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The *Eleocharis mamillata* H. Lindb. fil. aggregate (Cyperaceae) in the British Isles

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ABSTRACT

We analysed stylopodium characters, perianth bristle number, vascular bundle number, stomatal length and fruit density for 50 stems of *Eleocharis mamillata* agg. throughout its British range. Stylopodium shape varies considerably within a spikelet and it is necessary to measure a large sample of fruits to establish an accurate reading. However there is highly significant variation between individuals for stylopodium shape and relative stylopodium width. Variation in these attributes between individuals is continuous. Nine individuals sampled, eight from N.W. Yorks (v.c. 64) and one from Selkirk (v.c. 79), have a stylopodium shape considered typical of subsp. *mamillata*, which has not been previously recorded from the British Isles. However, this material does not correspond to subsp. *mamillata* in any other character. Most individuals from the Borders region (v.cc. 67 and 70) are clearly referable to subsp. *austriaca* (Hayek) Strandhede, but many individuals in N.W. Yorks, and one from Selkirk belong to a distinctive intermediate type which is also distinguished by a high fruit density and vascular bundle number. We hypothesise that these may represent hybrids between previously isolated populations which have been recently transported into water bodies by ducks.

KEYWORDS: stylopodium, vascular bundle, hybrid vigour, Spike-rush.

INTRODUCTION

Eleocharis mamillata H. Lindb. fil. and its close relatives including *E. austriaca* Hayek are distinguished from *E. palustris* (L.) Roemer & Schultes in having fragile stems with an orbicular rather than oval cross-section, fewer vascular bundles, conical flowering heads, and the number of perianth bristles at the base of the fruit usually exceeding four (Walters 1980). The *E. mamillata* aggregate are plants of a boreal or montane distribution and ecology in Europe, rarely inhabiting the lowland, more eutrophic locations that are typical of *E. palustris*.

E. austriaca was first collected in the British Isles in July 1947 by N.Y. Sandwith in a marshy ox-bow of the infant R. Wharfe below Buckden, Mid-W. Yorks. (v.c. 64) but was not identified until 1960 (Walters 1963). Shortly afterwards, it was discovered in similar habitats by streamsides in montane, usually forested areas, in S. Northumberland (v.c. 67), Cumberland (v.c. 70) (Walters 1963, Swan 1993, Halliday 1997), in Selkirk (v.c. 79) (Corner 1975) and in a number of further localities in the valleys of the R. Wharfe and R. Ribble in v.c. 64 (Roberts 1977). The exact habitats favoured by this species are impermanent since several are artificial water bodies and all are colonised by seral development resulting in conditions which become unsuitable to this primary coloniser. In v.c. 67 at least, the species has become very rare in recent years.

Although it has been traditional to separate *E. austriaca* from *E. mamillata* (Hayek 1910, Hegi 1966, Hess *et al*. 1967, Walters 1980), the two taxa are very similar in general appearance and are clearly closely related to one another. The character by which they are most readily separated is the shape of the stylopodium (the small discrete organ which links the top of the fruit to the style base) which all authors agree is wider than long in *E. mamillata* and longer than wide in *E. austriaca*. The perianth bristle number is said by Hayek to be more commonly six or more in the former species, but five in the latter, although neither Strandhede (1966) nor Walters (1953) confirm this. *E. mamillata* has also been said by Hayek to have, on average, fewer vascular bundles in the stem (not exceeding 12). These are plants with very few quantifiable characters, so the possibility should be borne in mind that any character that shows variability, however trivial, had been given undue importance. This may be particularly true of stylopodium characters which we have found can vary greatly depending on the position of the fruit in the spike. It has been suggested that *E. austriaca* occurs in mountainous, calcareous areas, and is localised to parts of Norway within Scandinavia, whereas *E. mamillata* is more typical of peaty pools without competing vegetation and is more widespread in Scandinavia, although both species are common in central Europe and the Alps (Strandhede & Dahlgren 1968).

However, Strandhede (1966) recombined *E. austriaca* as *E. mamillata* H. Lindb. fil. subsp. *austriaca* (Hayek) Strandhede and recently he has been followed by others, especially Gregor (2003), who provided considerable biometric support for this treatment; it is evident, therefore, that the correct name for the British plant at specific rank should be *E. mamillata*. All the material that has been examined previously from v.cc. 67 and 70 had a long and narrow stylopodium and were presumably correctly referred to subsp. *austriaca* (*E. austriaca).* However, fruits from a Yorkshire population in Strandhede (1966; see Fig. 7e) appear to have characters intermediate between *austriaca* and *mamillata* whilst drawings of some fruits in Walters (1963) and Roberts (1977) also led Gregor (2003) to consider plants from northern England to be typical of neither subspecies. Furthermore, some material sent to G. A. Swan (GAS) from Ribbledale and Wharfedale by F.J. Roberts (FJR) was characterised by a broader and wider stylopodium. At the time GAS considered that this material fell within the limits of subsp. *mamillata*, which had not been recorded from the British Isles. For many years, GAS had been aware that the fruits of the plant drawn by Roberts (1977) differed from those of the plant which he (GAS) named subsp. *austriaca*. However, it was only when A. J. Richards (AJR) sent to GAS a copy of Gregor (2003) that GAS felt compelled to try and clarify the situation and he is grateful to AJR and FJR for catalysing and promoting the (albeit inconclusive) work published here.

MATERIALS AND METHODS

Growth in *E. mamillata* agg. is such that it is impossible to satisfactorily distinguish the limits of clonal individuals in the field. Populations typically have a rather even distribution of shoots that may represent many individuals that overlap one another, or may consist of only one or very few individuals. A total of 50 shoots were examined from 24 populations from various parts of the British range (Table 1). Voucher specimens of these are to be lodged at the Hancock Museum, Newcastle upon Tyne (HAMU). Most populations are represented by only a single specimen, but where more than one specimen was examined, it is not known for certain whether more than one individual was involved, although measurements suggest that this was the case. In order to eliminate bias due to the position of the fruit within the spike, all fruits in a spike were sampled as far as this was possible, and their position in the spike noted. 2300 fruits were analysed in total. Often, some fruits were missing or had dehisced, but it is doubtful if these absences seriously affected the data. In order to count perianth bristle number, fruits need to be mounted in water on a microscope slide but it did not prove possible to accurately count this in some specimens as the bristles on many fruits had been broken or lost.

Dry fruits were measured by means of a calibrated eye-piece scale at ×20 using a Swift dissecting microscope. For each fruit, the following characters were noted:

- Ratio of the length to the maximum width of the stylopodium, known as 'stylopodium shape' (s.s.). (The length of the stylopodium is unambiguous in material which has lost style branches, although the style may not always break in the same position, causing a possible source of inaccuracy; in the few cases where style branches were still intact, the end of the stylopodium was judged to be where the style base reached its minimum width, which probably accords with the definition of Strandhede (1966), although this position is not always assessed readily).

- Ratio of the maximum width of the stylopodium to the maximum width of the fruit, known as 'relative stylopodium width' (r.s.w.).

TABLE 1. DETAILS OF SHOOTS EXAMINED. SHOOTS WERE CONSIDERED TO BELONG TO THE SAME POPULATION WHEN THEY OCCURRED IN THE SAME WATER BODY WITHIN ABOUT 100 M

Code	No. of fruits	V.C.	Site name and code	Grid Ref.	s.s.*	r.s.w.*	Date	Collector
5 m	39	64	Lodge Pond, Settle 5	SD822621	0·912	0·496	28/09/75	FJR
31 m	36	64	Ribble 12	SD777790	0·898	0·496	28/08/75	FJR
32 m	25	64	Ribble 7	SD782786	0·948	0·459	15/09/03	FJR
40 m	67	64	Ribbledale SLQ 8	SD773785	0·973	0·441	12/07/03	FJR
51 m	35	64	Ribblehead SLQ 8	SD773784	0·885	0·429	12/07/03	FJR
53 m	27	64	Ribblehead SLQ 8	SD773784	0·881	0·445	12/07/03	FJR
42 m	26	64	Ribble 21	SD785769	0·957	0·455	15/09/03	FJR
30 m	12	64	Buckden, Wharfe 11	SD944760	0·925	0·482	11/09/03	FJR
8 m	22	79	Tima Water ?pop	NT20	0·960	0·445	06/07/77	OM Stewart
7 i	53	64	Ribblehead Quarry 3	SD7678	1·156	0·414	04/09/04	FJR
9 i	45	64	Ribble 7	SD782783	1·084	0·436	15/09/03	FJR
14 i	51	64	Ribble 7	SD784780	1·100	0·418	15/09/03	FJR
10 i	84	64	Ribblehead SLQ 8	SD773785	1·073	0·426	26/08/75	FJR
39 i	74	64	Ribbledale SLQ 8	SD773785	1·043	0·442	12/07/03	FJR
11 i	77	64	Ribble 9	SD785778	1·013	0·436	15/09/03	FJR
12 i	36	64	Selside, Ribble 10	SD788787	1·017	0·419	18/10/73	FJR
41 i	77	64	Ribble 12	SD778789	1·049	0·407	03/09/03	FJR
38 i	75	64	Ribble 20	SD798745	1·156	0·417	15/09/03	FJR
45 i	41	64	Horton, Ribble 22	SD79.74.	1·068	0·428	14/07/75	FJR
57 i	28	64	BenRhydding gravel pit 24	SE146475	1·086	0·420	—/07/77	FJR
15 i	59	64	Buckden, Wharfe 11	SD943760	1·168	0·419	12/07/75	FJR
1 a	24	67	Byrness, Rede 1	NT770022	1·451	0·320	22/07/62	GAS
2 a	31	67	Kielder Burn 2	NY649955	1·426	0·340	06/05/62	GAS
4 a	30	70	Irthing. Gowk Bank 4	NY682737	1·412	0·407	16/09/63	GAS
6 a	36	79	Tima Water 6	NT283107	1·140	0·369	09/08/03	RWMCorner
16 a	50	64	Ribble 12	SD778789	1·355	0·391	02/09/03	FJR
17 a	16	64	Ribble 12	SD778789	1·257	0·406	02/09/03	FJR
18 a	58	64	Ribblehead SLQ 8	SD773784	1·209	0·363	03/09/03	FJR
20 a	36	70	Irthing, below Butterburr 13	NY6873	1·196	0·386	—/—/90	FJR
50 a	48	70	Churnsike bridge, Irthing 23	NY6876	1·517	0·406	—/—/91	FJR
26 a	47	67	Whitehill quarry pond 16	NY701777	1·222	0·353	—/08/02	T&D Hardy
29 a	17	67	White Kielder Burn 19	NY677989	1·486	0·303	13/08/67	GAS
28 a	41	67	N Tyne, Charlton 18	NY809846	1·228	0·319	11/08/63	GAS
58 a	16	64	Ribble 7	SD782786	1·558	0·403	15/09/03	FJR
22 a	38	64	Ribblehead SLQ 8	SD773784	1·167	0·381	03/09/03	FJR
25 a	62	64	Ribblehead SLQ 8	SD772785	1·287	0·404	03/09/03	FJR
33 a	51	64	Ribblehead Quarry 3	SD7678	1·277	0·405	04/09/04	FJR
34 a	40	64	Ribblehead Quarry 3	SD7678	1·272	0·392	04/09/04	FJR
35 a	33	64	Ribblehead Quarry 3	SD7678	1·262	0·415	04/09/04	FJR
36 a	43	64	Ribblehead Quarry 3	SD7678	1·381	0·363	04/09/04	FJR
37 a	66	64	Ribblehead Quarry 3	SD7678	1·160	0·383	04/09/04	FJR
46 a	87	64	Ribblehead Quarry 3	SD7678	1·136	0·369	04/09/04	FJR
3 a	68	64	Ribblehead Quarry 3	SD7678	1·405	0·373	04/09/04	FJR
13 ?	64	64	Ribble 7	SD782785	1·125	0·456	15/09/03	FJR
19 ?	49	64	Ribblehead SLQ 8	SD773784	1·069	0·366	03/09/03	FJR
56 ?	35	64	Ribblehead SLQ 8	SD773784	0·884	0·365	12/07/03	FJR
24 ?	71	64	Ribblehead Quarry 3	SD7678	1·207	0·455	03/09/03	FJR
21 ?	55	70	Irthing, Shank End 14	NY6876	1·303	0·424	—/—/91	FJR
23 ?	45	70	Irthing. Churnsike bridge 15	NY6873	1·142	0·424	28/09/75	FJR
27 ?	25	67	Bells Braes, Irthing 17	NY691724	1·272	0·416	27/09/64	GAS

Code – a = plants identified as subsp. *austriaca*, m = plants identified as subsp. *mamillata*, i = plants belonging to the intermediate group with high indices for bundle number and fruit density, ? plants which do not fall readily into any category , *s.s. stylopodium shape, *r.s.w. relative stylopodium width

The mean and standard error of these characters were calculated for each shoot. In addition, for each shoot the following characters were recorded:

- Number of vascular bundles
- Stem diameter after soaking in hot water
  - Number of mature fruits in spikelet
  - Length of spikelet
  - Stomatal length (measured by compound microscope ×400 from epidermal peels of dried material soaked in warm water, and mounted in tap water).

RESULTS

Across all 50 shoots there was highly significant variation between individuals for both stylopodium shape (s.s.: F = 17·48, P<0·0001) and relative stylopodium width (r.s.w.: F = 39·72, P<0·0001). For s.s., the mean reading varied between individuals by a factor of almost two, from 0·881 to 1·558, and for r.s.w. the mean reading varied from 0·303 to 0·496. There was a significant negative relationship between s.s. and r.s.w. (Fig. 1) as might be expected because these characters share the attribute of stylopodium width in which r.s.w. tends to increase and s.s. tends to decrease. The regression between these characters is identical for Yorkshire (v.c. 64) and "Borders" (vcc. 67, 70) material but, although there is some overlap between the "Borders" and about one third of the Yorkshire material, the majority of the Yorkshire material has a lower average s.s. and a higher average r.s.w. than any of the "Borders" material. Taken as a whole, the variation in mean readings of both characters is continuous, showing no obvious discontinuities.

We observed exceptional variability within shoots for both stylopodium shape and relative stylopodium width which, for both attributes, usually varied by a factor of two or more so that most specimens would have some fruits which were typical for subsp. *austriaca* and some typical for subsp. *mamillata* (for each of these attributes). For two individuals, both identified as subsp. *austriaca*, we investigated the relationship between these attributes and the position of the fruit on the spike. For individual 50 (from v.c. 70), an extreme 'austriaca' phenotype of mean s.s. (1·517), there was a significant relationship between fruit position and s.s. which tended to increase up the spike (F = 7·27, P = 0·010) (Fig. 2). All the fruits on this plant fell within the range of subsp. *austriaca* for s.s.. However for individual 46 (from v.c. 64) with a mean s.s. of 1·136, there was no relationship between s.s. and fruit position (F = 1·25, P = 0·267), and s.s. values of individual fruits varied from 0·64 (typical for subsp. *mamillata*) to more than 2·0 (an extreme value, even for subsp. *austriaca*). We found no relationship between fruit position on the spike and r.s.w. (F = 1·87, P = 0·178 for individual 50; F = 2·27, P = 0·135 for individual 46).

Almost all specimens examined had fruits with either four or five bristles and an average bristle number in the range 4·5–5·0. Only one specimen, number 5 from Lodge Pond, Settle (Table 1), deviated from this, having an average of 5·75 bristles (n = 18 fruits, four of which had seven bristles). In this character as well as for s.s., this specimen more or less accorded with Hayek's (1910) concept of *E. mamillata*.

Stomatal length varied relatively little, from 44 µm to 58 µm, and showed no significant relationship with any other character. The number of fruits in a spikelet was expressed as fruit density, by calculating the number per cm. This figure is usually higher, above 80, for shoots with an intermediate average stylopodium shape between 1·0 and 1·2 which is typical for neither taxon. Vascular bundle number also tended to be greatest for such intermediate individuals from v.c. 64, averaging over 20·5 (Fig. 3).

DISCUSSION

Based on an extensive biometric study from most of the range of *E. mamillata* agg., Gregor (2003) suggested that the morphological limits of the subspecies with respect to stylopodium characters are best given as:

Gregor considered that specimens with an r.s.w. of more than 0·5 can be attributed to subsp. *mamillata* and those with an r.s.w. of less than 0·4 to subsp. *austriaca,* although many of the specimens he attributes to subsp. *mamillata* in his Figure 4 and the appendix to his paper (Gregor 2003) have an r.s.w. that falls

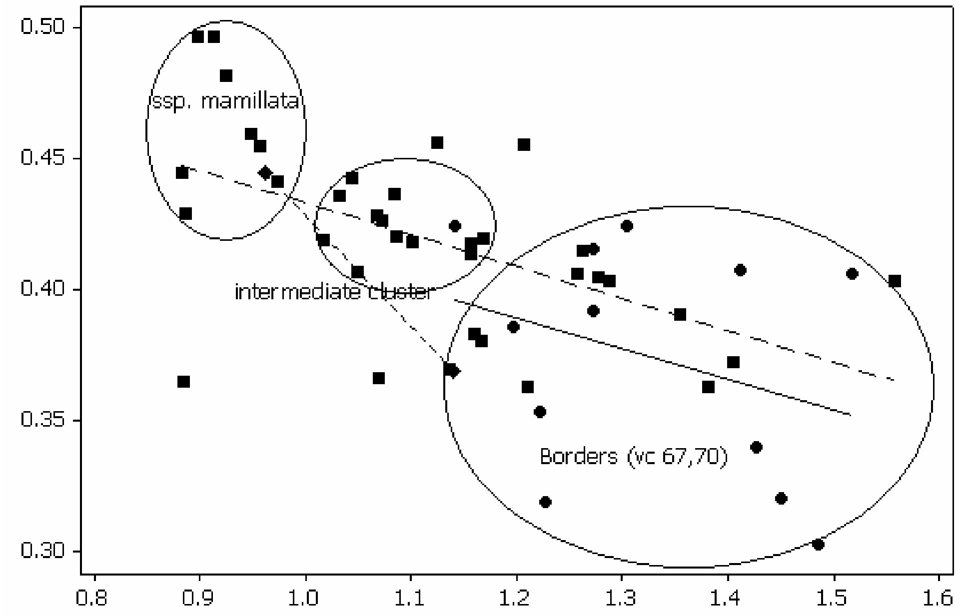

FIGURE 1. Scatter diagram of average stylopodium shape (s.s.) for a shoot (x-axis) against average relative stylopodium width (r.s.w.) (y-axis). Symbols: circles, samples from Borders populations (v.cc. 67, 70); squares, samples from N.W. Yorks (v.c. 64); diamond, samples from Selkirk (v.c. 79). Regression lines are shown: solid, Borders samples; heavy dashing, N.W. Yorks. Ellipses encircle (from the left) samples considered to represent subsp. *mamillata*, all from v.c. 64; samples representing the ‘intermediate cluster’; and all the samples from the “Borders” region (v.cc. 67, 70) with one exception.

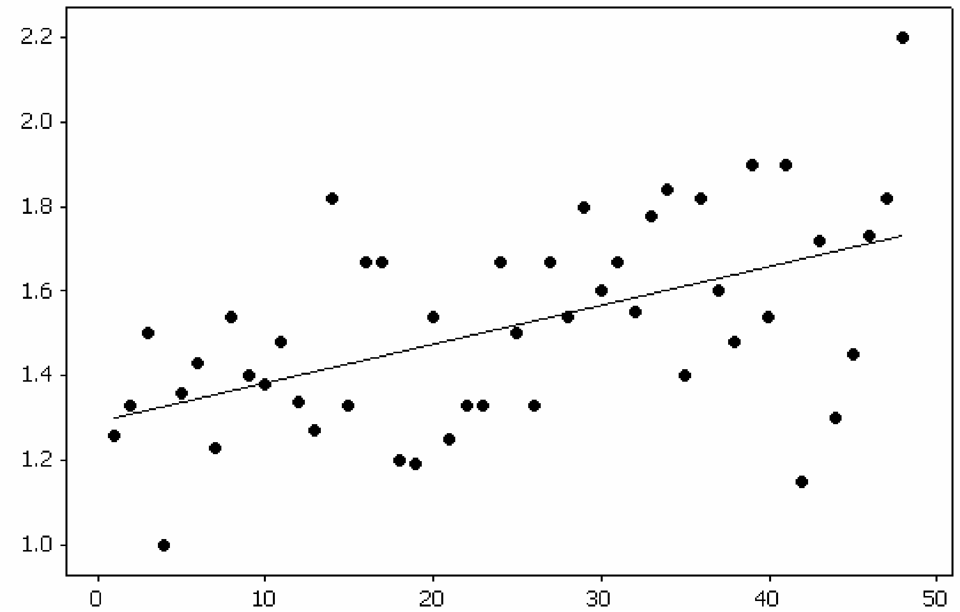

FIGURE 2. Scatter diagram of position of fruit on spike (x axis) against individual fruit stylopodium shape (s.s.) for individual 50. The regression line is shown. This relationship is significant (F = 7·27, P = 0·010).

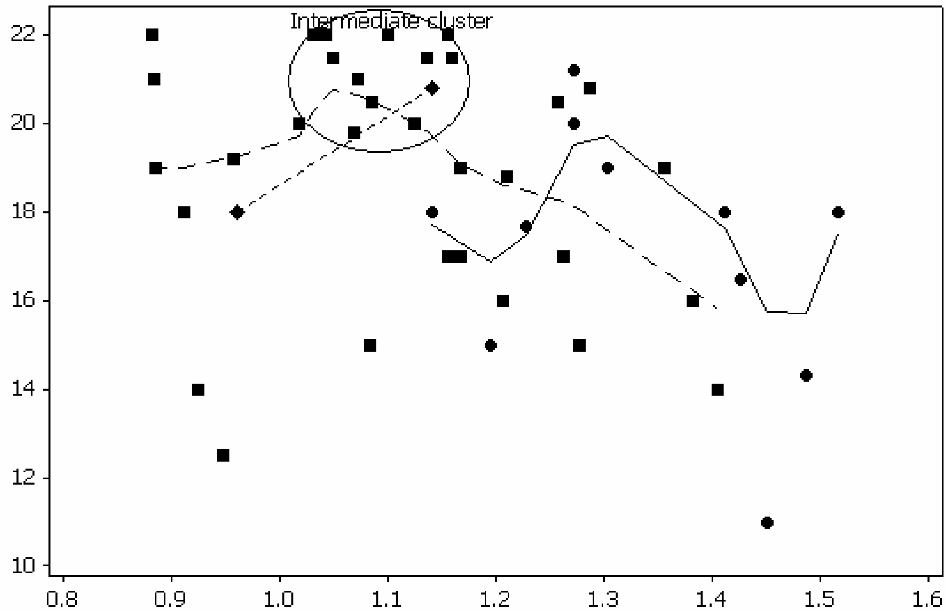

FIGURE 3. Scatter diagram of average stylopodium shape (s.s.) for a shoot (x-axis) against average fruit density on a spikelet (y-axis). Symbols: circles, samples from "Borders" populations (v.cc. 67, 70); squares, samples from N.W. Yorks (v.c. 64); diamond, samples from Selkirk (v.c. 79). Smoothing lines of best fit are shown: solid, Borders samples; heavy dashing, N.W. Yorks. Plants considered to represent the intermediate cluster are encircled. Data was missing for some plants in Fig. 1 and these are excluded.

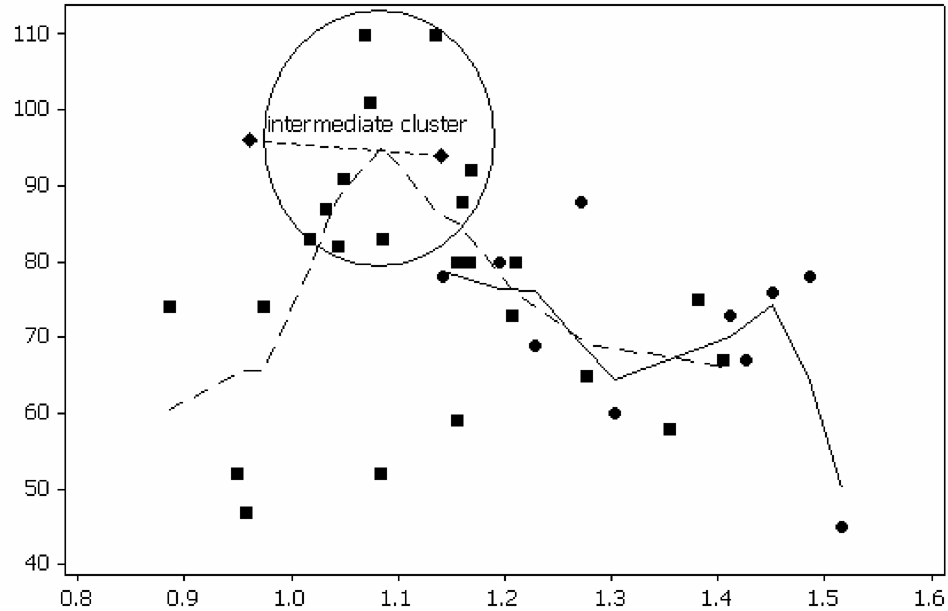

FIGURE 4. Scatter diagram of average stylopodium shape (s.s.) for a shoot (x-axis) against number of vascular bundles on that shoot (y-axis). Symbols: circles, samples from Borders populations (v.cc. 67, 70); squares, samples from N.W. Yorks (v.c. 64); diamond, samples from Selkirk (v.c. 79). Smoothing lines of best fit are shown: solid, Borders samples; heavy dashing, N.W. Yorks. Plants considered to represent the intermediate cluster are encircled. Data was missing for some plants in Fig. 1 and these are excluded.

between 0·4 and 0·5. In fact, no British plant measured had an average r.s.w of greater than 0·50. However, eight individuals from Yorkshire had an average s.s. of less than 0·97 which Gregor considered typical for subsp. *mamillata*. These plants also gave a relatively high r.s.w. reading of more than 0·429 (Fig. 1). A further plant from Selkirk also falls within this group. All the plants from the Borders region (vcc. 67 and 70) had an s.s. of more than 1·10 and so fall within Gregor's definition of subsp. *austriaca* for this character. For all (except five) the r.s.w. falls below 0·40 which is also diagnostic of subsp. *austriaca* according to Gregor. It is clear that it is necessary to measure a large number of fruits from all parts of the spikelet before a consistent average reading is obtained. Measurements of single fruits, or even much larger samples from the same part of the spikelet might give highly misleading readings. For instance, the average s.s. for the bottom half of spike 50 was 1·39. and that for the top half was 1·64 (n = 24 in each case). Gregor (2003) measured either three or five fruits per spike and does not state from which part of the spike these were taken from. It is our experience that such small samples would be liable to considerably bias average readings for s.s. and r.s.w., particularly if the part of the spike from which they were taken was not standardised. Nevertheless, when large samples are taken from the total spike, as in the present study, there is considerable statistically significant variation between individuals.

However, like Gregor, we conclude that there is no clear discontinuity in the distribution of the data across all populations which could have provided a natural basis to the delimitation of the subspecies. Also, like Gregor, we note that a proportion of individuals are intermediate in character and cannot be readily referred to either taxon. In fact, amongst our material, there is a distinct cluster of 12 shoots originating from Yorkshire with an average s.s. between 1·00 and 1·18 and an average r.s.w. between 0·40 and 0·45 which form a distinctive morphological group. This group of individuals has on average more vascular bundles than any other with a single exception (between 20·5 and 22·0) (Fig. 4), and a higher fruit density than any other (more than 80/cm) with three exceptions (Fig. 3). The only shoot from elsewhere which resembles this intermediate group comes from the Tima Water, Selkirk, but this has a much lower r.s.w. average (0·37).

We are uncertain as to the significance of the high readings for fruit density and vascular bundle number for this intermediate group. Both characters have been regarded as having taxonomic significance in earlier work. Beauverd (1921) considered that a fruit density of 60–70 was typical of *E. benedicta* Beauverd which Walters (1953) regarded as synonymous with *E.* (*mamillata* subsp.) *austriaca*. This agrees well with our findings for plants classified (according to mean s.s.) as both subsp. *mamillata* and subsp. *austriaca*, but is lower than we find for our 'intermediates'.

Hayek (1910) stated that subsp. *mamillata* tends to have fewer vascular bundles than subsp. *austriaca* (i.e less than 12). Gregor (2003) found that 61% of individuals he classified as subsp. *mamillata* had 13 bundles or fewer. However, all our shoots except two had more than 13 bundles, and there is no clear distinction in bundle number between our material which, according to mean s.s., was classified as 'typical' subsp. *mamillata* and 'typical' subsp. *austriaca*. Indeed, the number of bundles in the eight individuals that fall clearly within the s.s. character range for subsp. *mamillata* for which bundle number is known, shows the complete range present, from 12·5 to 22 (Fig. 3). Strandhede (1966) considered that bundle number was proportionate to stem diameter, and thus had no taxonomic significance, although in our opinion high bundle number could be a measure of vigour.

We believe two interpretations of this data are possible. Either, the intermediate individuals with high bundle and fruit density readings should be regarded as a distinct taxon, or these attributes can be considered as measures of vigour, in which case individuals with an intermediate stylopodium shape might be considered to show hybrid vigour.

If we regard these intermediate individuals as a distinct taxon, they have several features in common with the little-known *E. benedicta* Beauverd (1921), described from Lac Benit, Haute-Savoie, at 1500 m., notably: the stylopodium shape, said to average 1·07, the relative stylopodium width, said to average 0·39, the fruit density of 80/cm and the number of perianth bristles (5). However, *E. benedicta*, regarded by Walters (1953) as a synonym of *austriaca*, was stated to have a low vascular bundle number (averaging 12, rather than more than 20 in our 'intermediates'). As the high bundle number is one of the main attributes of the latter, we hesitate to identify it with *E. benedicta*.

With regard to the vigour hypothesis, this assumes that two previously isolated demes have come together in Yorkshire and have hybridised. Some support for this hypothesis can be derived from the finding that three of the four Yorkshire sites from which three or more individuals were collected (Ribble 7, Ribble 12, and Ribblehead SLQ 8) contained spikes showing stylopodium characters of subsp. *austriaca*, subsp. *mamillata* and the intermediate. We have considered the possibility that plants of intermediate phenotype and characteristics of vigour are allotetraploids, but the only chromosome counts recorded are diploid (2n = 16, 18) (Walters 1953, Strandhede 1966). Stomatal length commonly differs between related diploids and tetraploids (e.g. Stebbins 1950) and there is no suggestion from stomatal length that intermediates are tetraploid.

Eleocharis fruits are readily dispersed, especially by ducks (Gregor & Barth 1998). Some of the localities for *E. mamillata* agg. in Britain are artificial (i.e. quarries, gravel pits and reservoirs) and most are impermanent. Whether or not this group has persisted within these islands for much of the post-glacial period, it is quite likely that immigrant wildfowl have mediated repeated colonisations of both subspecies over thousands of years, as is suggested by the Yorkshire sites. In this context, it is perhaps remarkable that most individuals in the Borders populations are clearly referable to subsp. *austriaca*, suggesting that they may have originated from relatively few founder events.

The question remains as to the correct name for the plants from N.W. Yorks and Selkirk which have a stylopodium shape (s.s.) within the range given by Gregor (2003) for subsp. *mamillata*. We suggest that it would be unacceptable to record this taxon from the British Isles for the first time on the basis of this single character. Using relative stylopodium width (r.s.w.), none of these plants fall within Gregor's stated limit for subsp. *mamillata* (although this is also true of many of his so-called subsp. *mamillata*), and they have a vascular bundle number well in excess of that considered to be typical for this taxon. Except for one specimen, all of the material which we examined appeared to have an average perianth bristle number of five or less (i.e. typical of subsp. *austriaca*) including individuals such as number 31 which have an average s.s. typical of subsp. *mamillata*. Only individual 5 had an average bristle number typical of Hayek's concept of subsp. *mamillata*. Gregor (2003) shows that individuals assigned to subsp. *mamillata* can have the full range of average bristle number recorded, from 4·0 to 7·0. Although he found that no individual of subsp. *austriaca* had an average of more than 5·5 bristles, this character seems at best to be of very limited value.

Unfortunately, very few characters seem to separate these two taxa reliably and those that do so (s.s. and r.s.w.) are both based on the same basic character: the shape of the stylopodium. Nevertheless, our material is not typical of subsp. *mamillata* for r.s.w., perianth bristle number or vascular bundle number, and further work is needed before it can be safely assigned to ssp. *mamillata*. It has been suggested that the ecology of the two subspecies differs considerably, at least within Scandinavia. However, some of the British sites are man-made and appear to differ considerably from the natural localities in which they typically occur abroad, although Gregor (*in litt*. to F. J. Roberts) notes that in Germany both taxa occur predominantly in derelict ponds. As yet, there are no ecological data from British sites that can be compared with that gathered by Strandhede (1966) and Gregor & Barth (1998).

We conclude that plants in which the clear majority of fruits have a stylopodium longer than wide should be recorded as *E. mamillata* subsp. *austriaca*. All other British material should at present be referred to as *E. mamillata* agg.

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