

# EVOLUTION IN CLOSELY ADJACENT PLANT POPULATIONS

## II. *AGROSTIS STOLONIFERA* IN MARITIME HABITATS

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### 1. INTRODUCTION

THE occurrence of distinct populations within plant species adapted to local habitat conditions has long been realised. However, only recently has it become clear that such population differentiation occurs within small distances over which there can be considerable gene flow. Whether or not populations can diverge from one another under such conditions depends on the outcome of the interplay between differential selection on the one hand, and gene flow on the other. A general survey and the theoretical outcome of such an interplay has been considered earlier (Jain and Bradshaw, 1966). With a knowledge of the amount of differentiation that can occur in specific natural habitats it may be possible to assess more precisely values for the parameters of gene flow and selection in natural conditions about which we know little.

An intensive study has therefore been made of populations of *Agrostis stolonifera* occupying exposed maritime habitats in Wales. The degree of differentiation that can be found in this species is considerable. In inland habitats it is a loose widely spreading stoloniferous plant, whereas in coastal regions it is sometimes a small compact tufted plant with many short stolons. Such differences are retained in cultivation and in plants grown from seed. The character of length of stolon was therefore studied intensively since it appeared to be of adaptive significance.

A number of experiments were carried out to examine (a) the occurrence of differences between closely adjacent and other populations, (b) the potency of the forces of natural selection that maintain them, (c) the extent and effects of gene flow.

### 2. THE GENERAL CHARACTERISTICS OF CLIFF POPULATIONS

The first survey assessed the variation between populations within a range of cliff and maritime habitats, some closely adjacent. An intense sampling was made in the Abraham's Bosom region of Anglesey (near Holyhead): this region of exposed cliff and pasture, occupying about two hectares presented a wide range of habitat contrasts. Populations were collected from areas of about 50 sq. metres.

Two population trials were conducted. The first was of twenty populations laid down in a randomised block design with five replicates each with four plants from each population. The second was of

four populations only, with replication of individual genotypes: a balanced lattice of 81 genotypes was used with five replicates, and in each replicate the individual genotypes were duplicated side by side to guard against loss, etc. In both experiments the plants were spaced a metre apart and stolon length recorded after a nine week growing period.

(i) *The populations*

The first thirteen populations came from the Abraham's Bosom region. Their geographical relationships to each other are shown in fig. 1, and they are listed below.

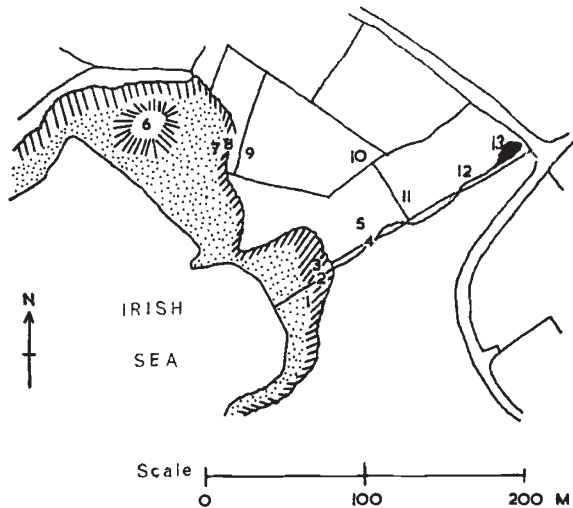


FIG. 1.—Map of Abraham's Bosom showing locations of sampling sites.

1. Rocky crevices at the base of low cliffs, extremely exposed to wind and salt spray and without any place for nodal roots to take hold. When collected the plants were small and tufted.
2. Edges of rocky pools at the base of a gully, with a small stream ensuring constant waterlogging. Somewhat creeping.
3. Dry exposed site a few metres above 2, with other maritime perennials, on shaley soil. Tufted.
4. Marshy region higher up the same stream as 2, sheltered and more fertile. Long and creeping.
5. Open, exposed pasture with a thin and windswept top soil. Small and grazed.
6. Low dry exposed bluff close to the sea. Tufted.
7. Base of a 30 metre cliff, growing in rocky crevices and on ledges in a wet region, somewhat sheltered from strong wind. Generally tufted with a few creeping stolons.
8. Open habitat on the cliff top above 7, extremely exposed to all winds. Dwarf and stunted.

9. Sheltered damp region of a pasture less than 10 metres from 8, in densely matted turf in sheltered hollows behind a low wall. Long.

10. Damp area of grazed pasture, the turf of which could afford tillers some shelter. Short, due to grazing.

11. Moderately exposed section of pasture, between 5 and 12. Long.

12. Marshy stream area, some 80 metres upstream from 4. Long and creeping.

13. Extremely waterlogged region another 30 metres upstream. Long and creeping.

The rest of the populations were collected from various maritime sites in Wales.

14. Beaumaris, Anglesey. Relatively sheltered coast on boulder clay cliffs, somewhat more fertile than Abraham's Bosom, but still subject to salt spray. Loosely tufted with creeping stolons.

15. Great Orme, Llandudno. Exposed north west face of a limestone cliff, growing in rocky crevices in a generally poor dry habitat. Densely tufted.

16. Little Orme, Llandudno. Cliff top sward, with other calcicolous grasses under fairly sheltered conditions. Short, due to sheep grazing.

17-20. Nash Valley, Glamorgan. Four populations from the stream bank in a flat alluvial valley flowing into the sea. Population 20 was only some 15 metres from high water tide line, 19-50 m., 18-100 m., and 17-200 m.

The populations from Abraham's Bosom can be put into three particular transects.

(a) Populations 6, 7, 8, 9, 10, 12. A transect up and over the cliffs, from the sea to the hinterland, passing through a severe habitat change, designed to determine whether a sudden and sharp environmental change would be matched by a corresponding sudden change in the populations.

(b) Populations 1, 3, 5, 11, 12. An adjacent transect, from the sea to the hinterland over a relatively smooth ecological gradient, contrasting with transect (a), to determine whether in this case a gradual change in habitat would be matched by a gradual change between populations.

(c) Populations 2, 4, 12, 13. A transect along the stream at Abraham's Bosom, to contrast with transect (b) adjacent to it.

#### (ii) *The results—twenty population trial*

The general range of stolon lengths are shown in table 1. A detailed topographical representation of the Abraham's Bosom transects is given in fig. 2.

Between the cliff populations in general there is a considerable amount of variation which forms a more or less continuous series, and which can be related to the types of cliff habitat. The five exposed

populations from Abraham's Bosom were all small. The exposed population from the Great Orme was also small, but the more protected Little Orme cliff population was larger. The Beaumaris cliff population, the largest, comes from steep cliffs, but being by the Menai Straits, it was relatively sheltered.

In the sudden change transect at Abraham's Bosom the transition from cliffs to pasture occurs over a few metres. The two populations at this point bear little resemblance to each other, and the transect falls into two very distinct halves.

TABLE I

*General variation in mean stolon length of various maritime populations (significant differences at 5 per cent. level using Duncan's multiple range test (1955) lie outside the lines)*

Population	Stolon length cms.	Statistical significance
1. Cliff base, exposed	14.5	
15. Great Orme, exposed	15.9	
8. Cliff top, exposed	16.5	
3. Dry cliff, exposed	17.0	
6. Dry exposed bluff	18.0	
7. Cliff base, exposed and wet	24.1	
16. Little Orme, cliff top pasture	32.2	
2. Stream, exposed near sea	33.6	
5. Pasture, exposed	35.5	
18. Nash Valley (b)	41.9	
11. Pasture, moderately exposed	42.3	
14. Beaumaris cliff	44.0	
17. Nash Valley (a)	45.4	
10. Pasture, normal	46.7	
4. Stream	47.5	
9. Pasture, sheltered	47.9	
12. Stream	48.7	
20. Nash Valley (d)	49.8	
19. Nash Valley (c)	51.2	
13. Stream	57.0	

The gradual change transect at Abraham's Bosom was from a graded series of habitats with no sharp changes. The pattern of the transect is in clear contrast to the previous one. There is little evidence of a sudden population change, but rather a gradual cline.

The stream transect which runs parallel to the previous transect suggests that the stream provides an environment which is very different and is almost unaffected by exposure. This can be seen from the comparison of populations 3 and 5 from the cliff, which show considerable adaptation to exposure, with populations 2 and 4 only a few metres away which show little or none.

In contrast with all these, the Nash Valley populations from a flat, even habitat failed to show any significant variation.

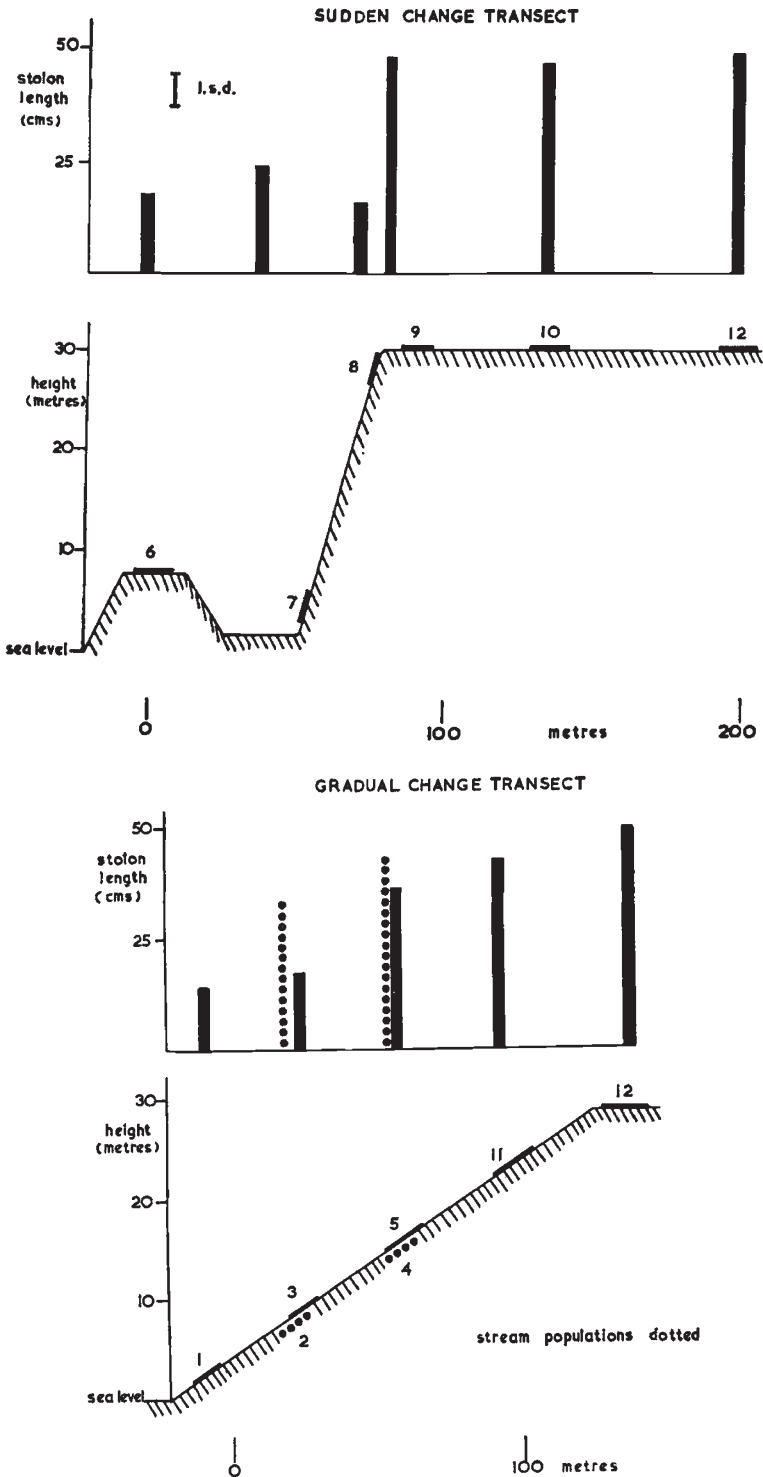


FIG. 2.—Mean stolon lengths in cultivation of the populations, and the topography of the sampling sites at Abraham's Bosom.

## (iii) Results—four population trial

The values of stolon length for individual plants are shown in fig. 3. Colour differences were also apparent and the plants fell into two distinct categories, the normal green colour or a glaucous blue-green colour, the frequency of which is given in table 2.

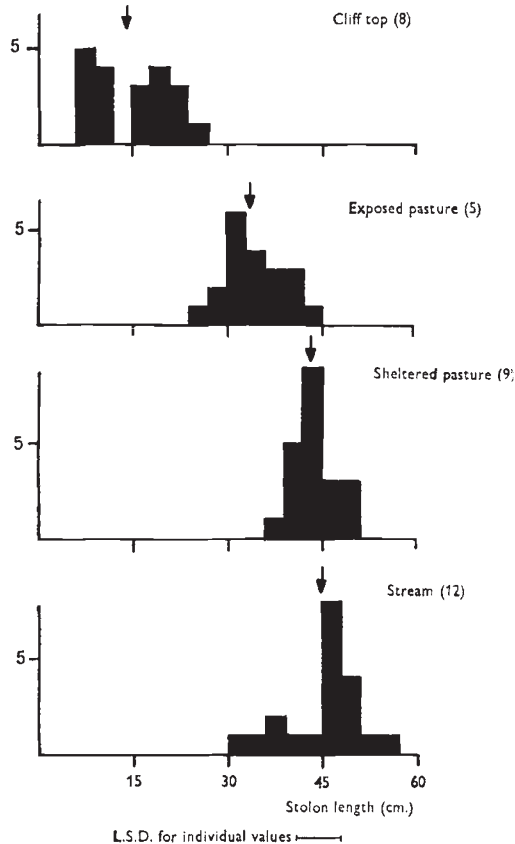


FIG. 3.—Histograms of stolon length in cultivation of four populations from Abraham's Bosom (arrows indicate population means).

The differences found in the previous trial remain just as clear cut. Thus, no plants of the cliff top population have values approaching any of those of the pasture and stream populations. The values of the exposed pasture only overlap the others slightly. The distinctness is further shown by the frequency of the blue-green character. Although the cliff population sample appears bimodal, this appears to a sampling artifact, as a second sampling (unpublished) shows no sign of this bimodality.

## (iv) Discussion

The variation found between populations is considerable, both generally, and in the very small area of Abraham's Bosom. It can only suggest a selective relationship between exposure and plant form.

The populations in general show differentiation of a continuous nature in relation to exposure similar to that described by Gregor (1946) for *Plantago maritima*. In the small area of Abraham's Bosom the complex pattern of differentiation forms a "graded patchwork" similar to that found in *Agrostis tenuis* (Bradshaw, 1959) and *Eschscholtzia californica* (Cook, 1962) but on a much smaller scale.

Contrasting gradients in environmental change have related contrasts in population change. A sudden change in populations occurs where there is a sudden change in environment, and a gradual change in populations, or cline, occurs where there is a gradual environmental change.

TABLE 2

*Number of plants showing blue-green phenotype in four populations from Abraham's Bosom*

Population	Blue-green	Green
Cliff top (8)	20	...
Exposed pasture (5)	16	4
Sheltered pasture (9)	...	20
Stream (12)	...	20

At first sight, it is difficult to accept the magnitude of the differences found between the populations. The distances between some populations are very small indeed, so that the possibility of gene flow by cross pollination from one population to another, which would tend to obliterate the differences, is very great. This is studied in the next section.

### 3. GENE FLOW—COMPARISON OF SEED AND ESTABLISHED POPULATIONS

In this experiment two contrasting but adjacent populations from Abraham's Bosom, from the cliff and the stream, were used. Population samples grown from natural seed were compared with actual natural tiller material of the same populations.

Seedling material may differ from adult population (a) in its mean population value or (b) in its variability. The former is likely to be due mainly to gene flow from neighbouring populations (*Agrostis stolonifera* is highly self incompatible). The latter is likely to be due to segregation or to gene flow. Any discrepancies found between seedling and adult populations will therefore throw light on these phenomena. At the same time, whatever the cause of the discrepancies, their occurrence points to the existence of selection maintaining the *status quo* of the adult populations. Therefore information can also be obtained on the nature and potency of natural selection in such situations.

Twenty seedlings from the two populations were grown on, transplanted and divided until sufficient material was obtained to make five

replicates of each plant. At the same time, single small tillers taken from the earlier trials of adults were treated similarly. The experiment was set out in boxes in a green-house in May, 1962, using a split plot design.

The following measurements were made on each plant: the length of three longest stolons, the length of the fourth leaf from the apex from the longest stolon, the width of this leaf at its widest point, a visual density assessment on the number of tillers present.

### (1) The results

The results are presented in fig. 4. The stolon length character has been analysed (after Cooper and Edwards, 1961) for the respective components of variation between the populations in table 3.  $V_G$  is the component due to genetic variability,  $V_B$  is a general measure of developmental stability,  $V_S$  gives an assessment of the stability of development within the plant and  $V_{GB}$  is an indication of individual plant variation between blocks.

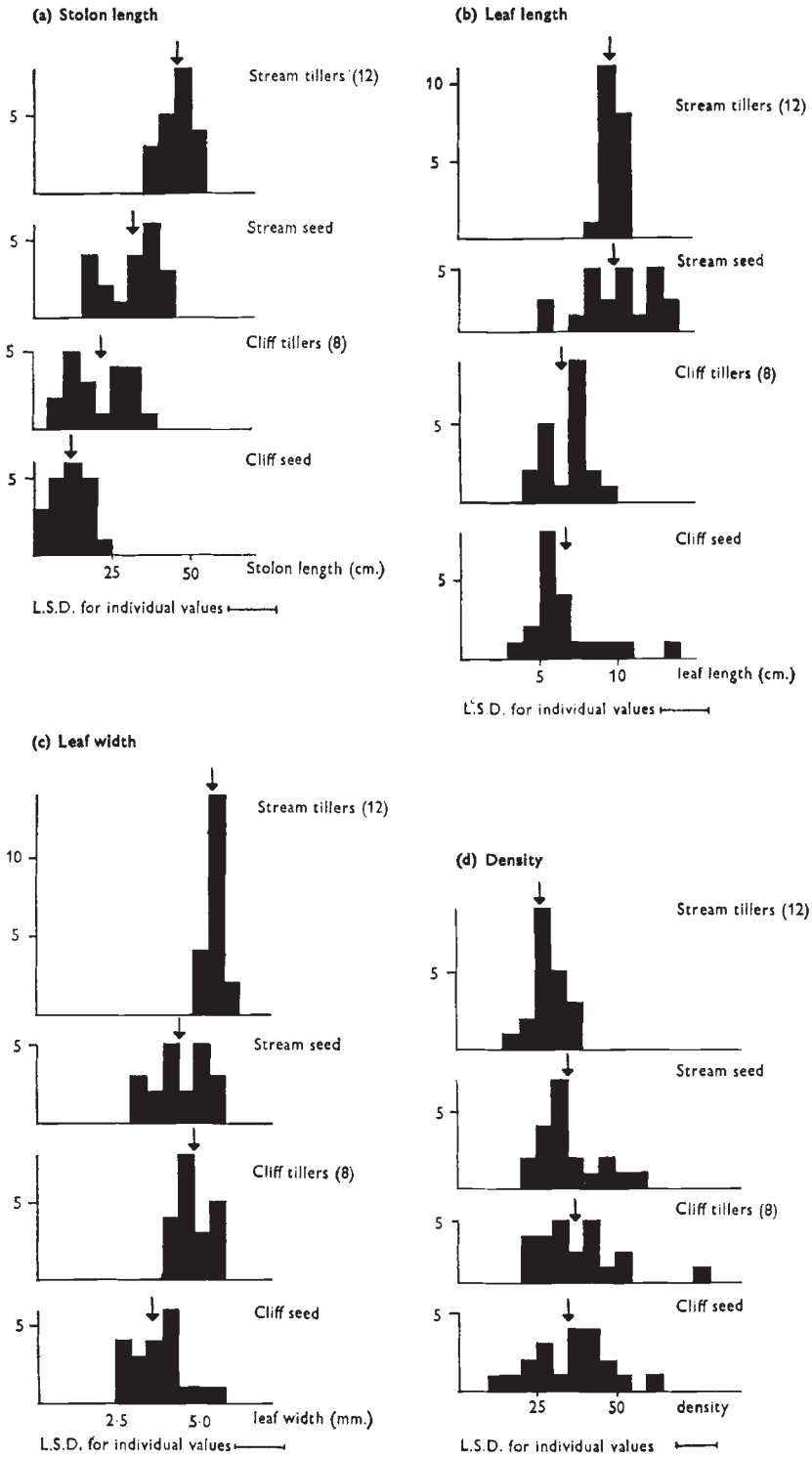
TABLE 3  
*Components of variability of stolon length*

Population	$V_G$	$V_B$	$V_S$	$V_{GB}$
Stream tillers	9.52*	5.00*	16.67	42.36
Stream seed	54.15***	3.87**	14.03	21.56
Cliff tillers	66.7***	-2.42ns	7.60	17.2
Cliff seed	18.73***	2.11*	2.59	7.23

The stolon length results showed that the tiller populations behaved very similarly to the tiller populations in the previous trial. But the stream seedling plants were not in general as long as the tiller plants. Many dwarf forms were found which were often blue-green in colour. The cliff seedling plants were also in general shorter than their parents, and the population contained several extremely weak dwarf plants. Some 25 per cent. of the seedling plants were *Agrostis stolonifera* × *A. tenuis* hybrids. These were vigorous and strong; yet it is surprising that no hybrid plants were found in the natural tiller population. *Agrostis tenuis* and hybrid plants had been noticed nearby.

The leaf length and width measurements showed clearly that while the means of the seedling populations were similar to those of their respective tiller populations, there was much more variation within the seedling populations than the tiller populations. The density measure, although a rough assessment, shows that the seedling populations resemble one another more than the tiller populations. Other discrepancies between tiller and seed populations were noted but were not recorded. Colour differences were again obvious and marked variation between stolon thickness and internode length were seen.





**FIG. 4.**—Histograms of morphological characters in cultivation of two populations from Abraham's Bosom sampled as tillers and as seed.

### (ii) Discussion

The stream population seems to be in an area where gene flow is great. Dwarf cliff plants are about 100 metres away, but as the prevailing wind blows inland from the sea, it is not perhaps surprising that these inland populations get much pollen from the cliff population blown onto them. Further evidence that gene flow has occurred is provided by the occurrence of blue-green seedlings in the stream seed population, although the dominance relationship of this character needs examining.

The reverse, however, does not appear to happen, or at least did not appear to happen in the year of sampling, for the cliff seed population is not longer but shorter than the adult. With pollen flow from the west, the plants may have been pollinated by more consistently dwarf plants further down the cliff to the west. Alternatively, seed production might have been predominantly by the smaller plants of the population.

The seedling populations are generally much more variable than their tiller counterparts. The stream seedling population in particular, is very variable for all characters by comparison with its tiller counterpart. The low proportion of genetic variability (see table 3) in this population tends to suggest that the adult stream tiller population consist of only a very few clones, a situation similar to that reported by Harberd (1961).

The discrepancies between seed and adult samples not only offer evidence for gene flow but also *per contra* evidence for selection. If selection were not acting the adult populations would resemble the seedling populations. Therefore, there must be directional selection counteracting the effects of gene flow, particularly in the stream population. Such selection is directional if we consider individual populations, but it is an example of disruptive selection if we consider the whole complex. Secondly, there must be stabilising selection, maintaining the low level of variability of the adults: this is probably due to the superiority of a few clones in the population, causing them alone to occupy the habitat. In the cliff population the evidence of hybridisation with *Agrostis tenuis* which is not found in the adults is further evidence of stabilising selection. Such evidence for stabilising selection is equivalent to that produced by Weldon (1900) and Cesnola (1907). It is likely to be widespread in plants with strong powers of vegetative propagation, and has recently been shown by Charles (1964).

#### 4. POSSIBLE SELECTIVE FORCES

All the previous evidence points to the existence of strong selective forces, which should be demonstrable. However, the experimental assessment of the effect of ecological factors is fraught with difficulties, so that experiments which can only be pointers to the situation in nature have to be accepted.

(i) *Survival of plants under inland conditions*

The plants of the second population trial were allowed to overwinter. In the early spring it became apparent that there were differences in survival related to the wet and heavy soil conditions of the experimental garden. Survival fitness, scored on a 3, 2, 1, 0 basis, is shown in table 4. Normal inland *A. stolonifera* is well adapted to such conditions, but it is clear that the cliff population is not. This is

TABLE 4

*Fitness of four populations from Abraham's Bosom growing on heavy soil after winter of 1961/2 (maximum score 100)*

	Fitness	S.D.
Cliff top (8)	50.3	17.1
Gradient pasture (5)	98.7	4.8
Sheltered pasture (9)	97.3	5.9
Stream (12)	96.0	7.5

interesting since the conditions were similar to those in pasture habitats of Abraham's Bosom, except that the plants were spaced.

(ii) *Survival of plants under waterlogging*

Material of the cliff and the stream populations from Abraham's Bosom together with two other populations were grown in boxes just covered with water: further material was grown in normally watered

TABLE 5

*Growth of various populations in normal and waterlogged conditions*

Population	Stolon length (cm.)		Fresh weight (gm.)	
	Normal	Pond	Normal	Pond
St Catherine's Hill (down)	76.5	68.0	198.8	50.0
Winchester (ditch)	79.1	91.1	249.4	131.8
Abraham's Bosom (cliff)	30.8	14.8	87.3	15.9
Abraham's Bosom (stream)	83.4	73.3	194.1	63.8
Level of significance of population $\times$ treatment interaction (from analysis of variance log data)	P < 0.001		P n.s.	

boxes alongside. The results (table 5) show that the cliff population was not at all happy in these conditions.

A second experiment was carried out using deeper water. While this does not occur in pasture habitats occupied by *A. stolonifera*, it is very possible in streams where *A. stolonifera* is very common, e.g. at Abraham's Bosom. Unfortunately material from South Stack, a cliff habitat similar and near to that of Abraham's Bosom, had to be used with three other marsh and pasture populations (table 6). This time

the short cliff form died completely, being unable to elongate stolons enough to reach the water surface. The population from arid Breckland conditions behaved similarly to the other long stolon types, and

TABLE 6

*Growth of various populations under 6 in. of water*

Population	Stolon length (cm.)		Fresh water (gm.)	
	Normal	Deep pond	Normal	Deep pond
Hythe (salt marsh)	57.7	57.1	135.7	5.6
South Stack (cliff)	14.0	0.0	63.1	0.0
Cors Gierch (ditch)	75.0	70.4	209.7	20.0
Weeting (heathland)	91.6	92.5	225.6	23.0
Level of significance of population $\times$ treatment interaction (from analysis of variance of log data)	P < 0.001		P < 0.001	

suggest that it is the ability to produce long stolons more than any other character which enables *A. stolonifera* to inhabit wet ditches.

### (iii) Survival of plant under exposure

Winds in coastal regions, particularly on cliff edges etc., are very much stronger than elsewhere. The short tufted growth habit of the cliff populations is assumed to be an adaptation to wind exposure.

TABLE 7

*Tatter flag wear, at 2 ft. above the ground in the Abraham's Bosom sites (number of sq. in. of flag lost in 14 days), and nature of ground surface*

Population	Flag loss (sq. in.)	Nature of ground surface
1. Cliff base	44.41	Bare rock and crevices
2. Stream base	48.69	Bare rock with water trickle
3. Cliff, above 2		Bare rubble and soil
4. Stream	5.46	Mud and shallow water
5. Exposed pasture		Partially bare soil and stones
6. Dry bluff	5.87	Bare rock and soil
7. Wet cliff base	0.36	Bare rock and crevices
8. Cliff top	55.00	Bare rock and soil
9. Sheltered pasture	1.70	Damp soil
10. Wet pasture		Damp soil
11. Exposed pasture		Damp soil
12. Stream	15.84	Mud and shallow water
13. Stream	0.99	Mud
Roof (Bangor)	10.10	

By using tatter flags (Lines, 1957), which accumulate the degree of exposure by the loss of the cotton material of which they are made (table 7), the enormous contrast in the exposure of habitats is very

evident, particularly between habitats 8 and 9. The lack of exposure suggested by the values for habitat 7 was perhaps because local protection during the period of observation, for the vegetation of the area gives indication of severe exposure with some storms. The exposed habitats all tend to be dry and rocky and unsuitable for rooting of

TABLE 8

*Loss of weight of artificial plants made of paper in strong air stream*

Strip length (cm.)	Strip number	Per cent. loss (weight)
80	8	61.5
40	16	34.3
10	64	15.5
Level of significance of differences due to length (from analysis of variance)		$P < 0.01$

stolons (table 7). This is added reason why the populations of these sites should have short stolons.

However, it is dangerous to presume that short stolons are an adaptation to exposure without experimental proof. To test this, plants of contrasting growth form, representing cliff and pasture types, were simulated from 4 mm. wide strips of tissue paper. The same

TABLE 9

*Stolon length of various populations remaining after exposure to storm conditions (mean of three occasions)*

Site	Per cent. remaining after exposure
Newborough Warren (dunes)	84.5
Abraham's Bosom (stream)	77.5
Abraham's Bosom (cliff)	105.0
Bangor (weed)	79.3
Level of significance of population differences (from analysis of variance)	$P < 0.001$

quantity of paper was used to make paper models representing either cliff plants—a large number of short pieces, or pasture plants—a smaller number of longer pieces. These plants were subjected to a wind speed of 25 metres per sec. for a short period and the damage was assessed by loss of material (table 8). Clearly, the longer models, representing plants of the inland pasture growth habit, are damaged far more severely by wind than the shorter models, representing plants of the cliff growth habit.

In a second experiment the effect of exposure on the length of live

stolons of actual plants was investigated. Plants of four populations were exposed on a roof top in Bangor during a period of strong winds; two other sets were exposed later in other periods. Although the general level of exposure indicated by tatter flag loss (table 7) was not as great as at Abraham's Bosom, considerable damage was done to the plants (table 9). Only the cliff population was not damaged by the exposure, and indeed, managed to continue normal growth. The other populations all suffered damage even though the periods of exposure were only about a fortnight. Subsequently one set of plants was left out the whole winter. At the beginning of spring the long stolon types were nothing but scraggy tufts, alive but very reduced in size. By contrast the cliff population showed little damage to its stolons; further tillering had occurred so that the plants were of the same "hedgehog" shape as in their natural habitats.

### 5. CONCLUSIONS

Natural situations provide a great range of very different environments. Some of these are represented by the great climatic regions of the world. Some however are represented by the very local variations in topography, soil, etc., which cause very localised environments. Although some regions of the world are so uniform that such localised environmental variation does not exist, in most regions such variation is commonplace.

A species faced with such conditions may remain restricted to one particular environment. Other species however may possess (a) the phenotypic flexibility (Thoday, 1953) or (b) the genetic variability to permit it to invade several of the localised environments. Although phenotypic flexibility permits a species to occupy a number of environments without genetic change, genetic variability can permit occupation of several environments only if differentiation of distinct populations occurs.

It has been argued (Jain and Bradshaw, 1966) that such differentiation of localised populations is dependent on the outcome of the interplay of natural selection and gene flow. Over short distances gene flow is likely to be high and differentiation seems therefore unlikely. Yet much local variation in environment is over short distances. It might be considered possible that evolution of localised populations cannot be part of the processes of adaptation of a species to such environmental variation. The data presented suggest that this is not so. Highly localised differentiation can clearly occur, brought about essentially by the impact of high selection pressures. Despite high levels of gene flow, the selection pressures determined experimentally seem on theoretical grounds to be adequate to explain the differentiation found; this is shown by a comparison of the findings given here with the theoretical analysis given previously.

*Agrostis stolonifera* is, however, strongly perennial. A perennial growth habit means that replacement by new seedlings is less frequent

than in an annual species, and that selective forces can accumulate on individual genotypes over many years. This means that ultimate coefficients of selection for individual genotypes, if they could be calculated, must be very high indeed, higher than those suggested by simple experiments done over short periods in the absence of competition. At the same time individuals of the species can spread from their point of origin by purely vegetative means into new habitats, thereby evading problems of gene flow altogether. These two aspects of perenniality must contribute considerably to the occurrence of some of the very highly localised populations, *e.g.*, in the stream at Abraham's Bosom.

Similar patterns of differentiation in parapatric situations are now becoming apparent in other perennial grasses (Jain and Bradshaw, 1966), and it is likely that they will be found to be commonplace. But it would be dangerous to speculate that such localised differentiation could not also occur in annual species. We are only now beginning to appreciate the intensity of selective forces into natural conditions, and surprising results appear (*e.g.*, Allard and Workman, 1963). In animals we have already seen that localised differentiation is possible not only in relatively sedentary species such as *Cepea memorialis* (Sheppard, 1952) but also in more mobile species such as *Maniola jurtina* (Creed, Ford and McWhirter, 1964).

It was suggested (Jain and Bradshaw, 1966) that the situation in nature is not as straightforward as that analysed by a simple two environment model. The situation in Abraham's Bosom readily demonstrates this. The three transects, although they are all in close proximity, are all entirely different. It would be bold to describe such a pattern of differentiation in taxonomic terms (Bradshaw, 1962). If any description is necessary it is only possible to say that these are a series of parapatric populations showing a graded patchwork of differentiation.

The overall picture of evolutionary differentiation in *Agrostis stolonifera* suggests a very effective species/environment strategy. Within the confines of various edaphic limitations which it cannot overcome, it occupies a wide range of habitats. It can be argued that it is only enabled to invade some of these by the evolution of distinct populations. Certainly, typical pasture forms are unlikely to be able to survive any length of time in exposed maritime situations and vice versa. The ability of *A. stolonifera* to differentiate on such a local scale is therefore not only an effective means of increasing its overall fitness but also its general range. Such evolutionary change is not only adaptive, it is also permissive.

## 6. SUMMARY

1. Populations of *Agrostis stolonifera* from maritime habitats were examined as spaced plants in cultivation.
2. The degree of exposure of the populations was related to the length of stolon growth.



3. Sampling of one region showed marked differentiation within an area of only 2 hectares, related to the local environments, particularly to exposure. Both a sharp discontinuity between two extreme types and a gradual ecocline were found.

4. Natural seed from two neighbouring contrasted populations showed that the plants produced deviated from the parents in a manner suggestive of gene flow between populations.

5. Ecological experiments on contrasting populations revealed a very different tolerance of conditions of waterlogging, exposure, etc. These suggest that high coefficients of selection are operating in the natural habitats of *A. stolonifera*, sufficient to initiate the differentiation of the populations, and to maintain it against considerable gene flow.

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