An eco-physiological study of sesleria caerulea (L.) Ard. subsp. calcarea

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An eco-physiological study of *Sesleria caerulea* (L.) Ard. subsp. *calcarea*.

A dissertation submitted in partial fulfilment of the requirements for the degree of Master of Science in Ecology at the University of Durham.

by Ian M. West

Durham. September 1975.

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Introduction

In order for a plant to survive in a particular habitat, it must be adopted both morphologically and physiologically to its environmental conditions. Turesson in his series of papers (1922, 1923, 1925, 1930), observed that in many plants there was a spatial variation in their morphology and physiology, and that this intraspecific variation could be correlated with habitat differences. He recognized that variation resulted from the plastic response of plants to the environment, and the action of natural selection on the genotype variation within the whole population. He first used the term "ecotype" to describe the genetically different strains of a species occurring in particular habitats.

Many ecotypes have now been described, and these may involve adaptations to any environmental factor, including temperature, moisture, soil conditions, light, fire or salinity. Studies have produced much evidence for the morphological and phenological variation of populations from different habitats (Heslop-Harrison, 1964); investigations have also shown that the physiological variation of populations is related to the environmental conditions, (Bradshaw, 1960; Björkman et. al., 1960; Mooney and Billings, 1961; Björkman and Holmgren, 1963; Milner and Hiesey, 1964; Björkman, 1968; Lloyd, 1974).

In studying the relationship between a plant and its environment, ecotypes have often been used, and many studies

on the variation within a plant species over an altitudinal range been made, as it is possible to study the morphological and physiological changes in response to gradual environmental differences. For example, Clausen, Keck and Hiesey (1948) observed differences in the height and flowering of Achillea landulosa over an altitudinal range in the Sierra Nevada; these differences were largely maintained when seeds were collected and grown under uniform conditions. Myers and Bormann, (1963), found morphological variation in Abies balsamina, leaf length being connected with altitude; Ward, (1969), and Pearcy and Ward, (1972), found changes in the phenology and growth of Deschampsia caespitosa, the high elevation plants being earliest in development, shorter in height and having shorter periods of growth. However, when grown in uniform conditions, there were essentially no differences indicating large ecotype plasticity. Physiological changes with altitude have also been recorded; Whitfield, (1932), observed a decrease in the transpiration and growth rate of Helianthus annuus at higher altitudes; Mooney, (1963), found that plants of Polygonum bistortoides originating from a warm coastal environment had growth and respiration rates considerably lower than alpine plants; Fryer and Ledig, (1972), found that when Abies balsamea is grown from seed, the photosynthetic temperature optimum of the seedlings decreases with the increased elevation of the seed source.

Many studies have shown correlations between growth form and habitat, but comparatively little is known about the

adaptive significance of the observed differences. Because morphological changes due to environmental and genetic factors often resemble one another, the structural differences have been considered to be of adaptive value without any knowledge of the physiological consequences, (Heslop-Harrison, 1964). However, Lewis (1969, 1972) considers that in the understanding of the adaptation of plants, it is important to study the relationship between the structure, the physiological functioning and the environmental complex. He uses this approach in his investigation of the physiological significance of different leaf structure in Geranium sanguineum. Lloyd (1974) used a similar approach in his study of the morphology, photosynthesis and transpiration of Sesleria caerulea collected from sites in Europe. He demonstrated the close relationship between the morphology and physiology of a plant, as the photosynthetic and transpiration rates were affected by differences in the stomatal depression depths.

The morphological and physiological adaptation of plants to their environment can readily be studied on species with a wide distribution or which occupy diverse habitats, as these have a larger number of ecotypes than species with a narrower distribution (Turesson, 1930). The existence of edaphic and climatic ecotypes of Sesleria caerulea was postulated by Round-Turner (1968), who studied the anatomy, growth and mineral relationships of two populations from different geographic areas. This species occurs mainly in open habitats

and on basic soils, has a wide tolerance of various soil-water conditions, and occurs over a large altitudinal range. There has been little detailed study of its morphology and physiology in relation to its environment, except for the work by Round-Turner (1968) and Lloyd (1974), thus it was decided to use this species for study.

The aims of this present work are:-

(a) to study the relationship between the morphology and physiology of a plant species and its environment, by investigating both the morphology and transpiration rates of various populations of Sesleria caerulea from different habitats and altitudinal sites.

(b) to determine the extent to which variation in this species is due to the plastic response of the plants or the expression of the genotype, by studying the change in the morphology and transpiration, when plants from different populations are transplanted and grown under the same conditions.

(c) to investigate the extent to which high altitude plants are adapted to lower soil temperatures, by measuring the effect of root chilling on the water uptake of plants collected from various altitudes.

Distribution of Sesleria caerulea and details of sites studied

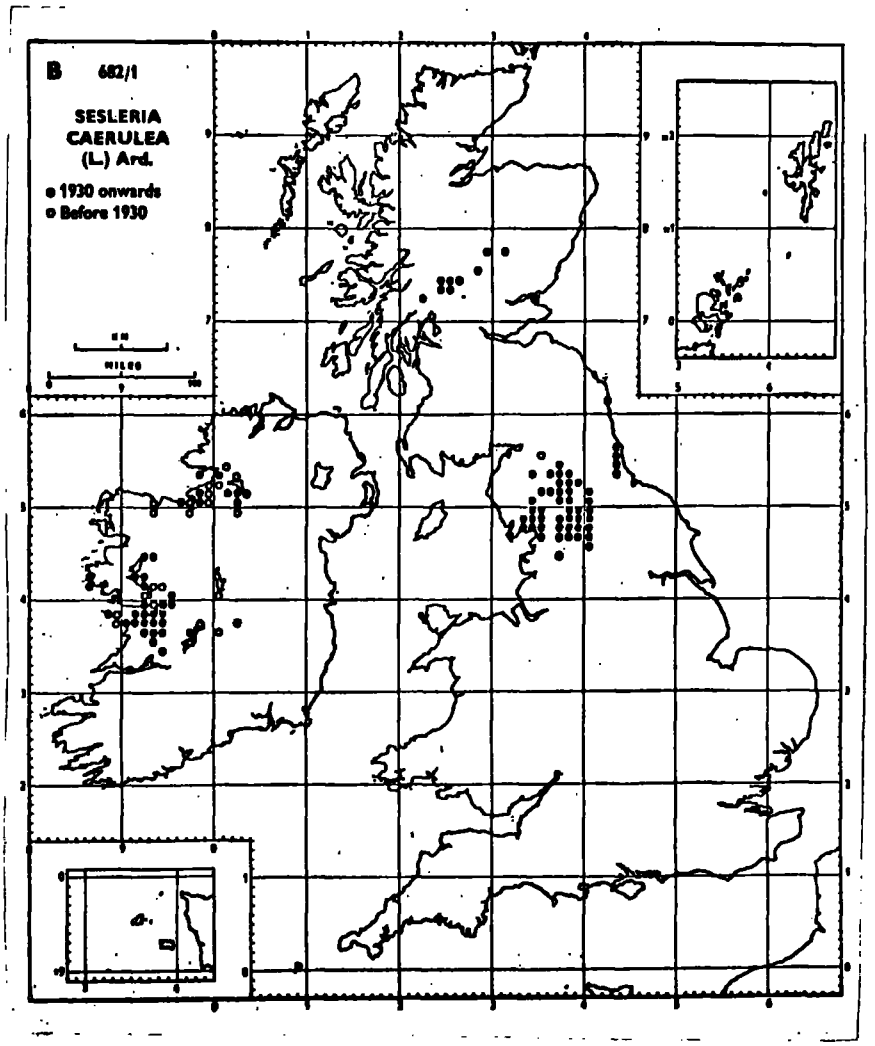
i) Distribution

Sesleria caerulea (L) Ard. subsp. calcarea, hereafter referred to as Sesleria, is a species with a very disjunct distribution. It occurs in South-West and Central Europe in a variety of habitats at different altitudes, being common on limestone hills and mountains. It is, however, absent from Scandinavia and has only a few populations in Iceland.

The distribution of Sesleria in Britain is shown on the map (Figure 1). In Northern England it is found mainly in upland areas on limestone, but also occurs in lowland and coastal sites. In Scotland, it is found on the limestone and mica-schists of the mountains, and in West Ireland it is widely distributed on the carboniferous limestone. It does not occur, however, on the limestone or chalk further south than Malham, although it is found on both soil types across the channel in France.

Figure 1. Distribution map of Sesleria caerulea (L) Ard.

Fig. 1.



"By permission of the Botanical Society of the British Isles, taken from their Atlas of the British Flora and updated by the Biological Records Centre, Monks Wood Experimental Station, Abbots Ripton, Huntingdon."

ii) Description of Sites

Sesleria was collected as living material from five different populations at Cassop Vale, near Durham, and eight other sites at different altitudes in Britain, (seven in N. England and one in Scotland). These sites were studied either because it was relatively easy to obtain plants from the location, and/or the site was at a particular altitude. At each site the altitude, aspect, slope and depth of soil were recorded; soil pH was determined later in the laboratory. At Cassop it was possible to carry out a more detailed description of the habitats, by doing a phyto-sociological survey.

Table 1.

Sites at Cassop Vale

National Grid Reference: NZ 341 383

Altitude: 160 m. O.D.

Underlying rock: Magnesian limestone

Site letter	Site description	Soil depth (cm)	Soil moisture (%)	pH of soil
A	Shallow dry soil on limestone cliffs. Easterly aspect	<10	3	7.35
B	Relatively deep soil at the base of a limestone cliff. Westerly aspect	10-20	16	7.4
C	Deep, well drained soil. Open aspect	>20	14	7.25
D	Damp soil, gently sloping. Southerly aspect	10-20	22	7.4
E	Wet soil due to drainage from above, sloping. Northerly aspect	10-20	28	7.4

Tables 2-6.

Phytosociology of sites at Cassop Vale

(Braun-Blanquet's system used)

Cover value scale

+ sparsely or very sparsely present; cover very small
1 plentiful but of small cover value
2 very numerous or covering at least 1/20 of the area.
3 any number of individuals covering $\frac{1}{4}$ to $\frac{1}{2}$ of the area
4 any number of individuals covering $\frac{1}{2}$ to $\frac{3}{4}$ of the area
5 covering more than $\frac{3}{4}$ of the area

Sociability scale

1 growing singly, isolated individuals
2 grouped or tufted
3 in small patches or cushions
4 in small colonies, in extensive patches or forming carpets
5 in pure populations

Table 2

Phytosociology of Site A

Cover 80%

Species	Cover value	Sociability
Sesleria caerulea	3	3
Centaurea scabiosa	2	2
Lotus corniculatus	1	2
Leontodon hispidus	1	2
Plantago media	1	2
Festuca ovina	1	1
Briza media	+	1
Plantago lanceolata	+	1

Table 3.

Phytosociology of Site B

Cover 100%

Species	Cover value	Sociability
Sesleria caerulea	4	4
Festuca ovina	3	1
Lotus corniculatus	2	3
Centaurea scabiosa	2	2
Centaurea nigra	2	2
Plantago lanceolata	2	2
Dactylis glomerata	1	2
Plantago media	1	2
Briza media	1	1
Leontodon hispidus	1	1
Euphrasia officinalis	+	1
Linum catharticum	+	1

Table 4.

Phytosociology of Site C

Cover 100%

Species	Cover value	Sociability
Sesleria caerulea	3	3
Festuca ovina	1	2
Lotus corniculatus	1	2
Poterium sanguisorba	1	2
Trifolium repens	1	2
Centaurea nigra	1	1
Plantago lanceolata	+	2
Agrostis tenuis	+	1
Briza media	+	1
Dactylis glomerata	+	1
Potentilla erecta	+	1
Viola riviniana	+	1

Table 5.

Phytosociology of Site D

Cover 80%

Species	Cover value	Sociability
Sesleria caerulea	3	3
Thymus drucei	1	2
Trifolium repens	1	1
Festuca ovina	+	2
Plantago lanceolata	+	2
Viola riviniana	+	2
Achillea millefolium	+	1
Briza media	+	1
Centaurea nigra	+	1
Lotus corniculatus	+	1
Polygala vulgaris	+	1
Succisa pratensis	+	1
Vicia hirsuta	+	1

Table 6.

Phytosociology of Site E

Cover 90%

Species	Cover value	Sociability
Sesleria caerulea	3	3
Cteridium moluscum	2	3
Thymus drucei	2	2
Festuca ovina	1	1
Potentilla erecta	+	2
Briza media	+	1
Carex panicea	+	1
Gentiana amorella	+	1
Pinguicula vulgaris	+	1
Sambucus nigra	+	1
Succisa pratensis	+	1
Valeriana officinalis	+	1

Plate 1. Site A at Cassop Vale
(at base of limestone cliff).

Plate 2. Site B at Cassop Vale
(shallow soil on limestone cliffs).

Plate 1.

Plate 2.

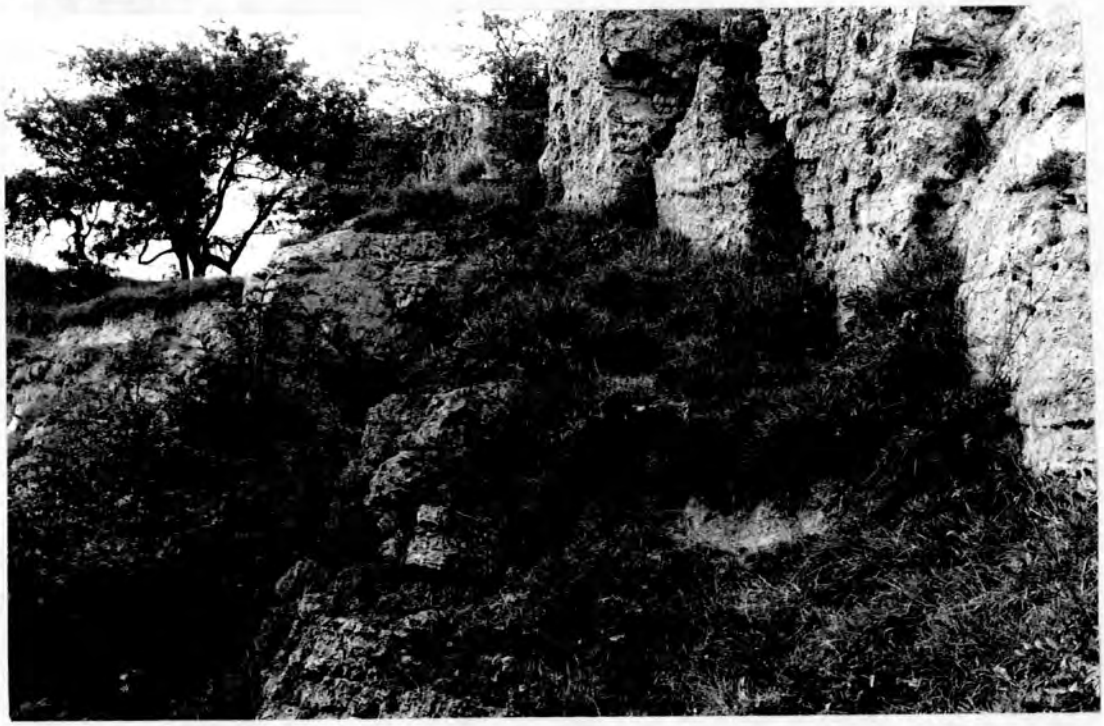


Plate 3. Site C at Cassop Vale

Plate 4. Site D and E at Cassop Vale
(E on the left, D on the right of photo).

Plate 3.

Plate 4.

Table 7.

Sites at different altitudes

National Grid Reference	Location	Altitude (m)	Underlying rock	Description of Site	Soil Depth (cm)	Soil pH
SD 457 772	Arnside, Westmorland	60	Carboniferous limestone	Roadside verge, Open aspect	10-20	7.2
SD 924 712	Arncliffe, Yorkshire	240	Carboniferous limestone	At base of limestone cliffs, Sheltered, Northerly aspect	10-20	7.2
NY 684 091	Sunbiggin Tarn, Westmorland	320	Carboniferous limestone	Limestone pavement, Open aspect	<10	6.95
SD 895 674	Malham Tarn, Yorkshire	430	Carboniferous limestone	Deep soil at top of cliffs, Open aspect	>20	7.2
SD 962 923	Askrigg, Yorkshire	440	Carboniferous limestone	Shallow dry soil on limestone cliff, Southerly aspect	<10	6.9
SD 964 924	Askrigg, Yorkshire	515	Carboniferous limestone	Shallow dry soil on limestone cliff, Southerly aspect	<10	7.1
SD 957 783	Buckden Pike, Yorkshire	600	Carboniferous limestone	Shallow dry soil on limestone cliff, Southerly aspect	< 10	6.9
NN 639 427	Ben Lawers, Scotland	910	Mica-schist	Shallow dry soil, South-easterly aspect	<10	-

iii) Climatic data

As the Durham University Observatory was very close to the Botany Gardens, it was possible to obtain climatic data from this meteorlogical station for the duration of the experiments.

National Grid Reference: NZ 267416

Altitude: 102 m. O.D.

Hour of observations: 0900 G.M.T.

Table 8.

Climatic data for Durham (May-July 1975)

Month	Mean temp. (^{o}C)	Total rain-fall (mm)	Humidity (%)	Total Sunshine (hrs)	Mean Wind Speed ($km.\ hr^{-1}$)
May	7.9	49.6	-	149.7	12.7
June	13.1	24.8	45 (Av. for 1300 hrs. G.M.T)	218.8	11.7
July	15.9	61.5	74 (Av. for 0900 hrs. G.M.T)	144.3	8.5

Materials and Methods

i) Collection and establishment of plants

Plants of Sesleria caerulea were collected from the various sites during early May. At each site about thirty inflorescences were collected at random, and approximately one hundred plants were carefully removed, leaving the soil around their roots. Each sample was then divided so that plants were available for either morphological or physiological/growth studies.

It was decided to use a standard soil in the growth and physiology experiments, so that any differences observed could be attributed to the nature of the plant material, and not to the edaphic conditions. Loam, peat and sand were mixed in the ratio of 5 : 2 : 1 and 30gm. of John Innes Base, and 120gm. of chalk were added to each litre of soil obtained, which was then sterilised by heating it to 80^{o}C for 10 minutes. Twenty small plants, each with approximately three leaves were then selected, and planted in the soil using 6cm. diameter plastic pots. These were placed in the gardens at Durham University, watered regularly, and left to establish themselves during the succeeding weeks.

Leaf length measurements were initially made at regular intervals, so that growth rates could be obtained. However, very little new leaf material was produced during the next 4-6 weeks, and there was sometimes an initial dying of some of the leaves; it was therefore decided that no useful measurements of growth rate could be obtained by this method

during the available time.

In July, plants were again collected from all sites at Cassop Vale and leaf lengths were measured, so that a measure of the rate of growth of each population could be obtained.

ii) Morphological studies

Plants from the other part of each original sample were used for morphological studies. Thirty plants were removed at random and measurements of leaf lengths, maximum leaf width, height of inflorescence and length and dry weight of the inflorescence spike were recorded for each specimen. Studies of leaf anatomy were also made using nail varnish impressions and transverse sections of the youngest fully expanded leaf of six plants from each population. The number of stomata in five areas of 1 mm^2 near the centre of each leaf were counted, and measurements of the lengths of five interstomatal spacings in a longitudinal direction were made, together with the lengths of five stomatal pores. Thirty measurements of each parameter were therefore obtained for each population. These were recorded for the upper leaf surface only, as very few stomata could be found on the lower surface. Sections of the same leaves were then cut using a hand microtome, and measurements of the depth of the stomata below the surface of the epidermis were made. These measurements were made in the light of the report by Lloyd (1974) who found that the depression depth of the stomata was a significant factor affecting the rates of photosynthesis and transpiration

in this species.

In July, when the potted plants from Cassop Vale and the shallow soils at different altitudes had produced new leaves, anatomical measurements were again made, in order to determine the extent to which variation is due environmental or genetic factors.

iii) Transpiration studies

A number of different methods are available for measuring transpiration in the field and laboratory. Many of them, however, require a large amount of apparatus or are not suitable for use with grass species, so it was necessary to use comparatively simple methods in this study.

(a) Field measurements

Rates of transpiration in the field were measured using the cobalt chloride (or thiocyanate) method on the populations at Cassop Vale. Small strips of cobalt thiocyanate paper were cut, placed across the upper surface of the leaf, and held in place by two cover slips on either side of the leaf. Vaseline was then placed around the edges to prevent water vapour from the air affecting the paper, and the time taken for the paper to change to a standard colour was recorded. However, it was very difficult to decide exactly when the colours were the same, so instead the time taken for a detectable colour change in the thiocyanate paper was recorded for ten plants from each population. Measurements of light intensity, relative humidity and temperature 20cm. above the ground and 10cm. below it were also made at each site. However, large

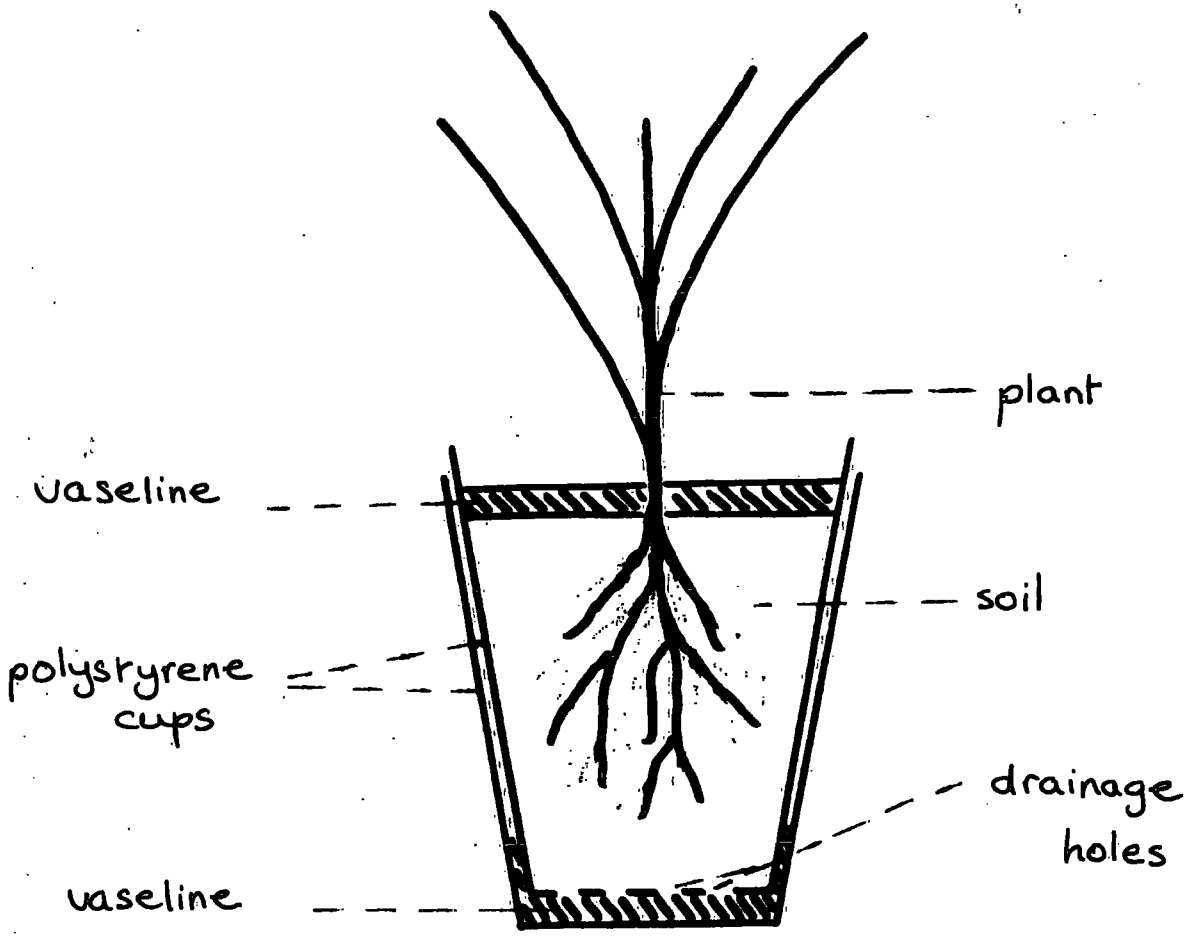
variations in the time taken for a colour change to occur were recorded for each population; it was considered that the method was too inaccurate for meaningful results to be obtained therefore no further measurements were made using this technique.

(b) Laboratory measurements

One month after planting, the potted plants in the gardens have become established, and some were beginning to produce new leaves, so it was possible to begin measuring the transpiration rates of these plants. A phytometer method was used; the loss in weight of a potted plant was recorded over a period of time, the soil surface being covered to prevent evaporation. It was originally intended to leave the plants in their pots, and seal the holes at the base, but this was not effective in many cases, and it was necessary to transfer the plants to polystyrene cups a few days before experiments were carried out. As the polystyrene cups were the same size as the original pots, this procedure involved very little disturbance of either the roots or the soil surrounding them. Holes were made in the base of each cup to allow free drainage, and the soil was brought to field capacity just before the pots were sealed at the base and soil surface. This was achieved by pouring molten vaseline, just above its melting point, on the soil, and then placing the cup in another similar one which contained a small amount of molten vaseline in the bottom (Figure 2). The total leaf length of each plant was measured, and each pot was then

Figure 2. Diagram of the phytometer used for the transpiration experiments.

Fig. 2.


plant
vaseline
soil
polystyrene cups
drainage holes
vaseline

weighed at the same time each day. Temperature and relative humidity measurements were made continually in the laboratory using a hair hygrometer, and the light intensity was also recorded at frequent intervals. However, because the main illumination in the laboratory was always provided by fluorescent bulbs, the light intensity did not vary greatly either on any individual day or from day to day. Therefore only occasional checks were made during the subsequent experiments. Weighings were continued for a week or less, as after this time changes in weight and leaf area occur, as plants begin to die (either due to lack of water or the presence of anoxic conditions around the roots) or show signs of growth. Leaf lengths were measured at the end of each experiment to check that no significant increase had occurred, and the dry weights of both root and shoot for each plant were found. Leaf area was calculated by multiplying the leaf length by the width, and then correcting for leaf shape by using the relationship determined by Lloyd (1974). Rates of transpiration were found for:-

1) the populations from various habitats at Cassop Vale

2) the populations from sites with shallow soils at different altitudes.

3) plants grown in Durham under the same environmental conditions, having been originally collected from various sites at Cassop Vale

(It was decided not to use the altitudinal populations from deep soils for transpiration measurements, as the preliminary

morphological studies had indicated that the variation between populations was too great to include all populations).

In each experiment five plants of approximately the same size were used. A control was also set up which consisted of a polystyrene cup containing only soil at field capacity. It was sealed in the same way as the other pots, and was used to find out if weight changes occurred other than those due to the water loss by the plants.

iv) Water uptake at low soil temperatures

The effect of low soil temperatures on the water uptake from different habitats and altitudes was investigated by measuring the transpiration of plants with roots and soil chilled by an ice/water mixture. Water loss was determined using the same method as in the previous experiment. As it was necessary to change the environment around the pots with water of different temperatures, each pot was placed in another polystyrene cup before being placed in a water bath. In this way it was possible to remove and weigh each sealed pot without the necessity of drying the outside first. The temperatures outside and inside the pot were recorded by placing one thermometer in the water bath and another, sealed in with vaseline, in the soil next to the plant.

On the first day the water bath was filled with water at room temperature, and the loss in weight during 24 hours was found for all plants. On the following day the water was replaced by an ice/water mixture at 0-1^{o}C., and after the soil temperature had been stable for several hours, the loss

in weight over 24 hours was again found. The reduction in transpiration was then found; this is equal to the reduction in water uptake if uptake is equal to loss of water over a 24 hour period. Measurements of air temperature, relative humidity and light intensity were recorded on the successive days, so that any change in the environmental conditions was known.

In the preliminary experiments with low soil temperatures, the weighings were inaccurate because of condensation on the surface of the vaseline (the cold/warm interface). This was prevented by covering the surface of the vaseline with paper tissue between weighings, so that the water vapour in the air did not come into contact with the cold vaseline.

The effect of low root temperatures on water uptake was investigated on:-

1) populations from various habitats at Cassop Vale
2) populations collected from sites with shallow soils at different altitudes.

Results

i) Morphology and growth of populations from Cassop Vale

Sesleria growing in the various habitats at Cassop Vale showed considerable morphological variation, (Figure 3), with both plant and inflorescence size being influenced by the depth and water relations of the soil. On the relatively deep, well-drained soils, (Sites B and C), large plants with long leaves and tall inflorescences were growing, but on the shallow, dry soils on the limestone cliffs, (Site A), and the constantly moist/wet soils, (Sites D and E), significantly smaller plants with shorter inflorescences were present. The leaf width and seed production, (as measured by length and dry weight of the inflorescence spike), were also found to be related to the soil-water conditions, as plants from the drier, well-drained sites had significantly wider leaves and larger inflorescence spikes than those from the moist sites (Figure 4).

A variation in the leaf anatomy of *Sesleria* from the different sites was also found, (Figure 5) and some of the features were related to the soil-water conditions, as leaves from plants on the shallow, dry soils had a higher stomatal frequency than those from the wetter soils. However, no other anatomical feature studied seemed to be related directly in this way; there were no significant differences in the depth of stomatal pores, and although the pore length varied in different populations, it could not be correlated

Plate 5. Nail varnish impression of a Sesleria leaf

Plate 6. Nail varnish impression of stomata of Sesleria leaf

(Epidermal cells out of focus as stomatal pores are sunken below the surface).

Plate 5.

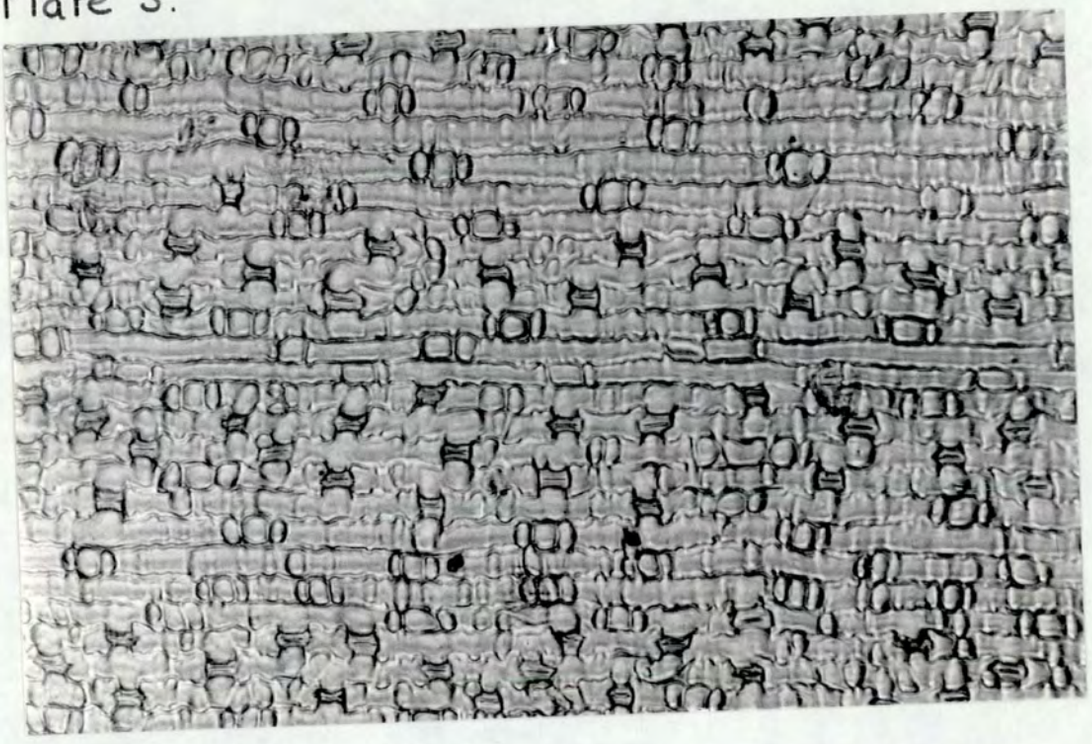


Plate 6.

Figure 3. Morphology of Sesleria from Cassop Vale.
(Explanation of site letters A-E on Table 1.
Sample size = 30.
Mean and standard error of the mean plotted).

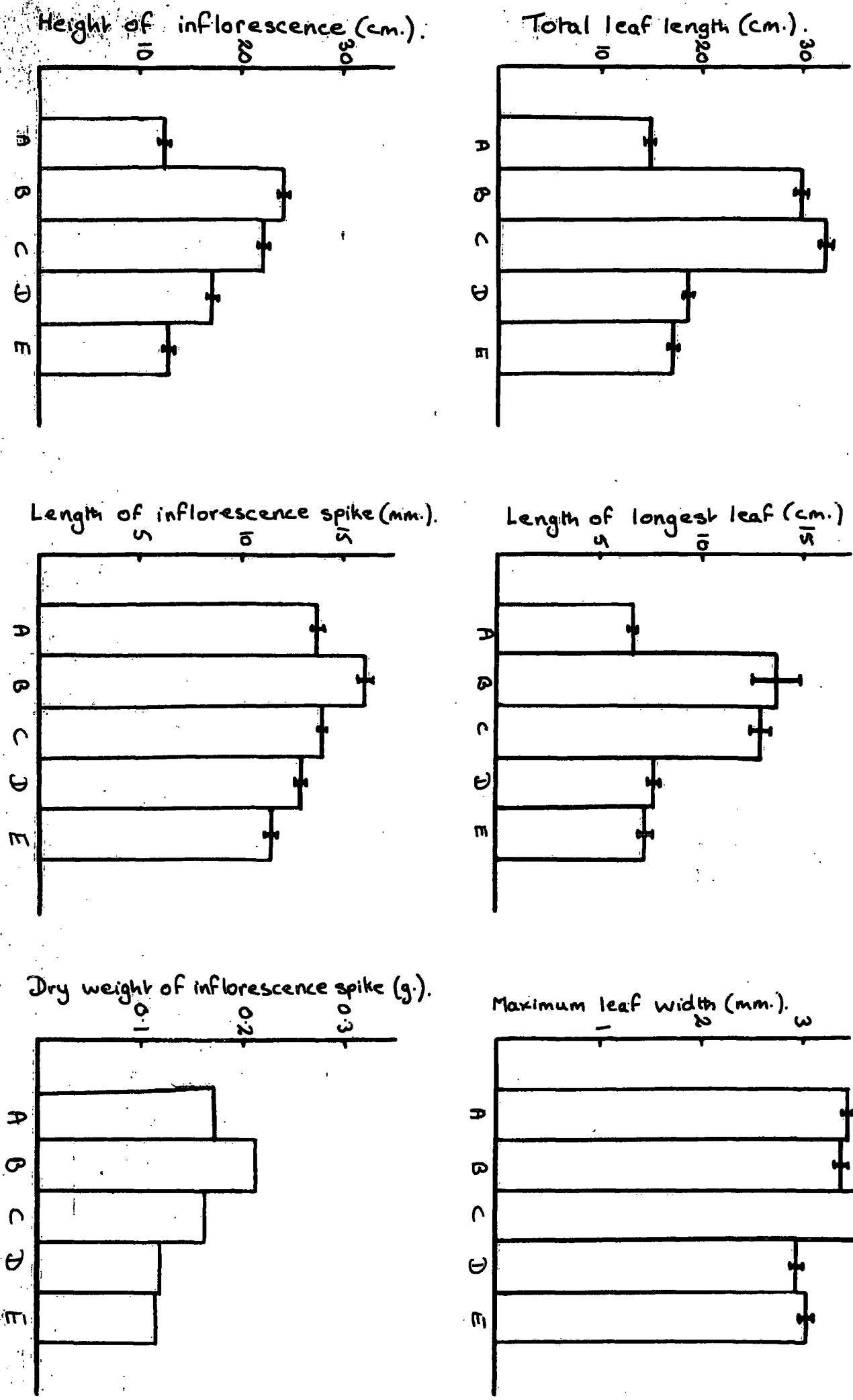

Height of inflorescence (cm.).
10
20
30
A
B
C
D
E
Total leaf length (cm.).
10
20
30
A
B
C
D
E
Length of inflorescence spike (mm.).
5
10
15
A
B
C
D
E
Length of longest leaf (cm.)
5
10
15
A
B
C
D
E
Dry weight of inflorescence spike (g.).
0·1
0·2
0·3
A
B
C
D
E
Maximum leaf width (mm.).
2
3
A
B
C
D
E

Fig. 3.

Figure 4. Significance tests on the morphology of populations from Cassop Vale.
(Explanation of site letters A-E on Table 1.
Sample size = 30. Student's t-test used).

Figure 4.

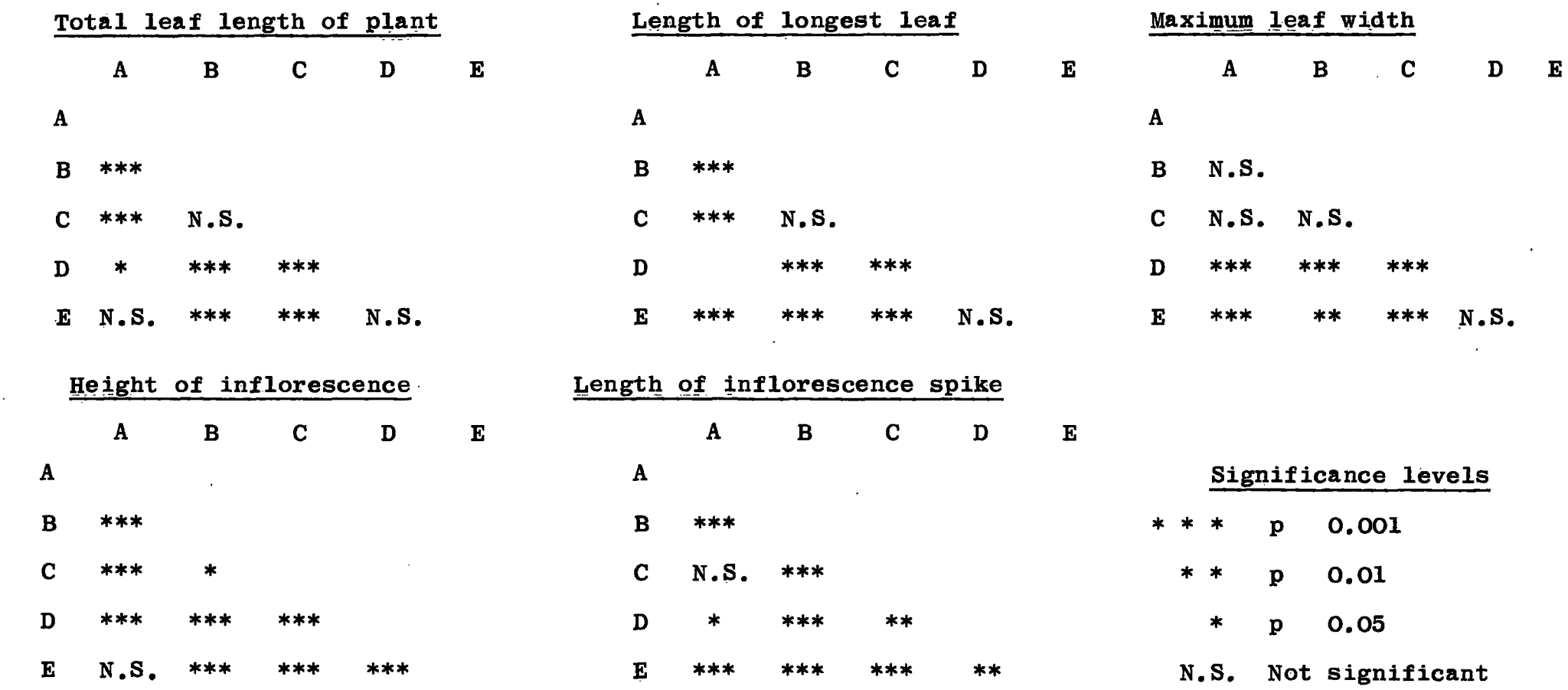
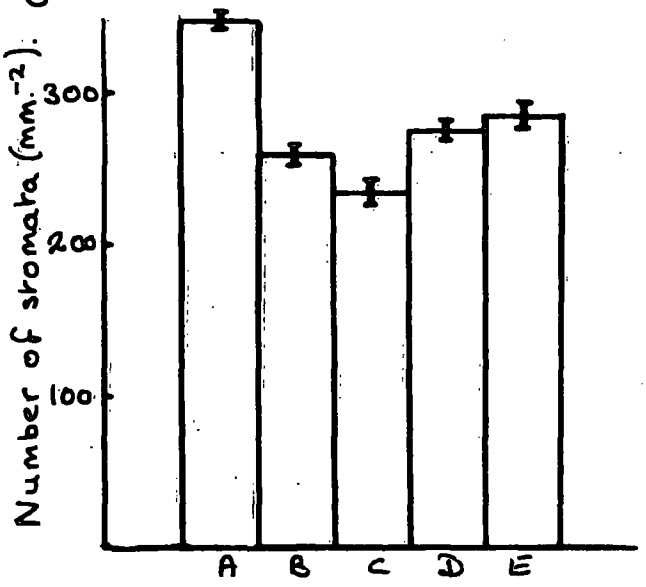

Total leaf length of plant
A B C D E
A
B ***
C *** N.S.
D * *** ***
E N.S. *** *** N.S.
Length of longest leaf
A B C D E
A
B ***
C *** N.S.
D *** ***
E *** *** *** N.S.
Maximum leaf width
A B C D E
A
B N.S.
C N.S. N.S.
D *** *** ***
E *** ** *** N.S.
Height of inflorescence
A B C D E
A
B ***
C *** *
D *** *** ***
E N.S. *** *** ***
Length of inflorescence spike
A B C D E
A
B ***
C N.S. ***
D * *** **
E *** *** *** **
Significance levels
* * * p 0.001
* * p 0.01
* p 0.05
N.S. Not significant

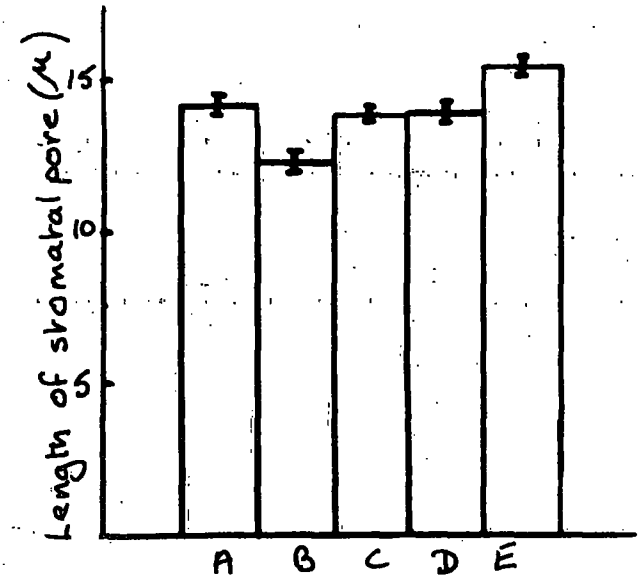
Figure 5. Leaf anatomy of Sesleria from Cassop Vale, (including significance tests on the data). (Explanation of site letters A-E on Table 1. Explanation of significance levels on Fig. 4. Sample size = 30. Mean and standard error of the mean plotted). Student's t-test used).

Fig. 5.

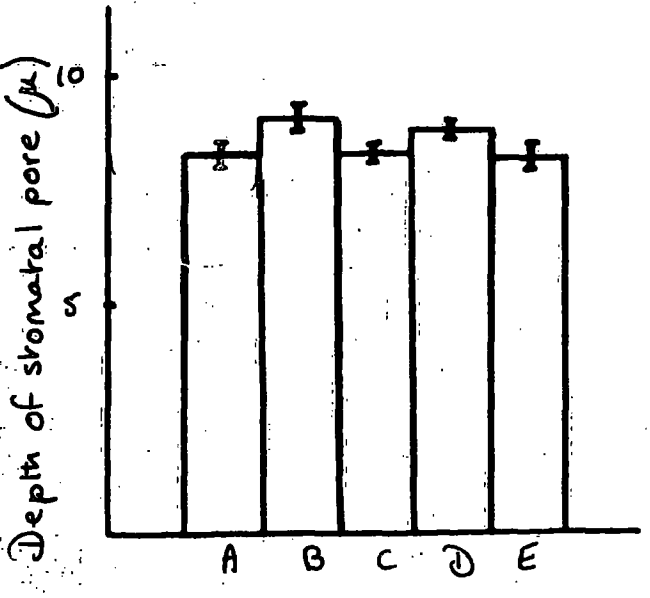


Student's t-tests

	A	B	C	D	E
A					
B	***				
C	***	*			
D	***	N.S.	***		
E	***	*	***	N.S.	



	A	B	C	D	E
A					
B	***				
C	N.S.	***			
D	N.S.	***	N.S.		
E	***	***	***	***	



	A	B	C	D	E
A					
B	N.S.				
C	N.S.	N.S.			
D	N.S.	N.S.	N.S.		
E	N.S.	N.S.	N.S.	N.S.	

with any measured habitat feature. The ratio of interstomatal spacing to length of stomatal pore also varied in these populations (Table 9). (This value was calculated as it may have an effect on the transpiration rate, which would be measured later).

Table 9. Ratio of interstomatal spacing to length of stomatal pore for the populations from Cassop Vale

Site letter	Interstomatal spacing / Length of stomatal pore
A	4.3
B	6.0
C	6.1
D	5.5
E	4.3

(Explanation of site letters on Table 1)

Growth rates of plants in the field from May to July also varied in the different sites, with greatest increase in size, (as measured by longest leaf length and total leaf length), occurring in the open site with the deep, well-drained soil, (Site C), and least where there was a constantly waterlogged soil, (Site E). At this site no significant increase in size was observed during the two months (Table 10),

Table 10. Changes in leaf length in populations of Sesleria at Cassop Vale, during the period May-July.

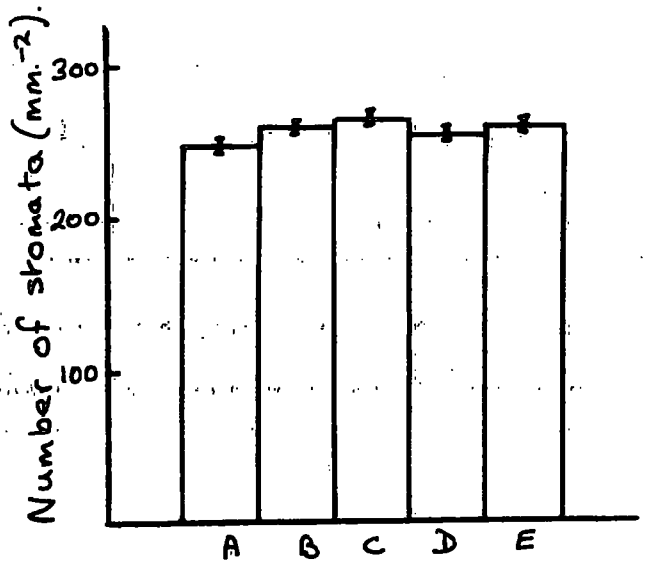
Site letter	Increase in total leaf length of plant (%)	Significance test on change in total leaf length of plant	Increase in length of longest leaf (%)	Significance test on change in length of longest leaf
A	22	* *	40	* * *
B	4	N.S.	34	* * *
C	28	* * *	48	* * *
D	9	N.S.	35	* * *
E	- 1	N.S.	10	N.S.

(Sample size = 30) Key to significance levels on Fig. 4
Explanation of site letters on Table 1.

When plants from the sites were collected and grown under the same environmental conditions at Durham University, very few differences in the leaf anatomy were found, as the new leaves of all plants had similar stomatal frequencies and pore depths. Variation in the length of the pore was still present, but was less than that found in field populations (Figure 6), and as a result there were also differences in the ratio of interstomatal spacing/pore length (Table 11).

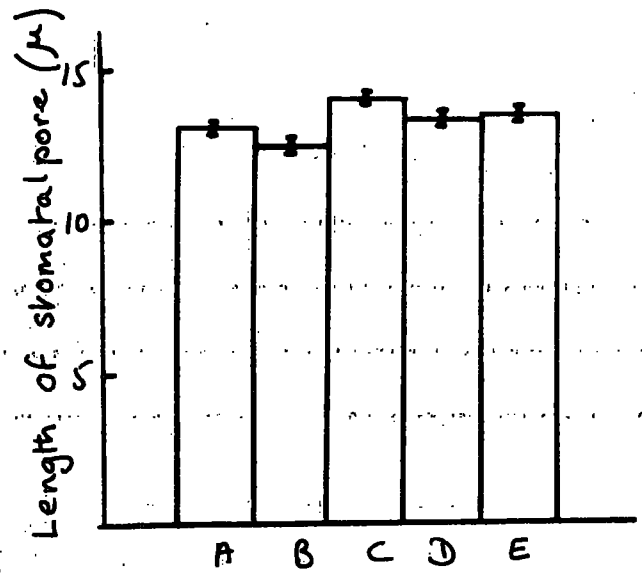
Figure 6. Leaf anatomy of Sesleria collected from Cassop Vale and grown under the same environmental conditions.
(Explanation of site letters A-E on Table 1.
Sample size = 30.
Mean and standard error of the mean plotted).

Fig. 6.

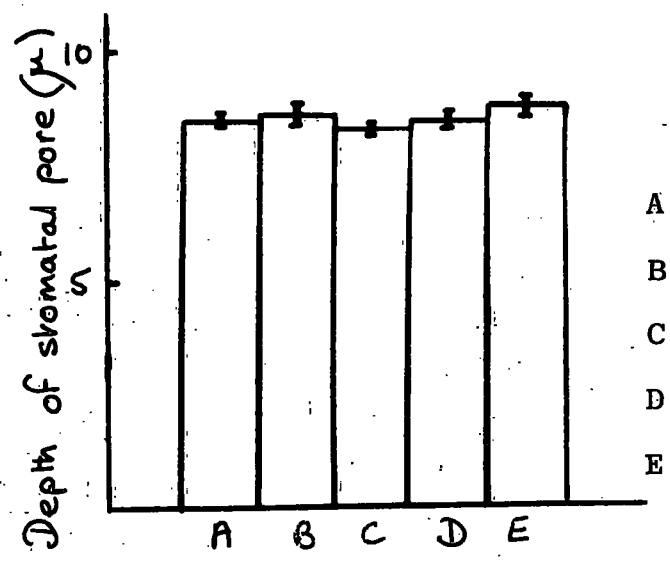


Student's t-tests

	A	B	C	D	E
A					
B	N.S.				
C	*	N.S.			
D	N.S.	N.S.	N.S.		
E	N.S.	N.S.	N.S.	N.S.	



	A	B	C	D	E
A					
B	*				
C	***	***			
D	N.S.	*	*		
E	N.S.	**	*	N.S.	



	A	B	C	D	E
A					
B	N.S.				
C	N.S.	N.S.			
D	N.S.	N.S.	N.S.		
E	N.S.	N.S.	N.S.	N.S.	

Table 11. Ratio of interstomatal spacing to length of stomatal pore for the plants from Cassop Vale which had been grown under the same conditions

Site letter	Interstomatal spacing / Length of stomatal pore
A	8.3
B	8.0
C	7.5
D	6.5
E	6.1

(Explanation of site letters on Table 1)

It was not possible to measure the growth rate of potted plants as they required several weeks to become established before new leaves were produced. However, all plants appeared to produce new growth at approximately the same rate as they were a similar size at the end of the experiment, but no measurements were made as only a few plants from each population were available at this time. Therefore many of the differences in morphology (and growth?) which existed in the field were not maintained when the plants were grown under the same environmental conditions.

ii) Transpiration of plants from Cassop Vale

Differences in the transpiration rate of Sesleria from the various populations at Cassop Vale were observed both in the field and in the laboratory.

(a) Field measurements

When cobalt thiocyanate paper was used, small differences

in the rate of water loss from plants in the various habitats were recorded (Table 11). Sesleria in the sunny dry habitat had a faster water vapour loss than that in the shady dry habitat, but the measured rates were not very accurate as the method depends on the human eye to match colours. Therefore no significance tests were applied to the data.

Table 12. Field measurements of the transpiration rate of plants in Cassop Vale (using the cobalt thiocyanate paper method)

Site letter	Average time for a detectable colour change to occur (secs).	Temperature 20cm. above ground (°C)	Temperature 5cm. below ground (°C)	Soil moisture (%)	Relative Humidity (%)	Light intensity (Arbitory units)
A	51.0 ± 3.2	22.0	21.0	3.3	50	17
B	52.0 ± 3.9	24.0	20.5	17.3	52	18
C	50.6 ± 4.1	23.5	22.0	15.5	52	18
D	36.4 ± 3.8	25.0	23.0	18.8	49	19
E	40.2 ± 3.5	21.0	19.0	25.7	53	17

(Explanation of site letters on Table 1)

(b) Laboratory measurements

Analysis of variance showed that differences in the rates of transpiration of the various populations existed in the laboratory. Generally, Sesleria from the wettest sites, (Sites D and E) and from the dry shallow soil, (Site A), had higher rates of transpiration than plants from the deeper, well-drained soils (Fig. 7). However, when comparisons were

Fig. 7.

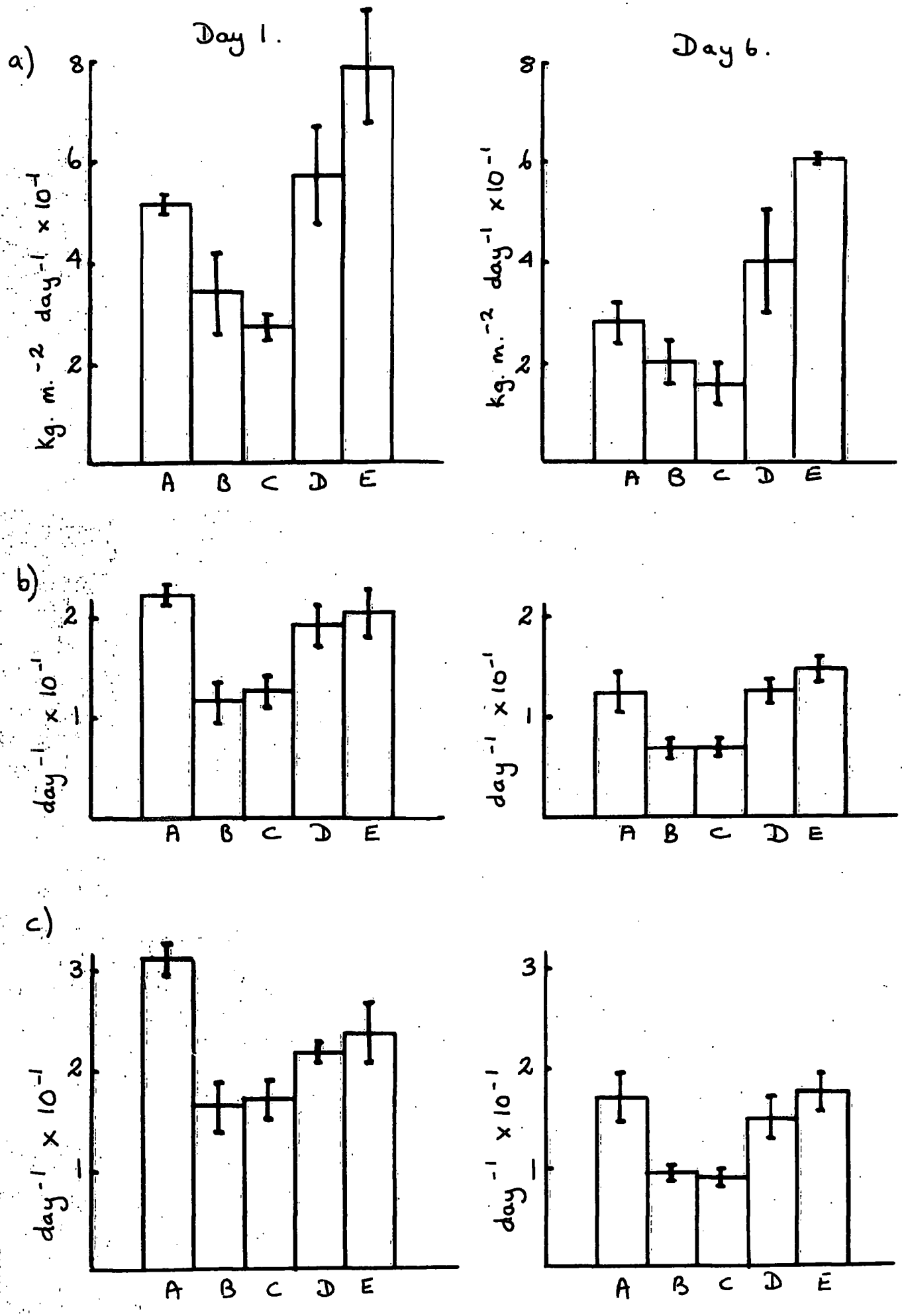

a)
Day 1.
Day 6.
kg. m.$^{-2}$ day^{-1} x 10^{-1}
8
6
4
2
A B C D E
b)
day^{-1} x 10^{-1}
2
1
A B C D E
c)
day^{-1} x 10^{-1}
3
2
1
A B C D E

Figure 7. Transpiration rates of Sesleria from Cassop Vale, (laboratory measurements).

(a) On a leaf area basis for Day 1 and Day 6.

(b) On a dry weight of plant basis for Day 1 and Day 6.

(c) On a dry weight of root basis for Day 1 and Day 6.

(Explanation of site letters A-E on Table 1.

Sample size = 5.

Mean and standard error of the mean plotted).

made between the mean rates for the populations using a multiple-range test (shortest significant ranges), the significant differences found on Day 1 depended on the basis on which the rate was calculated (Figure 8). The population from Site E showed a large variation in the rate of transpiration when expressed on a leaf area basis, and as this affected the total variance, the significance tests between all pairs of populations were affected, which made an important difference when populations A and B were considered. When analysis of variance was used, the transpiration rates were not significantly different from one another, but when only these two populations were compared using a Student's t-test, they were found to be different, ($p < 0.01$). Greater sample numbers are therefore required in these experiments, because of the large variation in rate of transpiration of plants from one population.

During the succeeding days, there was a reduction in the rate of transpiration of Sesleria from all populations, but this was greater in plants from the deeper or drier soils. By the sixth day, plants from the wettest sites, (Sites D and E), had significantly higher rates of transpiration than plants from the deeper, well-drained soils, (Sites B and C), regardless of the basis on which the rate was calculated. Some other differences were also found, but these were dependant on a particular basis for the transpiration measurement (Fig. 8).

Figure 8. Significance tests on the transpiration rates of plants from Cassop Vale.
Analysis of variance and shortest significant ranges (S.S.R.) tests used, ($p = 0.5$).
(Explanation of site letters A-E on Table 1).

Figure 8.

DAY 1

(a) On a leaf area basis

	A	B	C	D	E
A					
B	N.S.				
C	N.S.	N.S.			
D	N.S.	N.S.	*		
E	*	*	*	N.S.	

(b) On a dry weight of plant basis

	A	B	C	D	E
A					
B	*				
C	*	N.S.			
D	N.S.	N.S.	N.S.		
E	N.S.	N.S.	N.S.	N.S.	

(c) On a dry weight of root basis

	A	B	C	D	E
A					
B	*				
C	*	N.S.			
D	N.S.	*	*		
E	N.S.	*	*	N.S.	

DAY 6

(a) On a leaf area basis

	A	B	C	D	E
A					
B	N.S.				
C	N.S.	N.S.			
D	N.S.	*	*		
E	*	*	*	*	

(b) On a dry weight of plant basis

	A	B	C	D	E
A					
B	*				
C	*	N.S.			
D	N.S.	*	*		
E	N.S.	*	*	N.S.	

(c) On a dry weight of root basis

	A	B	C	D	E
A					
B	*				
C	*	N.S.			
D	N.S.	*	*		
E	N.S.	*	*	N.S.	

Plants from all populations had similar shoot/root ratios, except those from Site E, which had a significantly lower ratio ($p < 0.01$) than plants from Sites A, B and C (Table 13). The environmental conditions were also approximately constant for the duration of the experiment (Table 14)

Table 13. Shoot/Root Ratios of plants from Cassop Vale used in the transpiration experiment

Site letter	Shoot/Root Ratio
A	0.41 ± 0.03
B	0.44 ± 0.09
C	0.38 ± 0.02
D	0.27 ± 0.03
E	0.16 ± 0.03

(Mean ± Standard Error)

(Sample size = 5)

Explanation of site letters on Table 1.

Table 14. Environmental data for the transpiration experiment using plants from Cassop Vale

Environmental factor	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Temperature (°C)						
24 hr. period	22.5	22.0	21.5	22.0	21.0	22.0
Daylight hours	22.5	22.0	21.5	22.0	21.0	21.5
Relative humidity (%)						
24 hr. period			Data not available			
Daylight hours	47	51	52	49	51	47

(Averages of temperature and relative humidity for 24 hours and daylight hours (0500-2100 hours G.M.T.) recorded).

When the transpiration rate of plants grown under the same environmental conditions were studied, very small differences were found (Figure 9), for although plants from Sites A, D and E still had higher rates of transpiration, analysis of variance showed that no significant differences existed except when the rate was expressed on a leaf area basis. In this case only the transpiration rates of plants from Sites C and E were significantly different from one another ($p < 0.05$) on Day 1 and Day 4. A large variation in the transpiration rate of plants from Site E was also found in this experiment and this again affected comparisons between all populations.

All plants used had similar shoot/root ratios, and the environmental conditions were approximately constant for the duration of the experiment. (Appendix).

iii) Effect of low root temperatures on the transpiration of plants from Cassop Vale.

Low root temperatures caused a large reduction in the rate of transpiration of Sesleria from Cassop Vale. Using the ice/water mixture it was possible to obtain a soil temperature of $2^{o}C \pm 1^{o}C$, and the transpiration rate under these conditions was about 20% of that at $23^{o}C$ for all populations, there being no significant difference between the sites (Table 16).

Figure 9. Transpiration rates of Sesleria collected from Cassop Vale and grown under the same environmental conditions.

(a) On a leaf area basis for Day 1 and Day 4.

(b) On a dry weight of plant basis for Day 1 and Day 4.

(c) On a dry weight of root basis for Day 1 and Day 4.

(Explanation of site letters A-E on Table 1

Sample size = 5

Mean and standard error of the mean plotted).

Fig. 9.

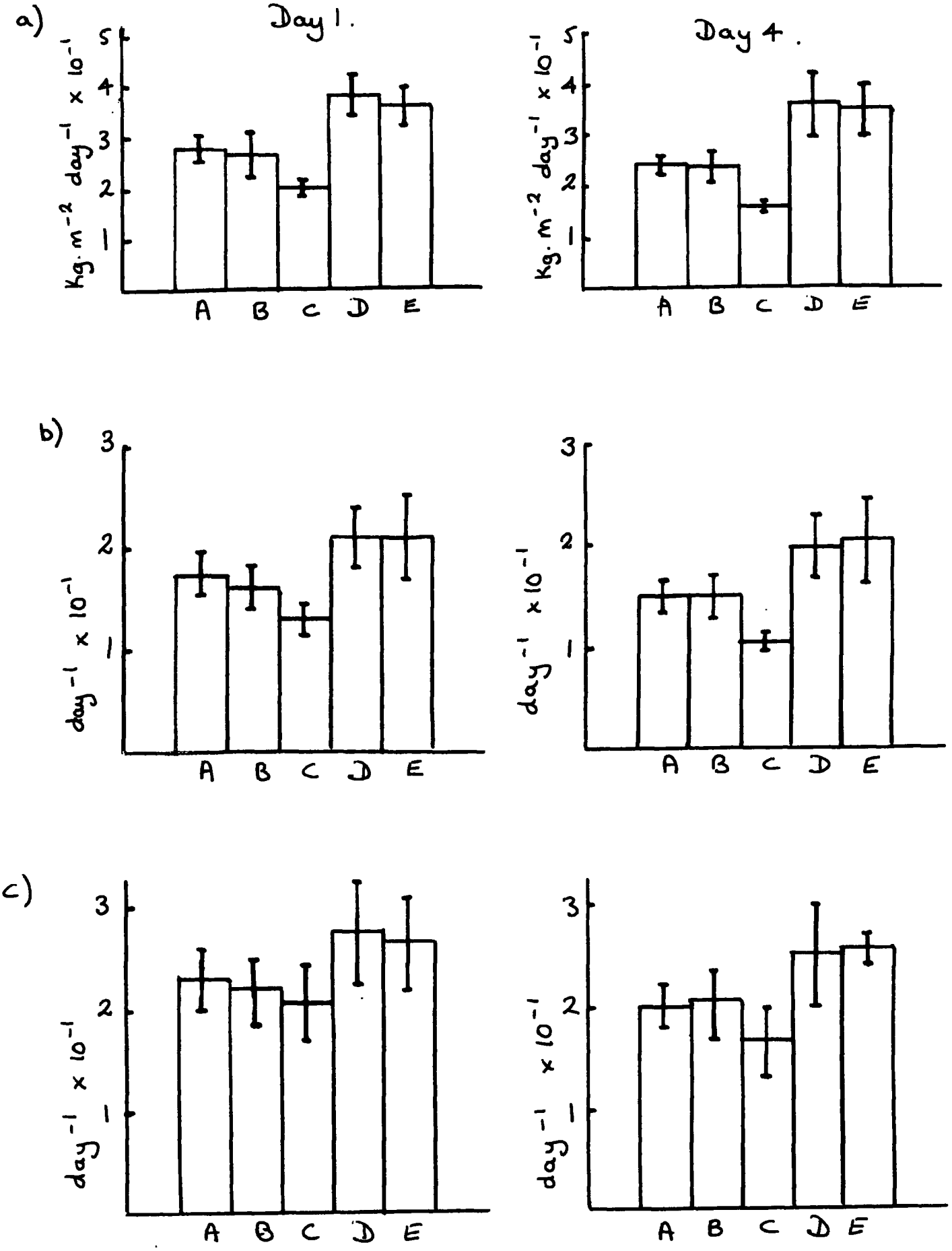


Table 15. Effect of low root temperatures on the transpiration rate of plants from Cassop Vale.

Site letter	Transpiration rate at 2°C root temperature as a percentage of transpiration rate at 23°C root temperature
A	16.6 ± 1.9
B	27.4 ± 5.2
C	28.2 ± 5.7
D	18.8 ± 2.1
E	22.8 ± 3.2

(Explanation of site letters on Table 1).

iv) Morphology of populations from different altitudes

When many populations of Sesleria from different altitudes were studied, an even greater variation in the morphology was observed, but no trend with altitude was found in any of the morphological features studied (Figures 10 and 11). However, the sites varied considerably in the depth of soil present, and as this had been found to be an important factor affecting the morphology of Sesleria at Cassop Vale, it was used as a basis for dividing the altitudinal sites into two groups. Populations growing on shallow, dry soils, (less than 10cm deep) on limestone cliffs were studied separately from those growing in deep, well-drained soils, (more than 10cm deep). A clear separation was possible because the limestone cliff habitat was clearly defined, and nearly all the sites with deeper soils had at least 20cm of soil present. There was a clear difference in the morphology of the plants from the two groups. As at Cassop Vale, Sesleria

Figure 10. Morphology of Sesleria from sites at different altitudes, (including sites A and C at Cassop Vale).

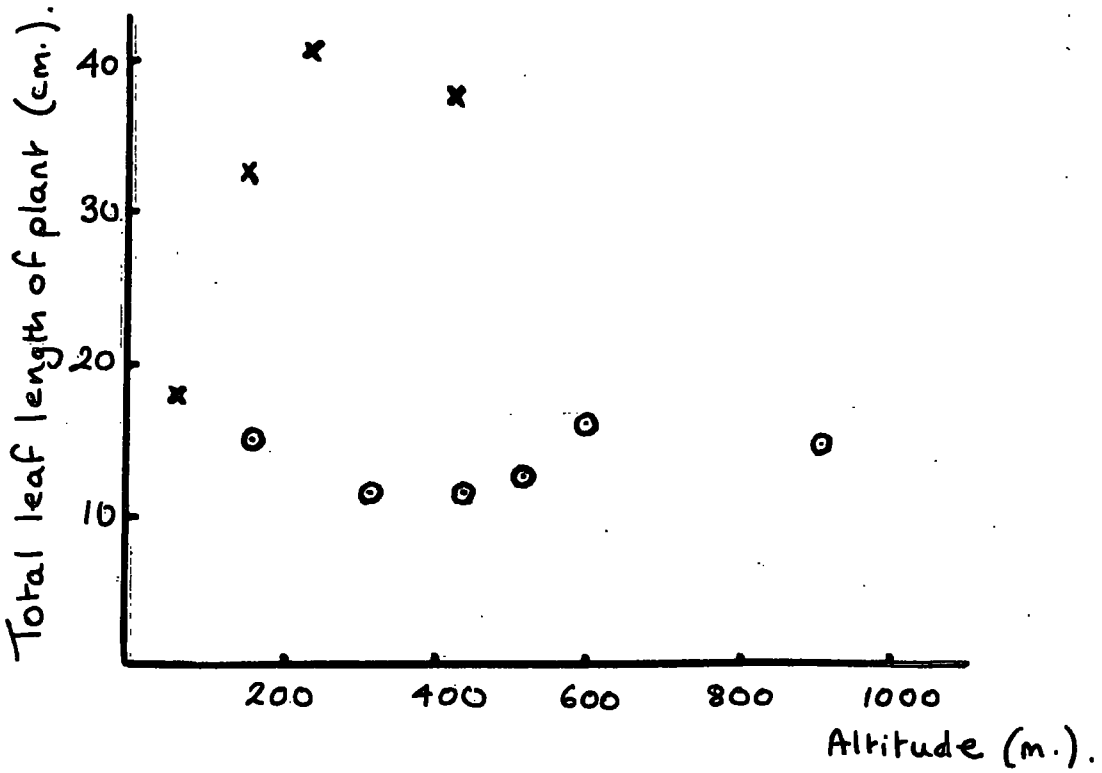
(i) Total leaf length of plant and length of longest leaf.

⊙ shallow soils (< 10 cm)

× deep soils (> 10 cm)

(Sample size = 30. Mean value plotted).

Fig. 10.


Total leaf length of plant (cm.).
40
30
20
10
200
400
600
800
1000
Altitude (m.).

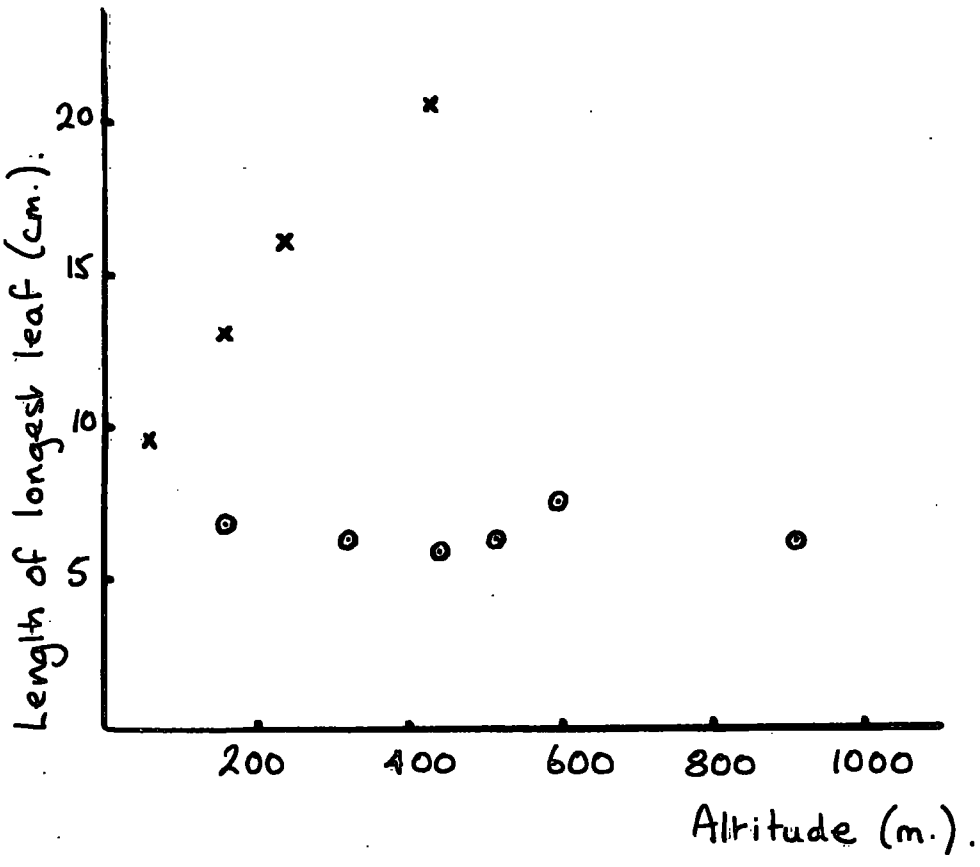

Length of longest leaf (cm.).
20
15
10
5
200
400
600
800
1000
Altitude (m.).

Figure 11. Morphology of Sesleria from sites at different altitudes, (including sites A and C at Cassop Vale).

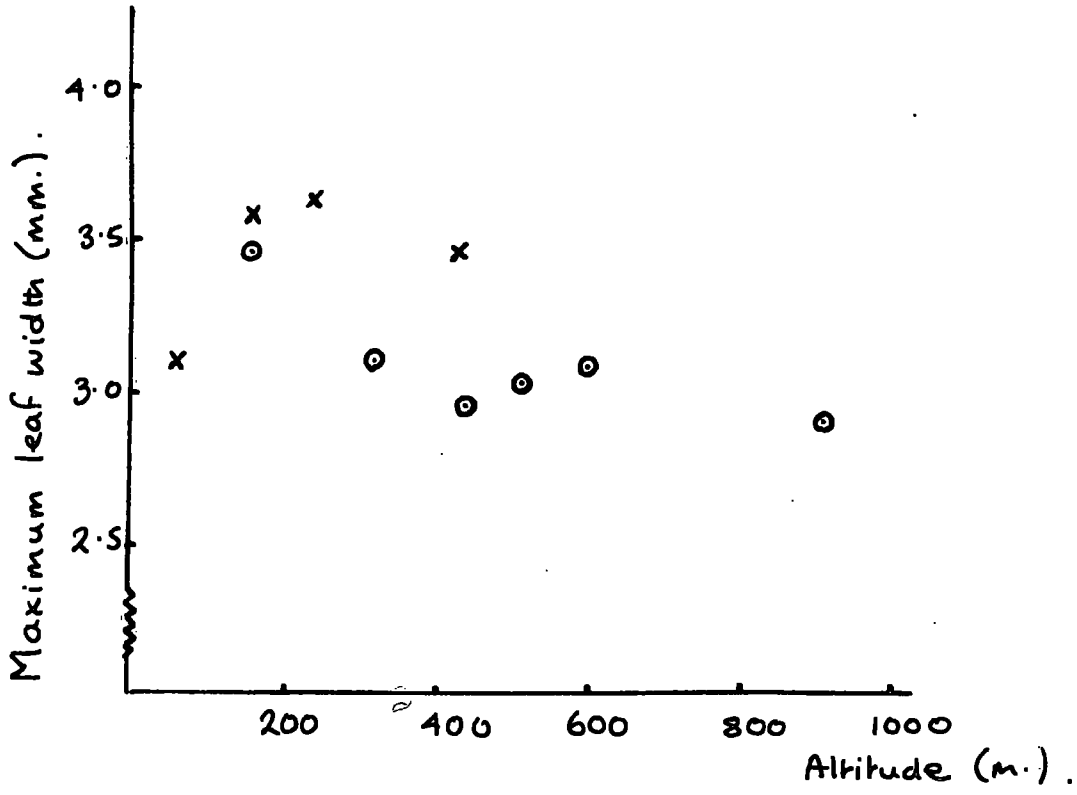
(ii) Maximum leaf width and height of inflorescence.

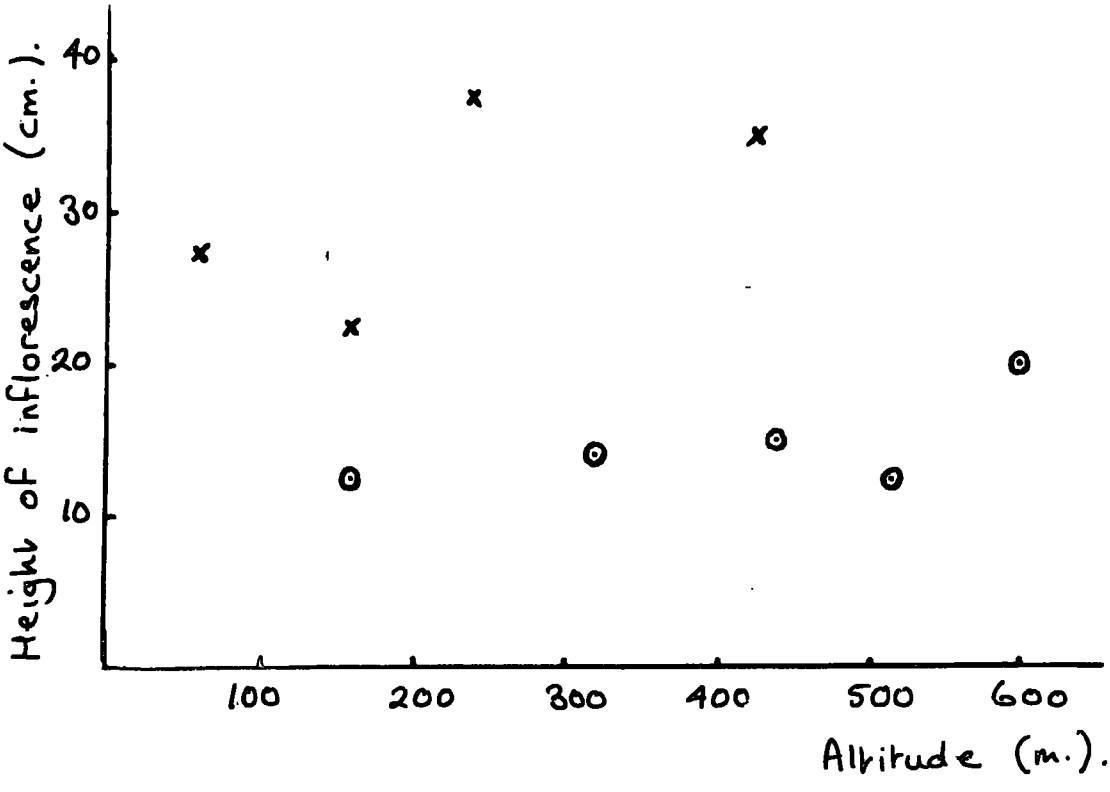
⊙ shallow soils (< 10 cm)

X deep soils (> 10 cm)

(Sample size = 30. Mean value plotted).

Fig. 11.


Maximum leaf width (mm.).
4·0
3·5
3·0
2·5
200
400
600
800
1000
Altitude (m.).


Height of inflorescence (cm.).
40
30
20
10
100
200
300
400
500
600
Altitude (m.).

growing in deep soils was much larger, had wider leaves and greater seed production than that on the shallow, dry soils. This difference was present irrespective of the altitude of the site.

When the sites with shallow soils were compared, very few differences in morphology and no trends with increasing altitude were observed, except for a small increase in size (Figure 12). All populations had similar leaf lengths and widths, and only at one site, (600 m. O. D), was the plant size and height of inflorescence significantly larger than at other sites ($p < 0.01$). When the population from the dry, shallow soil at Cassop Vale, (Site 1), was compared with those from different altitudes, some other small differences were observed, particularly the significantly wider leaves of Sesleria at Cassop Vale (Figure 13).

Similarly, no trends with altitude were observed in the morphology of the populations from the deeper soils, but very few sites of this type were studied, and soil depth was not measured accurately enough for a comparison to be made between these populations.

The leaf anatomy of Sesleria from deep and shallow soils was also studied separately, as differences at the same altitude relating to soil depth and dryness had already been found at Cassop Vale. Similarly differences were found in these populations; plants from the dry, shallow soils had a higher stomatal frequency than those from the deeper soils at a similar altitude, except for the population from Arnside,

Figure 12. Morphology of Sesleria from sites at different altitudes, (including sites A and C at Cassop Vale).

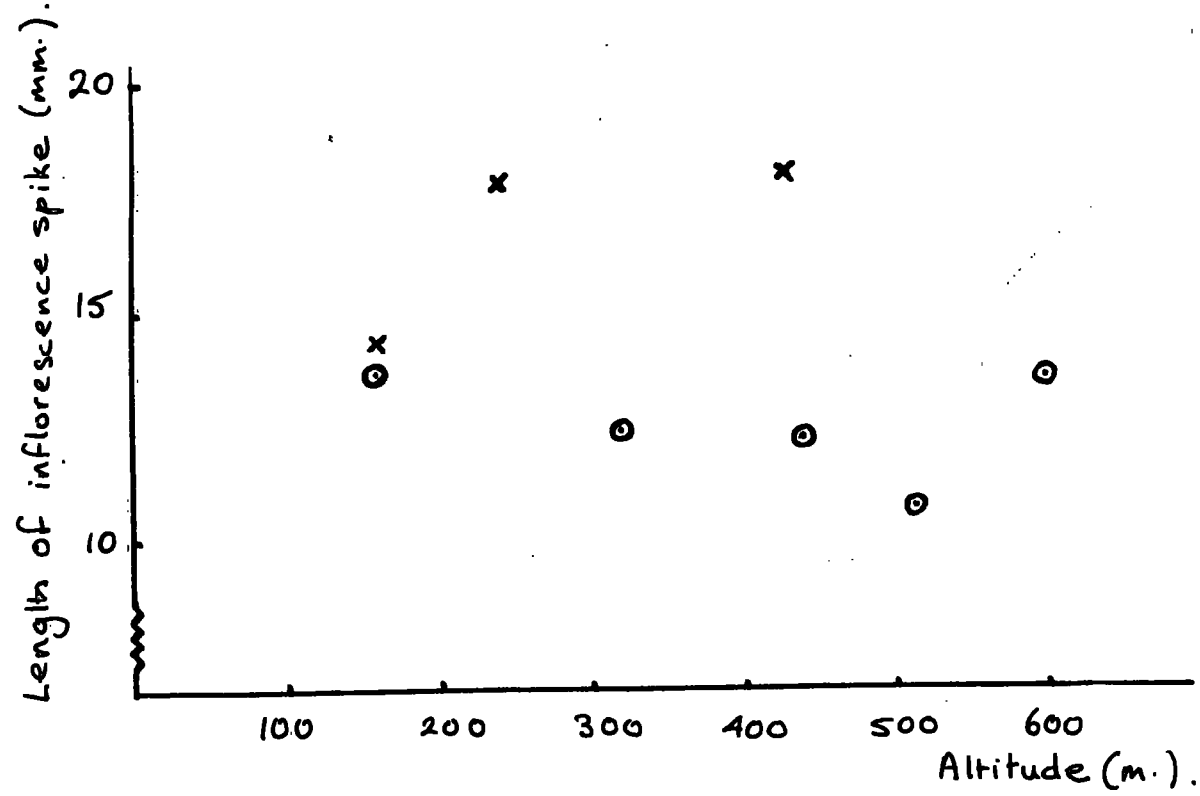
(iii) Length and dry weight of inflorescence spike.

⊙ shallow soils (< 10 cm)

× deep soils (> 10 cm)

(Sample size = 30. Mean value plotted).

Fig. 12.


Length of inflorescence spike (mm.).
20
15
10
100
200
300
400
500
600
Altitude (m.).

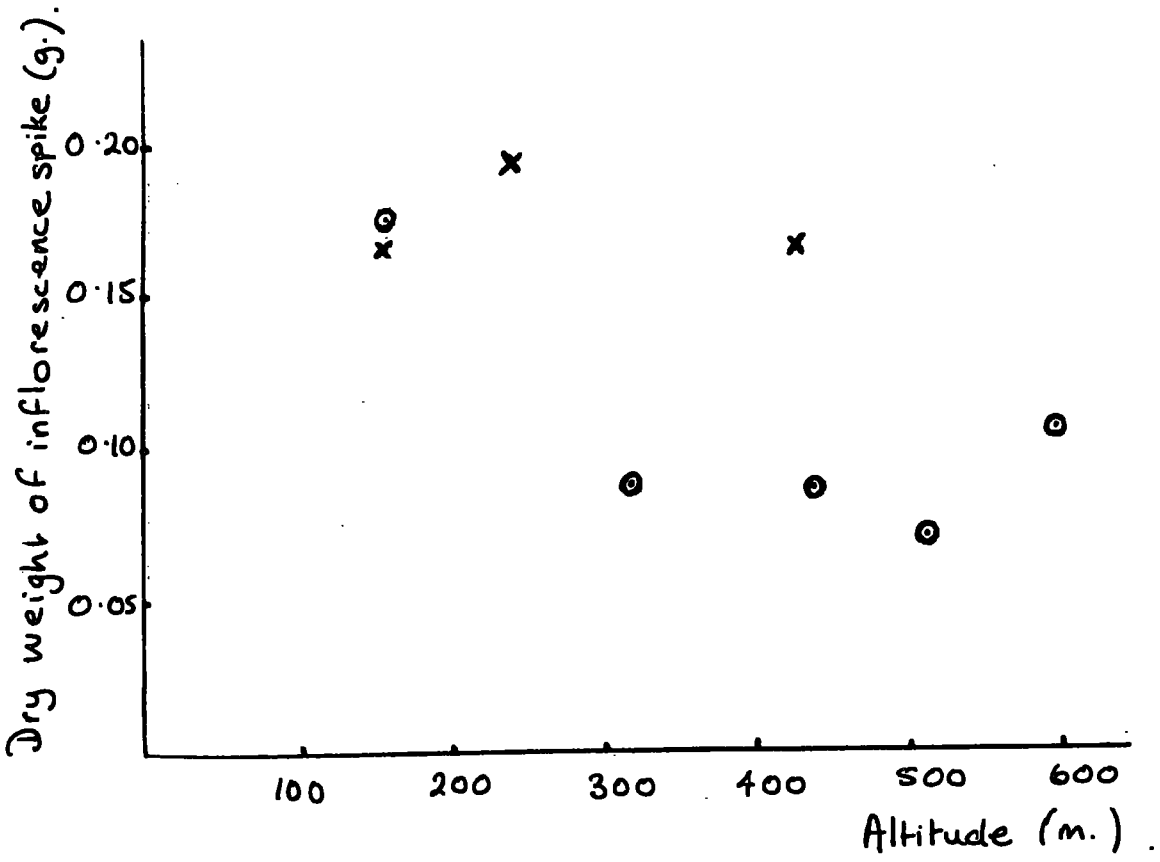

Dry weight of inflorescence spike (g.).
0·20
0·15
0·10
0·05
100
200
300
400
500
600
Altitude (m.).

Figure 13. Significance tests on the morphology of populations from shallow soils at different altitudes.

Key to site letters used.

1.	Cassop Vale (site A)	160 m O.D.
2.	Sunbiggin Tarn	320 m O.D.
3.	Askrigg	440 m O.D.
4.	Askrigg	515 m O.D.
5.	Buckden Pike	600 m O.D.
6.	Ben Lawers	910 m O.D.

(Explanation of significance levels on Fig. 4. Student's t-test used).

Figure 13.

(a) Total leaf length of plant

	1	2	3	4	5	6
1						
2	***					
3	***	N.S.				
4	*	N.S.	N.S.			
5	N.S.	***	***	**		
6	N.S.	*	*	N.S.	N.S.	

(b) Length of the longest leaf

	1	2	3	4	5	6
1						
2	N.S.					
3	*	N.S.				
4	N.S.	N.S.	N.S.			
5	N.S.	*	***	*		
6	N.S.	N.S.	N.S.	N.S.	*	

(c) Maximum leaf width

	1	2	3	4	5	6
1						
2	**					
3	***	N.S.				
4	***	N.S.	N.S.			
5	***	N.S.	N.S.	N.S.		
6	***	N.S.	N.S.	N.S.	N.S.	

(d) Height of inflorescence

	1	2	3	4	5
1					
2	N.S.				
3	*	N.S.			
4	N.S.	N.S.	N.S.		
5	***	***	***	***	

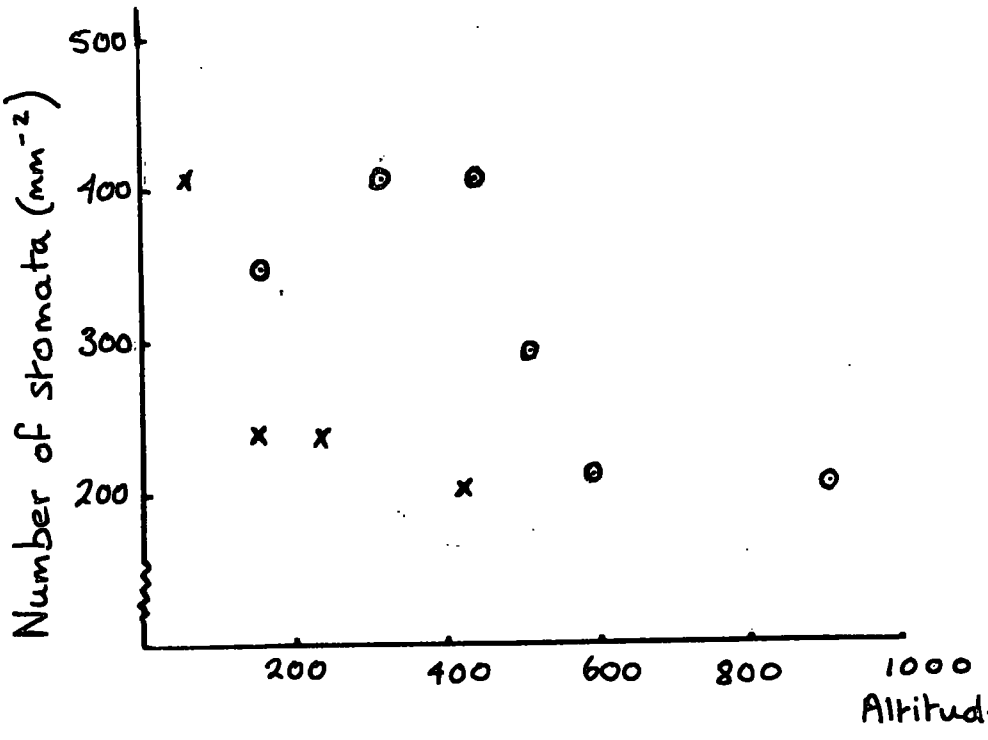
(60m. O. D), which had a high stomatal court similar to those from dry soils (Figure 14). It is possible that this site is relatively dry despite the depth of soil, as both general morphology and leaf anatomy measurements indicate this, but no measurements of soil moisture were made in the field.

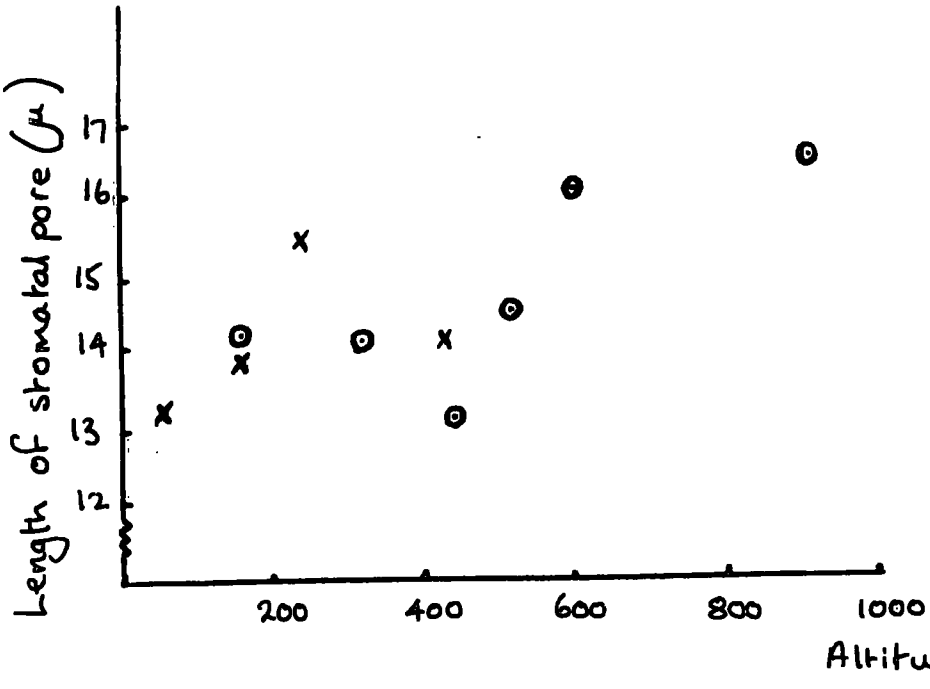
The populations from the shallow, dry soils were collected mainly from sites in the same geographic area and with the same soil type. However, as Cassop Vale has a magnesian limestone bedrock, and Ben Lawes is located at a different latitude to the other sites, it was decided to omit them from the preliminary analysis. For the other populations, a decrease in stomatal frequency and increase in the depth of the stomatal pore with increasing altitude was observed, together with a general increase in the length of the stomatal pore (Figures 14 and 15). The leaf anatomy of the Ben Lawers and Cassop Vale populations was similar to that of other high and low altitude plants, but slight differences in the stomatal frequency of plants at Cassop Vale and the depth of pore of plants at Ben Lawers were observed, possibly due to the different soil type or latitude of the site. For populations from deeper soils a similar decrease in stomatal frequency, and a slight increase in length and depth of the stomatal pore was observed with increasing elevation of the site (Figure 14).

Also, in populations from both shallow and deep soils an increase in the ratio of interstomatal spacing to length

Figure 14. Leaf anatomy of Sesleria from sites at different altitudes, (including sites A and C at Cassop Vale).
(Sample size = 30. Mean value plotted).

Fig. 14.


Number of stomata (mm^{-2})
500
400
300
200
200
400
600
800
1000
Altitude (m.).


Length of stomatal pore (μ)
17
16
15
14
13
12
200
400
600
800
1000
Altitude (m.).

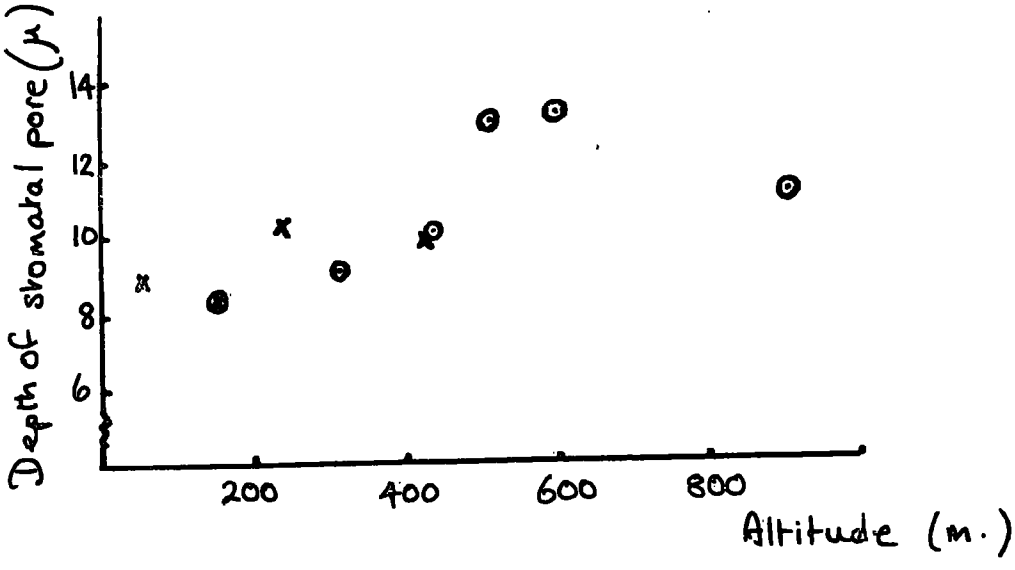

Depth of stomatal pore (μ)
14
12
10
8
6
200
400
600
800
Altitude (m.)

Figure 15. Significance tests on the leaf anatomy of populations from shallow soils at different altitudes.
(Explanation of site letters 1-6 on Fig. 13. Explanation of significance levels on Fig. 4. Student's t-test used. Sample size = 30).

Fig. 15.

(a) Number of stomata

	1	2	3	4	5	6
1						
2	***					
3	***	N.S.				
4	***	***	***			
5	***	***	***	***		
6	***	***	***	***	N.S.	

(b) Length of stomatal pore

	1	2	3	4	5	6
1						
2	N.S.					
3	**	***				
4	N.S.	N.S.	***			
5	***	***	***	***		
6	***	***	***	***	N.S.	

(c) Depth of stomatal pore

	1	2	3	4	5	6
1						
2	N.S.					
3	***	*				
4	***	***	***			
5	***	***	***	N.S.		
6	***	***	N.S.	**	**	

of stomatal pore with increasing altitude was recorded (Table 16).

Table 16. Ratio of interstomatal spacing to the length of the stomatal pore for populations from different altitudes

Altitude (m)	Depth of soil (cm)	Interstomatal spacing / Length of stomatal pore
60	deep	5.0
240	deep	6.5
320	shallow	2.9
430	deep	6.5
440	shallow	4.0
515	shallow	5.6
600	shallow	9.0
1030	shallow	5.9

When plants from shallow soils at different altitudes were collected and grown under the same environmental conditions, the new leaves produced were more similar than those from the original populations. Stomatal frequency still decreased and the depth of the stomatal pore still increased with increasing elevation of the original site, but the differences between the populations were not so great. There was only a small variation in the length of the stomatal pore in the different populations (Table 17).

Table 17. Leaf anatomy of plants collected from shallow soils at different altitudes and grown under the same environmental conditions.

Altitude (m)	Number of stomata (mm^{-2})	Length of stomatal pore (μ)	Depth of stomatal pore (μ)
320	289 ± 5	14.5 ± 0.3	8.9 ± 0.2
440	286 ± 7	14.4 ± 0.3	9.3 ± 0.3
515	259 ± 8	13.4 ± 0.3	10.6 ± 0.3
600	214 ± 6	14.5 ± 0.3	10.5 ± 0.4

v) Transpiration of plants from different altitudes

Laboratory measurements showed that slight differences in the average rate of transpiration were present when Sesleria from the same geographic area was studied (Figure 16). However, although the rate of transpiration of plants from high altitudes was lower, analysis of variance showed that there were no significant differences between the populations, regardless of the basis of the transpiration measurement.

A repeat of the experiment, using the same populations and those from Cassop Vale and Ben Lawes, yielded similar results, as there was generally a non-significant decrease in the rate of transpiration with altitude (Figure 16). Both the Cassop Vale and Ben Lawers populations had transpiration rates which did not always agree with the general trend, but these differences depended on the basis of the transpiration measurement. In both experiments a large variation in the transpiration rate was observed, and so

Figure 16. Transpiration rates of Sesleria from shallow soils at different altitudes.

(a) On a leaf area basis for Experiments 1 and 2.

(b) On a dry weight of root basis for Experiments 1 and 2.

(c) On a dry weight of plant basis for Experiments 1 and 2.

(Sample size = 5

Mean and standard error of the mean plotted).

Fig. 16.

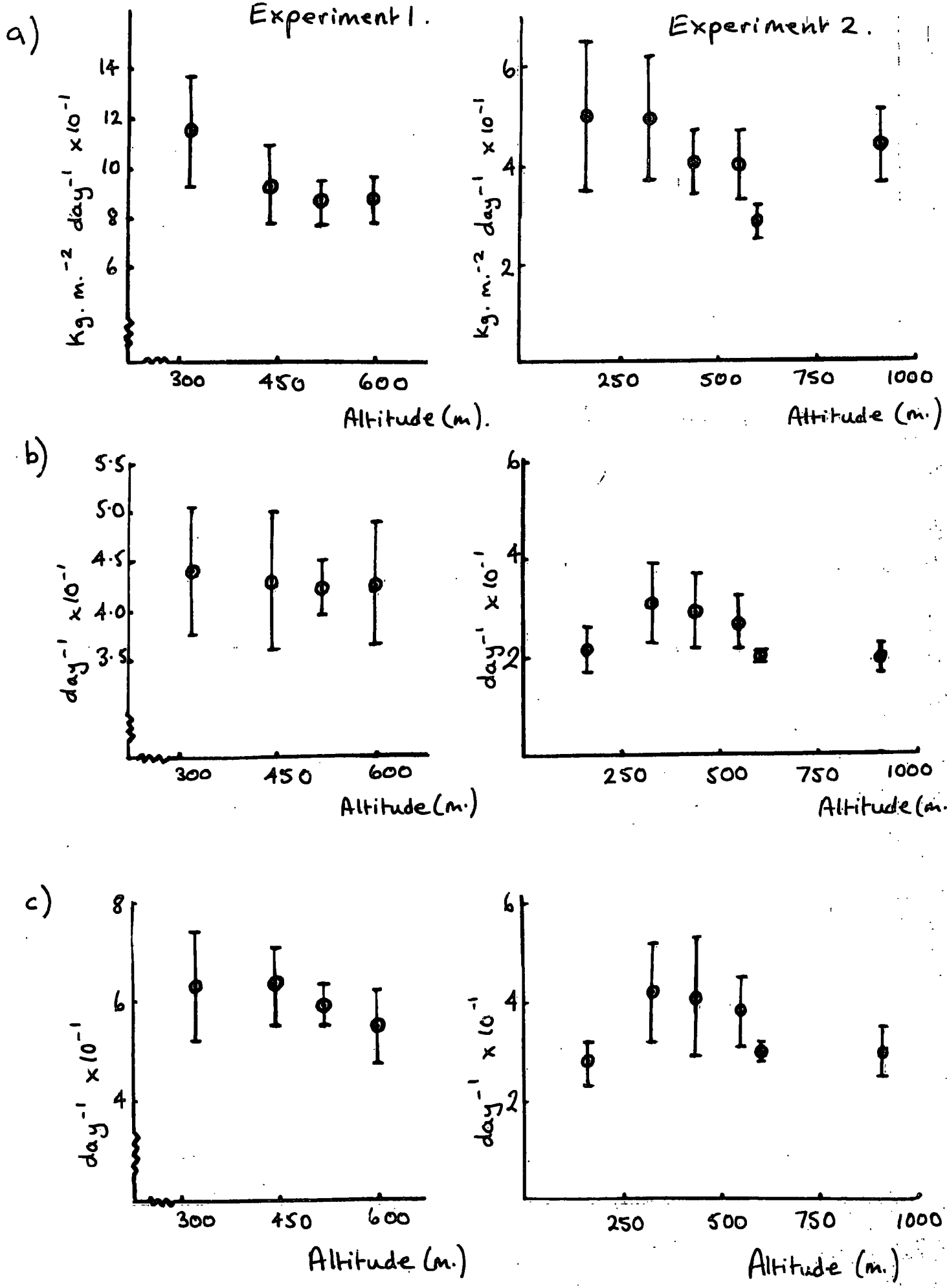
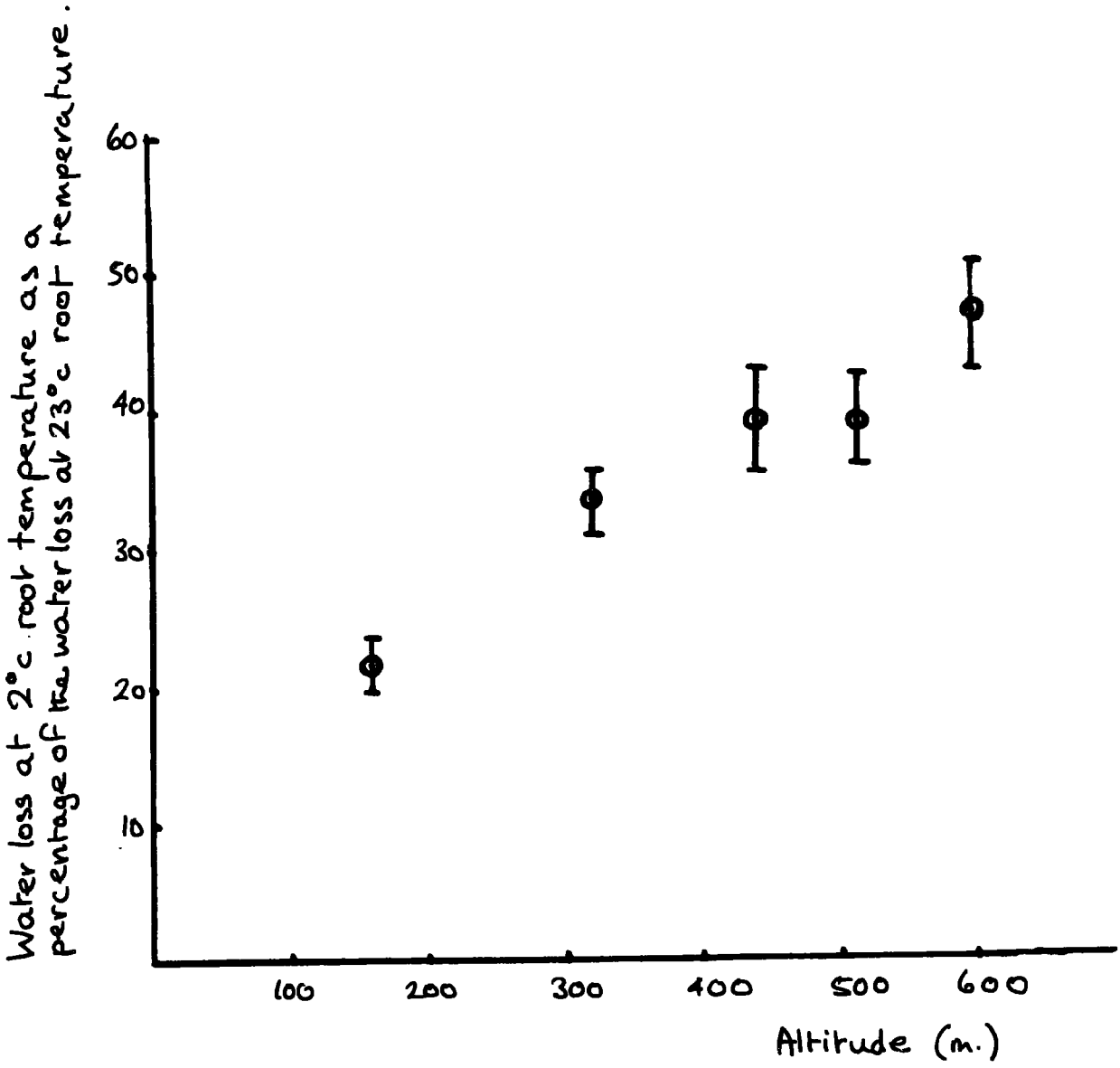

a)
Experiment 1.
Experiment 2.
kg. m.$^{-2}$ day^{-1} x10^{-1}
14
12
10
8
6
300
450
600
Altitude (m).
6
4
2
250
500
750
1000
Altitude (m.)
b)
day^{-1} x10^{-1}
5·5
5·0
4·5
4·0
3·5
300
450
600
Altitude (m.)
6
4
2
250
500
750
1000
Altitude (m.)
c)
day^{-1} x10^{-1}
8
6
4
300
450
600
Altitude (m.)
6
4
2
250
500
750
1000
Altitude (m.)

Figure 17. Effect of low root and soil temperatures on the transpiration rate of Sesleria from shallow soils at different altitudes, (including significance tests on the data). (Explanation of site letters 1-5 on Fig. 13. Explanation of significance levels on Fig. 4. Sample size = 15 Analysis of variance and S.S.R's used).

Fig. 17.


Water loss at 2°c root temperature as a percentage of the water loss at 23°c root temperature.
60
50
40
30
20
10
100
200
300
400
500
600
Altitude (m.)

a large sample size is necessary to determine if there are significant differences between the populations.

vi) Effect of low root temperatures on the transpiration of plants from different altitudes.

Low root temperatures caused a reduction in the transpiration rate of Sesleria collected from shallow soils at different altitudes. The greatest reduction was observed in populations from low elevations, and this gradually decreased with increasing altitude, so that there was a significant difference in the effect of low temperatures on the various populations (Figure 17). The population from the shallow soil at Cassop Vale has also been included for comparison, as the reduction in transpiration of plants from this site was significantly greater than any other site studied.

Discussion

Morphological variation in plant species has been attributed to the effect of various environmental factors on the growth form (Heslop-Harrison 1964). In Northern England, the growth of Sesleria, (as measured by plant size) is mainly related to the edaphic conditions of the habitat in the sites studied, with both soil depth and water relations being important (Figures 3 and 10). The species favours a deep, well-drained soil, which provides an adequate water supply and rooting depth, and grows less well on a dry or constantly wet soil. On the dry, shallow soils the very low moisture content (Table 1) may be important, as it is well known that a water deficit limits plant growth, (Richards and Wadleigh 1952, Stanhill 1957), but other factors such as nutrient deficiency or rooting depth should also be considered, and further investigation involving measurement of these factors is necessary. Sesleria was only found on one wet site, and the poor growth here may be a direct effect of the waterlogged soil, (e.g. low oxygen concentration around the roots), or an indirect effect of competition from other species more suited to this type of habitat (Table 6).

Many environmental factors change with altitude, (air temperature, soil temperature, light intensity, wind speed, rainfall, soil water and nutrient content), and these may all affect growth (Warren Wilson 1959, Hunter and Grant 1971). For certain factors approximate rates of change with increasing

altitude have been determined, and these can be applied to the field situation provided that topographical features are also considered. Manley (1952) quotes an observed temperature lapse of 0.67°C/100m. of altitude in Northern England and an increase in rainfall of approximately 100mm/100m. in North-West England, and Woodward (1973) quotes an increase in the mean daily windspeed of 0.66 ms^{-1}/100m. of altitude, so this data may be used when studying morphological variation with altitude. In field investigations, it is however very difficult to study the effect of one environmental factor, as they are not independent of one another.

With increasing altitude there is often a decrease in the growth rate and height of plants (Clausen, Kech and Hiesey 1948, Ward 1969, Hunter and Grant 1971, Pearcy and Ward 1972, Woodward 1973). This was not found in populations of Sesleria in Northern England, over the range of altitude studied, and other environmental factors not directly related to altitude seem to be more important in determining plant size. Soil depth has a large influence on the growth even at relatively high altitudes, as at Malham (430m. O. D) plants were over three times the size, and had wider leaves than those found on shallow soils at lower altitudes (Figure 10). A deep soil will provide a larger water and nutrient supply of longer duration, and a greater rooting medium, but insufficient evidence is at present available to decide if any one factor has more effect. Soil moisture is likely to

be important as Turesson (1925) demonstrated that the populations of a number of species growing on dry limestone soils were genetically smaller, or narrower-leaved than populations from less xeric habitats. It has since been shown by several workers that size reduction and narrowing of the leaf is a common feature of plants of dry habitats (Shields 1950, Stocker 1960).

As soil depth has such a large influence on the morphology of Sesleria, it is necessary to consider sites with similar soil depth, in order that the effect of the changing climate with altitude can be studied. Plants growing on shallow soils at different altitudes have very similar morphological features and no altitudinal trend can be observed, (Figure 12), so although higher altitudes have a less favourable climate, and the growing season is reduced by 20 days/100m altitude in N. England, (Manley 1952), this has little effect on the size of Sesleria over the altitudinal range studied. At greater elevations the more severe climate is more important, as plant size decreases in populations of Sesleria in the Dolomites with an increase in altitude from 3000m to 6000m (Alexander 1975, unpublished). In Britain, the low growth rates of Sesleria, (Woodward 1973), combined with the water deficiency on shallow soils seem to be more important in determining plant size. A slight increase with altitude is observed if sites from only one geographic area are considered, Cassop Vale and Ben Lawers populations being excluded.

The slightly greater growth of plants at higher altitudes may be due to greater water availability as Woodward, (1973), found that the increase in rainfall and fall in air temperature and total daily short wave radiation flux density leads to a reduction in the evaporation from the soil with increasing altitude. Hunter and Grant (1971) also found a significant correlation ($p = 0.05$) between decreasing soil moisture tension and increasing altitude, when studying the growth of Lolium perenne on Scottish mountains. Yield of Lolium perenne on a yearly basis decreased with altitude, as temperature was the most important climatic variable affecting growth for most of the year. However, during the summer months, when the temperature was at an optimum, yield actually increased with altitude, due to the development of moisture stress at lower altitudes. The adverse effect on growth of a soil moisture deficit was also shown by comparing growth on two soils with different moisture tensions at the same altitude. It is possible, therefore, that growth of Sesleria in Britain is largely determined by the soil moisture tension, but much more detailed study on this aspect is required before any definite conclusions can be made.

Studies on the leaf anatomy of Sesleria from Northern England have been made previously by Lloyd (1974) on laboratory grown plants, and he obtained results very similar to those obtained in this investigation. Average values of approximately 350 stomata/mm^2, 16μ pore length and 11-12μ pore depth found

by Lloyd, are within the ranges found in the field of 200-400 stomata/mm^2, 12-16.5μ pore length and 8-13μ pore depth (Figures 5, 6 and 14). This wide range of values can be explained when it is considered that leaf structure is modified significantly by the environment in which the leaves develop, and several factors are known to influence leaf shape and anatomy (Stocker 1960, Lewis 1969, 1972). High light intensity and soil dryness have similar effects on leaf structure in many species, as leaves produced under these conditions often have a smaller area, thicker lamina, greater stomatal frequency, greater vein density, more compacted mesophyll, smaller epidermal cells and thicker cuticle. It was not possible to measure many of these in this investigation, but results obtained in this study indicate that Sesleria from dry habitats does have smaller leaves with a greater stomatal frequency than that collected from soils with a higher moisture content (Figures 5 and 14). Although soil moisture was not measured at different altitudinal sites, it can be assumed that shallow soils would dry out more quickly than deep ones. This fact is reflected in the stomatal frequencies of the plants, as the higher stomatal frequencies were found in plants growing in a shallow soil. The decrease in stomatal frequency with increasing altitude found in the populations from shallow and deep soils can be explained by a change in soil moisture tension with altitude which has been recorded by Woodward, (1973), and Hunter and Grant (1971).

Soil dryness is known to influence stomatal frequency, and as a decrease in stomatal frequency and a decrease in moisture tension with increasing altitude have been recorded, it is possible that this is a casual effect, but other factors such as light intensity should also be considered. The higher stomatal frequency found in plants from shallow lowland soils, also corresponds to the higher drought situation recorded by Woodward (1973) for similar lowland habitats in N. England where Sesleria was growing.

Differences in both length and depth of the stomatal pore were also found in the populations studied. The length of pore was inversely correlated with stomatal frequency ($r = 0.7$) and a decrease in the size of the pore with increasing soil dryness has also been recorded for some species, (Stocker 1960), so the causes of pore length changes are probably similar to those of stomatal frequency.

Sunken stomata occur in many species, especially those from extreme environments, (Slatyer, 1967), or dry habitats, (Stocker 1960), and as Sesleria is often found in the latter, their presence could be mainly a morphological adaptation to reduce water loss. However, this is unlikely, as there was no correlation between depression depth and dryness of the habitat. With increasing altitude there is an increase in the depth of the pore, and as the depression depth affects the length of the diffusion pathway for water vapour and carbon dioxide into and out of the leaf, this will affect the rate of transpiration and photosynthesis. At high altitudes there

is less need to control water loss as the rainfall is higher, and the lower temperatures will also reduce the rate of evaporation from both plant and soil. Lloyd (1974) suggested that the deep depression depths in Sesleria help to raise leaf temperatures relative to air temperatures by increasing the boundary layer resistance and reducing transpiration. He showed experimentally that plants with deeper stomatal pores had higher leaf temperatures, and predicted that these plants would have higher rates of photosynthesis in the temperature range of 5-15^{o}C, as a small increase in leaf temperature will produce large increases in the photosynthetic rate of 5-6% per ^{o}C at 10^{o}C. The predominant effect of increasing altitude is a fall in the mean air temperature, (Woodward 1973), and this reduces the photosynthetic rate and growth of many plant species. In Sesleria however, leaf temperatures greater than air temperatures may be present at high altitudes, so the rate of photosynthesis is reduced less. This may help to explain why there is no reduction in the size of Sesleria with increasing altitude.

Morphological investigations of Sesleria collected from different habitats and grown under the same environmental conditions indicate that a large variation which exists in the field is mainly due to the plastic response of the plants to their environment, as plants grown at Durham had similar morphology (Figure 6). Ecotypes may exist in different geographic locations, as populations from different areas and altitudes still have some significant differences in leaf anatomy when grown under the same environmental

conditions (Table 17). However, within one site, although a large variation may be present in the field, the plants appear to have similar genotypes, as no significant differences in leaf anatomy are present when grown in the same environment. It is likely that the Cassop Vale population is an edaphic ecotype as Round-Turner (1968) postulated, since it is geographically separate, and many aspects of the morphology and physiology of plants from this site are significantly different from that of plants from similar habitats in areas of carboniferous limestone (Figure 12).

Lloyd (1974) found that populations of Sesleria collected from Malham and Teesdale had similar morphology (leaf width, stomatal frequency, length and depth of stomatal pore) and similar physiology (photosynthesis and transpiration), so no evidence of ecotypes was found. However the two populations, although from different geographic areas, were collected from sites only 100m in altitude apart, (Malham 395m, Teesdale 500m), and over this altitudinal range very few differences in leaf anatomy were recorded when plants were grown under the same environmental conditions (Table 17).

In studying the physiological responses of the plant to its environment, two different approaches may be used. If populations from different geographical areas are collected and grown in uniform conditions, any differences in physiology would be genetic in nature and it may be possible to relate

these to the ecology of the species. However this approach may not be considered valid, as the physiological responses of the plant measured in the laboratory may bear little relation to the responses in the field. Field measurements should really be made, but these usually involve considerable practical differences if accurate results are required, and a comparison of different populations would give no information about the genetic differences. Ideally laboratory measurements under uniform conditions should be made together with measurements in the field.

This approach was used by Mooney and Billings, (1968), Mooney, Wright and Strain (1964) and Bazzaz (1973) who measured the rate of photosynthesis in both field and laboratory. They found differences between the two situations because it was not possible to exactly reproduce field conditions in the laboratory. Acclimatisation of plants should also be considered when plants are grown under uniform conditions, as there are many examples of different growth temperatures affecting physiological processes (Drake and Salisbury 1972, Pasternak and Wilson 1972, Beardsall and Mitchell 1973). If acclimatisation of plants has taken place, it is then no longer possible to extrapolate laboratory data to the field, so it is necessary to make careful use of any measurements made under controlled conditions.

In this investigation an attempt was made to obtain some measure of water loss from plants in the field and laboratory, but because of the nature of the plant material

and the equipment available the methods chosen were not ideal. The cobalt chloride (or thiocyanate) paper method gives a measure of the escape of water vapour from a leaf, but involves the removal of the boundary layer around the leaf, so that wind has no effect and the leaf below the paper is transpiring into almost completely dry air. Milthorpe (1955) therefore states that this method is inapplicable for measuring rates of transpiration in the field, and is more truly an estimate of the diffusive conductance of the stomata. Despite these limitations, it was originally considered that any field measure of water loss would be useful, but the inaccuracies involved were too large for any definite conclusions to be drawn from the results, and some other method of measuring transpiration in the field is necessary. Although the environmental conditions around the leaves were different at all sites studied, the results do agree with those of Mooney and Billings (1968), who found that the transpiration sites were related to the water supply to the habitat (Table 12).

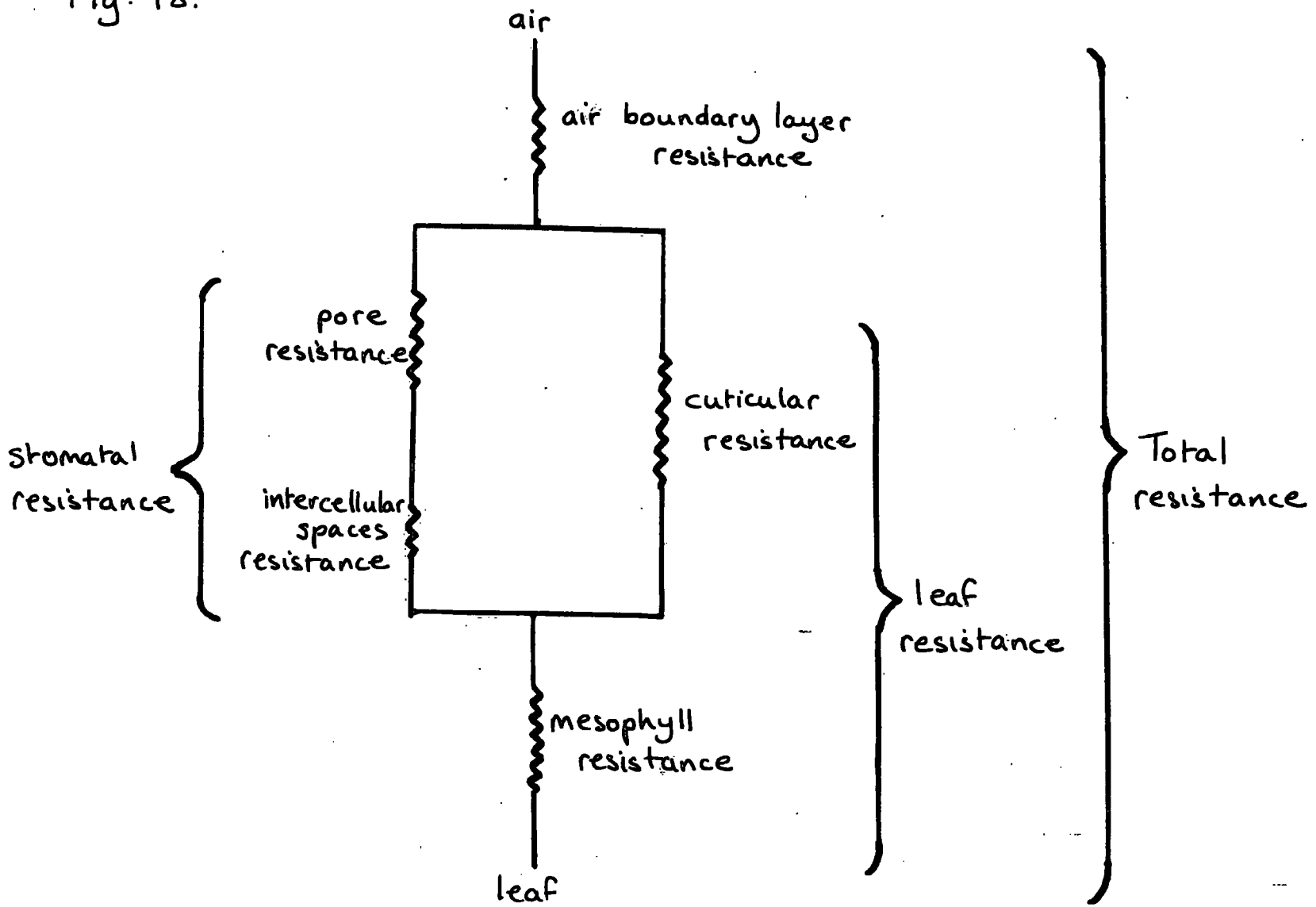
In the laboratory the phytometer method gives an accurate measure of the rate of transpiration under constant conditions, and is useful for studying the reaction of plants to different environments. It does, however, have certain limitations in its use, as extrapolation of transpiration rates of plants in the laboratory to estimates in the field is unreliable, because of the difference in environmental conditions (Statyer 1967, Kramer 1969). The edaphic conditions of a

potted plant may be considerably different from those in the natural environment, as it is necessary to confine the roots to a small space and use a standard soil at field capacity for phytometry experiments. Therefore, because of the difficulty of extrapolation to the field, and the fact that rates measured in this way do not agree with rates obtained using cobalt thiocyanate paper, (Bailey et. al., 1952), results from this method were used mainly for studying the relationship between structure and physiology.

In the field the nature of the soil, plant and environment around the leaves all influence transpiration. In laboratory experiments, however, both the soil and atmospheric conditions are approximately the same for all plants, so any differences observed should be related to the plant structure, particularly the surface area, external morphology and internal structure of the leaves (Sutcliffe 1968). Leaf structure affects the transpiration rate because the stomata, mesophyll and cuticle of the leaf, and the air boundary layer adjacent to it all contribute to the total resistance to the diffusion of water vapour (Figure 18). The rate of transpiration is influenced to some extent by all these structures, as it is inversely proportional to the total diffusive resistance if there is a constant vapour pressure difference between the leaf and the bulk air outside (Kramer 1969). As the boundary layer resistance is primarily determined by wind speed and leaf geometry, leaf width will affect transpiration. Lewis (1972) considers the effect of this resistance on transpiration to be small, but

Figure 18. Diagram of resistance to diffusion of water vapour from a leaf. (after Kramer, 1969).

Fig. 18.


air
air boundary layer resistance
pore resistance
cuticular resistance
stomatal resistance
intercellular spaces resistance
leaf resistance
Total resistance
mesophyll resistance
leaf

from values quoted by Slatyer (1967) and Kramer (1969) it may make a significant contribution to the total resistance when the stomata are open. Lloyd (1974) also concluded that the differences in leaf width in Sesleria influenced the transpiration and photosynthesis, and related this to the ecology of the populations.

The diffusive resistance due to the stomata can be closely estimated from equations produced by Parlange and Waggner (1970) for pores of known geometry, but insufficient data are available from this study to use these formulae. Lewis, (1972), however, found that the stomatal resistance was inversely proportional to the product of stomatal frequency and pore depth, so it should be possible to apply this to Sesleria provided that populations with similar pore depths are considered. Mesophyll resistance is difficult to measure experimentally, but appears to be inversely proportional to leaf thickness, and the value of the cuticular resistance is high compared with the other diffusive resistances (Slatyer 1967, Kramer 1969).

Most of the differences in the rates of transpiration recorded for the plants from Cassop Vale in this investigation can be explained by differences in the stomatal resistance. As there are no significant differences in pore depth, stomatal resistance is approximately inversely proportional to the product of stomatal frequency and pore length. A correlation between this product and the rates of transpiration for the various populations gave values of $r = 0.68$ for leaf

area, r = 0.98 for total dry weight of plant and r = 0.93 for dry weight of root bases of transpiration, so the stomatal resistance seems to be the main factor influencing the rate of water loss. The high rate of transpiration of plants from a dry soil was initially quite surprising, but this has been observed several times in watered dry habitat plants (Schneider and Childers 1941, Van der Paauw 1949), and can be explained by the value of the stomatal resistance.

In the wet site plants the boundary layer resistance will also be lower, as these populations have significantly narrower leaves, and this may help to explain the higher transpiration rates (Figure 7). Although no measure relating to mesophyll or cuticular resistance was made, there does not seem to be any important differences in these values in the various populations, as the transpiration rates can be explained by consideration of other diffusive resistances only.

Other structural features which also affect the rate of transpiration are the size of shoots and roots and the shoot/root ratio. It has been found that on a per unit area basis, smaller plants often transpire at a greater rate than larger plants, (Miller 1938), and this may also partly explain why populations from the wet sites (D and E) have a higher transpiration rate; for although every attempt was made to use plants of the same size, it was necessary to use slightly smaller plants on average from these populations. Parker (1949)

found that transpiration increases with a decrease in the shoot/root ratio, but there was no significant difference in this ratio for all populations used, except for the population from the very wet site (Table 12). At this site a lower ratio was found, and this may also contribute to the higher rate observed in this population.

In the transpiration experiments on the plants grown under the same conditions, very few differences in both the morphology and the transpiration rate were observed, so a relationship between structure and physiology is again evident. Although most of the plants used had new leaves, a very small amount of the original plant material collected from the field was sometimes still present; this may have contributed to any measurements made, so that a closer relationship was not obtained. In both experiments the size of the root system was approximately the same in all populations, but any differences were accounted for by expressing the transpiration on several bases.

Although non-significantly different transpiration rates were obtained from the altitudinal populations, this may be due entirely to the variation in transpiration rate recorded for each population. As the sample size was small (5), and the variation large, this resulted in large standard errors and non-significant differences, so it is necessary to use many more plants in each experiment. If, however, average rates of transpiration are used, some relationship between structure and physiology is still evident, as stomatal

resistance (as calculated by Lewis' formula, 1972) and transpiration rate both change with altitude. There is a good correlation between the transpiration rate and the product of stomatal frequency and pore length ($r = 0.62$ for leaf area, $r = 0.80$ for dry weight of plant, $r = 0.67$ for dry weight of root bases of transpiration), but the values of r are not so high as obtained from the Cassop Vale populations. It is necessary to include the populations from Cassop Vale and Ben Lawers in this correlation, as otherwise the sample size would be too small for statistical tests. These populations, however, provide the greatest differences observed, and so reduce the value of r.

In these populations the effect of the different depression depths must also be considered, as depression depth increases with altitude. It would be expected that this would also contribute to a reduction in transpiration rate, as Lloyd (1974) found a correlation between depression depth and minimum stomatal resistance in Sesleria. It is therefore surprising that only small non-significant differences in transpiration rate are observed, and it is necessary to consider other possible factors which may affect the rates.

As Sesleria has a relatively high number of stomata, it is possible that these interfere with one another, and so change the stomatal resistance. Parlange and Waggner (1970) state that interstomatal interference is unlikely to be of importance if interstomatal spacing is at least 3x stomatal length. Values of less than 3 were obtained by Lloyd (1974)

in British populations of Sesleria, which contributed to their high stomatal resistance and low rates of transpiration and photosynthesis compared with other populations. In this investigation a value of less than 3 was found in only one population, collected from a lowland habitat with a dry shallow soil (Table 16). Stomatal resistance will therefore be higher and transpiration lower in this population than would be expected from consideration of only the frequency and geometry of the pores. This reduction in transpiration may be related to the ecology of the population, as higher water deficits occur in lowland sites (Hunter and Grant 1971 Woodward (1973)). Also, the effect of stomatal interference may help to explain why there is only a small reduction in transpiration rate with increasing elevation of the populations, as the ratio of interstomatal spacing/length of pore increases in populations from higher altitudes and stomatal interference has less effect. Other factors which may affect the rate of transpiration do not seem to be important in this experiment, as plants used were similar in size, and had similar shoot/root ratios and leaf widths, (Figure 10). Transpiration rates recorded in this investigation (a range from 0.2 - 1.1 kg. m^{-2} day^{-1}) were similar to those obtained by Lloyd (1974). Over a short time period he recorded rates of approximately 1 x 10^{5} kg. m^{-2} s^{-1} (1.2 kg.m^{-2} day^{-1}) at 20°C and a vapour pressure deficit of 7nb.

Possible errors in the measurement of the rates in this investigation must be considered as it was not possible to measure the transpiration under controlled conditions; this

may explain the large variation in the rate measurements. The important environmental factors affecting transpiration are light intensity, humidity of the air, temperature, wind speed and availability of soil water, and as it was not possible to control these in the laboratory, changes in any one of these factors will influence the rate of water loss recorded. All plants were in approximately the same environment, so changes in the environmental factors should affect them all equally; but, however, plants from different populations may not respond in the same way, as shown by the daily measurements of transpiration of the 5 populations from Cassop. As the soil dried out (or became anoxic?) the rates of transpiration of all populations decreased, but a much greater percentage decrease was observed in the plants from dry habitats than those from wetter habitats (Figure 7). It is possible, therefore, that changes in other environmental factors may also have differential effects on the populations, but these are likely to be small as the average temperatures and relative humidities were approximately constant during each experiment. Another possible error resulting from the laboratory arrangement, is that with a large number of pots, each plant may have a slightly different microclimate around it. Different local conditions may contribute to the large variation observed in the transpiration experiments, for although the average conditions in the laboratory remain constant, these can only be recorded at one place in the laboratory, and environmental conditions around individual plants may be considerably different. Therefore, to obtain

accurate estimations of the rate of transpiration, all environmental factors should be kept constant throughout the experiment around individual plants.

Low soil temperatures are known to reduce the growth of many plant species, and a variety of factors have been considered as causal including effects on root growth, water uptake, root metabolism, oxygen supply and mineral nutrition (Richards et. al., 1952, Nielson and Humphries 1966). It has been known since the time of Hales in the eighteenth century that low soil temperatures reduce the absorption of water by plants, (Kramer 1969). More recently Kramer (1942, 1969) from studies on the effect of low soil temperatures on water absorption in a large number of species, suggested that plants native to colder climates might possess root systems with greater water permeability at low soil temperatures than do plants native to warmer climates, as absorption was reduced more in species which normally grow in warm soils. It is therefore possible that as soil temperature decreases with altitude at approximately the same rate as air temperature, (Mueller 1970) high elevation populations are better adapted to water uptake at lower temperatures. This has been studied in recent years, and the results indicate that only some species respond in the manner suggested by Kramer (1942). Anderson and McNaughton (1973) found that in 17 populations of 12 plant species studied neither transpiration or photosynthesis was reduced at $3^{o}C$ soil temperature compared with rates at $20^{o}C$ in plant populations from different altitudes, although leaf

relative water content and growth were reduced in response to low soil temperatures. However, McNaughton (1974) found that in altitudinal ecotypes of Typha latifolia, root chilling reduced both water and phosphate uptake. This effect was greater in the lower altitudinal ecotypes, suggesting natural selection at high altitudes for ability to function efficiently in cold soils. Similar results to those of McNaughton (1974) were found for altitudinal populations of Sesleria in this investigation. With increasing elevation of the population, low soil temperatures reduced the water uptake less, and several populations were significantly different from one another (Figure 17). High altitude populations therefore appear to be adapted to lower soil temperatures, and they may have more permeable root membranes as suggested by Kramer (1942). This would be of ecological importance in a species such as Sesleria, which grows in soils which are often just above freezing and whose growth is largely determined by the available water supply. This change in water uptake ability appears to be related only to the elevation (and presumably soil temperature) of the site, and not to the water availability, as plants from several sites with different soil moisture contents at the same altitude all had similar reductions in water uptake, as a result of low soil temperatures (Table 11).

In these experiments it was necessary to measure the transpiration (and water uptake) rates at 23°C and 2°C on successive days, using the same plants, as only a few plants were available and the variation in rates was large. This

may have, however, caused some errors in the actual value of the percentage reduction, as changes in the environmental conditions, other than soil temperature, during the time of the experiment, may have affected the water loss. Both temperature and relative humidity measurements showed no change in the average daily values, but the edaphic conditions will have changed slightly. In previous experiments a small daily reduction in transpiration rate was sometimes observed, but as this was not constant, it could not be included in the calculations.

As the same plants were used for both warm and cold soil measurements, rapid cooling of the soil was necessary. This may have caused a greater reduction in absorption than would be normally experienced, as Böhning and Lausanandana (1952) found that water absorption in kidney bean was reduced less if the roots were cooled gradually over a period of days. Most of the previous experiments on root chilling and transpiration used control plants at the higher temperatures on the same day, and plants which had been kept with low root temperatures for some time. However, comparable results for the percentage reduction were still obtained from this investigation (Kramer 1969).

The populations of Sesleria which occur in a large number of habitats are therefore adapted to their environment, as field and laboratory studies have shown that the morphology of the plant is related to both its habitat and its physiology. The species has a large plastic response to its environment which accounts for many of the observed differences in the

field, but evidence was also found of genetic differences between populations in different geographic areas.

SUMMARY

Studies on the morphology of Sesleria caerulea have shown that there was a large variation in plants from different habitats and altitudes in Northern England. Leaf lengths and widths, height of inflorescence and size of inflorescence spike were generally greater, and stomatal frequency lower, in plants growing on deep than on shallow soils, irrespective of the altitude, indicating that the edaphic conditions are a main factor influencing the growth of this species. In plants from similar soil depths, no relationship between plant size and altitude was found, but the stomatal frequency and length of the stomatal pore both increased with increasing elevation of the site. These features were considered to be related to the changes in soil moisture tension with altitude. The depth of the stomatal pore was also greater in plants from high elevations; such differences were related to the physiology and ecology of the populations. Morphological studies on field and laboratory grown plants have shown that the large variation is mainly due to the plastic response of the plants to their environment, but evidence of genetic differences was also found, indicating that ecotypes of Sesleria may exist in different geographic locations.

Laboratory measurements of the transpiration of potted plants demonstrated the close relationship between the morphology and physiology of the species, as water loss was correlated with leaf anatomical measurements. Low soil temperatures caused a reduction in the transpiration rate

of all populations, but this was greatest in plants from low altitude sites, suggesting natural selection at high altitudes for ability to function efficiently in cold soils.

Appendix

List of Tables

16A. Effect of low root temperatures on the transpiration rate of Sesleria collected from sites at different altitudes.

17A. Analysis of variance data.

Table 1A.

Morphology of Sesleria from Cassop Vale

Site letter	Total leaf length of plant (cm)	Length of longest leaf (cm)	Maximum leaf width (mm)	Height of inflorescence (cm)	Length of inflorescence spike (mm)	Dry weight of inflorescence spike (g)
A	15.2 ± 0.8	6.7 ± 0.3	3.45 ± 0.07	12.5 ± 0.4	13.7 ± 0.3	0.176
B	29.9 ± 1.7	13.7 ± 1.2	3.41 ± 0.08	23.9 ± 0.4	15.9 ± 0.4	0.215
C	32.6 ± 1.7	12.9 ± 0.6	3.58 ± 0.06	22.2 ± 0.5	14.0 ± 0.2	0.166
D	18.7 ± 1.1	7.8 ± 0.3	2.93 ± 0.07	16.9 ± 0.5	12.9 ± 0.3	0.121
E	17.4 ± 1.2	7.2 ± 0.4	3.05 ± 0.08	12.7 ± 0.5	11.6 ± 0.4	0.117

Table 2A.

Site letter	Number of stomata (mm^{-2})	Interstomatal spacing (μ)	Length of stomatal pore (μ)	Depth of stomatal pore (μ)
A	347 ± 6	61 ± 4	14.2 ± 0.3	8.3 ± 0.3
B	260 ± 5	74 ± 4	12.3 ± 0.2	9.1 ± 0.3
C	236 ± 8	84 ± 5	13.8 ± 0.3	8.4 ± 0.2
D	273 ± 5	77 ± 4	13.9 ± 0.3	8.9 ± 0.2
E	284 ± 8	66 ± 6	15.5 ± 0.2	8.3 ± 0.3

Table 3A.

Site letter	Number of stomata (mm^{-2})	Interstomatal spacing (μ)	Length of stomatal pore (μ)	Depth of stomatal pore (μ)
A	248 ± 5	108 ± 6	13.1 ± 0.2	8.5 ± 0.2
B	259 ± 6	100 ± 6	12.4 ± 0.2	8.7 ± 0.3
C	266 ± 6	106 ± 6	14.1 ± 0.2	8.3 ± 0.2
D	256 ± 5	87 ± 6	13.3 ± 0.3	8.5 ± 0.2
E	260 ± 6	82 ± 5	13.4 ± 0.2	8.9 ± 0.3

(Sample size = 30 Results expressed as Mean ± Standard Error.
Explanation of site letters on Table 1.

Transpiration rate of Sesleria collected from Cassop Vale (laboratory measurements)

Table 4A. a) Transpiration rate on a leaf area basis

Results expressed as loss in weight/unit leaf area/day (kg m^{-2} day^{-1} x 10^{-1})

Site letter	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
A	5.14 ± 0.22	5.10 ± 0.26	4.31 ± 0.38	3.95 ± 0.35	2.97 ± 0.32	2.82 ± 0.40
B	3.41 ± 0.78	3.11 ± 0.69	2.60 ± 0.66	2.33 ± 0.59	1.67 ± 0.37	2.03 ± 0.45
C	2.76 ± 0.28	2.74 ± 0.35	2.09 ± 0.32	1.82 ± 0.37	1.56 ± 0.32	1.54 ± 0.37
D	5.73 ± 0.91	5.50 ± 0.93	5.36 ± 1.09	4.78 ± 1.03	4.22 ± 0.95	3.96 ± 1.02
E	7.84 ± 1.15	8.49 ± 0.64	8.04 ± 0.68	6.91 ± 0.41	5.78 ± 0.51	5.97 ± 0.07

Table 5A. b) Transpiration rate on a dry weight of whole plant basis

Results expressed as loss in weight/unit dry weight of plant/day (day^{-1} x 10^{-1})

Site letter	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
A	2.19 ± 0.12	2.14	1.86	1.64	1.24	1.21 ± 0.19
B	1.16 ± 0.20	1.05	0.87	0.78	0.55	0.68 ± 0.11
C	1.27 ± 0.17	1.25	0.94	0.81	0.69	0.67 ± 0.08
D	1.91 ± 0.22	1.83	1.70	1.51	1.33	1.23 ± 0.14
E	2.03 ± 0.26	2.10	1.92	1.66	1.40	1.47 ± 0.14

Table 6A. c) Transpiration rate on a root dry weight basis

Results expressed as loss in weight/unit dry weight of root/day (day^{-1} x 10^{-1})

Site letter	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
A	3.08 ± 0.15	3.00	2.62	2.29	1.86	1.70 ± 0.26
B	1.65 ± 0.25	1.47	1.20	1.07	0.78	0.94 ± 0.1
C	1.70 ± 0.19	1.68	1.27	1.09	0.93	0.90 ± 0.1
D	2.16 ± 0.13	2.06	1.94	1.73	1.53	1.50 ± 0.2
E	2.35 ± 0.30	2.44	2.24	1.93	1.64	1.76 ± 0.18

Transpiration rate of Sesleria from Cassop Vale with leaves grown under the same environmental conditions

Table 7A. a) Transpiration rate on a leaf area basis

Results expressed as loss in weight/unit leaf area/day (kg m^{-2} day^{-1} x 10^{-1})

Site letter	Day 1	Day 2	Day 3	Day 4
A	2.74 ± 0.24	2.96 ± 0.28	2.61 ± 0.34	2.38 ± 0.22
B	2.64 ± 0.41	2.79 ± 0.42	2.29 ± 0.29	2.36 ± 0.32
C	2.00 ± 0.14	1.94 ± 0.15	1.62 ± 0.11	1.63 ± 0.11
D	3.83 ± 0.40	3.97 ± 0.44	3.35 ± 0.39	3.63 ± 0.63
E	3.58 ± 0.39	3.59 ± 0.39	3.03 ± 0.37	3.50 ± 0.49

Table 8A. b) Transpiration rate on a dry weight of whole plant basis

Results expressed as loss in weight/unit dry weight of plant/day (day $^{-1}$ x 10^{-1})

Site letter	Day 1	Day 2	Day 3	Day 4
A	1.73 ± 0.20	1.85	1.59	1.49 ± 0.14
B	1.62 ± 0.21	1.72	1.43	1.49 ± 0.21
C	1.30 ± 0.16	1.24	1.05	1.06 ± 0.12
D	2.11 ± 0.30	2.08	1.84	1.94 ± 0.31
E	2.09 ± 0.42	2.04	1.74	2.05 ± 0.38

Table 9A. c) Transpiration rate on a dry weight of root basis

Results expressed as loss in weight/unit dry weight of root/day ($day^{-1} \times 10^{-1}$)

Site letter	Day 1	Day 2	Day 3	Day 4
A	2.32 ± 0.31	2.48	2.14	1.99 ± 0.22
B	2.21 ± 0.33	2.34	1.95	2.04 ± 0.33
C	2.06 ± 0.37	1.95	1.65	1.67 ± 0.28
D	2.75 ± 0.47	2.79	2.39	2.50 ± 0.49
E	2.65 ± 0.43	2.60	2.19	2.56 ± 0.13

Table 10A. Shoot/root ratios of plants

Site letter	Shoot/root ratio
A	0.33 ± 0.04
B	0.35 ± 0.03
C	0.48 ± 0.11
D	0.28 ± 0.04
E	0.30 ± 0.06

Tables 7A - 10A
Sample size = 5
Explanation of site letters on Table 1.
Results expressed as Mean ± standard Error

Table 11A. Environmental data

Environmental factor	Day 1	Day 2	Day 3	Day 4
Temperature (°C)				
24 hr. period	23.0	24.0	23.0	21.5
Daylight hours	22.5	23.0	22.5	21.0
Relative humidity (%)				
24 hr. period	70	75	73	71
Daylight hours	70	74	73	70

(Averages for 24 hours and daylight hours (0500 - 2100 hours G.M.T.)

Table 12A.

Morphology of Sesleria from sites at different altitudes (excluding Cassop Vale)

Altitude (m)	Total leaf length of plant (cm)	Length of longest leaf (cm)	Maximum leaf ,width (mm)	Height of inflorescence (cm)	Length of inflorescence spike (mm)	Dry weight of inflorescence spike (g)
60	18.3 ± 0.9	9.6 ± 0.4	3.10 ± 0.08	27.0 ± 0.8	-	-
240	40.4 ± 2.1	15.9 ± 0.7	3.63 ± 0.09	37.5 ± 1.2	17.8 ± 0.7	0.192
320	11.5 ± 0.6	6.2 ± 0.4	3.10 ± 0.07	14.0 ± 1.0	12.3 ± 0.3	0.088
430	37.4 ± 1.9	20.6 ± 0.9	3.46 ± 0.1	35.3 ± 1.3	17.9 ± 1.0	0.166
440	11.5 ± 0.5	5.8 ± 0.3	2.95 ± 0.06	14.9 ± 1.0	12.2 ± 0.3	0.086
515	12.7 ± 0.6	6.3 ± 0.2	3.02 ± 0.08	12.4 ± 0.7	10.6 ± 0.4	0.069
600	16.2 ± 1.0	7.5 ± 0.4	3.07 ± 0.06	20.1 ± 0.8	13.5 ± 0.4	0.106
910	14.5 ± 1.0	6.3 ± 0.3	2.89 ± 0.1	-	-	-

Table 13A.

Leaf anatomy of Sesleria from sites at different altitudes

Altitude (m)	Number of stomata (mm^{-2})	Interstomatal spacing (μ)	Length of stomatal pore (μ)	Depth of stomatal pore (μ)
60	402 ± 8	67 ± 3	13.2 ± 0.2	8.8 ± 0.4
240	236 ± 7	100 ± 6	15.4 ± 0.3	10.1 ± 0.3
320	405 ± 6	41 ± 4	14.1 ± 0.2	9.1 ± 0.3
430	199 ± 5	92 ± 7	14.1 ± 0.4	9.8 ± 0.4
440	404 ± 8	52 ± 3	13.1 ± 0.2	10.1 ± 0.3
515	288 ± 5	81 ± 6	14.5 ± 0.2	13.0 ± 0.5
600	212 ± 7	119 ± 8	16.1 ± 0.3	13.2 ± 0.5
910	206 ± 5	97 ± 4	16.5 ± 0.2	11.1 ± 0.4

(Sample size = 30 Results expressed as Mean ± Standard Error).

Transpiration rate of Sesleria collected from sites at different altitudes (laboratory measurements)

Table 14A. Experiment 1.

Altitude	loss in weight/unit leaf area/day ($kg\ m^{-2}\ day^{-1} \times 10^{-1}$)	loss in weight/unit dry weight of plant/ day ($day^{-1} \times 10^{-1}$)	loss in weight/unit dry weight of root/ day ($day^{-1} \times 10^{-1}$)
320	11.46 ± 2.22	4.40 ± 0.65	6.42 ± 1.08
440	9.26 ± 1.52	4.28 ± 0.70	6.44 ± 0.79
515	8.54 ± 0.90	4.22 ± 0.28	6.00 ± 0.42
600	8.68 ± 0.95	4.24 ± 0.61	5.56 ± 0.78

Average temperature = 25.5°C Average relative humidity = 46%

Table 15A. Experiment 2.

Altitude	loss in weight/unit leaf area/day ($kg\ m^{-2}\ day^{-1} \times 10^{-1}$)	loss in weight/unit dry weight of plant/ day ($day^{-1} \times 10^{-1}$)	loss in weight/unit dry weight of root/ day ($day^{-1} \times 10^{-1}$)
160	5.01 ± 1.47	2.15 ± 0.43	2.79 ± 0.53
320	4.95 ± 1.29	3.10 ± 0.77	4.21 ± 0.96
440	4.05 ± 0.61	2.93 ± 0.75	4.12 ± 1.22
515	3.98 ± 0.66	2.72 ± 0.53	3.82 ± 0.67
600	2.85 ± 0.36	2.03 ± 0.11	2.98 ± 0.18
910	4.42 ± 0.77	2.00 ± 0.29	2.97 ± 0.54

Average temperature = 21.5°C Average relative humidity = 77%

(Sample size = 5 Results expressed as Mean ± Standard Error

Table 16A.

Effect of low root temperatures on the transpiration rate of Sesleria collected from sites at different altitudes

Altitude (m)	Water loss at 2°C root temperature as a percentage of the water loss at 23°C root temperature
160	21.6 ± 1.9
320	33.3 ± 2.1
440	39.2 ± 3.8
515	39.1 ± 3.3
600	46.7 ± 3.9

(Sample size = 15)

Table 17A.

Analysis of variance data

Experiment	Basis of Transpiration rate	Source of variation	Degrees of freedom	Mean Squares	F value	F p = 0.05
Transpiration rate of Sesleria collected from Cassop Vale (laboratory measurements (Day 1)	Leaf area	Between populations	4	20.24	6.97	2.87
		" replicates	20	2.90		
	Dry weight of plant	Between populations	4	1.09	5.52	2.87
		" replicates	20	0.20		
	Dry weight of root	Between populations	4	2.02	3.37	2.87
		" replicates	20	0.60		
Transpiration rate of Sesleria collected from Cassop Vale (laboratory measurements (Day 6)	Leaf area	Between populations	4	15.57	10.11	2.87
		" replicates	20	1.54		
	Dry weight of plants	Between populations	4	0.66	6.88	2.87
		" replicates	20	0.10		
	Dry weight of root	Between populations	4	0.94	6.30	2.87
		" replicates	20	0.15		
Transpiration rate of Sesleria grown under the same environmental conditions (laboratory measurements (Day 1)	Leaf area	Between populations	4	6.03	3.13	2.87
		" replicates	20	1.92		
	Dry weight of plant	Between populations	4	0.58	1.53	2.87
		" replicates	20	0.38		
	Dry weight of root	Between populations	4	0.42	0.57	2.87
		" replicates	20	0.75		
Transpiration rate of Sesleria grown under the same environmental conditions (laboratory measurements (Day 4)	Leaf area	Between populations	4	7.06	3.58	2.87
		" replicates	20	1.97		
	Dry weight of plant	Between populations	4	0.80	2.50	2.87
		" replicates	20	0.32		
	Dry weight of root	Between populations	4	0.69	1.12	2.87
		" replicates	20	0.62		

Experiment	Basis of Transpiration rate	Source of variation	Degrees of freedom	Mean Squares	F value	F p = 0.05
Transpiration rate of Sesleria collected from sites at different altitudes (laboratory measurements) Experiment 1.	Leaf area	Between populations	3	9.18	0.82	3.24
		" replicates	16	11.19		
	Dry weight of plant	Between populations	3	0.03	0.02	3.24
		" replicates	16	1.70		
	Dry weight of root	Between populations	3	0.86	0.23	3.24
		" replicates	16	3.76		
Transpiration rate of Sesleria collected from sites at different altitudes (laboratory measurements) Experiment 2.	Leaf area	Between populations	5	3.18	0.71	2.62
		" replicates	24	4.47		
	Dry weight of plant	Between populations	5	2.04	0.71	2.62
		" replicates	24	2.88		
	Dry weight of root	Between populations	5	1.20	0.83	2.62
		" replicates	24	1.45		
Effect of low root temperatures on Cassop Vale populations	-	Between populations	4	131.05	1.69	2.87
	-	" replicates	20	77.74		
Effect of low root temperatures on populations from different altitudes	-	Between populations	5	1683.3	10.49	2.36
	-	" replicates	70	160.5		

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