

An analysis of the characters of *Bromus racemosus* L., *B. commutatus* Schrad. and *B. secalinus* L. (Poaceae)

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ABSTRACT

The characters currently used to distinguish *Bromus racemosus*, *B. commutatus*, and *B. secalinus* are analysed. The lengths of the spikelets, lemmas, anthers and rhachillas and the shape of the lemma margins were found to be often unreliable. Two more diagnostic characters are proposed to separate *B. racemosus* from *B. commutatus*. The characters of *B. secalinus* are discussed. A new key for these species is proposed.

KEYWORDS: Brome-grasses, morphological characters, panicle structure, key.

INTRODUCTION

Ever since Linnaeus described *B. secalinus* in 1753 and *B. racemosus* in 1762 and Schrader described *B. commutatus* in 1806, botanists have encountered difficulties in distinguishing these three annual brome-grasses.

In *Bromus* it is rarely possible to determine a taxon using only one character and an appraisal of all the information provided by several different characters is usually necessary. The couplets in the keys in Clapham *et al.* (1987), Smith (1980) and Stace (1997) use the lengths of the spikelets, lemmas, anthers, and rhachillas and the shape of the lemma-margins. Unfortunately, all too often, not all the characters lead to the same conclusion. *B. secalinus* is readily identified when it is in fruit but it is often difficult to determine before fruiting. Consequently an analytical study of the characters of these three species was undertaken to evaluate the reliability of the existing criteria and to seek new criteria that might be helpful.

MATERIALS AND METHODS

846 specimens (281 of *B. racemosus*, 392 of *B. commutatus* and 173 of *B. secalinus*) were assessed using the characters and potential characters in Table 1. 742 were herbarium specimens from **BDD, BM, BRISTM, CGE, DBN, E, GL, HANU, K, LTR, NMW, OXF, RAMM, RNG, SLIB, SUN, TCD, TOR, and WARMS**. 104 were fresh or new specimens collected by the author and others during the four years 1998 to 2001. All specimens had been collected in the British Isles. The technique involved in preparing material for observation was described in Spalton (2001) and is greatly assisted by pre-soaking the lemmas.

The data listed in Table 1 include all the characters of these grasses mentioned in Clapham *et al.* (1962, 1987), Hubbard (1954, 1968), Sell & Murrell (1996), Smith (1973, 1980), and Stace (1997), together with some others from Acedo & Llamas (1999), Ammann (1981), Bomble & Scholz (1999), Conert (1997, 2000), Kerguelen (1995), Portal (1995), Scholz (1970, 1997 & pers. comms., 2000, 2001) and Tzvelev (1976), plus some other data selected by the author.

MORPHOLOGICAL OBSERVATIONS

All specimens had lemmas of leathery texture and in dried specimens the veins of the lemmas did not protrude. This very important character distinguished the three species from the *B. hordeaceus* group where the lemmas were of papery texture and the veins protruded when dried.

TABLE 1. DATA COLLECTED ON *BROMUS RACEMOSUS*, *B. COMMUTATUS*, AND *B. SECALINUS*

Character	Measurement
Culm:	height.
Lower leaf-sheath:	indumentum.
Panicle:	appearance; structure; length; length of pedicels and of branches.
Spikelets:	shape; length; width before and after divarication.
Glumes:	shape; length; length in relation to spikelet length.
Lemmas (2nd lowest):	texture, papery or leathery; whether veins protrude in dried specimens; glabrous, scabrid or pubescent; type of pubescence and its location; shape of margin; depth of hyaline area; width and depth of apical notch if present.
Paleas:	length and its relationship to length of the lemma; width; whether surfaces are pubescent, scabrid or smooth; whether 'eyelash' hairs continue to palea apex.
Awns:	length; width; shape; shape at fruiting.
Rhachillas:	length of lowest before fruiting; tough or brittle at fruiting; whether some are clearly visible at fruiting.
Anthers (from lowest florets):	length of mature undehisced anthers; length of dehisced anthers and evidence of chasmogamy.
Caryopses (mature):	length and width; length in relationship to lengths of lemma and of palea; thickness and shape in cross-section.

The indumentum of the lower leaf-sheath, which is much used by continental European botanists, proved to be a useful character, especially in fresh material but was less reliable if the sheath had been damaged or became shrivelled. In *B. racemosus* and *B. commutatus* the hairs were patent and appeared to be stiff because they did not bend at the ends. In *B. hordeaceus* subsp. *hordeaceus* the hairs were dense and softly villous (Fig 1). However in *B. hordeaceus* subsp. *longipedicellatus* the sheath had long and short patent hairs which, while not villous, were often slightly bent at the ends. 41% of the *B. commutatus* specimens were *B. commutatus* var. *pubens* Wats. which had hairy lemmas and the indumentum of the sheath varied from that of *B. commutatus* var. *commutatus* to that of subsp. *hordeaceus*. The latter character also separated *B. secalinus* from the other species, since its sheath was glabrous, though, especially in *B. secalinus* L. var. *hirtus* (F. Schultz) Aschers. & Graebn., sparse, thin, usually short hairs often also occurred on the sheath.

BROMUS RACEMOSUS AND *B. COMMUTATUS*

It was found that the most important character to distinguish *B. racemosus* from *B. commutatus* was the panicle structure (Fig. 2) including the lengths of the pedicels and panicle branches, especially the latter. In fresh mature specimens, the narrow \pm lax, usually unbranched (96.3%), panicle of *B. racemosus* was markedly different from the broad, often robust, panicle of *B. commutatus* with its long panicle branches and/or pedicels. It will be seen from the scatter diagram (Fig 3.) that the length of the longest pedicel or panicle branch (whichever was the longer) of *B. racemosus* did not usually exceed 4 cm but the longest pedicel or panicle branch (whichever was the longer) of mature *B. commutatus* was longer than 4 cm. For the purpose of this study panicle branches were measured from the node to the base of the terminal spikelet.

These differences were not immediately obvious in many herbarium specimens because the panicles constrict on drying and the spikelets then lie close to the rhachis. Only a minority of herbarium specimens examined were mounted to display the panicle in its natural state at anthesis. In examining herbarium specimens, it became obvious that C. E. Hubbard, P. M. Smith and T. G. Tutin must also have considered the appearance and structure of the panicle to be very important, since, in many of the specimens seen, they could not have separated *B. racemosus* from *B. commutatus* in any other way.

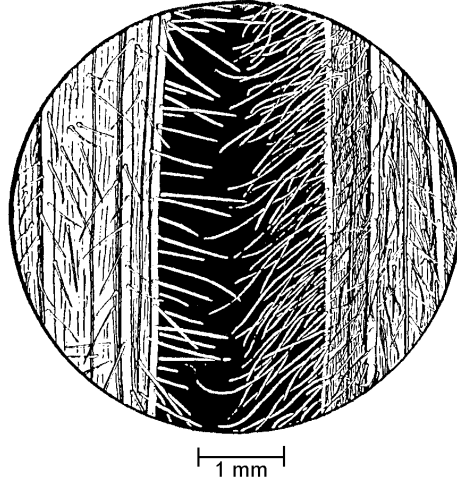


FIGURE 1. Indumentum of the lower sheath. Left: *Bromus commutatus*. Right: *B. hordeaceus* subsp. *hordeaceus*. Drawing by A. Tröger.

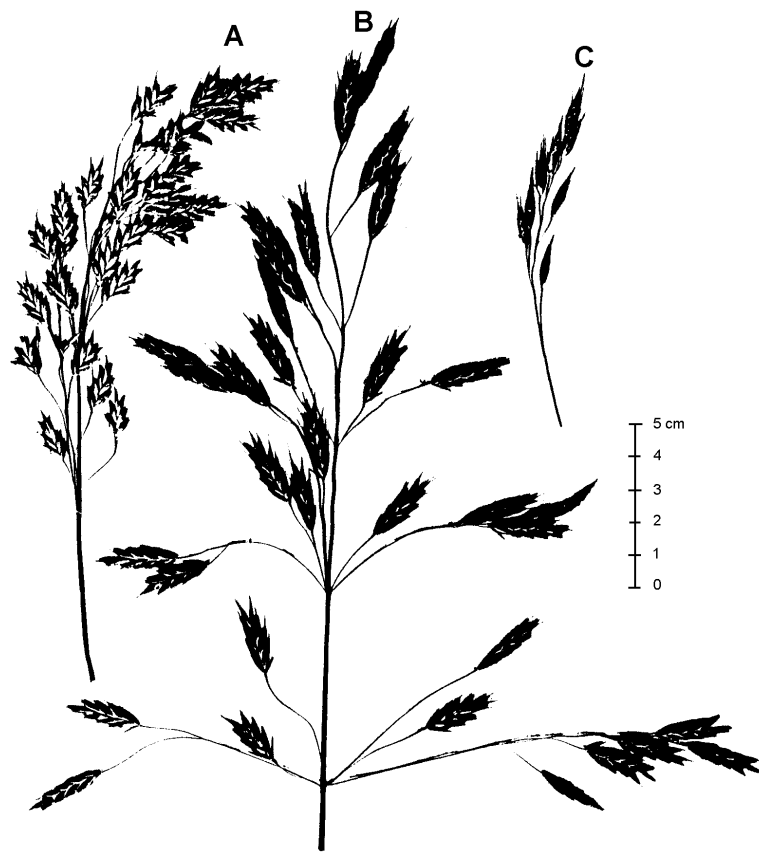


FIGURE 2. A. Scan of panicle of *Bromus secalinus*, Hooperton, Devon, waste ground, 28/7/2000, acc. 3438. B. *B. commutatus*, Hatch Beauchamp, Somerset, edge of wheat, coll. 21/7/1999, acc. 392. C. *B. racemosus*, Honiton, Devon, moist pasture, 13/5/1999, acc. 103. L. M. Spalton.

H. Scholz (pers. comm., 2001) suggested that the relative length of the awns of the lowest lemmas might be worth investigating in British specimens of these two species. This proved to be good character. In *B. commutatus* the awn of the lowest lemma was usually shorter than the other awns while in *B. racemosus* they were \pm equal.

The indumentum of the lemma was definitive but only in some of the taxa investigated. The lemmas of *B. racemosus* and *B. commutatus* var. *commutatus* were always glabrous, though often very minutely scabrid, but the lemmas of *B. commutatus* var. *pubens* Wats. were pubescent.

The lemma-length character has been much used to distinguish these two species, and most floras have continued to quote the measurements in Hubbard (1954): *B. racemosus* 6.5–8 mm and *B. commutatus* 8–11 mm (Table 2). In this study, no specimens of *B. racemosus* had lemmas shorter than 7 mm and 42% had lemmas exceeding 8 mm, up to 9 mm in length.

From an analysis of 673 specimens (281 of *B. racemosus* and 392 of *B. commutatus*) it was clear that the appropriate lemma-lengths should be: *B. racemosus* 7–9 mm and *B. commutatus* 7.5–11 mm and these figures were used throughout this study. There was an overlap at 7.5–9 mm in these lemma-measurements and 496 specimens (74%) had lemmas with lengths within this overlapping range (Fig. 3). So it is suggested that the lemma-length character should only be accepted if the length is outside the overlapping range *viz.* less than 7.5 mm, indicating *B. racemosus*, or more than 9 mm, indicating *B. commutatus*, and then only as a secondary, indicative character.

The spikelet-lengths quoted in the floras are listed in Table 2. From the 673 specimens examined it was found that the most appropriate lengths were *B. racemosus* 11–18 mm and *B. commutatus* 15–30 mm. The overlapping lengths were 15–18 mm and 37% of the specimens fell within this range. Consequently, it is suggested that the spikelet-length character should only be used when the length of the spikelets is less than 15 mm, indicating *B. racemosus*, or more than 18 mm, indicating *B. commutatus* and then only as a secondary, indicative character.

The lemma-margin of *B. racemosus* has been described as smoothly curved and that of *B. commutatus* as broadly angled. It was found, however, that the shape was frequently unclear and often varied in the same panicle. After a cultivation study of *B. commutatus*, Vivant (1964) reported that in young specimens of *B. commutatus* the lemma-margin was smoothly curved and only appeared broadly angled towards anthesis. This phenomenon was also observed during this study.

There is no doubt that in many mature specimens of *B. commutatus* the lemma-margin is definitely broadly angled and that of *B. racemosus* is definitely smoothly curved but in 61% of the specimens examined it was indeterminate. So it is suggested that this is also a secondary indicative character, which should only be accepted when the conclusion is certain and consistent throughout the panicle.

TABLE 2. *BROMUS RACEMOSUS* AND *B. COMMUTATUS*: LENGTHS OF LEMMAS, SPIKELETS AND ANTHERS

	LEMMAS (mm)		SPIKELETS (mm)		ANTHERS (mm)	
	racemosus	commutatus	racemosus	commutatus	racemosus	commutatus
Clapham <i>et al.</i> (1962)	c. 7	c. 9	c. 15	15–20	2–2.5	1–1.5
Clapham <i>et al.</i> (1987)	6.5–8	8–11	15	15–25	1.5–3	1–1.5
Conert (1997)	6.5–8	8–11	16–20	16–28	1.5–2.5	1–1.5
Conert (2000)	6.5–8	8–11	12–16	8–18	1.5–2.5	1–1.5
Hubbard (1954, 1968)	6.5–8	8–11	12–16	18–28	Mostly 2–3	Mostly 1.5–2
Portal (1995)	6.5–8	8–11	10–15	15–30	(1.5) 2–3	1–1.5
Sell & Murrell (1996)	6–8.5	8–11	10–16	15–28	Mostly 2–3	1–1.5
Smith (1973)	6.5–8	8–11	10–15	15–25	1.5–3	up to 1.5
Smith (1980)	6.5–8	8–11.5	10–15	15–25	1.5–3	c. 1.5
Stace (1997)	6.5–8	8–11	10–16	15–28	Mostly 1.5–3	Mostly 1–1.5
Tzvelev (1976)	6.5–8	7.5–11	12–20	18–28	1.5–3.2	0.8–2.3
Spalton (2001)	7–9 (1)	7.5–11 (1)	11–18	15–30	1.5–3.5 (2)	1.3–2.5 (2)

(1) 2nd lowest lemma.

(2) Mature undehisced anthers from the lowest florets, others less

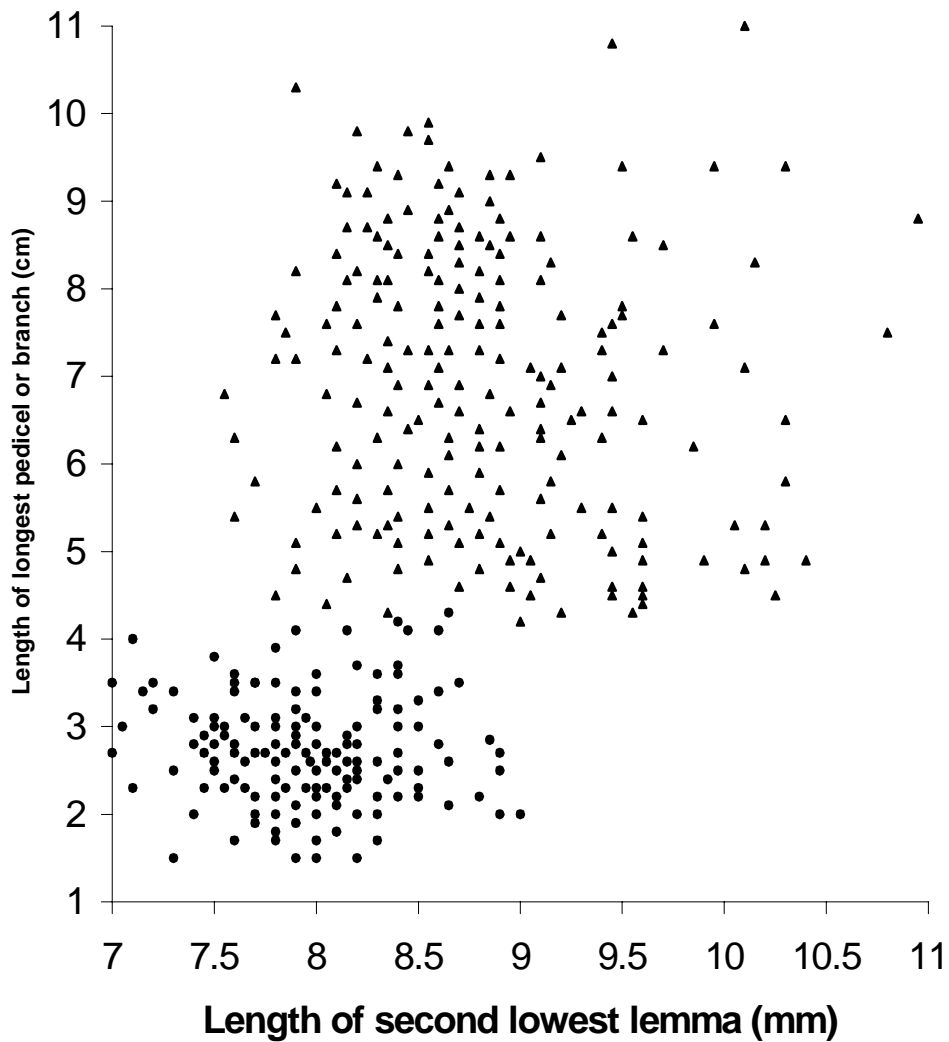


FIGURE 3. Scatter diagram of the lengths of the longest pedicels or branches in panicles plotted against length of second lowest lemma of *Bromus racemosus* ● and of *B. commutatus* ▲. Note the large overlap in the length of the lemmas.

Anther lengths are listed in Table 2. Between the figures for *B. racemosus* (1.5–3.5 mm) and *B. commutatus* (1.3–2.5 mm), established in this study, there is an overlap. Consequently this character should only be used if the mature undehisced anthers from the lowest florets exceed 2.5 mm, indicating *B. racemosus*. There was also a practical difficulty with this character. Spalton (2001) reported that the lengths of dehisced anthers are unreliable. They are usually less than those of undehisced anthers and very variable. As soon as the anthers matured the filaments lengthened, the florets opened, the anthers were extruded, dehisced and were then dropped. So there was only a very short period during which mature undehisced anthers could be measured and in very many specimens this was not possible. Consequently 89% of the specimens could not be determined by anther-length.

In all the mature specimens of *B. racemosus*, *B. commutatus* and *B. secalinus*, the length of the lowest rhachilla exceeded 1.3 mm (and thus differed from c.1 mm in *B. hordeaceus*), but the variations in length were too great to be of use in separating the three species. None of the other features listed in Table 1 were found to be of significant value in distinguishing *B. racemosus* from *B. commutatus* in the British Isles.

Only 2.5% of the specimens studied were indeterminate using panicle-structure and the 4 cm length of the longest pedicel or branch character. 9.4% were indeterminate using the relative length of the lowest awn. Taken together these proved to be good diagnostic characters which could sometimes be supplemented by the secondary indicative characters already described.

Because separating these two species has often been very difficult, some botanists have reported that there are 'intermediates'. It is suggested that many of these 'intermediates' may have been specimens that were indeterminate using the current characters but might have been determined by the two new characters proposed in this report and more precise use of traditional characters.

Immature *B. commutatus* (and immature *B. secalinus*) with small spikelets, short pedicels and branches and apparently smoothly curved lemma-margins frequently resembled *B. racemosus*. Glumes became mature before the upper florets develop, so in immature spikelets they appeared rather longer than usual in relation to the length of the spikelet. Immaturity in *B. commutatus* was suggested if the length of the spikelet was significantly less than twice the length of the upper glume. Immaturity was confirmed by examining the anther cuticle and pollen grains under a high-power microscope. In immature specimens the cuticle was fragile and \pm translucent and the pollen was transparent.

In all the herbarium specimens of *B. commutatus* and *B. racemosus* examined only three had been determined as an (?)intermediate or (?)hybrid of the two taxa. There are no confirmed reports of *B. commutatus* \times *B. racemosus* in the British Isles. P. M. Smith (pers. comm., 2001) tried very hard to hybridise *B. racemosus* and *B. commutatus* and failed to do so, though he considered that this may have been a technical problem. He and his co-worker, F. Sales, and the present author have examined a great many *Bromus* specimens in British herbaria, and we have all failed to find any material of certain hybrid origin. The status of 'intermediates' of *B. racemosus* and *B. commutatus* is still being investigated and may be the subject of a later report. Fresh specimens are being sought in the field, especially in those few places where *B. racemosus* and *B. commutatus* still grow together. Putative specimens will be analysed and some cultivated. The author will be pleased to receive specimens for examination.

BROMUS SECALINUS

The panicle of *B. secalinus* usually had long pedicels or branches, but not always, and the spikelets were very different when fruit formation commenced. At this time the spikelets became much wider as the florets divaricated and the lemma wrapped around the developing caryopsis eventually causing many of the rhachillas to be visible (Fig. 2). In addition the rhachillas became tough, which could be detected by gently pulling an upper floret with forceps. Consequently the spikelets were slow to disarticulate and when this eventually occurred some florets were often dropped still joined together.

In cross-section, the mature caryopses of *B. secalinus* were U or V shaped and those of *B. commutatus* and *B. racemosus* were \pm flat with upturned ends, or crescent shaped. Although the caryopsis has been described as 'thick' in *B. secalinus* and 'thin' in *B. commutatus* and *B. racemosus*, this was not confirmed (data in Table 3). Bomble & Scholz (1999) have also recognised that *B. secalinus* can have thin fruits and have referred such specimens to a proposed new taxon, *B. secalinus* subsp. *decipiens* Bomble & Scholz. This taxon has not yet been found in Britain but may occur on the edges of wheat-fields.

The panicles of young specimens of *B. secalinus* and *B. commutatus* were often rather similar but *B. secalinus* had a glabrous lower leaf-sheath which differed from the pubescent sheath of *B. commutatus* (Fig. 1). However, sparse thin, usually short, hairs were sometimes present, especially in *B. secalinus* var. *hirtus*, which constituted 49% of the specimens of *B. secalinus* examined. This variety could be readily distinguished from other *Bromus* taxa by the characteristic very dense and very short patent hairs on its lemmas.

The awns of *B. secalinus* were frequently shorter and stouter in relation to their varied lengths (0 to 7 mm) than in the other two species. Eventually they often became bent, curved, or sinuous, specially in *B. secalinus* var. *secalinus*. The awns of *B. commutatus* and *B. racemosus* remained straight.

KEY

The following key is proposed to separate *B. racemosus*, *B. commutatus*, and *B. secalinus* in the British Isles.

1. Spikelets substantially widening by divarication as fruit forms with eventually many rhachillas becoming visible as the lemmas wrap around the caryopsis which is U or V shaped in section. Rhachillas becoming tough and slow to disarticulate. Some florets often dropped still joined together. Lower leaf-sheath glabrous or with sparse, thin, usually short hairs. Lemmas glabrous or with very dense very short patent hairs. Awns short, stout, 0–7 mm often becoming bent, curved or sinuous.2
1. Spikelets not substantially widening in fruit. Lemmas continuing to obscure most of the fragile rhachillas. Florets readily disarticulating. Caryopsis flat or crescent shaped in section. Lower leaf-sheath with many patent hairs (Fig. 1). Lemmas glabrous or pubescent.3
2. Lemmas glabrous *B. secalinus* L. var. *secalinus*
2. Lemmas with very dense, very short patent hairs *B. secalinus* L. var. *hirtus*
3. Panicle narrow, ± lax, usually unbranched; pedicels (and branches) less than 4 cm in length. Spikelets 11–18 mm long*. 2nd lowest lemma 7–9 mm long*, glabrous, often with a definite smoothly curved margin. All awns ± equal. Mature undehisced anthers from the lowest florets 1.5–3.5 mm long* *B. racemosus* L.
3. Panicle broad and spreading with some pedicels or branches exceeding 4 cm in length. Spikelets 15–30 mm long*. 2nd lowest lemma 7.5–11 mm long*, glabrous or pubescent, often with a definite broadly angled margin. Awn of the lowest lemma shorter than the others. Mature undehisced anthers from the lowest florets 1.3–2.5 mm long*4
4. Lemmas glabrous *B. commutatus* var. *commutatus*
4. Lemmas pubescent *B. commutatus* var. *pubens* Wats.

*These characters should only be used when the measured lengths are outside the overlapping lengths.

There is a summary of these data in Table 3.

DISCUSSION

B. racemosus occurs in wet pasture and old hay-meadows; it was formerly found in water-meadows. It is now rare in the British Isles because of habitat destruction. *B. commutatus* also grew in water-meadows but is now mainly a plant of disturbed ground and arable weed (especially wheat-fields). The arable weed form is usually more robust, with longer branches than the earlier water-meadow plants and is therefore more distinctive from *B. racemosus*. *B. commutatus* var. *pubens* is found in the same habitats but also in grassland. It is believed to be under-recorded because it only has varietal status and is usually not quite so robust as the arable weed form. *B. secalinus* occurs on the margins of wheat-fields and waste ground. It was traditionally associated with rye and was probably a grain contaminant. It is now rare but can occasionally still be found.

TABLE 3. SIGNIFICANT CHARACTERS USED FOR THE DETERMINATION OF *BROMUS RACEMOSUS*, *B. COMMUTATUS* AND *B. SECALINUS*

	<i>B. racemosus</i>	<i>B. commutatus</i>	<i>B. secalinus</i>
Lower leaf-sheath indumentum	stiff patent hairs	stiff patent hairs	glabrous or sparse thin short hairs
Panicle structure	narrow \pm lax usually unbranched	broad with long branches	spreading or compact
Longest branches/ pedicels (cm) (1)	<4	>4	2.1–9.5
Spikelets* length (mm) (2)	11–18	15–30	11–27
Lemma* length (mm)	7–9	7.5–11	7–9
Lemma indumentum	glabrous (3)	glabrous (3) or pubescent	glabrous or dense v. short patent hairs
Lemma margin	definitely curved	definitely angled	indistinct
Rachillas at fruit	\pm concealed, brittle	\pm concealed, brittle	many visible, tough
Awn shape	straight	straight	often bent, curved or sinuous
Awn length* (mm)	5–9 \pm same	5–10 lowest <	0–7 stout variable
Anther length* (mm) undehisced (4)	1.5–3.5	1.3–2.5	1.2–2.5
Caryopsis section	\pm flat or crescent shaped	\pm flat or crescent shaped	U- or V-shaped
Caryopsis thickness (mm)	0.2–0.7 mean: 0.45	0.2–0.6 mean: 0.35	0.2–0.8 mean: 0.5

(1) Branches measured from the node to the base of the terminal floret.

(2) Before divarication.

(3) Often glabrous and very minutely scabrid.

(4) From the lowest floret.

* These characters should only be used when the measured lengths are outside the overlapping lengths.

All three species are related tetraploids ($2n = 28$), though according to Bomble & Scholz (1999) an octoploid ($2n = 56$) population of *B. commutatus* has been reported. This has not been identified in Britain. Most floras and most authors have described the three taxa as species, however in North Africa Maire (1955), in France Vivant (1964) but not Kerguelen (1995) and not Portal (1995), in Switzerland Ammann (1981) and Lauber & Wagner (1996), in the Netherlands Meijden (1996) and in Iberia Acedo & Llamas (1999) treated *B. commutatus* as a subspecies of *B. racemosus*.

In Britain, Stace (1997) described *B. commutatus* as a species but added that *B. commutatus* might be better as *B. racemosus* subsp. *commutatus*. In North America, Pavlick (1995) and in South America Planchuelo & Peterson (2000), after listing the two taxa as species, suggested that *B. racemosus* might be a depauperate form of *B. commutatus*. Smith (1973), in the last major study of the taxa in Britain, concluded that, at least until the distribution of *B. racemosus* and *B. commutatus* is better known, they should be regarded as species and added (pers. comm., 2001) something is keeping them apart; they are not identical but overlap ecologically.

In Germany, Bomble & Scholz (1999) have identified a new subspecies of *B. secalinus*, which morphologically resembles *B. commutatus* to some degree and *B. racemosus* to a lesser extent. They have named the new subspecies *B. secalinus* subsp. *decipiens*, but they have retained *B. commutatus* and *B. racemosus* as species. In Spain, Lloret (1993) regarded *B. commutatus* as a subspecies of *B. secalinus*. As, morphologically, *B. commutatus* appears to be in a central position between *B. racemosus* and *B. secalinus*, if subspecies status is indicated, "*B. commutatus* subsp. *secalinus*" and "*B. commutatus* subsp. *racemosus*" should not be excluded as possibilities. It is possible that the three taxa may have originated from an unidentified common diploid ancestor which may no longer exist.

The author believes that more information is required and suggests that DNA sequence studies and isozyme analyses together with more field work using the characters suggested in this paper may eventually enable taxonomists to come to more definite conclusions.

Using isozyme analyses, Oja (1998) found that *B. secalinus* and *B. commutatus* had very similar enzyme phenotypes, indicating their strong genetic affinity, but still differed in PRX-F homoeozymes of one composite genome. Unfortunately, at that time, she had no seed of *B. racemosus* and the *B. secalinus* and *B. commutatus* seed was from continental European countries. There may be some differences between British and continental taxa. For instance, according to H. Scholz (pers. comm., 2001), *B. commutatus* var. *pubens* and *B. secalinus* var. *hirtus*, which are frequent forms of these taxa in Britain, are very rare in Germany. Seed of most British *Bromus* taxa has been sent to T. Oja and these plants are being analysed in her study. This may provide some useful information not only about these three species but also about other *Bromus* taxa as well. T. Oja (in prep.) has already found that the isozyme phenotypes of *B. racemosus* L. distinguish it as a separate species from *B. commutatus* Schrad.

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REFERENCES

- ACEDO, C. & LLAMAS, F. (1999). *The Genus Bromus L. (Poaceae) in the Iberian Peninsula*. J. Cramer, Berlin.
- AMMANN, K. (1981). Bestimmungsschwierigkeiten bei Europäischen Bromus-Arten. *Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie* **102**: 459–469.
- BOMBLE, W. & SCHOLZ, H. (1999). Eine neue Unterart des *Bromus secalinus* (Gramineae) eine Sekundäres Unkraut. *Feddes Repertorium* **110**: 425–438.
- CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1962). *Flora of the British Isles*, 2nd ed. Cambridge University Press, Cambridge.
- CLAPHAM, A. R., TUTIN, T. G. & MOORE, D. M. (1987). *Flora of the British Isles*, 3rd ed. Cambridge University Press, Cambridge.
- CONERT, H. J. (1997). *Bromus*, in HEGI, G. *Illustrierte Flora von Mitteleuropa* **1**: 737–757. Parey Buchverlag, Berlin.
- CONERT, H. J. (2000). *Parey's Gräserbuch*. Parey Buchverlag, Berlin.
- HUBBARD, C. E. (1954). *Grasses*. Penguin Books, London.
- HUBBARD, C. E. (1968). *Grasses*, 2nd ed. Penguin Books, London.
- KERGUÉLEN, M. (1995). In PORTAL, R. *Bromus de France*. 16 Rue Louis Brioude, 43750 Vals-Pres-Le-Puy, France.
- LAUBER, K. & WAGNER, G. (1996). *Flora Helvetica*. Zurich.
- LLORET, F. J. (1993). Sobre Nomenclatura del género *Bromus* L. Poaceae. *Collectanea Botanica (Barcelona)* **22**: 151. Instituto Edita, Barcelona.
- MAIRE, R. (1955). *Flore de l'Afrique du Nord*. **3**. Paul Lechevalier, Paris.
- MEIJDEN, R. van der (1996). *Heukels' Flora van Nederland*, ed 22. Groningen.
- OJA, T. (1998). Isozyme diversity and phylogenetic affinities in the section *Bromus* of the grass genus *Bromus* (Poaceae). *Biochemical Systematics and Ecology* **26**: 403–413.
- PAVLICK, L. E. (1995). *Bromus L. of North America*. Royal Museum, Victoria, British Columbia, Canada.
- PLANCHUELO, A. M. & PETERSON, P. M. (2000). The species of *Bromus* (Poaceae: Bromeae) in South America, in JACOBS, S. W. L. & EVERETT, J., eds. *Grasses: Systematics and Evolution* pp. 89–101. C.S.I.R.O., Melbourne.
- PORTAL, R. (1995). *Bromus de France*. 16 Rue Louis Brioude, 43750, Vals-Pres-Le-Puy, France.
- SCHOLZ, H. (1970). Zur Systematik der Gattung *Bromus* L. Subgenus *Bromus* (Gramineae). *Willdenowia* **6**: 139–159.
- SCHOLZ, H. (1997). *Bromus pseudosecalinus* – auch in Deutschland. *Floristische Rundbriefe* **31**: 17–20.
- SELL, P. & MURRELL, G. (1996). *Flora of Great Britain and Ireland* **5**. Cambridge University Press, Cambridge.

- SMITH, P. M. (1973). Observations on some critical Brome-grasses. *Watsonia* **9**: 319–323.
- SMITH, P. M. (1980). *Bromus* L., in TUTIN, T. G. *et al.* eds. *Flora Europaea* **5**: 182–189. Cambridge University Press, Cambridge.
- SPALTON, L. M. (2001). A new subspecies of *Bromus hordeaceus* L. (Poaceae). *Watsonia* **23**: 525–531.
- STACE, C. A. (1997). *A New Flora of the British Isles* 2nd ed., Cambridge University Press, Cambridge.
- TZVELEV, N. N. (1976). *Grasses of the Soviet Union*. Leningrad. (1984). Translation by A. A. Balkema, Rotterdam.
- VIVANT, J. (1964). Au sujet de *Bromus commutatus* Schrader. *Bulletin Société Botanique de France* **111**: 97–100.

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