Variation in some populations of *Calamagrostis stricta* (Timm) Koeler in the British Isles and the putative past hybridization with *C. canescens* (Wigg.) Roth

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ABSTRACT

The variability of *Calamagrostis stricta* (Timm) Koeler (Poaceae) at some sites in the British Isles has been investigated using hybrid index analysis and polygonal graphs. Most of the variation in *C. stricta* in the British Isles can be explained as the result of past hybridization with *Calamagrostis canescens* (Wigg.) Roth and subsequent backcrossing to *C. stricta*. Putative backcrosses occur in most English and Scottish *C. stricta* localities and signs of introgression are present in some Irish *C. stricta* plants, although *C. canescens* does not now occur in Ireland. The ecology and putative history of *C. stricta* in the British Isles, the conditions for hybridization with *C. canescens* and the likely roles of changing environment, hybridization and introgression in evolutionary change are discussed. A key to British *Calamagrostis* taxa based on the Leven, S.E. Yorks., v.c. 61, studies is presented.

KEYWORDS: Poaceae, variability, introgression, adaptation, (*C.* × *gracilescens*).

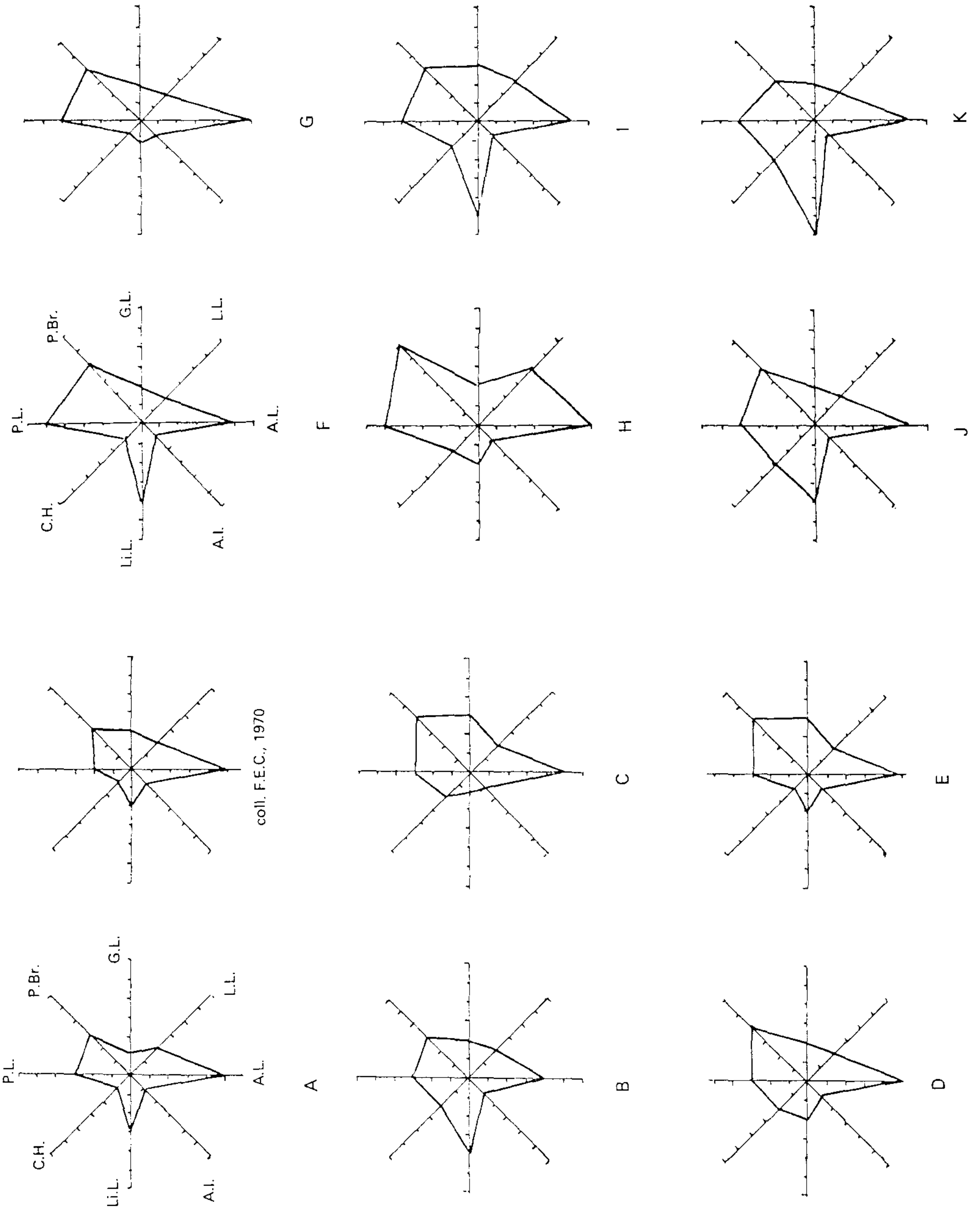
INTRODUCTION

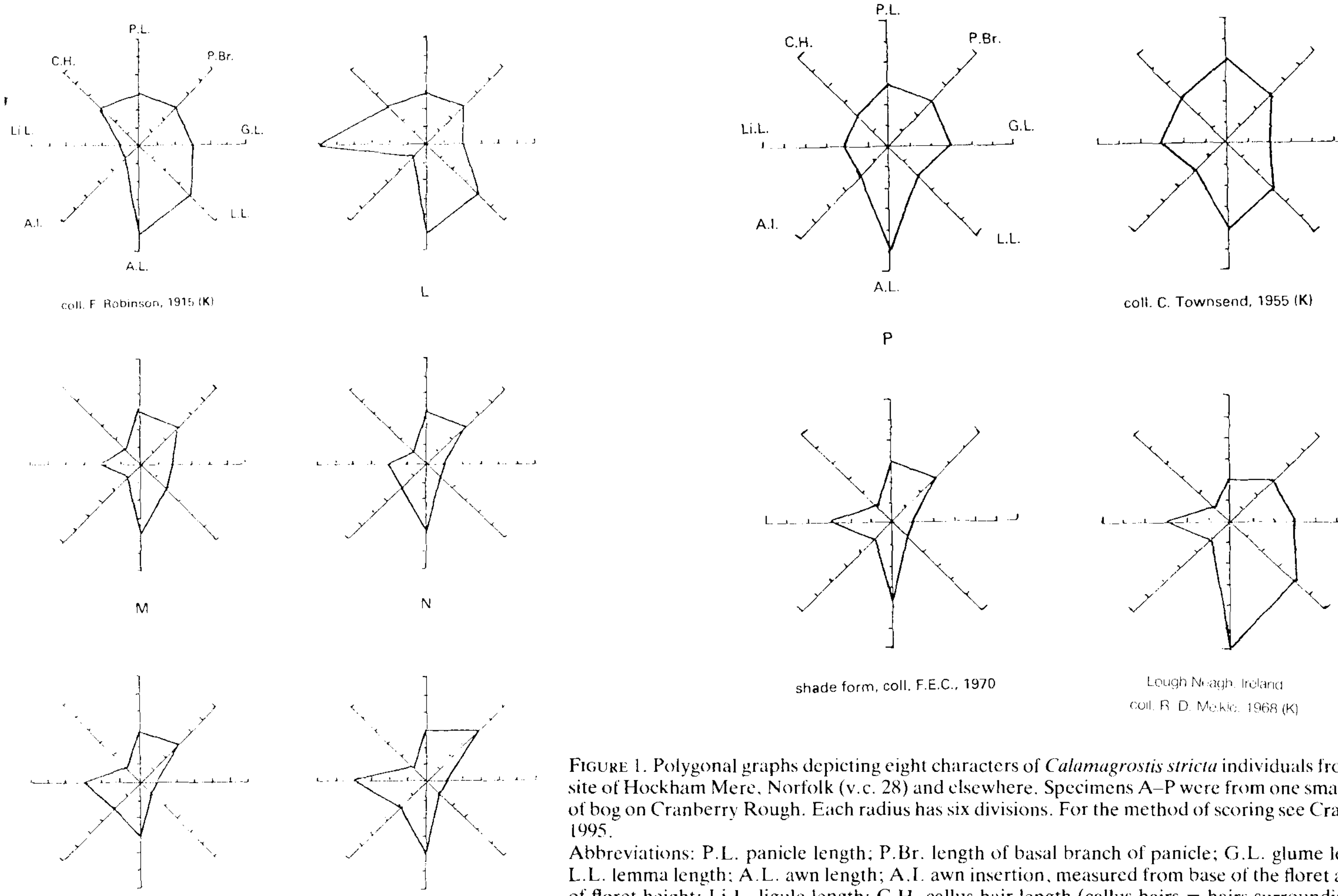
Soon after the discovery in 1951 of the S.E. Yorks., v.c. 61, site for *Calamagrostis stricta* (Poaceae) my interest in its taxonomy was aroused by the realisation that *C. stricta* is a variable grass. Plants from well separated localities in the British Isles were said to show slight morphological differences (Hubbard 1968).

On a visit to Cranberry Rough, Great Hockham, W. Norfolk (v.c. 28) in July 1970 I found plants with long white hairs on the upper leaf surface and long ligules, features which on the basis of the Leven (v.c. 61) studies (Crackles 1994) are believed to be characteristic of *C. canescens* and not *C. stricta*. Also, shoots I collected from two English localities were found to have florets with a short awn leaving the lemma about half-way from its base. These characters are found in both Leven *C. canescens* × *C. stricta* (H_2, $2n = 28$ and H_1, $2n = 56$) (*C.* × *gracilescens*) populations and not in Leven *C. stricta* (Crackles 1994).

The relevant British literature was found to include not only the range of variation in *C. stricta* but also almost the full range of variation of *C. stricta* × *C. canescens* H_2 ($2n = 28$). The account of *C. stricta* in Hubbard (1968) was found to include almost the full range of variation found in the Leven *C. canescens* × *C. stricta*, H_2 ($2n = 28$) population, as well as in Leven *C. stricta* for some morphological characters, but not for all. Notably the panicle length is given as 7–20 cm long (Leven *C. stricta* panicle length (6–)9–13(–15) cm, Leven H_2 panicle length 13·7–19·2 cm, Leven H_1 ($2n = 56$) panicle length 13·5–20·8 cm); the basal branch of panicle as up to 6 cm (that of Leven *C. stricta* less than 4 cm, that of Leven H_2 (3·5–)4·6–7·4 cm and that of Leven H_1 3·8–6·6 cm) and the awn leaving the back of the lemma for one-third to half-way above the base (the awn of Leven *C. stricta* arises from one-third of the way up the lemma or below). This suggested that plants of hybrid origin had been named *C. stricta*. Further, Tutin (1987) gives the awn as arising from about the middle of the lemma as a diagnostic character of *C. stricta* while in the Leven studies this character proved to be consistent in the hybrids, both the H_2, $2n = 28$ and the H_1, $2n = 56$ (Crackles 1994) and not in *C. stricta*.

The taxonomy, biology, phytogeography and putative Quaternary history in the British Isles of *Calamagrostis stricta* are discussed in this paper. The opportunity is taken to assemble my thoughts on *Calamagrostis stricta*, its variability in the British Isles as revealed by the measurements of the


P.L.
P.Br.
G.L.
L.L.
A.L.
A.I.
Li.L.
C.H.
A
B
D
coll. F.E.C., 1970
C
E
F
H
J
G
I
K



coll. F. Robinson, 1915 (K)

L

P

coll. C. Townsend, 1955 (K)

M

N

shade form, coll. F.E.C., 1970

Lough Neagh, Ireland
coll. R. D. Meikle, 1968 (K)

Thompson Common, coll. F.E.C., 1970

O

FIGURE 1. Polygonal graphs depicting eight characters of *Calamagrostis stricta* individuals from the site of Hockham Mere, Norfolk (v.c. 28) and elsewhere. Specimens A–P were from one small area of bog on Cranberry Rough. Each radius has six divisions. For the method of scoring see Crackles, 1995.

Abbreviations: P.L. panicle length; P.Br. length of basal branch of panicle; G.L. glume length; L.L. lemma length; A.L. awn length; A.I. awn insertion, measured from base of the floret as a % of floret height; Li.L. ligule length; C.H. callus hair length (callus hairs = hairs surrounding the base of the lemma).

Norfolk specimens and those from other localities as given in the "Results" and also the research carried out at the Leven Canal, S.E. Yorks. (v.c. 61) (Crackles 1994 & 1995).

A key to the *Calamagrostis* species, their hybrids and putative backcrosses is given at the end of the paper.

METHOD OF STUDY

During 1971, I was in regular correspondence with Dr C. E. Hubbard and in August of that year he collected a number of individual shoots of *C. stricta* from Cranberry Rough, W. Norfolk, (v.c. 28) from two populations, each about 20 m across in the same small area of bog. I spent a week in the Herbarium at Kew in August, 1971, when the specimens collected by Hubbard were examined. Measurements of five florets, removed at random, were recorded to provide average values as in the Leven studies (Crackles 1994). Each Norfolk variant was subject to hybrid index analysis based on the measurements of the Leven *Calamagrostis* populations (Crackles 1994) using the previous method of scoring (Crackles 1995).

Other *C. stricta* specimens in **K** and in the author's possession were examined and their parts measured as in the case of the Norfolk specimens already mentioned.

A polygonal graph using the same scheme as in the Leven studies (Crackles 1995) was constructed for each Norfolk variant collected by Hubbard and in **herb. F.E.C.** and in **K** (Fig. 1). This series of polygonal graphs are arranged to demonstrate most clearly the degree and nature of the difference between these taxa. They can also be compared with the polygonal graphs for Leven *C. stricta* and other Leven *Calamagrostis* populations (Fig. 2)

A polygonal graph is also presented for a specimen from Lough Neagh, Ireland (v.c. H39) (Fig. 1), for each specimen examined from Oakmere, Cheshire (v.c. 58) (Fig. 3) and Ashkirk Loch, Selkirkshire (v.c. 79), and for a specimen from Alemoor Loch, Roxburghshire (v.c. 80) (Fig. 4).

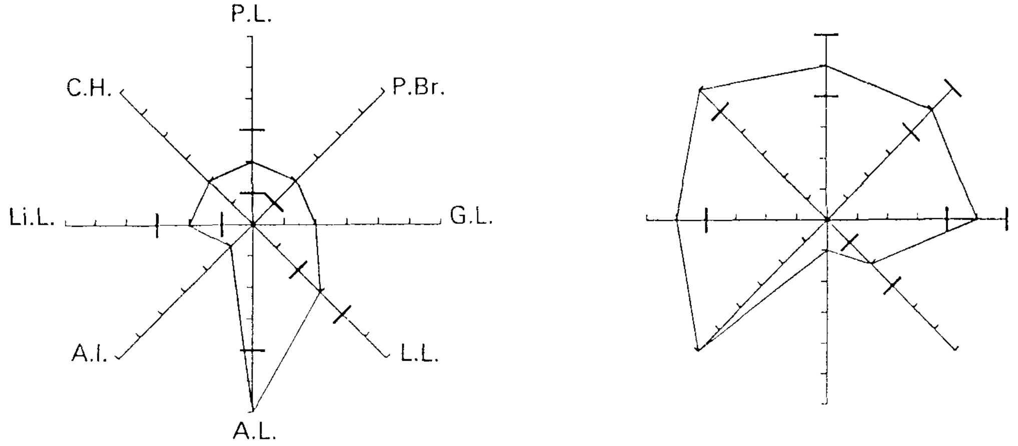
RESULTS

The 16 variants of *Calamagrostis stricta* collected by Dr C. E. Hubbard from a small area of Cranberry Rough, W. Norfolk, were found to resemble *C. stricta* generally, but to possess two or more characters of the Leven hybrid, *C. canescens* × *C. stricta* (H_2 population, $2n = 28$) in various combinations. This is also true of most specimens from Cranberry Rough in **K** and in **herb. F.E.C.** In a few specimens a single putative hybrid character only was found; no specimen from this site exactly matched an individual of the Leven *C. stricta* population. By comparing the polygonal graphs for these specimens (Fig. 1) with that for Leven *C. stricta* (Fig. 2), most of these variants are seen to resemble Leven *C. stricta* with regard to ligule length, panicle length, glume length, lemma length, awn length and point of insertion of awn on lemma. Almost all the Norfolk variants resemble Leven *C. stricta* with regard to panicle and glume width. The length of the basal branch of the panicle is longer than in Leven *C. stricta*, but usually not markedly so. A character which frequently occurs in Norfolk *C. stricta* is white hairs on the upper leaf surface. This is a *C. canescens* character which commonly occurs in the Leven hybrids (Crackles 1994). The range of hybrid scores for the Norfolk variants examined is 2–9 (*C. stricta* = 0, *C. canescens* = 20, Leven H_2 population 8–14, Leven H_1 population 9–15).

I shall use the term partial hybrid to describe specimens which have characters of both Leven *C. stricta* and Leven hybrids.

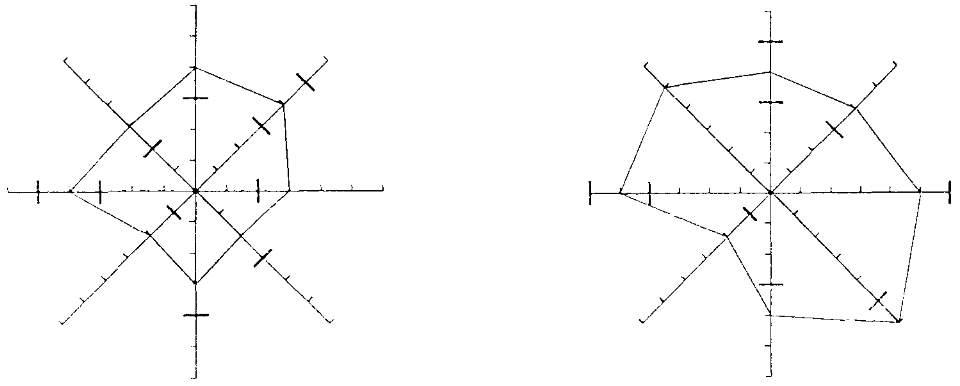
Among partial hybrids from Cranberry Rough collected by me was the shade form of *C. stricta* (Fig. 1). Specimens I collected from Thompson Common, Stow Bedon, a site 3 km from Cranberry Rough, have awns of intermediate length which leave the lemma from about its mid point as in the Leven hybrids. A polygonal graph is given for one of these specimens (Fig. 1).

Of the Norfolk specimens examined, the one which has the most characters with measurements falling within the range of those found in the Leven *C. canescens* × *C. stricta*, H_2 population, is that collected by C. C. Townsend in **K**. The polygonal graph for this specimen (Fig. 1) shows similarities to that of the Leven H_2 population, although the specimen has some characters of Leven *C. stricta* including panicle width, ligule length, and length and width of glumes.



C. stricta

C. canescens



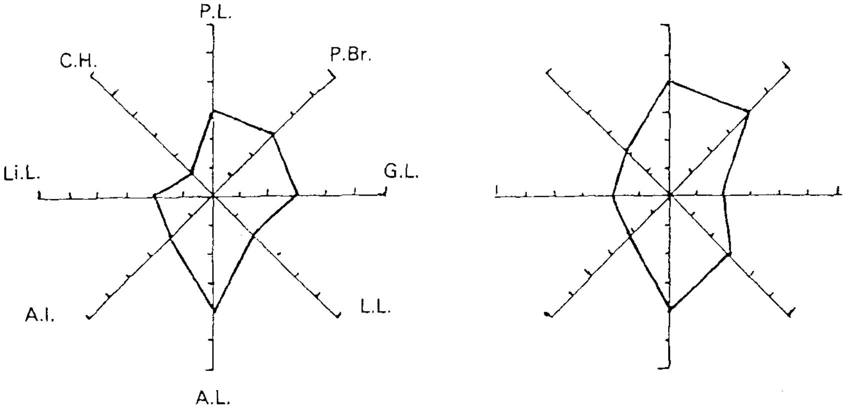
H_2 population

H_1 population

FIGURE 2. Variation in eight characters of Leven (v.c. 61) *Calamagrostis stricta*, *C. canescens* and *C. canescens* × *C. stricta*, 2n = 28 (H_2) and 2n = 56 (H_1) populations. Each radius has six divisions. For method of scoring see Crackles (1995). Each polygonal graph was drawn using the mean of measurements for each character of the population sample of 25 shoots; standard deviations are shown along each axis. Abbreviations are given under Fig. 1.

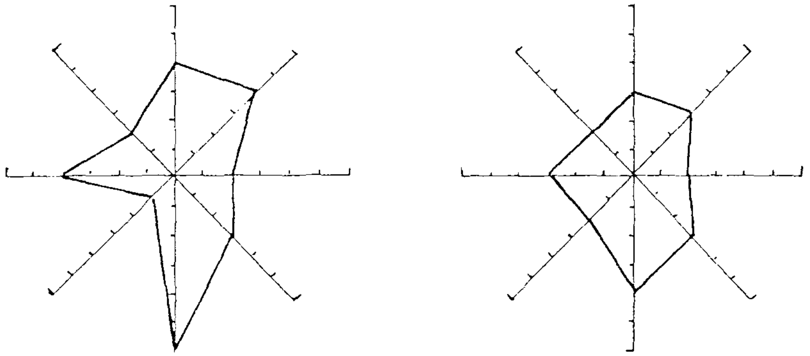
Some Norfolk variants of *C. stricta* have very short glumes, lemmas and callus hairs with measurements less than those found in Leven *C. stricta* or *C. canescens* × *C. stricta* populations (Figs 1 & 2). Two of these characters, i.e. short glumes and short lemmas, are found in the same four specimens, i.e. specimens N & O collected by Hubbard on Cranberry Rough (Fig. 1), a shade form collected there by the author (Fig. 1) and a specimen collected on Thompson Common (Fig. 1) and in no others.

Characters of the Norfolk specimens with measurements not within the range of measurements for Leven *C. stricta* are usually within the range of measurements for the Leven H_2 population. Only rarely do measurements exceed those found in that population, i.e. the ligule length of specimens K & L (Figs 1 & 2), the panicle length of specimen F and the basal branch of panicle of specimen F



coll. G. Holt, 1893 (K)

coll. S. H. Bickham, 1878 (K)



coll. G. Last, 1940 (K)

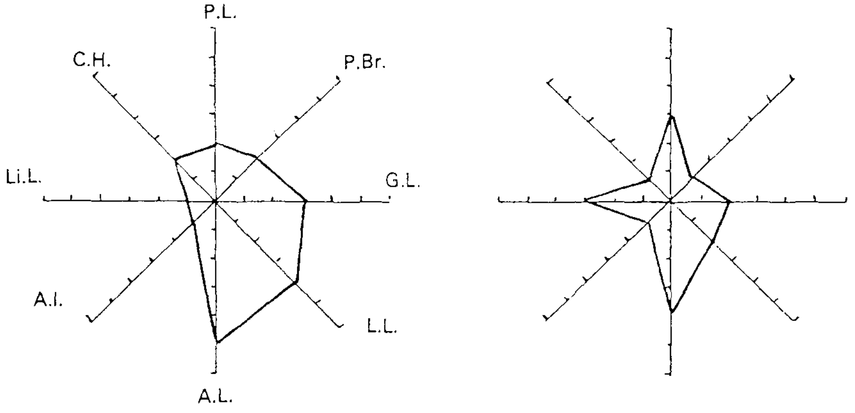
coll. C. Waterfall, 1877 (K)

FIGURE 3. Polygonal graphs depicting eight characters of *Calamagrostis stricta* individuals from Oakmere, Cheshire (v.c. 58) collected at different times. Abbreviations are given under Fig. 1.

(Fig. 1). These measurements are in the range for the character concerned for the Leven H_1 population except for the length of the basal branch of panicle for specimen F which is in the *C. canescens* range for that character (Fig. 2).

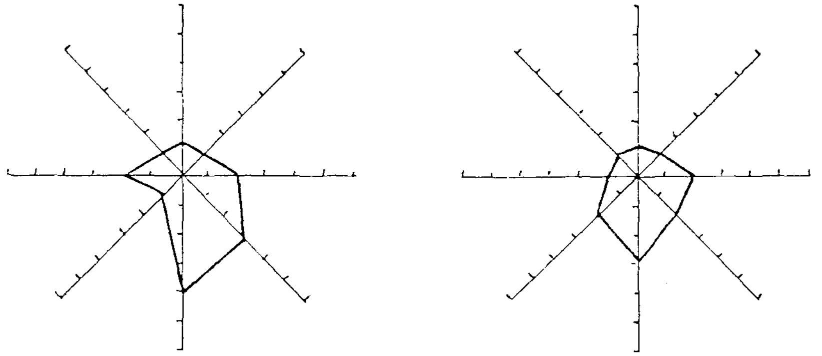
Partial hybrids have been discovered among specimens from Oakmere, Cheshire (Fig. 3) and several Scottish sites including Alemoor Loch, Roxburghshire and Ashkirk Loch, Selkirkshire (Fig. 4); various combinations of putative hybrid characters are found in these specimens. The greatest variability has been found in the Cranberry Rough, Norfolk populations.

Some putative hybrid characters were found to occur more frequently than others in *C. stricta* British specimens examined. Characters occurring in the Leven H_2 range are (83 specimens examined): panicle length (31% of specimens), length of basal branch of panicle (42%), awn arising from near the middle of the lemma (35%) and hairs on upper leaf surface (55%). These same putative hybrid characters occurred in a higher percentage of specimens from the Norfolk sites (33



Alemoor Loch

Ashkirk Loch



Ashkirk Loch

Ashkirk Loch

FIGURE 4. Polygonal graphs depicting eight characters of a *Calamagrostis stricta* individual from Alemoor Loch, Roxburghshire (v.c. 80) and of *C. stricta* individuals from Ashkirk Loch, Selkirkshire (v.c. 79). Specimens collected by H. Milne-Redhead, 1971, **herb F.E.C.**. Abbreviations are given under Fig. 1.

specimens examined): panicle length in the Leven H_2 range, 67%; length of basal branch of panicle, 74%; awn arising from near the middle of the lemma, 57% and hairs on upper leaf surface, 73%.

Intermediate awn length and awn arising from near the middle of the lemma often, but not invariably, occurred together. Both characters were found in specimens from Cranberry Rough and Thompson Common, Norfolk; Oakmere, Cheshire; Ashkirk Loch, Selkirkshire; Alemoor Loch, Roxburghshire and Loch Watten, Caithness (v.c. 109).

In some *C. stricta* specimens, a single putative hybrid character was found. The most frequent single putative hybrid characters found were hairs on the upper leaf surface and long basal branch of the panicle.

One or two putative hybrid characters were found in specimens from Lough Neagh, Ireland i.e. ligule length in the Leven H_2 range and/or white hairs on the upper leaf surface.

Specimens with all the characters of Leven *C. stricta* (Crackles 1994) have been found in the following localities: Malham, Mid-W. Yorks. (v.c. 64); Alemoor Loch, Roxburghshire; Bogton Loch, Ayrs. (v.c. 75); St John's Loch and Loch Scarmclett, Caithness (v.c. 109).

DISCUSSION

VARIATION IN *C. STRICTA* SENSU STRICTO AND *C. CANESCENS* SENSU STRICTO

The assumption is made that the range of variation in Leven *C. stricta* and *C. canescens* gives a reliable indication of variation usually found in populations of these species. In the case of the very variable British *C. stricta*, this assumption is based on an examination of Scandinavian literature (Crackles 1994) and of Swedish specimens possessed by the author. Leven *C. canescens* closely matches the description of this species in British literature (Hubbard 1968; Tutin 1987; Rose 1989; Stace 1991).

VARIATION IN *C. STRICTA* SENSU LATO

Most of the variation in *C. stricta* is most satisfactorily explained by postulating that there has been past hybridization between *C. canescens* and *C. stricta* and subsequent backcrossing of the F_1 and later generations to *C. stricta*, a different combination of hybrid characters occurring in different backcrosses.

Beds of *C. canescens* and of *C. stricta*, the latter showing only slight signs of hybridity, occur side-by-side on Cranberry Rough, Norfolk, the site of Hockham Mere, but no intermediates possessing all the characters of the Leven hybrids were found. The specimen in **K** collected by Townsend approaches the Leven hybrid, population H_2 ($2n = 28$). It has a number of characters of the hybrid, but some characters of Leven *C. stricta* as specified in the results section and would seem to be best regarded as part of the Norfolk series of backcrosses.

The fact that the shade form of *C. stricta* (var. *viridis*) from Cranberry Rough is one of the putative backcrosses is of great interest. Apart from this rare form, *C. stricta* only occurs in unshaded situations whereas *C. canescens* is notably shade tolerant so that it appears that *C. stricta* var. *viridis* may have inherited its shade tolerance from *C. canescens*. I have also examined two specimens of the shade form from Loch Watten, Caithness (v.c. 109), 1907, *C. Druce* (**K**). Both specimens are partial hybrids, one with an awn of intermediate length and awn position, the other with just an intermediate awn position on the lemma.

Variants of *C. stricta* which are satisfactorily explained as products of hybridization with *C. canescens* and subsequent backcrossing have been found among specimens from most of the British localities from which the species has been recorded. Variants with different hybrid characters have been collected from a single locality, notably from Cranberry Rough, Norfolk, and from Oakmere, Cheshire.

The short glumes, florets and callus hairs of some Norfolk *C. stricta*, outside the range of variation for these characters in any of the Leven *Calamagrostis* populations, may be explicable as a result of the long isolation of the populations concerned and the opportunity for mutations to have occurred. Some diminution of parts is a possible result of hybridization resulting in negative heterosis (Stace 1975).

Some specimens of *C. stricta* from Cranberry Rough, Norfolk, and other British localities show only slight morphological signs of hybridity. The single character of the Leven hybrids most commonly found in putative introgressants is long white hairs on the upper leaf surface, a *C. canescens* character (Crackles 1994; Nygren 1946). Such slight signs of hybridity are satisfactorily explained as the result of repeated backcrossing from *C. canescens* × *C. stricta* i.e. by introgression. During introgression, there is gradual infiltration of genes from one species to another. Anderson (1949) pointed out that this process may continue until the introgressant is morphologically indistinguishable from the pure species. There are specimens from a number of British stations which answer to the description of *C. stricta* sensu stricto as understood by the Leven studies; these may or may not be introgressed.

It seems desirable to regard the putative backcrosses from *C. canescens* × *C. stricta* to *C. stricta* as variants of *C. stricta*, particularly when the number of hybrid characters is small. If this policy is adopted, the question arises as to where the line should be drawn between *C. stricta* variants and the hybrid. For example should the Townsend specimen, which shows a number of hybrid characters, be regarded as a *C. stricta* variant or as *C. canescens* × *C. stricta*? The specimen would seem to be best regarded as part of the Norfolk series of backcrosses. In any study relating to the evolution of *C. stricta*, *C. canescens* and their hybrid derivatives, it is desirable to distinguish between:

1. *C. stricta* where introgression cannot be demonstrated;
2. backcrosses in which hybrid characters found in the Leven H_1 or H_2 populations occur, but some characters found in Leven *C. stricta* persist;
3. *C. canescens* × *C. stricta* (2n = 56), Leven H_1 population; and
4. *C. canescens* × *C. stricta* (2n = 28), Leven H_2 population (Crackles 1994).

Localities from which *C. stricta* is recorded, but where *C. stricta* sensu stricto specimens, as understood by the Leven studies, have not been found, need to be searched for pure *C. stricta*. There may have been a tendency to select specimens of hybrid origin because of their larger panicles.

DISTRIBUTION OF *C. STRICTA* AND *C. CANESCENS*: THE HISTORY OF *C. STRICTA* IN VARIOUS LOCALITIES

The discontinuous distribution of *C. stricta* in the British Isles becomes meaningful if regarded as a relict distribution of a species once widespread. Influenced by the writing of Pigott & Walters (1954) and Rose (1957), I put forward the theory that this sub-arctic grass has been in the British Isles since the Late Glacial (Crackles 1968). As the ice retreated, great floods of melt water formed extensive lakes and marshes on lower ground, such as occur today between the mountains of Scandinavia, so that suitable habitats for *C. stricta* would abound. At Leven, *C. stricta* occurs at the edge of the canal and I believe *C. stricta* sensu stricto to be primarily a species of lake edges in fenland areas. As the climate became warmer and extensive afforestation and acid peat formation followed, the species would be obliterated from most localities and in time extensive drainage would cause a further reduction in its distribution. It would persist in those few places where environmental conditions remained favourable to the species. I suggested that the low-lying area of the Leven Carrs with its meres was one of these (Crackles 1968).

C. stricta is more or less circumpolar in Arctic and sub-arctic regions (Polunin 1959); it is found in Greenland and Spitsbergen (Nygren 1946) and is common in northern Norway and Sweden, Finland, Estonia, Latvia, Lithuania and Poland. It also occurs in northern Russia and Siberia (Hultén 1950). It occurs in scattered localities in southern Norway and Sweden, Denmark and islands in the Baltic; it is rare with a disjunct distribution in central Europe, including the British Isles (Tutin 1962) (Fig. 5). It is classified by Matthews (1955) as Northern Montane i.e. a species with its main centre of distribution in northern Europe, but reappearing further south in Europe, usually only in montane areas. *C. stricta* is an exceptional member of the group in remaining a lowland species at the southern edge of its range.

The present distribution of *C. stricta* in the British Isles may be related to winter temperatures. Most localities are in the north or east of Great Britain where the lowest mean February temperatures are recorded (Perring & Walters 1962). It occurs in Ireland, but only in the north and it may be limited by the 2·2°C February isotherm.

Rose (1957) points to evidence that highly calcareous water seeping steadily through the ground is inimical to the growth of coarse mesotrophic vegetation so that succession to woodland is indefinitely suppressed. At Leven, extensive annual flooding of the carrland, which still occurred in winter until c. 40 years ago, could have prevented the formation of woodland, at any one time, over at least part of the area. It is also worthy of note that most of the English sites for *C. stricta* are spring-fed and Rose (1957) remarked that "such spring-fed habitats may have remained permanently open since Late Glacial times". There is a spring in the Leven Canal, the ripples from which reach the bank where a *Phragmites australis* (Cav.) Trin. ex Steudel bed ends and a bed of *C. stricta* begins. Cranberry Rough, in the parishes of Great Hockham and Stow Bedon, Norfolk, is on the site of Hockham Mere and there are still springs in the area, but no permanent standing water. At Malham Tarn, Yorks., GR SE 88.67, *C. stricta* occurs at the junction of the two inflow streams as they enter the tarn, an area subject to flooding when the spring-fed streams are in spate. At Oakmere, Cheshire, GR SK 57.68, *C. stricta* occurs at the edge of the lake which is spring-fed (Lind 1949) "in places subject to periodic inundation" (Lind 1951).

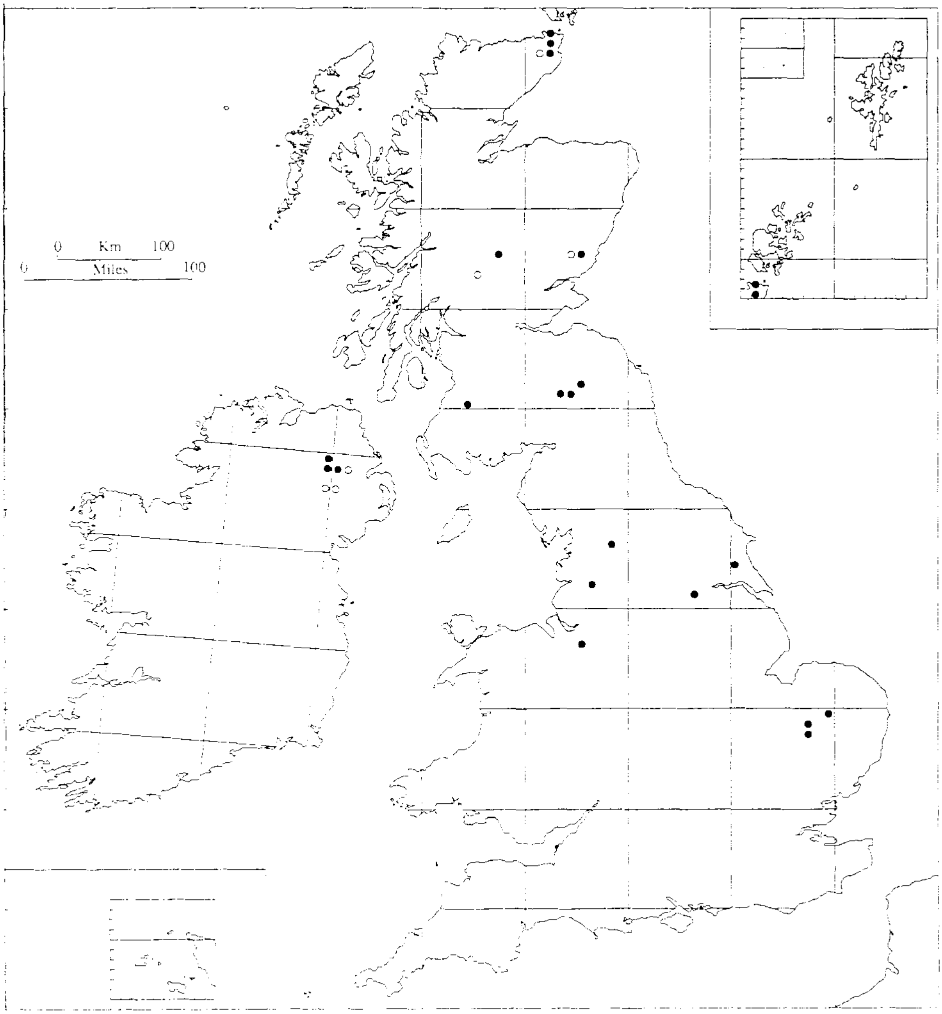


FIGURE 5. Distribution of *Calamagrostis stricta* in the British Isles, on a 10-km square basis. ● post-1950 record, ○ pre-1950 record.

Calamagrostis canescens is classified by Matthews (1955) as belonging to the European Continental Element i.e. species characteristic of central Europe, thinning out westwards. It is believed to have spread into the British Isles as the climate became warmer, but while the British Isles were still attached to the continent. It occurs in central and northern Europe, southwards to northern Spain, northern Italy and Bulgaria and also in western Siberia (Tutin 1962). Hultén (1950) in his distribution map shows that it is fairly common in parts of southern Sweden, locally frequent in Denmark and in parts of central Russia and southern Finland as well as in Latvia and Lithuania and that there are scattered localities in western Norway, parts of Sweden, in Estonia and on islands in the Baltic Sea.

C. canescens occurs in marshes, fens and wet open woodland, here and there in the lowlands of England to the Border (Hubbard 1968), mainly in the east (Perring & Walters 1962); it is rare in Scotland and absent from Ireland (Rose 1989) (Fig. 6).

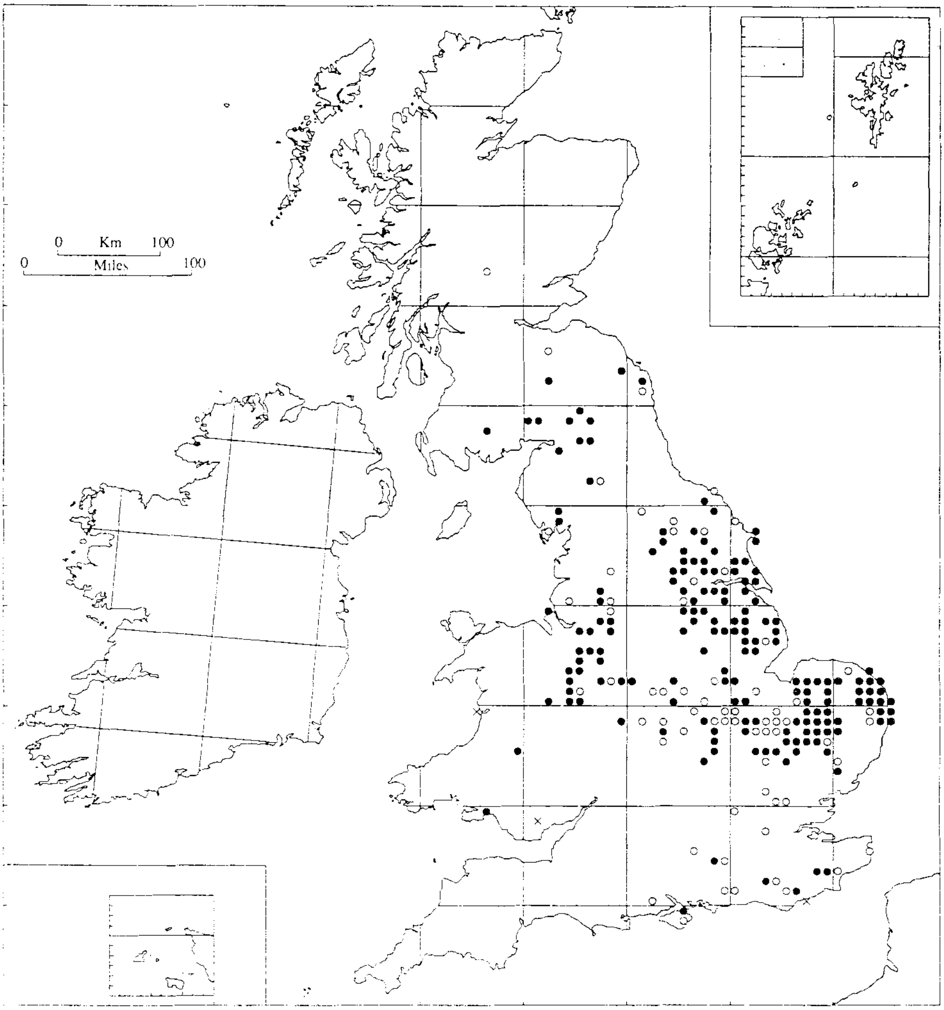


FIGURE 6. Distribution of *Calamagrostis canescens* in the British Isles, on a 10-km square basis. ● post-1950 record, ○ pre-1950 record.

CONDITIONS FOR HYBRIDIZATION BETWEEN *C. STRICTA* AND *C. CANESCENS*

I have previously given an account of the area in which Leven Canal, GR TA/056.449 – 108.449, is situated and its history. Map evidence suggests that the canal, cut in 1802, passed through two meres or their sites, including the edge of one where I first found *C. stricta*. I also listed the scarce and local British species recorded for the canal and its banks, the occurrence of which strongly supports the view that the canal and its banks derived their flora from the former meres and adjacent marshes (Crackles 1994). The meres in Leven Carrs were still present at least towards the end of the eighteenth century and were finally drained soon after the publication of the drainage plan of 1831 (Page 1831).

I believe that *C. stricta* which grows at the edge of the canal formerly grew at the margin of one or more meres in Leven Carrs, while *C. canescens* would grow in large beds in adjacent marshes, as it does today at Pulfin Bog by the River Hull, less than 2 km south of the canal and by Hornsea Mere, GR TA/18.46. The construction of the canal and its banks brought the two species close together so enabling hybridization to occur. *C. canescens* grows in quantity on the canal bank, particularly on its top and outer slope. Anderson (1949) stated that "hybridization of the habitat" is necessary before the establishment of hybrid populations becomes possible. The sloping bank adjacent to the water provides a suitable intermediate habitat for the H_1 population, while the H_2 population grows at the canal edge where competition is at a minimum.

C. canescens and *C. stricta* are both tetraploids with $2n = 28$. No sterility or internal crossing barriers appear to exist between *Calamagrostis* tetraploids (Nygren 1946). *C. canescens* and *C. stricta* are maintained as separate entities and hybridization prevented by differences in distribution, different ecological requirements and differences in flowering times. Historical factors may have operated to alter the distribution of the species; there may have been barriers to spread or extinction of one or both species from localities where they formerly occurred.

The flowering times of *C. stricta* and *C. canescens* growing by Leven Canal, S.E. Yorks., were studied. *C. stricta* is usually in full flower by mid-June, while *C. canescens* is not normally in full flower until the first week in July. There may be a slight overlap of flowering times, a few spikes of *C. stricta* being still open when the first spikes of *C. canescens* are also open. When the early part of the summer is cold, flowering of *C. stricta* may be delayed by as much as ten days. In some years, tightening of the spikes of *C. stricta* is delayed so that only some spikes are in the closed condition by the first week in July. In both these situations, there may be a significant overlap of flowering of the two species (Crackles 1994).

The occurrence of several different *C. stricta* variants, believed to be backcrosses from *C. canescens* × *C. stricta* to *C. stricta*, on Cranberry Rough, Norfolk, on the site of Hockham Mere, GR TL/92.93, many close together in a small area, points to the existence of F_1 hybrids on this site in comparatively recent times. Godwin & Tallantire (1951) stated that Hockham Mere was a lake of 750 acres [303·5 ha] in Tudor times, that it was not known when it was drained, but that there were indications that it was overgrown by 1737. It is probable that during the period of drainage suitable intermediate habitats for F_1 and F_2 hybrids occurred. Eventually, natural selection has apparently favoured the survival of a range of backcrosses and it seems that a number of different microhabitats still exist on the Hockham Mere site where the different backcrosses can still thrive. Stace (1975) points out that the significance of "hybridized habitats" becomes much more important in the F_2 and later generations, where the range of variation and therefore ecological requirements are so much greater.

C. stricta spread from the Hockham Mere site to the nearby Thompson Common, GR TL/93.96, between 1955 and 1970 (E. L. Swann, in litt. 18 February 1970). It occurs by the side of a pond and shows little variation.

The occurrence of different partial hybrids in other parts of the British Isles suggests that F_1 and F_2 hybrids once occurred in these localities also. Past hybridization and backcrossing to *C. stricta* and stabilization of the taxa may have occurred a very long time ago, particularly in areas where *C. canescens* is now absent.

In recent times, the two species were known to occur on the same site only in three British localities: Leven, S.E. Yorks (v.c. 61); Thorne, S.W. Yorks. (v.c. 63) and Cranberry Rough, W. Norfolk (v.c. 28).

C. canescens is rare in Scotland. There are post-1950 records for Dumfriesshire (v.c. 72) (Plant records, *Watsonia* **17**: 197); Kirkcudbrightshire (v.c. 73) (Stace 1991); Peeblesshire (v.c. 78) (Biological Records Centre) and Roxburghshire (v.c. 80) (Plant records, *Watsonia* **13**: 143). The scattered occurrence of partial hybrids in Scotland suggests that *C. canescens* was once more widespread there. It is of interest in this connection that Nygren (1946) states that the overlap of distribution of *C. canescens* and *C. stricta* in Scandinavia was once much greater than it is today suggesting that the hybrid *C. canescens* × *C. stricta* is now far more widely spread there than *C. canescens*.

It is of interest that some of the Irish specimens of *C. stricta* show signs of introgression, these signs of hybridity being slight in the specimens I have examined. *C. canescens* has not been recorded for Ireland. It may be that *C. canescens* did once occur in Ireland or that the hybridization and subsequent backcrossing which gave rise to the *C. stricta* variants occurred before Ireland was cut off from the rest of the British Isles.

The evidence suggests that infiltration of genes from *C. canescens* may have played an important part in the survival of *C. stricta* in the British Isles, near the edge of its climatic range, as well as making possible adaptation to changed environmental conditions, e.g. drier conditions and shade.

The perennial nature of *Calamagrostis* taxa is important, enabling beds of hybrids to provide gene pools derived from both species for considerable periods of time.

WHY DOES BACKCROSSING TAKE PLACE MAINLY TO *C. STRICTA* AND NOT *C. CANESCENS* AND WHY DO SUCH BACKCROSSES SURVIVE?

The question arises as to why backcrossing appears to be almost always to *C. stricta* and not to *C. canescens*. The flowering time of the F_1 hybrid ($2n = 28$) is usually intermediate between that of the two parents, although I have seen it in flower at Leven at the same time as *C. canescens*. However, in years in which flowering or closing of the spikes of *C. stricta* is significantly delayed the chance of backcrossing to *C. stricta* rather than to *C. canescens* is greatly increased.

C. stricta and *C. canescens* have very different ecological requirements. *C. stricta* sensu stricto characteristically occurs by open water whereas *C. canescens* occurs often some distance from the water's edge in areas subject to winter flooding but dry in summer. Hybridization has probably only occurred when there have been changes which have brought populations of the two species close together. The reason for the tendency for *C. stricta* backcrosses to survive and *C. canescens* to disappear from mixed populations is likely to be complex and to involve both environmental and climatic factors and their interaction. Also the explanation may be different in different parts of the British Isles. As changes occurred which favoured the survival of *C. stricta* backcrosses, suitable habitats for *C. canescens* may have been lost. The fact that *C. canescens* was once more widely distributed at the northern edge of its range in Scotland and in Scandinavia suggests that a minimum winter temperature, higher than that required for *C. stricta* may have been vital for the survival of *C. canescens*. Further studies of populations of *C. stricta*, including backcrosses, and of *C. canescens* and their requirements, particularly in Scotland and the study of the history of localities where *C. stricta* backcrosses occur may help to answer these questions.

The following key is provided to encourage other field workers to engage in the study of this particularly interesting group of plants.

KEY TO THE SPECIES OF *CALAMAGROSTIS* AND THEIR HYBRIDS

1. Hairs at base of lemma longer than lemma 2
1. Hairs at base of lemma shorter than or ± equal to the lemma 4
2. Leaves hairless; hairs at base of lemma >1·5 × as long as lemma .... *C. epigejos*
2. Leaves hairy on upper surface; hairs at base of lemma <1·5 × as long as lemma 3
3. Ligules 2–6 mm; anthers purple, dehiscent, pollen well formed .... *C. canescens* i*
3. Ligules 7–10(–13) mm; anthers yellow, indehiscent, pollen absent .... *C. purpurea* ii*
4. Hairs markedly < lemma; awn arising from one-quarter to one-third above the base of the lemma; no hairs on upper leaf surface 5
4. Hairs usually ± equalling the lemma; awn arising from one-third to half-way above the base of the lemma; usually white hairs on upper leaf surface 6
5. Spikelets 3–4 mm; lower glume acute; one or more lower leaf sheaths usually hairy; culm usually rough near panicle .... *C. stricta* iii*
5. Spikelets 4·5–6·0 mm; lower glume acuminate; leaf sheaths glabrous; culms smooth .. *C. scotica*
6. Glumes 3·5–4·2 mm long and 0·8–0·9 mm wide; callus hairs mainly slightly < floret; anthers yellow when exserted; pollen 0; tightened panicle after flowering slightly wider than that of *C. stricta* .... *C. canescens* × *C. stricta*, $2n = 28$ (Leven H_2)
6. Glumes 4·9–5·9 mm long and 1·0–1·2 mm wide; callus hairs mainly equal to floret; or slightly > floret; anthers purple; pollen well formed; tightened panicle after flowering twice as wide as that of *C. stricta*. .... *C. canescens* × *C. stricta*, $2n = 56$ (Leven H_1)

i* Backcrosses from *C. canescens* × *C. stricta* to *C. canescens* may have culm rough near panicle; panicle not lax as in *C. canescens* sensu stricto, not nodding after flowering; awn arising >0·3 mm below tip of lemma; glumes variable in length in one panicle.

ii* *C. purpurea* in the British Isles is described as having hairs on upper leaf surface (Stace 1991; Stewart 1988). However, note that Nygren (1946) considered lack of hairs on upper leaf surface to be a significant character of this species which he used to distinguish it from *C. canescens*.

iii* Backcrosses from *C. canescens* × *C. stricta* to *C. stricta* generally resemble *C. stricta* but have one or more hybrid characters, e.g. white hairs on the upper leaf surface as in *C. canescens*; ligule > 3·0 mm; panicle >15 cm; basal branch of panicle >4 cm; glumes >4 mm; callus hairs ± equalling the lemma; awn arising from one-third to half-way above the base of the lemma.

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REFERENCES

ANDERSON, E. (1949). *Introgressive hybridization*. Wiley, New York.

CRACKLES, F. E. (1968). Some plant associations of the River Hull valley. *East Yorkshire field studies* **1**: 13–24.

CRACKLES, F. E. (1994). *Calamagrostis stricta* (Timm) Koeler, *C. canescens* (Wigg.) Roth and their hybrids in S.E. Yorks, v.c. 61, northern England. *Watsonia* **20**: 51–60.

CRACKLES, F. E. (1995). A graphical analysis of the characters of *Calamagrostis stricta* (Timm) Koeler, *C. canescens* (Wigg.) Roth and their hybrid populations in S.E. Yorks, v.c. 61, northern England. *Watsonia* **20**: 397–404.

GODWIN, H. & TALLANTIRE, P. A. (1951). Studies in the post glacial history of British vegetation, XII. Hockham Mere, Norfolk. *Journal of ecology* **39**: 285–307.

HUBBARD, C. E. (1968). *Grasses*, 2nd ed. Penguin Books, Harmondsworth.

HULTÉN, E. (1950). *Atlas of the distribution of vascular plants in N.W. Europe*. Generalstabens Litografiska anstalts förlag, Stockholm.

LIND, E. M. (1949). The history and vegetation of Cheshire meres. *Memoirs and proceedings of the Manchester Literary and Philosophical Society* **90**: 1–20.

LIND, E. M. (1951). Notes on the natural history of Oakmere, Cheshire (1) Vegetation of the exposed shore. *Memoirs and proceedings of the Manchester Literary and Philosophical Society* **92**: 1–11.

MATTHEWS, J. R. (1955). *Origin and distribution of the British flora*. Hutchinson, London.

NYGREN, A. (1946). The genesis of some Scandinavian species of *Calamagrostis*. *Hereditas* **32**: 131–262.

PAGE, E. (1831). *The report of Mr Edward Page upon the better drainage of the land within the level of Holderness drainage*. Unpublished report, Beverley. [Copy in Hull local history library.]

PERRING, F. H. & WALTERS, S. M., eds. (1962). *Atlas of the British flora*. Nelson, London.

PIGOTT, C. D. & WALTERS, S. M. (1954). On the interpretation of discontinuous distribution shown by certain British species of open habitats. *Journal of ecology* **42**: 95–116.

POLUNIN, N. (1959). *Circumpolar arctic flora*. Oxford University Press, Oxford.

ROSE, F. (1957). The importance of the study of disjunct distributions to progress in understanding the British flora. *Botanical Society of the British Isles. Conference reports* **5**: 61–67.

ROSE, F. (1989). *Colour identification guide to the grasses, sedges, rushes and ferns of the British Isles and north-western Europe*. Viking, London.

STACE, C. A. (1975). *Hybridization and the flora of the British Isles*. Academic Press, London.

STACE, C. A. (1991). *New Flora of the British Isles*. Cambridge University Press, Cambridge.

STEWART, O. (1988). *Calamagrostis* Adanson in RICH, T. C. G. & RICH, M. D. B., eds. *Plant crib*, pp. 135–136. B.S.B.I., London.

TUTIN, T. G. (1962). *Calamagrostis* Adanson in CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F., eds. *Flora of the British Isles*, 2nd ed., pp. 1170–1171. Cambridge University Press, Cambridge.

TUTIN, T. G. (1987). *Calamagrostis* Adanson in CLAPHAM, A. R., TUTIN, T. G. & MOORE, D. M., eds. *Flora of the British Isles*, 3rd ed., pp. 643–644. Cambridge University Press, Cambridge.

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