of *B. grossus*. In earlier work on the species relationships of annual bromes (Smith 1972) it was not possible to provide serological evidence of the affinities of this interesting species. From knowledge of morphology and crossability, a strong relationship with *B. secalinus* and *B. bromoideus*, and a slightly weaker one with *B. racemosus* and *B. commutatus*, were suspected. The techniques and theory underlying serological assessment of species affinities have already been described (Smith 1968b). The spectrum of seed proteins revealed in *B. grossus* extracts is in all respects exceedingly similar to those previously demonstrated for *B. bromoideus*, *B. secalinus*, *B. racemosus* and *B. commutatus* (Smith 1972). This confirms the

B

close relationship, forecast earlier, of *B. grossus* with these four better-known bromegrasses.

2. Bromus commutatus Schrad. and B. racemosus L.

These two species are very similar morphologically and are often confused by collectors. Because of this their ranges and abundances are uncertain. *B. racemosus*, with a narrow, rather erect panicle, is easily overlooked in roadside populations of *B. hordeaceus*. In Britain, and probably western Europe in general, *B. racemosus* is certainly under-recorded.

Many workers have been tempted to lump these two taxa into a single species (e.g. Bentham 1858, Wilson 1956) because of the difficulty they experienced in distinguishing between them. Some of the difficulty has been caused by too great an attention to the shape of the panicle, which is often narrow and erect in *B. racemosus*, but rarely racemose. This type of panicle may quite commonly be seen in specimens of *B. commutatus*, which normally has a larger, more branched and spreading panicle. Plates 1C & 1D indicate the typical appearance of panicles of the two taxa.

The chief differences between *B. racemosus* and *B. commutatus* are summarised in Table 2. Figs. 1 & 2 include illustrations of the mature lemmas of both taxa from adaxial, abaxial and side views, and show significant differences. *B. racemosus* has a cucullate lemma which is narrower in relation to its length than is that of *B. commutatus*. The markedly convex lemma-back of *B. racemosus*, seen from the side, lends a distinctive appearance to the spikelets (Plates 1D & 2E) in which the upper part of each lemma appears to be slightly bulged outwards below its hyaline tip and margin. This striking feature has not been observed in material of *B. commutatus*. The shape of the lemma-margin (Fig. 2 and Plate 2) is a widely used character. In *B. racemosus* it is gradually rounded in the upper third whereas in *B. commutatus* there is a blunt marginal angle. The character has proved difficult for generations of field botanists to distinguish reliably, and it must be confessed that intermediate conditions are not infrequently seen.

Characters of the two taxa have been scored for a large number of herbarium specimens from different parts of Britain, and the most useful characters are represented in a scatter diagram (Fig. 3). The diagnostic characters and their variation are now thought to be better established, and it is these revised measurements that are given in Table 2.

From these data there seems to be little doubt that two taxa can be recognised but also that there are a significant number of intermediates. Interspecific hybridisation may well be the explanation for this. Wilson (1956) managed to produce completely fertile F_1 and F_2 hybrids of the two taxa, which were morphologically intermediate between the parents. Plants of both taxa often grow together, especially in the lush water-meadows of southern and southwestern England, and both frequently have exserted anthers. Self-pollination is undoubtedly usual, but crossing to some degree is highly likely.

Ecological differences between the two taxa are obscured by the difficulties in identification encountered by collectors. My personal impression is that *B. racemosus* is more often a plant of waysides than *B. commutatus*, which is commoner in hayfields and water-meadows. The data (Smith 1971) in the *Flora of Warwickshire* do not support this view. In Warwickshire 34% of *B. commutatus* records are from roadside habitats compared with only 14% for *B.*

OBSERVATIONS ON SOME CRITICAL BROMEGRASSES

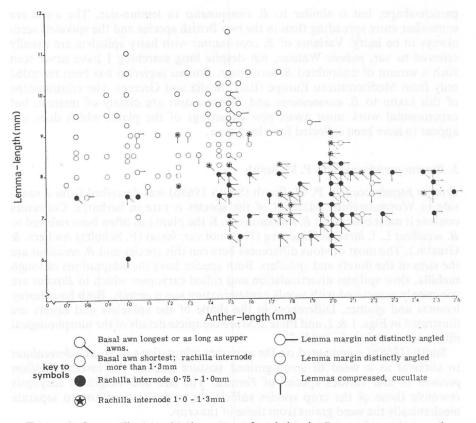


FIGURE 3. Scatter diagram showing range of variation in *Bromus commutatus* and *B. racemosus*.

racemosus. I am sure, however, that this does not represent the actual situation. B. commutatus is more easily noticed than B. racemosus, therefore appearing to be the commoner plant. In wet grassland habitats B. racemosus is perhaps sought for with greater diligence by collectors. On roadsides it is frequently overlooked because it is obscured by the very common B. hordeaceus. These populations may appear uniform and somewhat dull, but they will repay more careful scrutiny.

With the demonstration of interfertility of the taxa and their notable similarity of form, there might be a school of thought suggesting lumping them together as one species. Wilson (1956) has already proposed this. I believe the morphological differences are sufficient to be easily recognised once they are communicated adequately, and that the ecological preferences of the two taxa will eventually be shown to be different. Lumping them as one species solely on the basis of interfertility and possibly ephemeral difficulties of identification would be premature. At least until the distributions of the two taxa are better known they should be recognised as species.

B. neglectus (Parl.) Nyman is a Continental taxon very similar to B. commutatus and B. racemosus. It closely resembles B. racemosus in anther-length and panicle-shape, but is similar to *B. commutatus* in lemma-size. The awns are somewhat more spreading than in the two British species and the spikelets seem always to be hairy. Variants of *B. commutatus* with hairy spikelets are usually referred to var. *pubens* Watson, but despite long searching I have never seen such a variant of undoubted *B. racemosus. Bromus neglectus* has been recorded only from Mediterranean Europe (Italy, Sicilia and Greece). The relationships of this taxon to *B. commutatus* and *B. racemosus* are clearly of interest, but experimental work must await new gatherings of the plant, which does not appear to have been collected for a long time.

3. Bromus pseudosecalinus P. M. Smith

Bromus pseudosecalinus P. M. Smith (Smith 1968b) was described from a roadside in Worcestershire. Material of the species is rare in herbaria. Collectors confuse it most often with *B. racemosus*. In **K** the plant has often been referred to *B. secalinus* L. f. hirsutus Kindberg (N.B. not var. hirtus (F. Schultz) Aschers. & Graebn.). The most obvious differences between this species and *B. secalinus* are the sizes of the florets and spikelets. Both species have the adaptations of tough rachilla, slow spikelet disarticulation and rolled caryopses which in *Bromus* are commonly associated with weeds contaminating sown cereals. Both have horny lemmas and glumes. Differences in the shape of the spikelets and florets are illustrated in Figs. 1 & 2, and Plate 2. More complete details of the morphological differences are given in Table 2.

Smith (1968b) commented on the apparent adaptations of *B. pseudosecalinus* to survival as a weed of small-grained pasture grasses, for instance *Lolium perenne* L. and various species of *Festuca*. The size and weight of caryopsis resemble those of the crop species sufficiently to frustrate efforts to separate mechanically the weed grains from those of the crop.

B. pseudosecalinus is a diploid species (2n = 14) unlike *B. secalinus* which is tetraploid (2n = 28). The saline-soluble seed proteins of *B. pseudosecalinus* are very different from those of *B. secalinus* (Smith 1972) and from those of *B. grossus*, *B. bromoideus*, *B. racemosus* and *B. commutatus*. *B. pseudosecalinus* hence appears serologically only distantly related to the other species considered to belong to Holmberg's Coriacei (Holmberg 1924), or to P. M. Smith's 'Group 2' (Smith 1972). Morphological similarities between *B. pseudosecalinus* and *B. secalinus* probably arise from convergent evolution.

The genetic relationships of *B. pseudosecalinus* are very incompletely known, but one possibly significant finding is that it will not hybridise with *B. arvensis* (Smith 1968b) – a diploid species thought to be a probable parent of *B. secalinus* and its close relatives (Wilson 1956, Smith 1972). The relationships of *B. pseudosecalinus* to other diploids, and to tetraploid species, are at present obscure.

Since the recognition of *B. pseudosecalinus* in 1968 it has been possible to investigate its distribution in a little more detail. Fig. 4 is a dot-map of the known distribution of the plant in the British Isles based on herbarium material and personal collection. All records known to date are listed in Appendix 1. The species resembles most other bromes with which it is sympatric in having a mainly southern distribution in the British Isles. It should be looked for in areas where small-seeded grasses or clovers are sown. It is likely to be commoner than its known distribution may suggest, and probably far commoner in the British Isles than *B. secalinus*.

OBSERVATIONS ON SOME CRITICAL BROMEGRASSES

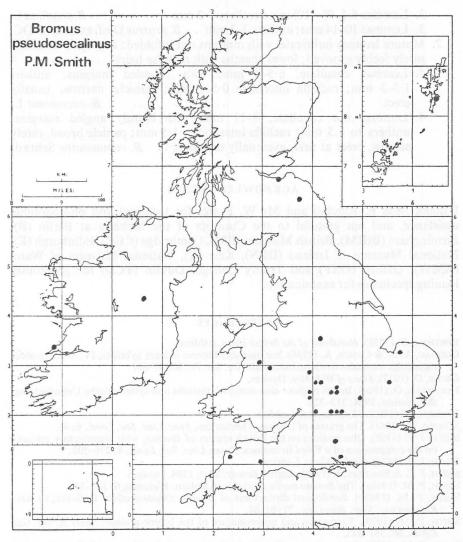


FIGURE 4. Distribution map showing records of *Bromus pseudosecalinus* in the British Isles.

KEY TO SPECIES

Measurements refer to basal florets in mature spikelets.

- 1. Lemmas 5–6 mm, divaricate at maturity; lower sheaths hairy

P. M. SMITH

- 3. Lemmas $6 \cdot 5 9(-10)$ mm; anthers 1 2 mm $\dots B$. secalinus L.
- 3. Lemmas 10-14 mm; anthers 2-3 mm .. B. grossus Desf. ex Lam. & DC.
- 2. Mature lemmas imbricate, with margins not infolded; caryopsis thin, flat, rarely feebly grooved; lower sheaths with retrorse hairs ... 4
 - 4. Lemmas cucullate, 6.5–8 mm, with rounded margins; anthers 1.5–3 mm; rachilla internode 0.5–1 mm; panicle narrow, usually erect ... B. racemosus L.
 - 4. Lemmas not cucullate, 8–11 mm, with bluntly angled margins; anthers to 1.5 mm; rachilla internode c 1.5 mm; panicle broad, rarely narrow, erect at first, eventually drooping ... B. commutatus Schrad.

ACKNOWLEDGMENTS

I thank Miss E. Randall and Mr W. Foster for technical and photographic assistance, and am grateful to the Curators of the herbaria at Berlin (B), Birmingham (BIRM), British Museum (BM), Cambridge (CGE), Edinburgh (E), National Museum of Ireland (DBN), Kew (K), National Museum of Wales (NMW), Oxford (OXF) and Trinity College, Dublin (TCD) for generously loaning specimens for examination.

REFERENCES

BENTHAM, G. (1858). Handbook of the British Flora. Ashford.

CUGNAC, A. DE & CAMUS, A. (1936). Sur quelques bromes et leurs hybrides, IV. Deux espèces messicoles menacées de disparition. *Bull. Soc. bot. Fr.*, 83:47–68.

GROSE, D. (1957). Flora of Wiltshire. Devizes.

HOLMBERG, O. (1924). Bromi molles – eine nomenklatorische und systematische Untersuchung. Bot. Notiser, 1924: 313–328.

HUDSON, W. (1762). Flora Anglica. London.

MUNRO, W. (1861). The grasses of Linnaeus' herbarium. Proc. Linn. Soc. Lond., 6: 46.

SMITH, J. E. (1798). Observations on the British species of *Bromus*, with introductory remarks on the composition of a Flora Britannica. *Trans. Linn. Soc. Lond.*, 4: 276–302.

SMITH, J. E. (1824). English Flora. London.

SMITH, J. E. & SOWERBY, J. (1808). English Botany, 27: t. 1584. London.

SMITH, P. M. (1968a). The Bromus mollis aggregate in Britain. Watsonia, 6: 327-344.

SMITH, P. M. (1968b). Serological distinctness of Bromus pseudosecalinus P. Smith, sp. nov. Reprium nov. Spec. Regni veg., 77: 61–64.

SмITH, P. M. (1970). Taxonomy and nomenclature of the brome-grasses. Notes R. bot. Gdn Edinb., 30: 361–375.

SMITH, P. M. (1971). Bromus L. sect. Bromus, in CADBURY, D. A., HAWKES, J. G. & READETT, R. C. A Computer-Mapped Flora. London.

SMITH, P. M. (1972). Serology and species relationships in annual bromes (Bromus L. sect. Bromus). Ann. Bot., n.s., 36: 1-30.

TOURNAY, R. (1968). Le brome des Ardennes, 'B. arduennensis', et ses proches, B. secalinus et B. grossus. Bull. Jard. bot. État. Brux., 38: 295–380.

WILSON, D. (1956). Cytogenetic studies in the genus Bromus. Ph.D. thesis, University of Wales, Aberystwyth.

APPENDIX 1

Records of Bromus pseudosecalinus P. M. Smith in the British Isles

v.c.3, S. Devon: In clover fields at Cove, near Tiverton. Eleven collections from different parts of the Cove area were made in June 1943 by A. L. Still. K.

- v.c.3, S. Devon: Clover-field margin, Cobbacombe, near Tiverton. June 1943, A. L. Still. K.
- v.c.4, N. Devon: Hayfield, Woolfardisworthy. June 1945, R. M. Payne. K.
- v.c.12, N. Hants.: Andover. July 1890, C. B. Clarke. K.
- v.c.22, Berks.: South Hinksey. June 1892, H. Baker. OXF.
- v.c.22, Berks.: On roadside at Woodend, between Botley and Swinford. June 1941, C. E. Hubbard 10394. K.
- v.c.23, Oxford: In grassland on heavy soil by Oxford by-pass, near Wolvercote. July 1941, C. E. Hubbard 10290. K.
- v.c.28, W. Norfolk: Appleton, on roadside in partial shade, on sandy soil with Bromus hordeaceus agg. July 1936, C. E. Hubbard A.B.X. K.
- v.c.29, Cambs.: Wicken. June 1901, A. H. (sic). CGE.
- v.c.30, Beds.: Tingrith. J. G. Dony. K.
- v.c.33, E. Gloucester: Around an old stack bottom, 1 mile north of Fairford, on the Hatherop road. June 1944, C. E. Hubbard 11919. K.
- v.c.33, E. Gloucester: Around an old stack bottom, 1–2 miles north of Fairford on the Quenington road. June 1944, C. E. Hubbard 11957. K.
- v.c.33, E. Gloucester: Rye-field at Ashchurch. June 1951 & June 1957, C. W. Bannister A/3-6. K.
- v.c.37, Worcester: Defford Common. July 1936. K.
- v.c.37, Worcester: Halesowen, growing among roadside population of *Bromus* hordeaceus agg. and *B. lepidus* on the verges of the new by-pass. July 1963, *P. M. Smith.* E (holotype).
- v.c.38, Warwick: Drayton Manor Farm, near Stratford-upon-Avon, by farm track. June 1945, C. E. Hubbard 12796. K.
- v.c.38, Warwick: In pasture, cultivated field and on roadside, near Upper Tysoe. BIRM.
- v.c.38, Warwick: in a mortuary (? cemetery) under trees, about half a mile east of Studley. **BIRM**.
- v.c.38, Warwick: Roadside near Hardwick Farm, south of Kineton. June 1958, C. M. Goodman. BIRM.
- v.c.38, Warwick: Pasture at Edge Hill. 1960, B. M. Daulman. BIRM.
- v.c.38, Warwick: Grove Park, near Warwick. Margin of cultivated field. June 1964, *P. M. Smith.* **BIRM**.
- v.c.47, Montgomery: Bettws, Lower Garth, in rye grass and clover ley, in upland pasture. July 1955, *E. Milne-Redhead* 6657. K.
- v.c.47, Montgomery: Carno. July 1956, I. A. Williams. BM.
- v.c.57, Derby: Ashbourne. July 1888, W. R. Linton. E.
- v.c.80, Roxburgh: Fields near Kelso. June 1870. OXF.
- v.c.83, Edinburgh: Field near Caroline Park, Edinburgh. July 1834. E.
- v.c.83, Edinburgh: Near Leith. July 1878, D. Douglas, K.
- v.c.112, Zetland: Ham, Isle of Bressay, in a meadow. July 1959, R. C. Palmer. OXF.
- v.c.H9, Clare: Near Glencolumkille House, north of Kilkee. July 1955, D. A. Webb. TCD.
- v.c.H23, Westmeath: meadows at Knock Drin, near Mullingar. June 1894, H. C. L. Ewing. DBN.

APPENDIX 2

Sources of material represented in Plates and Figures (Accession numbers refer to author's seed collection).

B. commutatus Schrad.

Spain, High Aragon, pathsides in Vallibierne, near Benasque. August 1961. Seed accession no. 42.

B. racemosus L.

Wales, Cardiganshire, roadside near Lampeter. July 1963. Seed accession no. 425. *B. pseudosecalinus* P. M. Smith

England, Worcestershire, roadside at Halesowen. July 1963. Seed accession no. 489. *B. secalinus* L.

Raised from seed received from Dijon Botanic Garden. Seed accession no. 336. (Plate 1).

B. secalinus L.

Raised from seed received from the State Botanic Garden, Brussels. Seed accession no. 330. (Plate 2).

B. grossus Desf. ex Lam. & DC.

Raised by Professor A. de Cugnac, Rumigny, Ardennes, France, 1970. Seed accession no. 1049.

(Accepted October 1972)

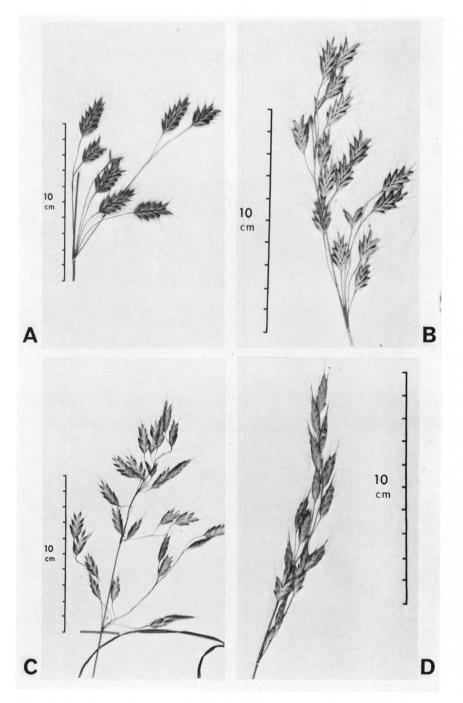


PLATE 1. Panicles of *Bromus* species: A. *B. grossus* (one node only); B. *B. secalinus*; C. *B. commutatus*; D. *B. racemosus*.

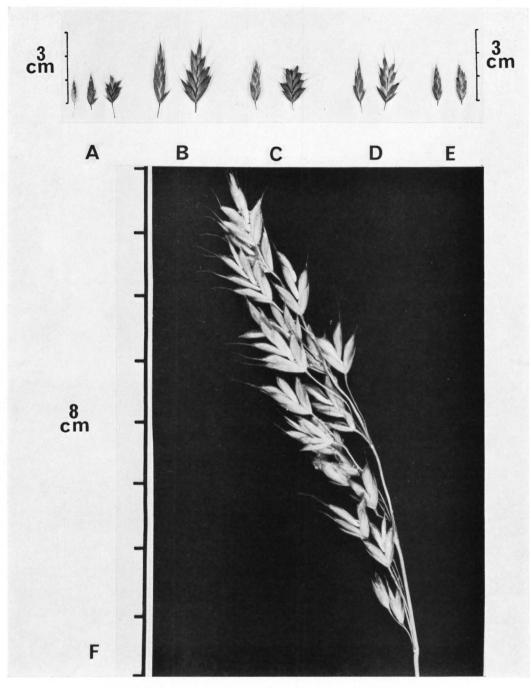


PLATE 2. A-E: Young and mature spikelets of *Bromus* species: A. *B. pseudosecalinus*; B. *B. grossus*; C. *B. secalinus*; D. *B. commutatus*; E. *B. racemosus*. F: Mature panicle of *Bromus pseudosecalinus*.