

# ADAPTATION IN THE REPRODUCTIVE PERFORMANCE OF *Phleum alpinum* L. AT A SUB-ANTARCTIC STATION

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**ABSTRACT.** Investigations were undertaken into phases of the life cycle of *Phleum alpinum* growing *in situ* on South Georgia to provide comparisons between widely differing micro-environments. The flowering tiller performance showed that the time needed for complete development was similar in differing habitats and that this stabilization of overall performance was achieved by differentiation of contributory processes. Vegetative reproduction proved to be very similar at the various sites but reproduction by inflorescences, as assessed by seed and floret numbers per flowering tiller and per unit ground area, were generally negatively correlated with habitat severity. Comparisons of reproduction by inflorescences at the various sites also indicated the existence of compensatory mechanisms aimed at the stabilization of development at the various sites. Seed germination trials showed that vernalization treatments were unimportant and that the seeds, although capable of germinating at low temperatures, germinated earlier at higher temperatures. Between-site comparisons of tiller dry weights and living biomass gave some assessment of the success of the developmental and reproductive phases in maintaining plant populations under contrasting environmental conditions; they were found to be negatively correlated with habitat severity and to be generally low in comparison with Arctic and alpine regions.

THE paucity of polar terrestrial vegetation and the low levels of primary productivity are evidence of the fact that the environmental complex of polar regions imposes severe limitations on plant growth and survival. Within these regions, however, great variation in aerial and edaphic micro-climates is found (Wilson, 1966; Lewis and Greene, 1970). This produces a variety of stresses which may differentially select for plant responses.

The present study of the patterns of variation between populations of the same species growing in contrasting habitats concentrates on two of the basic factors important to plant survival, that is, growth as expressed by dry-matter accumulation and reproductive performance. A detailed consideration of these factors is essential to a fuller understanding of the modes of adaptation of plants to environmental extremes and also of the component processes involved in primary production. Comparisons of biomass and reproductive capacities per unit ground area in the various habitats allows some assessment of the "fitness" of the plants, that is, their ability to contribute to the next generation (Thoday, 1953), as well as the integrated efficacy of the individual processes involved in growth and reproduction (Harper, 1967).

The present investigations were carried out on tetraploid *Phleum alpinum* L. (= *P. commutatum* Gaud.) growing naturally in the vicinity of Grytviken, South Georgia (lat. 54°17'S., long. 36°31'W.). On this island, *P. alpinum* exhibits a wide ecological tolerance, being found in most of the habitats capable of supporting vascular plant growth.

## SITE DESCRIPTIONS

The behaviour of *Phleum alpinum* was studied in detail at four sites representative of its ecological range on South Georgia. The main environmental features of the study sites, together with their floristic composition, are presented in Tables I and II.

It can be seen from Tables I and II that increase in altitude is associated with an increase in wind exposure, a deterioration in soil quality and the gradual reduction in the number of species until at the highest altitude the vegetation is restricted to a few hardy species, most of which are cryptogamic. In contrast to most of the island's other vascular species, which show a rapid decline in frequency of occurrence with altitude, *P. alpinum* remains an important element in the vegetation even at the most exposed situations.

## OUTLINE OF REPRODUCTIVE CYCLE

During winter, *P. alpinum*, on South Georgia, in Scotland (Gregor, 1931) and presumably elsewhere, undergoes a period of dormancy which is quickly broken by the retreat of over-

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TABLE I. DESCRIPTION OF *Phleum alpinum* STUDY SITES

	<i>Whaling station</i>	<i>Phleum sward</i>	<i>Rostkovia flush</i>	<i>Fell-field</i>
Locality	Paths around buildings Grytviken	South shore of King Edward Cove	Behind whaling station Grytviken	North shore of Gull Lake
Altitude (m.)	4	10	20	100
Aspect and slope	Level ground	North-facing; 30°	North-facing; 20°	Exposed top of small hill
Insolation	Low to normal, variable	High	High	Normal
Wind exposure	Low	Moderate	Moderate	High
Soil description	Enriched soil, drained	Black peat, well-drained	Brown peat, flushed	Gravelly, dry

TABLE II. PERCENTAGE FREQUENCY IN 50 RANDOMIZED 25 cm. BY 25 cm. QUADRATS OF *Phleum alpinum* AND ASSOCIATED SPECIES AT THE SOUTH GEORGIA STUDY SITES

	Whaling station	Phleum sward	Rostkovia flush	Fell-field
<i>Cerastium fontanum</i>	46	—	—	—
<i>Acaena decumbens</i>	54	88	100	—
<i>A. tenera</i>	—	—	—	2
<i>Galium antarcticum</i>	—	—	86	—
<i>Rostkovia magellanica</i>	—	—	100	—
<i>Uncinia smithii</i>	—	—	4	—
<i>Festuca erecta</i>	22	96	6	—
<i>Poa flabellata</i>	—	2	—	—
<i>P. annua</i>	92	—	—	—
<i>P. pratensis</i>	12	—	2	—
<i>Deschampsia antarctica</i>	86	6	—	24
<i>Phleum alpinum</i>	100	96	88	58
<i>Polytrichum alpinum</i> Hedw.	—	—	—	10
<i>P. piliferum</i> Hedw.	—	—	—	100
<i>Ceratodon</i> cf. <i>grossiretis</i> Card.	—	2	—	—
<i>Dicranoweisia</i> sp.	—	—	—	24
<i>Tortula robusta</i> Hook. & Grev.	2	—	100	—
<i>Grimmia</i> sp.	—	—	—	4
<i>Racomitrium</i> sp.	—	—	—	6
<i>Bryum</i> sp.	34	—	—	—
<i>Marchantia berteroana</i> Lehm. & Lindb.	7	—	—	—
Lichens	—	—	—	28

— Denotes the absence of the species.

Nomenclature of phanerogams follows Greene (1964, 1969).

lying snow. Flowering tillers are produced after floral initiation in vegetative tillers at least 1 year old, which is in agreement with Nordenskjöld's (1945) findings that inflorescences are only produced in the second year of growth. A flowering tiller may be readily distinguished in the field at an early stage as it comprises an elongated culm bearing leaves which decrease in size from the base to the top, rather than increasing as in the case of vegetative tillers; in addition, the long in-rolled uppermost leaf, always present in vegetative tillers, is absent in flowering ones.

Growth of the inflorescence takes place inside the youngest leaf sheath which is itself developing inside the sheath of the next youngest leaf; inflorescences reach maximum size

whilst still within the sheath. Elongation of the uppermost culm internode, which takes place very slowly during the growth of the inflorescence, now accelerates, pushing the inflorescence out of the sheath and raising it above the level of the leaves (Fig. 1).

Anther exertion and anthesis start in late summer after the main phase of culm elongation has occurred. Following anthesis, the leaves on the flowering culm begin to die. On South Georgia, seed appears to be set only a short time before the establishment of winter snow, whilst in years with particularly adverse climatic conditions seed may not be set at all. It is assumed that germination occurs in the spring and dormancy during the winter is probably environmentally imposed, there being no evidence for any inherent dormancy system in seed of *Phleum alpinum* (Bliss, 1958; see below).



Fig. 1. Developmental stages of flowering tillers of *Phleum alpinum*.

- a. Inflorescence enclosed in upper culm leaf sheath (the stage at which observation commenced).
- b. Inflorescence emergent.
- c. Inflorescence fully emerged on elongated culm.

#### BEHAVIOUR OF FLOWERING TILLERS

##### *Elongation of culm*

Before pollination the inflorescence is usually carried clear of the surrounding vegetation, mainly by the elongation of the youngest culm internode. The rate of elongation of this internode was compared at the *Phleum* sward, *Rostkovia* flush and fell-field by measuring to the nearest millimetre the internodes of 25 widely spaced flowering tillers growing *in situ* at each site. Initially, all 25 tillers were matched at the same developmental stage, that is, when the inflorescence was only partially protruding through the youngest leaf sheath (Fig. 1a). Observations were taken at intervals of a few days between 24 January and 21 March 1968 at the *Rostkovia* flush and fell-field sites and between 12 February and 19 March 1968 at the *Phleum* sward site.

Mean internode length, with the standard deviation of the mean for each site, is plotted against time in Fig. 2. It can be seen that elongation at the *Rostkovia* flush and *Phleum* sward sites resulted in a greater mean internode length than at the fell-field. The initial rate of elongation, however, was very similar at all three sites, despite the fact that elongation was measured from a later starting date at the *Phleum* sward. The reduced final length of the youngest internode of the flowering culm at the fell-field means that elongation takes place here in a shorter time than at the other two sites.

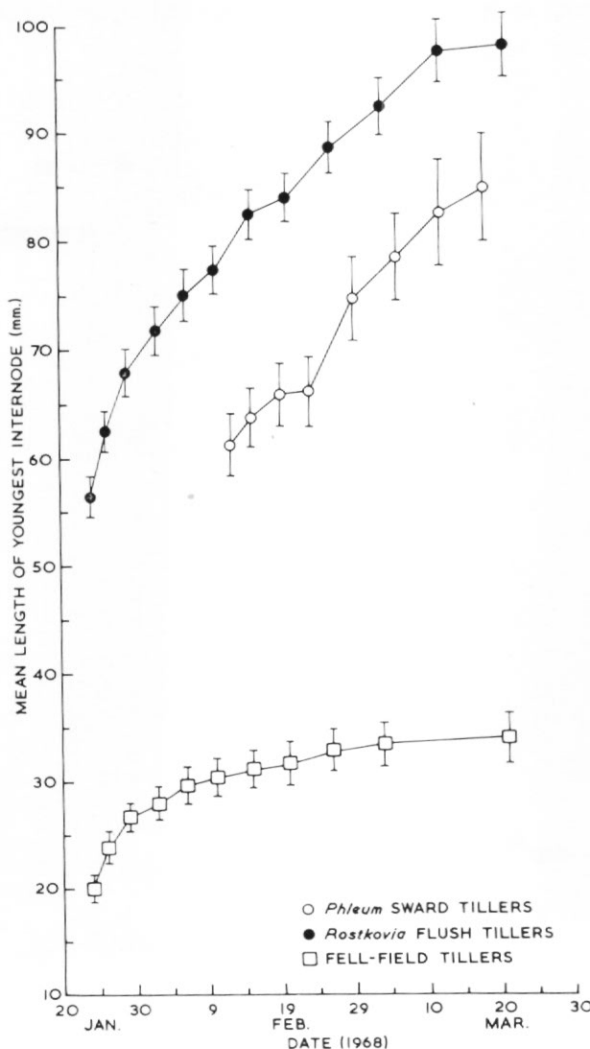


Fig. 2. Increase with time in youngest internode length, at three sites. Vertical lines indicate a 0.5 standard deviation on either side of the mean.

#### *Inflorescence maturity*

Concurrently with the assessment of internode elongation, observations were made on the stages of maturity attained by the inflorescences of the same tillers. These tillers were scored according to the following index comprising five categories of anther exertion:

0. No anther exertion visible.
1. Up to 25 per cent of the inflorescence in or past anther exertion.
2. Between 26 and 50 per cent of the inflorescence in or past anther exertion.
3. Between 51 and 75 per cent of the inflorescence in or past anther exertion.
4. Above 76 per cent of the inflorescence in or past anther exertion.

Means of the maturity indices were calculated for each site and are plotted against time in Fig. 3. Although environmental conditions were very different at the fell-field, *Rostkovia* flush and *Phleum* sward, maximum anther exertion was attained over the same time interval, with the rate of increase in the percentage of the florets in or past anther exertion being very similar at all sites.

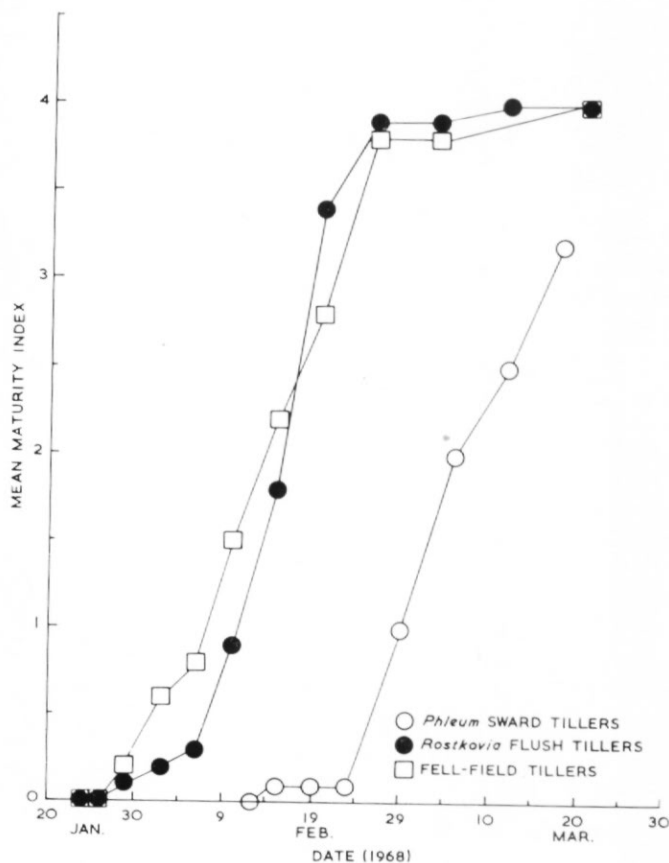


Fig. 3. Increase with time in mean inflorescence maturity index at three sites.

#### *Culm leaf senescence*

Field observations indicated that the leaves of flowering tillers often died before the inflorescence reached maturity. Quantitative estimates of the rate of death were obtained by recording the date on which half or more of the blade area of the youngest culm leaf was discoloured or dead. Means for the number of leaves at this stage on the same tillers as used in the maturity assessments are plotted against time in Fig. 4. It can be seen that death of the youngest leaf proceeded more rapidly at the fell-field than at the *Rostkovia* flush or *Phleum* sward. It can also be seen that, whereas all the youngest leaves of the fell-field flowering tillers were dead when observations ceased, many were still alive at the other two sites at the same late stage in the growing season.

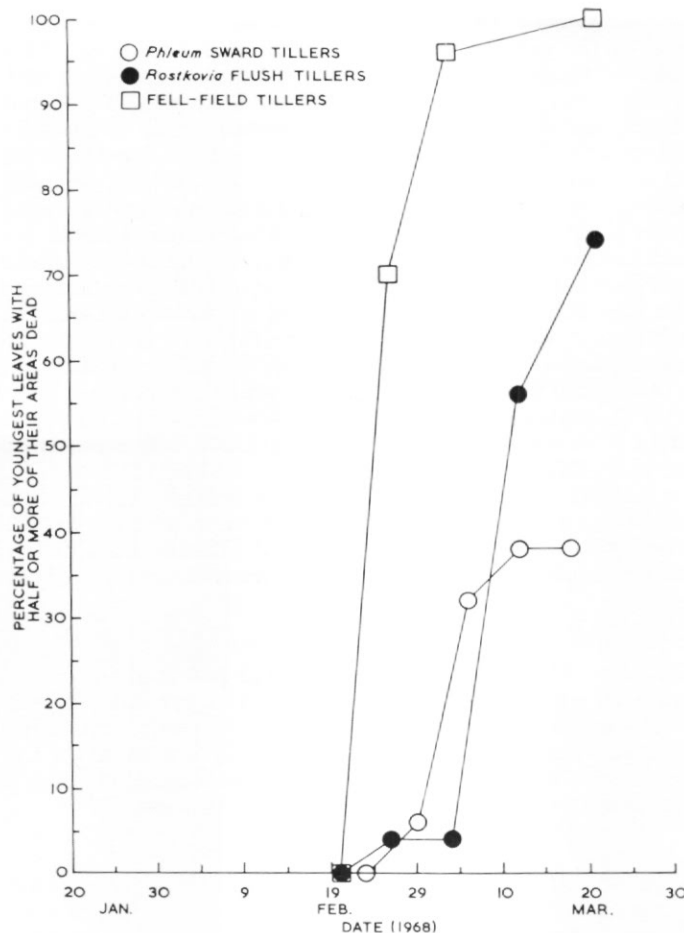


Fig. 4. Increase with time in the percentage of youngest culm leaves, with half or more of their blade area dead.

Some indication of the extent to which senescence in the youngest culm leaf is representative of parallel changes in the remaining leaves on the flowering tillers is provided by a comparison of the total number of living leaves per tiller assessed at the beginning and end of the observations (Table III). Although the data are fragmentary, it is clear that the older leaves on the flowering tillers followed a pattern similar to that of the youngest leaf.

TABLE III. MEAN NUMBER OF LIVING LEAVES PER FLOWERING TILLER OF *Phleum alpinum* AT THE BEGINNING AND END OF THE REPRODUCTION OBSERVATIONS

	<i>Rostkovia</i> <i>flush</i>	<i>Phleum</i> <i>sward</i>	<i>Fell-</i> <i>field</i>
24 January 1968	4.4	—	2.9
12 February 1968	—	3.9	—
18 March 1968	—	1.5	—
21 March 1968	1.2	—	0.0

*Dry-matter partitioning*

Towards the end of the growing season (11 March 1968) between 32 and 50 flowering tillers were collected at random within the same quadrats as used in the floristic analysis (Table II). Each tiller was divided into inflorescence, stem and non-photosynthetic leaf sheaths, photosynthetic leaf parts, root system and standing dead, the fractions being dried at 80° C and weighed to the nearest 0.0001 g. Mean inflorescence dry weight was calculated and compared between sites. In addition, the investment of dry weight by the tiller into its inflorescence, i.e. proportional partitioning, was assessed by calculating the ratio of inflorescence dry weight to the dry weight of the whole tiller excluding standing dead.

Analyses of variance were carried out on the results for the above parameters, the within-population variance estimate being used in "t" tests to determine the significance level of differences between population means. The results are presented in Table IV.

It can be seen from a comparison of the data in Table IV that inflorescence dry weight falls into three classes. Inflorescences from the whaling station population gave the highest mean dry weight, those from the fell-field the lowest, whilst the inflorescences from the *Phleum* sward and *Rostkovia* flush sites gave intermediate values which were not significantly different. A somewhat different relationship between the populations becomes evident when the proportional partitioning of dry matter between the inflorescence and the rest of the flowering tiller is considered. The greatest dry weight investment was made by the fell-field tillers, those at the whaling station having a lower value. Although the mean absolute dry weights of inflorescences at the remaining two sites were not statistically different, the *Rostkovia* flush inflorescences represent a significantly smaller dry weight investment than those of tillers in the *Phleum* sward.

*Number of florets and seeds*

The number of florets and seeds per inflorescence was also counted for a sub-sample of 12 inflorescences from each site. The mean number of florets per inflorescence (Table IV) was found to be positively associated with the dry weight of the inflorescence. However, the mean number of seeds per inflorescence showed an unexpectedly low value for the whaling station population. This is possibly explained by differences in the average maturity of inflorescences, in this case, between the whaling station and the other three sites.

## VEGETATIVE REPRODUCTION

Many workers (Löve, 1959; Billings and Mooney, 1968) have shown that vegetative reproduction is of prime importance in polar regions where conditions may be too severe in some growing seasons for reproduction by seed to be effected. The absence of seedlings in the field, although only assessed on subjective observations, indicates the importance of vegetative propagation in this species on South Georgia.

Daughter tillers arise from nodes at the junction of the rhizome and aerial stem, from the activities of a lateral meristem which develops inside an old leaf sheath, the latter being eventually ruptured by the growing lateral shoot (Fig. 5). After the expansion of two or three leaves, the daughter tiller develops its own root system from the node at the point of attachment to its parent tiller. Following the interpolation of rhizome internodes by the daughter tiller and/or the parent tiller, together with the decay or fracture of one of these, organic connection is broken and propagation effected.

The ability of plants to produce lateral tillers was investigated by counting the number of rootless daughter tillers attached to each of a sample of primary tillers. Counting was undertaken on the same flowering tillers used in the analysis of inflorescence reproduction and on an equal number of vegetative tillers collected from the same quadrats. The results are presented in Table IV.

It can be seen that the number of rootless daughter tillers attached to flowering tillers at the end of the season does not vary significantly between the populations, whereas the number of these tillers attached to vegetative tillers at the *Rostkovia* flush site is significantly less than the numbers attached to vegetative tillers at the other sites. It is also evident that the mean number of daughter tillers per flowering tiller was higher than that for vegetative tillers at all sites.

Although the values for the mean number of daughter tillers per parent tiller were low, it



TABLE IV. BETWEEN-SITE COMPARISONS OF FLOWERING TILLERS AND VEGETATIVE REPRODUCTION IN *Phleum alpinum*

	<i>Whaling station</i>	<i>Phleum sward</i>	<i>Rostkovia flush</i>	<i>Fell-field</i>	<i>Least significant difference</i>		
					For $P \leq 5\%$	For $P \leq 1\%$	For $P \leq 0.1\%$
Mean dry weight of inflorescence (mg.)	113.2	82.7	80.0	19.4	12.3	16.2	20.7
Mean $\frac{\text{dry weight of inflorescence}}{\text{dry weight of whole tiller}}$	0.274	0.218	0.183	0.388	0.020	0.027	0.034
Mean number of florets per inflorescence	265	176	202	77	43	57	73
Mean number of mature seeds per inflorescence	48	103	67	22	52	69	88
Mean number of rootless daughter tillers per parent flowering tiller	0.7	0.8	0.8	0.8	0.33	0.43	0.55
Mean number of rootless daughter tillers per parent vegetative tiller	0.3	0.5	0.1	0.4	0.26	0.34	0.43

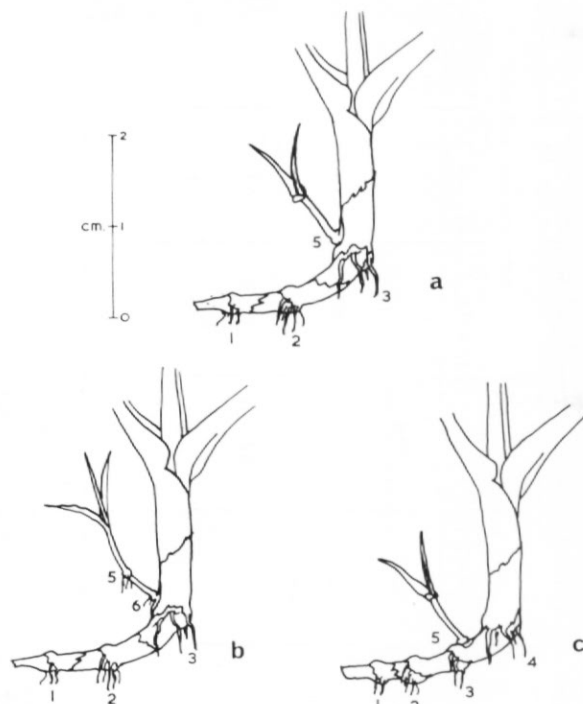


Fig. 5. Stages in the production of daughter tillers in *Phleum alpinum*.

- a. Parent tiller with young lateral lacking roots.
  - b. Parent tiller with young lateral with interpolated internode (5-6) bearing roots.
  - c. Parent tiller with interpolated internode (3-4) and young lateral lacking roots.
- 1-6 Nodes.

should be borne in mind that they include only daughter tillers without roots. It is likely that a proportion of the rooted daughter tillers had also been produced within the current growing season, although an estimate of actual numbers was not possible owing to the difficulty of distinguishing these from rooted daughter tillers of previous years.

#### REPRODUCTIVE CAPACITY PER UNIT GROUND AREA

The parameters of seed and vegetative reproduction already considered give some estimate of the performance of individual tillers at the various sites. However, the successful maintenance and growth of a population depends not only on the performance of individual tillers but also on its size and tiller density, as well as the number of propagules produced per unit area (Harper, 1967). The reproductive capacity in the sense of Salisbury (1942, 1961), i.e. the average annual output of propagules with regard to their normal viability on a ground area basis, was estimated from the product of the mean number of seeds or daughter tillers per primary tiller and the tiller density per population as given in Table IV. Tiller density was obtained by counting the number of both vegetative and reproductive tillers in each of 50 randomized 25 cm. by 25 cm. quadrats per site. At sites where clumping occurred the number of tillers per clump and the number of clumps/m.<sup>2</sup> were estimated for the same quadrats. The results are presented in Table V.

The data show that the whaling station population had the largest reproductive capacity by seed, resulting mainly from a high tiller density, the number of seeds per inflorescence being very low. Seed capacity at the *Phleum* sward reflects both high density and increased seed output per inflorescence, whilst the low level at the fell-field is due to reduction in both seed output and tiller density.

TABLE V. A COMPARISON BETWEEN POPULATIONS OF REPRODUCTIVE CAPACITIES PER UNIT GROUND AREA OF *Phleum alpinum*

	<i>Whaling station</i>	<i>Phleum sward</i>	<i>Rostkovia flush</i>	<i>Fell-field</i>
Number of florets/m. <sup>2</sup>	68,900	9,574	4,141	963
Number of mature seeds/m. <sup>2</sup>	12,480	5,603	1,373	275
Number of daughter tillers/m. <sup>2</sup>	>482	>168.5	29.7	50.2
Number of quadrats (m. <sup>2</sup> ) per site	50	50	50	50
Number of flowering tillers/m. <sup>2</sup> (with standard error)	260.0	54.4 ± 8.0	20.5 ± 3.4	12.5 ± 4.3
Number of vegetative tillers/m. <sup>2</sup> (with standard error)	>1,000	>250	133.4 ± 15.1	100.5 ± 20.3
Total number of tillers/m. <sup>2</sup> (with standard error)	>1,260	>304	153.9 ± 17.3	113.0 ± 23.9
Tiller distribution	Clumped	Non-clumped	Non-clumped	Clumped
Number of tillers per clump	>30	—	—	8.4
Clumps/m. <sup>2</sup>	16.8	—	—	15.7

Table V also shows that the mean number of daughter tillers/m.<sup>2</sup> is more related to density than to the number of daughter tillers per plant. Except for the *Rostkovia* flush, the values of vegetative reproductive capacity follow the same pattern between populations as the seed capacity. It can be seen that the highest reproduction was at low-altitude sites which were sheltered, well-drained and with high, sometimes enriched, nutrient status.

#### SEED GERMINATION

The effectiveness of reproduction by seed will depend to a great extent on the proportion which is viable and therefore capable of germination. Experiments were carried out at Birmingham in constant-environment chambers to investigate the effect of certain environmental factors on the rate and percentage (i.e. viability) of germination. These factors were:

- i. The temperature of vernalization.
- ii. The duration of vernalization.
- iii. The temperature during germination.

Seeds of approximately 100 inflorescences were collected at random on 26 March 1968 from the *Phleum* sward site, and after being homogenized were stored at room temperature for 9 months. The seeds were vernalized dry, preliminary trials having indicated that wet vernalization did not improve the rate or percentage of germination. Vernalization was undertaken at  $-5^{\circ}$  and  $-15^{\circ}$  C for 2, 4 and 8 weeks on 50 seeds per treatment. The seeds were sown on moist filter paper in petri dishes and tested for germination at  $5^{\circ}$ ,  $10^{\circ}$ ,  $20^{\circ}$  and  $25^{\circ}$  C under a 16 hr. photoperiod provided by mercury vapour lamps. The number of seeds germinating was recorded daily, the results being presented in Tables VI and VII, and Fig. 6.

TABLE VI. FINAL PERCENTAGE GERMINATION AFTER 48 days FROM SOWING

Vernalization treatments	Germination temperatures ( $^{\circ}$ C)			
	5	10	20	25
None	34	14	36	32
2 weeks at $-5^{\circ}$ C	44	52	38	30
4 weeks at $-5^{\circ}$ C	22	24	34	22
8 weeks at $-5^{\circ}$ C	—	32	14	34*
2 weeks at $-15^{\circ}$ C	36	14	52	40
4 weeks at $-15^{\circ}$ C	32	26	44	30

\* After only 20 days.

TABLE VII. NUMBER OF DAYS BETWEEN SOWING AND GERMINATION OF THE FIRST SEED

Vernalization treatments	Germination temperatures ( $^{\circ}$ C)			
	5	10	20	25
None	26	13	5	5
2 weeks at $-5^{\circ}$ C	18	13	6	5
4 weeks at $-5^{\circ}$ C	16-18	8-14	4	6
8 weeks at $-5^{\circ}$ C	—	9-11	6	5
2 weeks at $-15^{\circ}$ C	20	13	6	5
4 weeks at $-15^{\circ}$ C	22	14	5	6

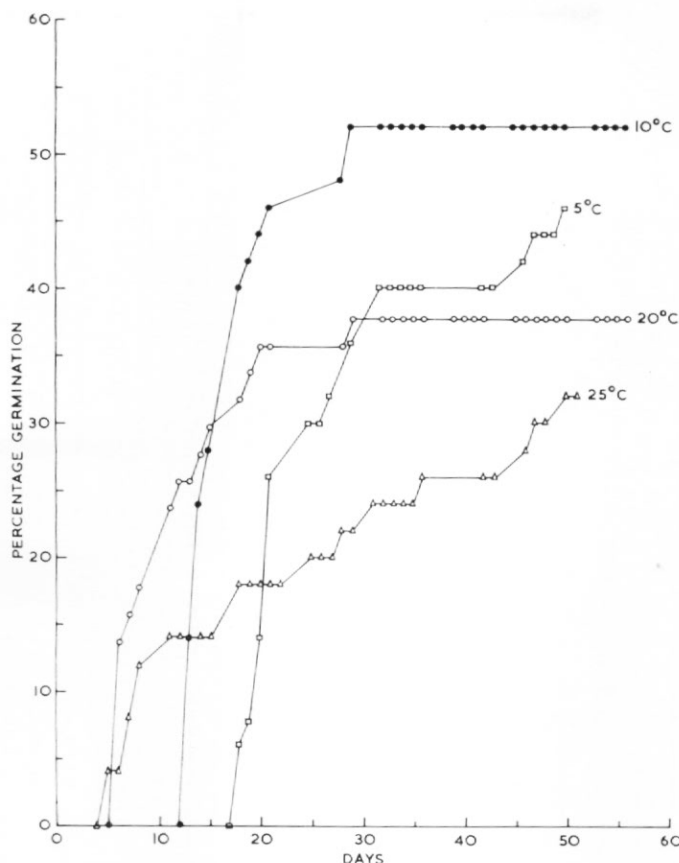


Fig. 6. The effect of different temperatures on the germination of *Phleum alpinum* seed after vernalization for 2 weeks at  $-5^{\circ}\text{C}$ .

From Table VI it can be seen that the temperature of vernalization, as well as its duration, had very little effect on the final percentage germination at the end of the experiment, 48 days after sowing; the final percentage was also unaffected by the temperature of germination. However, from Table VII and Fig. 6 it can be seen that the onset of germination is clearly correlated with temperature but is independent of the vernalization pre-treatments. Thus the period between sowing and onset of germination decreases with increase in temperature up to an optimum of about  $20^{\circ}\text{C}$ .

#### BIOMASS

Within a species, biomass values are to some extent a reflection of the overall success of the growth and reproductive processes involved in the maintenance of populations in different environments. Biomass, on a ground-area basis, was calculated from the product of mean tiller dry weight per population and tiller density, using estimates of the mean dry weight of flowering and vegetative tillers from the four study sites.

From Table VIII it can be seen that the mean dry weight of flowering tillers is greater than that of vegetative tillers, although in the case of the fell-field the difference is not significant. The mean dry weight of fell-field vegetative tillers is the lowest of the four populations, whilst the highest values were obtained at the *Phleum* sward and whaling station sites. Mean dry weight of flowering tillers was greatest at the *Rostkovia* flush and lowest at the fell-field.

TABLE VIII. MEAN TILLER DRY WEIGHTS AND BIOMASS OF *Phleum alpinum* AT STUDY SITES

	<i>Whaling station</i>	<i>Phleum sward</i>	<i>Rostkovia flush</i>	<i>Fell-field</i>	<i>Least significant difference*</i>		
					For $P \leq 5\%$	For $P \leq 1\%$	For $P \leq 0.1\%$
Mean dry weight per flowering tiller (g.)	0.417	0.359	0.428	0.048	0.053	0.070	0.089*
Mean dry weight per vegetative tiller (g.)	0.238	0.266	0.181	0.039	0.053	0.070	0.089
Total dry weight of living matter/m. <sup>2</sup> (g.)	>300	>80	32.92	4.52	—	—	—

\* These values may also be applied to weight differences between flowering and vegetative tillers.

The decrease of biomass with increasing severity of the habitat follows the same pattern as reproductive capacity. The 7-fold difference in biomass between the fell-field and *Rostkovia* flush site can be attributed mainly to differences in mean tiller dry weight, as densities did not differ greatly (Table 1). On the other hand, the 70-fold difference in biomass between the fell-field and the whaling station sites, is the result of large differences in both tiller dry weight and density.

#### DISCUSSION

The data presented indicate that, although environmental differences between the habitats have resulted in some morphological differentiation, critical stages in the reproductive cycle, namely internode elongation of the flowering culm and the period of maximum anther exsertion are relatively synchronous at the various sites. Although the period of flowering for a population may last longer at a more favourable site, the duration of the development of an individual flowering tiller is very similar at all the sites.

One of the ways in which comparability between the fell-field and the other sites has been attained is by the great reduction in the final length of the youngest internode at the former. This will reduce the amount of dry matter incorporated into the youngest internode and may facilitate an earlier switch to floret and seed development. In addition, the more abrupt death of the leaves on the flowering tillers at the fell-field may be the result of the re-mobilization of metabolic substrates and their re-direction into seed development. Thus the stages of maximum internode length and maximum maturity index at the relatively favourable *Rostkovia* flush and *Phleum* sward sites, and at the more severe fell-field, were attained over comparable time intervals, i.e. stabilized by a number of compensatory mechanisms involving contributory processes.

It can be argued that the comparability of the time taken for the development of reproductive structures at the different sites is imposed by the shortness of the growing season in that this development must meet a "deadline". Sørensen (1941) has shown an extreme example of developmental adaptation to the very short growing season of north-east Greenland where, in many species, floral initiation takes place in the year preceding flowering. This enables the remaining developmental phases to be completed in a very short period beginning as soon as conditions are favourable. No data are at present available for the time of floral initiation in *P. alpinum*.

The between-site differences in floret and seed production can also be interpreted as adaptations to environmental inequalities. In general, the number of seeds and florets was found to decrease with increasing severity of the habitat; this is in agreement with results presented by Bliss (1956), who found that flowering intensity and seed production decreased with increasing severity of the micro-environment. The reduction in floret and seed numbers may be a further compensatory mechanism aimed at stabilizing this part of the life cycle. At all sites, florets and seeds must attain a minimum dry weight and size in order to be fully functional, although there may be considerable differences between sites in the amount of dry matter available for growth of the reproductive structures of a particular plant. Attainment of this weight and size has been facilitated at the more severe fell-field by modification of a number of contributory parameters, inflorescences being smaller with fewer florets and hence fewer seeds. In other words, the smaller amount of available dry matter is partitioned between fewer "sinks", each of which is thus capable of maintaining the rate of growth necessary for the production of functional florets and seeds. Furthermore, the inflorescences although smaller actually represent a greater proportional dry-weight investment than at the more favourable sites, an additional partitioning within the plant which reinforces the first modification and may be considered as a further mechanism aimed at ensuring the success of the reproductive cycle.

The large differences observed between the sites in the number of florets and seeds produced/m.<sup>2</sup> of ground are due to inequalities in both the density of reproductive tillers and the number of seeds per inflorescence. Although the overall picture is complex, there is a tendency for the more severe habitats to have lower tiller densities with fewer florets and seeds per inflorescence, thus resulting in lower reproductive capacities as expressed on a ground-area basis.

Differences in vegetative reproduction between the various sites closely parallel floret and seed capacities. Vegetative reproductive capacity per unit ground area is higher at the more

favourable sites but this is mainly a reflection of differences in tiller density. There is some evidence to suggest that differences in tiller production per plant exist between the various populations, i.e. the number of daughter tillers per vegetative tiller was significantly lower for the *Rostkovia* flush than elsewhere. The tillers were also more widely spaced at this site and less clumped, possibly as a result of the lower rate of lateral production. This could well be an ageing effect similar to that described for *Carex bigelowii* by Kershaw (1962), the pronounced clumping at the fell-field and whaling station indicating juvenile colonizing populations. However, the differences may be environmentally imposed or genetically determined. Mooney and Billings (1961) showed that genecological differentiation existed between populations of *Oxyria digyna* in the production of rhizomes. Other data on the production and growth rates of daughter tillers of *P. alpinum* suggest that similar genetic differences may exist between South Georgian populations.

In its germination, the seed of *P. alpinum* exhibits apparently adaptive features, it being found that intrinsic seed dormancy mechanisms were absent. From other work (Sørensen, 1941; Bliss, 1958; Amen, 1966) it would appear that intrinsic seed dormancy is comparatively uncommon amongst polar and alpine species. Billings and Mooney (1968) have suggested that this is of adaptive significance in that these species are "thermally opportunistic" as regards germination, i.e. they will germinate whenever temperature conditions rise above a minimum threshold.

Billings and Mooney (1968) have also commented that the optimum germination temperatures for tundra species are surprisingly high, being in the range of 20° to 30° C, temperatures very comparable with those of more temperate species. The optimum of about 20° C for *P. alpinum* supports this generalization but germination at 5° C is to some extent atypical for polar species, most of which appear to remain inactive at these low temperatures. It is of interest that seed of another grass from South Georgia, *Deschampsia antarctica*, also germinated at 5° C (Holtom and Greene, 1967). It is possible that establishment under conditions of the South Georgian growing season, which is relatively more overcast and colder than many Arctic areas, requires this ability.

The variation in mean dry weight of both vegetative and flowering tillers between the various habitats is considerable, the values for the fell-field being between five and nine times lower than those for the other sites. This reduction is probably a consequence of growth limitation at severe sites. Living biomass estimates of *P. alpinum* show a simple correlation with site conditions, the environmentally more favourable sites supporting the greatest biomass. Differences may be compounded of both tiller density and their mean dry weight. Thus the difference in biomass between the fell-field and *Rostkovia* flush is due to the greater mean dry weight of the *Rostkovia* flush tillers. In contrast, the difference between the *Rostkovia* flush, whaling station and the *Phleum* sward is mainly due to variation in tiller density, whilst that (approximately 70-fold) between the fell-field and whaling station reflects variation in both density and mean dry weight per tiller. It must be noted, however, that whereas *P. alpinum* is the main constituent of the communities at the fell-field and whaling station, the communities were more complex at the *Rostkovia* flush and, to a lesser extent, at the *Phleum* sward. Thus only the biomass of that part of the community composed of *P. alpinum* plants is available for these two latter communities, the total biomass of the whole communities being considerably higher. Nevertheless, biomass values for the South Georgian populations are relatively low when compared with those presented by Scott and Billings (1964) for both mesic (1,350 g./m.<sup>2</sup> being a maximum biomass estimate for above- and below-ground fractions from the same site) and xeric (600 g./m.<sup>2</sup> being a maximum biomass estimate as above) sites. They are also low when compared with figures presented by Bliss (1966) of 3,634 g./m.<sup>2</sup> for the root and rhizome biomass alone, of a sedge meadow on Mount Washington.

The data in the present paper indicate the ways in which both differences and similarities in developmental processes may be adaptive to the environment. The question remains, however, to what extent these differences between populations are direct responses to environmental inequalities or have their basis in genecological differentiation. Preliminary trials, both at Birmingham and in controlled environment chambers at York, indicate that considerable genecological differentiation in morphological, phenological and growth characters exists between the populations.



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