

A BIOSYSTEMATIC STUDY OF SOME *GLYCERIA* SPECIES IN BRITAIN*

3. BIOMETRICAL STUDIES

By MARTIN BORRILL

Welsh Plant Breeding Station, Aberystwyth**

INTRODUCTION

The British representatives of section *Glyceria* are paludal species, they occupy a wide range of habitats and are occasionally found growing together (Hubbard, 1942); nevertheless each shows slightly different ecological tolerances. *G. declinata* ($2n = 20$) can grow in turf likely to be trampled and to dry out in summer. *G. fluitans* ($2n = 40$) is ubiquitous, and like *G. declinata* is able to flourish in both acidic and base-rich soils, whereas *G. plicata* ($2n = 40$) is intolerant of acid soils. Both *G. plicata* and *G. × pedicellata* ($2n = 40$) are stoloniferous, forming large stands in shallow water. The hybrid flourishes in swift flowing water.

Because these grasses are restricted to paludal habitats they are divided into many small, spatially isolated, local populations which occur in ponds, on mudbanks, or at the bends of rivers and streams. Many populations have minor differences in floral morphology, and they are often very distinct vegetatively. Examples are: a luxuriant form of *G. declinata* sometimes found in humus-rich ponds (Hopedale, Stafford, H.506)[†], a form of *G. fluitans* in which the palea-apex greatly exceeds the lemma (Broad oak, Monmouth, H.426 and in Herb. Kew), and the *triticea* forms or varieties of *G. fluitans* and *G. plicata*, characterised by simple spiciform inflorescences (H.460, H.423).

Previous authors (Hubbard, 1942; Lambert, 1949; Jungblut, 1953) regard the varieties as ecological forms dependent on habitat conditions and changing with them, and they are not chromosomal races (Borrill, 1956b). Consequently some of these forms were compared in the same environment to see whether their phenotypic differences had a genetic basis.

MATERIAL

Seeds were collected from 15 populations, the characteristics of which are shown in Table 1. The limits of individual plants were explored in an attempt to ensure that seed was not derived from one clone. The plants raised from this seed formed samples of the potential biotypes in the populations (Baker, 1953). Each will be referred to as a 'race.' The plants were grown in the same environmental conditions from germination, namely 960 ft.-candles fluorescent light for 17 hours at a mean temperature of 28.5°C., with 7 hours darkness at a mean of 18.5°C. When the fourth leaf in each species appeared, a randomised block with three replicates was planted. The blocks were irrigated with a lawn spray.

DATA RECORDED

All the measurements were based on homotypes, i.e., organs of similar position and maturity (Pearson, 1901; Gregor *et al.*, 1936). A list of those used is given in Table 2.

* Part of a thesis for the degree of Ph.D. of the University of London.

** The experimental work for this investigation was carried out in the Botany Department at the University of Leicester.

† Specimen citations are given in the following form: H.506 = specimen No. 54506 in Herb. Univ. Leicester.

TABLE 1. *Seed parents for garden trial.*

Herb. No.	Race	Locality	Vice County	pH	Habitat	Morphology				
						Habit	Leaf	Culm	Lemma	Anthers
<i>G. declinata</i> 468	A	Malham Beck	64	7.6	Mudbanks in limestone stream	Small, rather spreading	Narrow, tapering towards apex. Pale green, purplish on sheath	Short, slightly curved	4.0—4.5 mm. 3-toothed, occasionally lobed at spikelet extremities, nerve tips purple	0.75—1.00 mm. purple
464	B	Malham Cove	64	7.3	Mudbanks at foot of limestone cliff	Large, prostrate, 'cup' type	Rather narrow, scarcely tapering, apex abruptly contracted, mucronate, slightly glaucous	Few, of medium length, slightly curved	4.0—4.5 mm., usually 3-toothed, sometimes obscurely lobed	0.75—1.00 mm. purple
413	C	Ulverscroft	55	4.6	Gravel bed of small stream	Large, erect	Broad, more or less tapering, occasionally slightly mucronate at apex	Many, long, erect and more or less curved	4.0—4.5 mm., conspicuously 3-toothed	0.8—1.25 mm. purple
427	D	Cadgwith	1	—	Quarry pond at cliff top	Large, spreading	Somewhat tapering, occasionally slightly mucronate at apex, more or less glaucous	Few, long, curved	4.0—4.5 mm., somewhat acute at apex, 3-toothed	Up to 1.00 mm. purple
506	E	Hopedale	39	5.4	Muddy pond rich in humus	Very large, massive	Very long and broad, scarcely tapering, apices contracted, abruptly mucronate	Long, spreading, curved - ascending, thick	About 4.0 mm., 3-5 toothed, sometimes lobed	0.8 to 1.0 mm. yellow or purple
<i>G. plicata</i> 400	F	Fulborn	29	8.2	Chalky soil, bank of clear chalk stream	Slender, stiff, erect, bushy	Rather small, tapering, often folded, rather dark green for species	Many, stiff, and straightly erect	4.0—4.5 mm., rounded or obscurely lobed at apex	1.0—1.25 mm. yellow
—	G	Breedon	55	6.9	Gravel bed of small stream	Large, spreading	Medium size, more or less tapering	Few, long, lax, spreading, erect	4.0—4.25 mm., rounded or more or less lobed	ca. 1.25 mm. yellow
444	H	Wistow	55	5.3	Edges of pond in marl pit	Erect, bushy	Long and broad, tapering towards apex	Many, long, stiff, straightly erect	4.0—4.5 mm., rounded or lobed, nerves purple-tipped when in fruit	1.0—1.25 mm. yellow

TABLE 1.—continued. *Seed parents for garden trial.*

Herb. No.	Race	Locality	Vice County	pH	Habitat	Morphology				
						Habit	Leaf	Culm	Lemma	Anthers
G. plicata 466	I	Malham	64	7.2	Freshet on limestone	Small, compact	Slender, short, tapering and often folded, purplish on leaf sheaths	Few, geniculate ascending-erect	3.5—4.0 mm., obscurely lobed or 3-toothed, scarlet-bordered	ca. 1.0 mm. purple
423	J	Wittering	32	6.2	Small spring on limestone	Small, spreading	Medium size, more or less tapering	Rather short, spreading-ascending	4.0—4.5 mm., more or less rounded, black-tipped in fruit	1.0—1.25 mm. yellow
G. fluitans —	K	Breedon	55	6.9	Bed of canal, mud rich in humus	Stiff, ± erect	Medium size, rather stiff, and often folded, dark green	Spreading, ascending, to erect	ca. 6.0 mm., apices acute and more or less sinuous	ca. 2.0 mm. purple
454	L	Ulverscroft	55	4.3	Muddy ditch	Large, rather spreading	Long, lax, often flat, rather pale green	Long, straight-ascending	6.0—6.5 mm., noticeably exceeded by palea points, apex acute often lobed	2.0—2.5 mm. yellow
437	M	Loddington	55	5.5	Wet place in fields at Loddington Reddish	Large, spreading	Long and more or less folded, later flat. Rather lax, pale or medium green	Long, straight-ascending	6.0—6.5 mm., usually exceeded by palea points, apex acute and smooth	2.0—2.5 mm. yellow or purple
490	N	Acle	27	4.1	Trodden ground by dike	Small, slender	Stiff, short, often folded and dark green	Few, short	6.0—6.5 mm., equals length of palea, acute, irregularly lobed, nerve-tips blackish	1.5—2.0 mm. yellow or purple
475	O	Acle	27	3.9	ca. 30 cm. water in dike	Very large, coarse, and stiff	Medium size, stiff, often folded, dark green, blackish on sheaths	Very long, woody, nodally rooting	5.5—6.0 mm., more or less equals palea, apices smooth or slightly sinuous, acute	ca. 2.0 mm. purple

TABLE 2.

Details of the homotypic characters.

Measurements averaged to obtain the mean value for each plant. <i>G. declinata</i> , <i>G. fluitans</i> and <i>G. plicata</i> :	
Lemma length	= Lemma of supra-basal floret in terminal spikelet of major pedicel at each node on the first three culms.
Florets per spikelet	= Number of florets in each spikelet measured.
Spikelet length	= Length of each spikelet measured.
Culm length	= Length of the three longest culms.
Panicle length	= Length of the panicle in each culm measured.
Number of internodes	= The internodes of each panicle.
Emergence date	= Interval from germination up to the emergence of the second culm.
Leaf length } Leaf width }	= Length and width of the three longest leaves on the three longest culms and tillers (The averages of the culm leaves and tiller leaves used separately).
Leaf index	= Ratio $\frac{\text{Mean leaf length}}{\text{Mean leaf width}}$
Number of culms	= Total number of culms on the plant.
Number of shoots	= Total number of shoots on the plant.
Dry weight	= Weight of the whole plant excluding the root system.
For <i>G. plicata</i> only:	
Major tillers	= Number of long stolons on the plant.
Major tiller length	= Length of these stolons.
Crown tillers	= Number of vegetative shoots at the crown of the plant.
Secondary tillers	= Number of tillers borne on each culm.
Tiller number	= Number of tillers borne on each stolon.

In the case of the consistently stolon-forming *G. plicata*, with both heading and non-heading plants, these two forms were considered separately as follows :—

In the heading plants the numbers of short vegetative shoots at the centre, and of secondary tillers borne on the culms; *in the non-heading*, the number and length of the long stolons, and number of short vegetative shoots at the centre, and of secondary tillers borne on the stolons.

At the end of the experiment, the plants themselves were lifted (leaving the roots in situ), partially dried and stored; before measurement, leaves were floated on a detergent solution to restore their normal size.

The data were subjected to an analysis of variance, and the homotype-means for all the races are shown in Table 3, where differences significant at $P = 0.01$ are indicated.

DISCUSSION

Highly significant differences were shown by the population samples grown in the same environment (Table 3); consequently there are genetic differences between them. In general, they retained the characteristic morphological features of the parental populations.

The numerical differences between the homotypes give precision to visible variations between the races. Ideographs (Fig. 1), based on the suggestion of Anderson (1949), have been prepared for each population sample, consisting of (1) a base representing the vegetative part of the plant and (2) an erect portion showing the culm, with leaf and spikelet homotypes. The height of the leaf from the base is proportional to the interval between sowing and heading.

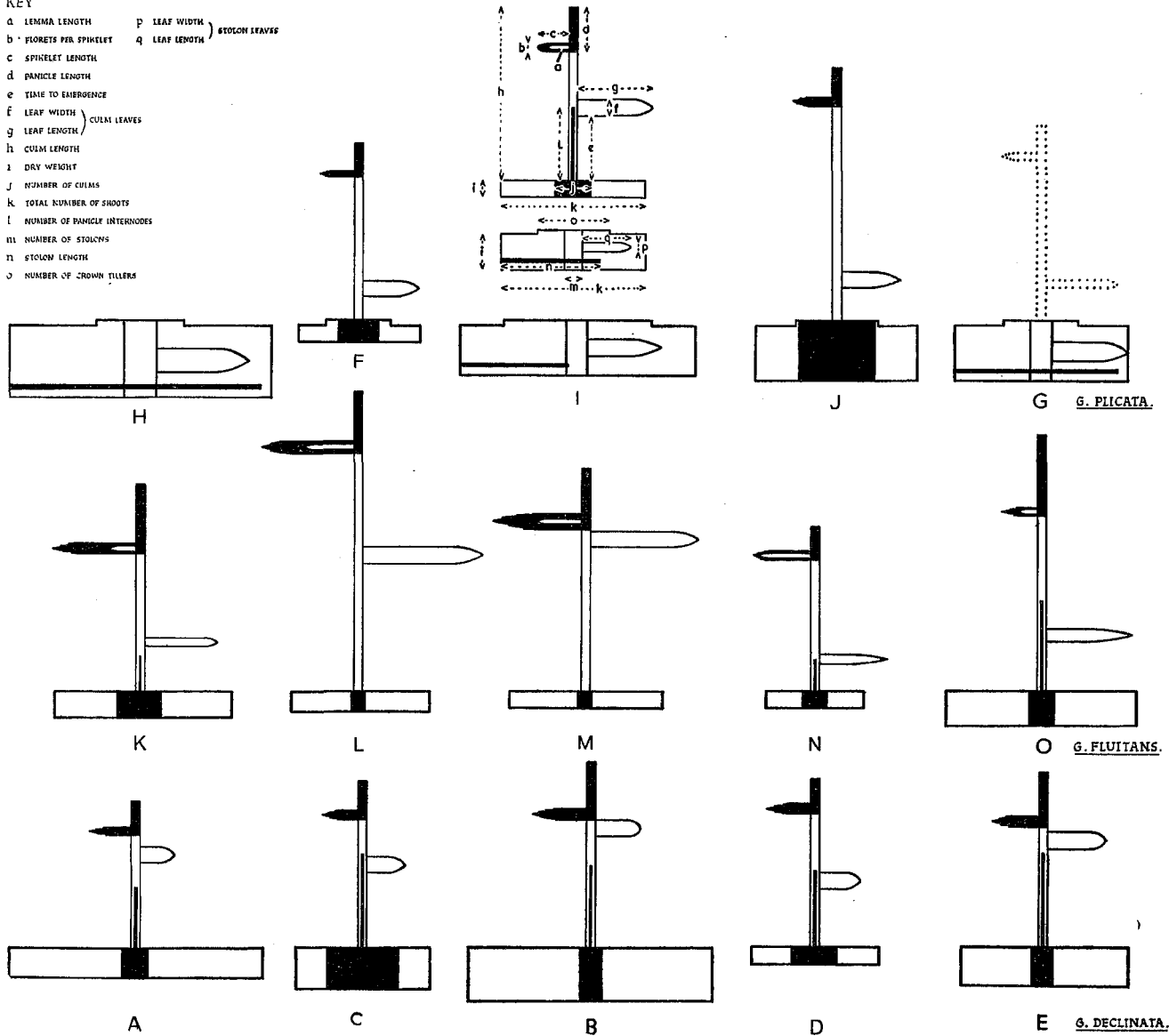
TABLE 3.
The occurrence of significant differences between race means.

Character	Mean values				
	A	B	C	D	E
<i>G. declinata</i>					
Florets per spikelet	6.27	(7.87)	(7.09)	(7.37)	(7.73)
Spikelet length (mm.)	(15.0)	16.4	14.3	(15.2)	(15.4)
Culm length (cm.)	47.6	(52.9)	(52.4)	(50.5)	(51.7)
Panicle length (cm.)	[23.2]	(27.5)	24.2	[24.0]	(28.0)
Number of internodes	10.5	[11.3]	(11.8)	[11.2]	(11.8)
Emergence date	29/7	5/8	27/7	20/7	1/8
Leaf length (mm.)	(77.7)	96.2	(72.7)	(76.3)	105.4
Leaf width (mm.)	[5.91]	(6.66)	[5.99]	(6.43)	[7.09]
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	13.0	[14.5]	(12.0)	(11.9)	[14.7]
Total culms	(15.1)	(12.9)	41.2	24.9	(11.6)
Total shoots	154.0	175.0	(116.0)	(111.0)	(132.0)
Dry weight (gm.)	(24.2)	37.5	(30.7)	17.1	(28.8)
<i>G. plicata</i>					
Florets per spikelet	8.09	—	—	—	8.61
Spikelet length (mm.)	16.3	—	—	—	17.8
Culm length (cm.)	69.3	—	—	—	79.4
Panicle length (cm.)	(24.9)	—	—	—	(24.7)
Leaf length (mm.)	[104.3]	(142.9)	165.2	(139.5)	[109.5]
Leaf width (mm.)	(6.20)	7.45	9.25	(6.18)	(6.25)
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	(16.0)	18.9	(17.7)	22.4	(17.3)
Number of culms	21.6	—	—	—	42.3
Total shoots	92.1	(165.9)	279.9	236.3	(153.0)
Dry weight (gm.)	31.2	(53.1)	80.3	(50.0)	(52.8)
Total major tillers	—	(12.8)	18.9	(12.3)	—
Length major tillers	—	90.6	139.0	60.1	—
Crown tillers	(51.8)	(62.3)	(73.3)	123.9	(69.6)
Secondary tillers	23.4	—	—	—	41.3
Mean tiller number	—	(7.14)	(10.33)	(8.48)	—
<i>G. fluitans</i>					
Lemma length (mm.)	[5.86]	(6.39)	(6.24)	(6.42)	[5.73]
Florets per spikelet	10.10	11.20	12.42	9.16	8.48
Spikelet length (mm.)	(24.5)	(25.9)	(25.4)	20.80	18.0
Culm length (cm.)	(62.7)	75.3	(64.8)	59.30	71.9
Panicle length (cm.)	[29.5]	[27.1]	[28.0]	22.90	[31.6]
Number of internodes	9.68	—	—	9.50	11.64
Emergence date	17/7	8/8	14/8	12/7	18/7
Leaf length (mm.)	(126.6)	217.5	197.5	(127.5)	158.5
Leaf width (mm.)	(6.33)	[7.99]	[7.49]	(6.65)	(7.03)
Leaf index $\frac{\text{Length}^1}{\text{Breadth}}$	[20.1]	(27.1)	(26.3)	[19.1]	22.8
Total culms	24.3	[8.0]	[8.14]	(14.84)	(14.42)
Total shoots	(97.1)	[76.7]	[84.9]	55.4	(105.1)
Dry weight (gm.)	21.1	(18.0)	(16.2)	(16.0)	26.4

Unbracketed figures differ from all others. Figures in like brackets similar. Bracketed figures underlined or barred differ. All differences significant at $P = 0.01$.

1. A 't' test. 2. Plants almost or entirely non-heading.

- KEY
- a LEMMA LENGTH
 - b FLORETS PER SPIKELET
 - c SPIKELET LENGTH
 - d PANICLE LENGTH
 - e TIME TO EMERGENCE
 - f LEAF WIDTH) CULM LEAVES
 - g LEAF LENGTH)
 - h CULM LENGTH
 - i DRY WEIGHT
 - j NUMBER OF CULMS
 - k TOTAL NUMBER OF SHOOTS
 - l NUMBER OF PANICLE INTERNODES
 - m NUMBER OF STOLONS
 - n STOLON LENGTH
 - o NUMBER OF CROWN TILLERS
 - p LEAF WIDTH) STOLON LEAVES
 - q LEAF LENGTH)



The main differences between the populations are shown in Fig. 1. In *Glyceria declinata* and *G. plicata*, plant bulk is the main feature, measured by dry weight and number of culms and shoots (i, j and k); floral differences are less pronounced.

Race E of *G. declinata* retained the luxuriant habit characteristic of the parent population, and, with race B, is a distinct type characterised by large vegetative and floral parts. The leaves are long, broad and conspicuously mucronate (Fig. 3), those on the vegetative shoots being significantly longer than those on the culms, as shown below.

Analysis of variance, leaf morphology

Race	Character	Type of shoot	Mean (mm.)	Diff. (mm.)	Minimum significant numerical difference (P = 0.01)
B	Leaf length	Tiller	10.71	1.09	0.471
		Culm	9.63		
E	Leaf length	Tiller	11.75	1.34	0.865
		Culm	10.41		

In *Glyceria plicata*, grown, like the other species, without low-temperature treatment, two races headed, two did not, and race G was intermediate in behaviour. This is interesting, since Lambert (1949) considered that delay of flowering until the second season distinguished *G. plicata* from the other British species of section *Glyceria*. In fact, the position is more complex.

Fig. 1 shows that the non-heading plants made more growth and that races H and I are opposite in habit, the former being very spreading with long, broad leaves (Fig. 3) and the latter with a tufted crown and short stolons. A difference was seen between the parents and offspring of race H. In the field these were slender, erect, floriferous plants resembling race F. The larger size and increased vigour of the progeny are due to suppression of heading.

Homotype correlation was studied by means of scatter diagrams. An example is the relation between spikelet length and number of florets in *Glyceria fluitans*. Fig. 1 and the histograms in Fig. 2 show that these are closely correlated, whereas lemma length is independent.

The homotypes fall into three correlation groups (Fig. 1):—

1. Those concerned with the size of the vegetative parts of the shoots, i.e. culm length, panicle length, number of internodes per panicle, leaf length, leaf width.
2. Those providing a measure of plant bulk i.e. dry weight and number of shoots.
3. The spikelet characters.

Quite strict correlation is the rule within a population but there are departures from this when passing from one population to another. The fact that populations tend to have independent centres of variation enhances their phenotypic distinctness. A similar situation has been described in *Panicum virgatum* by Nielson (1944).

In *G. fluitans* (Fig. 1) the differences between the races are in spikelet—(Fig. 2), leaf—(Fig. 3), and culm—length, in contrast to the other species, where bulk was most important. Races L and M are similar with spreading habit, long, lax, flat, pale green leaves, and large spikelets. Race N, at the other extreme, was compact, with short, stiff,

dark green and more or less folded leaves, and short spikelets with very long lemmas. One local population sample, an extreme form of *G. fluitans* var. *triticea* from an acid pool at Great Close Mire, Malham, Mid West York (H.460), was grown alongside the others and retained the varietal form. It was not analysed statistically. The characteristics of this population have a genetic basis.

The large differences in lemma-length in this species are interesting when considering *G. fluitans* var. *islandica* Löve (1951), largely because of its short lemmas (mean 5.9 mm., range 5.3-6.4 mm.). The British material studied by Löve had a range of 6.3-7.6 mm. Fig. 2, however, shows that races K and O have short lemmas very similar in range to var. *islandica* (5.4-6.4 mm., mean 5.86 mm., in race K; and 5.2-6.2, mean 5.73 mm., in race O). This variety is therefore to a large extent paralleled by British material.

Glyceria fluitans has a greater range of variation in race means for spikelet and leaf homotypes than the other species (Fig. 1). This is shown for leaf index in Fig. 3, and for spikelet characters of *G. declinata* and *G. fluitans* in Table 4. The existence of a greater range of race-means in *G. fluitans* could be due to greater variability or to accidents

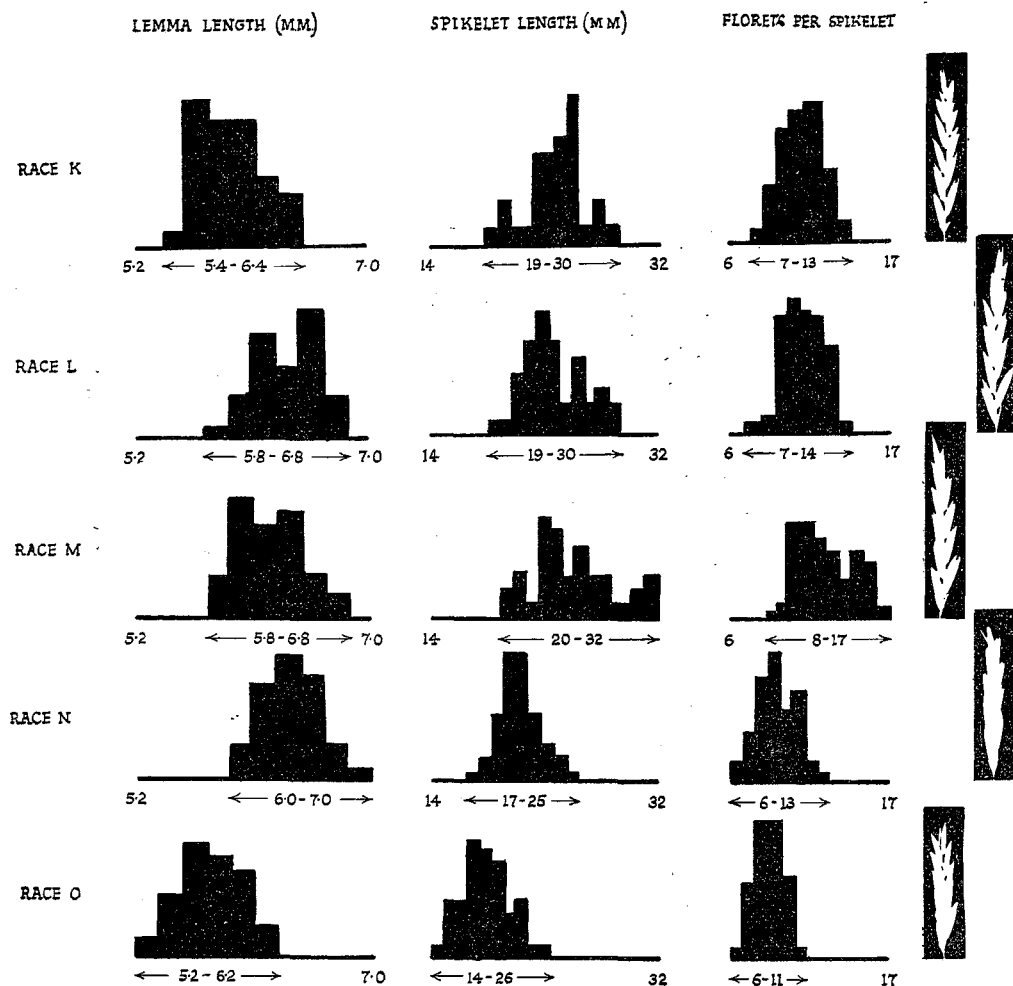


Fig. 2. Spikelet characteristics in five races of *Glyceria fluitans*. The three characters illustrated show a wide range of variation. Spikelet length and number of florets per spikelet are closely correlated. Lemma length varies independently.

of sampling, since it is possible that another five populations could show a smaller range of variation. The intrinsic variability therefore was studied.

The standard deviation is generally used to measure variation and this is expressed as a percentage of the mean, and the resulting coefficient used as an index of phenotypic variation. For this to be reliable, an increase in the mean must be accompanied by a proportional increase in the standard deviation. Day & Fisher (1937) pointed out that there is no logical reason for this, and evolved the more complex analysis of covariance which has been used in population studies by Gregor & Lang (1950), and Baker (1953).

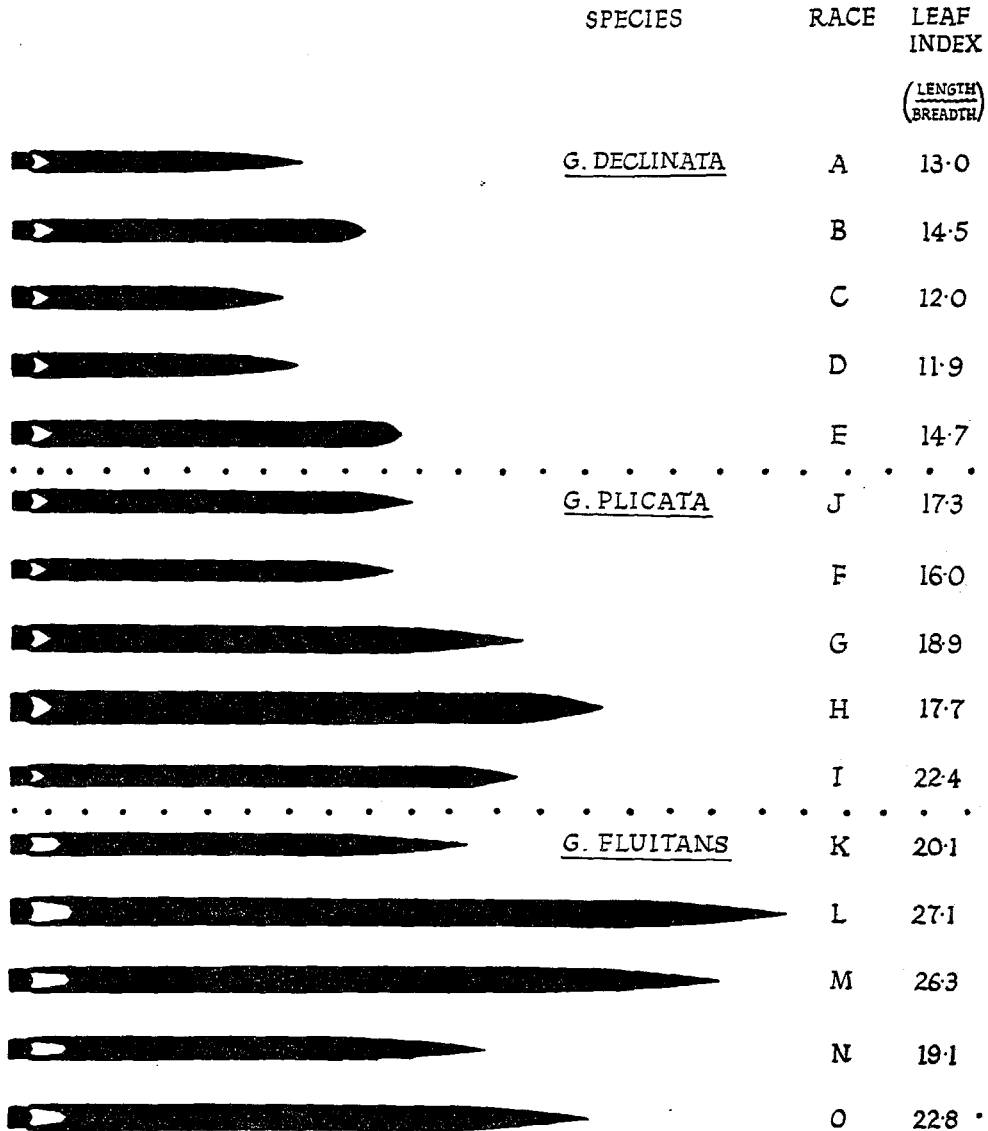


Fig. 3. Leaf morphology.

Variation in leaf morphology in *Glyceria* species. Differences significant at $P = 0.01$ occur between BE : CD : A, FJH : G : I, KN : LM : O, in leaf index, which is a measure of leaf shape. *G. declinata* has the least range of variation, 2.8 units, *G. plicata* a greater range, 6.4 units, and *G. fluitans* the largest range, 8.0 units.

TABLE 4. Range of subpopulation means in *Glyceria* species.

Characters	<i>G. declinata</i>					Range	<i>G. fluitans</i>					Range
	Race						Race					
	A	B	C	D	E		K	L	M	N	O	
Lemma length	4.73	4.87	4.58	4.84	4.72	0.29	5.86	6.39	6.24	6.42	5.73	0.69
Spikelet length	15.00	16.36	14.32	15.22	15.43	1.36	24.50	25.90	25.40	20.80	18.00	7.90
No. of florets per spikelet	6.27	7.87	7.09	7.37	7.73	1.60	10.10	11.20	12.42	9.16	8.48	3.94

The standard deviations of the races of *Glyceria* were therefore plotted against the means in order to see whether they were related. Fig. 4 illustrates the results for spikelet-length in *G. fluitans* and *G. declinata*; for lemma-length in *G. fluitans*, and for the species as a whole, based on the pooled data of the races.

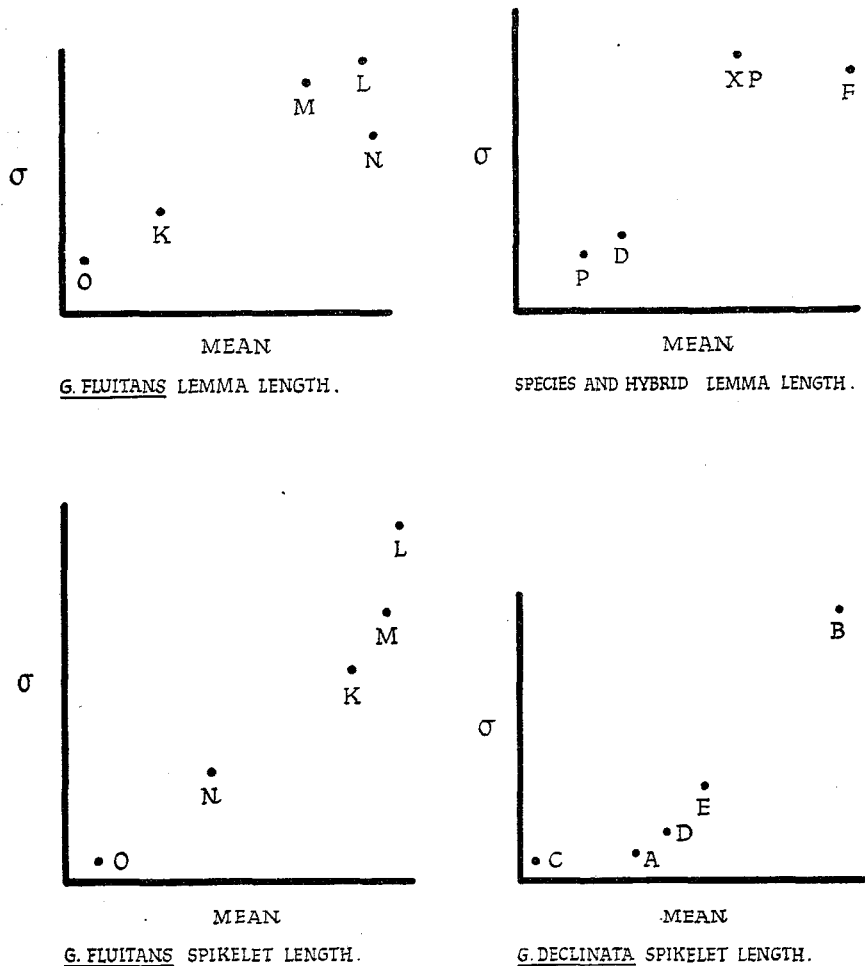


Fig. 4. Relation between mean and standard deviation in *G. fluitans* and *G. declinata*. Race letters: *G. fluitans* K L M N O; *G. declinata* A B C D E. Symbols for species: D = *G. declinata*; P = *G. plicata*; F = *G. fluitans*; XP = *G. × pedicellata*.

TABLE 5.
Coefficients of variation in *Glyceria*.

Character	Species	Details of data	Population ¹ mean (mm.)	Standard deviation (σ)	(per cent) Coefficient of variation
Lemma length	<i>G. plicata</i>	Pooled	4.45	0.175	4.06
		Most variable Race J	4.51	0.189	4.18
" "	<i>G. declinata</i>	Pooled	4.73	0.200	4.22
		Most variable Race D	4.84	0.232	4.79
" "	<i>G. fluitans</i>	Pooled	6.21	0.402	6.48
		Least variable Race O	5.73	0.345	6.07
Spikelet length	<i>G. × pedicellata</i> ²	Pooled	5.47	0.434	8.11
		<i>G. declinata</i>	Pooled	15.26	0.872
		Most variable Race B	16.36	1.166	7.12
	<i>G. fluitans</i>	Pooled	22.89	3.967	17.31
		Least variable Race O	18.00	2.491	13.83

1. All differences between species significant at $P = 0.01$

2. Data from specimens in Herb. University of Leicester.

The coefficients of variation for lemma-length, given in Table 5, based on the pooled data, show that *G. fluitans* is the most variable species; and this is confirmed by the fact that the coefficient of variation for the least variable race of *G. fluitans* exceeds the coefficient of variation for the most variable races of the other species.

The vegetatively propagated hybrid, *G. × pedicellata*, has a similar ecological distribution to the sexually-reproduced species, but a very different genetic population-structure, and it is therefore impossible to carry out sampling on a comparable basis. Data for lemma-length were therefore collected from a random selection of herbarium specimens. The results are shown for comparison in Table 5. *G. × pedicellata* has a smaller mean-lemma-length than *G. fluitans* but a larger standard deviation and therefore the highest coefficient of variation. In the first paper of this series (Borrill 1956a), it was concluded that *G. × pedicellata* had a greater range of phenotypic variation than either parent in panicle characters; the present data suggest that it might also have a higher variability.

CONCLUSIONS

1. The small, spatially isolated, local populations sampled have many statistically significant phenotypic differences which show that underlying genetic differences exist.

2. In one population of *G. fluitans* var. *triticea*, the varietal type of morphology was found to have a genetic basis.

3. *G. fluitans* var. *islandica* Löve is similar to two British populations of *G. fluitans* with short lemmas.

4. The phenotypic characters fall into three correlation groups: those concerned with the dimensions of the vegetative parts, those providing a measure of plant bulk, and the spikelet characters. *Lemma-length was independent.*

5. *G. fluitans* is more variable than *G. declinata* and *G. plicata*.

6. In an earlier paper (Borrill 1956a), *G. × pedicellata* was shown to have a greater range of variation than either parental species; the present data suggest that it may have a greater variability. The evidence obtained is not conclusive, because population-sampling could not be put on the same basis in parents and hybrid.

7. All the populations of *G. declinata* and *G. fluitans* studied headed in the first season, whereas, in *G. plicata*, two of the populations headed in the first season, two remained non-heading, and one was intermediate. All the seed- and population-plants were without low temperature treatment.

8. There was no obvious relation between the nature and extent of morphological differentiation in the populations examined and the type of habitat in which they grew. The implications of this will be discussed in a further paper.

ACKNOWLEDGEMENTS

My thanks are due to Professor T. G. Tutin for his interest and encouragement in the course of the work, to the Research Board at the University of Leicester who financed the collection of the material, and to Professor E. T. Jones, the Director of the Welsh Plant Breeding Station and Mr. A. R. Beddows, Grass Breeding Section, for facilities to write up the results.

REFERENCES

- ANDERSON, E., 1949, *Introgressive Hybridization*. New York.
- BAKER, H. G., 1953, Race formation and reproductive method in flowering plants. *S. E. B. Symposia*, **7**, (Evolution), 114-145.
- BORRILL, M., 1956a, A biosystematic study of some *Glyceria* species in Britain, 1. Taxonomy, *Watsonia*, **3**, 291-298.
- , 1956b, A biosystematic study of some *Glyceria* species in Britain, 2. Cytology, *Watsonia*, **3**, 299-306.
- DAY, B., & FISHER, R. A., 1937, The comparison of variability in populations having unequal means, *Ann. Eugen. Lond.*, **7**, 333.
- GREGOR, J. W., DAVEY, J. McM., & LANG, J. M. S., 1936, Experimental Taxonomy, 1. Experimental garden technique in relation to the recognition of small taxonomic units, *New Phytol.*, **35**, 323-350.
- GREGOR, J. W. & LANG, J. M. S., 1950, Intra-colonial variation in plant size and habit in *Plantago maritima*, *New Phytol.*, **49**, 135-141.
- HUBBARD, C. E., 1942, The collective species *Glyceria fluitans*, *J. Ecol.*, **30**, 233.
- JUNGBLUT, F., 1953, Les espèces du genre *Glyceria* au Grand-Duché de Luxembourg, *Bull. Soc. Bot. Belg.*, **86**, 25-37.
- LAMBERT, J. M., 1949, The British species of *Glyceria*, *B.S.B.I. Conference Report*, **1**, British flowering plants and modern systematic methods, 86-89.
- LÖVE, Å., 1951, The Icelandic type of *G. fluitans*, *Bot. Notiser*, **5**, 229-240.
- NIELSON, E. L., 1944, An analysis of variation in *Panicum virgatum*, *J. Agric. Res.*, **69**, 327-353.
- PEARSON, K., 1901, Homotyposis in the vegetable kingdom, *Phil. Trans. Roy. Soc. A.*, **197**, 285-379.