Sesleria caerulea (l.) ard. ssp calcarea (celak) hegi scop, in the North East of England an ecological study

Guiti Seyed Yagoobi

CONTENTS

SESLERIA CAERULEA (L.) ARD. SSP CALCAREA (Celak.) Hegi Scop. in the North East of England. An Ecological Study.

by

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The contents of this thesis are, apart from any text references to published work, entirely the product of my own research and have not been submitted for the candidature of any other degree or diploma.

G. Seyed-Yagoobi

June, 1977

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LIST OF FIGURES, TABLES AND PLATES

AUTHORITIES

Phytosociological Nomenclature Throughout is based on that Advocated by

LOHENMEYER W et al.

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INTRODUCTION

Sesleria caerulea (L) Ard. ssp. calcarea (Celak.) Hegi Scop. is a member of the tribe Festucae of the family Graminae. It is a gregarious grass which forms an important component of sub arctic and arctic alpine grasslands throughout Europe and Fennoscandia.

Apart from being found mainly on limestone substrata it appears to tolerate a wide range of soil types and locations from calcareous syrozems and protorendzinas to mature rendzinas, cf Bryan (1967); from Coastline situations along the Atlantic seaboard of Europe to the higher pastures and screes of the Central Alps, and from wet mountain flushes to dry south facing slopes in lowland situations.

Its distribution in the North East of England is perhaps unique for here in a quite small area it is found in habitats which span the full range of wet to dry, skeletal to mature soils and lowland to montane sub-arctic alpine situations see Fig. 1.

The range of calcareous grassland in the North East of England has been intensively studied from the phytosociological stand point by Shimwell (1968). A synopsis of the phytosociological units in which Sesleria is a dominant or important member which have been used in this study is given below.

Class Festuco-Brometea

Order Brometalia erecti

Alliance Mesombromion

Sub-Alliance Seslerio-Mesobromion

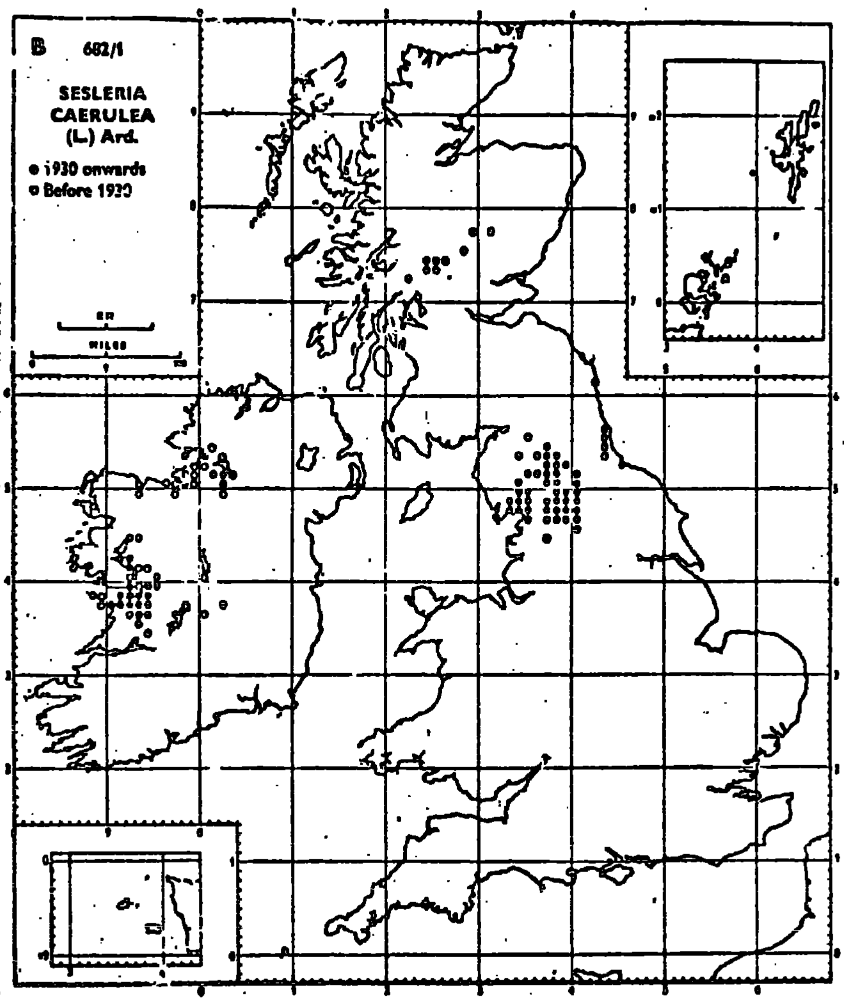
Association of Sesleria-Helictotrichon

Association Seslerio-Caricetum pulicariae

Association Asperulo-Seslerietum

Sub Alliance Eu-Mesobromion

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."

Association Helictotricho-Caricetum flaccae

Class Violetea calaminariae

Alliance Thlaspeion calaminariae

Association Minuartio-thlaspeetum

Class Festuco-Brometea Br-Blanq. R.T.X. 1943

A class which contains the dry anthropogenic, base-rich grasslands of Central and Western Europe. The limits of these grasslands are somewhat obscure. In the Mediterranean region they are confined to north facing slopes on mountains (Braun Blanquet 1951) being replaced in the lowlands by the more xeric grasslands of the class Thero-Brachypodietea Br-Bl 1947, and on the majority of the mountains by the class ONONIDO-ROSMARINETEA Br-Bl 1947

In the North and especially in the sub arctic climate such grasslands are replaced by grass heaths of the class Elyno-sesleriatea Br-Bl-1948. In the East their limit is obscured by intergradation with the grasslands of the steppes of Poland.

Order-Brometalia Erecti Br-Bl-1936

This order contains the bulk of the dry calcareous grasslands dominated by coarse grasses such as Bromus erectus, Brachypodium pinnatum, Festuca ovina and Helictotrichon pratense

Alliance Mesobromion-erecti Br-Blanq. Moor 1938 emend Oberd 1949

The alliance contains most of the familiar chalk and limestone grasslands of the British Isles and also includes some communities on stabilised calcareous dune systems. The majority of them must be considered to be secondary in nature being formed on the steeper scarp slopes layed bare by early deforestation.

Sub Alliance Eü-Mesobromion Oberd 1957

This sub-alliance was created to include almost all the lowland Mesobromion associations which are free from the de-alpine species (Meusel 1939) such as Sesleria caerulea.

Association Helictotricho-Caricetum flaccae

An association which in many ways represents a zone of communities poor in order and alliance character species found around the Northern and Western limits of the Cirsio Brometum. It forms a definite link with the sub-alliance Seslerio-Mesobromion.

The outlier communities of County Durham form part of a succession which proceeds to a low scrub community best referred to the alliance Salicion arenariae R.T.X. 1952.

Sub-Alliance Seslerio Mesobromion Oberd 1957

A group of grasslands which occur in a marked zone across Northern England and Western Ireland and form a floristic link between the classes. Festuco-Brometea and Elyno-seslerietum.

Association Seslerio-Helictotrichetum

An association peculiar to the magnesian limestone escarpment of Eastern Durham at altidues varying between 60 and 160 m above sea level. The climate of the escarpment is an extension of the drier eastern climate of South England, climate type Vlib, Walter and Leith (1967), although the average minimum winter temperatures are somewhat cooler, average $\bar{2}5^{o}$C.

This is the most thermophilous association in the sub-alliance and forms an important link between the Eu-Mesobromion associations to the South and the damper upland associations of the Seslerio-Mesobromium to the west, four sub-associations are recognisable in the area.

1. Sub-ass. of Encalypta and Plantago maritima although representing a second stage of colonization of disturbed areas, is typical of the shallowest soils where summer drying will be most prevalent.

2. Sub-ass. of Helictotrichon pubescens is fairly widespread above the escarpment being found in small areas which have been disturbed in the past and are now grazed to varying extents.

3. Sub-ass. Typicum occurs in areas of least disturbance on deeper soils which retain their moisture well throughout the summer.

Sub-Ass. Caricetosum pulicariae is found on damp north and west facing slopes which enjoy a more humid micro-climate. The dampness of the habitat is made clear by the abundance of Ctenidium molluscum, Acrocladium cuspidatum and Fissidens cristatus, and locally Pinguicula vulgaris and Primulia farinosa, showing a distinct affinity with the association of the Seslerio-Caricetum pulicariae described from the montane limestones of the Pennines.

Association Seslerio Caricetum pulicariae

Montane grasslands found at attitudes between 290 m and 730 m above sea level, on steep south and west facing slopes soils ranging from calcareous syrozems to shallow rendzinas.

1. Sub-ass. Typicum is the most widespread and the driest of grassland series being typically found on steep south facing slopes where drainage after rain is rapid.

a. Ditrichum flexicaule-Rhytidium variant is found on the shallow soils which are the most primitive of the calcareous syrozen series.

b) Calluna-Empetrum variant on steep slopes with deeper soils which show an accumulation of raw humus in the surface horizon and are best termed a slightly podzolized red-brown calcareous soil.

c) Typical variant developed over the deeper, protorendzina soils, root depth being up to 15 cm.

2. Sub-ass. Kobresietosum

Is found exclusively on Widdy Bank Fell, being typified by the abundance and often dominance of Kobresia simpliciuscula a plant of calcareous alpine flushes of the order Tofieldietalia.

Two facies are represented here; in the dampest Carex lepidocarpa becomes an important member of the flora where the water is almost at the surface during all except the driest periods of the year. Typically the soil shows marked signs of gleying and the effective rooting depth appears to be the top few cms. only.

Class Violetea calaminariae R.T.X. 1961

Order Violetalia calaminariae Br-Bl RTX 1943

Grassland communities of metaliferous strata and metal mine spoil heaps characterized by the presence of Viola calaminaria Lej. a species as yet unrecognized in Britain. Of the three alliances recognized by Ernst (1965) only one occurs in Britain and that is the:-

Alliance Thlaspeion Calaminariae Ernst 1965 a single association Minuartio-Thlaspeetum has been recognized by Shimwell (1968) from metal spoil heaps. The soils are very skeletal and although and there may be some accumulation of humus no soil profile can be said to exist.

It is thus obvious that, (1) Sesleria caerulea Ssp. calcarea hence referred to as Sesleria is found in a whole range of habitat conditions from rapidly drying shallow soils in thermophilous lowland situations, to deep wet soils in cold 'sub-alpine' situations, (2) the north east of England presents an ideal situation for detailed study of its ecology.

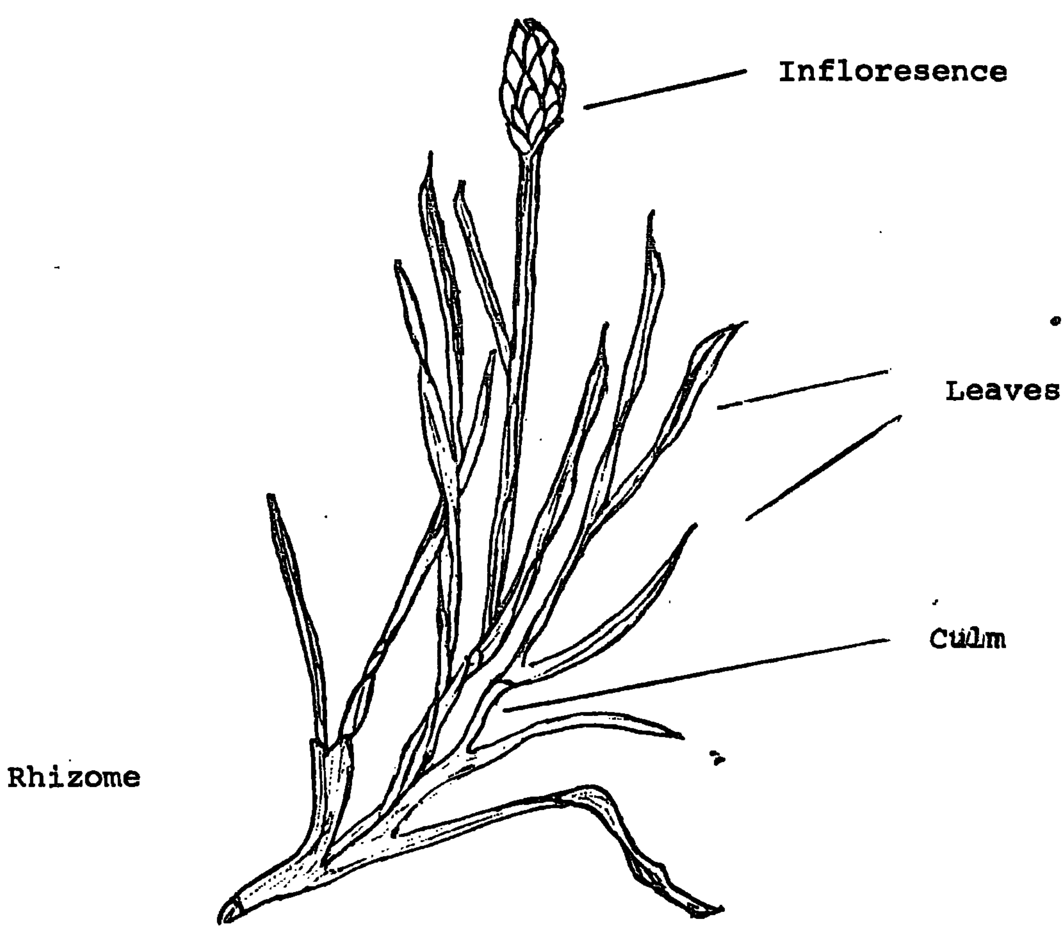


FIG 2 SESLERIA CAERULEA

Preliminary work (West 1975) has indicated that Sesleria is very plastic especially in relation to size of the leaves, and number and distribution of stomata on the adaxial surface of leaves.

His conclusions based on a study of 9 populations, 8 of them in northern England and one in Scotland were as follows

1. The size of plants measured both as total leaf length, length of longest leaf and length of the inflorescence were greater the deeper the soil.

2. Stomatal frequency is negatively correlated with soil depth at any one altitude.

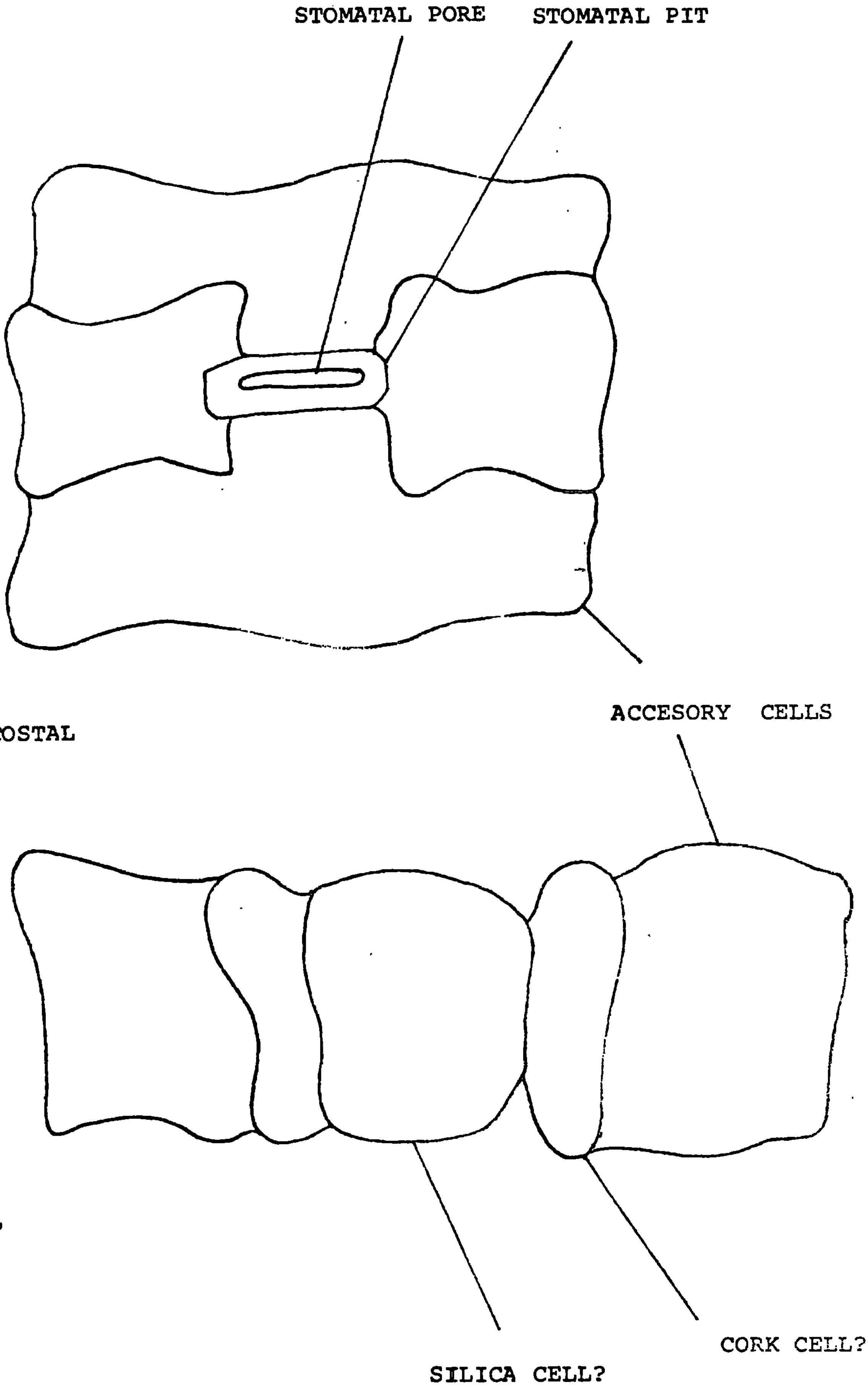
3. In plants from a similar soil depth, no relationship was found between plant size and altitude, however stomatal frequency, length of stomatal pore and depth of stomatal pore were significantly greater at higher elevations. West stated that the variation is mainly due to the plastic response of the plants to their environment, but evidence of genetic differences were also found.

It was therefore decided to attempt to extend our knowledge of the physiological anatomy of the species across the range of habitat conditions found in the north east of England.

MORPHOLOGY AND ANATOMY

Sesleria is an erect wiry, tufted (Fig. 2) perennial which varies greatly in stature both as regards size of leaves and inflorescence. Clapham et al. (1965) give a size range of 15-40 cms. The leaf blades are more or less flat although being keeled and supplied with bulliform cells may become folded to produce

FIG. 3.



I INTERCOSTAL

2 COSTAL

a boat shape leaf especially near the tip.

The most striking feature of the leaf anatomy Prat (1936) Peelaby (1898) see Fig. 3 and Plates 1 and 2 is the presence of sunken stomata arranged along the intercostal regions in rows of two or more. The stomata are supported in the main by rectangular 'long-cells' (sensu Metcalfe 1960), which may, where the stomata are crowded become shorter with concave ends making them appear distinctly saddle shaped.

The costal (above vein) cell rows are devoid of stomata, their place appears to be taken by groups of three 'short-cells' (sensu Metcalfe 1960). Each group appears to consist of one central silica cell between two cork cells although staining reactions are not very conclusive.

Aims of the Work

1. To compare the distribution of stomata and short cell groups on the leaf of Sesleria caerulea from the full range of habitats in which is found growing in the N.E. of England.

2. To investigate the plasticity of the above anatomical attributes under cultivation.

3. To investigate the relationship between stomatal number and transpiration rate in two contrasting field populations.

Study 1 Lowland populations on magnesian limestone

Two populations were studied from the Cassop Vale area of lowland County Durham both at approximately 160m above sea level.

Population A is situated on the N.E. facing ledges of a disused quarry where maximum soil depth does not exceed 2 cms, in a position where rapid drying out between rains is inevitable.

Plate 1.

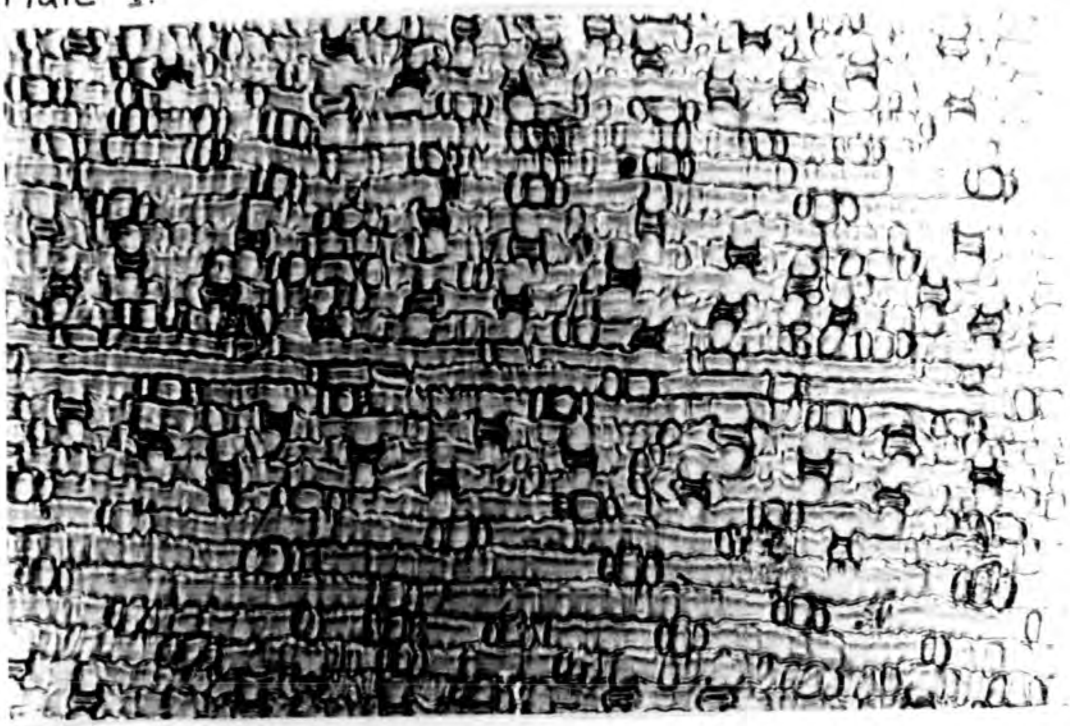


Plate 2.

Table A presents phytosociological data for the closed communities of the ledges

V-Sesleria caerulea 3.3
IV-Carex flacca +.1
III-Helianthemum chamaecystus +.2
V-Plantago maritima 1.2
V-Encalypta vulgaris +.2

(In the table, the roman figures given before the plant names is a measure of constancy of occurrence in 10 sample plots and the arabic figures are the abundance sociability estimates Braun Blanquet (1956) for the plot from which the samples were taken. This format is used throughout the thesis.
N.B. only the important (characteristic) species are listed.)

The community is best classified with the sub association of Encalypta and Plantago maritima of the Seslerio Helictotrichetum

Population B

In contrast is taken from a wide area of deep soil (up to 40 cm). Its aspect is north and the site is supplied by seepage water from a considerable area of magnesian limestone. Table B presents phytosociological data from the relevant communities.

Table B

V Sesleria caerulea 3.4
V Carex panicea +.1
IV Carex flacca +.2
III Pinguicula vulgaris +.2
IV Carex pulicaris 1.2
IV Ctenidium molluscum +.2
V Acroccadium cuspidatum 1.2

The community of the area is best referred to the Sub. ass. Caricetosum pulicariae

Experiment 1

Collection and laboratory study

20 plants collected at random from the communities were stored in polythene bags at $0^{o}C$ before the following measurements were made on each.

1. Length of the longest leaf; 2. number of stomata per unit area in the mid section and top section of the longest leaf;* 3. number of short cell groups (hence called short cells) per unit area in the mid section and top section of the longest leaf.*

Results

The results are summarised in Table 1 in which the significance levels derived from student t tests are shown.

TABLE 1

	Pop A	Significance of Difference	Pop B
Length of longest leaf (mm)	4.9 ± 0.4	* * *	13.8 ± 1.8
Number of Stomata/Unit area Mid section	669 ± 24	* * *	417 ± 18
Number of Stomata/Unit area Top section	649 ± 73	* * *	454 ± 31
Number of Short Cells/Unit area Mid section	372 ± 36	NS	336 ± 25
Number of Short Cells/Unit area Top section	315 ± 25	NS	302 ± 25

Significance Levels (this notation is used throughout the thesis)

* * * p = 0.001; * * p = 0.01; * p = 0.05; NS - not significant

Conclusions

The longest leaves in population A are significantly shorter than those of population B. The number of stomata per unit leaf

(* All measurements of stomatal and short cell numbers refer to the adaxial leaf surface, throughout the thesis.)

are
area/significantly greater in population A than in population B. There is no significant difference between the number of short cells per unit area of leaf of the two populations.

Experiment 2

Aim to investigate the "plasticity" of the two populations

Method

50 plants were collected at random from each population. On return to the laboratory they were potted separately in 20 cm. plastic pots filled with John Innes No. 1 compost. The pots were then arranged in two latin squares in the greenhouse, each one a mixture of 25 of each type of plant. One set designated 'wet treatment' were watered every day, the other set designated dry treatment were watered once every 7 days. The length of all leaves of every plant were measured. The experiment was terminated after 6 weeks, when the following measurements were made:

1) Length of all leaves (hence it could be calculated which leaves had grown the most); 2) length of the longest leaf; 3) the following measurements were then made on a) the five leaves that had grown the most, and b) five new leaves.

Number of stomata and the number of short cells in the mid section of the leaf. The results are summarised and statistical comparison of each data set using the student t test is shown below

TABLE 2

							Stomata	Cells
1.	Population	A	Field	mid	section		669 ± 24	372 ± 36
2.	"	A	"	top	"		649 ± 73	315 ± 25
3.	"	B	"	mid	"		417 ± 17	336 ± 25
4.	"	B	"	top	"		454 ± 30	302 ± 35
5.	"	A	Laboratory wet grown most				482 ± 50	225 ± 27
6.	"	A	Laboratory wet new leaves				495 ± 35	234 ± 48
7.	"	A	Laboratory dry grown most				466 ± 35	255 ± 21
8.	"	A	Laboratory dry new leaves				503 ± 34	258 ± 25
9.	"	B	Laboratory wet grown most				403 ± 72	375 ± 23
10.	"	B	Laboratory wet new leaves				507 ± 52	306 ± 34
11.	"	B	Laboratory dry grown most				513 ± 23	517 ± 53
12.	"	B	Laboratory dry new leaves				548 ± 20	401 ± 55

TABLE 3

STOMATA

	1	2	3	4	5	6	7	8	9	10	11	12
1		NS	***	***	***	***	***	***	***	***	***	***
2			NS	**	*	*	*	*	**	*	*	NS
3				NS	*	*	NS	**	NS	**	**	***
4					NS	NS	NS	*	NS	*	*	**
5						NS	NS	NS	NS	NS	NS	NS
6							NS	NS	NS	NS	NS	NS
7								NS	NS	NS	NS	NS
8									NS	NS	NS	NS
9										NS	NS	*
10											NS	NS
11												NS
12												

TABLE 4

SHORT-CELLS

	1	2	3	4	5	6	7	8	9	10	11	12
1		NS	NS	NS	**	**	**	**	NS	*	**	NS
2			NS	NS	**	*	**	NS	NS	NS	**	*
3				NS	*	*	**	**	NS	NS	**	*
4					*	NS	NS	NS	NS	NS	**	*
5						NS	NS	NS	**	NS	**	**
6							NS	NS	*	NS	**	**
7								NS	*	NS	**	NS
8									*	NS	**	NS
9										NS	**	NS
10											**	**
11												**
12												

CONCLUSIONS

STOMATA

Under the conditions of the experiment new leaf tissue produced by the plants of population A (dry), produce significantly fewer stomata per unit leaf area than in the field situation. In contrast the new leaf tissue produced by the plants of the population B (wet), produce significantly more stomata than when in the field situation.

Short-Cells

Under the conditions of the experiment the new leaf tissue produced, by the plants of population A (dry) show a significant decrease in the number of short-cells in the treatments. In contrast those of population B (wet) show a significant increase in the number of cells when grown in the dry although there is no significant change in the wet treatment.

Experiment 3

The summer of 1976 was exceptionally dry for a period of some two months when the drought was terminated by torrential rains. It was decided to attempt to make use of these extreme climatic conditions to test anatomical variability in a field population. To this end the longest new leaves were collected from 20 selected plants at random from the contrasting populations at Cassop in late autumn. Counts were made of the stomata and short-cells in the top section (grown during the drought period) and the basal section (grown during the rainy period).

Although it is felt that direct comparison between years is impossible because of the multitude of environmental variations, it at least seems safe to compare the number of stomata in the leaf tissue produced during the drought with that produced in the autumn rains.

Statistical analyses of the results are summarised below.

Results

Table 5

Sample (20 of each)	Stomata	Cells
1) Population A. Top (Drought)	642 ± 39	302 ± 23
2) Population A. Base (Rains)	532 ± 15	338 ± 15
3) Population B. Top (Drought)	614 ± 20	410 ± 17
4) Population B. Base (Rains)	437 ± 23	296 ± 21

Table 5 (Con'd)

STOMATA

	A top	A base	B top	B base
A top		***	NS	***
A base			*	*
B top				***
B base				

SHORT-CELLS

	A top	A base	B top	B base
A top		NS	***	NS
B top				**
B base				

Conclusions

Stomata

During the drought period both populations were producing leaf tissue with a similar number of stomata per unit area. In contrast during the wet period population A is producing more stomata per unit area of leaf tissue than population B, thus reverting to the normal field situation.

Short-Cells

During the drought period, population B was producing significantly more cells per unit area of leaf tissue than population A. This backs up the findings of experiment 2.

STUDY 2 Thrislington Plantation

Experiment 4

A series of six contrasting populations were selected for study from the lowland area of Thrislington plantation in County Durham, altitude 140 m above sea level. Details of the ecology and phytosociology of the chosen populations are given in each section below. Collections were made in late autumn 1976 and measurements of the following were made from each population. Number of stomata and number of short cells, from the top section of each leaf that is of tissue formed during the drought period. To allow further study of the possible effects of the drought measurement were also made to allow comparison between the top and the base of the leaf, the latter being produced during the wet autumn period.

Population C

Habitat

Skeletal grassland on the edge of an old trackway. The soil is a protorendzina, maximum rooting depth approximately 2 cms.

Phytosociology

V Sesleria caerulea 2.2
V Hypochaeris radicata +.1
III Hypericum montanum +.1
V Ceratodon purpureus +.2
IV Encalypta vulgaris 1.2
II Epipactis atrorubens +
II Crataegus monogyna +

Syntaxonomy

Association Seslerio Helictotrichetum

Sub-Ass. Encalypta and Plantago maritima

Results (Sample size 10)

	Stomata	Cells
Drought	837 ± 11	351 ± 14
Autumn rain	725 ± 27	300 ± 15

Population D

Short turf grassland found on or near marked breaks of slope. The soils are rendzinas, the maximum rooting depth being 6 cms.

Phytosociology

V Sesleria caerulea 2.3
V Helictotrichon pubescens 1.1
IV Daucus carrota +.1
IV Centaurea nigra 1.1
V Plantago media 1.1

Syntaxonomy

Association Seslerio Helictotrichetum

Sub-Ass. Helictotrichon pubescens

Results

	Stomata	Cells
Top (Drought)	715 ± 43	359 ± 14

Population E

Restricted tracts of grassland, although on gentle south facing slopes are but little effected by grazing by farm stock.

The soils are best described as rendzinas, maximum rooting depth 30 cm.

Phytosociology

II Sesleria caerulea 1.2
V Helictotrichon pubescens 1.1
V Helictotrichon pratense 1.1
V Poterium sanguisorba +2
IV Carlina vulgaris +2
III Anthyllis vulneraria +.1
II Linum anglicum +2

Syntaxonomy

Sub-Alliance *Mesobromion-erecti*
Association *Helictotricho-Caricetum-flaccae*

Results (Sample size 10)

	Stomata	Cells
Top (Drought conditions	650 ± 15	284 ± 23

Population F

A single small stand of grassland which is being invaded by a hybrid population of willows. (Salix repens x Salix nigra). It is in reality a damper version of the above being situated close to the base of a main south east facing slope and in part is subject to seepage water draining off the slope.

Phytosociology (NB a single stand)

Sesleria caerulea 1.2
Helictotrichon pubescens 2.3
Carex flacca 1.1
Koeleria cristata 1.1
Primula farinosa +2
Valeriana dioica 1.1

Syntaxonomy

Association *Helictotricho-Caricetum-flaccae*

Border Community with developing scrub related to the Alliance *Salicon arenariae* R.T.X. 1952

Results (Sample Size 10)

	Stomata	Cells
Top (Drought)	604 ± 33	250 ± 9

Population G

Tracts of grassland on a range of slopes which are subject to little or no-grazing by farm stock. Soils are rendzinas with a maximum depth of 50 cms.

Phytosociology

V Sesleria caerulea 2.3
V Helictotrichon pratense 1.1
II Epipactis atrorubens +2
III Betonica officinalis +1
III Campanula rotundifolia +1
IV Carex flacca

Syntaxonomy

Association Seslerio Mesobromion

Sub-Ass. Typicum

Results (Sample Size 10)

	Stomata	Cells
Top (Drought)	505 ± 17	241 ± 70
Base (Wet)	450 ± 27	216 ± 12

The results are summarised in Table 6, where the results of comparison using student t test are given.

TABLE 6

Number of Stomata per unit area ± Standard Error

	Dry Shallow ———	Soil ———		Range ———	Damp Deep
Population	C	D	E	F	G
Top (Drought)	837 ± 11.8	715 ± 43.6	640 ± 16.0	604 ± 33.5	505 ± 18
Base (Wet)	725 ± 27.3	NR	NR	NR	450 ± 27.1

	C Top	C Base	D Top	E Top	F Top	G Top	G Base
C Top		**	**	***	***	***	***
C Base			NS	**	*	***	***
D Top				NS	NS	***	***
E Top					NS	***	***
F Top						*	***
G Top							*
G Base							

TABLE 7

Number of Short-Cells per unit Area ± Standard Error

Dry Shallow ——— Soil ——— Range ——— Damp Deep

Population	C	D	E	F	G
Top (Drought)	352 ± 14	359 ± 14	284 ± 23	250 ± 9	216 ± 70
Base (Wet)	300 ± 15	NR	NR	NR	741 ± 12

	C Top	C Base	D Top	E Top	F Top	G Top	G Base
C Top		**	NS	NS	***	*	***
C Base			**	NS	**	NS	***
D Top					***	**	***
E Top					NS	NS	***
F Top						NS	***
G Top							***
G Base							

Conclusions

There is a positive correlation between the stomata and the arbitrary scale of depth/dampness of the soil. The number of stomata decrease significantly with increasing depth/dampness of the soil. The effect of the rain after the drought has been similar to decrease significantly the number of stomata formed on the leaves of both plants of the extreme 'wet' and extreme 'dry' populations.

The correlations and 'effects' on the short cells are not nearly as clear cut. Increasing depth/dampness of the soil goes hand in hand with a decrease in the number of the short cells. The effect of rain compared to drought is to significantly decrease the number of cells in the extreme dry population, and exactly the opposite in the population G from the wet field conditions.

Study 3 Montane populations

Experiment 5

All the following populations are situated at about 540 m OD on the Widdy Bank Fell National Nature Reserve in County Durham.

The following attributes were measured from each:
1) Number of stomata; 2) Number of cells, per unit area in the top section of the leaves formed in 1975 and during the drought and the basal section formed during the autumnal rains of 1976.

Population H

Habitat details

Skeletal grassland developed on an old spoil heap from the Cow Green lead/barytes mine. No soil as such exists, the plants are rooted in the fines between the spoil. The soils are subject to very rapid drying after rain.

Phytosociology

III Sesleria caerulea +2
IV Thlaspi alpestre +1
IV Anthoxanthum odoratum +1
III Carex capillaris +2
IV Plantago lanceolata +2
III Minuartia verna +2

Syntaxonomy

Association Minuartio Thlaspeetum

Results (Sample size 10

	Stomata	Cells
1975		
	385 ± 17	91 ± 2
1976 Autumn		
Top	532 ± 17	395 ± 11
Base	521 ± 17	362 ± 11

Population I

Grassland on soils developed on steep slopes or close to breaks of slope. The soils are at the best considered to be calcareous syrozems providing a maximum rooting depth of 2 to 3 cms.

Phytosociology

V Sesleria caerulea 2.1
V Gallium sterneri +
V Cornicularia aculeata 1.1
IV Ditrichum flexicaule +2
IV Hieracium pilosella 1.1
III Barbula fallax +2
III Helictotrichon pratense 1.1
III Carex ericetorum +
IV Carex pulicaris 1.2

Syntaxonomy

Association Seslerio-Caricetum pulicariae

Sub-Ass. Typicum

Variant Ditrichum and Rhytidium

Results (Sample size 10)

1975	Stomata	Cells
Top	677 ± 37	194 ± 23

Population J

Grassland with a mixture of heath species developed on gentle slopes on slightly podsolised red-brown calcareous soils, rooting depth not more than 10 cms.

Phytosociology

V Sesleria caerulea 2.3
IV Gallium sterneri 1.1
IV Cornicularia aculeata 1.2
V Calluna vulgaris +2
III Empetrum nigrum +2
III Carex pulicaris 1.2

Syntaxonomy

Association Seslerio Caricetum pulicariae

Sub-Ass. Typicum

Variant Calluna/Empetrum

Results (Sample size 10)

1975 late	Stomata	Cells
	645 ± 55	279 ± 15
1976 Top (Dry)	660 ± 2	453 ± 14
Base (Wet)	576 ± 19	358 ± 12

Population K

Extensive grasslands developed over a range of slopes on undulating ground, the soils are protorendzinas up to 15 cms deep.

Phytosociology

V Sesleria caerulea 3.3
IV Gallium sterneri 1.1
IV Cornicularia aculeata 2.2
III Carex pulicaris 1.2

Syntaxonomy

Association Seslerio Caricetum pulicariae

Sub-Ass. Typicum

Variant typicum

Results (Sample size 10)

	Stomata	Cells
1975	614 ± 17	277 ± 28
1976 top	643 ± 21	361 ± 11
base	596 ± 20	364 ± 12

Population L

Habitat details

Grasslands developed in damper areas, in some cases depressions in others near the base of main slopes adjacent to flushes. Soil profile deep, to 30 cms.

Phytosociology

V Sesleria caerulea 1.2
III Carex pulicaris 2.2
IV Kobresia simpisiuscula 2.3
V Carex flacca 1.2
IV Carex panicea +1

Syntaxonomy

Sub-Ass. Kobriesietosum

Results (Sample size 10)

1976	Stomata	Cells
Top	549 ± 18	445 ± 14
Base	541 ± 17	378 ± 12

Population M

As above but taken in the areas where there is an abundance of Carex lepidocarpa in the community. Rooting depth less than 4 cms.

Results (Sample size 10)

	Stomata	Cells
1975	796 ± 68	88 ± 10

The results as summarised in Table 8 and 9 where the results of comparison using the student t test are shown

Conclusions

In the main the same trends are shown as for the lowland populations. The populations situated on the dry skeletal soils have more stomata than those on the deeper wetter soils, the differences are however in many cases not significant.

There are however two marked exceptions. The plants on the thin skeletal soils on heavy metal spoil heaps have significantly fewer stomata, and those on the very wet flush soils appear to have significantly more stomata than they should if the wet to dry series is correct.

TABLE 8

Number of Stomata per unit area ± Standard Error

Soil Type	Shallow Dry (Heavy Metals)	Shallow Dry	Deeper Dry	Deeper Moist	Deep Damp	Shallow (wet)
Population	H	I	J	K	L	M
1975	[1] 385 ± 17	[4] 677 ± 37	[5] 645 ± 55	[8] 614 ± 17	NR	[13] 796 ± 68
1976 Top (Drought)	[2] 532 ± 17	NR	[6] 660 ± 21	[9] 643 ± 21	[11] 549 ± 18	NR
1976 Base (Rain)	[3] 521 ± 17	NR	[7] 576 ± 19	[10] 596 ± 20	[12] 541 ± 17	NR

Results of t tests where significant					
	1	***	4,5,8,13	6	** 11
	4	***	13	2	*** 6,9
	5	***	13		

TABLE 9

Number of Stomata per unit area ± Standard Error

Soil Type						
Population	H	I	J	K	L	M
1975	[1] 91 ± 2	[4] 194 ± 23	[5] 279 ± 15	[8] 277 ± 28	NR	[13] 88 ± 10
1976 Drought	[2] 395 ± 11	NR	[6] 453 ± 14	[9] 361 ± 11	[11] 445 ± 14	NR
1976 Rain	[3] 362 ± 12	NR	[7] 358 ± 12	[10] 364 ± 12	[12] 378 ± 12	NR

Results of	1	***	4,5,8	4	***	5,8
t tests where	2	***	6,11	6	**	9
significant				3	***	4,5,8

In all cases where comparable data is available, the seasonal charges are the same, stomatal numbers were highest in leaf tissue formed during the drought of 1976 falling again in tissue produced during the wet autumn. It must be noted that these differences were not as marked as with the lowland populations. The changes and trends in the numbers of short-cells are less easy to interpret.

Experiment 5a

Aim

To test the plasticity of the above attributes under experimental conditions.

20 plants were collected at random from populations H, J, K, L. They were potted out in 20 cms. plastic pots, filled with John Innes No. 1 potting compost. The 80 pots were randomised in a latin square in the greenhouse where they were watered daily for a period of 4 weeks.

At the end of the experiment the plants were harvested and the following attributes were measured on leaf samples from each. 1) Number of stomata; 2) Number of cells, on the new leaf tissue at the base and on the old leaf tissue produced during the autumn prior to collection. The results are summarised in Table 10 in which the results of statistical comparisons are presented.

TABLE 10

Stomata and cells (sample size 10)

	Field	Stomata	Cells	Field
1) Population H top	(521)	497 ± 29 **	373 ± 14 NS	(355)
2) " H base		641 ± 27	403 ± 8	(362)
3) " J top	(576)	574 ± 30 **	438 ± 65 NS	(453)
4) " J base		770 ± 38	511 ± 56	(358)
5) " K top	(596)	518 ± 16 ***	360 ± 27 *	(361)
6) " K base		713 ± 42	496 ± 38	(364)
7) " L top	(541)	400 ± 38 NS	384 ± 28 NS	(445)
8) " L base		478 ± 35	366 ± 36	(378)

Conclusions

In all cases the number of stomata per unit area of leaf produced in the greenhouse were greater than that produced in the field. The increases were significant in all cases except population L from the deep wet soil.

This is in marked contrast to the greenhouse experiments carried out on the lowland population which, in every case, showed a decrease of stomata in the wet treatment. The number of short-cells showed no significant pattern of change under the experimental conditions.

Study 4

Transpiration

Experiment 6

Aim

To compare the rate of transpiration of plants collected from field populations A and B in Cassop Vale.

Methods

One hundred plants collected at random from each population in the field were potted individually in 20 cms polystyrene cups filled with commercial vermiculite.

All plants were kept under the same conditions of light and temperature in the laboratory. Fifty of each batch being watered daily (wet treatment), the other 50 being watered every 7 days (dry treatment). The experiment was begun after 14 days of laboratory growth.

Ten plants from each treatment were watered until the vermiculite was fully saturated after which they were allowed to drain for 10 minutes before being sealed as shown in Fig. 4

Each transpirometer was then weighed to an accuracy of 0.005 gms and the leaf area of each plant was calculated after measurement of the length and maximum width of each leaf.

The plants were then placed in a line on the laboratory bench, at right angles to the incident sunlight.

For the first four days each transpirometer was reweighed every 8 hours and then every 24 hours for a further 13 days after which all plants were showing signs of stress. Each time a transpirometer was weighed it was randomly replaced in another position in the line.

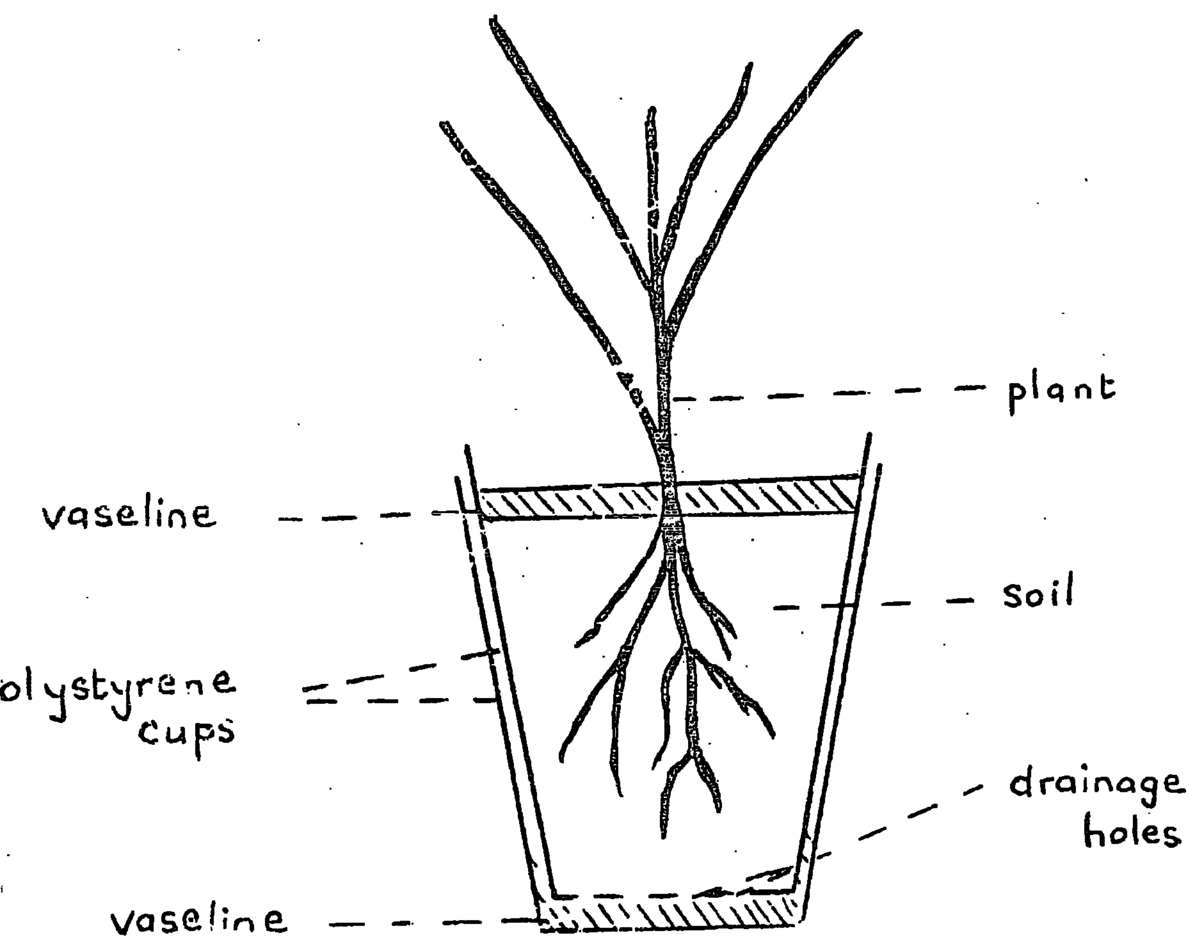

plant
vaseline
soil
olystyrene
cups
drainage
holes
vaseline

Fig 4

At the end of the experiment the leaf area of each plant was again measured.

Results

The results are summarized in Table 11 below, and in Figs. 5 and 6.

TABLE 11

Experiment 7

	gms/cm²/Day ± standard error			
Days	Dry in Dry	Dry in Wet	Wet in Dry	Wet in Wet
1	0.12 ± .04	0.43 ± .05	0.56 ± 0.07	0.33 ± .03
2	0.31 ± .03	0.32 ± .03	0.48 ± 0.04	0.46 ± .06
3	0.32 ± .05	0.16 ± .01	0.97 ± .06	0.55 ± .01
4	0.11 ± .04	0.07 ± .02	0.53 ± .03	0.61 ± .02
5	0.52 ± 0.06	0.52 ± .04	0.52 ± .01	0.55 ± .02
6	0.34 ± 0.04	0.31 ± .07	0.40 ± .03	0.56 ± .04
7	0.21 ± 0.03	0.51 ± .04	0.47 ± .02	0.49 ± .03
8	0.01 ± 0.03	0.43 ± .03	0.41 ± .04	0.18 ± .07
9	0.43 ± 0.03	0.16 ± .01	0.36 ± .01	0.32 ± .02
10	0.32 ± 0.04	0.31 ± .02	0.18 ± .01	0.36 ± .02
11	0.51 ± 0.04	0.33 ± .06	0.26 ± .03	0.45 ± .01
12	0.26 ± 0.02	0.36 ± .03	0.22 ± .02	0.28 ± .04
13	0.13 ± 0.01	0.14 ± .01	0.17 ± .01	0.21 ± .02
14	0.10 ± 0.03	0.21 ± .01	0.18 ± .06	0.22 ± .03
15	0.12 ± 0.02	0.09 ± .02	0.09 ± .03	0.19 ± .07
16	0.07 ± 0.01	0.13 ± .01	0.16 ± .01	0.19 ± .01
17	0.09 ± 0.01	0.26 ± .07	0.23 ± .06	0.46 ± .02
18	0.06 ± 0.01	0.20 ± .03	0.29 ± .04	0.28 ± .04
MEANS	0.22	0.27	0.36	0.37

Table 11 (Cont'd)

Student t test

		1	2	3	4
Dry in Dry	1		NS	NS	**
Dry in Wet	2			NS	NS
Wet in Dry	3				NS
Wet in Wet	4				

Conclusions

The rates of transpiration show a definite gradation being greater in the plants of treatment 4 (wet in the wet) and least in treatment 1 (dry in the dry).

1	2	3	4
0.22	0.27	0.36	0.37

Only when the results of treatment 1 and 4 are compared is there any significant difference

It was concluded from the results of experiments 2 and 3 above that the number of stomata formed per unit leaf area was very plastic responding quickly to change in environment conditions. It was therefore decided to carry out a further experiment.

Transpiration

Experiment 7

Aim

To compare the rate of transpiration of the two populations A and B from Cassop Vale after a longer period of growth under the experimental conditions in the greenhouse.

In the light of the results of experiment one only the two extreme treatments were used, dry in the dry, and wet in the wet. The plants were grown under the experimental conditions in the greenhouse for 28 days prior to the beginning of the experiment.

The method employed were exactly the same as those used in experiment 1.

Results

The results are summarised in Table 12.

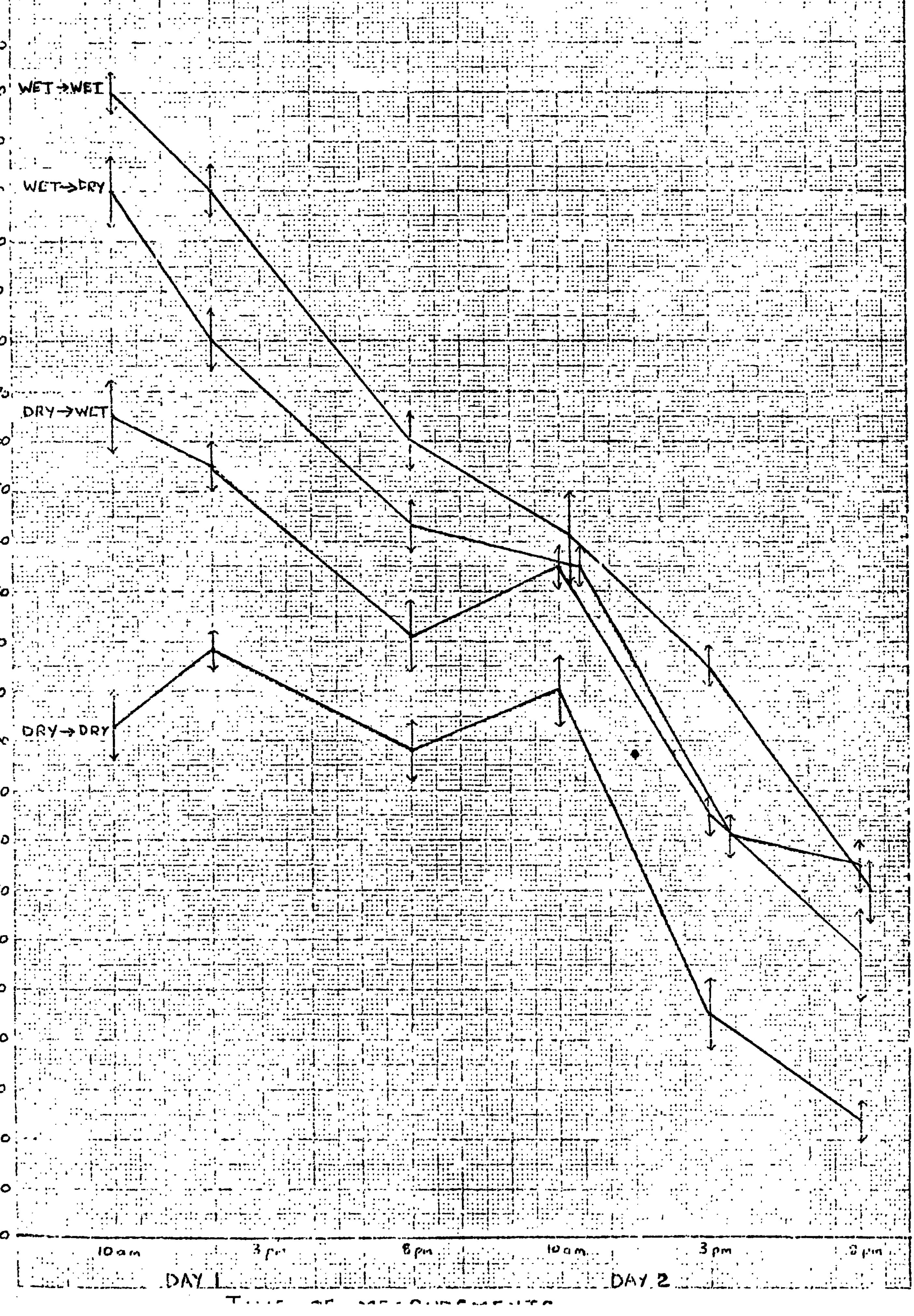
TABLE 12

Days	Dry Dry	Wet Wet
1	0.63 ± .03	0.52 ± .06
2	0.44 ± .03	0.43 ± .06
3	0.38 ± .07	0.91 ± .05
4	0.42 ± .06	0.26 ± .03
5	0.31 ± .05	0.23 ± .03
6	0.11 ± .06	0.13 ± .07
7	0.36 ± .04	0.21 ± .03
8	0.27 ± .05	0.14 ± .05
9	0.13 ± .03	0.08 ± .06
10	0.34 ± .06	0.32 ± .05
11	0.45 ± .06	0.36 ± .03
12	0.35 ± .04	0.34 ± .05
13	0.42 ± .07	0.51 ± .06
14	0.41 ± .03	0.32 ± .06
MEANS	0.358	0.340

T Test on Means

	DD	WW
DD		NS
WW		

FIG 5 WATER LOSS OVER 1ST TWO DAYS OF EXPERIMENT



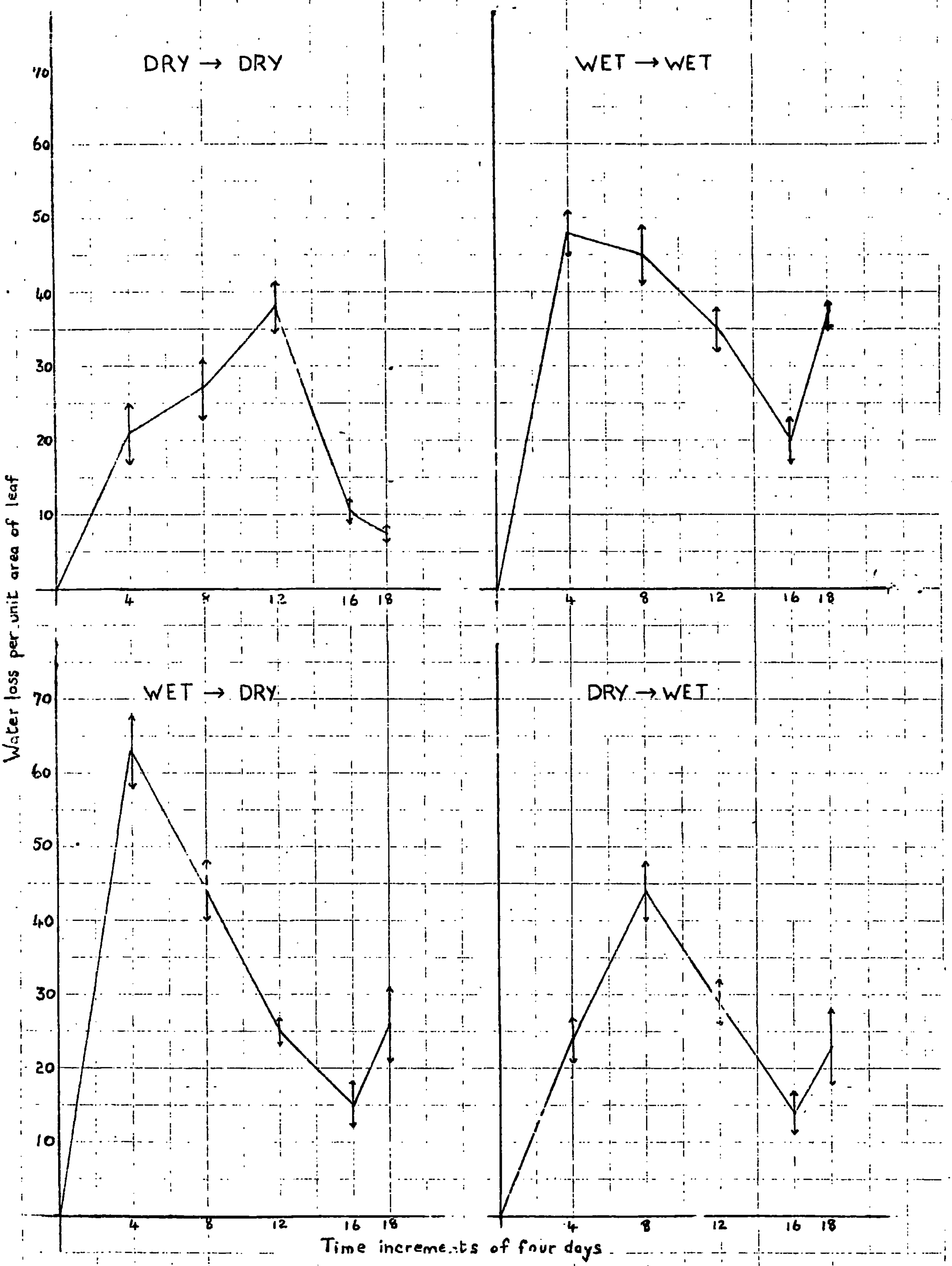


FIG. 6 WATER LOSS 4 DAY MEANS THROUGHOUT EXPERIMENT

Conclusions

There is no significant difference between the rates of transpiration in the two treatments.

Overall conclusions

It is impossible to come to any firm conclusion on the basis of these few, crude experiments.

However the indications are that the plants of population A (under the conditions of experiment 6) can control water loss from their leaves more efficiently than those of population B.

The graphs lend weight to this conclusion indicating that even over the first two days of the experiment when it appears that the plants are "settling down". A pattern of difference in the rate of transpiration between the population and the treatments is set up and this pattern is more or less maintained throughout the experimental period.

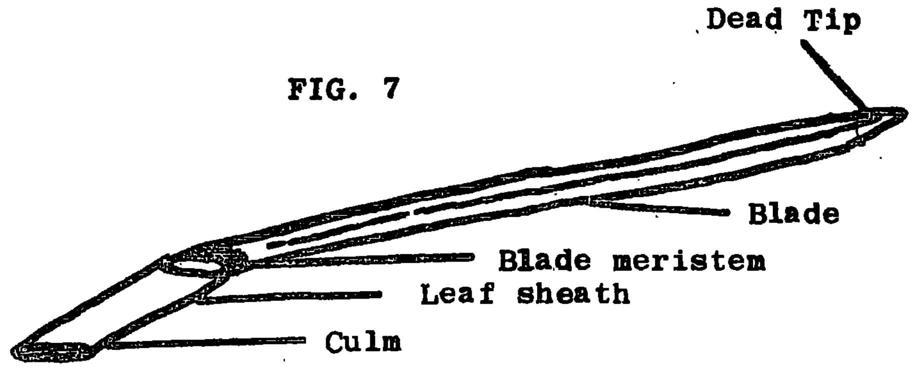
The fact that these differences become obscured after 28 days of growth in the greenhouse are best explained by 1) the great plasticity in the number of stomata per unit leaf area shown above and 2) the supposition that the bulk of transpiration takes place via the youngest leaf tissue.

Supporting although circumstantial evidence for the latter is provided by the fact that the main visible effect of stress over the period of the experiment was the rapid death of the leaves from the tip backwards toward the meristem.

GENERAL DISCUSSION AND FURTHER EXPERIMENTS

In order to attempt to understand the effects of the environment on the structure and anatomy of the leaf of Sesleria a model of the development of the leaf blade is presented below

FIG. 7



Initiation of the structure of the epidermis including the frequency of the stomata and the short cell groups must take place in the leaf blade meristem, Thiele (1951).

Investigations were made into development in the region of the meristem, Feulgen method but all attempts at revealing the pattern of mitotic divisions failed. The actual process of initiation and early development of the stomata is thus a matter of pure conjecture.

From the experimental work described above and summarised in Table 13 it may be concluded that there is no correlation between the number of stomata and the number of short cell groups formed per unit area of epidermis. In the light of this together with the absence of any overall pattern of response of the number of short cells to environmental conditions either in the field or greenhouse it was decided to omit the short cells from further discussion.

TABLE 13

Summary of Results of all counts Number of Stomata per unit area and number of short-cells per unit area in the same Tissue

Stomata	Short-Cells	Stomata	Short-Cells
837	351	505	241
796	88	503	258
770	511	497	373
725	300	495	234
713	496	485	91
677	194	482	225
669	372	478	366
660	543	466	255
649	315		
645	279	454	302
643	361	450	216
642	302	437	296
641	403		
640	284	417	336
614	410	403	375
614	277	400	384
604	250		
596	364		
576	358		
574	438		
549	445		
548	401		
541	378		
532	395		
532	338		
521	362		
518	360		
513	517		
507	306		

STOMATA

All the field data indicates that the number of stomata produced per unit area of epidermis is in some way related to a "scaler" linking depth and dampness of soil and water supply. The differences are most marked in the lowland populations, but nevertheless the trends throughout the montane populations are the same see summary table, 14.

TABLE 14

Soil Type		Dry/Shallow			Damp/Deep	
Lowland	Drought	837	715	640	604	505
	Rains	725	NR	NR	NR	450
Montane	Drought	677	660	643	549	NR
	Rains	NR	576	596	541	

It is of interest to note that for each subjectively comparable step in the depth/dampness scaler the stomatal numbers are fewer in the montane populations. It must however be emphasised that the soil step units are in no way directly comparable.

Measurements of the soil moisture content (amount of water present in the air dried samples) of each soil type summarised in Table 15, bear out the subjective assessment of depth and dampness.

TABLE 15

Soil Moisutre % (5 replicates)

Soil Type	Dry/Shallow			Damp/Deep	
Lowland	3 ± 0.7	10 ± 3.6	15 ± 6.0	23 ± 7.3	34 ± 1.6
Montane	5 ± 2.2	8 ± 4.1	12 ± 1.7	20 ± 11.2	36 ± 14.1

It was impossible to collect relevant data on the microclimate of the two sites during the experimental work. However data, see Table 16 from the Upper Teesdale (Widdybank Fell) and Durham Observatory Meterological stations do help to indicate the macro-differences between the climates of the two study areas throughout 1976.

The experimental work on plasticity back up the trends shown in the field populations at least as far as the lowland populations are concerned. The plants from the population A (dry shallow soil) produced significantly fewer stomata when grown under the "wet" conditions. In marked contrast the plants of population B (deep damp soils) produced significantly more stomata when grown under "dry" experimental conditions. These significant changes were found both on new leaf tissue and on new leaves produced during the experimental period.

As the depth of the potting compost was the same in each of the experimental treatments it must be concluded that water supply, 'hydrature' of the soil/precipitation/evaporation system Walter (1973) is the main factor controlling the structure of the epidermis of Sesleria. The conditions of humidity in the greenhouse experiments were not kept stable although the fluctuations were similar for all plants in each experiment. However it is realised that the humidity microclimate in and around the pots subject to more regular watering could be higher than that around those in the "dry" treatment.

The effect of 'hydrature' on the stomatal number is also shown by comparison of the leaf tissue produced in the field during the summer drought and the autumnal rains of 1976.

TABLE 16 Monthly means rainfall and temperature throughout 1976 at relevant lowlands and montane meterological stations

		Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Durham Observatory	Rainfall mm	46.2	17.5	2.6	31.4	78.9	24.9	30.0	18.4	193.2	142.6	22.8	50.9
	Temp °C	4.7	3.7	3.6	7.7	11.4	16.8	18.2	16.9	12.2	10.0	4.5	1.7
Widdybank Fell	Rainfall mm	150.8	88.0	140.5	65.5	133.0	38.1	66.7	22.1	218.8	236.7	99.0	201.0
	Temp °C	2.2	1.4	0.7	4.2	7.5	13.2	14.5	14.8	9.3	7.4	3.6	-0.6

In all cases the number of stomata produced during the rains were significantly fewer than the number produced during the drought.

Turning to the montane populations the results of the experimental work, though at first sight puzzling are of great interest. In all cases except for the wettest field population, the number of stomata produced in greenhouse culture whether "wet or dry" were greater than the number produced in the field. This can only be explained by supposing that the conditions of both experimental treatments are more 'xeric' in terms of 'hydrature' than those usually encountered by the montane populations in the field. Unfortunately it was impossible to make meaningful recordings of the humidity at the field sites during the growing period.

The fact that all the 1976 field comparisons showed that the leaf tissue produced during the drought had significantly more stomata per unit area than that produced during the autumnal rains is good supporting evidence indicating similar behaviour of all the populations to an effective scale of 'hydrature.'

PLASTICITY

Perhaps the most surprising results of the work outlined above is the rapid response in the number of stomata produced per unit leaf area in relation to hydrature both in the field and the laboratory.

It would appear that as soon as the leaf blade meristem is put under a new regime of 'hydrature' the rate of initiation of stomata changes, perhaps to compensate for the change, in water supply.

The importance of such plasticity to the success of a plant able to live across a range of habitats cannot be overstressed, cf. the findings of Clausen Keck & Hiesey for Achillea millefolium (1948). It is however obvious from the distribution of Sesleria that it is unable to compete with the ranker growing grasses of the Mesobromion proper Shimwell 1968, Bellamy et al. (1969). It has been suggested Lloyd (1974) that its inability to compete in the warmer conditions more typical of the Mesobromion may be due to its slow rate of growth compared with the more thermophilous grasses.

TRANSPIRATION

The experiments on transpiration rate although of a very 'crude' nature do give backing to the above conclusion. The rate of water loss being significantly less from the dry population A than from the 'wet' population B. West (1975) had attempted and failed to get meaningful estimates of transpiration in the field using a simple cobalt thiocyanate paper technique. His laboratory experiments using the same technique as employed in this study were less conclusive than those reported here. However the marked plasticity of the number of stomata reported here and the fact that Wests plants were grown in the greenhouse for one month prior to comparative study provides an adequate explanation for this.

More accurate measurements on a range of contrasting populations would be necessary before valid conclusions could be drawn. However it does appear safe to suggest that an increased number of stomata per unit area of epidermis afford better control of transpiration. The mechanism of such control has long been understood from the investigations of Browne & Escombe (1905), Kramer (1969).

The tentative indications are that Sesleria plants collected from populations from a range of environmental conditions in which it grows in N.E. England respond to water stress by increasing the number of stomata per unit area of leaf tissue which help to control water loss from the plant.

The two exceptions to this rule, populations H & M are of interest. Population H although growing on very shallow rapidly drying soils has significantly fewer stomata per unit area of epidermis than any of the other montane populations. An explanation is sought in the fact that the soils of population H are rich in heavy metals. A definite effect of the heavy metals on the biogeochemistry of the leaf tissue is shown by the following investigation.

HEAVY METALS IN POPULATION H

In order to investigate further the effects of heavy metals (if any) on Sesleria the following analyses were undertaken.

Leaves were collected from the two populations, H (on heavy metal spoil) and J an adjacent dry shallow soils free from the effects of mining spoil.

On return to the laboratory the dead tips were removed from all leaves the dead material being discarded. Six replicate samples of live leaf material were selected at random from each of the two population samples. After drying to constant weight at 105°C they were wet digested with a mixture of perchloric and nitric acids using the method of Johnson & Ulricht (1959).

The digests were analysed using a Perkin Elmer 480 atomic absorption spectrophotometer for Mg, Ca, Pb, Zn, Al & K. All results corrected for matrix enhancement Waughman (pers. comm.) are summarized in Table

TABLE 17

mg per gm dry weight of plant tissue means + standard errors

Mg		Cu		Pb		Zn		Al		K	
H	J	H	J	H	J	H	J	H	J	H	J
0.559	0.565	5.15	5.14	0.200	0.141	0.205	0.144	0.181	0.134	10.55	10.14
±0.01	±0.012	±0.169	±0.233	±0.017	±0.021	±0.010	0.008	±0.019	±0.012	±0.152	±0.233

Results of student t test, comparing element concentrations in leaf tissue of population H & J.

Mg	NS
Ca	NS
Pb	*
Zn	**
Al	*
K	NS

The levels of Pb, Zn and Al all of which are present in larger than 'normal' amounts in the soils associated with heavy metal spoil heaps in Upper Teesdale Kookorinis (1976) are present in significantly greater concentrations in the tissues of population H than in the tissues of population J.

The mechanism if any linking the significantly higher levels of heavy metals and the reduced number of stomata is obscure. Indeed it might be expected that high levels of such metals could result in physiological drought Raman (1911) which might be expected to result in an increase in the number of stomata rather than a decrease.

The results from population M are more readily explained. In this case although the soil was without doubt the 'wettest' studied being along the edge of a flush dominated by vegetation referable to the Eriophoretum latifoliae, it had significantly more stomata per unit area of epidermis than all the populations from 'drier' situations. Despite the fact all the plants were very small and stunted and their rooting depth was limited to less than 3 cm due to marked gleying of the flush soils.

West (1975) reported some measurements of the root/shoot ratio of the plants he studied. Attempts were made to gain similar information for the plants used in this study. However, because of the length of time required to excavate the roots and the inaccuracies inherent in such work due to breakage of the finer roots it was abandoned early in the study.

The experimental work in which changes in the number of stomata were obtained in similar depth of soil and over a time scale in which it was found that in all cases only limited growth of new roots had occurred are of interest. They indicate that the amount of roots present on a plant is not the most important factor controlling stomatal number.

Further studies on populations found growing in other extreme conditions are required before any conclusions can be drawn.

MECHANISM OF MORPHOGENETICAL CHANGE

West (1975) showed for the population he studied that there was a significant difference between the size of the Sesleria plants and soil depth at any one altitude. This is in the main borne out by this study, for in the majority of cases the plants growing on the dry shallow soil were smaller than those growing on the adjacent damp/deeper soils. In the light of these observations it would appear possible that the mechanism of change in the number of stomata per unit leaf area could be brought about by a simple reduction in the growth rate of the leaf, providing that the rate of production of stomata was a fixed attribute of the leaf meristem system.

In order to gain information concerning this relationship the following investigations were carried out.

METHODS

The longest leaf of the twenty plants selected at random from the field populations A, B, C, G, H, J, K and L were collected and the following measurements made on each

(1) Length of the longest leaf

(2) Length of five stomata (see Fig.

(3) Longitudinal distance between adjacent stomata in one cell line.

All the above measurements were made on tissues produced during the drought of 1976. In addition the same measurements were made on the contrasting leaf tissue of population H, J, K & L produced during the autumnal rains of 1976. A final set of measurements were also made on the tissues produced in experiment 4 described above.

TABLE 18

		LOWLAND (160m OD)				MONTANE (460m OD)			
Soil Type		Shallow Dry	Deep Moist	Shallow Dry	Deep Damp	Heavy Metal	Shallow Dry	Medium Moist	Deep Damp
Population		A	B	C	G	H	J	K	L
	Top (Drought)	(642) 0.095 ± 0.004	(614) 0.100 ± 0.005	(837) 0.090 ± 0.003	(505) 0.060 ± 0.003	(532) 0.086 ± .003	(660) 0.074 ± .004	(643) 0.062 ± .008	(549) 0.092 ± .005
istance etween djacent tomata mm	Base (Rains)	NR	NR	NR	NR	(521) 0.096 ± .006	(576) 0.008 ± .003	(596) 0.084 ± .004	(541) 0.100 ± .006
ength of tomata	Top (Drought)	0.026 ± 0.004	0.033 ± 0.006	0.040 ± 0.006	0.030 ± 0.008	0.032 ± .004	0.036 ± .007	0.048 ± .007	0.046 ± .008
	Base (Rains)	NR	NR	NR	NR	0.042 ± .006	0.036 ± .007	0.038 ± .005	0.054 ± .005
		5.5 ± 1.2	151 ± 2.6	6.5 ± 0.9	16.4 ±2.3	3.2 ± 1.3	6.4 ± 1.8	12.9 ± 1.2	164 ± 6.8
umber of tomata	Top	642	454	537	505	532	660	643	549
	Base	532	437	725	450	521	576	596	541

TABLE 19

SUMMARY

No. of Stomata per unit area	Distance mm	Length mm
837	0.090	0.040
660	0.074	0.036
643	0.062	0.048
642	0.095	0.026
614	0.100	0.033
596	0.084	0.038
576	0.068	0.036
549	0.092	0.046
541	0.100	0.054
521	0.096	0.042
505	0.060	0.030
454	0.100	0.033

FIG. 20

	Population	H	J	K	L
Length of Stomata	Top	0.044 ± 0.01	0.044 ± 0.007	0.048 ± 0.01	0.048 ± 0.01
	Base	0.028 ± 0.005	0.028 ± 0.005	0.042 ± 0.009	0.036 ± 0.007
Distance between Stomata mm	Top	0.072 ± 0.005	0.084 ± 0.004	0.08 ± 0.006	0.06 ± 0.006
	Base	0.072 ± 0.005	0.084 ± 0.004	0.08 ± 0.004	0.06 ± 0.007

RESULTS

The results are summarized in Tables 18, 19 and 20.

DISCUSSION

Inspection of the data shows that there is no simple relationship between the number of stomata per unit area and either of the cell measurements. It is therefore obvious that the adjustment in the number of stomata both in the field and in the laboratory are not brought about by a simple increase in the number of stomata produced in each cell line.

The greenhouse experiment further shows that the longitudinal distance between the stomata does not change significantly although the actual length of the stomata would appear to be more plastic.

Fig 8 a and b shows tracings of representative sections of the epidermis of the two contrasting populations A & B.

In both the intercostal cell lines with stomata are in ranks of 3 sometimes 2 or 1. However in population A these are separated in the main by 3 lines of costal cells while in population B the number is usually 6.

It would thus appear that adjustment in the number of stomata present per unit area of epidermis is brought about by an adjustment in the proportion of costal to intercostal cell lines. Unfortunately time did not allow further measurements to be made.

MAIN DISCUSSION CONTINUED

The above findings are also of importance in relation to stomatal control of transpiration.

Parlange & Waggner (1970) state that interstomatal interference is likely to take place when interstomatal spacing is less than 3 times stomatal length. Lloyd (1974) obtained values of less than 3 for some British populations of Sesleria and suggested that this factor might contribute to their high stomatal resistance and low rates of transpiration and photosynthesis. In West's (1975) investigation he only found a value of less than 3 from one population on shallow soil from a lowland habitat.

Unfortunately because of the marked grouping of the stomata, the measurements recorded above are of no use in calculating a meaningful figure for the ratios distance between stomata to length of stomatal pore. It is nevertheless obvious that in all cases the individual stomata within the stomatal groups are close enough to invoke some effects of interference. It is also clear that in the case of population A even the stomata of adjacent groups could lie within the sphere of each others influence.

CONCLUSIONS

The work detailed above indicates that for the plants of the populations studied:-

(1) The number of stomata produced per unit area of the adaxial epidermis of the leaf of Sesleria is related to

the 'hydrature' <u>sensu</u> Walter (1973) of the system in which the plants are growing

(2) That the less readily available water is to the leaf blade meristem the greater the number of stomata are formed per unit area of epidermis.

(3) That the morphogenetic response to 'hydrature' is very rapid and hence the morphology of the epidermis as regards to stomatal number is very plastic.

(4) That the increased number of stomata is produced by a decrease in the number of files of intercostal cells.

(5) That the increased number of stomata helps to control the rate of water loss from the leaf.

(6) That part of this control may be due to interstomatal interference.

(7) That much more work is required before any of the above conclusions may be regarded as anything more than mere indications.

(8) That a fruitful line of research would be studies of both the anatomy and transpiration of cloned material grown under a variety of controlled conditions in a growth cabinet.

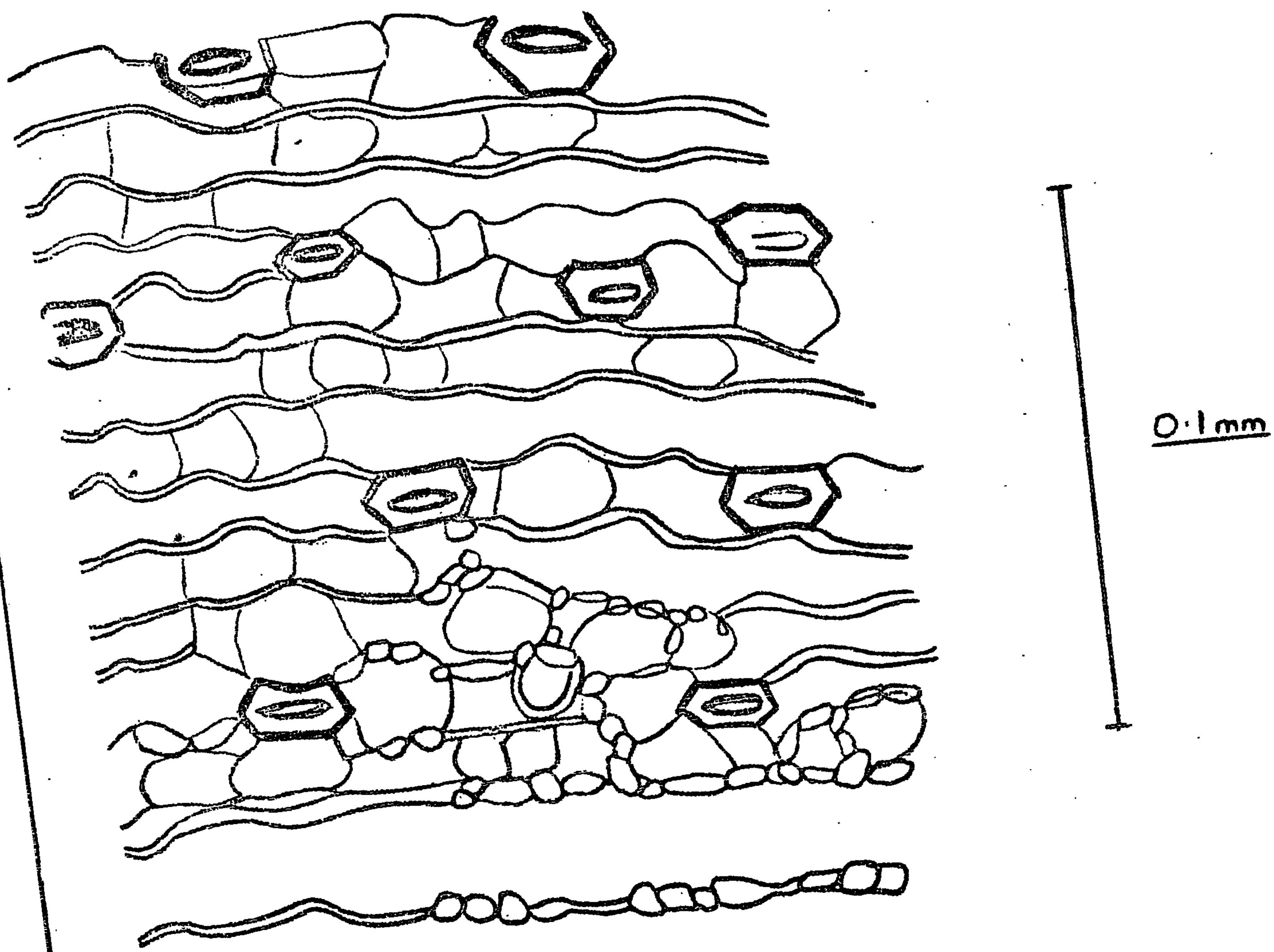


FIG 8A POPULATION A

Tracing of photograph of acetate peel of epidermis

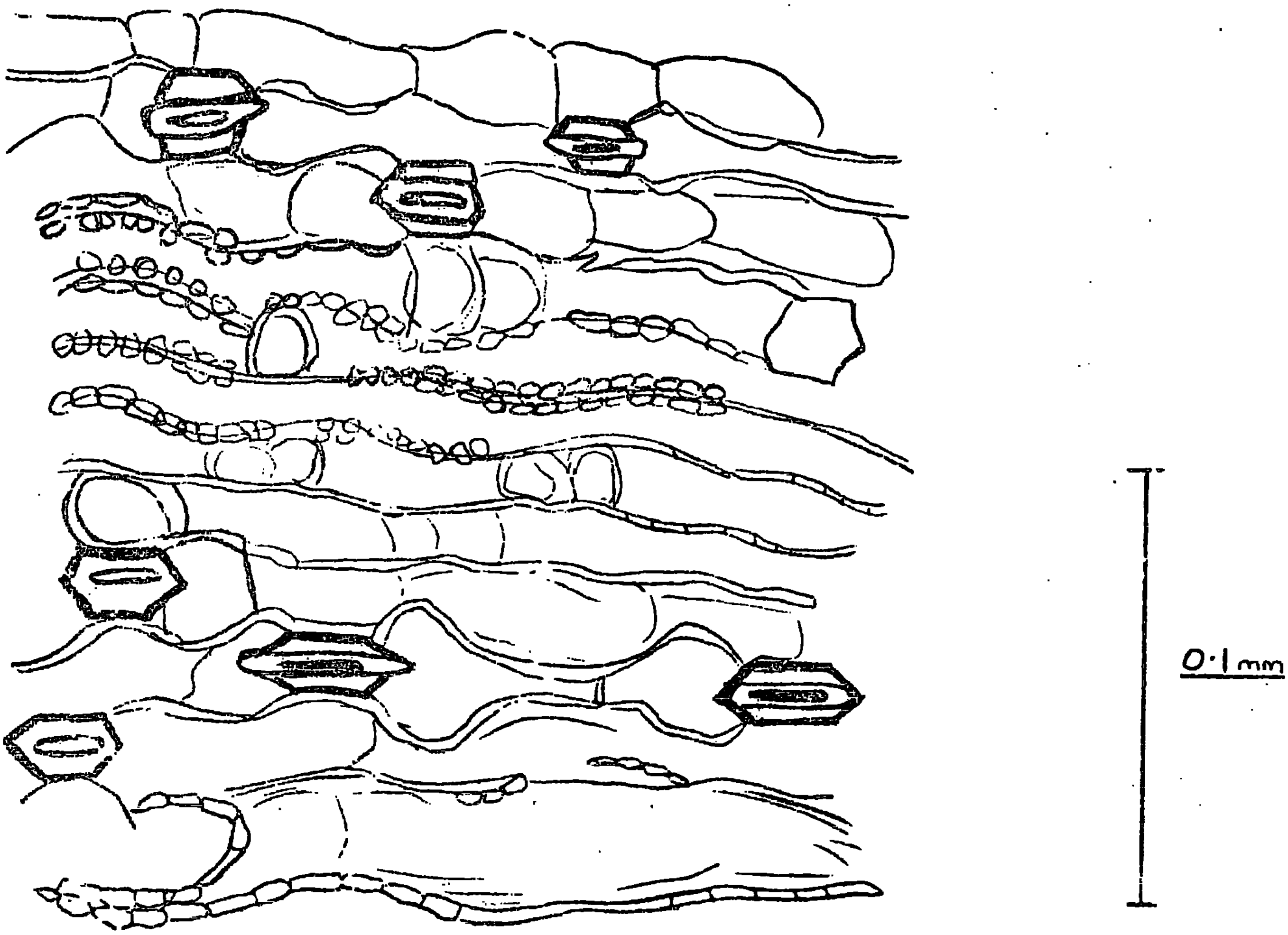


Fig 8B Population B

Tracing of photograph of

acetate peel of epidermis

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