On the status of the genus *Koeleria* Pers. (Poaceae) in Britain

J. M. DIXON

Dept. of Environmental Science, University of Bradford, Bradford BD7 1DP

ABSTRACT

Since 1980 there has been confusion over the number of species in the genus *Koeleria* found in Britain. Prior to 1980, only two species - *Koeleria macrantha* (= *cristata*) and *K. vallesiana* - were reported; *Flora Europaea* added *K. glauca* to these. Results of an extensive programme to clarify the status of the *Koeleria macrantha* group (containing both *K. macrantha* and *K. glauca*) in Britain are presented here. Detailed morphological measurements and observations were made on plant material collected from 51 sites throughout Britain. The material was then grown under standard conditions; repeat measurements and observations were then made. Chromosome determinations were also carried out on samples of all populations. Whilst field specimens sometimes had morphological characteristics which might have identified them as either *K. macrantha* or *K. glauca*, all plants grown under standard conditions in the glasshouse converged in all their characteristics and were clearly referable to *K. macrantha*. The results are supported by cytological evidence: all plants were tetraploid (*K. macrantha* is reported as $2n = 28$ and *K. glauca* as $2n = 14$ in Britain). The results strongly suggest that only two species of *Koeleria* - *K. macrantha* and *K. vallesiana* - occur in Britain, and that confusion might have arisen as a result of the wide morphological variation inherent in *K. macrantha*.

KEYWORDS: *Koeleria macrantha, Koeleria glauca,* morphological measurement, chromosome determination.

INTRODUCTION

During the latter part of the 19th century and early part of the 20th, the genus *Koeleria* in Britain was divided into at least five species: *K. vallesiana* (Honck.) Gaudin, *K. albescens* DC., *K. gracilis* (*eugracilis*) Pers., *K. britannica* Domin and *K. pseudocristata* Domin. There were nine varieties and several forms distributed between them, together with the hybrid *K.* × *mixta*, considered to be the hybrid between *K. vallesiana* and *K. britannica* (Howarth 1933).

Hubbard (1954) reduced the species to two (*K. vallesiana* and *K. cristata*), with a comment that a coastal sand dune variant had been named *K. albescens.* However, he noted that the British plant referred to as *K. albescens* was scarcely distinguishable from inland *K. cristata*, except perhaps by its whitish panicles. A further note stated that *K. britannica* is a dwarf variant with short dense panicles.

The delimitation of two species continued to be adopted in British Floras throughout the 1960s and 1970s (Clapham *et al.* 1962, 1987; Keble-Martin 1965; Hubbard 1984). However, Humphries (1980) described the genus *Koeleria* in *Flora Europaea* in which species 5–13 of the genus are listed under the *K. macrantha* group. The author comments that the group is an imperfectly understood complex, with much variation as a result of polyploidy and adaptation to a wide range of ecological conditions. He goes on to state that many populations which have been given specific, subspecific and varietal rank might well represent only ecotypes and variants of different ploidy levels. As a result, the species in the *K. macrantha* group, which are based entirely on morphology, might only represent minor taxa (Tutin *et al.* 1980).

Within the *K. macrantha* group the species *K. macrantha* (Ledeb.) Schultes (a re-naming of the older *K. cristata*) and *K. glauca* (Schrad.) DC. are both recorded as occurring in Britain, along with *K. vallesiana* which in Britain is confined to a handful of sites in Somerset, and will not be discussed further here.

British Floras and related publications from 1980 onwards have, for the most part, contained the three species: *K. vallesiana*, *K. macrantha* and *K. glauca,* the last-named also belonging to the *macrantha* group. Clapham *et al.* (1987) recorded the distribution of *K. macrantha* as " in turf on well-drained, base-rich soils particularly on chalk and limestone. Locally common" and *K. glauca* as "on sandy soils. Widely distributed throughout the British Isles". Rose (1989) recorded *K. macrantha* as "frequent to locally common on dry sandy or calcareous grassland, dunes" and *K. glauca* as "common. On sandy soils, especially dunes". Fitter & Fitter (1984) recorded the two species as occurring in Britain but commented that the distribution of *K. macrantha* is not yet distinguishable from that of *K. glauca*.

Some authors were rather more cautious: Grime *et al.* (1988) merely noted that "recently *K. glauca* has been separated from the more common taxon formerly called *K. cristata*", Rodwell (1992) only referred to *K. macrantha*, while Stace (1997) under the sub-heading for *macrantha* noted that "despite several claims the diploid *K. glauca* has not been confirmed from BI".

This paper offers a detailed examination of the status of the *Koeleria macrantha* group in Britain.

MATERIALS AND METHODS

FIELD WORK

Observations and measurements were made on material belonging to the *macrantha* group from 51 sites throughout Britain, using the B.S.B.I. distribution map as a guide (Perring & Walters 1962). The majority were coastal sites but a number of inland sites were also sampled. Site descriptions are given in Appendix 1 and Fig. 1 indicates their approximate geographical location; at three of the sites (numbers 5, 41 and 44) two or more different habitats were sampled. At each site estimates were made of the average height of stands of vegetation containing *K. macrantha* (apart from sites 1, 2 and 3), and an assessment was made of the status and habit of the species. Accompanying species were also recorded but are not presented here. An estimate of soil depth was made, and a soil sample collected from the top 10 cm for analysis. The soil was collected with a stainless steel trowel, after removing any surface vegetation and litter, and placed in self-sealing polythene bags. Measurements of pH were made on fresh soil and the rest of the analyses, comprising loss on ignition, extractable Ca, K, Mg and PO_4 - P and total organic nitrogen, were carried out on air-dried soil: methods were according to Allen (1989). Soil analyses are presented in Appendix 2.

Wherever possible about ten ramets of *K. macrantha* were collected from each site, far enough apart to be separate genotypes, and an additional number of inflorescences were gathered from the same population to ensure sufficient measurements were available. The ramets were wrapped in damp newspaper and placed in polythene bags, as collection took place over several days.

LABORATORY AND GLASSHOUSE WORK

The length and width of the three longest leaves of eight selected ramets were measured and the length of the three longest stems; their panicle lengths and widths (measured in the middle of the panicle) were also measured. Where a ramet did not have three inflorescences, measurements were included for that population from the extra ones collected. Thus for most populations a total of 24 measurements for each variable were obtained. Three populations could not be sampled extensively and these are indicated by an asterisk in Appendix 1. In addition, for each population six inflorescences were selected at random (from different ramets) and one or two spikelets were removed from the middle of the panicle and measured to the nearest 0·5 mm. Observations were also made on whether stem thickening was present, the shape of the glumes and lemmas, and the degree of hairiness present on both leaves and floral parts. Hairiness was subjectively assessed as glabrous, sparsely hairy, moderately hairy and densely hairy.

After the measurements had been made all the ramets were potted up in 9 × 9 cm plastic pots containing John Innes No 1 compost and transferred to an unheated glasshouse. Each pot was moved one position horizontally and laterally every three weeks to ensure any variations in environmental conditions were evened out. The plants were watered as necessary, and in the spring were given four feeds of seedling strength commercial fertilizer 'Tomerite' to encourage flowering.

Sampling had taken place during the summers of 1997 (northern Britain) and 1998 (southern Britain). Each set of plants was grown in the glasshouse for approximately one year under standard conditions and then harvested.

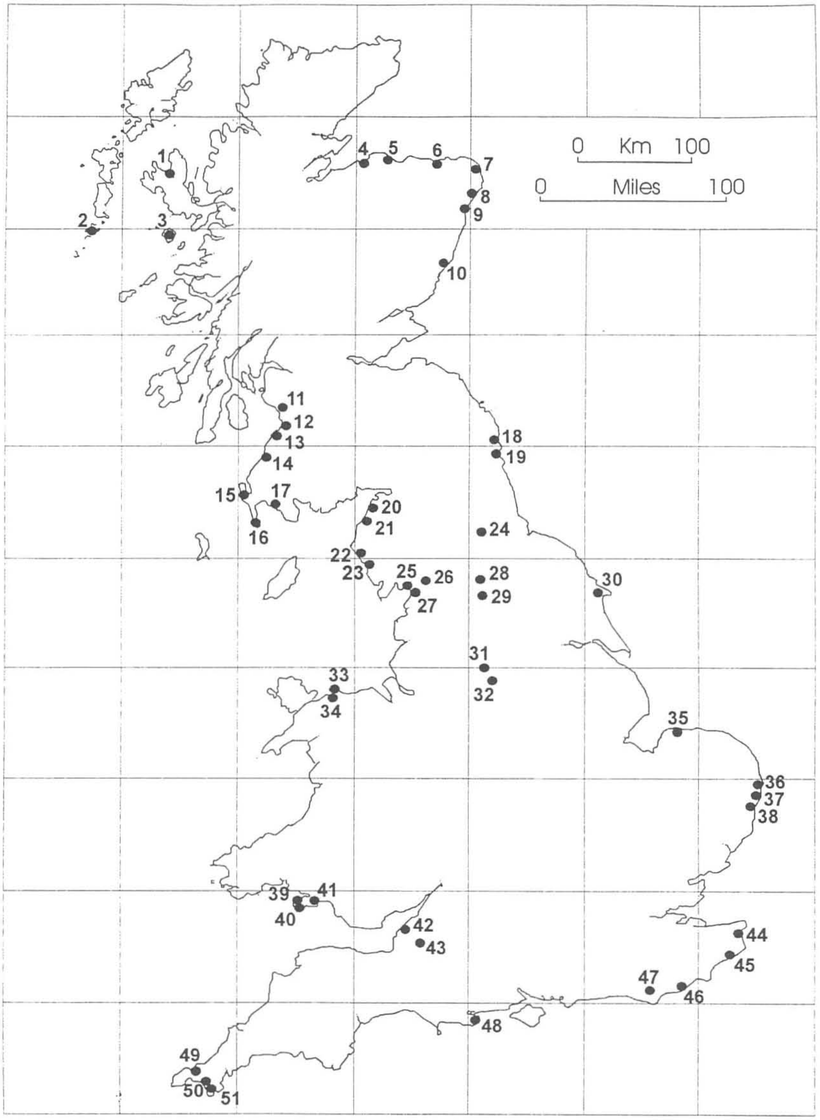

FIGURE 1. Approximate locations of sites sampled for *Koeleria*.

Measurements were then made, where possible, on each population for the same set of variables as had been made for the field samples. However, glasshouse populations from sites 15, 20 and 22 did not flower.

In addition, chromosome determinations were carried out for each population. During the spring of 1998 and of 1999, when new roots were being produced, three pots were selected at random from each population and about six new, healthy white root-tips were snipped off from those emerging through the sides of the soil/root mass. These were fixed in 3:1 absolute ethanol / glacial acetic acid fixative and kept in the refrigerator for periods not exceeding one week until they could be processed. The root tips were washed in tap water and hydrolysed for 12 minutes at 65° C in MHCl. This extended hydrolysis was found to be necessary to ensure efficient squashing. The root tips were stained in Feulgen's solution for 1–2 hours and then squashed in 45% acetic acid.

From the literature *K. macrantha* in Britain is described as tetraploid (2n = 28) and *K. glauca* as being diploid (2n = 14) (Clapham *et al.* 1987). Therefore, for the current study it was only necessary to ascertain whether 14 or 28 chromosomes were present. In view of the quantity of material being processed, to save time it was decided that any squashes with countable spreads of 20+ could safely be deemed to belong to the tetraploid and this method was adopted. For each population two out of three plants sampled were considered acceptable if good counts were obtained (not all plants had actively dividing roots); where necessary further plants were sampled.

RESULTS

MEASUREMENTS

These are presented in Appendix 3. Leaf length is highly plastic and mean leaf length was longer in all the glasshouse plants with the exception of populations from site 39 (Broughton Bay), which had almost the same mean lengths for field and glasshouse plants, and from site 4 (Nairn) where the field population had a significantly longer ($p = 0{\cdot}05$) mean leaf length (Nairn had the longest mean leaf length of any field population). The increase was not significant in only five populations - sites 5a (Branderburg), 6 (Portgordon), 21 (Allonby), 30 (Staxton) and 44a (Sandwich Bay). These were all populations with mean field leaf lengths >11 cm. All the shortest populations, that is with mean field leaf lengths < 6 cm, showed the greatest increase in leaf length in the glasshouse populations and were all significantly ($p = 0{\cdot}001$) longer, increasing to at least twice the field length.

Leaf width is not very variable in *K. macrantha*, only ranging from 1–4 mm. However, all populations increased their mean leaf width in the glasshouse, many of them significantly so. The populations which had not increased significantly in leaf length also tended to be those not showing significant increases in leaf width either.

Stem length was more variable but showed an increase in all glasshouse populations apart from site 21 (Allonby) and site 24 (Coxhoe), with mean field lengths of 27·3 and 29·7 cm respectively. These two populations had the longest mean field stem lengths.

Panicle length increased in most populations in the glasshouse; only one population had a mean measurement less than that of the field population site 13 (Mull of Galloway), but this was not significant. Some populations increased significantly in panicle length in the glasshouse while others did not.

Panicle width also generally increased, but it is difficult to measure this with any degree of accuracy and it depends on the age of the panicle, which becomes more contracted as it matures.

Spikelet length, which in the field ranged from 3·5–6 mm, increased in all populations in the glasshouse apart from site 46 (Camber) which remained the same. However, unlike the leaf length measurements, there was no significant variation between the ratio of increase for any of the populations. Whatever the mean field length the mean increase in spikelet length was around 1:1·2, with the glasshouse spikelet lengths ranging from 4·5–7·5 mm.

OBSERVATIONS

Field populations varied considerably in their habit, with some very rigid, tufted populations such as from sites 2 (Barra), 12 (Ayr), 17 (Auchenmalg Bay), 23 (Silecroft), 27 (Jenny Brown's Point); 43 (Cheddar) and 44 (Sandwich Bay - foreshore). Some were very dwarf, prostrate populations such as from sites 36 (Sizewell), 37 (Thorpeness Sluice) and 42 (Brean Down), some prostrate "trailing" populations such as from sites 39 (Broughton Bay) and 40 (Rhossili Cliff) and some tall, bushy populations as at sites 24 (Coxhoe) and 46 (Camber). These habit forms became much less pronounced in the glasshouse, but populations from sites 2, 12, 17 and 23 remained tufted and fairly rigid.

Although the field populations varied in leaf colour from light blue-green to glaucous to dark green on the adaxial surface, and from mid-green to dark green on the abaxial surface, with coastal populations being generally more glaucous than inland populations, after a year in the glasshouse there was much closer correspondence in leaf colour, varying from blue-green to mid-green on the adaxial surface and a uniform mid-green on the abaxial surface.

Leaf hairiness is extremely variable, with plants from the same population being glabrous to densely hairy and the degree of hairiness even varying on the same plant. Hairs can be minute and downy, to long (1·5 mm) on both surfaces and on the margins. Generally leaves are less hairy towards the tip, but in some populations, for example from site 24 (Coxhoe), the leaves were densely hairy on both sides almost to the tip, while in others, for example from site 27 (Jenny Brown's Point) the leaves were almost entirely glabrous apart from a few hairs around the ligule, with not even any marginal teeth. In most populations the abaxial surface is more hairy than the adaxial. In general, leaves tend to be more hairy in southern populations than in northern, but extremes have been found in both the north and the south of Britain.

None of the c. 1200 stems examined had any sign of thickening; some stems were very robust but there were no bulbous swellings at the base.

All glasshouse inflorescences were greenish-purple until flowering, becoming silvery and losing their greenness as the panicles closed, and finally straw-coloured as the panicles matured. Panicles were variable in shape, and narrowly oblong, spiciform, pyramidal and some almost round panicles were observed; these variations were maintained in cultivation. The majority of plants had a moderately to densely hairy rachis, sometimes very fine and downy, sometimes with longer hairs to 0·5 mm. In only five populations were plants found which had a glabrous to sparsely hairy rachis - 13 (Ayr), 11 (Troon), 33 (Great Orme), 35 (Holme-next-the-sea) and 44 (Sandwich Bay - fixed dunes).

Glumes varied from aristate to acuminate (most common) to mucronate; none were blunt when flattened. Glumes were densely hairy with some hairs to 0·5 mm, to minutely hairy on the keel and near the tip, to completely glabrous. Awned and very sharply-pointed glumes occurred more frequently in northern populations, with mucronate glumes more frequent in southern populations. Lemmas were also either aristate, acuminate (most common) or, rarely, mucronate. Lemmas also varied in hairiness with some being glabrous and some minutely hairy on the keel and near the tip: lemmas are never as densely hairy as glumes.

CHROMOSOME COUNTS

All populations were tetraploid with 2n = 28. No diploid plants were found.

TABLE 1. DIFFERENTIAL CHARACTERISTICS FOR *KOELERIA MACRANTHA* AND *K. GLAUCA*

Characteristic	*Koeleria macrantha*	*Koeleria glauca*
1) Habit	Tufted	Rigid tufted
2) Stems	Not thickened, 10–40 cm	Robust and with bulbous thickening towards the base, 10–45(–60) cm
3) Leaves	Green or glaucous, flat or folded, sometimes slightly rough, up to 15 cm × 1–2 mm	Leaves of non-flowering shoots glaucous, more or less inrolled and rough to touch, at least above, densely silvery, not more than 5 cm
4) Leaf sheaths	Persistent, with parallel veins	Persistent, breaking down into filaments when old
5) Panicle	20–80(–100) mm × c. 10 mm. Narrowly oblong, silvery-green purplish	20–110 mm × c. 8 mm. Spiciform, interrupted below; whitish/silvery; rachis densely puberulent
6) Spikelets	2–5(–6) mm	4–5 mm
7) Glumes	Acuminate,aristate or mucronate green, brown or purplish with a silver hyaline margin	Blunt when flat, pale green or brown
8) Lemma	Acuminate and glabrous	Subobtuse or mucronate, puberulent, at least towards the base
9) Chromosomes	2n = 28 (for Britain)	2n = 14 (for Britain)

Sources: Humphries (1980); Clapham *et al.* (1987).

DISCUSSION

Taxonomic differences between *K. macrantha* and *K. glauca* are listed in Table 1.

If each character is examined in turn a comparison can be made between the samples collected in the field and the glasshouse material grown under standard conditions:

1) A number of the field populations of *K. macrantha* had a tufted habit but with flexible leaves, while several could be described as having a rigid tufted habit, which in four populations remained so in the glasshouse.
2) Examination of the stem did not reveal any thickening or bulbous swelling in these four populations nor indeed in any other population; not a single plant exhibited this characteristic. Stem length is similar for the two species, but with *K. glauca* extending less commonly to 60 cm. Most of the *K. macrantha* populations, both in the field and in the glasshouse, did not generally extend beyond 40 cm, but in three field populations and 19 glasshouse populations, stems 44–57 cm long were recorded.
3) None of the plants collected from the field had densely silvery leaves; a few were rough enough to be described as scabrid, but were not so in their glasshouse counterparts. Sixteen populations had mean leaf lengths equal to or less than 5 cm, but in the glasshouse, in all these populations, leaf length increased significantly, with minimal mean lengths of not less than 10 cm. Leaves of *Koeleria* plants fold or inroll (*K. macrantha* does both) when subject to water stress - a common occurrence on sand dunes and shallow soils over limestone, but are flat when not subject to a water deficit: all glasshouse plants, watered freely, had flat leaves.
4) Observations on leaf sheath breakdown did not reveal the presence of filaments in either field or glasshouse populations.
5) Panicles varied in size and shape as described in the results: none exceeded 9 cm either in the field or in the glasshouse, and the rachis in the majority of populations varied from moderately to densely hairy, only five populations had a sparsely hairy or glabrous rachis. These included three small populations, an intermediate one and a tall population (based on leaf length).
6) Spikelet length for the two species is an overlapping range, with *K. macrantha* extending to 6 mm and *K. glauca* stated to be not less than 4 mm. In the field only two populations had spikelets with measurements less than 4 mm, but these had increased to 5 mm in the glasshouse. Nine populations contained spikelets of 6 mm or over in the field and in the glasshouse this had increased to 41 populations containing spikelets measuring 6 mm or longer.
7) No plants had glumes that were blunt when flattened. Some had a well-developed hyaline margin and others much less so. Colouring was variable, depending on the state of maturity.
8) Lemmas varied in shape and also in hairiness as described in the results, and at maturity the thickened median rib was found to extend into the folded acute apex.
9) All plants were tetraploid.

Koeleria glauca is described as a plant of sand dunes and sandy soils, habitats which are susceptible to drought and are often nutrient poor. Willis & Yemm (1961) investigated the nutrient status of three types of dune soils in Devon, and reported that while these had sufficient minor nutrients they were very deficient in nitrogen, phosphorus and often potassium. The vegetation of these dune soils produced some forms of several of the common species which were very depauperate, and which had even been recognised as dwarf varieties. Addition of the major nutrients led to an increase in height and weight, often two to three times greater than the control plants. Ivimey-Cook & Proctor (1966) also commented that the sparse cover and dwarfing of plants on calcareous grey dunes in the Burren, Co. Clare (v.c. H9) may reflect nitrogen, phosphorus and potassium deficiencies in the skeletal soil.

In the present study, although no sites were deficient in calcium and magnesium (see Appendix 2), several sites, 9 (Balmedie), 11 (Troon), 12 (Ayr), 19 (Druridge Bay), 23 (Silecroft) and 36 (Sizewell), all from sand dunes or raised beaches are very low in nitrogen and all the plants are of small stature. Site 36 is also deficient in phosphorus and potassium. Other short populations occurred in very shallow soils, some were heavily grazed and some occurred on exposed cliffs, usually in shallow soils. Plants in such stressed habitats are often dwarfed and very tufted relative to plants from more favourable habitats. If the stature of the short populations was a genetic adaptation to such stressed habitats (as it is perhaps in *K. glauca*), then one would have expected the ratio of increase in leaf length brought about by the more favourable conditions of the glasshouse to be roughly the same regardless of the initial length of the leaf. Figure 2 shows that this is not so and that the shorter the field population in leaf length the greater the ratio of increase in the glasshouse, leading to the conclusion that the plants were suffering from environmental stress in their original habitat, as were those investigated by Willis & Yemm (1961). This is borne out by the fact that spikelet length, and thus the floral parts, which are generally much less plastic than the leaf and stem characteristics, did not increase in the linear manner demonstrated by the regression line in Fig. 2.

The results show that *K. macrantha* is very variable in many of its morphological characteristics, and some plants collected in the field had a number of features which might lead them to being identified as *K. glauca*, such as leaf length, spikelet length, inrolled leaves and indumentum. However, after a year of growth under standard conditions all plants had converged in these (and other) features and were unmistakably *K. macrantha*, an identification supported by the cytological evidence of the constant tetraploid state. Wall (1988) investigated the role of B chromosomes in *K. macrantha* and sampled extensively from 27 sites (mainly coastal) throughout Britain, including two sites sampled by the present author. All plants that she examined were tetraploid and clearly *K. macrantha*. Thus sampling in depth from 78 sites covering a wide range of geographical locations and substrate types in Britain has yielded only tetraploid plants.

Wall also commented that plants with high numbers of B chromosomes (*K. macrantha* can have up to 6) lack vigour and set fewer seeds. Thus it is possible that the shortest populations might be those with high numbers of these accessory chromosomes; for example, in the present study populations from sites 23 (Silecroft), 36 (Sizewell) and 41b (Porthcawl) all produced mean leaf lengths of less than 11 cm in their glasshouse populations compared with the mean overall glasshouse leaf length, for all populations, of 16·2 (± 0·5) cm.

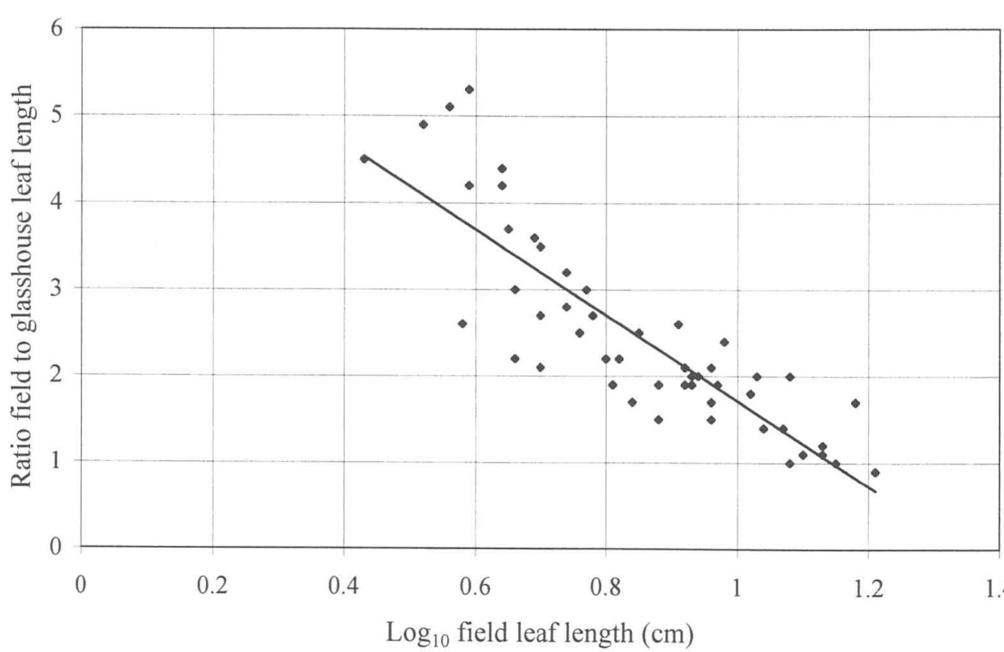

FIGURE 2. Log. mean field leaf length vs. ratio of field to glasshouse leaf length for sampled *Koeleria* populations

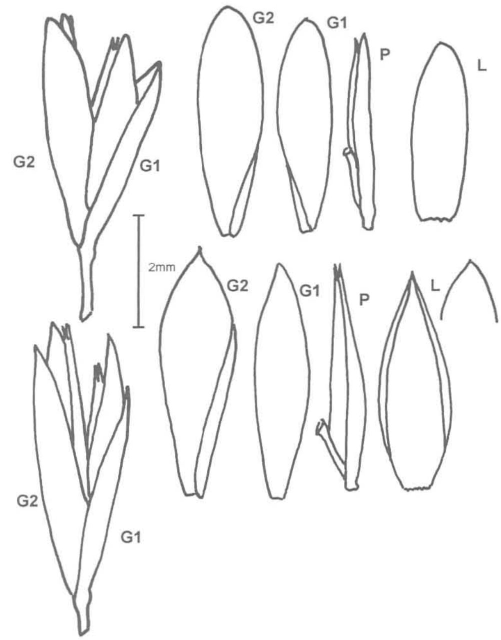

FIGURE 3. Comparison of spikelets and spikelet parts of *Koeleria macrantha* and *Koeleria glauca*. Top row *K. glauca* ; bottom row *K. macrantha*. G 1 = lower glume; G2 = upper glume; P = palea and pedicel; L = lemma. Entire spikelets on left. Indumentum not shown.

Because many of the coastal sites are stressed habitats it is possible that some plants exhibiting some characeristics of *K. glauca* may well have been misidentified from field specimens, as a result of the inherent variation in *K. macrantha,* which is described in *Flora Europaea* (Tutin *et al.* 1980) as " very variable in habit, leaf-size and indumentum". Confusion may have arisen by the inrolling of leaves by *K. macrantha* where water deficits occur.

To ascertain the degree of confusion which might arise in comparing *K. macrantha* and *K. glauca* an examination was made of European material of *K. glauca* held in **K**. Measurements and observations are summarised below.

Stems of *K. glauca* were mostly very sturdy but in only two specimens was there any slight thickening which could be described as bulbous. Leaves of non-flowering shoots, which are presented as an identifying characteristic in *Flora Europaea* as being not more than 5 cm, surprisingly turned out to be in many cases considerably longer than this: mean leaf length was 6·1 (± 0·2) cm, and the range for western Europe was 2·6–10·0 cm. Only about 37% of leaves had a length less than 5·5 cm. Thus leaf length does not appear to be a strong differentiating feature for the species. However, the maximum leaf length of 10 cm is considerably shorter than that recorded by the author for British *K. macrantha* (24·8 cm). The majority of leaves were inrolled, but some were folded and some flattened. However, this might have been an artefact of the preservation process. Leaves of *K. glauca* were all "felted" with minute rough teeth, giving the silvery, scabrid characteristic described for the species (see Table 1). This felting extends to the tip of the leaf and is in contrast to *K. macrantha* where the leaves have longer, true hairs rather than teeth (which are confined to the margins) and in most populations these do not extend to the tip. The leaf sheaths of *K. glauca* break down into a network of filaments, in a similar manner to those of *K. vallesiana*, in contrast to those of *K. macrantha,* where the leaf sheaths are persistent.

Panicle lengths to 115 cm were measured and there is less variation in the shape of the panicles in *K. glauca* compared with *K. macrantha*: 90% were spiciform with the rest exhibiting a slight pyramidal shape. *Koeleria glauca* is characterised as having the panicles interrupted below and

77% of the specimens examined were interrupted compared with only 14% in specimens of *K. macrantha* (from a much larger sample) with interrupted panicles.

Spikelets of *K. glauca* ranged from 2·5–5·5 mm with a mean of 4·7 mm (median 4·0 mm) which was very little different from those of *K. macrantha* for British specimens (range 3·5–6·0 mm, mean 4·9 mm and median 4·8 mm). These figures do not agree with those quoted in *Flora Europaea* (see Table 1).

Illustrations of the spikelets and the spikelet parts are provided in Fig. 3, and it can be seen that the glumes of the two species are different, with those of *K. macrantha* being pointed and *K. glauca* being blunt. The lemmas of *K. macrantha* are also more pointed than those of *K. glauca* and the median rib is thicker and more rigid than in *K. glauca,* and extends into the point.

Some of the differential characteristics listed in Table 1, such as the rigid tufted habit of *K. glauca* and panicle width, were not possible to determine from herbarium specimens. However, these aspects notwithstanding, and in spite of the greater convergence of the two species than is indicated in their descriptions in *Flora Europaea*, there is a marked separation of the two species as far as the leaf sheath breakdown, leaf pubescence and floral characteristics are concerned, together with the more slender and uniform spiciform shape of the panicle, which even in herbarium specimens is more intensely silvery than those of *K. macrantha*.

Thus the presented measurements and observations provided in this paper do not support the presence of *K. glauca* in Britain. In the most recent Floras, British authorities have more-or-less discarded *K. glauca* from the British list (see Cope 1998); the current paper affirms this view.

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APPENDIX 1. SITE DETAILS FOR *KOELERIA* SAMPLING. NUMBERS REFER TO APPROXIMATE LOCATION ON MAP FIG. 1

No	Location	NGR	Alt.	Slope	Aspect
1*	Nr. Dunvegan, Isle of Skye, Highland	NG223549	3 m	flat	-
	Koeleria frequent on basalt; also occasional on sandy beach with broken coral				
2*	Eoligarry, Barra, Western Isles	NL695054	1 m	flat	-
	Machair. *Koeleria* common to abundant in ungrazed areas				
3	Fonchra, Rhum, Highland	NG337003	350 m	28°	SE
	Base of steep, vegetated cliff over basalt. *Koeleria* frequent				
4	Nairn, Highland	NJ866569	2 m	flat	-
	Pebbly track *Koeleria* dominant, also in longer vegetation at side of track				
5	Nr Branderburgh, Grampian	NJ204714	15 m	20°	N
	Dune-heathland with mix of calcicoles and calcifuges, also on rocks at edge of sea				
6	Portgordon, Grampian	NJ401645	3 m	flat	-
	Sandy soil over pebbles, *Koeleria* scattered but frequent				
7	St. Combs, Grampian	NK059630	15 m	12°	NE
	Raised beach,vegetation to 40 cm high, *Koeleria* in isolated clumps				
8	Cruden Bay, Grampian	NK096358	15 m	40°	WSW
	All plants scattered in pockets across face of granite cliff, *Koeleria* frequent				
9	Balmedie, Fife	NJ977182	15 m	10°	NNE
	Short grazed turf, *Koeleria* common, plus longer ungrazed turf, with scattered *Koeleria*				
10	Lunan Bay, Tayside	NO691502	10 m	5°	NW
	Lightly grazed, fixed dunes, vegetation 3–6 cm. *Koeleria* scattered but frequent				
11*	Troon, Strathclyde	NS324305	3 m	flat	-
	Fixed dunes, *Koeleria* scattered but frequent				
12	Ayr, Strathclyde	NS328205	10 m	20°	W
	Edges of fixed dunes (top was mown), *Koeleria* very scattered				
13	Dunure, Strathclyde	NS254158	2 m	flat	-
	On rocks (hornfels) at top of beach in shallow pockets of soil, isolated plants				
14	Girvan, Strathclyde	NX160943	10 m	90°	N
	In shallow pockets of soil on rocks (phyllite) at top of shore, also on flat tops of rocks, isolated plants, an abundance of ants here				
15	Labarax, Dumfries & Galloway	NX972601	5 m	flat	-
	Koeleria scattered on fixed dunes, isolated plants also in rock crevices (slate)				
16	Mull of Galloway, Dumfries & Galloway	NX159307	50 m	15°	E
	On grassy slope and also on flat cliff top. *Koeleria* frequent but scattered				
17	Auchenmalg Bay, Dumfries & Galloway	NX243515	6 m	flat	-
	Very short, prostrate turf on track, vegetation 10–15 cm. *Koeleria* dominant here				
18	Alnmouth, Northumberland	NZ256115	3 m	flat	-
	Fixed dunes, vegetation 30–45 cm high. *Koeleria* frequent but scattered				
19	Druridge Bay, Northumberland	NZ292936	10 m	flat	-
	Fixed dunes, vegetation 10–15 cm high, grazed (horses). *Koeleria* frequent				
20	Silloth, Cumbria	NY090493	10 m	flat	-
	Fixed dunes, vegetation to 45 cm high. *Koeleria* frequent				
21	Allonby, Cumbria	NY080440	7 m	flat	-
	Partially fixed dunes,. *Koeleria* on top but not sides of dunes, vegetation to 45 cm				
22	St. Bees, Cumbria	NY957118	50 m	5°	E
	Short, but ungrazed, turf on cliff top. *Koeleria* frequent to abundant				
23	Silecroft, Cumbria	SD123805	10 m	flat	-
	Top of bank of consolidated pebbles, short, ungrazed turf. *Koeleria* common, also on track, trampled and very short				
24	Coxhoe, Durham	NZ326364	132 m	flat	-
	Dolomite quarry spoil heap. *Koeleria* in scattered small patches				
25	Far Arnside, Cumbria	SD453760	12 m	20°	SW
	Grassy slope over Carboniferous limestone, just above beach. *Koeleria* frequent in small patches				
26	Thrang End, Yealand Redmanyne, Cumbria	SD494766	70 m	10°	NNW
	Carboniferous limestone pasture, sheep grazed. *Koeleria* frequent				

* = only small samples available for measurements and observations

No	Location	NGR	Alt.	Slope	Aspect
27	Jenny Brown's Point, Silverdale, Lancashire	SD463734	5 m	20°	S
	Sandy bank over Carboniferous limestone, sloping into sea. *Koeleria* scattered among rocks				
28	Bishopdale, North Yorkshire	SD943803	419 m	20°	S
	Grassy bank over Carboniferous limestone, ungrazed vegetation to 45 cm high. *Koeleria* frequent				
29	Langcliffe, North Yorkshire	SD833656	366 m	flat	-
	Koeleria isolated but frequent in pockets of soil on clints of limestone pavement, and in shallow grikes				
30	Staxton, North Yorkshire	TA011782	107 m	5°	E
	Koeleria scattered among tall vegetation on overgrown path of disused chalk pit				
31	Wormhill, Derbyshire	SK107756	372 m	18°	S
	Isolated plants in pockets on Carboniferous limestone outcrop. Turf 3–12 cm high				
32	Monyash, Derbyshire	SK160661	274 m	flat	-
	On top of Carboniferous limestone outcrop. *Koeleria* scattered in small clumps. Some also present on more or less vertical rock face.				
33	Great Ormes Head, Gwynedd	SH780836	76 m	15°	N
	On Carboniferous limestone sea cliff, above tidal limits but within splash zone. *Koeleria* abundant, some on vertical face nearer the sea				
34	Little Ormes Head, Gwynedd	SH813823	130 m	45°	W
	Very shallow soil over Carboniferous limestone. *Koeleria* abundant				
35	Holme-next-the-Sea, Norfolk	TF708448	2 m	flat	-
	Partially fixed dunes, long loose vegetation to 60 cm. *Koeleria* occasional and very scattered, mostly at edge of board-walk				
36	Sizewell, Suffolk	TM475628	3 m	flat	-
	Raised beach, just above sea level. Sparse, very short turf on almost pure sand. *Koeleria* scattered but frequent				
37	Thorpeness Sluice, Suffolk	TM472593	2 m	flat	-
	On inland side of a shingle bar, shingle mixed with sand. *Koeleria* abundant				
38	Aldeburgh, Suffolk	TM465575	3 m	6°	NW
	Sandy bank at side of car park. *Koeleria* dominant				
39	Broughton Bay, West Glamorgan	SN416928	30 m	13°	SE
	Early fixed dunes, dense tall vegetation to 60 cm. *Koeleria* restricted to path edges where vegetation was rather shorter				
40	Rhossili Cliff, West Glamorgan	SN405878	50 m	25°	N
	Sloping cliff top, shallow soil over Carboniferous limestone. *Koeleria* scattered				
41	Nr. Porthcawl, Mid Glamorgan	ST804782	6 m	5°	NE
	Fixed dunes, dense tall vegetation to 60 cm. *Koleria* very scattered, mostly on path edges. Also on limestone outcrop nearby				
42	Brean Down, Somerset	ST286587	45 m	flat	-
	Dwarf population on exposed Carnoniferous limestone cliff top; very shallow soil. *Koeleria* abundant				
43	Nr Cheddar, Somerset	ST504517	245 m	15°	S
	Koeleria frequent on Carbonifeous limestone outcrop, occasional in pasture				
44	Sandwich Bay, Kent	TR364578	3 m	10°	WSW
	Roadside bank, also on flat fixed dunes and on flat sandy/pebbly foreshore. *Koeleria* common on bank and in dunes, more scattered on foreshore				
45	St. Margaret's At Cliffe, Kent	TR372447	80 m	12°	ESE
	In short to moderately long vegetation (12–40 cm) on top of chalk cliff. *Koeleria* scattered in small populations				
46	Camber Golf Course, East Sussex	TR946194	5 m	25°	ESE
	Partially fixed dunes of deep sand. *Koeleria* on edges of banks, frequent				
47	Nr. Beachy Head, East Sussex	TQ592973	154 m	90°	W
	Koeleria virtually limited to roadside vertical bank, not in the pasture behind it				
48	Durlston Head, Dorset	SZ025769	61 m	22°	S
	Very shallow (c. 5 cm) soil over limestone. Very short (2–7 cm) grazed turf. *Koeleria* frequent but scattered				
49	Carbis Bay Golf Course, Cornwall	ST294588	95 m	12°	W
	Fixed dunes, *Koeleria* mainly on edges of banks and paths				
50	Mullion Cove, Cornwall	SW666106	61 m	29°	N
	In short turf on top of cliff over serpentine. *Koeleria* scattered but frequent				
51	Kynance Cove, Cornwall	SW686135	64 m	10°	SW
	Koeleria abundant in very short turf over serpentine				

APPENDIX 2. SOIL ANALYSES FOR SITES SAMPLED FOR *KOELERIA*

Site No	pH	% Loss on Ignition	Ca mg $100g^{-1}$	Mg mg $100g^{-1}$	K mg 100 g^{-1}	PO_4 - P mg $100g^{-1}$	Total N (%)
1	5·8	56·1	205	88	39	1·12	1·92
2	6·4	5·5	292	41	17	1·12	0·23
3	6·2	30·8	198	66	25	0·88	0·84
4	6·2	19·3	268	99	28	1·44	0·66
5a	5·9	6·8	205	52	14	0·56	0·02
5b	6·0	5·0	190	51	14	1·12	0·03
6	5·8	4·5	255	41	16	0·90	0·20
7	5·7	10·4	365	51	15	0·92	0·39
8	6·1	17·1	348	119	34	0·92	0·56
9	6·0	3·7	183	41	16	0·90	0·10
10	5·9	4·1	198	40	15	0·88	0·21
11	6·5	1·8	218	38	14	1·12	0·06
12	6·0	1·7	190	41	15	0·80	0·04
13	6·2	3·4	210	61	17	1·20	0·06
14	5·9	24·2	185	83	28	0·68	0·80
15	6·1	8·4	203	60	21	0·76	0·31
16	soil analysis not available						
17	5·8	4·0	188	51	15	1·12	0·22
18	6·0	3·9	255	44	14	1·12	0·11
19	6·3	3·2	205	58	14	0·76	0·10
20	5·7	5·4	250	52	17	0·60	0·21
21	6·0	7·8	360	56	18	0·70	0·24
22	6·5	8·4	150	60	24	0·88	0·27
23	6·4	5·4	210	75	17	1·12	0·15
24	6·3	4·4	255	50	15	0·79	0·10
25	6·3	11·8	448	39	20	0·60	0·48
26	5·9	23·0	490	40	24	0·90	0·97
27	6·5	7·9	320	58	22	0·88	0·36
28	6·3	19·2	650	58	26	0·76	0·69
29	6·9	n/a	278	38	16	0·80	0·36
30	7·0	5·4	364	59	17	0·68	0·47
31	6·6	32·1	625	13	20	0·96	0·99
32	6·6	11·9	350	14	12	2·80	0·57
33	6·2	17·2	550	56	25	0·56	0·33
34	6·3	7·6	383	39	19	0·68	0·27
35	5·5	1·7	69	13	5	0·48	1·00
36	5·8	0·3	56	16	5	0·12	0·10
37	6·4	8·6	175	35	14	3·20	0·37
38	6·5	4·5	200	25	8	0·96	0·24
39	6·2	5·4	144	16	8	0·58	0·18
40	6·4	16·4	460	55	40	0·46	0·75
41a	6·6	6·6	356	25	11	0·48	0·25
41b	6·3	32·9	431	n/a	39	1·12	1·18
42	6·3	17·4	420	125	39	1·00	0·77
43	6·0	17·7	363	20	13	0·48	0·61
44a	6·7	8·3	356	26	19	0·90	0·19
44b	6·8	4·0	119	24	8	1·80	0·12
44c	6·8	5·1	194	29	10	0·48	0·24
45	7·0	28·8	750	44	54	1·44	0·16
46	6·6	4·1	131	23	9	0·90	0·16
47	6·8	7·2	231	25	11	0·94	0·26
48	7·0	16·7	500	100	54	1·00	0·59
49	7·0	7·4	313	29	5	0·46	0·29
50	6·1	31·3	150	388	50	1·58	1·05
51	6·0	35·2	106	200	46	0·31	0·88

5a = dune heathland; 5b = rocks; 41a = dunes; 41b = outcrop; 44a = roadside; 44b = foreshore; 44c = fixed dunes

APPENDIX 3. MEAN FIELD AND GLASSHOUSE MEASUREMENTS (± SE) AND SIGNIFICANT DIFFERENCES FOR *KOELERIA* SAMPLES

Site	Leaf length (cm)	Leaf width (mm)	Stem length (cm)	Panicle length (cm)	Panicle width (mm)	Spikelet length (mm)
1 Field	5·7 (0·5)	1·2 (0·1)	9·7 (0·5)	2·7 (0·2)	3·6 (0·3)	5·4 (0·1)
Glass.	19·8 (0·6) **3**	2·9 (0·1) **3**	24·3 (1·3) **3**	5·0 (0·3) **3**	5·5 (0·4) **1**	6·8 (0·2) **3**
2 Field	6·0 (0·4)	1·5 (0·1)	18·2 (0·9)	4·0 (0·1)	5·5 (0·6)	5·0 (0·3)
Glass.	16·4 (0·9) **3**	2·7 (0·1) **3**	33·5 (1·2) **3**	5·0 (0·2) **3**	6·4 (0·2) **N**	6·8 (0·1) **3**
3 Field	8·5 (2·3)	1·4 (0·1)	22·6 (1·2)	3·4 (0·2)	4·3 (0·2)	5·2 (0·1)
Glass.	16·5 (0·8) **3**	2·8 (0·1) **3**	32·1 (1·3) **3**	6·5 (0·2) **3**	6·3 (0·2) **3**	6·3 (0·2) **3**
4 Field	16·3 (1·7)	2·2 (0·1)	21·7 (1·7)	4·7 (0·3)	4·0 (0·2)	5·1 (0·1)
Glass.	14·7 (0·5) **1**	2·7 (0·2) **N**	25·0 (1·0) **N**	6·0 (0·2) **2**	4·5 (0·1) **1**	5·8 (0·2) **3**
5a Field	5·9 (0·3)	2·1 (0·2)	10·9 (0·9)	2·8 (0·2)	3·7 (0·2)	4·8 (0·1)
Glass.	16·5 (0·7) **3**	2·4 (0·1) **1**	20·8 (0·9) **3**	6·2 (0·1) **3**	5·5 (0·1) **3**	5·2 (0·1) **1**
5b Field	12·7 (0·7)	1·8 (0·1)	17·4 (1·7)	3·1 (0·2)	3·3 (0·3)	4·8 (0·1)
Glass.	14·0 (0·5) **N**	2·2 (0·1) **1**	19·1 (0·7) **N**	5·6 (0·2) **3**	5·0 (0·2) **2**	5·9 (0·2) **3**
6 Field	13·6 (0·8)	2·0 (0·1)	24·9 (1·7)	4·0 (0·2)	3·9 (0·1)	4·7 (0·1)
Glass.	15·3 (0·5) **N**	2·5 (0·1) **1**	36·5 (1·5) **3**	7·0 (0·2) **3**	5·2 (0·2) **3**	6·9 (0·1) **3**
7 Field	11·9 (0·7)	1·9 (0·1)	21·2 (1·2)	3·5 (0·2)	4·9 (0·1)	5·2 (0·2)
Glass.	23·8 (0·4) **3**	2·6 (0·1) **3**	22·2 (0·7) **N**	3·5 (0·1) **N**	5·2 (0·2) **3**	6·0 (0·3) **1**
8 Field	9·2 (1·2)	2·3 (0·1)	18·6 (1·6)	3·1 (0·2)	4·5 (0·2)	5·0 (0·3)
Glass.	15·5 (0·7) **2**	2·9 (0·1) **3**	30·7 (1·9) **3**	5·1 (0·1) **3**	5·8 (0·2) **3**	5·6 (0·2) **N**
9 Field	4·5 (0·4)	1·6 (0·1)	17·5 (1·9)	3·2 (0·2)	3·9 (0·2)	5·0 (0·1)
Glass	16·5 (0·5) **3**	2·4 (0·1) **3**	28·0 (1·1) **3**	5·6 (0·3) **3**	5·6 (0·3) **3**	5·7 (0·1) ·**2**
10 Field	7·1 (0·5)	1·8 (0·1)	9·6 (0·6)	3·1 (0·3)	3·2 (0·2)	4·6 (0·2)
Glass.	18·0 (0·6) **3**	2·5 (0·1) **3**	31·0 (1·2) **3**	5·7 (0·2) **3**	4·6 (0·2) **3**	6·2 (0·2) **3**
11 Field	3·9 (0·2)	1·6 (0·1)	3·9 (0·4)	1·7 (0·2)	3·4 (0·2)	4·8 (0·1)
Glass.	16·5 (0·6) **3**	2·1 (0·1) **3**	25·4 (1·0) **3**	4·7 (0·2) **3**	4·7 (0·2) **3**	5·3 (0·1) **1**
12 Field	3·6 (0·4)	1·7 (0·1)	11·4 (0·6)	3·8 (0·3)	4·5 (0·2)	4·4 (0·2)
Glass.	18·5 (0·5) **3**	2·3 (0·1) **3**	24·9 (0·3) **3**	6·9 (0·1) **3**	5·0 (0·3) **N**	5·6 (0·2) **3**
13 Field	10·8 (0·6)	2·8 (0·1)	17·0 (0·9)	5·9 (0·4)	7·1 (0·5)	5·5 (0·2)
Glass.	22·1 (1·7) **3**	2·9 (0·2) **N**	23·4 (1·3) **N**	6·0 (0·3) **N**	4·6 (0·2) **3**	5·8 (0·1) **N**
14 Field	7·5 (0·6)	1·9 (0·1)	13·2 (1·3)	3·0 (0·2)	4·6 (0·2)	4·9(0·2)
Glass.	11·1 (0·3) **3**	2·4 (0·2) **2**	17·1 (1·0) **1**	4·1 (0·1) **3**	5·1 (0·2) **2**	5·5 (0·2) **1**
15 Field	3·3 (0·3)	1·8 (0·1)	5·9 (0·7)	2·3 (0·1)	4·1 (0·2)	4·3 (0·1)
Glass.	16·2 (0·6) **3**	2·3 (0·1) **3**	n/a	n/a	n/a	n/a
16 Field	8·6 (0·9)	2·0 (0·1)	14·9 (2·5)	3·6 (0·3)	4·9 (0·3)	4·7 (0·2)
Glass.	17·6 (0·4) **3**	2·6 (0·1) **3**	22·9 (1·6) **3**	3·3 (0·2) **N**	5·0 (0·1) **N**	6·1 (0·2) **3**
17 Field	4·6 (0·2)	2·0 (0·1)	12·3 (1·2)	2·7 (0·2)	4·8 (0·2)	5·3 (0·2)
Glass.	13·9 (0·9) **3**	2·6 (0·1) **3**	29·3 (0·9) **3**	4·5 (0·1) **3**	5·8 (0·2) **2**	5·4 (0·2) **N**
18 Field	8·1 (0·5)	2·3 (0·1)	14·8 (0·6)	2·8 (0·2)	4·5 (0·2)	4·6 (0·2)
Glass.	21·1 (0·9) **3**	2·9 (0·1) **3**	26·4 (1·9) **3**	5·1 (0·2) **3**	5·7 (0·2) **2**	5·7 (0·2) **2**
19 Field	3·9 (0·2)	1·8 (0·1)	11·4 (0·7)	2·6 (0·1)	4·4 (0·2)	4·8 (0·2)
Glass.	20·7 (0·7) **3**	2·4 (0·1) **3**	24·7 (0·2) **3**	4·5 (0·2) **3**	5·0 (0·2) **1**	5·3 (0·2) **N**
20 Field	11·7 (0·9)	2·0 (0·1)	24·3 (1·5)	5·2 (0·2)	4·5 (0·2)	5·2 (0·2)
Glass.	16·4 (0·2) **3**	2·7 (0·1) **3**	n/a	n/a	n/a	n/a
21 Field	13·7 (0·6)	2·1 (0·1)	27·3 (0·9)	3·9 (0·5)	5·0 (0·3)	4·7 (0·1)
Glass.	15·3 (0·5) **1**	2·5 (0·1) **2**	20·9 (0·9) **3**	4·6 (0·2) **N**	5·0 (0·2) **N**	5·2 (0·2 **1**
22 Field	5·5 (0·3)	2·1 (0·1)	8·0 (0·8)	3·4 (0·2)	4·6 (0·2)	5·5 (0·2)
Glass.	15·3 (0·4) **3**	3·1 (0·1) **3**	n/a	n/a	n/a	n/a
23 Field	3·8 (0·2)	2·1 (0·1)	3·8 (0·3)	2·3 (0·05)	4·2 (0·2)	5·3 (0·1)
Glass.	10·0 (0·4) **3**	2·7 (0·2) **1**	11·0 (0·8) **3**	4·7 (0·2) **3**	4·4 (0·2) **N**	5·4 (0·2) **N**
24 Field	15·1 (0·9)	2·0 (0·1)	29·7 (2·9)	5·4 (0·4)	4·8 (0·3)	4·8 (0·2)
Glass.	25·8 (0·9) **3**	2·5 (0·1) **3**	25·5 (0·8) **N**	7·1 (0·1) **3**	4·1 (0·3) **N**	5·7 (0·2) **2**
25 Field	8·4 (0·6)	2·3 (0·2)	15·5 (0·7)	3·6 (0·3)	4·0 (0·2)	4·9 (0·2)
Glass.	17·9 (0·4) **3**	3·0 (0·1) **3**	33·9 (1·3) **3**	7·0 (0·1) **3**	5·7 (0·4) **3**	5·3 (0·2) **N**
26 Field	4·9 (0·3)	1·5 (0·1)	21·4 (1·3)	3·5 (0·2)	n/a	4·7 (0·3)
Glass.	17·7 (0·7) **3**	2·5 (0·1) **3**	37·6 (1·6) **3**	5·6 (0·1) **3**	4·5 (0·1)	5·8 (0·3) **2**

n/a = not available 5a = dune heathland; 5b = rock.
Numbers in bold indicate levels of significance for t-tests between the field and glasshouse populations. N = not significant, 1 = p at 0·05, 2 = p at 0·01 and 3 = p at 0·001

Site	Leaf length (cm)	Leaf width (mm)	Stem length (cm)	Panicle length (cm)	Panicle width (mm)	Spikelet length (mm)
27 Field	5·5 (0·7)	1·8 (0·1)	20·1 (2·3)	3·5 (0·3)	n/a	4·9 (0·2)
Glass.	17·8 (0·6) **3**	2·5 (0·05) **3**	26·9 (1·7) **3**	6·2 (0·1) **3**	4·6 (0·2)	5·8 (0·2) **3**
28 Field	10·4 (1·1)	2·2 (0·1)	17·5 (2·3)	3·9 (0·2)	3·8 (0·2)	5·1 (0·2)
Glass.	18·3 (0·4) **3**	2·8 (0·1) **3**	32·4 (2·3) **3**	6·2 (0·2) **3**	4·4 (0·2) **N**	5·6 (0·2) **N**
29 Field	5·9 (0·3)	1·4 (0·1)	16·2 (1·6)	3·1 (0·2)	3·4 (0·2)	4·8 (0·2)
Glass.	17·9 (0·9) **3**	2·4 (0·05) **3**	29·6 (1·1) **3**	6·0 (0·1) **3**	5·0 (0·2) **3**	5·4 (0·1) **2**
30 Field	13·2 (0·7)	1·5 (0·1)	22·5 (1·2)	3·1 (0·2)	3·7 (0·1)	4·8 (0·1)
Glass.	13·6 (1·1) **N**	2·3 (0·1) **3**	25·9 (1·8) **N**	5·5 (0·2) **3**	4·9 (0·2) **3**	n/a
31 Field	6·3 (0·7)	1·8 (0·1)	10·2 (1·1)	2·5 (0·2)	3·6 (0·2)	4·3 (0·2)
Glass.	13·7 (0·6) **3**	2·1 (0·1) **2**	20·5 (2·6) **2**	4·5 (0·3) **3**	4·6 (0·3) **2**	5·9 (0·3) **2**
32 Field	6·6 (0·6)	1·9 (0·1)	17·7 (1·1)	3·5 (0·2)	3·6 (0·2)	4·8 (0·3)
Glass.	14·2 (0·8) **3**	2·0 (0·1) **N**	29·8 (1·2) **3**	5·5 (0·2) **3**	4·2 (0·2) **1**	5·6 (0·1) **1**
33 Field	4·4 (0·2)	1·7 (0·1)	8·5 (0·8)	2·8 (0·3)	4·2 (0·2)	4·8 (0·2)
Glass.	18·4 (0·8) **3**	2·6 (0·1) **3**	23·6 (1·2) **3**	5·5 (0·1) **3**	4·9 (0·2) **2**	6·1 (0·2) **3**
34 Field	4·4 (0·2)	1·7 (0·1)	8·5 (0·8)	2·8 (0·3)	4·2 (0·2)	5·2 (0·2)
Glass.	19·6 (0·5) **3**	2·4 (0·1) **3**	30·9 (1·7) **3**	5·4 (0·2) **3**	4·4 (0·2) **N**	5·8 (0·2) **N**
35 Field	9·6 (0·6)	1·9 (0·1)	17·5 (1·2)	4·1 (0·2)	3·3 (0·1)	5·2 (0·2)
Glass.	22·9 (1·0) **3**	2·3 (0·1) **2**	34·4 (2·4) **3**	6·8 (0·1) **3**	3·9 (0·2) **2**	6·0 (0·1) **3**
36 Field	4·6 (0·3)	1·8 (0·1)	11·8 (0·8)	3·2 (0·2)	2·9 (0·1)	4·4 (0·2)
Glass.	10·0 (0·2) **3**	2·3 (0·1) **3**	28·0 (1·1) **3**	5·5 (0·2) **3**	4·6 (0·1) **3**	5·3 (0·1) **2**
37 Field	5·0 (0·3)	2·0 (0·1)	12·0 (0·9)	2·8 (0·1)	2·9 (0·1)	4·2 (0·1)
Glass.	13·3 (0·5) **3**	2·1 (0·1) **N**	44·1 (1·9) **3**	6·9 (0·2) **3**	4·9 (0·2) **3**	5·2 (0·2) **2**
38 Field	7·0 (0·3)	2·1 (0·1)	19·3(1·0)	4·1 (0·1)	3·8 (0·2)	4·3 (0·2)
Glass.	13·5 (0·3) **3**	2·3 (0·1) **N**	39·4 (1·8) **3**	6·5 (0·2) **3**	4·7 (0·2) **1**	5·7 (0·3) **2**
39 Field	12·1 (1·0)	2·2 (0·1)	13·8 (0·6)	3·9 (0·2)	3·7 (0·2)	4·8 (0·1)
Glass.	12·0 (0·4) **N**	2·4 (0·1) **1**	19·6 (1·1) **2**	4·4 (0·2) **N**	5·7 (0·2) **3**	5·1 (0·2) **N**
40 Field	5·0 (0·3)	1·7 (0·1)	7·9 (0·9)	2·3 (0·1)	3·1 (0·2)	4·8 (0·1)
Glass.	17·7 (0·8) **3**	2·3 (0·1) **3**	22·3 (1·4) **3**	5·0 (0·2) **3**	6·0 (0·7) **3**	5·3 (0·1) **1**
41a Field	6·5 (0·3)	1·8 (0·1)	14·7 (0·5)	3·3 (0·1)	3·9 (0·2)	4·9 (0·1)
Glass.	12·3 (0·3) **3**	2·4 (0·1) **3**	25·1 (1·4) **3**	5·8 (0·3) **3**	5·8 (0·3) **3**	6·4 (0·1) **3**
41b Field	5·0 (0·3)	1·7 (0·1)	10·4 (0·6)	2·9 (0·3)	3·4 (0·3)	4·3 (0·1)
Glass.	10·6 (0·4) **3**	2·3 (0·1) **3**	28·0 (0·9) **3**	4·6 (0·2) **3**	4·7 (0·1) **3**	5·3 (0·2) **N**
42 Field	2·7 (0·2)	1·5 (0·05)	8·2 (0·8)	2·2 (0·1)	2·9 (0·1)	4·3 (0·1)
Glass.	12·2 (0·3) **3**	2·0 (0·1) **3**	25·4 (0·9) **3**	5·7 (0·2) **3**	4·2 (0·1) **3**	5·3 (0·2) **2**
43 Field	5·7 (0·3)	1·5 (0·1)	21·7 (1·3)	3·5 (0·2)	3·3 (0·1)	4·8 (0·2)
Glass.	14·1 (0·7) **3**	2·1 (0·1) **3**	42·9 (2·1) **3**	6·2 (0·2) **3**	3·9 (0·3) **1**	5·4 (0·2) **1**
44a Field	14·1 (0·6)	2·3 (0·1)	29·9 (2·8)	5·9 (0·3)	3·9 (0·1)	4·5 (0·2)
Glass.	14·9 (0·3) **N**	2·5 (0·1) **N**	30·9 (0·8) **N**	6·8 (0·2) **N**	5·1 (0·2) **3**	5·4 (0·1) **N**
44b Field	13·6 (0·5)	2·4 (0·1)	26·4 (2·2)	4·8 (0·2)	3·8 (0·2)	4·7 (0·2)
Glass.	16·7 (0·6) **3**	2·6 (0·1) **1**	41·4 (0·8) **3**	6·6 (0·1 **3**	4·7 (0·1) **3**	5·0 (0·1) **2**
44c Field	11·0 (0·8)	2·0 (0·1)	30·4 (1·4)	5·4 (0·3)	3·7 (0·2)	4·9 (0·1)
Glass.	15·4 (0·4) **3**	2·4 (0·1) **3**	39·1 (1·0) **3**	6·9 (0·2) **3**	4·8 (0·2) **2**	5·3 (0·2) **N**
45 Field	9·4 (0·6)	2·0 (0·1)	20·3 (1·0)	4·3 (0·2)	3·9 (0·2)	4·9 (0·2)
Glass	18·1 (0·8) **3**	2·5 (0·1) **3**	32·8 (2·6) **3**	6·6 (0·3) **3**	4·5 (0·3) **N**	5·4 (0·1) **N**
46 Field	9·2 (0·6)	2·1 (0·1)	28·1 (0·9)	5·6 (0·3)	4·1 (0·1)	5·3 (0·3)
Glass.	19·0 (0·7) **3**	2·5 (0·1) **N**	28·7 (1·6) **N**	5·6 (0·1) **N**	4·6 (0·2) **N**	5·3 (0·3) **N**
47 Field	8·8 (0·7)	1·8 (0·)	14·8 (0·7)	3·1 (0·2)	3·3 (0·1)	4·3 (0·3)
Glass.	17·5 (0·6) **3**	2·4 (0·1) **3**	23·5 (0·2) **3**	5·3 (0·2) **3**	4·4 (0·1) **3**	5·0 (0·2) **N**
48 Field	4·6 (0·3)	1·5 (0·1)	10·8 (1·0)	2·7 (0·2)	3·0 (0·2)	4·8 (0·2)
Glass.	13·7 (0·5) **3**	2·3 (0·1) **3**	25·2 (1·9) **3**	5·4 (0·2) **3**	4·5 (0·3) **3**	5·7 (0·1) **1**
49 Field	8·4 (0·6)	1·8 (0·1)	15·5 (0·8)	3·3 (0·2)	4·1 (0·2)	4·8 (0·2)
Glass.	16·2 (0·9) **3**	2·7 (0·1) **3**	16·4 (1·1) **N**	4·1 (0·1) **2**	5·6 (0·3) **3**	5·3 (0·2) **N**
50 Field	9·1 (0·4)	2·1 (0·1)	13·7 (1·0)	4·1 (0·2)	4·3 (0·2)	4·8 (0·1)
Glass.	13·8 (0·4) **3**	2·3 (0·2) **N**	20·8 (0·8) **3**	5·0 (0·1) **2**	5·4 (0·2) **2**	5·9 (0·3) **2**
51 Field	6·9 (0·4)	2·1 (0·1)	10·8 (0·7)	3·3 (0·2)	4·9 (0·2)	5·0 (0·2)
Glass.	11·9 (0·3) **3**	2·6 (0·1) **3**	14·5 (0·4) **3**	4·4 (0·1) **3**	6·1 (0·3) **2**	5·6 (0·1) **1**

41a = dunes; 41b = outcrop; 44a = roadside; 44b = foreshore; 44c fixed dunes
Numbers in bold indicate levels of significance for t-tests between the field and glasshouse populations. N = not significant, 1 = p at 0·05, 2 = p at 0·01 and 3 = p at 0·001