TAXONOMY AND CULTIVAR DEVELOPMENT OF *POA PRATENSIS* L.

David P. Byres

PhD. University of Edinburgh 1984

Declaration.

This thesis was composed by myself, and the work described herein is my own.

David P. Byres

CONTENTS

Acknowledgements

I am very grateful to my supervisors, Dr P.M.Smith at the Botany Department, Edinburgh University, and Mr G.Wallace and Dr R.N.Eckersall at Scottish Agricultural Industries Plc., for their advice, assistance and encouragement during the course of this study. I would also like to thank Dr J.H.Lennard for advice on the identification of fungal pathogens, and Dr M.Talbot for the use of his 'Duncan's Multiple Range Test' computer program.

I am greatly indepted to the following, who provided me with land for experimental sites : Mr J.Reid, of Balbridie, Crathes, Mr I.Blackhall of Milton, Kirktown of Durris, Mr J.McLaren of Craigs Farm, Dalmally, Dr F.Harper of the Edinburgh School of Agriculture, and Dr R.Armstrong of the Hill Farming Research Organisation, Sourhope.

The work described in this thesis was carried out while I was in receipt of an S.E.R.C. Case award, for which I am very grateful.

ABSTRACT

Poa pratensis L. *s.l.* (Gramineae) is a common wild plant in Britain, but despite its economic importance - primarily as an amenity grass - the taxonomy and cultivar development of this species has been relatively neglected in this country. The two main aims of this work were to investigate the taxonomy of *Poa pratensis*, in Britain primarily, and to assess the potential for producing cultivars with improved performance, using the indigenous biotypes from Scotland.

The morphology of plants from three separate populations in Scotland was examined, as well as herbarium specimens from the whole of Britain, and the other main areas of distribution of *Poa pratensis s.l.*. Great morphological variability was evident, both within populations and over a wide geographical range, and this transcended the boundaries of the putative intra-specific taxa: subsp *angustifolia*, subsp *pratensis* and subsp *subcaerulea*. Many plants were found which had a mixture of morphological characters normally attributed to two or more subspecies. From these results, and also the geographical overlap of the supposed subspecies in Britain, it was concluded that the use of specific or subspecific rank was inappropriate for the taxa *subcaerulea* and *angustifolia*, and that these should be considered to be part of the spectrum of variation within the single species *Poa pratensis* L. Insufficient material of subsp *alpigena*, which does not grow in Britain, was examined to allow any conclusions to be drawn about the validity of the subspecific rank attributed to this taxon.

Twenty three biotypes of Poa pratensis were collected from around Scotland, and these were grown in three main experimental sites - near Aberdeen, at Edinburgh, and in the Cheviots. Four cultivars were used as controls. Approximately twenty visits were made to each site over two years, and on each occasion the plants were cut to a height of 2.5cm. The characters recorded at the experimental sites were : plant survival, dry matter production, ground cover, disease resistance and plant colour. The wild biotypes showed considerable physiological diversity, and the cultivars were outperformed, in all the characters examined, and at almost every site, by one or more biotypes. Four of the biotypes showed considerable potential as possible future cultivars.

No correlation was apparent between the taxonomic position of plants within Poa pratensis and their performance in experimental plots. The initial tillering rate of the plants was the best character found for predicting their future performance.

SECTION A.

CHAPTER 1. INTRODUCTION

1.1 Introduction

The subject of this study is Poa pratensis L. s.l., which is one of over four hundred species in the genus Poa. Although it is a grass of economic importance, the taxonomy of this species has been relatively neglected, particularly in Britain. One of the aims of the present work was to examine Scottish plants and also herbarium specimens of Poa pratensis s.l. from other parts of the world in order to investigate the taxonomy of this species.

Cultivated varieties ('cultivars') of Poa pratensis are used in Britain primarily for amenity grass for lawns, sports turf and roadside verges. Poa pratensis is a common plant growing wild throughout Britain, but at present all the cultivars used in Britain are imported from abroad. There has been little work done on improvement of Poa pratensis cultivars, and no cultivars are available that originate in Britain. This species has therefore been neglected in terms of cultivar development in Britain. The second aim of this thesis was to compare the performance in experimental plots of indigenous Scottish Poa pratensis with some of the imported cultivars, to find out whether cultivars with improved performance could be produced from wild plants. These two aspects of the work are discussed below.

1.2 Taxonomy

The genus Poa is in the Pooideae (Gramineae), a subfamily

of mainly north temperate distribution [1]. Temperature is probably the main limiting factor in the distribution of Poa itself [2]: generally, Poa is more tolerant of cold than of heat, and so in the tropics it is found only at high altitude [3], however it flourishes in temperate areas.

Poa pratensis is distributed as a wild plant throughout Europe, especially in the north, also North Africa, temperate Asia and North America [4]. It is a species with wide morphological variation [5], and there is debate as to the number and taxonomic position of inter-specific groups. Previous workers have divided Poa pratensis s.l. into between 4 and 22 entities [6]. Recent floras have treated these taxa variously as species [7,8], subspecies [9] or varieties [10]. Modern British floras generally divide Poa pratensis s.l. in Britain into three species: Poa pratensis L., Poa angustifolia L. and Poa subcaerulea Sm. [7], although as Barling points out [11], very little taxonomic work has been done on Poa pratensis s.l. in Britain.

The taxonomy of Poa pratensis is complicated by the fact that it reproduces by facultative apomixis [12,13]. In Poa pratensis this takes the form of agamospermy, with seed being genetically identical to the mother plant. This is achieved by apospory and parthenogenesis [14,15]: the embryo sac is produced from an unreduced nucellus cell, which forms the seed without fertilisation by a male gamete. Pollination is still required for seed set, as apomictic embryos cannot develop until the endosperm has been fertilized [16].

Although Poa pratensis is predominantly apomictic, there is wide variation from completely sexual plants to almost complete

apomixis, and this balance depends on both the maternal genotype and on environmental conditions [17,18,19].

Facultative apomixis allows plants with unbalanced chromosome complements to reproduce, and so a wide range of variation is often found within apomictic groups [20]. Another of the results of facultative apomixis is that small populations containing only one or two genotypes can be produced, so that apparently discrete units are formed. However these are unstable and will alter over time due to the resumption of some sexual reproduction. This may mean that no useful classification of the variation into stable units may be practicable [21].

There are two main definitions of species :

a) 'Taxonomic' species - groups of morphologically similar individuals, separated from other groups by morphological discontinuities.

b) 'Biological' species - groups of interbreeding individuals, separated from other groups by reproductive barriers [21].

Use of the 'biological' species concept would cause problems with Poa pratensis L., as it hybridises readily with other species of Poa that are morphologically very different from it [22-24]. There is also the problem that two taxa may be capable of interbreeding, but do not hybridize in the wild due to ecological or geographical barriers [25]. Therefore in this study, a species is defined as a group of morphologically similar individuals, separated from other groups by correlated morphological discontinuities. This definition produces units that are subjective, in that the degree of difference permitted between individuals of the same species varies

to some extent with the observer. The limits put on the variation pattern may be broad ('Linneon species') or very narrow ('Jordanons') [26]. It is now generally recognised that there is a range of variation within each species, and so very narrow delimitations of species are not appropriate [21].

The term subspecies was originally used for a major, morphologically distinct variation in the species [27]. More recently, subspecies have been defined as ' a considerable segment of a species with a distinct area, and fairly distinct morphology' [21]. It is in this latter sense that 'subspecies' is used in this study. As Davis and Heywood point out [21], some overlap, both morphological and geographical, is permissible between subspecies, but the great majority of individuals must be morphologically different from individuals of the other subspecies.

Throughout this thesis, reference is made to the subspecies of Poa pratensis (such as subsp subcaerulea). It should be stressed that this is for reference purposes only, and does not imply acceptance of these putative taxa as actual subspecies as defined above. This is discussed further in Chapter 8.

1.3 Cultivar Development

Poa pratensis has been used in agriculture in Britain since the 17th century [28], and it was one of the first grasses recommended for cultivation [29]. Since then, however, its use as an agricultural grass has declined steadily, being largely replaced by Lolium perenne [30]. However its use as an amenity grass for sports

grounds, lawns and roadside verges has increased, as it has several useful characterisitics [31]. It has a high tillering capacity and creeping rhizomes to form a dense turf [31]. Winter hardiness is good [32-37], and this is especially important in Scotland where winterkill of Lolium is widespread in cold winters [38]. Excellent resistence to wear and mowing make Poa pratensis a very persistent species [31,39,40]. It has better root growth [41], and is more heat tolerant than Lolium [42], and is therefore used extensively as an agricultural grass in the relatively dry U.S.A.. On the other hand, Poa pratensis also has better tolerance to flooding than Lolium [43], so it is a grass of wide climatic tolerance.

There was very little organised plant breeding in Britain until the Welsh Plant Breeding Station was set up in 1919. The emphasis there was on the important agricultural grasses Lolium perenne and Dactylis glomerata, and the breeding material was obtained from adapted indigenous species [44]. In many cases the local grass gave a better productivity than the imported cultivars, and the superiority of local plants which are adapted to the climatic conditions of the area has been shown many times in grass breeding [45,46].

Work on improving the cultivars of Poa pratensis by selecting indigenous plants has been carried out in the U.S.A. for some time [22], but has only started fairly recently in Europe. At the moment, the main breeders of Poa pratensis are in the U.S.A., Holland, Sweden and Denmark. There are no cultivars that originate in Britain available on the market. Russia and Eastern Europe have an essentially independent trade in Poa pratensis [47]. On the whole, the market for amenity grass is expanding in Europe; the

increased use of amenity grass seed can be exemplified by the area used in Holland for producing Poa pratensis for seed. In 1950, no Poa was sown, but by 1962 the area of Poa pratensis sown by breeders exceeded the total area devoted to all other grass species, and this trend has since been maintained [48].

The realization that adapted local grass may offer improvements on the performance of imported cultivars has meant that selection of indigenous Poa pratensis for possible use as new cultivars has recently started in Norway [49], Japan [50] and Poland [51]. Due to the facultative apomixis of Poa pratensis, cultivars are normally obtained by selecting wild plants with the required characteristics, rather than actually crossing plants to produce a new genotype [52]. Most of the selection and breeding are done by private companies, and the origin and selection procedure are often undeclared, and perhaps often unrecorded and hence effectively unknown. This study is intended to provide an example of the initial stages in the development of a cultivar.

CHAPTER 2. LITERATURE REVIEW : TAXONOMY

2.1 Introduction

Poa pratensis L. *s.l.* is distributed throughout Europe, especially in the north, also North Africa, temperate Asia and North America [4], extending up to 83 degrees north in Greenland, making it one of the most northerly vascular plants [23]. In Great Britain, *Poa pratensis* is very widely distributed, and although rarely dominating it is a common grass found in several habitats and over a wide range of soil pH [53-55]. It is found on sand dunes, pastures, riverbanks, roadsides, waste ground, and hill and mountainsides [4]. It is a species with wide morphological variation [8,56], and there is debate as as to whether to treat the various groups as separate species or as subspecies. However cross fertilization can occur between all the different groups, and intermediates exist between them [6], so the taxa will here be referred to tentatively as subspecies. Apart from *Poa pratensis* L. *s.s.*, there are three other taxa, one of which (*Poa pratensis* subsp *alpigena*) is not found in Britain. The taxa are :

Poa pratensis L. subsp. *pratensis*

Poa pratensis subsp *angustifolia* (L.) Lindberg

Poa pratensis subsp *subcaerulea* (Sm.) Hiitonen.

Poa pratensis subsp *alpigena* (Fr.) Hiitonen.

The concept of 'ecotype' has gradually changed from the original definition - of a group of plants genetically adapted to a particular environment - to, an adapted population with no internal barriers to hybridization [21]. This latter definition would give

impracticably wide limits to ecotypes of Poa pratensis s.l., as it hybridises freely with several other species of Poa [22-24]. So ecotype is here taken to mean a group of plants within a species adapted to a certain environment. Several ecotypes of Poa pratensis have been reported, differing from each other in physiology [49,57], or in both physiology and morphology [58]. As Stebbins points out [59], Turesson - who first proposed the term ecotype - tended to emphasize the distinctness of different ecotypes, but later authors, such as Gregor, have found a more or less continuous series of intergrading populations. It is clear that in many cases the apparent distinctness of ecotypes is caused by sampling a few biotypes from widely different localities and habitats [59], so that continuous variation may appear to be discontinuous. How far this is true of ecotypes of Poa pratensis s.l. is not known. Occasionally, plants of Poa pratensis from different areas are referred to as separate ecotypes even though no physiological or morphological differences are reported between them [36]; in this study, such plants are referred to as biotypes. The term biotype is discussed below.

In Europe, subsp pratensis and subsp angustifolia are reported to differ ecologically; the former being found in wetter, fertile soil and on high ground, and the latter in dry, infertile soil [60]. In Britain, the subspecies overlap in range, but generally subsp angustifolia grows in drier, southern regions, and subsp subcaerulea is found in wet, northerly areas, with subsp pratensis between the other two [61]. The taxonomic characteristics of the British subspecies are given in Table 2.1..

Table 2.1. Taxonomic Characters of British Subspecies of Poa Pratensis

KEY : Sub = subcaerulea, Pra = pratensis, Ang = angustiolia
CTW = A.R.Clapham, T.Tutin and E.Warburg. Flora of the British Isles. 1952
Bar = D.M.Barling. Watsonia 5(3), 163-173 (1962)
Hub = C.E.Hubbard. Grasses. 1968.
CT2 = A.R.Clapham, T.Tutin and E.Warburg. Flora of the British Isles. 1962
Edm = J.R.Edmondson, in T.Tutin et al, Flora Europaea, 5, 161-162. 1980

An asterisk in brackets refers to the values for that character that are shown in identical brackets. For example Hubbard has the ligule length of subspecies pratensis as 1 - 3 mm, and Edmondson has it as about 1mm. Similarly only Barling shows the panicle length of subsp subcaerulea extending up to 11cm.

Character	SUBSPECIES Sub	Pra	Ang	REFERENCES CTW	Bar	Hub	CT2	Edm
Ligule length	~1mm (up to 2mm)	~1mm (1-3mm)	1-3mm (~1mm)			(*)		*
Leaf blade width	2 - 4 mm (1.5 - 2.5)	2 - 4 mm (2 - 3)	1 - 2 mm (0.8 - 2)	*		*	*	(*)
Lemma length	3 - 5mm	3 - 5mm	2 - 3mm			*		
Culms	Solitary	Tufted	Tufted	*	*	*		*
Panicle branches	usually 2	3 - 5	3 - 5	*	*	*	*	*
Lower glume	3 veined	1 veined (1-3 veined)	1 veined		*	(*)	*	*
Glumes	Tapering	Abruptly Pointed	Abruptly Pointed	*		*	*	*
Glumes	Almost Equal	Unequal	Unequal	*		*	*	*
Culm height	10 - 40cm (mainly) (15 -30cm)	6 - 15cm (mainly) (20-50cm)	6 - 10cm (mainly) (50 - 70cm)		*	*		(*)
Panicle length	4 - 6.5cm (2-8)[-11]	6 - 15cm (2-20)	6 - 19 cm (3 - 14)		[*]	(*)		*
Florets per Spikelet	2 - 4	2 - 5	2 - 5			*		
Spikelets per panicle	Few (20 - 80)	Numerous (>80)	Numerous (>80)	*	(*)		*	
Seed length	2.6 - 4mm	?	2 - 3.2mm		*			
Pollen diameter	32 - 40 m	?	22 - 32 m		*			
Spikelet length	4 - 7mm	4 - 6mm	2.5 - 5mm			*		

2.2. History of the Taxonomic Treatment of *Poa pratensis* s.l.

The taxonomic treatment of *Poa pratensis* L. *s.l.* varies from Flora to Flora. Table 2.2. shows how the four taxa have been treated in different Floras. The position is slightly complicated by synonymy; thus *Poa irrigata* Lindm. is considered to be a synonym of *Poa subcaerulea* Sm.[11], but both Druce [62] and the first edition of C.T.W. [63] list them separately. Similarly Weber [64] had *Poa agassizensis* as a separate species, while other authors [65] consider *Poa agassizensis* to be a synonym of *Poa pratensis* L. In both these cases the classification in the more recently published Flora is followed.

Table 2.2. is arranged in chronological order for each area. *Poa pratensis* subsp *alpigena* is not found in Southern Europe, and so the European Floras have been divided into those dealing with northern areas and those concentrating on the south. Flora Europaea, which covers the whole of Europe, is listed under Northern Europe.

Table 2.2. Taxonomic Treatment of *Poa pratensis* s.l.

Key: A = species; S = subspecies; V = variety; - = not mentioned; Ref = Reference number in bibliography

P = *pratensis*; N = *angustifolia*; C = *subcaerulea*; L = *alpigena*

Ref	Author	P	N	C	L
A) BRITAIN					
66]	Smith (1802)	A	A	A	-
67]	Lindley (1829)	A	V	V	-
68]	Hooker (1860)	S	S	S	-
69]	Bentham (1865)	A	-	S	-
62]	Druce (1932)	A	-	A	-
70]	Stewart (1938)	A	-	V	-
63]	CTW (1952)	S	S	S	S
71]	Butcher (1961)	A	A	A	-
72]	CTW (1962)	S	S	S	-
11]	Barling (1962)	A	A	A	A
4]	Hubbard (1968)	A	A	A	-
7]	CTW (1981)	A	A	A	-
73]	Wigginton (1981)	A	A	A	-
B) NORTHERN EUROPE					
74]	Linnaeus (1753)	A	A	-	-
75]	Hartman (1843)	A	-	S	-
76]	Norman (1894)	A	-	-	-
77]	Hiitonen (1933)	S	S	S	S
78]	Grontved (1941)	A	-	-	-
79]	Lid (1952)	A	A	A	A
80]	Hylander (1953)	S	S	S	S
81]	Hulten (1962)	A	S	-	A
82]	Lindman (1964)	S	-	-	S
83]	Love (1977)	A	A	A	A
8]	Edmondson (1980)	A	A	A	A
84]	Andersson (1981)	A	S	S	A
C) SOUTHERN EUROPE					
85]	Suter (1821)	A	A	A	-
86]	Willkomm (1861)	S	S	S	-
87]	Ascherson (1902)	S	S	S	-
88]	Coste (1906)	A	V	V	-
89]	Hegi (1907)	V	V	V	-
90]	Bonnier (1934)	A	V	V	-
91]	Fournier (1940)	A	V	V	-
92]	Caballero (1940)	A	-	-	-
93]	Jirasek (1964)	S	S	S	-
94]	Lopez (1974)	A	A	-	-
95]	Guinochet (1978)	A	S	S	-

Table 2.2.(cont). Taxonomic Treatment of *Poa pratensis* s.l.

Key: A = species S = subspecies
V = variety - = not mentioned
Ref = Reference number in bibliography

P = *pratensis* N = *angustifolia*
C = *subcaerulea* L = *alpigena*

Ref	Author	P	N	C	L
D) NORTHERN ASIA					
96]	Maximiowicz (1859)	A	V	-	-
97]	Komarov (1934)	A	A	A	A
98]	Kolakovski (1938)	A	A	-	-
99]	Lavrenko (1940)	A	A	-	-
100]	Makashvili (1941)	A	A	-	-
101]	Gorodikov (1953)	A	A	A	A
102]	Pavlov (1956)	A	A	-	-
103]	Koie (1958)	A	A	-	A
104]	Ohwi (1965)	A	-	-	-
9]	Tzvelev (1972)	S	S	S	S
E) AMERICA					
105]	Gray (1950)	A	A	A	A
106]	Mohlenbrock (1959)	A	-	-	-
107]	Moss (1959)	A	-	-	-
108]	Wiggins (1962)	-	-	-	A
109]	Roland (1963)	A	V	A	V
110]	Steyermark (1963)	A	-	-	-
111]	Lakela (1965)	A	A	-	-
112]	Braun (1967)	A	-	-	-
113]	Hulten (1968)	A	A	A	A
114]	Strausbaugh (1970)	A	-	-	-
115]	Voss (1972)	A	V	-	-
64]	Weber (1972)	A	-	-	-
65]	Hitchcock (1973)	A	-	-	-
116]	Welsh (1974)	A	?	?	?
117]	Gould (1975)	A	-	-	-
118]	Scoggan (1978)	V	V	V	A
10]	Dore (1980)	V	V	-	V

Table 2.2. illustrates the lack of agreement on the appropriate rank which the taxa should be given. In Britain, most of the earlier Floras have treated the different taxa as subspecies or varieties but recent ones divide them into species. Although Poa pratensis subsp. subcaerulea Sm. was first described from Britain in 1802 [66], very little work was done on British Poa pratensis s.l. until Barling's studies of subsp subcaerulea [11,119] and subsp angustifolia [120]. Barling treated these taxa as species separate from Poa pratensis L. and since then other authors have concurred with this view. The most recent edition of the Excursion Flora of the British Isles, for example, has the taxa as species [7]; earlier editions did not mention subcaerulea or angustifolia [121], but in the Flora of the British Isles they were treated as subspecies [72].

The distribution of Poa alpigena does not include Britain or Southern Europe, accounting for the relatively few mentions of this taxon in the literature from these areas. The Northern European Floras are split roughly equally between considering the taxa as subspecies and as species, while in Southern Europe most references have been to subspecies or varieties. In contrast Asian Floras refer almost exclusively to species. In America little reference is made specifically to the taxa, some authors such as Welsh [116] considering that all forms intergrade without discontinuity, presumably therefore even varietal rank is considered inappropriate.

2.3. Taxonomic Characters used by previous workers

This distinction in Floras from different areas could reflect a genuine difference in the plants of each region, or could be due to authors choosing, or emphasising, different characters. Traditionally, overwhelming reliance is placed on morphological characters, especially floral ones [21]. The characters that are commonly used for differentiating between the subspecies were determined, the characters used by different authors are shown in Table 2.3.. As far as possible, characters have been chosen for analysis in this study that are quantitative rather than qualitative; this removes the problem of inconsistent and subjective use of qualitative terms by different taxonomists. Where possible, any valuable character that is normally expressed qualitatively - such as panicle size - has been recorded quantitatively in this study. Useful qualitative characters that cannot be easily quantified have been retained, so no valuable evidence has been discarded.

Table 2.3. Taxonomic Characters used in Poa pratensis

CHARACTER

1 Culm height in cm.
2 Ligule length in tenths of mm
3 Leaf width in tenths of mm
4 Leaf length in mm
5 Panicle length in mm
6 Number of lower panicle branches
7 Number of spikelets per panicle
8 Spikelet length in tenths of mm
9 Lemma length in tenths of mm
10 Glume length in tenths of mm.
11 Glume tip shape
12 Number of florets per spikelet
13 Panicle width in mm
14 Panicle branches scabrous
15 Tufted
16 Colour of spikelets
17 Hairy ligule and area around ligule

Key: X = measurements given 0 = qualitative information, or information from diagrams

Ref	AUTHOR	CHARACTER																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
A) Britain																		
66]	Smith (1802)	X	0	0	0		0	0					X				0	
67]	Lindley (1829)		0										X					
68]	Hooker (1860)		0										X					
69]	Bentham (1865)	X	0	0		X	0	0			X		X					
63]	CTW (1952)	X	X	X		X	X	0	X				X			0		
71]	Butcher (1961)	X	X	X	0	0	0	0	X	X	X	0	X	0		0	0	
72]	CTW (1962)	X	X	X		X	X	0	X			0	X			0		
11]	Barling (1962)	X		X	X	X	X	X					X					
4]	Hubbard (1968)	X	X	X	X	X	X	0	X	X	X	0	X	X	0	0	0	0
7]	CTW (1981)	X	X	X		X	X		X			0	X			0		0
73]	Wigginton (1981)			X			X			X						0		0
B) Northern Europe																		
74]	Linnaeus (1753)		0										X					
75]	Hartmann (1843)		0				X						X		0			
77]	Hiitonen (1933)		X				X						X					
78]	Grontved (1941)	X																
79]	Lid (1952)	X	X				X				X	0				0	0	
80]	Hylander (1953)	X		X	X		X				X					0	0	
82]	Lindman (1964)		0										X					
83]	Love (1977)	X	0	X		X												
81	Edmondson (1980)	X	X	X	X	X	X					0	X			0		
C) Southern Europe																		
85]	Suter (1821)												X				0	
86]	Willkomm (1861)	X				X							X					
87]	Ascherson (1902)	X	X	X		X	X		X		X		X		0		0	
88]	Coste (1906)	X	0	X			X						X					
89]	Hegi (1907)	X	X	X			X		X	X	X		X		0		0	
90]	Bonnier (1934)	X	0	X			X					0	X				0	
91]	Fournier (1940)	X		X			X								0			
92]	Caballero(1940)												X					
93]	Jirasec (1964)								X	X		0				0	0	0
94]	Lopez (1974)	X																
95]	Guinochet(1978)	X	X															
D) Northern Asia																		
97]	Komarov (1934)	X	X	X		X	X		X			0	X		0	0	0	
98]	Kolakovski(1938)	X	X	X									X					
99]	Lavrenko (1940)	X	X	X		X	X		X				X		0		0	
100]	Makashvili (1941)	X	X	X					X				X					
101]	Gorodikov (1953)	X	X	X	X	X			X	X	X		X	X				
102]	Pavlov (1956)	X	X	X		X	X		X				X					
104]	Ohwi (1965)	X	X	X	X	X			X	X	X		X		0		0	
9]	Tzvelev (1974)	X		X		X			X	X								
E) North America																		
105]	Gray (1950)	X		X		X	X		X			0		X		0		
106]	Mohlenbrok (1959)		X	X		X			X				X					
107]	Moss (1959)	X		X			X		X	X			X					
108]	Wiggins (1962)	X	X	X	X	X			X	X	X		X	X	0	0	0	
109]	Roland (1963)		X	0		0	0		0	0			0			0		
110]	Steyermark (1963)	X							X									
111]	Lakela (1965)	X	X	X			X						X					
112]	Braun (1967)		X				X	0	0	X								
113]	Hulten (1968)	0	X	X	0		X	0				0				0	0	
114]	Strausbaugh (1970)	X		X	X		X		X	X								
115]	Voss (1972)		X															0
64]	Weber (1972)		X	X						X			X					
65]	Hitchcock(1973)		X	X			X			X								
116]	Welsh (1974)	X	X	X		X			X				X					0
117]	Gould (1975)	X	X	X		X	X	0	X				X	X		0		
118]	Scoggan (1978)	X		X								0						
Total References :		39	39	38	11	23	31	10	25	15	10	12	37	6	9	16	15	6

Table 2.3. shows that the most frequently mentioned characters are : Culm height, leaf width, ligule length, number of florets per spikelet and number of lower panicle branches. The characters about which the least information is given are : glume length, number of spikelets per panicle, scabrousness of panicle branches, hairiness of the area around the ligule, and panicle width. Only Barling [11] provides values for the number of spikelets per panicle, other data on this character are interpolated from diagrams in Floras, which give no idea of variability, and may not accurately represent a typical specimen of each subspecies.

Comparing the Floras from different regions, on the whole the Northern European ones use relatively few characters compared to the others; also European Floras generally give less importance to panicle length (character 5) and spikelet length (character 8) than the others. However similar characters tend to be stressed in Floras of different areas, so there is little evidence that the disagreement over taxonomic treatment is due to uncertainty about which characters are most important, useful or reliable.

There is general agreement on the key characters that distinguish Poa pratensis L. s.l. from other species of Poa. From Linnaeus onwards [74], the shortness of the ligule of Poa pratensis has been emphasised [4,8,64,65,67,77,115]; Smith in 1802 mentions the five prominent nerves of the lemma and the web of hairs on the callus at the base of the lemma [66], which are still frequently mentioned [8,95,104,105,115]. Also, Poa pratensis is rhizomatous [7,11,64,66-68,72,113-115] and the culm is round or slightly compressed but never two edged [8,88-91,105,107]. The culm leaves are usually between 1 and 4mm wide [4,72,81,88,99]. The number of

branches at the lowest node of the is between two and five [65,75,79,90,99,105]; each spikelet contains 2 - 5 florets [64,66,67,75,77,88].

Some of the characters above have been used as key characters for distinguishing the subspecies of Poa pratensis L. s.l.. Linnaeus [122], in the first edition of Species Plantarum separated Poa pratensis L. from Poa angustifolia L. partly by the number of florets per spikelet : 3 in pratensis and 4 in angustifolia. However in the second edition [123], he had pratensis with 5 florets per spikelet, changing it back to 3 florets in the 4th edition [74]. Since then, the number of florets per spikelet has been only occasionally used for separating subspecies most recently by Kolakovski in 1938 [98]. The other key Linnaean character - leaf width, has been extensively used for separating the subspecies, especially subsp. pratensis and subsp. angustifolia [4,7,8,64,68,72,73,79,81,83,87,90,97,98,105,111,117].

The number of lower panicle branches is said to vary between subspecies [4,8,72,73,81,90]; and the degree to which plants are tufted is also commonly refered to as an important character at this level [4,8,11,65,72,73,79,81,97,105]. Other characters that are less frequently used include the ligule length [4,8,11,87,98], and number of veins on the lower glume [4,8,11,72,73,80,83], although with both of these there is disagreement about the values attributable to the different subspecies (see Table 2.1.).

Recently published works vary in their selection of key characters for distinguishing between the subspecies. In Canada, Scoggan (1978) uses glume shape, leaf width, hairiness of the nerves

of the lemma, degree of tufting and culm thickness, to separate subspecies alpigena, subsp pratensis and subsp angustifolia [117]. In contrast, Tzvelev (1972) employs culm height, rhizome length, leaf colour and width, panicle length and spikelet length, amongst other characters, and describes 10 subspecies [9].

Edmondson in Flora Europaea (1980) concentrates on leaf width, leaf tip shape and number of panicle branches to separate subsp alpigena, and distinguishes between the three subspecies found in Britain (subsp angustifolia, subsp pratensis and subsp subcaerulea) by the degree of tufting, number of dead leaf sheaths, glume shape, relative length of the glumes, leaf shape, number of nerves on the lower glume and whether or not the ligule is decurrant on the sheath margins [8].

Although subsp subcaerulea was first described from Britain [66], very little work was done on British Poa pratensis until Barling's studies of subsp subcaerulea [11,119] and subsp angustifolia [120,124].

Barling's transplant experiments showed that short culms, small spikelets and small panicles - features seen in the wild in subsp. subcaerulea - are often environmental effects [11]. He regarded production of single tillers, presence of three-nerved glumes, presence of hairs at the mouth of the leaf sheath, large pollen diameter, long seeds and few spikelets per panicle as features differentiating subsp subcaerulea from subsp angustifolia [11,119]. There was also an ecological difference: subsp subcaerulea being found in moist environments, with subsp angustifolia preferring dry areas. The narrow sterile leaves of subsp angustifolia, with few stomata, were presumed to be a xeromorphic

feature [120]. Generally, subsp subcaerulea and subsp angustifolia were considered to be more or less extreme forms of Poa pratensis [11]. Since then, no new taxonomic information about Poa pratensis s.l. in Britain has been published.

CHAPTER 3. MATERIALS AND METHODS

3.1 Environmental Variation

The degree to which different taxonomic characters can be affected by the environment is of great importance. Traditionally, characters which are greatly modified by the environment in which the plant is growing are regarded as poor taxonomic characters [21]. Biotypes of Poa pratensis s.l. from several areas of Scotland were grown in plots at three sites to determine susceptibility of different characters to environmental influence. Biotypes are normally defined as a group of individuals with the same, or essentially the same, genotype [21]. In this study, plants are assumed to be the same biotype if they are morphologically similar, and growing within 5 cm of each other. Six biotypes grown in three sites, and one biotype grown in two sites were used; in each case ten panicles were sampled. The biotype from Barra was only grown in two sites because it tillered slowly, and so not enough material was available to plant three sites. The experimental sites, and initial collection sites of the biotypes are shown in Table 3.1.1. Map references are given which refer to the metric, 1:50,000 scale Ordnance Survey maps, and these give the position accurate to the nearest 100m.

Table 3.1.1. Position of Experimental Plots and Collection Sites

SITE	AREA	MAP REFERENCE	ALTITUDE
Experimental Plots			
Bush (Bush)	Edinburgh	NT 244635	190m
Sourhope (Sour)	Cheviots	NT 858204	285m
Banchory (Aber)	Aberdeen	NJ 955736	50m
Collection sites			
Aviemore (Avie)	Grampians	NH 896126	200m
Quanterness (Quant)	Orkney	HY 416134	15m
Stromness (Strom)	Orkney	HY 257079	0m
Yetholm (Yetholm)	Cheviots	NT 841273	140m
Dalmelington (9Dal)	SW uplands	NS 527089	340m
Barra (High)	Outer Hebrides	NF 705024	100m

Further information on the collection sites is shown in Table 9.1. A commercial cultivar - Baron - from Holland was also used in the experiment. The biotype from Barra was grown at Sourhope and Bush, the other biotypes were grown at all three sites.

All plants in the same biotype ie. from one particular collection site, were collected from a circle of turf approximately 5cm in diameter. This maximises the chance of genotype reduplication. Plants were divided up into clonal groups - all tillers that were joined together by a rhizome were separated, and then grown in the greenhouse in Fisons 'Levington' potting compost for several weeks until they had established roots. So plants in the same clonal group were originally all physically attached by rhizomes, and therefore genetically identical. Plants that were from the same patch of turf, but were not definitely attached to each other by rhizomes were put in different clonal groups. While tracing each rhizome through the turf, it was necessary to cut several other rhizomes, and therefore it is likely that several plants that are in

different clonal groups are in fact all the same clone. So the number of different clonal groups is an indication of the maximum number of different genotypes present.

Individual seeds of the cultivar 'Baron' were sown separately, and tillers from each plant were separated and treated as one clonal group; these were also grown in the greenhouse until root establishment.

Plots were planted out in July 1981, with six tillers in each 1m square plot. The number of tillers from each clonal group planted in the plots is shown in Table 3.1.2. The clonal group is given as a number prefixed by 'C'. The number of tillers of that clonal group that were planted is shown in brackets. Thus C1(6) means that six tillers were used from clonal group 1. The total number of tillers used is shown in the right hand column of Table 3.1.2.

Table 3.1.2. Clonal Groups planted out

Biotype	Clonal Group	Total Number
Aviemore	C1(6)	6
Quanterness	C5(1), C6(3), C10(2)	6
Stromness	C1(2), C3(2), C8(2)	6
9Dal	C1(1), C2(1), C4(1), C6(3)	6
Yetholm	C2(3), C3(2), C13(1)	6
Barra	C1(3), C2(2), C4(1)	6
Baron	C1(2), C3(2), C5(2)	6

In most cases the same proportion of the different clonal groups were planted in each of the three experimental sites, so that the plots in different areas contained genetically identical material. The only exception to this was '9Dal', where one tiller of group C3 was used at Sourhope, instead of C2.

Plants were cut after establishment at approximately three weekly intervals, to a height of 2.5cm. Panicles were collected from the plots on 31st May at Bush, 9th June at Sourhope and 3rd of July at Aberdeen. The number of days since the plots were cut prior to collection was 14 days at Bush, 14 days at Sourhope and 44 days at Aberdeen.

The same biotypes were also grown in plots at the Botany Department, Edinburgh University (Map reference : NT 268706 ,

Altitude 70m), and were left uncut. They were harvested on 12th June and ten culms of each biotype (except Quanterness) were examined. The biotype from Quanterness produced insufficient panicles to be included in this study.

The following measurements were made on the panicles :

1) Culm height - in cms, from ground level to the tip of the panicle
2) Panicle length - in cms from the lowest panicle node to the tip of the panicle
3) Panicle width - in cms, at the widest point of the panicle
4) Lower panicle branches - the number of branches at the lowest node of the panicle
5) Second panicle branches - the number of branches at the second lowest node of the panicle
6) Top spikelet length - in tenths of millimetres, length of spikelet from near the top of the panicle.
7) Bottom spikelet length - length of a spikelet from near the bottom of the panicle (mm/10)
8) Florets per top spikelet - number of florets per spikelet, from near the top of the panicle
9) Florets per bottom spikelet - number of florets in a spikelet near the bottom of the panicle
10) Top floret length - in tenths of millimetres, the lowest floret from a spikelet near the top of the panicle
11) Bottom floret length - the lowest floret from a spikelet near the bottom of the panicle (mm/10)
12) Top glume top - length of upper glume in tenths of millimetres, from near the top of the panicle

13) Lower glume top - length of lower glume, from near the top of the panicle (mm/10)

14) Top glume lower - length of upper glume, from near the bottom of the panicle (mm/10)

15) Lower glume lower - length of lower glume, from near the bottom of the panicle (mm/10)

16) Spikelets per panicle - total number of spikelets in the panicle

Although culm height has a wide range of phenotypic plasticity [21], there is still a considerable genetic influence; the heritability is about 60% in Poa pratensis [125]. It is one of the most important characters affecting the overall morphology of the plant, and is reported to vary between different subspecies of Poa pratensis [8,98].

Panicle length and width determine the overall shape of the panicle, which is regarded as important by several authors [4,8,72,88,89,93,99]; the dimensions of the panicle are more useful than a subjective assessment of overall shape. The number of lower panicle branches affects the number of spikelets per panicle and therefore the number of seeds produced. It is likely therefore to be under fairly strong selection pressure, and it apparently varies between subspecies [4,8,72,73,90].

Spikelet and floret lengths will both affect the size of the seed, and being reproductive characters they are likely to be less plastic than vegetative ones [21]. There are reports that the subspecies differ in both spikelet [93,97] and floret [4,73,93]

length. Characters such as spikelet and floret length and glume length will vary with the maturity of the individual spikelet, and possibly also with position of the spikelet on the panicle; these characters were therefore measured from two spikelets per panicle - one from near the top of the panicle, the other from near the bottom.

Since Linnaeus [74], the number of florets per spikelet has been recorded as a useful character that is not very susceptible to environmental variation. Occasionally at the tip of the spikelet there is a small, empty lemma which is ignored - only complete florets are counted. The number of florets per spikelet will influence the seed production of a plant, and is likely to be under relatively strong selection pressure.

Glume length, and the relative length of the upper and lower glumes are mentioned as key characters for separating the subspecies [7,8,93], but relatively little quantitative information is available about this (see Table 2.3.).

The number of spikelets per panicle is a major determinate of the total seed production per panicle. Seed production in Poa pratensis can be affected by the environment [126,127], but selection pressure will ensure that this is kept within reasonable limits.

3.2 Populations and Herbarium Studies

The pattern of local variation is important in

understanding the total range of variation shown in Poa pratensis. To investigate this, three populations were chosen and between fifty and sixty panicles from each population were studied. The populations were at New Cumnock, near Ayr; Lyne Water, south of Edinburgh, and Cleish, in Fife. The populations were all in ungrazed areas where human disturbance was minimal, and there were no obvious habitat discontinuities within each area sampled. The sites were all fairly level, with no evidence of obvious variation in the micro-environment. These particular sites were chosen because they were far enough apart from each other to be considered different populations, they were not grazed or cut and they had sufficient plants of Poa pratensis to make a reasonable sample of the population possible within a small area.

Ideally, the individuals in a population are situated so that there is an equal probability of any two setting viable seed [128]. In practise, of course, plants are much more likely to be pollinated by nearby plants than by ones growing further away, and this means that in large populations it is possible to have divergent evolution of segments of the same population [59]. A population is therefore not always a homogeneous unit. Another problem caused by the pattern of pollen dispersal is that two or more populations may merge into one another [21], which means that populations have no tangible boundaries [129,130]. So the delimitation of a population is often subjective; plants are chosen from a fairly small, uniform site and assumed to be in the same population, but this is impossible to prove without very extensive and long term investigation. Finally populations are fluid in that they vary in size, and genetic composition, over time [21].

Therefore any single analysis of a population is bound to show the situation only at the time of sampling; the actual population is in a continual process of change. A population is here taken to be a group of plants of the same species growing together and able to exchange genes [131].

In this study, gene flow between members of the population was inferred rather than proved. Data on seed dispersal of Poa pratensis in the wild is not available, but is likely to be only a few metres on average [132,133]. Pollen dispersal is more important for gene flow, and in a variety of species the general pattern of gene flow over distance varies little : distances of up to 30m are common for pollen dispersal [134]. The distances between the three populations were greater than 40 km, so there is no real likelihood of direct gene exchange between the different populations except over very long time intervals.

When sampling local populations, especially with rhizomatous species such as Poa pratensis, there is the danger that several panicles will be collected from what are apparently different plants, but are in fact all from the same plant. Genotype reduplication leads to serious difficulties in analysis, because it means that intra-population variation is underestimated [135]. Harberd, studying this problem, collected samples from swards less than two yards across [135], which will tend to maximise reduplication. There is a conflict here, in that plants should be sampled from far enough apart to minimise multiple collections of one genotype, but should not be so far apart that plants cannot be considered to be in the same population. Gene flow falls off rapidly with distance : very little pollen travels 100m [134]. Therefore in

this study, each panicle was collected at least 2m from every other one, which meant that the greatest distance between panicles in the same population was about 32m. In the case of the populations at New Cumnock and Cleish, there was very little chance of genotype reduplication due to vegetative spread, as the sites were fairly bare and the rhizomes of plants could be easily followed. This contrasts with the situation examined by Harberd [132], where the ground was completely covered, seed survival was very rare, and so established genotypes are buffered against immigration. In this closed community, the population is not in delicate equilibrium with its environment. At Lyne Water, the ground cover was higher than in the other two sites, but was still not complete.

Three different populations were studied to determine the pattern of local variation. Between fifty and sixty plants, all growing at least 2m apart were collected from each population.

The populations were :

1) New Cumnock (Map reference : NS 595138 , Altitude : 175m).
Waste ground near a stream.
Sample area 15m by 25m

2) Lyne Water (Map reference : NT 164443 , Altitude : 190m).
River bank.
Sample area 30m by 5m

3) Cleish (Map reference : NT 102953 , Altitude : 270m).
Top of disused quarry.
Sample area 32m by 5m

For both the examination of local populations, and study of herbarium material from around the world, the same characters were chosen. These were broadly the characters shown in Tables 2.1. and 2.3., with a few omissions. For example, preliminary analysis showed that the number of veins in the lower glume varied even

within one panicle. Barling [124] also noted the unreliable nature of this character. Also, frequently the central vein was prominent, but the two faint lateral veins were also visible, and it was debateable whether this should be scored as 1-veined or 3-veined; this character was therefore rejected. Another character - hairiness of the area around the ligule, has been put forward as a characteristic of subsp subcaerulea [4,7,8,11], but several plants which otherwise were typical subcaerulea lacked this character, and other plants which bore little resemblence to subcaerulea had conspicuous hairs around the ligule. For example, ten culms from a biotype collected from Lochans were examined. There were hairs easily visible around the ligule, but in other characters the plants were unlike subsp subcaerulea : the mean culm height was very high (77 cms), the panicles were long (mean 11.5cm) and wide (4.9cms), the lower panicle branches were not in pairs (mean number 3.5), there were more spikelets per panicle than in subsp subcaerulea (mean 95) and the glumes were unequal (differing by about 20% in length). So hairiness of the area around the ligule does not correlate well with other characters. This character was therefore also rejected. In most of the herbarium specimens, two other characters could not be reliably determined, these were seed length and pollen diameter, and so these were also omitted.

The following measurements and observations were taken from each panicle :

1) Culm height - in centimetres, from ground level to the tip of the panicle

2) Top ligule length - in tenths of millimetres, in the centre of the ligule, top culm leaf

3) Second ligule length - ligule of the second culm leaf (mm/10)

4) First leaf width - in tenths of millimetres at the widest point, top culm leaf.

5) Second leaf width - width of second culm leaf (mm/10)

6) First leaf length - in millimetres, from ligule to tip, top culm leaf.

7) Second leaf length - as above, second culm leaf (mm)

8) Panicle length - in millimetres, from tip of panicle to lowest panicle node.

9) Panicle width - in millimetres, at the widest point

10) Lowest panicle branches - number of branches at lowest panicle node

11) Second panicle branches - number of branches at second lowest panicle node

12) Spikelets per panicle - total number of spikelets

13) Top spikelet length - in tenths of millimetres,from near the top of the panicle

14) Bottom spikelet length - in tenths of millimetres, from the bottom part of the panicle

15) Floret number top - number of complete florets in a spikelet from near the top of the panicle

16) Floret number bottom - number of complete florets in a spikelet in the bottom part of the panicle

17) Floret length top - in tenths of millimetres, the lower floret in a spikelet near the top of the panicle

18) Floret length bottom - the lower floret in a spikelet near the bottom of the panicle (mm/10)

19) Top glume top - length of upper glume of a spikelet from near the top of the panicle (mm/10)

20) Lower glume top - length of lower glume from a spikelet near the top of the panicle (mm/10)

21) Top glume lower - length of upper glume from a spikelet near the bottom of the panicle (mm/10)

22) Lower glume lower - length of lower glume from a spikelet near the bottom of the panicle (mm/10)

23) Glume shape top - shape of glumes from a spikelet near the top of the panicle , on a 1 - 5 scale :

Side View of Glume:

1 = tapering gradually to the tip 

2 = slightly pointed at the tip 

3 = slightly pointed before the tip 

4 = moderately pointed 

5 = markedly pointed 

24) Glume shape bottom - shape of glumes from a spikelet near the bottom of the panicle

25) Tufted - number of culms in each tuft:

0 = one culm at the basal node

1 = 2 to 4 culms at the basal node

2 = over 4 culms at the basal node

26) Scabrousness of panicle branches :

0 = lower panicle branches unscabrous

1 = lower panicle branches scabrous

2 = lower panicle branches markedly scabrous

Short ligules are an important character of Poa pratensis s.l. [8,65,66,74,79,81,83] and ligule length has been used to separate the subspecies [87,98]. However there is some disagreement here; Hubbard [4] has the ligule length of subsp angustifolia 1mm or less, and subsp pratensis 1-3 mm in length, whereas Edmondson [8] has subsp angustifolia with ligules 1-3mm and subsp pratensis with ligules 1mm or less.

Leaf width is widely used to distinguish between subspecies of Poa pratensis [4,64,68,72,73,81,83,87,90,97,98,117]; it is usual in the taxonomy of grasses for vegetative characters to be important, due to the reduced floral structures [21]. In contrast leaf length is rarely mentioned, possibly because of the large amount of variation in this character within one plant [135]. The only specific mention of significant variation at the subspecific level is by Barling [124], who found a difference between subsp angustifolia and subsp pratensis in the leaf width to length ratio.

Several authors have commented on the differences in

glume shape between the subspecies [4,8,72,93,117]; subsp subcaerulea has tapering glumes compared to the abruptly pointed ones of subsp angustifolia and subsp pratensis.

The degree of tufting is an important character [8,93,97,117], which is often used to separate the three subspecies found in Britain [4,7,11,72,73]; subsp angustifolia is strongly tufted, subsp pratensis is intermediate and subsp subcaerulea normally has individual culms separated by long rhizomes.

Scabrousness is reported to be a good sectional character in Poa [135], and is usually assumed to be constant within Poa pratensis s.l.[8]. However there is some evidence of variation within the species of this character, and it has been used at the subspecific level [75,97].

All the herbarium specimens of Poa pratensis s.l. in the Royal Botanic Gardens, Edinburgh (E), that were in good condition were examined. This provided the bulk of the herbarium data. Other results, for areas not well covered by the Edinburgh material - Ireland, England and Wales and Northern Asia - were obtained from herbarium specimens at the Royal Botanic Gardens, Kew (K) and the British Museum (Natural History), London (BM). Measurements given in tenths of millimetres were made with an eyepiece micrometer, using X10 magnification, accurate to the nearest tenth of a millimetre. Glume shape was also examined using the eyepiece micrometer. Results expressed in centimetres and millimetres (such as culm height and leaf length) were made using a ruler, and were measured to the nearest millimetre. Estimates of the scabrousness of panicle branches were made by drawing the branches between the fingers.

A total of 412 herbarium specimens were examined; the geographical origin of these plants is summarised in Table 3.2.1..

Table 3.2.1. Geographical origin of Herbarium material

Area	Number of Plants examined	Percentage of Plants examined
Scotland	87	21 %
England and Wales	79	19 %
Ireland	27	7 %
Total (British)	193	47 %

Area	Number of Plants examined	Percentage of Plants examined
Europe (excl.Britain)	110	27 %
North America	47	11 %
Asia	62	15 %
Total (Non-British)	219	53 %

The herbarium specimens were classified into subspecies using the criteria outlined above; if a plant was labelled Poa pratensis , but had the characteristics of - for example - subsp subcaerulea, it was treated here as subsp subcaerulea. The identity of the herbarium specimens was :

subsp alpigena	3 %	subsp angustifolia	14 %
subsp pratensis	63 %	subsp subcaerulea	20 %

As mentioned before, subsp alpigena is not found in Britain, which accounts for the paucity of herbarium specimens of this subspecies.

3.3 Taxonomic Analysis of Biotypes and Cultivars

The biotypes and cultivars used in the cultivar development experiments (Section B) were analysed to determine the taxonomic position of the biotypes and cultivars, and to find out whether the cultivars could be distinguished from the biotypes morphologically.

Twelve tillers of each of the 23 biotypes and 4 cultivars used in the experimental plots (see Section B, Table 10.2.3.) were planted out in October 1981 at the Botany Department, Edinburgh University (Map reference NT 268706, Altitude 70m). The same proportions of the clonal groups were used as were planted in the experimental plot at Aberdeen (see Table 10.2.3.), there being the best supply of living material to achieve this. Ten culms were collected from each of these plants on 12th June, 1982, except for the biotypes 'Quanterness' and 'Port Patrick', and the cultivars 'Fylking' and 'Primo' which did not produce sufficient numbers of panicles to be included in this study.

The characters which distinguished between the putative subspecies most consistently in the herbarium material (see Table

6.2.5) were examined. These were:

1) Culm height (cm).
2) Mean leaf width of the 1st and 2nd culm leaves (mm/10).
3) Second leaf length (mm).
4) Panicle length (mm).
5) Mean number of panicle branches on the lowest two nodes of the panicle.
6) Number of spikelets per panicle.
7) Mean spikelet length of two spikelets, one from near the top of the panicle, the other from near the bottom (mm/10).
8) Mean floret length of the lower florets of the above spikelets (mm/10).
9) Mean top glume length of the two spikelets (mm/10).
10) Mean lower glume length of the two spikelets (mm/10).

3.4. Statistical Analysis

Unless stated otherwise, the following statistical methods were used to analyse the results:

1) To test whether two means were significantly different, the 't-test' was used [136].
2) To test whether more than two means were significantly different, 'Duncan's Multiple Range Test' was used [137].
3) To test for groupings within the data with maximum objectivity, Principal Components Analysis (PCA) was used. PCA identifies the 2 or 3 axes of variation (components) which show maximum discrimination between any groups present (235).

CHAPTER 4 EFFECT OF ENVIRONMENTAL VARIATION ON MORPHOLOGY.

4.1 Introduction

Six biotypes of Poa pratensis collected from Scotland, and one cultivar from Holland, were planted at three experimental sites. Ten culms of each were collected, and sixteen morphological characters were measured on each culm. The mean results for each biotype from the different sites were compared, to investigate how much each morphological character was modified by the environment.

4.2 Results

The mean results from the ten culms of each biotype for several of the characters are displayed in Table 4.2.1.. In Table 4.2.1. numbers that are followed by the same letter are not significantly different from each other at the 0.05 level.

The abbreviations used in Table 4.2.1 are shown in brackets in Table 3.1.1.

These results - from plants that were subject to cutting - are then compared in Table 4.2.2. to the results for uncut plants. The degree to which the characters distinguish between different biotypes without varying within a biotype is then quantified in Tables 4.2.3. and 4.2.4.

Table 4.2.1.i. Culm height and Panicle length of biotypes

Biotype	Site	Culm height (cm)		Biotype	Site	Panicle length (mm)	
High	Bush	17.9	a	Yetholm	Sour	61.1	a
Baron	Bush	22.8	ab	9 Dal	Aber	61.7	a
High	Sour	24.7	bc	High	Bush	63.1	ab
Yetholm	Sour	25.0	bc	Yetholm	Bush	63.4	ab
Yetholm	Bush	26.3	bc	Yetholm	Aber	63.7	ab
9 Dal	Bush	26.7	bc	9 Dal	Bush	64.8	abc
Strom	Sour	26.7	bc	Strom	Sour	71.6	abcd
Strom	Bush	28.2	bc	High	Sour	74.3	bcd
Baron	Sour	29.1	c	Baron	Aber	74.4	bcd
Quant	Bush	34.5	d	Avie	Sour	74.7	bcde
Avie	Sour	34.5	d	Baron	Sour	76.2	cde
9 Dal	Sour	36.7	de	Baron	Bush	76.8	cde
Avie	Bush	36.9	de	Avie	Bush	77.1	de
Quant	Sour	39.7	de	9 Dal	Sour	78.0	de
Yetholm	Aber	40.2	ef	Strom	Bush	80.8	de
9 Dal	Aber	45.0	fg	Avie	Aber	83.3	def
Baron	Aber	46.1	g	Quant	Aber	86.7	ef
Quant	Aber	53.5	h	Quant	Sour	93.4	fg
Avie	Aber	65.3	i	Quant	Bush	101.6	g
Strom	Aber	73.5	j	Strom	Aber	122.3	h

Table 4.2.1.ii. Top and Bottom Floret lengths of biotypes

Biotype	Site	Top Floret Length (mm/10)		Biotype	Site	Bottom Floret Length (mm/10)	
Quant	Sour	30.9	a	Strom	Aber	30.1	a
Baron	Sour	31.6	a	Quant	Sour	30.9	ab
Strom	Aber	31.9	a	Quant	Aber	31.8	abc
Quant	Bush	32.0	a	Quant	Bush	31.9	abc
Quant	Aber	32.3	a	Baron	Sour	32.5	bc
Avie	Sour	32.9	ab	Baron	Bush	33.4	cd
Baron	Bush	34.4	bc	Avie	Sour	34.7	de
Baron	Aber	34.4	bc	Avie	Bush	35.0	def
Avie	Aber	35.0	cd	9 Dal	Sour	35.1	def
9 Dal	Aber	35.3	cd	Strom	Bush	35.2	def
9 Dal	Sour	35.3	cd	Baron	Aber	35.2	def
Avie	Bush	35.8	cde	9 Dal	Aber	35.9	ef
9 Dal	Bush	36.6	de	Avie	Aber	36.0	ef
Strom	Bush	37.5	ef	9 Dal	Bush	37.2	fg
High	Bush	39.1	fg	Strom	Sour	38.7	gh
Strom	Sour	39.2	fg	High	Sour	39.9	h
Yetholm	Bush	40.1	g	High	Bush	40.0	h
Yetholm	Sour	40.3	g	Yetholm	Bush	40.0	h
High	Sour	40.4	g	Yetholm	Aber	40.6	h
Yetholm	Aber	41.1	g	Yetholm	Sour	41.0	h

Table 4.2.1.iii.. Florets per spikelet and Glume length

Biotype	Site	Florets per Bottom Spikelet		Biotype	Site	Top glume Length (mm/10)	
Baron	Sour	2.6	a	Strom	Aber	25.8	a
Baron	Bush	2.9	ab	Baron	Sour	26.6	a
Quant	Sour	3.0	abc	Baron	Bush	28.0	ab
Yetholm	Bush	3.1	abcd	Quant	Sour	29.1	bc
High	Sour	3.1	abcd	Baron	Aber	30.5	cd
High	Bush	3.3	bcde	Quant	Aber	30.9	cd
9 Dal	Sour	3.4	bcdef	Avie	Sour	31.2	cde
Avie	Sour	3.5	bcdef	9 Dal	Sour	31.4	cde
Quant	Bush	3.5	bcdef	Quant	Bush	31.7	de
9 Dal	Bush	3.5	bcdef	Avie	Bush	31.9	de
Yetholm	Sour	3.5	bcdef	Strom	Bush	32.7	def
Yetholm	Aber	3.5	bcdef	9 Dal	Aber	33.6	ef
Baron	Aber	3.6	cdef	9 Dal	Bush	34.3	f
Strom	Aber	3.6	cdef	Avie	Aber	34.6	fg
Quant	Aber	3.7	defg	Strom	Sour	36.9	gh
Strom	Bush	3.8	efg	High	Sour	37.8	hi
9 Dal	Aber	3.8	efg	High	Bush	37.8	hi
Avie	Bush	4.0	fg	Yetholm	Bush	39.8	ij
Avie	Aber	4.3	g	Yetholm	Sour	41.4	j
Strom	Sour	5.9	h	Yetholm	Aber	41.9	j

Table 4.2.1. shows that with certain characters (such as culm height), plants of the same biotype grown in different sites produce very different results, often significantly different. For example the culm height of '9Dal' is significantly higher at Aberdeen than at Sourhope, and significantly higher at Sourhope than at Bush. Obviously the fact that the culms had different lengths of time to grow since the last cut would partly explain this result, but other characters - such as floret length are less affected by cutting (Table 4.2.2.), and do not show any consistent tendency for one site to produce higher values . For example 'Quanterness' has its shortest florets at Sourhope, and longest at Aberdeen, whereas 'Stromness' has longest at Sourhope and shortest at Aberdeen. Therefore this difference between biotypes is not merely caused by

different times since the plants were cut. Top floret length of each biotype is similar in different sites, indicating that this character is less susceptible to environmental variation. However there are significant differences between different biotypes grown in the same site. For example, at Bush 'Quanterness' has significantly smaller florets than 'Aviemore', which in turn has significantly smaller ones than 'Yetholm'.

A comparison of the results for 'Quanterness' and 'Stromness is interesting, as both of these biotypes come from Orkney, and so grow in the same climatic area. At Sourhope, where plants had been cut only fourteen days before, 'Quanterness' was already significantly greater than 'Stromness' in culm height and panicle length, and significantly less than 'Stromness' in the number of florets per spikelet, floret length and glume length. In contrast at Aberdeen, where plants had the longest time to recover from cutting, culms and panicles of 'Stromness' were significantly longer than 'Quanterness', and the glumes of 'Quanterness' were significantly longer than those of 'Stromness' - a reversal of the previous situation. The floret lengths of 'Quanterness' and 'Stromness' are not significantly different at Aberdeen. This suggests that the culms and panicles of 'Quanterness' recover quickly from cutting, but eventually the slower growing 'Stromness' produces longer culms and panicles. With the glumes, 'Stromness' seems to grow rapidly to start off with, but 'Quanterness' eventually produces longer glumes. This shows that markedly different biotypes may exist within a fairly small area.

As would be expected, the culm heights of the uncut plants grown at Edinburgh are greater for all the biotypes than

those of the cut plants. However the positions of the biotypes relative to one another is very similar in the uncut and cut plants. The mean heights of the uncut plants were :

Stromness	72.4cm	9 Dalmelington	63.8cm
Aviemore	71.2cm	Baron	62.3cm
Yetholm	66.2cm	High	57.5cm

In comparison, for the cut plants at Bush (about 8 km from where the uncut plants were growing), the order of these biotypes in terms of culm height was : Aviemore, Stromness, 9 Dalmelington, Yetholm, Baron and High. At Aberdeen, where the plants had had the longest period since cutting, Stromness had the tallest culms, followed by Aviemore - the same as in the uncut material. Therefore the cut plants still reflect fairly accurately the uncut material, especially as culm height would be expected to be one of the characters most affected by cutting. This is important, because plants in the wild are often grazed or cut, and little information is available about the effects of this on taxonomic characters. The degree to which characters are affected by cutting can be estimated by comparing the mean results for the cut and uncut plants of the same biotypes. This is shown in Table 4.2.2..

Table 4.2.2. Mean results for cut and uncut plants

Percentage = Results from cut plants as a percentage of results from uncut plants

Character	Cut	Uncut	Percentage
Culm height	35.6 cm	65.6cm	54 %
Panicle length	74.5 mm	90.9 mm	82 %
Florets per bottom Spikelet	3.61	3.50	103 %
Top floret length	3.65 mm	4.12 mm	89 %
Lower floret length	3.65 mm	3.98 mm	92 %
Top Glume Lower	3.39 mm	3.77 mm	90 %

This shows that culm height is greatly affected by cutting, panicle length is less altered, and the other characters are not greatly reduced in size or number by cutting ; the number of florets per bottom spikelet is actually increased marginally.

The characters above thus differ in taxonomic 'value' - 'valuable' characters being defined as ones which will separate different biotypes but will not show a significant difference between plants of the same biotype grown in different environments. By summing the number of significant differences between biotypes, and dividing by the number of significant differences within biotypes, a quantitative figure can be given to this 'value'- higher numbers denoting more valuable characters. This method does not overcome all the problems of quantifying the data, because in

several cases the figures are only just significant, or almost significant, and so a slight variation one way or the other can affect the figure for 'value'. This problem cannot easily be overcome, but the data produced from this simple method may nevertheless provide some useful information. Some results for the data above are shown in Table 4.2.3.

Table 4.2.3. 'Value' of selected Taxonomic Characters

Culm height	29
Panicle length	64
Florets per bottom spikelet	29
Top floret length	87
Bottom floret length	84
Top glume lower	45

These results suggest that culm height and number of florets per bottom spikelet are relatively poor characters for separating biotypes, as they have a high environmental component. Glume length and panicle length are better, but floret length seems to be least altered by the environment, and discriminates best between biotypes.

Results for the other characters are of interest; these are shown in Table 4.2.4.

Table 4.2.4. 'Value' of Taxonomic Characters

Panicle width : 27	Top spikelet length : 57
Bottom spikelet length : 44	Spikelets per panicle : 58
Lower panicle branches : 48	Second panicle branches : 41
Top glume top : 37	Lower glume top : 53
Lower glume lower : 44	Florets per top spikelet : 75

For the characters listed above, the mean results of the cut plants ranged from 89 % of the uncut plants for panicle width to 107 % for number of florets per top spikelet; with a mean of 94 % over the ten characters. So of the 16 characters measured, culm height is definitely the one most affected by cutting ; spikelet length was least affected, the mean results of the cut plants being 101 % of uncut plants for the top spikelet, and 97 % for the lower spikelet.

Although these results on the whole confirm that floret length is a valuable character, the fact that the number of florets per top spikelet has a high value is rather anomalous. It is very unlikely that the number of florets per spikelet is a valuable character when examined in the upper spikelets of a panicle, but much less useful when a lower spikelet is used. This result is therefore probably due to the problems inherent in using this method of quantification, which were discussed earlier. Therefore these 'values' should be treated with some caution, and are best treated as broad guidelines rather than absolute fixed numbers.However they still offer some improvement over subjective, and assumed, 'value'

which is frequently used . Generally the results suggest that culm height and panicle width are not very useful characters, glume and spikelet length, number of spikelets per panicle and panicle length are better, and floret length is best.

These results agree with Barling's conclusion from transplant experiments with Poa pratensis in Wales, that culm height has a large environmental component [11]. He also suggested that panicle length and spikelet length were very susceptible to environmental changes; these two characters would seem from the results above to be less affected by environment than culm height. This result is consistent with the concept of reproductive conservatism ; in general characters directly involved with reproduction show less phenotypic plasticity [21].

Barling also found that plants from widely scattered areas showed no great difference in gross morphology when transplanted to the same site [11]. This is very different from the results above, where plants from different areas are often significantly different in morphology, and even plants from fairly close together, such as 'Quanterness' and 'Stromness' are frequently dissimilar when grown at the same site. The reason for this could be that in the experiment above, no a priori selection was made of a particular subspecies; any plant of Poa pratensis s.l. was collected. In contrast Barling specifically sought to collect only subspecies subcaerulea, and was therefore selecting a morphological group from only a small part of the total variation of Poa pratensis s.l.. It is thus perhaps not surprising that his plants were similar when transplanted.

Because characters which vary with the environment are regarded as poor taxonomic characters [21], one would expect that characters which are not greatly affected by the environment would be more frequently quoted by taxonomists than those more susceptible to environmental change. However this does not seem to be the case. The number of times that the characters above were used by the authors cited in Table 2.3. is :

Culm height	Panicle width	Glume length	Spikelet number
37	5	10	10

Panicle branches	Spikelet length	Floret length
29	24	15

Culm height was the most common character mentioned, even though its variation pattern has a high environmental component [11]. However the variation range for one particular biotype is less than the total range of all the biotypes, so the variation between different biotypes is greater than the variation within one biotype. Thus there can be discontinuous variation from one biotype to another, which is taxonomically important. As mentioned before, the estimated heritability of culm height in Poa pratensis is 60% [125].

Panicle width, which is not a useful character, is rarely used. Of the four characters of intermediate value, number of lower panicle branches and spikelet length were much more frequently mentioned than glume length or number of spikelets per panicle. The reason for this bias is unclear; possibly the glumes are neglected because of their small size - accurate measurement to the nearest tenth of a millimetre is required. The number of spikelets per

panicle depends on variables such as panicle length and number of panicle branches, which in themselves are regarded as important characters (see Table 2.1.). The evidence above suggests that the number of spikelets is no more sensitive to environmental change than characters such as the number of panicle branches, which are more often quoted. Possibly greater use should be made of spikelet number; Barling [11] is the only author to give quantitative information on this character. At a higher taxonomic level, spikelet number is used to separate different genera in the Gramineae [8,71,72]. Finally floret length, which seems a valuable character, is also cited relatively infrequently. It would seem that this important character has been relatively neglected.

CHAPTER 5. STUDY OF *Poa pratensis* POPULATIONS

5.1 Introduction

Three populations, from different parts of Scotland, were examined morphologically to determine the amount of variation both between and within populations. Between fifty and sixty plants were sampled from each population. Plants that were examined were growing at least 2m apart, which minimises the possibility of genotype reduplication.

5.2. Results

The mean results for each population are shown in Table 5.2.1. In this table, two asterisks (**) between two numbers on the same row indicate that the mean results are significantly different at the 0.01 level. Asterisks to the right of the 'Cleish' column refer to a significant difference between 'Cleish' and 'New Cumnock' populations. A single asterisk shows numbers differing at the 0.05 level. Thus the culm height of plants from New Cumnock is significantly less than those at Lyne Water, which in turn are significantly less than those from Cleish; all at the 0.01 level. However in terms of Top Ligule length, New Cumnock and Lyne Water are not significantly different, but both are significantly shorter than Cleish.

The population at Lyne Water was in a relatively dense sward, and presumably the plants had had longer to establish and spread here than in the other two populations, so the chances of genotype reduplication are higher. If genotype reduplication is high, only a few biotypes will be present, and so the variance of the results shown in Table 5.2.1 for that site should be low. Table

5.2.2. shows the variance and number of culms sampled for each character.

Figures 5.2.1. and 5.2.2. are scatter diagrams of several charaters from 20 plants from each population, which illustrate the variability of the three poopulations.

Table 5.2.1. Morphological Analysis of plants from three Populations

Character	Population: New Cumnock		Lyne Water		Cleish	
Culm height (cms)	25.3	**	32.8	**	39.3	**
Top ligule length (mm/10)	10.8		11.3	**	14.6	**
Second ligule length (mm/10)	10.3	**	7.4	**	11.8	
First leaf width (mm/10)	19.5	*	17.5		17.6	*
Second leaf width (mm/10)	23.5	*	20.7		22.0	
First leaf length (mm)	13.9	**	19.6	**	25.8	**
Second leaf length (mm)	24.2	**	34.6	**	53.2	**
Panicle length (mm)	43.3	**	56.7	**	74.8	**
Panicle width (mm)	30.1	*	34.8	*	40.2	**
Lowest panicle branches	2.84		2.53		2.88	
Second panicle branches	2.85	*	2.46	**	3.14	
Spikelets per panicle	53.8		49.9	**	73.9	**
Top spikelet length (mm/10)	39.9	**	47.2	**	50.6	**
Bottom spikelet length (mm/10)	37.6	**	43.8	**	47.4	**
Floret number top	2.45		2.68		2.84	**
Floret number bottom	2.20	**	2.47		2.44	**
Floret length top (mm/10)	32.5	**	37.1	**	39.9	**
Floret length bottom (mm/10)	32.0	**	36.4	**	39.2	**
Top glume top (mm/10)	29.6	**	35.4	**	38.9	**
Lower glume top (mm/10)	26.9	**	31.7	**	35.2	**
Top Glume Lower (mm/10)	29.0	**	33.7	**	36.8	**
Lower glume lower (mm/10)	24.9	**	29.1	**	32.4	**
Glume shape top	1.45		1.47		1.44	
Glume shape bottom	1.69		1.73		1.48	
Tufted	0.16		0.02		0.00	
Scabrous panicle branches	0.05		0.04		0.06	

Table 5.2.2. Variances and number of culms sampled

Key : V = Variance N = Number of culms examined

Character	New Cumnock V	N	Lyne Water V	N	Cleish V	N
Culm height	86	55	192	59	74	50
Top ligule length	17	52	10	45	19	50
Second ligule length	16	53	14	43	16	50
First Leaf width	20	53	15	48	16	50
Second Leaf width	30	53	21	38	31	50
First Leaf length	61	54	20	41	82	50
Second Leaf length	148	52	35	19	341	50
Panicle Length	195	55	160	59	211	50
Panicle Width	128	55	161	59	177	50
Lowest Panicle Branches	0.66	55	0.87	59	1.17	50
Second Panicle Branches	0.76	55	0.53	59	0.94	50
Spikelets per panicle	573	55	311	59	1015	50
Top Spikelet length	34	55	38	59	32	50
Bottom Spikelet Length	23	55	29	59	35	50
Floret number top	0.44	55	0.36	59	0.26	50
Floret number bottom	0.20	55	0.29	59	0.33	50
Floret Length top	14	55	17	59	16	50
Floret Length bottom	10	55	13	59	15	50
Top Glume Top	18	55	18	59	29	50
Lower Glume Top	16	55	13	59	25	50
Top Glume Lower	12	55	13	59	23	50
Lower Glume Lower	13	55	12	59	24	50

On the whole, the variances of the results from the Lyne Water population are similar to those of the other populations (Table 5.2.2). This shows that genotype reduplication is not significantly greater here than in the other two populations.

Populations of apomictic plants may contain only a small number of different biotypes [138]. If there are very few biotypes present in all three populations, then morphological variability in the populations will be low. Using variance directly as a measure of variability is complicated, as it depends on the units that the character is measured in. The coefficient of variation (square root of the variance divided by the mean then multiplied by a hundred) is a measure of variability which overcomes this problem. For most biological material, the coefficient of variability is 10 % - 15 %, and values around 25 % show great variability [139]. The mean coefficients of variability for the three populations are :

New Cumnock 27 % Lyne Water 25 % Cleish 23 %

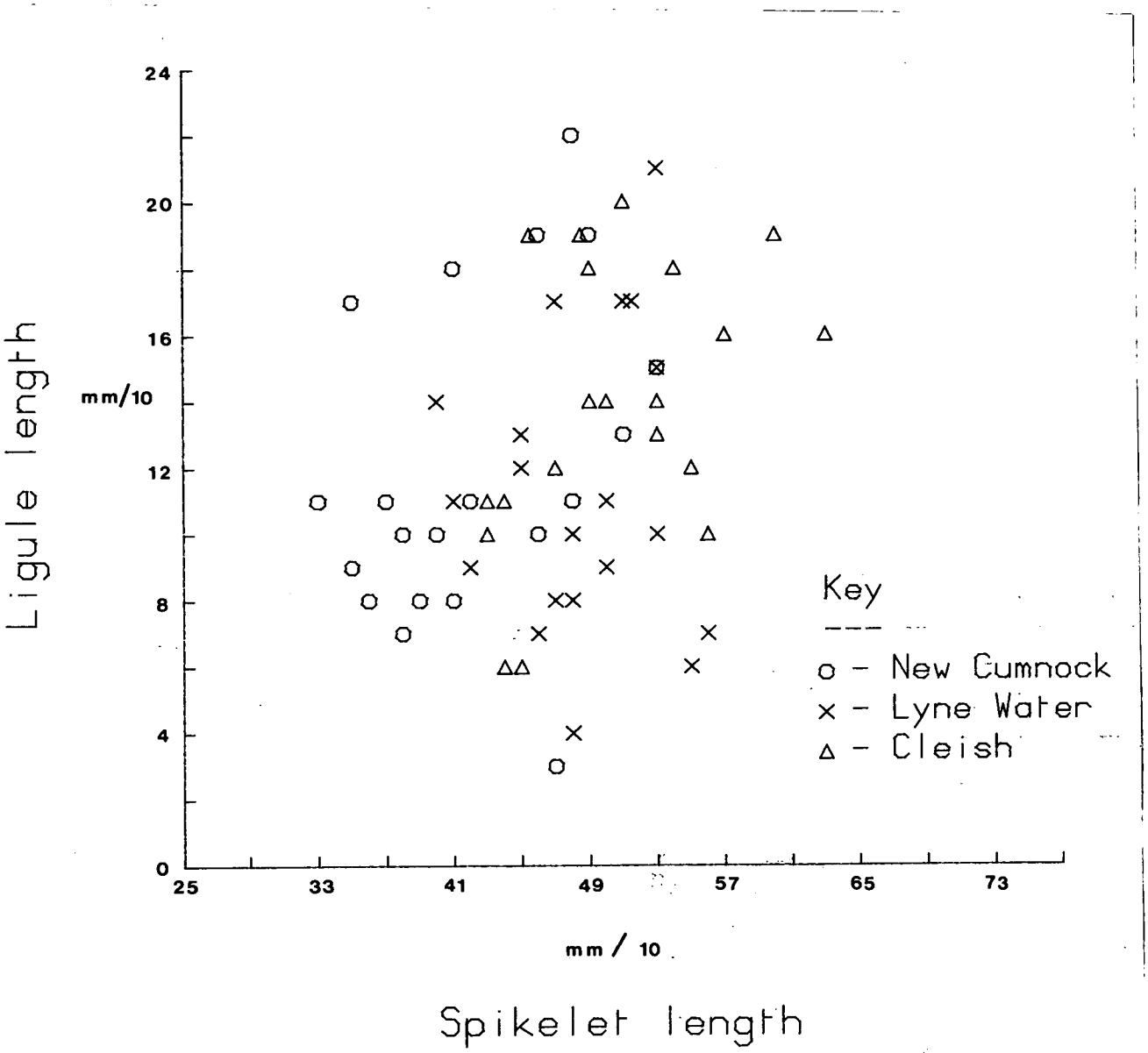
This suggests that variability is high, so genotype reduplication in all the populations is low, unless the plants are responding plastically to differences in the micro-habitat. This is unlikely, as the sites were specifically chosen for their uniformity of habitat. These coefficients also provide further evidence that there is no more genotype reduplication at Lyne Water than at the other two sites, so collecting panicles at least 2m apart seems to have solved this problem.

These results show that in most of the characters examined, the three populations differ significantly, showing that

Poa pratensis is not uniform within Scotland, but displays local variation. In some cases, such as culm height, the environment has an important effect on this variation, so it is not surprising that plants in different areas have culms of different lengths. However other characters, which are not so susceptible to environmental influence, such as floret length, are also significantly different in the three sites, indicating a probable genetic difference between the populations. Once this difference is established, either by genetic drift or by adaptation to local conditions, its persistence will be facilitated by the predominantly apomictic reproduction in Poa pratensis. Work on other grass species has revealed divergence even amongst adjacent populations [140]. Steep clines can exist over short distances due to strong selection pressure, for example heavy metal tolerance [141]; where selection pressures are less, changes will presumably occur over longer distances, as high gene flow will prevent local adaptation. In theory the reduction in gene flow caused by facultative apomixis means both that adapted genotypes can be retained despite some gene flow, and also that a population of only one or two genotypes - possibly not very well adapted - can be built up from a plant colonising a new area. The result is that populations in different areas will tend to diverge. In the case above the adaptive function of the taxonomic characters is unclear: they may be linked to adaptive, non-visible characters.

Although the populations are significantly different in several characters, there is considerable intra-population variation. This is displayed in Figure 5.2.1., showing the top ligule length and top spikelet length of 20 plants chosen at random from each population.

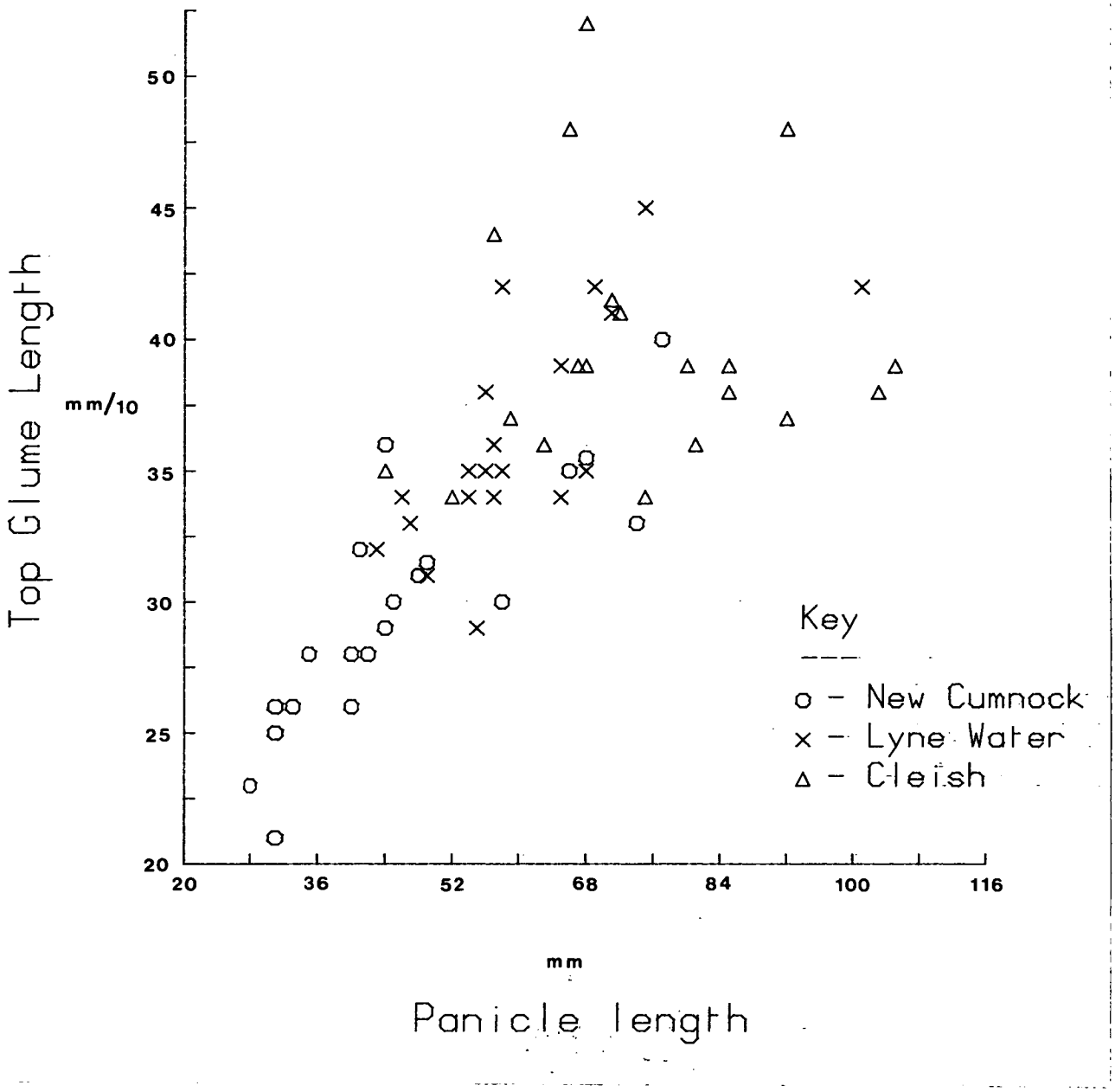
Figure 5.2.1. Ligule length and Spikelet length



Despite the fact that the mean values from all three populations differ significantly in spikelet length, and the plants from 'Cleish' have a significantly greater ligule length on average than the other populations, it is not possible on the basis of these two characters to ascribe any individual plant to a particular population ; there is very considerable overlap between the three populations. According to Edmondson [8], the ligule length of subsp subcaerulea and subsp pratensis is around 1mm, while that of subsp angustifolia is 1 - 3mm. However the data above show no evidence of discontinuity in ligule length in any of the populations. All three populations have plants with very short ligules (about 0.6mm) and long ligules (about 2 mm). It seems that the variability of this character within a population has been underestimated.

Figure 5.2.2 shows a scatter diagram of the panicle length and top glume length of 20 panicles chosen at random from the three populations.

Figure 5.2.2. Panicle length and Glume length



Again, there is considerable variation within each population and a large degree of overlap between the populations. This variation transcends the range for panicle length of subsp subcaerulea given in the Flora Europaea [8], and also exceeds the

values given by Hubbard [4] for glume length for this subspecies. Several of the plants have panicle lengths characteristic of subsp subcaerulea, and paradoxically, glume lengths indicative of subsp pratensis. None of the three populations seem to fit neatly into any of the subspecies outlined in Table 2.1.: the plants from New Cumnock are like subspecies subcaerulea in terms of culm height, leaf width, panicle length and spikelet number. However on average the upper and lower glumes differ in length by 13%, and it is unclear whether a difference of this magnitude would be described as 'almost equal' (subsp subcaerulea) or 'unequal' (subsp pratensis). Also the spikelet lengths are rather less than the values given in Table 2.1.. The Cleish population is more like subsp pratensis in culm, ligule and panicle length, but has narrower leaves than expected, fewer panicle branches, longer spikelets at the top of the panicle and upper and lower glumes differing by almost exactly the same amount as those from New Cumnock. Also the glumes are more tapering than those from New Cumnock, when they should be more abruptly pointed if the population is nearer to subsp pratensis. In most of the characters, Lyne Water is intermediate between the two other populations (Table 5.2.1.). However Lyne Water plants have relatively few panicle branches, which suggests that they are more like subsp subcaerulea, but also have more pointed glumes, which are more characteristic of subsp pratensis.

This illustrates one of the problems with the categories of subspecies revealed in Table 2.1., namely wild plants often do not fit into the categories shown, and the characters do not always occur in correlated groups. Often, plants have a mixture of characters that are generally ascribed to two subspecies. The

Division into species, rather than subspecies, on the basis of these characters, is even harder to defend.

It was decided on the basis of Principal Components Analysis of internationally collected herbarium data (see p. 82 ff) that it was not worthwhile to analyse the smaller population samples here discussed for possible entities other than the taxa which have traditionally been mooted within Poa pratensis.

CHAPTER 6. STUDY OF HERBARIUM MATERIAL

6.1. Introduction.

Over 400 herbarium specimens of Poa pratensis were examined, which had been collected from all the main areas of distribution of the species. Plants from the British Isles made up just under half of the total number of specimens examined, and Scottish material comprised 21% of the total. Twenty six morphological characters were scored for each herbarium specimen, including most of the key taxonomic characters used by previous workers for distinguishing between the subspecies of Poa pratensis. Results are analysed both in terms of the area of origin of the plants, and by the subspecific categories used by other workers. The term 'subspecies' is used in this chapter purely for reference to the categories employed by previous authors, and should not be taken to imply acceptance of the subspecies as sound taxa.

6.2 Results

The herbarium results were divided up into the following geographical areas :

A] Scotland B] England and Wales C] Ireland
D] Europe (including Eastern USSR, but excluding Britain and Turkey)
E] Middle East (including Turkey) and Asia F] North America.

The mean results for Poa pratensis s.l. in these areas are shown in Table 6.2.1.. The mean results from different areas that are significantly different in Table 6.2.1. are summarised in

Table 6.2.2.. In Table 6.2.2. the different areas are denoted by the following letters :

S = Scotland	E = England and Wales
I = Ireland	Eu = Europe
A = Asia	Am = America

For example, Eu > S,I shows that the mean result from Europe is significantly greater for that character at the 0.05 level than those from Scotland and Ireland. Similarly, I<< Am means that a mean value from Irish specimens is significantly lower than that from America at the 0.01 level.

The range of variation for each character in the herbarium material from British plants is compared in Table 6.2.3. with the total variation exhibited by all the herbarium specimens.

Table 6.2.4. summarises the distribution of the four subspecies amongst the herbarium specimens. There were only 13 specimens of subsp alpigena, which was too small a sample to provide useful information, but the mean results for the other three subspecies are shown in Table 6.2.5.

Table 6.2.1. Herbarium results analysed in terms of Area of origin

Character	Scotland	England and Wales	Ireland
Culm Length (cms)	28.5	37.9	27.5
Top Ligule (mm/10)	13.8	13.2	11.6
Second Ligule (mm/10)	11.7	10.8	11.6
1 Leaf Width (mm/10)	23.3	21.1	16.9
2 Leaf Width (mm/10)	28.1	24.6	22.3
1 Leaf Length (mm)	26.8	31.9	18.6
2 Leaf Length (mm)	48.1	52.3	31.5
Panicle Length (mm)	60.3	69.7	50.8
Panicle Width (mm)	33.0	30.0	25.9
Lower Panicle Branches	3.11	3.49	2.56
Second Panicle Branches	3.14	3.55	2.81
Spikelet number	80.8	103.1	65.2
Top Spikelet Length (mm/10)	46.8	44.9	45.0
Bottom Spikelet length (mm/10)	44.6	41.7	44.3
Floret Number Top	2.97	3.12	2.67
Floret Number Bottom	2.62	2.75	2.44
Floret Length Top (mm/10)	36.3	34.2	36.5
Floret Length Bottom (mm/10)	36.1	33.1	36.5
Top Glume Top (mm/10)	34.3	31.3	33.6
Lower Glume Top (mm/10)	30.7	27.8	29.5
Top Glume Lower (mm/10)	33.1	30.0	32.9
Lower Glume Lower (mm/10)	29.3	25.5	28.6

Table 6.2.1. (cont.) Herbarium results analysed in terms of Area

Character	Europe	Asia	America
Culm Length (cms)	44.8	47.7	48.5
Top Ligule (mm/10)	12.8	14.8	15.7
Second Ligule (mm/10)	11.9	13.4	15.5
1 Leaf Width (mm/10)	20.7	20.9	22.8
2 Leaf Width (mm/10)	23.1	25.6	26.1
1 Leaf Length (mm)	32.4	33.8	38.2
2 Leaf Length (mm)	54.1	53.3	58.5
Panicle Length (mm)	74.4	77.5	75.3
Panicle Width (mm)	29.3	24.8	29.7
Lower Panicle Branches	3.61	3.45	3.85
Second Panicle Branches	3.63	3.76	4.02
Spikelet Number	106.3	109.2	104.5
Top Spikelet Length (mm/10)	44.1	44.5	45.1
Bottom Spikelet length (mm/10)	41.4	41.1	42.6
Floret Number Top	2.95	3.16	3.02
Floret Number Bottom	2.59	2.85	2.77
Floret Length Top (mm/10)	33.8	32.7	34.5
Floret Length Bottom (mm/10)	32.9	31.8	34.1
Top Glume Top (mm/10)	30.7	29.8	32.6
Lower Glume Top (mm/10)	26.8	25.5	28.2
Top Glume Lower (mm/10)	29.4	27.6	30.5
Lower Glume Lower (mm/10)	25.3	22.7	26.0

Table 6.2.2. Summary of herbarium results analysed in terms of Area

Character	Results
Culm height	E >> S,I ; Eu > S,E,I ; A >> S,E,I ; Am >> S,E,I
Top ligule length	Am >> I,Eu ; Am > E
Second ligule length	Am >> S,E ; Am > Eu
First leaf width	I << S,A,Am ; I < E,Eu ; S > Eu
Second leaf width	S >> Eu ; S > E ; I << S ; I < A,Am
First leaf length	I << Eu,A,Am ; I < E ; Am >> S ; A > S
Second leaf length	I << E,Eu,A,Am ; I < S
Panicle length	I << E,Eu,A,Am ; S << E,Eu,A,Am
Panicle width	S > A
Lower panicle branches	S << Eu,Am ; S < E ; I << E,Eu,A,Am ; I < S
Second panicle branches	S << Eu,A,Am ; S < E ; I << E,Eu,A,Am; Am > E
Spikelet number	S << Eu,A ; S < E,Am ; I << Eu,A ; I < E,Am
Top spikelet length	S > Eu
Bottom spikelet length	S >> A ; S > E,Eu
Floret number top	I << A ; I < E
Floret number bottom	I << A ; I < E,Am ; A > Eu
Floret length top	S >> E,Eu,A ; I >> A ; I > E,Eu
Floret length bottom	S >> E,Eu,A ; S > Am ; I >> E,Eu,A ; Am > A
Top glume top	S >> E,Eu,A ; I > Eu,A ; Am > A
Lower glume top	S >> E,Eu,A ; S > Am ; I >> A ; I > Eu ; E > A ; Am > A
Top glume lower	S >> E,Eu,A ; S > Am ; I >> Eu,A ; I > E ; A << E,Am ; A < Eu
Lower glume lower	S >> E,Eu,A,Am ; I >> E,Eu,A ; I > Am; A << E, Eu,Am

The results in Tables 6.2.1. and 6.2.2. show that plants from Scotland are similar to those from Ireland, but with longer, wider leaves, longer panicles and more spikelets per panicle. Specimens from England and Wales are taller than Scottish or Irish material, and have slightly longer leaves, longer panicles, more panicle branches and spikelets, more florets per spikelet and shorter spikelets, florets and glumes. So the florets and spikelets in England and Wales are smaller but more numerous than in plants from the rest of Britain. Irish plants have relatively short culms, short and narrow leaves, short panicles with few panicle branches, few spikelets per panicle and large florets and glumes. In contrast to the English material, Irish plants have large florets, but small panicles with relatively few spikelets.

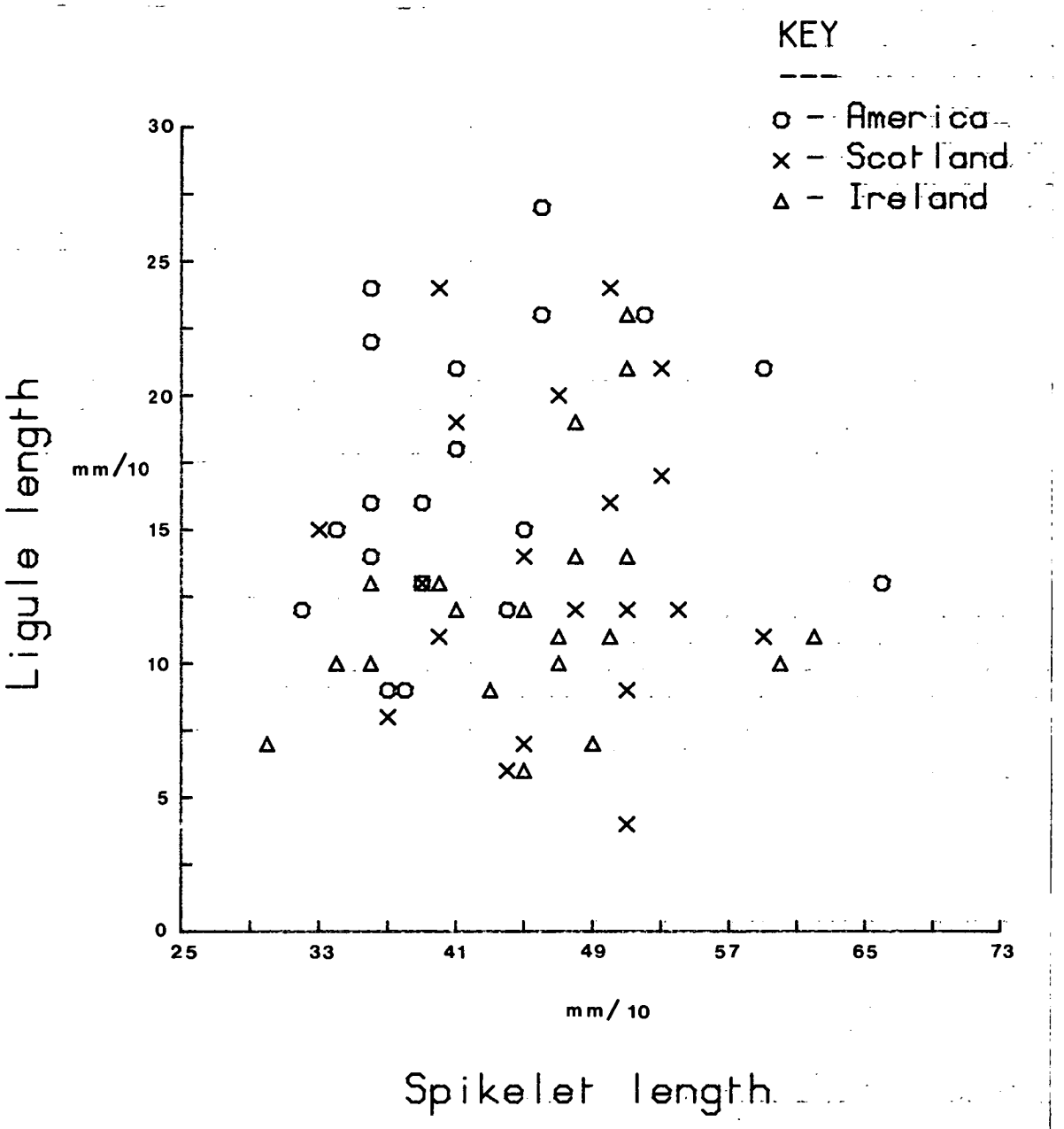
Herbarium specimens from Europe are generally taller than those in Britain, but have leaf dimensions very similar to those in England and Wales. Panicles of European plants are longer than those of British origin, with more panicle branches at the lowest node of the panicle. Florets and glumes are slightly shorter than in the British material.

Asiatic material has panicles which are long and narrow, with numerous spikelets per panicle, and short florets and glumes. Finally, American plants are tall, with long ligules, fairly large leaves and panicles and several panicle branches at the lowest node. American spikelet characters are similar to those in England and Wales.

Although the mean results for plants from different areas may differ, there is still considerable overlap in these characters between individual plants from different areas. Figure 6.2.1. shows

the ligule length and spikelet length of 20 plants chosen at random from the herbarium material from America, Ireland and Scotland.

Figure 6.2.1. Ligule length and Spikelet length

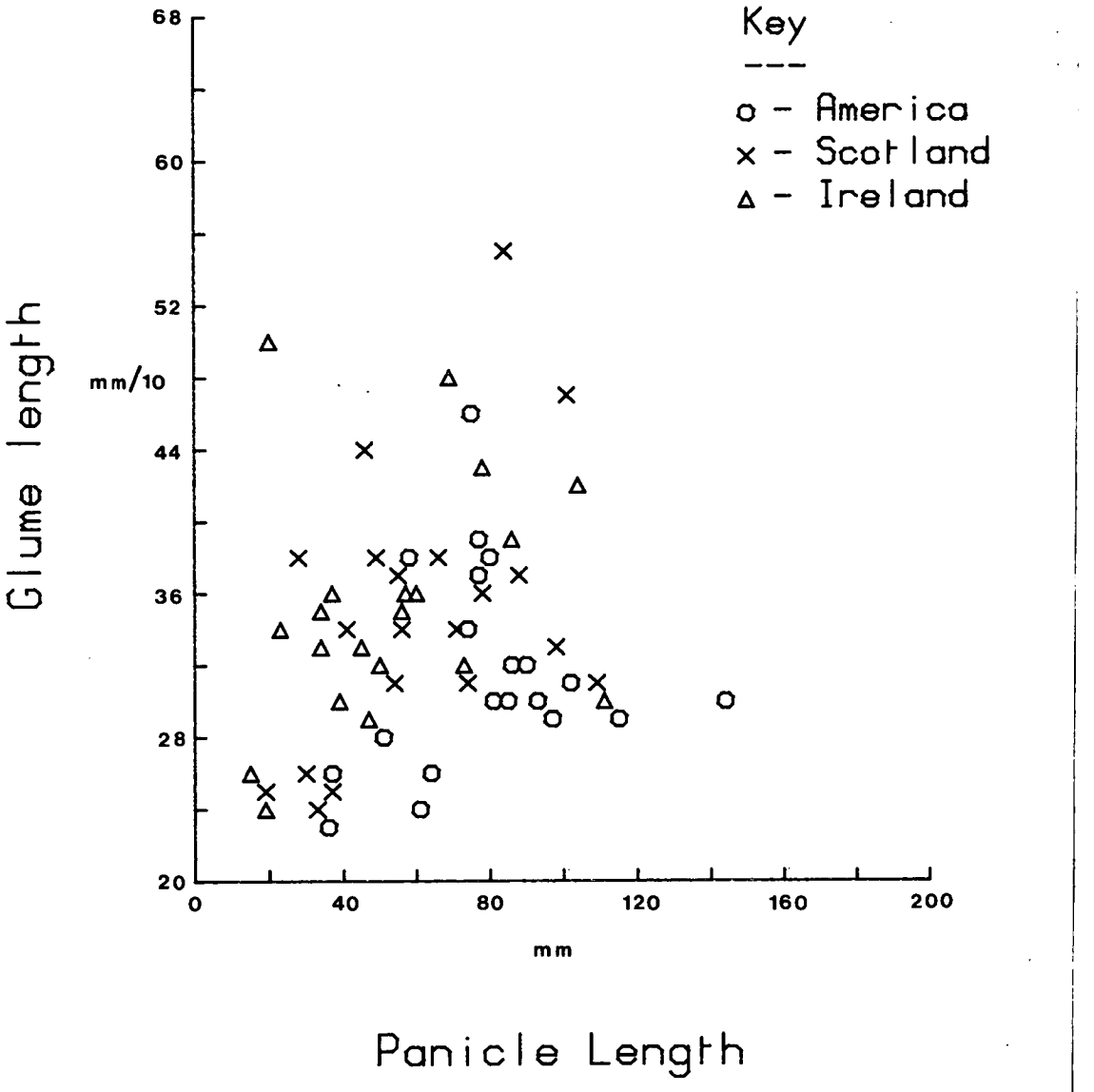


The mean ligule length of American plants is significantly greater than that of Irish material, yet, as Figure

6.2.1. illustrates, several Irish plants have longer ligules than the majority of American plants. Plants from each area show great variability in both ligule and spikelet length.

Figure 6.2.2. shows the panicle length plotted against top glume length for another 20 plants picked at random from herbarium specimens from America, Ireland and Scotland.

Figure 6.2.2. Panicle length and Glume length



There is considerable overlap between plants from different areas in terms of panicle length, even though American plants have, on average, significantly longer panicles than Irish or Scottish material. Therefore although the mean results of plants

from different areas may differ, the range of variation exhibited within each area means that it is impossible to ascribe any individual plant to a particular area.

The total range of variation in each character for the herbarium specimens from Britain (including Ireland) was calculated by subtracting the lowest value found for that character from the highest value. The total range of variation from all the specimens examined from around the world (including Britain) was obtained in a similar manner, and the results are shown in Table 6.2.3..

Table 6.2.3. Total Range of Variation exhibited by Herbarium Specimens

Character	Specimens: British	All
Culm height	78 cm	103 cm
Ligule length	3.5 mm	5.4 mm
Leaf width	4.8 mm	5.1 mm
Panicle length	14.0 cm	16.3 cm
Panicle branches	5	6
Spikelet number	517	521
Spikelet length	4.3 mm	4.3 mm
Floret number	5	5
Floret length	3.6 mm	3.6 mm
Top glume length	4.5 mm	4.5 mm
Lower glume length	3.8 mm	4.0 mm

Table 6.2.3 shows that the range of variation in British material is very considerable. Although British specimens made up less than half of the total number of herbarium sheets examined, the

range of variation is often very similar to the total range of variation for all the specimens from around the world. Thus herbarium specimens of Poa pratensis collected from Britain are almost as variable as plants collected thousands of miles apart.

There seems to be a cline in several characters as the origin of the plants moves east or west. Culm height, ligule length and leaf length are all relatively low in British material, and increase in value moving east through Europe and Asia, reaching a peak in America. In terms of spikelet characters, American plants have similar dimensions to British (especially English) plants. Scottish and Irish material generally has long spikelets, florets and glumes, and the length of these decreases in plants collected further east, reaching a minimum in Asia.

These differences in plants from different areas could be due to sampling error : the herbarium specimens may not be an accurate sample of the population of that area. There is evidence of selective sampling among museum collections of butterflies [142], but it is hard to determine the degree to which herbarium specimens are representative of the total population of the species. This is discussed in Chapter 7.

Furthermore, the subspecies of Poa pratensis s.l. as generally defined, are reported to differ in several of the characters above. The variation shown in Table 6.2.1. must therefore imply that the subspecies are unequally common in different regions. The subspecies represented in the herbarium material of each area are shown in Table 6.2.4. The criteria outlined in Table 2.1. were used to identify to which subspecies each plant should be allocated.

Table 6.2.4. Proportion of the subspecies in the Herbarium results

alp = subsp *alpigena* ang = subsp *angustifolia*

prat = subsp *pratensis* sub = subsp *subcaerulea*

Area	alp	ang	prat	sub
A] Scotland	-	-	51 %	49 %
B] England and Wales	-	24 %	55 %	21 %
C] Ireland	-	-	56 %	44 %
D] Europe	9 %	25 %	52 %	14 %
E] Asia	2 %	8 %	90 %	-
F] America	6 %	-	92 %	2 %

Table 6.2.4. hence reveals that the frequency of the subspecies is indeed different in different areas . The distribution of subsp *alpigena* does not include Britain [8], and within Britain subsp *subcaerulea* is reported to be common in the north, and subsp *angustifolia* to be rare in Scotland [4,61]; Table 6.2.4. provides further evidence for this. The herbarium results were therefore divided up according to subspecies, to check whether the mean results for the subspecies were different. If so, this would go some way towards explaining the differences between plants in different areas. Only 13 specimens of subsp *alpigena* were examined, so these have been excluded from Table 6.2.5., which shows the mean results

for the plants of only the other three subspecies.

The mean results for these subspecies are shown below. In the 'summary' column of Table 6.2.5.,

P = pratensis, S = subcaerulea, and A = angustifolia.

P > S means a value for pratensis is significantly greater than a value for subcaerulea at the 0.05 level, P >> S means a value for pratensis is greater at the 0.01 level. Results that do not follow a normal distribution are marked 'n.n.d.', and have not been tested for significance. The statistical test used here, 'Duncan's Multiple Range Test', assumes that values follow a normal distribution [137], and so cannot be used for results that are not normally distributed.

Table 6.2.5. Herbarium Results Analysed in terms of the defined Subspecies

Character	Pratensis		Subcaerulea	
	Mean	Range	Mean	Range
Culm height (cms)	43.7	7 - 108	20.9	5 - 55
Top ligule length (mm/10)	14.1	2 - 38	13.3	3 - 26
Second ligule length (mm/10)	12.8	3 - 43	11.3	4 - 31
First leaf width (mm/10)	22.7	7 - 51	20.1	8 - 46
First leaf length (mm)	35.4	3 - 137	18.2	2 - 52
Second leaf width (mm/10)	27.2	10 - 55	23.7	12 - 46
Second leaf length (mm)	56.7	12 - 167	30.9	5 - 97
Panicle length (mm)	74.8	19 - 182	47.0	19 - 130
Panicle width (mm)	32.1	7 - 179	24.2	9 - 60
Panicle branches	3.57	1 - 7	2.60	1 - 5
Second panicle branches	3.69	2 - 9	2.70	1 - 5
Spikelet number	110	16 - 529	52.8	8 - 154
Top Spikelet length (mm/10)	45.4	29 - 68	45.9	28 - 66
Bottom Spikelet length (mm/10)	42.4	28 - 71	44.4	29 - 70
Floret number Top	3.11	2 - 5	2.74	2 - 4
Floret number Bottom	2.74	2 - 7	2.49	2 - 4
Floret length Top (mm/10)	34.4	21 - 50	36.6	25 - 51
Floret length Bottom (mm/10)	33.6	23 - 47	36.5	23 - 56
Top Glume Top (mm/10)	31.9	16 - 49	34.1	15 - 55
Lower Glume Top (mm/10)	27.8	15 - 47	30.9	14 - 54
Top Glume Lower (mm/10)	30.1	20 - 44	33.6	17 - 60
Lower Glume Lower (mm/10)	25.7	16 - 41	29.9	15 - 52
Glume shape top	1.64	1 - 5	1.66	1 - 5
Glume shape bottom	1.73	1 - 5	1.89	1 - 5
Scabrousness	0.45	0 - 2	0.40	0 - 2
Tufted	0.44	0 - 2	0.23	0 - 1

Table 6.2.5. (cont.) Herbarium Results analysed in terms of subspecies

Character	Angustifolia Mean	Range	Summary
Culm height (cms)	52.4	26 - 96	A >> P >> S
Top ligule length (mm/10)	11.7	3 - 24	P >> A
Second ligule length (mm/10)	10.8	4 - 29	
First leaf width (mm/10)	17.6	4 - 33	P > S > A , P >> A
First leaf length (mm)	31.5	11 - 64	P >> S , A >> S
Second leaf width (mm/10)	18.0	4 - 40	P >> S >> A
Second leaf length (mm)	61.9	24 - 123	P >> S , A >> S
Panicle length (mm)	80.3	42 - 127	P >> S , A >> S
Panicle width (mm)	25.0	8 - 83	P >> S , P > A
Panicle branches	3.86	2 - 6	P >> S , A >> S
Second panicle branche	3.95	2 - 5	P >> S , A >> S
Spikelet number	121	36 - 251	P >> S , A >> S
Top Spikelet length (mm/10)	40.9	30 - 52	P >> A , S >> A
Bottom Spikelet length (mm/10)	37.9	28 - 48	P >> A , S >> A
Floret number Top	2.93	2 - 5	P >> S
Floret number Bottom	2.65	2 - 4	P >> S
Floret length Top (mm/10)	31.4	25 - 40	P >> A , S >> A
Floret length Bottom (mm/10)	30.4	25 - 40	S >> P >> A
Top Glume Top (mm/10)	28.0	21 - 38	S >> P >> A
Lower Glume Top (mm/10)	24.1	17 - 35	S >> P >> A
Top Glume Lower (mm/10)	26.3	19 - 35	S >> P >> A
Lower Glume Lower (mm/10)	21.8	16 - 35	S >> P >> A
Glume shape top	1.61	1 - 4	n.n.d.
Glume shape bottom	1.67	1 - 5	n.n.d.
Scabrousness	0.46	0 - 2	n.n.d.
Tufted	0.47	0 - 2	n.n.d.

These data agree with those from previous authors, whose subspecific definitions were, in any case, used to define the specimens here examined, in the following results : culm height is highest in subsp angustifolia, and lowest in subsp subcaerulea [8,98]; subsp angustifolia has narrow leaves [4,68,97]; subsp subcaerulea has short panicles [4,8,11], few lower panicle branches [72,73,90], and relatively few spikelets per panicle [11]; subsp angustifolia has short spikelets and florets [4,93], and subsp subcaerulea has large florets [11,73], but few florets per spikelet [4]; the glumes of subsp subcaerulea are long, and of subsp angustifolia are short [4]. In all these characters, subsp pratensis is intermediate between the other two.

On the basis of this analysis, which is probably the biggest numerical comparison made of Poa pratensis, the characters defined for each subspecies can indeed be regarded as correlates in the herbarium material. It should be stressed, however, that means are being compared here; the range of variation within one subspecies is very great, and therefore there is considerable overlap between the subspecies (see Table 6.2.5.). This means that many individual plants seem to be intermediate between two subspecies.

For example, one plant had a culm height of 24 cm, a panicle length of 4.1 cm, and 51 spikelets per panicle - which are all characteristic of subsp subcaerulea - but also had a second culm leaf only 1.6mm wide, a top spikelet 3.0 mm long and a top glume 2.2 mm long - which are characteristic of subsp angustifolia. Similarly, another plant with a culm 84 cm high and top spikelet 4.1 mm long (like subsp angustifolia), had a second culm leaf 3.7 mm wide and

panicle 10.5 cm long (like subsp pratensis), and also had 41 spikelets per panicle and a top glume length of 3.9 mm (like subsp subcaerulea). These are not isolated, rare examples: there are a large number of plants with a combination of characters that are normally ascribed to more than one subspecies.

Leaf length is very rarely mentioned by other workers, perhaps because it varies greatly within one plant depending on which leaf is measured. However Table 6.2.4 shows that both the culm leaf and the second leaf of subsp subcaerulea are significantly shorter than the leaves of the other two subspecies.

The difference in length between the upper and lower glumes is shown in Table 6.2.6..

Table 6.2.6. Length of Upper glume compared to Lower Glume

Values show the length of the upper glume as a percentage of the lower glume length

Spikelet	pratensis	subcaerulea	angustifolia
Top	115 %	110 %	116 %
Bottom	117 %	112%	121 %

The results in Table 6.2.6 are lower for subsp subcaerulea than for the other two subspecies, which gives weight to reports that the glumes of subspecies subcaerulea are more equal in length than those of subsp pratensis or subsp angustifolia [4,7,8,72]. There was previously very little quantitative information about the degree to which subsp subcaerulea differed in

this from the other two subspecies. As with several of the other characters, the mean results for the subspecies may differ, but individual plants within a subspecies vary greatly, so it is very hard to allocate a particular plant to a subspecies using this character. Evaluations of some of the other characters, based on herbarium observations, are given below.

The shape of the glumes is very similar for the top spikelets of all three subspecies, but in the lower spikelets subcaerulea has more pointed glumes than the other two subspecies. This contradicts the results of several authors [4,7,8,11,72], who characterise subsp subcaerulea as having glumes that are gradually tapering. This anomaly may be due to nomenclatural differences; in this study, 'tapering gradually' is restricted to glumes with straight edges, those with curved edges being referred to as pointed (see diagram on page 32). However it is clear from the illustrations that Hubbard applies 'tapering gradually' to glumes that have both straight and curved edges [4]. So glumes that other authors would describe as tapering are here listed as pointed. This demonstrates the difficulty of making accurate comparisons of results where subjective classifications are used, the boundaries of which vary with different authors.

There is little evidence of significant variation between the subspecies in the scabrousness of the panicle branches. This character has been reported to vary between subspecies [75,97], although not specifically between the three subspecies reported here.

Subspecies subcaerulea seems to be much less tufted than

subsp pratensis or subsp angustifolia, which has been noted by several authors [4,7,11,72], but there is very little difference between subsp pratensis and subsp angustifolia in the degree of tufting, yet several authors use this character to separate these two subspecies [7,10,72]. It is possible that herbarium specimens give an inaccurate estimate of tufting, because specimens that are tufted may be separated, to facilitate pressing and mounting. Any plants that were mounted as single specimens, but were noted as tufted on the herbarium label were here scored as tufted. In the great majority of cases, no information on tufting was given on the label.

There is some dispute over the relative ligule lengths of subsp angustifolia and subsp pratensis (see Table 2.1.). The herbarium results in Table 6.2.5. show that the ligule length of subsp pratensis is significantly higher than that of subsp angustifolia; this supports Hubbard rather than Edmondson. In all of the characters, including ligule length, the range of values found within each subspecies is very large, and there is considerable overlap between the subspecies. This is illustrated in Figures 6.2.3. and 6.2.4.

Figure 6.2.3. Top ligule length

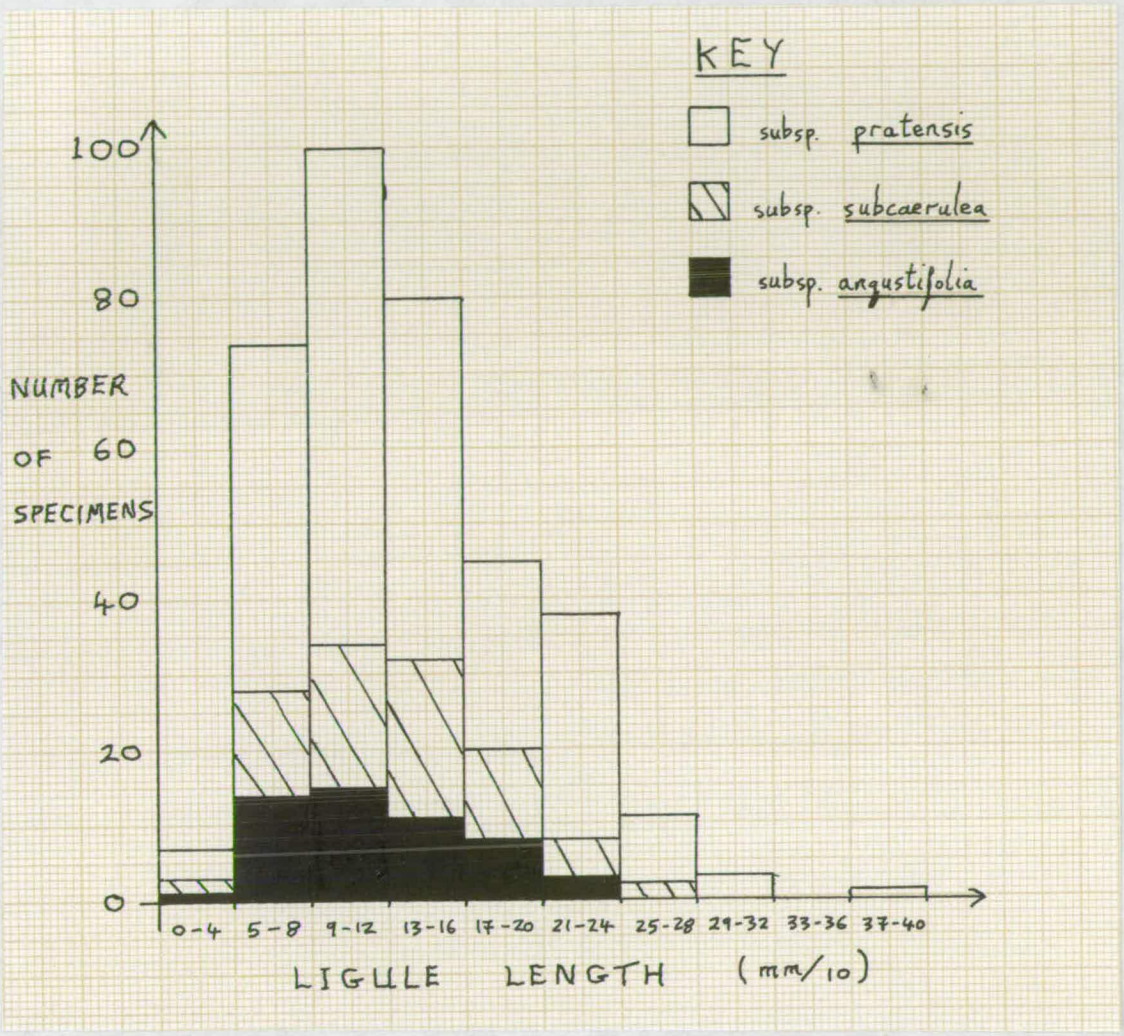
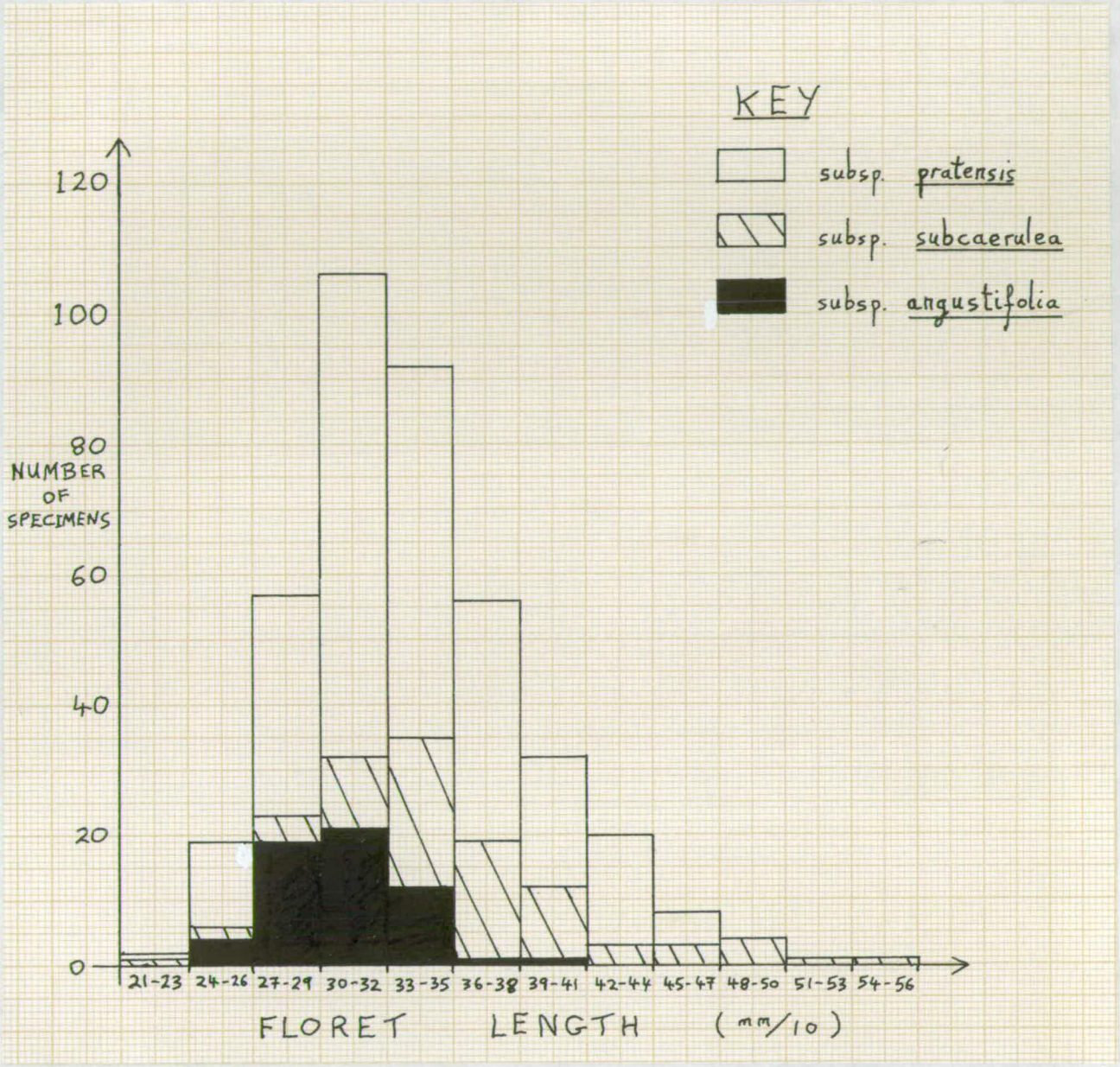


Figure 6.2.4. Bottom Floret length



This wide range of values for each subspecies means that it is essential to take as large a sample as possible; if only a few plants of each subspecies are examined, very different results may be obtained. A balance is necessary between sampling too few

individuals, which may give results very different from the actual population mean, and sampling so many individuals that only very few characters can be recorded in the time available. As a rough guide, about 40 individuals should be examined to give a fairly precise estimate of the mean and variance [143]. In the various divisions of the herbarium material above, only the sample of Irish plants (n = 27) was smaller than this, and this was due to the paucity of herbarium material available.

These differences between the subspecies undoubtedly account for some of the variation in plants from different areas; for example, Scottish plants, with a relatively high proportion of subsp subcaerulea, have shorter culms and panicles and longer florets and glumes than plants from most other areas. However there are still discrepancies : Irish plants have shorter and narrower leaves than Scottish material, even though Ireland has a slightly higher proportion of subsp pratensis. This could be because the mean results from the Irish plants are not representative of the Irish population, due to the relatively low numbers of plants sampled. Alternatively it could show an actual difference due to plants growing in different habitats. Of the herbarium material examined, information on the habitat was available for 64 % of Scottish plants and 89 % of Irish plants. The main difference in habitats is that 21% of Irish plants , but only 2 % of Scottish plants, were from bogs or moors. This implies that some of the Irish material may have been stunted through growing in nutrient poor soil. Leaf expansion is particularly susceptible to environmental influence, including variations in nutrient supply [144].

The herbarium results above therefore indicate that

plants from various areas of the world differed in several characters, and this is reflected in the different frequency of the defined sub-species in different areas. Possibly this reflects a genuine taxonomic difference, however it can also be interpreted that habitat types where the plants are growing may not be the same in different areas. Although the mean results of the three most numerous subspecies are often different, there is very considerable overlap between them in all the characters measured, so an individual plant often cannot be readily placed in a subspecies, as it has the characteristics of two or more subspecies.

Although the herbarium material examined did not fit neatly into the subspecific categories outlined by other workers, it is possible that certain character assemblages do exist, which have not been previously distinguished. In order to test this h pothesis, principal components analysis was carried out on the data. This analysis is used to display the relationships between plants in an objective and concise manner. If the variation within the species was partitioned into discrete groups, this would be revealed by principal components analysis.

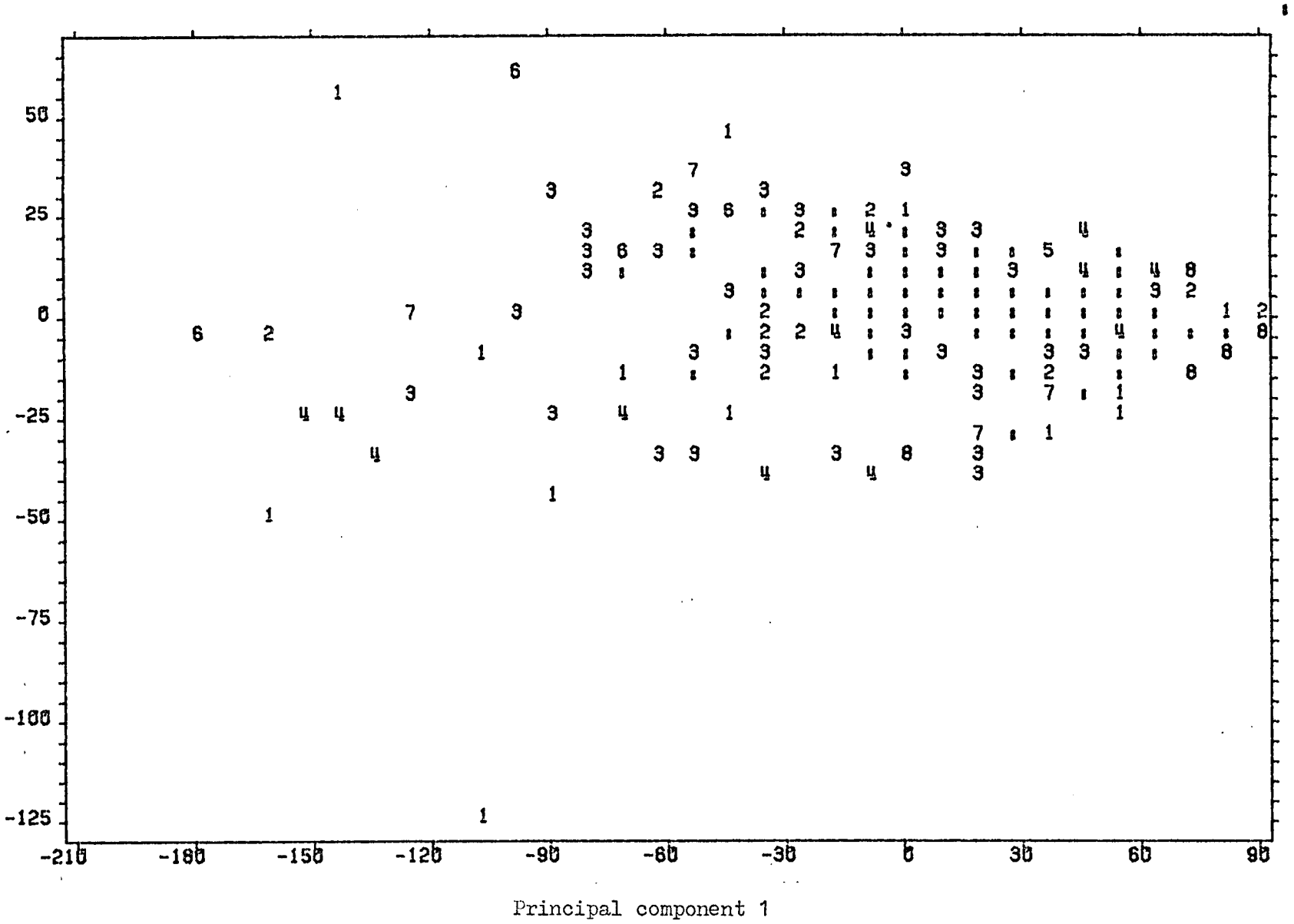
PCA (by GENSTAT V computer program) evaluates the variation of the twenty six characters (listed on pp. 30-33) in terms of which best showed entities within the sample. 406 individuals were analysed - those for which all data had been scored. The same analysis was applied to specimens from each of the geographical groupings inthe data (Scotland England, Europe, N.America, Middle East, Asia, Wales and Ireland) in case the scatter of points there revealed biologically significant differences.

As an initial check on whether part of the character array revealed groupings which the other did not, the characters were analysed in two parts. In the event the results from both were very similar, so the analysis might as well have been run all togeher, since neither showed groupings. Figure 6.2.5 is of of the plot of PC 1 vs PC 2 for the

Table 6.2.7. Latent vector loadings underlying Principal Components.

Characters	Analysis 1			Analysis 2	
	PC1	PC2	PC3	PC1	PC2
Second leaf length	-0.5342	0.4222	0.3992	-	-
Panicle length	-0.5250	0.1242	0.2382	-	-
Panicle width	-0.2572	0.7273	-0.2555	-	-
Culm height	-0.3306	0.1364	0.6666	-	-
First leaf length	-0.3194	0.1338	0.3664	-	-
Number of spikelets	-	-	-	0.9989	-0.0432
Top spikelet length	-	-	-	-0.0087	-0.4639
Bottom spikelet length	-	-	-	-0.0200	-0.4283
% variation					

Figure 6.2.5. Principal component analysis 1. Distribution of points, also showing geographical spread.



first PC analysis, covering characters (1-11) (see p. 29). Figures 6.2.6. is the same plot covering the distribution of plants using characters 12-26 (see p. 29), from the eight geographical areas. Separate plots of the PCA of different geographical samples appear as Appendix 1.

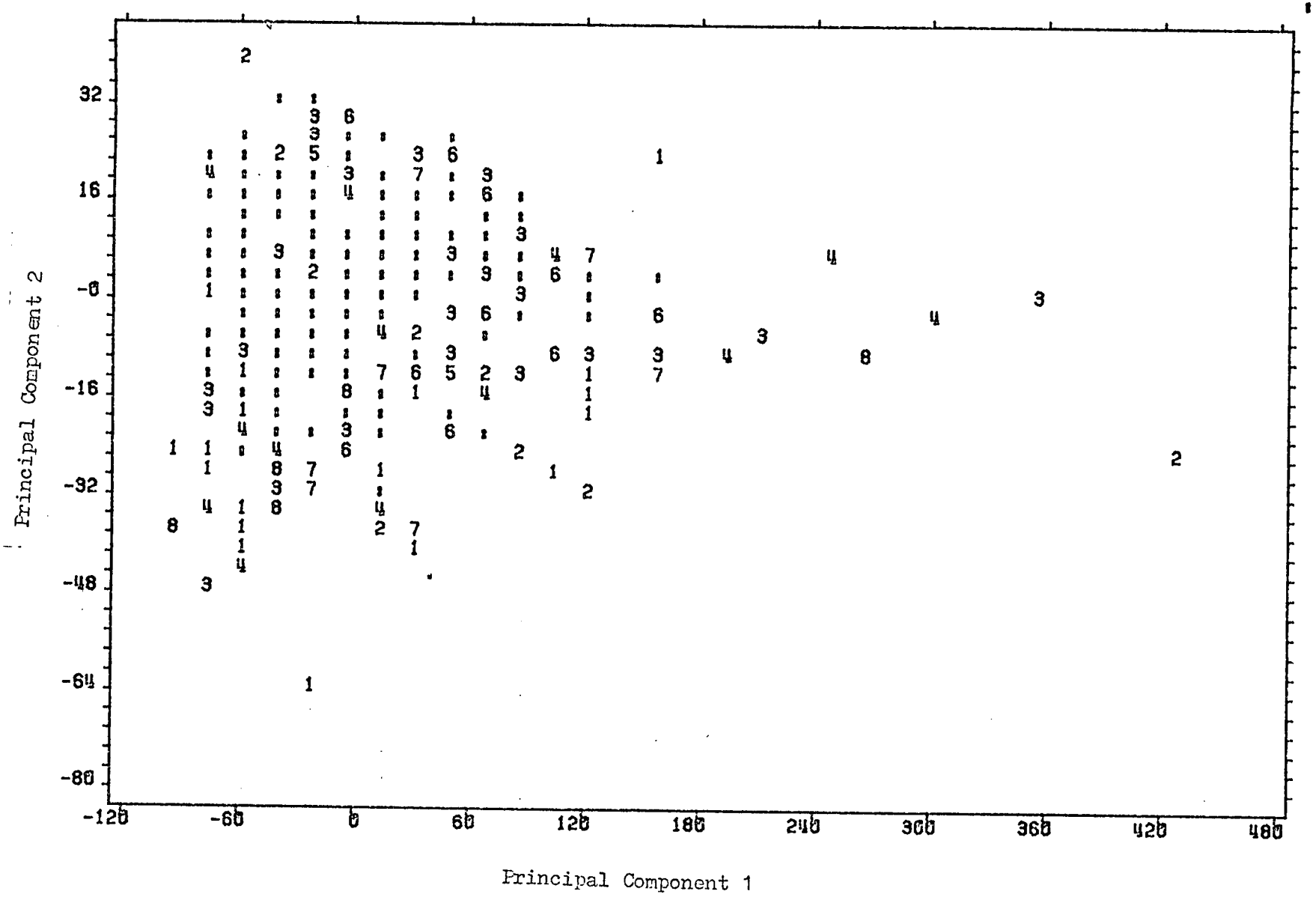
The first analysis showed that three components could account for over 88% of the total variation, none of the others being greater than 3.5%. The first three components hence rest upon those features in the data which are most likely to reveal entities within the population sampled. Table 6.2.7. shows the largest latent vector loadings for each of the principal components in each of the two parts of the analysis. In the first analysis, second leaf length and panicle length are the chief contributors to PC1, and panicle width is the chief factor in PC2.

Figure 6.2.5. shows that no taxonomic groupings are discernable. PC3 versus PC1 and PC2 showed a similar result. By definition arising from the PCA principle, other characters than those contributing largely to these first components can distinguish groupings in the data even less well.

The results of the second PC analysis (on characters 12-26) mirror those of the first. PC1 and PC2 here account for 98.7% of the variation. No other component reaches even 0.5%, so the characters on which they principally rest distinguish groups less well than those underlying the PC1 and PC2 components. The latent vector loadings (Table 6.2.7.) show that spikelet number is the largest contributor to PC1 and the two spikelet length characters are both important in PC2.

From these analyses, there is confirmation of the earlier evaluation of herbarium data, i.e. that there is clear distinction of neither potentially subspecific nor geographical groups. Figure 6.2.6. and the "geographical area" plots (see Appendix 1) are generally overlapping, though with some differences of spread which may betray the existence of minor geographical variants (grex) unworthy of taxonomic name. They are as likely to be explained by sample size difference.

Figure 6.2.6. Principal component analysis 2. Distribution of points, also showing geographical spread.



CHAPTER 7. MORPHOLOGICAL EXAMINATION OF BIOTYPES AND CULTIVARS

7.1 Introduction

Panicles from the biotypes and cultivars that flowered in 1982 were examined to investigate the taxonomic range of the biotypes and cultivars, and also to examine whether cultivars and biotypes could be differentiated morphologically.

7.2 Results

The mean results from 10 culms per biotype are shown in Table 7.2.1.. It has previously been demonstrated that one of the most consistent characters for separating the putative subspecies is the glume length (see Table 6.2.5). The biotypes and cultivars in Table 7.2.1. are therefore arranged in order of mean length of the lowest glume.

Table 7.2.1. Taxonomic Analysis of Biotypes and Cultivars

Key : 1 - Culm height (cm)
2 - Leaf width (mm/10)
3 - Leaf length (mm)
4 - Panicle length (mm)
5 - Number of Panicle Branches
6 - Number of spikelets per panicle
7 - Spikelet length (mm/10)
8 - Floret length (mm/10)
9 - Top Glume length (mm/10)
10 - Lower Glume length (mm/10)

Biotype	Character 1	2	3	4	5	6	7	8	9	10
West Coast	49	19	39	79	3.1	64	62	46	44	39
Yetholm	66	18	49	88	3.7	106	58	42	42	37
Tomintoul	58	19	48	89	3.9	86	54	40	42	37
West Cheviots	62	23	56	89	3.3	71	56	40	40	36
New Cumnock	70	21	63	108	4.2	140	53	40	41	36
9 Dalmelington	64	22	56	94	2.8	88	59	41	39	36
Airport	59	19	55	90	2.9	64	55	43	42	35
Fannich	64	25	54	103	4.3	140	51	40	37	33
Stromness	72	16	47	87	2.0	48	54	40	37	33
Knapdale	52	23	67	87	3.8	80	47	37	35	32
Lochans	77	23	70	115	3.7	95	50	38	37	32
Ben Obe	58	20	36	81	4.1	94	48	38	38	32
Kinlochleven	39	22	38	60	4.1	80	52	39	35	30
Newburgh	55	18	44	76	3.4	57	46	35	33	29
Birsay	46	17	37	72	3.3	65	50	35	33	29
8 Dalmelington	46	24	42	70	3.9	65	49	35	32	29
Aviemore	71	19	81	91	3.1	90	52	36	36	29
Wooler	44	19	45	85	4.0	65	53	37	32	28
Baron *	62	30	72	104	4.6	133	43	36	30	27
Arina *	86	20	69	101	3.8	108	49	36	34	27
Braemar	60	22	47	91	4.4	153	35	29	28	24
North Berwick	83	19	68	90	3.3	93	52	34	30	24
Cairngorm	52	24	59	81	2.8	102	39	26	24	22

Table 7.2.1. shows that the biotypes cover a wide range in terms of the characters examined. Using the subspecific categories outlined in Table 6.2.5., the biotypes range from plants such as 'West Coast' which has many of the characteristics of subsp subcaerulea, to 'Braemar', which is more like subsp pratensis. 'West Coast' has a short culm, and short, narrow leaves. The panicles are small and have relatively few spikelets. The individual spikelets, however, are large and the florets and glumes are long - all

characters associated with subsp subcaerulea. In contrast 'Braemar' has a taller culm, longer, wider leaves and a long panicle with numerous spikelets. The spikelets are fairly small and have short florets and glumes. The cultivars have more of the characters of subsp pratensis than of subsp subcaerulea, such as tall culms, long panicles and many spikelets per panicle. However there is no morphological character amongst those examined that clearly delimits the cultivars from the biotypes. The morphological characters were specifically chosen because they vary significantly between different subspecies (see Table 6.2.5.) and between plants from different areas (see Table 6.2.2.). However selection has not proceeded so far that plants can be reliably identified as cultivars or wild plants on the basis of these characters.

Table 6.2.5. showed that in herbarium specimens, plants with long glumes tend towards subsp subcaerulea and plants with short glumes are more likely to be subsp pratensis or subsp angustifolia. None of the biotypes or cultivars examined here had the characteristic rolled leaves of subspecies angustifolia, and so one would expect the plants towards the bottom of Table 7.1. - which have short glumes - to have the characters of subsp pratensis. These characters include: tall culms, long and wide leaves, long panicles with a large number of panicle branches and numerous spikelets per panicle (see Table 6.2.5.). However Table 7.2.1. shows that most plants do not have this combination of characters. For example, 'Wooler', which has very low culms indicative of subsp subcaerulea, has a relatively high number of panicle branches, which would normally be associated with subsp pratensis. Similarly, 'Yetholm' has a large number of spikelets per panicle but very narrow leaves.

Also 'New Cumnock' has tall culms, and long panicles containing many spikelets - all characters of subsp pratensis - combined with the long glumes associated with subsp subcaerulea. Even the cultivars 'Baron' and 'Arina', which have lower glumes of identical lengths, have different culm heights and leaf lengths, and even their upper glumes are different lengths.

So again there is evidence that the combinations of characters ascribed to the putative subspecies often are not found together. In many cases an individual plant has the characteristics of two separate subspecies.

The 21 biotypes were all collected from Scotland, and so a comparison can be made between the results in Table 7.2.1. and the herbarium results from Scottish material (Table 6.2.1.). This will give some idea of whether the herbarium specimens are representative of the population. The mean results for the biotypes and herbarium material for the 10 characters are shown in Table 7.2.2.

Table 7.2.2. Comparison of Biotypes and Herbarium Plants

Key: 1 - Culm height (cm)
2 - Leaf width (mm/10)
3 - Leaf length (mm)
4 - Panicle length (mm)
5 - Number of Panicle Branches
6 - Number of spikelets per panicle
7 - Spikelet length (mm/10)
8 - Floret length (mm/10)
9 - Top Glume length (mm/10)
10 - Lower Glume length (mm/10)

Specimens	1	2	3	4	5	6	7	8	9	10
Biotypes	59	21	52	87	3.5	88	51	38	36	31
Herbarium plants from Scotland	29	26	48	60	3.1	81	46	36	34	30

Table 7.2.2. shows that for most of the characters, the mean results for the biotypes and the herbarium material are within about 10 % of each other or less, so on the whole the results are similar. The characters in which there is the greatest difference are culm height and panicle length, both of which are longer, on average, in the biotypes. Part of this difference may be due to the fairly small sample size: with a total of 21 biotypes, the results from one or two aberrant plants can have a considerable effect on the value of the mean. The main part of this difference between the biotypes and the herbarium plants is however probably due to the conditions under which the plants were growing. In many cases the herbarium material would be subject to grazing or cutting, whereas the biotypes were not cut at all. Culm height and panicle length are much more likely to be affected by grazing or cutting than the other characters examined (see Chapter 4). Floret length is relatively unaffected by environmental variation (see Chapter 4), and the mean glume length often varies significantly between the subspecies of Poa pratensis (see Chapter 6). The possibility that herbarium material may not accurately reflect the total population, due to selective sampling by collectors has been mentioned before (see page 70).The fact that the floret length and glume length of the biotypes and herbarium specimens are very similar suggests, however, that there is no great taxonomic bias in the herbarium material.

On the whole, the results show that the cultivars are not morphologically different from the biotypes, and the biotypes cover a fair range of variation between the putative subsp pratensis and subsp subcaerulea. Several of the plants have the a mixture of characters that are normally attributed to two subspecies, as was

the case with the population analysis (see Chapter 5). None of the biotypes or cultivars have the characteristic rolled leaves of subsp angustifolia. As far as can be gathered from the limited sample of biotypes collected from Scotland, herbarium specimens from Scotland seem to give a fairly accurate cross-section of the total population.

CHAPTER 8. DISCUSSION

In Section A, the taxonomy of Poa pratensis was investigated. Plants of the same biotype were grown in experimental plots to determine which morphological characters were greatly modified by environmental conditions. Also, populations of Poa pratensis in Scotland were examined morphologically, and herbarium material of Poa pratensis collected from around the world was examined. In this chapter the results from the section dealing with the effect of the environment on morphological characters are related to the herbarium results.

A key point in the taxonomy of Poa pratensis is the treatment of the variation pattern. The degree of variability within a taxon, and the amount of overlap between taxa is crucial to determining the rank applicable to that taxon. Many of the results in Section A provide information on the variation pattern of Poa pratensis. The results from Section A are therefore discussed in relation to the taxonomic treatment of Poa pratensis by other authors.

The results in Chapter 4 indicated that floret length and glume length were relatively constant in plants of the same biotype grown in different environments, and were useful in distinguishing between different biotypes. The comparison between cut and uncut plants in Chapter 4 revealed that plants that were cut had their floret and glume lengths reduced by about 10 % (Table 4.2.2.) compared to uncut plants. This magnitude of difference is very similar to the mean difference between herbarium specimens from

different areas (Table 6.2.1.) and even to the mean difference between different subspecies (Table 6.2.5.). It is therefore theoretically possible that the mean differences between herbarium material attributed to different subspecies, and the mean difference between material from, for example, Scotland and North America, is an artefact of cutting or grazing. However this is unlikely for two reasons. Firstly there is no reason why plants from a particular area, or of a particular subspecies, should be cut or grazed more often than plants elsewhere. Secondly, only herbarium specimens that were in good condition were examined: any that had obviously been cut or grazed were not included in the study. The results in Table 4.2.2. were obtained from plants that had been cut between 14 and 44 days previously. Even in the case of those plants which had had 44 days to recover from cutting, it was clear that the plants had been cut - many of the leaf tips were missing. Any herbarium specimens that showed signs of damage were not examined in this study. Therefore any herbarium plants that were examined cannot have been recently cut or grazed, so this is unlikely to have affected the results.

The only author who has recently published papers on Poa pratensis collected in Britain is Barling [11,119,120,124]. Several of the results from the present work agree with Barling's results : for example, culm height seems to be relatively susceptible to environmental variation (chapter 4). However some of the results presented here do not confirm Barling's conclusions.

Firstly, Barling stated that many characters found in wild Poa pratensis, such as small spikelets, are usually environmental effects [11]. The work described here shows that the

spikelet lengths of cut and uncut plants are very similar (page 45). Also spikelet length can be used quite succesfully to distinguish between different biotypes (p 45), which would not be expected if spikelet length was controlled largely by environmental factors. Unfortunately the degree to which the environment alters the spikelet length of the plants examined by Barling is unclear, as he does not give any quantitative information about this character. It is therefore impossible to resolve this difference of opinion.

A more fundamental difference occurs in the treatment of the variation pattern of Poa pratensis s.l.. Barling treats Poa angustifolia and Poa subcaerulea as separate species from Poa pratensis s.s., and considers them to be extremes of the Poa pratensis s.l. group [11]. Several other authors, including Edmondson and Hubbard, also treat these three taxa as separate species (see Table 2.2.). In Flora Europaea, Edmondson states that intercrossing between the three taxa is now probably a rare event [8], however he does not provide any evidence for this. The great variability of plants within a small area, transcending the 'limits' of the three taxa (Figures 5.2.1. and 5.2.2.), suggest that intercrossing between the taxa is common. In neither his thesis [135], nor Flora Europaea [8] does Edmondson present quantitative data on the variation pattern in Poa pratensis s.l., and so it is not possible adequately to compare his database with that presented here.

The work carried out in this study indicates that the morphological variability of Poa pratensis seems in many cases to have been underestimated by previous workers. For example, most authors consider that five is the maximum number of florets per

spikelet in Poa pratensis [65,79,99,105], but the biotype collected from Stromness had a mean of 5.9 florets per spikelet (p40), and up to 7 florets per spikelet were found in the herbarium material (p73). In the three populations examined (chapter 5), the mean leaf width is relatively narrow compared to the values given by other workers [4,72,81], and the mean spikelet length of the plants from New Cumnock is lower than the minimum given by Hubbard [4]. Table 6.2.5 shows that the range of variation in the characters examined is much greater for the three subspecies than that recorded by other authors (see Table 2.1). The underestimation of the variability of intra-specific groups in Poa pratensis perhaps accounts for the disagreement between authors as to the range of values for characters such as ligule length attributable to the different taxa (Table 2.1). This large degree of variation within each taxon, and the resulting overlap in these characters between the taxa means that the validity of even subspecific rank for these taxa must be questioned.

In this study, the plants examined from Scotland tended to be intermediate between subsp pratensis and subsp subcaerulea (Tables 5.2.1. and 7.2.1.); none of the plants were typical specimens of subsp angustifolia. A characteristic feature of subsp angustifolia is that the vegetative leaves are rolled [47], and this was true of the herbarium specimens of this subspecies that were examined. None of the specimens of subsp pratensis or subsp subcaerulea had rolled leaves. Many of the other characters that are reported to distinguish subsp angustifolia from the other subspecies, however, show considerable variation within all three subspecies (Figures 6.2.3. and 6.2.4, and pages 75-76). Therefore

rolled leaves are the main distinguishing feature of subsp angustifolia. There is no single character analagous to the rolled leaves of subsp angustifolia, that separates subsp pratensis from subsp subcaerulea. In the material examined in this study, none of the characters which are normally used to distinguish between these subspecies (Table 2.1) showed a clear discontinuity. In fact the results indicate that individual plants often have the characteristics of more than one subspecies (chapters 5 - 7), and there is very considerable overlap between the subspecies in all the characters examined (Figures 6.2.3. and 6.2.4., and Table 6.2.5). As Davis and Heywood point out [21], some overlap can occur between subspecies, but the great majority of individuals must be morphologically different from individuals of the other subspecies. This is not true of the situation in Poa pratensis : the degree of overlap is so great between subsp pratensis and subsp subcaerulea that these taxa are not sufficiently distinct to be regarded as separate subspecies.

The validity of subsp angustifolia is more debatable, as the presence of rolled leaves was a constant character in this subspecies. However considering the large overlap in the other morphological characters between subsp angustifolia, subsp pratensis and subsp subcaerulea (Table 6.2.5.), the use of subspecific rank for this taxon does not seem to be justified.

Another reason for not treating subcaerulea and angustifolia as subspecies of Poa pratensis is the wide geographical overlap between them. Each subspecies should occupy a distinct geographical area, separate from other subspecies [21]. This is not true of Poa pratensis: in both Britain [61] and Europe [8] there is

considerable overlap between the three taxa that are found in Britain. The summary of the taxonomic treatment of Poa pratensis s.l., given in Table 2.2, indicates that all four taxa of Poa pratensis are also found in North America and Asia.

It is therefore concluded that subcaerulea and augustifolia should not be treated as subspecies, but should be included in the morphologically variable species Poa pratensis L.

The taxonomic position of subsp alpigena is unclear: there was insufficient material of this taxon examined in this study to clarify this point. A much larger sample, and further analysis, would be required before any conclusion could be reached concerning the validity of the subspecific rank ascribed to this taxon.

Principal Components Analysis confirmed the continuity of variation in gernal, and detected no groups worthy of rank in a test unweighted by preconceptions of what groups might exist, or which characters might be most important. Only minor geographic variations were detected, and these were ambiguous, being overlapping to a considerable degree, and possibly arising from sampling factors only.

SECTION B : Cultivar Development.

CHAPTER 9. LITERATURE REVIEW : CULTIVAR DEVELOPMENT..

9.1. Characters required in Poa pratensis cultivars.

Poa pratensis is used in Britain primarily as an amenity grass for sports grounds, lawns and roadside verges [31]. It is also used commonly in Europe as a forage grass [145]. Several characters are required in both amenity and forage grasses. These include winter hardiness, disease resistance, dense sward formation, high seed yield and good seed germination [31,41,47,146,147].

Winter hardiness is obviously important, especially in northern areas. In severe winters, the death of grass cultivars due to poor winter hardiness can be a major problem in Scotland [38]. The poor winter hardiness of imported cultivars of Poa pratensis in Norway was one of the main reasons for developing a cultivar from indigenous Norwegian material [37].

Compared to other species, disease resistance in Poa pratensis is relatively poor [58]. The most important disease affecting Poa pratensis is 'melting out', caused by the fungus Drechslera poae [148], but over 30 other diseases of Poa pratensis have been recorded [149]. The majority of these are fungal infections.

Normally, the high tillering capacity of Poa pratensis and its creeping rhizomes enable it to form a dense turf [31], but one of the main problems with this species is that it takes a long time to achieve this high ground cover [52]. The germination of Poa pratensis is fairly slow [41], and this could be a contributory factor in the slow establishment and initial ground cover of Poa

pratensis [40]. Seed production is often a problem with Poa pratensis: several plants with otherwise promising performance have a low seed yield [147,150].

In addition to these characters, dry matter production is very important for forage grasses [146,151,152], which will be used for feeding sheep and cattle, either as grass or as hay. Leaf colour is important in amenity grasses, especially those for use in sports turf and domestic lawns [31,153]. A consistent green colour is required; cultivars that turn yellow or brown over winter are unlikely to be used for lawns or sports turf, although they can be used for roadside verges [154].

Given the large overlap in the characters required in both amenity and forage grasses, plants can be screened simultaneously for both amenity and forage use [151]. This is the case in this study, the characters examined were: plant survival (hardiness), dry matter production, ground cover, disease resistance, colour, seed yield and germination.

An increase in the freezing tolerance of grasses occurs in autumn and winter, and the degree of damage done to the plants depends on the level of hardiness achieved during this time [155]. The hardiness of Poa pratensis is decreased by adding fertilizer in the late autumn [156,157], and in other grass species the frequency of cutting affects hardiness [158]. Also, prolonged snow cover results in a decrease in the hardiness of grasses [155]. Compared to Lolium perenne, winter hardiness is good in Poa pratensis [155]. Occasionally the hardiness of grass biotypes is tested in the laboratory [36], but the correlation is poor between laboratory tests and results from plants exposed to natural temperature

fluctuations outside [159]. Probably this is because several factors can affect hardiness, and they interact in a complicated pattern to increase or decrease hardiness under natural conditions [160]. So normally the hardiness of Poa pratensis is tested by growing plants outside in plots [33,161].

Non-destructive methods of estimating dry matter production are generally inaccurate [162], so dry matter yield is usually estimated from the weight of cuttings [163]. The frequency of cutting affects the total dry matter yield in Poa pratensis [127,164]. The amount of fertilizer provided, and the temperature both affect the dry matter production of Poa pratensis [165,166]. This means that the yield of Poa pratensis varies from place to place and from year to year [167].

Visual estimates of ground cover are relatively inaccurate, compared to using quadrats [168]. Mechanical quadrats using pins are widely used, but optical methods offer increased accuracy [169]. Grouping the points into frames makes the method quicker, but means that for statistical analysis, the results need to be angularly transformed so that they approximate to a normal distribution [170].

Disease resistance of Poa pratensis is affected both by cutting height [171] and by fertilizer application rates [172]. Disease resistance is heritable in Poa pratensis [125]. Normally, the resistance of plants outside in plots to natural infections is noted [161,173] rather than innoculation of plants outside with a certain disease [174], or laboratory tests of disease [175].

The colour of Lolium perenne is affected by its dry matter yield [176], and this is reportedly also true of Poa

pratensis [177]. The amount of fertilizer provided, which will affect the dry matter production, also affects colour in Poa pratensis [178].

Seed production of Poa pratensis depends on the environment in which the plants are growing [150]. Poa pratensis seed production is reportedly higher at soil temperatures of 22°C compared to temperatures of 14°C [126]. Seed production of the Poa pratensis cultivar 'Cougar' can apparently be increased by occasionally cutting the plants [127].

9.2. Germination

One of the main problems with Poa pratensis is that it has slow germination compared to other grass species [41,179], and this contributes to its relatively slow establishment. In several grasses, large seeds within a seed lot give better establishment than small seeds [180]. However the slow germination and establishment of Poa pratensis is not due to its small seed size: Phleum pratense, with almost identical seed weight to Poa pratensis, establishes much faster [181].

Three factors that strongly influence seed germination in the field are: temperature, light and nitrate ions [182]. Temperature has a greater effect on the germination of Poa pratensis than light [183] or nitrate [184]. Germination of Poa pratensis is increased by alternating temperatures compared to constant temperature [50,179,185]. Temperatures fluctuating by 10 °C are optimum for germination [186]. On the whole light promotes the germination of Poa pratensis [50], especially when given over fairly

short periods - continuous light inhibits germination [187]. Potassium nitrate solution stimulates the germination of Poa pratensis [188], and has a slightly greater effect on germination than gibberellic acid [184].

In order to increase the reproducibility of results obtained in different laboratories, a standardised germination test procedure has been published for agricultural and amenity grasses [189]. This defines the temperature, the light duration and the amount of potassium nitrate to be used in the germination test. Generally the conditions specified are those that give maximum seed germination. Cultivars of Poa pratensis must have at least 75% germination in this test before they can be sold in the E.E.C. [190]. In this test, four replicates each of 100 seeds are used.For Poa pratensis, the temperature specified is 20 ^{o}C for 16 hours and 30 ^{o}C for 8 hours, with 8 hours of light per day. A solution of 0.2% potassium nitrate is used to break dormancy [189].

9.3. Cultivar development in Poa pratensis

The facultatively apomictic reproduction of Poa pratensis means that unlike most cultivars, which are produced by crossing different biotypes, cultivars of Poa pratensis are normally obtained merely by selecting wild plants which have the desired characteristics [51,52]. The selected plants are multiplied up in open plots, aberrant plants are removed, and apomixis is relied upon to ensure uniformity [147]. The main advantage of apomixis for the plant breeder is the retention of good gene combinations, although of course with a facultative apomict such as Poa pratensis some sexual seed formation is inevitable. Thus cultivars tend to be

mixtures of apomictic strains [191].

Experimenters in the U.S.A. tried hybridizing Poa pratensis with other Poa species, and selecting the recombinants with the characteristics required [22]. A wide range of plants was produced, but after 20 years the study was concluded without producing a single new cultivar [192]. Later a similar method was used at the Scottish Plant Breeding Station , crossing Poa pratensis and Poa ampla [193]. Several hybrid plants were produced [171,194], and these are being evaluated for use as a forage grass in upland pastures at the Welsh Plant Breeding Station [195], to where the work has now been moved. The mean dry matter yield of the hybrid plants was, however, lower than that of the cultivar 'Troy' which was used as a control [163].

A few cultivars have been produced by crossing plants of Poa pratensis, but this is fairly rare: of the 25 cultivars for which the origin of the plants has been published, 22 are selected wild plants and only 3 are the result of crossing wild plants [52,196-201]. Normally Poa pratensis is sown in a mixture with other species; mixtures have the advantage of lower disease susceptibility [202] and greater tolerance of environmental and management extremes than pure swards [155].

CHAPTER 10. MATERIALS AND METHODS

10.1. Collection of Plant Material

Plants of *Poa pratensis* L. *s.l.* were collected from a wide variety of habitats and geographical areas of Scotland. Plants were not collected from any sites where it was likely that they had been sown, such as agricultural land, playing fields and the edges of major roads. It was assumed that all the plants had spread naturally into the areas where they were found, although it is of course impossible to tell a wild from a cultivated plant, especially if the cultivar was sown some time ago. The vast majority of cultivars are direct selections of wild plants, and so far no morphological differentiation has occurred between the cultivars and the wild plants (see Chapter 7). The collection sites of the biotypes are shown in Table 10.1., and Map 1.

Table 10.1 Collection Sites and Experimental Plots.

No	Name	Area	Map Reference	Latitude and Longitude
1.	North Berwick	East Coast	NT 516857	2°.45'W 56°.05'N
2.	Wooler	Cheviots	NT 952223	2°.05'W 55°.30'N
3.	Yetholm	Cheviots	NT 841273	2°.15'W 55°.30'N
4.	West Cheviots	Cheviots	NT 733137	2°.25'W 55°.25'N
5.	Port Patrick	SW coast	NW 999539	5°.05'W 54°.50'N
6.	Lochans	SW lowland	NX 067569	5°.00'W 54°.50'N
7.	8.Dalmelington	SW uplands	NS 426061	4°.30'W 55°.20'N
8.	9.Dalmelington	SW uplands	NS 527089	4°.20'W 55°.20'N
9.	New Cumnock	SW uplands	NS 605127	4°.10'W 55°.25'N
10.	Newburgh	NE coast	NK 004244	2°.00'W 57°.20'N
11.	Braemar	Grampians	NO 145853	3°.25'W 56°.55'N
12.	Tomintoul	Grampians	NJ 303050	3°.10'W 57°.10'N
13.	Aviemore	Grampians	NH 896126	3°.50'W 57°.10'N
14.	Cairngorm	Grampians	NH 992057	3°.40'W 57°.10'N
15.	Fannich	N lowland	NH 213607	5°.00'W 57°.45'N
16.	Stromness	Orkney	HY 257079	3°.15'W 58°.55'N
17.	Quanterness	Orkney	HY 416134	3°.00'W 59°.00'N
18.	Birsay	Orkney	HY 245285	3°.20'W 59°.10'N
19.	Kinlochleven	NW coast	NN 154613	5°.00'W 56°.45'N
20.	Knapdale	W coast	NR 840815	5°.30'W 56°.00'N
21.	West Coast	Barra	NF 652012	7°.30'W 57°.00'N
22.	Airport	Barra	NF 696054	7°.25'W 57°.00'N
23.	Ben Obe	Barra	NF 705024	7°.25'W 57°.00'N
Experimental Plots				
A.	Aberdeen	Banchory	NJ 955736	2°.25'W 57°.05'N
B.	Bush	Edinburgh	NT 244635	3°.10'W 55°.50'N
C.	Sourhope	Cheviots	NT 858204	2°.15'W 55°.30'N
D.	Dalmally	Argyll	NN 175279	4°.55'W 56°.25'N

Distances between Collection Sites

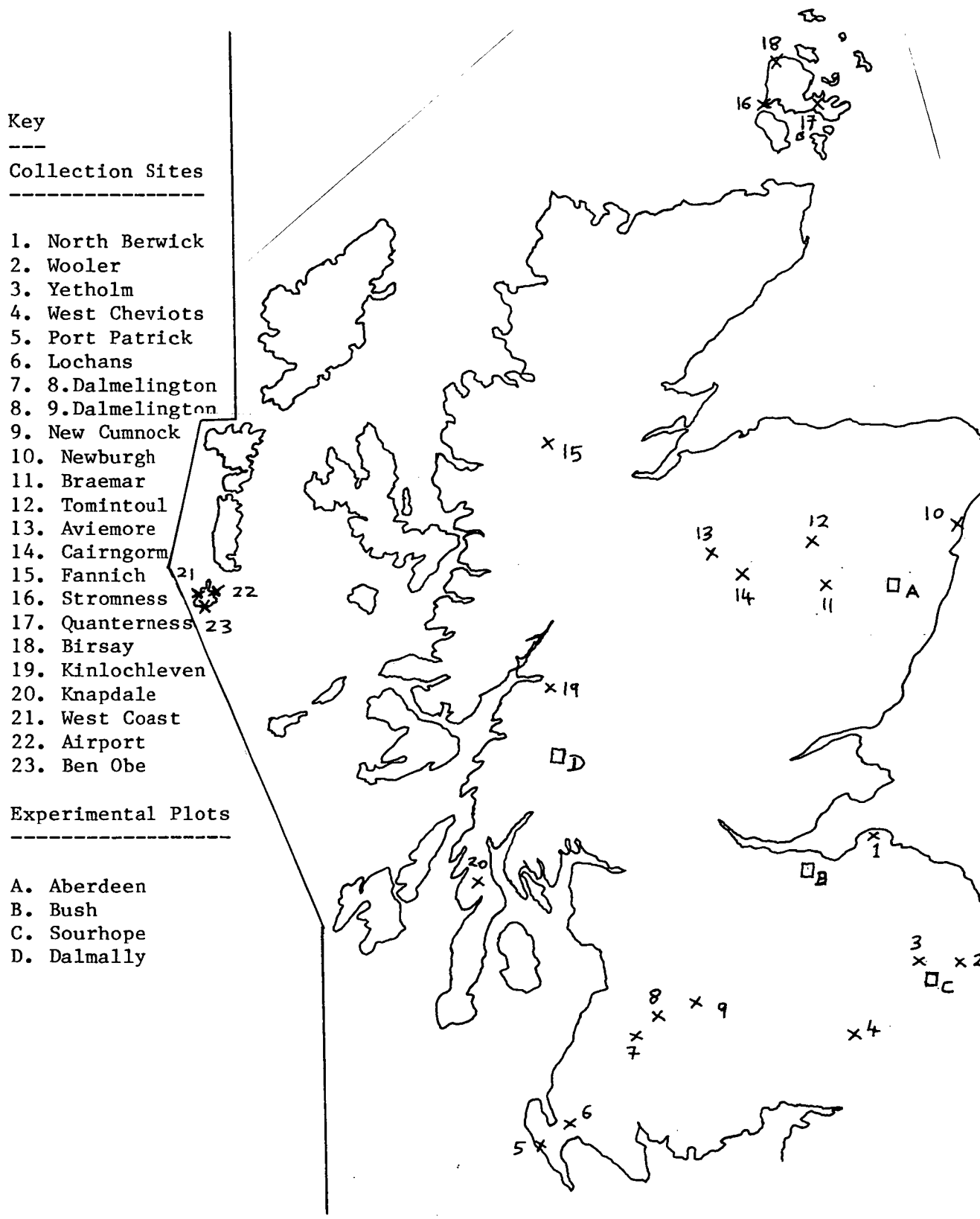
In the majority of cases, distances between collection sites were great enough to minimise the possibility of direct gene exchange between sites. The distance in a straight line between sites 15km or less apart is shown below :

Yetholm - West Cheviots	15km
Aviemore - Cairngorn	13km
Yetholm - Wooler	12km
9 Dalmelington - 8 Dalmelington	10km
9 Dalmelington - New Cumnock	8km
Port Patrick - Lochans	7km
West Coast - Airport	5km
West Coast - Ben Obe	5km
Ben Obe - Airport	4km

Table 10.1.(cont.) Collection Sites and Experimental Plots

No	Name	Area	Altitude	Site
1.	North Berwick	East Coast	5m	On top of wall
2.	Wooler	Cheviots	240m	Edge of pine wood
3.	Yetholm	Cheviots	140m	Bottom of wall near road
4.	West Cheviots	Cheviots	205m	Bank at side of stream
5.	Port Patrick	SW coast	5m	Top of harbour wall
6.	Lochans	SW lowland	40m	Grass on old road
7.	8.Dalmelington	SW uplands	270m	Hillside
8.	9.Dalmelington	SW uplands	340m	Gravel heap by roadside
9.	New Cumnock	SW uplands	190m	Ruined building
10.	Newburgh	NE coast	0m	Sand dunes
11.	Braemar	Grampians	410m	Side of road embankment
12.	Tomintoul	Grampians	530m	Roadside
13.	Aviemore	Grampians	200m	On stones by stream
14.	Cairngorm	Grampians	680m	Mountainside
15.	Fannich	N lowland	120m	On top of old wall
16.	Stromness	Orkney	0m	Drainage ditch by sea
17.	Quanterness	Orkney	15m	Waste ground
18.	Birsay	Orkney	5m	Grassy bank by sea
19.	Kinlochleven	NW coast	40m	Roadside
20.	Knapdale	W coast	50m	Edge of deciduous wood
21.	West Coast	Barra	5m	Rocks by the sea
22.	Airport	Barra	5m	Machair
23.	Ben Obe	Barra	100m	Hillside
Experimental Plots				
A.	Aberdeen	Banchory	50m	Corner of a field
B.	Bush	Edinburgh	190m	Agricultural trial area
C.	Sourhope	Cheviots	285m	Permanent pasture, upland
D.	Dalmally	Argyll	120m	Permanent pasture

Map 1. Collection Sites and Experimental Plots



At each of the collection sites, a circle of turf about 5 cm across was taken, and vegetatively propagated in the greenhouse. Culms that were definitely connected by a rhizome were separated and allocated to the same clonal group; plants that were not definitely connected, but were from the same patch of turf, were placed in different clonal groups, but in the same biotype. The number of clonal groups is therefore a measure of the maximum number of different genotypes present in one biotype, as explained on page 22. Plants in the same clonal group are assumed to be genetically identical.

Four cultivars were used as controls in the experimental plots: the breeder and country of origin of these cultivars are shown below :

Cultivar	Breeder	Origin of Cultivar
Arina-Dasas (Arina)	Dansk Planteforedling A/S	Denmark
Primo	Weibullsholms Vaxtf.	Sweden
Baron	Barenbrug	Holland
Fylking	Sveriges Utsadesforening	Sweden

These cultivars were chosen to reflect the range of different characters available in cultivars on the market. 'Arina' is a dual purpose cultivar, for both amenity and forage use. It has relatively good resistance to rust (Puccinia graminis Pers) and moderate resistance to mildew (Erysiphe graminis DC) [173].

'Primo' is also intended to be used as either an amenity or a forage grass. It has a rapid establishment rate and moderate resistance to mildew, but is very susceptible to 'melting out' (Drechslera poae) and rust [148]. It is reported to have poor

winter hardiness [58], and this is important because several cultivars of Poa pratensis suffer severe winterkill in Scotland [161]. One of the aims of this study is to provide information on the relative hardiness of Scottish biotypes.

'Baron' is a low-growing amenity grass with good winter hardiness [49]. It prefers soils of moderate to low fertility [161], but is apparently intolerant of acid soil [203]. It has good winter colour [148], and is moderately resistant to mildew [204].

'Fylking' is a fairly tall-growing amenity grass, which is winter hardy [49]. It is resistant to 'melting out' and moderately resistant to mildew [204]; resistance to rust is reported to be good [31]. It is tolerant of acid conditions [203].

'Primo', which was released in 1936, is rarely used now in Britain, but the other three cultivars - which were brought out more recently - are frequently sown in Scotland .

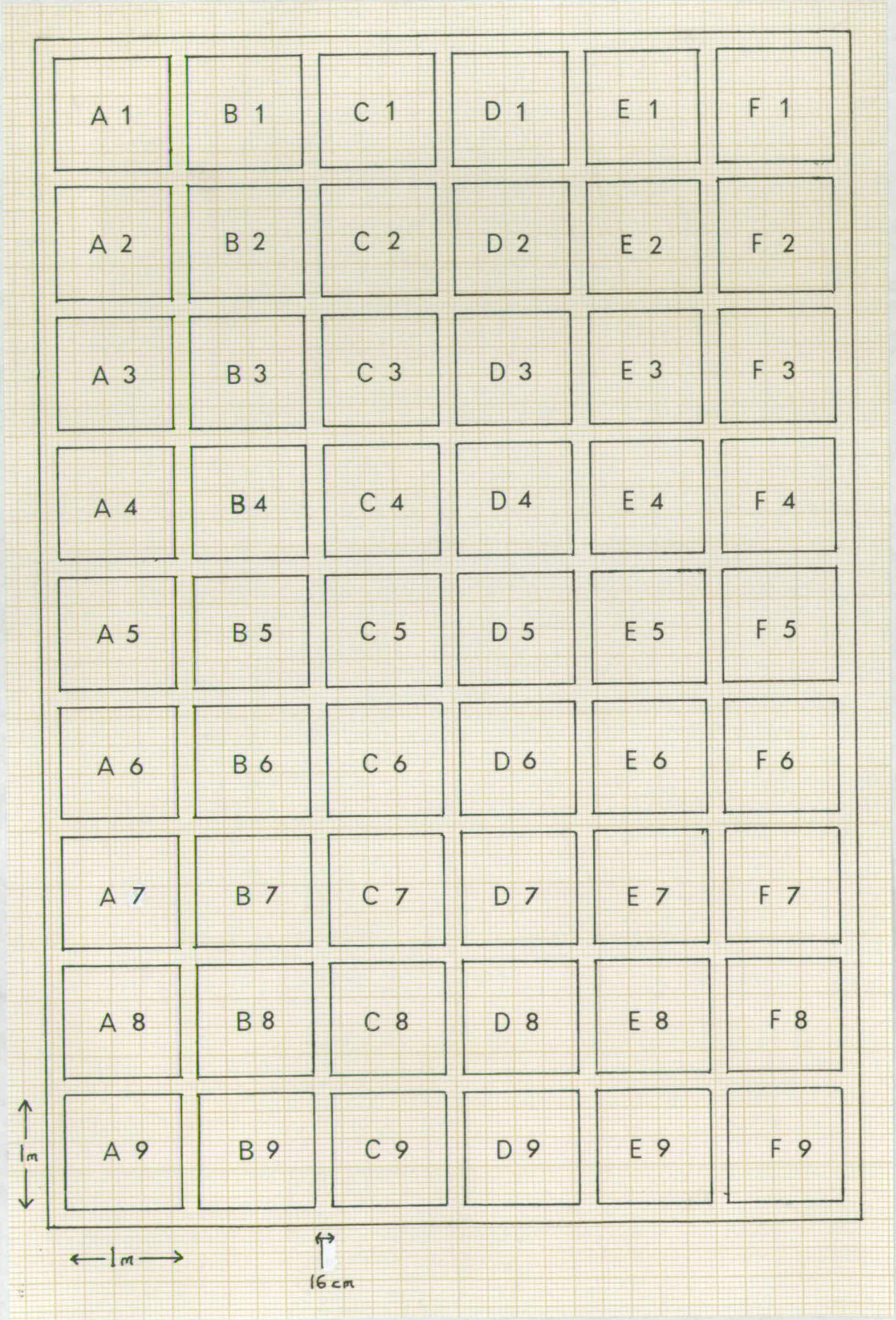
10.2. Experimental Sites

Three main experimental sites were used: Aberdeen, Bush and Sourhope. The location of these is shown in Table 10.1., and Map 1. At each of these sites, an area approximately 11m by 9m was chosen that was as level as possible. At each site, the ground was cleared using 'Paraquat' and then rotavated and hand rolled (Bush and Sourhope), or turned over with a fork and trampled flat (Aberdeen). Initially at Aberdeen, access to the site was around the edge of a field of barley, which prevented the use of any machinery for preparing the site. The barley was harvested soon after the plot

was planted out, making access easier.

At each site, fifty four plots, each of one square metre, were marked out in a rectangular pattern of six rows and nine columns. Between each row and column was a 16cm wide path of bare ground allowing access to each plot. The rows were labelled A to F, and the columns 1 to 9, so that each plot could be identified. The layout of the plots is shown in Figure 10.2.1.

Figure 10.2.1. Arrangement of the Plots at Experimental Sites



In March 1981, soil samples were collected with an auger from each site, and analysed by the Scottish Agricultural Industries laboratory at Sandilands. Access to the site at Aberdeen was restricted at this time, as mentioned before, and so only two soil samples could be taken here; in the other sites seven samples were collected. The results of the soil tests are shown in Table 10.2.1. In each case the sample was taken from the path just outside the plot mentioned, so that subsequent samples could be taken without disturbing the plants growing in the plots.

Table 10.2.1. Initial Soil Analysis at Experimental Plots

Site	Sampled	pH	Soil Phosphate (kg/hectare)	Soil Potassium (kg/hectare)
Aberdeen	A 1	6.8	7.3 (Low)	168 (Medium)
Aberdeen	F 9	6.4	8.4 (Medium)	278 (High)
Bush	A 1	5.8	10.6 (Medium)	385 (Very High)
Bush	A 5	5.8	15.7 (High)	316 (Very High)
Bush	A 9	5.7	10.6 (Medium)	340 (Very High)
Bush	C 5	5.8	12.3 (Medium)	340 (Very High)
Bush	F 1	5.8	10.1 (Medium)	324 (Very High)
Bush	F 5	5.5	12.9 (Medium)	348 (Very High)
Bush	F 9	5.7	12.9 (Medium)	316 (Very High)
Sourhope	A 1	4.8	9.5 (Medium)	340 (Very High)
Sourhope	A 5	4.6	8.4 (Medium)	413 (Very High)
Sourhope	A 9	4.7	8.4 (Medium)	466 (Very High)
Sourhope	C 5	4.5	8.4 (Medium)	242 (High)
Sourhope	F 1	4.7	9.0 (Medium)	348 (Very High)
Sourhope	F 5	4.7	8.4 (Medium)	332 (Very High)
Sourhope	F 9	4.7	8.4 (Medium)	278 (High)

The results in Table 10.2.1. show that pH was highest in the site at Aberdeen, and lowest at Sourhope. The pH at Sourhope was lower than that normally encountered in sites where either amenity or forage grass is grown [148], and so this site was limed with finely ground limestone (2.51 tonnes per hectare), to raise the pH slightly. One of the advantages of liming is that it increases the availability of soil phosphate [205].

There was no indication that soil potassium would limit plant growth in any of the sites, but soil phosphate was low at Aberdeen, and fairly low at Sourhope. All sites were therefore fertilized with a relatively high phosphate fertilizer to remedy this. Plots were fertilized just before planting : 3.37 kg of SAI No 3 fertilizer (N:P:K ratio of 12:24:12) was used on each site. This was an application rate of 50 kg N/ha.

The amount of fertilizer used in grass trials varies widely. In other countries, the rate of nitrogen application may be up to 224 kg/ha [166], 500 kg/ha [206], 672 kg/ha [207] , or even 800 kg/ha [208]. Generally, however, values over 350 kg/ha of nitrogen are not recommended [209]. Domska [210], working with Poa pratensis, found amounts up to 120 kg N/ha to be beneficial. More recently, fertilizer levels of 130 kg N/ha [190], 60 kg N/ha [211], and 44 kg N/ha [33] have been used for Poa pratensis in trials. In this study, six tillers are planted per metre square, and so the ground cover of Poa pratensis is low in the first year. Fairbridge [212] has estimated that a dense sward of Poa pratensis removes about 90 kg N/ha/annum, and so an initial amount in this study of 50 kg N/ha does not seem unreasonable.

Less information is available about the amount of phosphate in the fertilizers used by other workers. Jetne [33], uses 65 kg of phosphate per hectare; high initial phosphate (185 kg/ha) is recommended in swards used for grazing [213]. In this study the initial phosphate level used was 100 kg/ha.

In July 1982, one year after planting, a second series of soil samples was taken. Twelve samples were collected from each site, and showed the following results for pH :

Aberdeen : mean 6.6 (range 6.1 - 6.8)

Bush : mean 5.8 (range 5.4 - 6.3)

Sourhope : mean 5.0 (range 4.5 - 5.5)

The pH at Bush and Aberdeen has remained constant, while at Sourhope it has increased, presumably due to the lime added to the soil.

In July, 1982, the phosphate levels at Bush were all 'Very High', but at Sourhope they had declined to 'Medium' or 'Medium Low'(5 samples), and at Aberdeen to 'Low' or 'Very Low'(3 samples). 'Very Low' represents a value of less than 4.6 kg/ha. This was despite the fact that a high phosphate fertilizer had been used initially in all the sites. As the amount of phosphate at Bush was very high, it was considered inadvisable to use a high phosphate level here for fertilization in the second year, however the phosphate levels at Aberdeen and Sourhope obviously needed replenishing, so the fertilizer given in the summer of 1982 differed between these two groups.

At all three sites, 2.36 kg of SAI 'Triple 17' fertilizer (N:P:K ratio 17:17:17) was used, giving an application rate of 50 kg N/ha. In addition to this, at Aberdeen and Sourhope, 2.76 kg of Superphosphate (18 % soluble phosphate) was used, which provides an extra 60 kg of phosphate per hectare at these two sites.

In April 1983, a final soil sample was taken, again taking twelve samples from each site. The results are summarised in Table 10.2.2.

Table 10.2.2. Final Soil Analysis at Experimental Plots

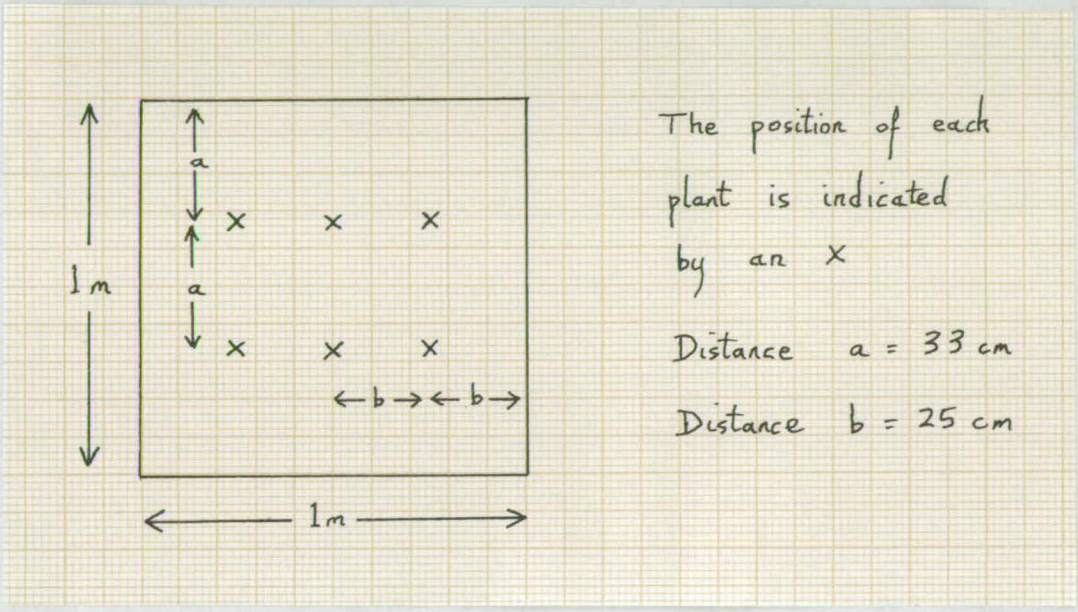
	Aberdeen	Bush	Sourhope
Mean pH	6.3	5.8	5.1
pH Range	5.7 - 6.7	5.6 - 6.0	4.6 - 6.1
Mean phosphate (kg/hectare)	9.5 (Medium)	37.5 (Very High)	18.0 (High)
Phosphate range	7.8 - 12.3	29.1 - 50.4	10.1 - 26.9

This shows that over the second year, the soil at Bush and Sourhope remained at about the same pH, but at Aberdeen the pH fell slightly, possibly due to the relative acidity of the rain. Rain acidity measured at Banchory showed a mean pH of 4.2 [214]. The phosphate levels at Aberdeen and Sourhope have risen over the year, presumably in response to the additional phosphate fertilizer used at these sites.

The sites were planted between 19th and 23rd July 1981 with six tillers per metre square plot. In each plot, tillers were planted in three

rows of two columns each. The rows were at 25cm, 50cm and 75cm from the edge of the plot, and the columns at 33cm and 66cm from the adjacent edge. This is illustrated in Figure 10.2.2. for plot A1, the other plots were all planted in an identical manner.

Figure 10.2.2. Arrangement of tillers within each plot



At each site, rows A to C contained one plot of each biotype, and rows D to F contained a replicate plot of each biotype. Biotypes were assigned to plots using random number tables, and rows A to C had a different randomisation than rows D to F (see Figure 10.2.1.). All three sites were also randomised independently of each other.

As far as possible, replicate plots of the same biotype were planted with an identical mixture of clonal groups, both within and between plots. Also within each biotype the number of different clonal groups planted was minimised. The actual clonal groups planted at each site are shown in Table 10.2.3.

Table 10.2.3. Clonal groups planted at each site

The clonal group is prefixed by the letter C, and the number of tillers of that clonal group planted is shown in brackets. For example, 'C2(4)' means four tillers of clonal group number 2. Cultivars are indicated with asterisks.
G = Number of different Clonal Groups planted
T = Total number of Tillers planted

Aberdeen

Biotype	Clonal Groups Planted	G	T
North Berwick	C1(3), C4(9)	2	12
Wooler	C1(4), C5(3), C6(3), C7(2)	4	12
Yetholm	C2(5), C3(5), C13(2)	3	12
West Cheviots	C1(4), C2(3), C4(1), C7(4)	4	12
Port Patrick	C1(12)	1	12
Lochans	C1(3), C2(3), C3(3), C4(3)	4	12
8 Dalmelington	C1(3), C2(2), C5(2), C7(3), C10(2)	5	12
9 Dalmelington	C1(2), C2(2), C4(2), C6(6)	4	12
New Cumnock	C2(5), C11(3), C12(4)	3	12
Braemar	C3(4), C4(4), C11(2), C13(2)	4	12
Newburgh	C1(2), C3(4), C4(2), C7(4)	4	12
Tomintoul	C4(2), C5(3), C9(2), C10(2), C11(3)	5	12
Cairngorm	C1(6), C2(6)	2	12
Aviemore	C1(12)	1	12
Fannich	C1(3), C2(6), C3(3)	3	12
Birsay	C1(5), C2(2), C3(2), C9(3)	4	12
Quanterness	C5(3), C6(6), C10(3)	3	12
Stromness	C1(4), C3(4), C8(4)	3	12
Kinlochleven	C2(12)	1	12
Knapdale	C6(2), C9(2), C11(2), C12(4), C17(2)	5	12
West Coast	C1(3), C2(1), C4(1), C5(2), C6(1),C10(4)	6	12
Airport	C1(3), C2(3), C3(4), C4(2)	4	12
Ben Obe	C1(6), C2(3), C4(3)	3	12
Primo *	C1(5), C2(4), C3(3)	3	12
Fylking *	C1(6), C2(6)	2	12
Baron *	C1(4), C3(5), C5(3)	3	12
Arina *	C1(5), C2(3), C3(4)	3	12

Bush

The same clonal groups, and number of tillers were used as at Aberdeen, with the following exceptions :

8 Dalmelington - C9(5) was used instead of C1(3) and C5(2)

Newburgh - C6(4) was used instead of C3(4)

Tomintoul - C6(3) was used instead of C5(3)

West Coast - C7(2) was used instead of C5(2)

Table 10.2.3.(cont.) Clonal Groups planted at each site

Sourhope

The same clonal groups, and number of tillers were used as at Bush, with the following exceptions :

Lochans	-	C1(2), C2(4), C4(2) were used instead of C1(3), C2(3), C4(3); also C5(4) was used instead of C3(3)
8 Dalmelington	-	C3(2) used instead of C2(2); C6(5) used for C9(5); C8(2) used for C10(2)
9 Dalmelington	-	C3(2) was used instead of C2(2)
New Cumnock	-	C14(4) was used instead of C12(4)
Newburgh	-	C5(2) was used instead of C4(2)
Tomintoul	-	C3(3) was used instead of C5(3); C12(2) was used for C9(2)
West Coast	-	C3(2) was used instead of C2(1) and C4(1)

Table 10.2.3 shows that of the total number of tillers planted at Bush and Sourhope, 92 % are genetically identical to those at Aberdeen. The majority of those that differ are clonal substitutions - one clonal group is used instead of another; 97 % of the plots at Bush and Sourhope have the same number of clonal groups for each biotype as at Aberdeen.

The biotype 'Ben Obe' only tillered slowly in the greenhouse, so not enough material of this biotype was available for planting in all three sites in July 1981. Consequently, at Aberdeen, no 'Ben Obe' was planted in the first year - the two plots were left empty. This biotype was however planted at the same time as the other biotypes at Bush and Sourhope. 'Ben Obe' was planted at Aberdeen in July,1982 , and so at the end of the experiment in July

1983, this biotype had only been growing here for one year, whereas the other biotypes had been growing for two years. In order to compensate for this, the average value for the other 26 biotypes for a particular character such as ground cover at Aberdeen after one year (from July 1981 to July 1982) was calculated (V1), and the value for the same biotypes after two years (from July 1981 to July 1983) was also calculated (V2). The quantitative results (dry matter production and ground cover) for 'Ben Obe' for a single year (July 1982 to July 1983) were then multiplied by the correction factor: (V2/V1), to give an estimate of the results for 'Ben Obe' if it had had the same growing period as the other biotypes. At the other two sites, 'Ben Obe' was in the plots for exactly the same length of time as the other biotypes, so no correction was necessary.

Only six tillers of the biotype 'New Cumnock' were available for planting at Sourhope, because of losses during transport, so only one of the two plots for 'New Cumnock' was planted in July 1981. However six replacement tillers of this biotype, of the correct clonal groups, were planted in March 1982, and as both the dry matter production and ground cover of all the biotypes planted earlier had been very low up to this time (see Figures 11.4.3 and 11.5.2.), no correction was deemed necessary.

The arrangement of the biotypes within each site is shown in Table 10.2.4.

Table 10.2.4. Randomisation of Biotypes at each Site

Biotype	Abbreviation	Biotype	Abbreviation
North Berwick	N.Ber	Fannich	Fannich
Wooler	Wooler	Birsay	Birsay
Yetholm	Yetholm	Quanterness	Quant
West Cheviots	W.Chev	Stromness	Strom
Port Patrick	Port P	Kinlochleven	Kinloch
Lochans	Lochans	Knapdale	Knap
8.Dalmelington	8 Dal	West Coast	W.Coast
9.Dalmelington	9 Dal	Airport	Airport
New Cumnock	Cumnock	Ben Obe	Ben Obe
Braemar	Braemar	Primo	Primo
Newburgh	Newbur	Fylking	Fylking
Tomintoul	Tomin	Baron	Baron
Cairngorm	Cairn	Arina	Arina
Aviemore	Avie		

ABERDEEN

Column	Row A	B	C	D	E	F
1	Avie	W.Coast	W.Chev	Tomin	Strom	Knap
2	Kinloch	Strom	Cumnock	Quant	Newbur	Avie
3	Baron	Airport	Fannich	8 Dal	Cumnock	Ben Obe
4	9 Dal	8 Dal	Birsay	Fylking	W.Coast	Wooler
5	Tomin	Newbur	Knap	Arina	W.Chev	Airport
6	Port P	Primo	Wooler	Kinloch	Cairn	Baron
7	N.Ber	Lochans	Quant	Yetholm	Port P	N.Ber
8	Braemar	Ben Obe	Cairn	Primo	Fannich	9 Dal
9	Arina	Yetholm	Fylking	Birsay	Lochans	Braemar

Table 10.2.4.(cont.) Randomisation of biotypes

BUSH

Column	A	B	C	D	E	F
	Row					
1	Birsay	9 Dal	Arina	Strom	Quant	Avie
2	Strom	Yetholm	Kinloch	Lochans	W.Coast	Yetholm
3	Fannich	Cairn	Knap	Baron	Port P	Arina
4	Primo	Airport	Wooler	Tomin	Fannich	Fylking
5	Ben Obe	Lochans	Newbur	Cairn	Newbur	Knap
6	N.Ber	Braemar	Baron	Primo	Braemar	Ben Obe
7	8 Dal	Quant	Fylking	Kinloch	Wooler	Birsay
8	W.Chev	Port P	W.Coast	W.Chev	N.Ber	9 Dal
9	Avie	Cumnock	Tomin	Airport	8 Dal	Cumnock

SOURHOPE

Column	A	B	C	D	E	F
	Row					
1	Kinloch	Lochans	W.Coast	Baron	Braemar	Strom
2	Newbur	Tomin	Primo	Port P	Fannich	Wooler
3	Yetholm	Arina	Port P	Newbur	Tomin	Knap
4	Wooler	W.Chev	Cairn	Cairn	Primo	Airport
5	Braemar	Ben Obe	Avie	W.Coast	N.Ber	Cumnock
6	N.Ber	Airport	Baron	Lochans	Ben Obe	Quant
7	Fylking	Quant	9 Dal	8 Dal	Kinloch	Avie
8	Cumnock	Knap	Fannich	9 Dal	Arina	Yetholm
9	Strom	8 Dal	Birsay	Birsay	W.Chev	Fylking

The sites were all surrounded by 1m high rabbit fencing, buried 15cm deep, to exclude rabbits and hares.

Results were collected from the plots at approximately fortnightly intervals during the summer, and less frequently over the winter. The dates of visits to the plots are shown in Table 10.4. The parameters recorded at each visit are discussed below.

10.3. Plant Survival

This is the number of plants with green leaves in each 1m square plot (maximum number 6). This is not necessarily the actual number of plants alive, since especially over winter some plants showed complete die back of leaves, but new shoots appeared in spring from the same plants. Therefore the 'Plant Survival' values will rise without any replanting. Also, plants that have died may retain green leaves for several days, which may result in a temporary overestimation of plant survival.

10.4. Dry Matter Production

The plots were cut using hand shears. These shears had a metal stand attached to the lower blade, so that when the stand was on the ground, the blades were level, and the cutting edge 2.5cm above the ground. This is about the middle of the range of cutting heights used for amenity grasses [161]. The cuttings (growth above 2.5cm) were collected into labelled polythene bags, and dried on trays in an oven at 80 degrees centigrade for 5 days; this is the normal temperature used for drying plant material [144]. After drying, the cuttings were allowed to equilibrate in air at room

temperature for an hour before weighing; air drying has been found to give accurate estimates of dry weight in other species [215].

In most cases, it was possible initially to cut all 54 plots at each site on the same day, but as the plants grew, cutting usually took two days. Whenever possible, rows A to C were cut on one day, and rows D to F the next day; this meant that all 27 plots in each replicate were cut on the same day. The number of days since the plants were last cut, and the date of each visit to the sites is shown in Table 10.4.

Table 10.4. Dates on which the plants were cut

BUSH

Date	Visit number	Days since the last cut, Row: A	B	C	D	E	F
30.11.81	1	0	0	0	0	0	0
02.02.82	2	64	64	64	64	64	64
22.02.82	3	20	20	20	21	21	21
08.03.82	4	14	14	14	14	14	14
22.03.82	5	14	14	14	14	14	14
05.04.82	6	14	14	14	14	14	14
03.05.82	7	28	29	29	38	38	38
17.05.82	8	14	13	13	4	4	4
31.05.82	9	14	14	15	14	15	15
14.06.82	10	14	14	14	14	13	14
30.06.82	11	17	16	15	16	17	16
13.07.82	12	12	13	13	12	12	12
26.07.82	13	13	13	14	14	13	13
16.08.82	14	21	21	20	21	21	21
06.09.82	15	21	21	21	21	21	21
02.03.83	16	177	177	177	177	177	177
11.04.83	17	39	39	40	39	39	39
03.05.83	18	22	22	22	22	24	24
23.05.83	19	20	20	19	19	18	18
13.06.83	20	21	21	22	22	21	22
27.06.83	21	14	14	13	14	14	14

Table 10.4.(cont.). Dates on which the plants were cut

ABERDEEN

Date	Visit number	Days since the last cut, Row : A	B	C	D	E	F
18.11.81	1	0	0	0	0	0	0
02.12.81	2	14	14	14	14	15	15
10.02.82	3	70	70	70	70	69	69
24.02.82	4	14	14	14	14	14	14
11.03.82	5	15	15	15	15	15	15
24.03.82	6	13	13	13	13	13	13
07.04.82	7	14	14	14	15	15	15
05.05.82	8	28	28	28	28	28	28
21.05.82	9	16	16	16	15	16	16
03.07.82	10	43	44	44	51	50	50
15.07.82	11	12	11	11	4	5	5
28.07.82	12	13	13	13	14	13	13
19.08.82	13	22	22	22	21	22	22
09.09.82	14	21	21	21	22	22	22
16.02.83	15	160	160	160	160	160	160
08.04.83	16	51	51	51	51	51	51
30.04.83	17	22	22	22	22	22	22
21.05.83	18	21	21	22	21	21	21
11.06.83	19	21	21	20	20	21	21
05.07.83	20	24	24	24	24	24	24

SOURHOPE

Date	Visit Number	Days since the last cut ; Row : A	B	C	D	E	F
24.11.81	1	0	0	0	0	0	0
09.12.81	2	15	15	15	15	15	15
20.01.82	3	42	42	42	42	42	42
03.02.82	4	14	14	14	14	14	14
17.02.82	5	14	14	14	14	14	14
17.03.82	6	28	28	28	28	28	28
30.03.82	7	13	13	13	14	14	14
28.04.82	8	29	29	29	28	29	29
11.05.82	9	13	13	13	14	13	13
25.05.82	10	14	14	16	15	15	15
08.06.82	11	14	14	13	13	13	24
25.06.82	12	17	17	17	17	17	6
08.07.82	13	13	13	12	13	13	13
22.07.82	14	14	14	14	14	14	14
14.08.82	15	21	21	21	21	21	21
31.08.82	16	17	17	17	17	17	17
27.04.83	17	149	149	149	149	149	149
05.04.83	18	68	68	68	68	68	68
27.04.83	19	22	22	22	21	22	22
13.05.83	20	16	16	16	16	16	16
06.06.83	21	24	24	24	24	24	24
22.06.83	22	15	15	15	15	15	15

10.5. Ground Cover.

A rigid , square metal frame, of internal area 1m square with 10 metal pegs at 10cm intervals along each side was constructed, and thin orange thread was tied to each metal peg across the centre of the frame. A lattice of thread was thereby produced of 10 lines intersecting at 90 degrees with another 10, forming a regular 100 point quadrat with points 10cm apart. As the lattice was over both the top and the bottom of the frame, each lower point had a point a few centimetres above it, enabling a vertical line to be taken through both points.

The lowest part of the frame was raised over 3 cm above the ground by four legs, and therefore once the grass had been cut, the quadrat could be laid over each plot and the percentage ground cover estimated by the number of points exactly over the plants. Only green leaf tissue was scored, dead or senescent leaf and leaf litter were ignored.

The arrangement of the points into a regular frame makes the method less accurate than individual random points [169], however for practical purposes an equal distribution of points is normally used [216] ;the main advantage being rapidity of ground cover estimation. Using a frame of 10 points set at 10 random orientations (100 points / plot), takes about 26 hours to estimate 54 plots [169], but in a frame of 100 points, this can be done in about 2 hours.

The diameter of the point used in a quadrat is very important : increasing the diameter of the point exaggerates ground cover, especially for grasses [217]. The use of thread, rather than the usual pins, has resulted in a reduction of the point diameter from 0.79 mm square [216] to about 0.1mm square.

10.6. Disease

Poa pratensis is susceptible to a large number of diseases, of which the fungal infections causing mildew, stem rust, 'melting out' and yellow leaf rust are reportedly the most important [46]. In this study, no yellow leaf rust developed, but infection with the other three diseases occurred at all three sites. Snow mould, caused by Fusarium nivale (Fr) Snyder and Hansen, which is an important disease of Poa pratensis in Canada [174], and contributes to winterkill of Lolium perenne in Europe [217], did not affect the plants in this study.

Erysiphe graminis DC, which is the pathogenic fungus that causes mildew, is an ascomycete. Initial infection is usually by wind borne conidia. The mycelium is not systemic in the host, but secondary conidia produced on the leaf surface can rapidly spread the disease to neighbouring leaves and plants [149]. The symptoms of mildew infection are areas of white mycelium visible on the leaf surface, which are eventually surrounded by large chlorotic lesions. Optimum conditions for the disease are low light intensities, reduced air circulation, high humidity and temperatures of around 10 to 15 degrees centigrade [149].

Stem rust is caused by Puccinia graminis Pers, which is a basidiomycete. The spores, which are wind dispersed, can infect plants several kilometeres away [218]. Infection results in the appearance of small yellow lesions on the leaves, which enlarge and run parallel to the leaf veins. Finally the cuticle and epidermis rupture, and the lesions develop into large pustules. The urediospores are a characteristic golden-brown colour [149]. Optimum disease conditions are reported to be low light intensities, high humidity and temperatures of 21 - 23 degrees Centigrade [149].

'Melting out' is caused by the ascomycete, Drechslera poae (Baudys.) Shoem. [syn. Helminthosporium vagans Drechs.] [161]. Light infection results in 'leaf spot', and severe infection causes 'melting out' which can kill large areas of turf [161]. The disease is normally spread from plant to plant by conidia in splashing water [149]. The disease symptoms are brown necrotic lesions with dark purple margins which spread over the leaf and sheath, resulting eventually in the browning of large areas of turf, and leaves dropping from the plants. The susceptibility of Poa pratensis to 'melting out' is a major impediment to sucessful cultivar development [219].

Disease incidence was scored in the field, and a rapid system of recording was required, so the scale below was used:

0 - no disease

1 - few lesions on 1 or 2 plants

2 - few lesions on 3 - 6 plants

3 - about 10 % of leaves infected, on 1 or 2 plants

4 - about 10 % of leaves infected, on 3 - 6 plants

5 - about 30 % of leaves infected, on 1 or 2 plants

6 - about 30 % of leaves infected, on 3 - 6 plants

7 - over 50 % of leaves infected, on 1 or 2 plants

8 - over 50 % of leaves infected, on 3 - 6 plants

For categories 3,5, and 7 , where the score was based on one or two plants, it was assumed that the other plants in the plot would be in the category immediately below. For example, if 2 plants had 30 % of their leaves infected, scoring the plot as '5' implies that most of the remaining plants had about 10 % of leaves infected. If none of the other plants were infected, then the score would be reduced to '3'. This method of scoring was chosen, because in many of the plots there was a mixture of 3 or 4 different clones of each biotype, and if only one of these was susceptible, it would give a much higher value to the biotype as a whole than was warranted. In the event, disease incidence was very uniform within each plot in most cases.

10.7. Colour

Initial trials comparing the leaf colour of plants to British Horticultural Society Colour Charts were unsuccessful, mainly because in each plant there is a wide range of colours. Also the proportion of green leaf to dead leaf varied from plot to plot, and so a plant with a good green colour - which would score well on a colour chart test - may have a lot of yellow or brown leaves,

which make it unsuitable as an amenity grass. Therefore the colour was measured on a 1 - 8 scale, representing the approximate amount of green leaf :

1 - very low proportion (25 %) of green leaf to total leaf, 3 - 6 plants

2 - very low proportion (25 %) of green leaf to total leaf, 1 or 2 plants

3 - low proportion (50 %) of green leaf to total leaf, 3 - 6 plants

4 - low proportion (50 %) of green leaf to total leaf, 1 or 2 plants

5 - several non-green areas of leaf (25 % of total), 3 - 6 plants

6 - several non-green areas of leaf (25 % of total), 1 or 2 plants

7 - few non-green areas of leaf, 1 or more plants

8 - all leaves green

In addition to this, any striking colour characters, such as light green or dark green leaves, were noted.

10.8. Flowering

The number of plants in each plot (maximum number 6) with panicles emerged, and with anthers dehisced were recorded.

All the results from the experimental plots were stored in the EMAS 2972 computer, and programs were written in Fortran to print the data in a suitable format. Data on Dry Matter Production

were multiplied by :

{ 6 divided by the plant survival (maximum 6) for that plot}

to allow for any plants that had died. The computer program then divided the dry matter production for each plot by the number of days since the plots were last cut, to produce a result in mg/plot/day. Data on Ground Cover were calculated to allow for any missing plants. Other data were printed out directly. In all cases the data were printed out both in the randomised plot layout - for checking against the original data - and also with the results tabulated for each biotype.

10.9. Meteorological Conditions

Any meteorological data collected at the experimental plots covers a long period, due to the infrequency of visits to the sites. At meteorological stations, data is recorded daily, and this will give a much more accurate idea of the climate in the experimental sites, as long as the conditions at the meteorological stations are similar to those at the plots.

A maximum/minimum thermometer and raingauge were placed in each site from August 1982, to enable the meteorological conditions in the experimental sites to be compared with those from the nearest meteorological station. The distance from each site to the nearest meteorological station is shown in Table 10.9.1.

Table 10.9.1. Distances from experimental sites to meteorological stations.

Experimental Site	Meteorological Station	Distance
Aberdeen	Finzean	7 km
Bush	Bush	0.3 km
Sourhope	Redesdale	22 km

At each site, the raingauge was set in the centre of the experimental area, at the corner of plots C4, C5, D4, and D5 (see diagram on page 109). The thermometer was attached to a fencepost on the edge of the site, approximately 1m above the ground. The thermometer was contained within a plastic tube with a metal shield over the top to prevent direct exposure to sunlight. At meteorological stations, thermometers are kept in slatted wooden containers, 1.25m above the ground.

At meteorological stations, the following temperatures are recorded : 'maximum air' and 'minimum air' temperatures are the highest and lowest daily temperatures recorded inside a slatted wooden box. The 'grass minimum' temperature is the lowest daily temperature recorded over a surface of short grass by an exposed thermometer, the bulb of which is 3cm above the ground, and in contact with the tips of the blades of grass. The 'grass minimum' is therefore a much more accurate measure of the minimum temperature to which grass is exposed than the 'minimum air' temperature.

The results for rainfall recorded at the experimental sites were very similar to those from the meteorological stations,

but the temperature data were often different. The maximum and minimum temperatures were recorded when the plots were visited, at approximately three weekly intervals (see Table 10.4.). The highest maximum and lowest 'grass minimum' temperatures over the same period were obtained from records from the nearest meteorological stations. Temperature is recorded daily at meteorological stations.

The mean correlation between the minimum temperature recorded at the plots and at the nearest meteorological station was 0.91, but for maximum temperatures, the correlation coefficient was only 0.56. The temperatures recorded at the experimental sites were usually higher than that at the meteorological stations. The mean temperature differences are shown in Table 10.9.2.

Table 10.9.2. Mean difference between the temperature recorded at the experimental sites and that recorded at the meteorological stations.

Values given are the mean temperature in ^{o}C recorded at the experimental sites minus the mean temperature recorded at the nearest meteorological station.

	Experimental Sites		
	Aberdeen	Bush	Sourhope
Maximum temperature	+ 3.2	+ 9.9	+ 7.0
Minimum temperature	+ 0.6	+ 5.0	+ 0.6

Table 10.9.2. shows that the maximum temperatures recorded are considerably higher than those at meteorological stations, especially at Bush. This is surprising, as the site at Bush was only about 300m from the meteorological station (see Table

10.9.1.). Part of this difference may be due to the relatively few records made at the plots; none of the sites was visited more than eight times after the beginning of August, 1982, when the thermometers were placed in the sites. A daily record of maximum and minimum temperatures was recorded at the site at Bush between 21st November and 4th December, 1982, to enable a more accurate comparison of temperatures with the daily meteorological records at Bush. Again, the results for minimum temperature were very similar (mean difference $0.4^{o}C$, correlation coefficient 0.67, $p<0.01$), but there was greater variation in maximum temperature results (mean difference $2.7^{o}C$, correlation coefficient 0.57, $p<0.05$). The results for maximum temperature, and the number of hours of sunshine recorded at Bush meteorological station for this period are shown in Table 10.9.3.

Table 10.9.3. Meteorological data from Bush

E = Maximum temperature recorded daily at the experimental site (^{o}C)

M = Maximum temperature recorded daily at Bush meteorological station

D = Difference in recorded temperature (E - M) in ^{o}C.

S = Hours of sunshine per day

Date	E	M	D	S
21st November	12	9.9	+2.1	0
22nd November	7	7.1	-0.1	0
23rd November	4	2.9	+1.1	0
24th November	8	3.6	+4.4	1.8
25th November	10	5.3	+4.7	4.5
26th November	11	3.9	+7.1	3.9
27th November	8	4.9	+3.1	0.8
28th November	5	4.7	+0.3	0.2
29th November	10	6.4	+3.6	2.0
30th November	9	7.9	+1.1	0.6
1st December	11	5.5	+5.5	5.2
2nd December	5	2.1	+2.9	0
3rd December	7	4.6	+2.4	0
4th December	8	7.6	+0.4	0

The discrepancy between the temperature recorded at the experimental site and at the meteorological station varies greatly from day to day. Part of the difference is due to the different accuracies of the thermometers. The thermometer used at the experimental site was only accurate to the nearest degree, whereas the meteorological station records the temperature to the nearest tenth of a degree. So if the maximum temperature at the experimental site on 4th December was in fact 7.6^{o}C, it would be recorded as 8^{o}C, resulting in an apparent difference of 0.4^{o}C.

A more important source of error could be due to sunshine. At meteorological stations, the maximum and minimum temperatures are recorded inside a slatted wooden screen, whereas

the 'grass minimum' thermometer is directly exposed. The thermometers in the sites were protected from direct sunlight by being positioned inside a plastic tube with a metal shield over the top. The insulating properties of this will be different from a meteorological screen, and so it is possible that although sunlight could not fall directly upon the thermometer, it could heat the tube around it sufficiently to affect the recorded temperature. Evidence for this is obtained from the data in Table 10.9.3. For the six days with no sunshine, the mean difference in maximum temperature recorded at the experimental site and at the meteorological station was 1.5°C, but on the eight sunny days, the mean difference was 3.7°C. Further, on the days with less than one hour of sunshine, the difference in temperature recorded was always less than the difference on the days with more than one hour. The values for the temperature difference and the number of hours of sunshine are significantly correlated ($r = 0.84$, $p<0.01$). The relatively high values recorded for maximum temperature at the experimental site were therefore probably due to sunshine warming the thermometer, rather than any actual temperature difference.

More evidence that the maximum/minimum thermometers in the experimental sites were less well insulated than those used at meteorological stations comes from the results for minimum temperature. Generally, the results correlated better with the 'grass minimum' temperature rather than the 'minimum air' temperature recorded at the meteorological stations. For example at Aberdeen, the correlation coefficient between the minimum temperature recorded at the experimental site, and the 'minimum air' temperature recorded at Finzean was 0.90, but the correlation with

'grass minimum' temperature was 0.98. The thermometer at meteorological stations recording 'grass minimum' temperature is directly exposed, whereas the 'minimum air' temperature is recorded inside a wooden screen. Thus 'grass minimum' temperatures are usually lower than 'minimum air' temperatures. The higher correlation with 'grass minimum' temperature shows that the thermometers at the experimental sites were less well insulated than those inside meteorological screens. For the purposes of this study, the 'grass minimum' temperature is more important than the 'minimum air' temperature, as it gives a much more accurate idea of the temperature to which grass is actually exposed. The higher correlation of the minimum temperature in the experimental plots with 'grass minimum' rather than 'minimum air' temperature is therefore very useful.

On the whole therefore, there is no evidence that the meteorological conditions at the experimental sites were significantly different from those at the nearest meteorological station. Any apparent difference is largely due to the different insulating properties of the material surrounding the thermometers. Data from the nearest meteorological station is therefore assumed to give a reasonably accurate view of conditions in the experimental sites. The results from the meteorological stations for the two years over which which the experimental sites were used (August 1981 to July 1983) are discussed below.

The mean results for 'maximum air' temperature and 'minimum grass' temperature at the meteorological stations are shown in Figures 10.9.1. and 10.9.2.

Figure 10.9.1. Maximum air temperature.

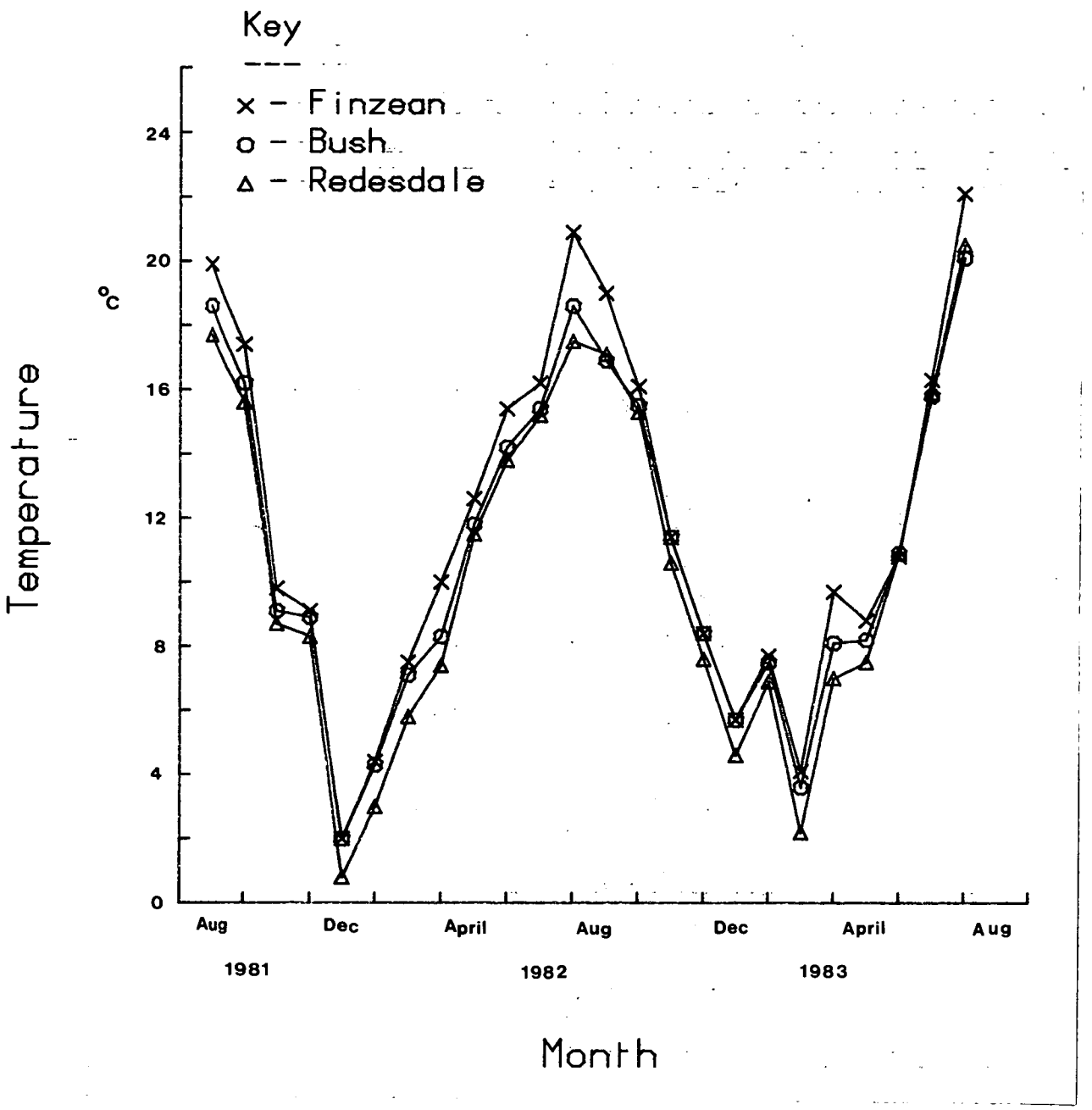
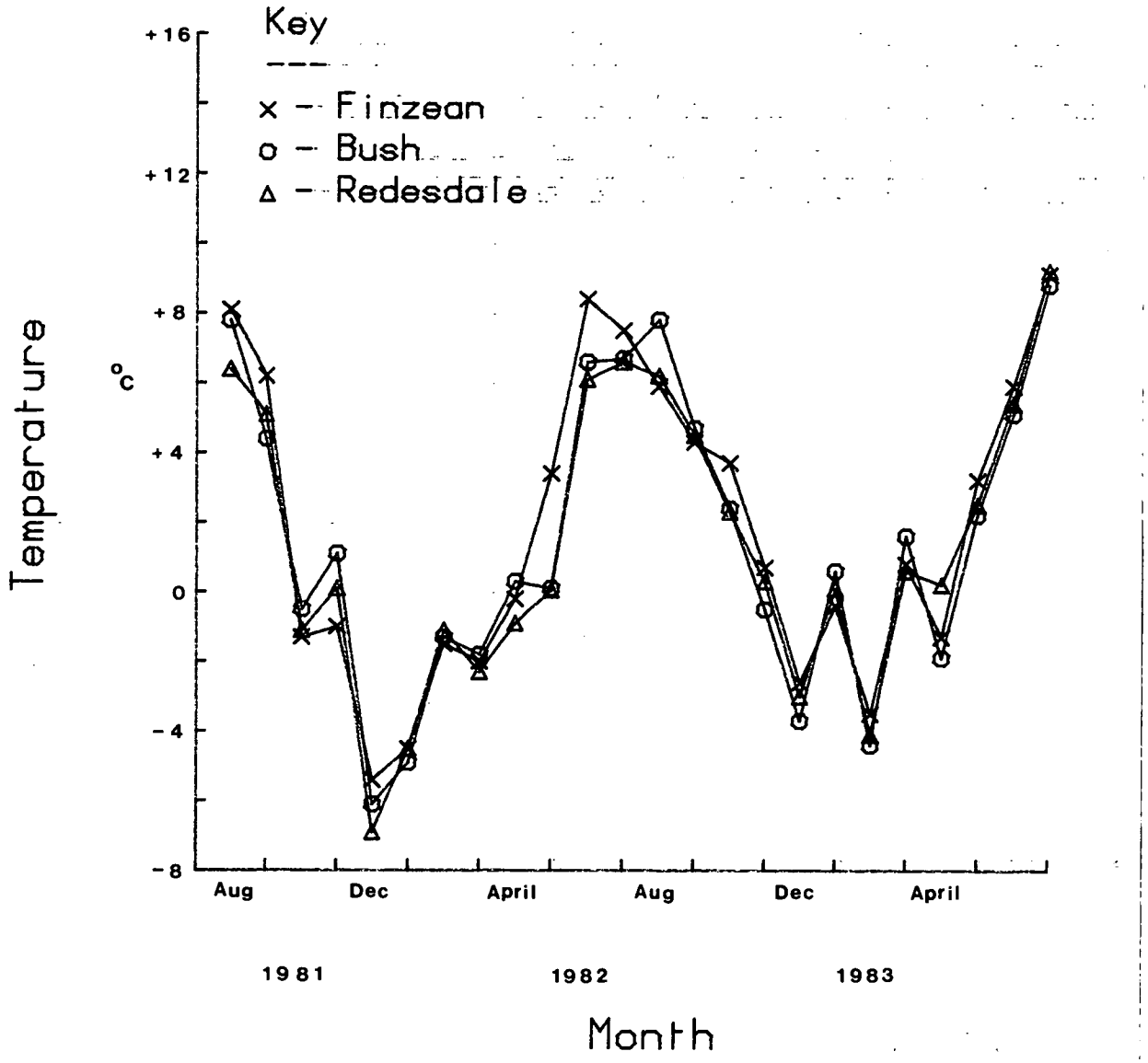


Figure 10.9.2. Minimum grass temperature.



The temperature was fairly similar at all three sites. The winter of 1981/82 was more severe than that of 1982/83, with

lowest mean temperatures recorded in December 1981. In contrast, lowest mean temperatures in 1983 were recorded in February. The temperature at Finzean was generally higher than at the other sites during the summer. Maximum temperatures over winter at Redesdale were lower than at the other sites.

Although the mean values were fairly similar, the fluctuations in temperature were generally highest at Finzean and lowest at Redesdale. The highest maximum and lowest 'grass minimum' temperatures recorded at the three meteorological stations over the period when the experimental plots were used are shown in Table 10.9.4.

Table 10.9.4. Temperature extremes recorded at meteorological stations

H = Highest maximum temperature in ^{o}C.

L = Lowest 'grass minimum' temperature in ^{o}C

F = Total temperature fluctuation (H + L) in ^{o}C.

Site	H	L	F
Finzean	28.5	-23.5	52.2
Bush	26.4	-25.5	51.9
Redesdale	25.3	-19.7	45.0

Finzean has the greatest temperature fluctuation (Table 10.9.4.), and this suggests that the climate here is more continental, compared to the more maritime climate at Redesdale.

There were also differences between the sites in the number of days of frost. In the winter of 1982/83, Finzean had 90 days where the air temperature was below $0^{o}C$, Redesdale had 86 days of frost and Bush had only 59 days.

The total rainfall over the two year period was fairly

similar in all three sites: the difference in total rainfall between the sites is less than the fluctuation at each site from year to year. This is shown in Table 10.9.5.

Table 10.9.5. Rainfall recorded at the meteorological stations

The '1st Year' is from 1st August, 1981 to 31st July, 1982
The '2nd Year' is from 1st August, 1982 to 31st July, 1983

Site	1st Year	2nd Year	Total
Finzean	791 mm	1110 mm	1.84 m
Bush	951 mm	1056 mm	2.01 m
Redesdale	864 mm	958 mm	1.82 m

At both Bush and Redesdale, the rainfall in the second year was about 11% higher than in the first year. At Finzean, however, the rainfall was 40% higher in the second year. Figures. 10.9.3. and 10.9.4. show the monthly distribution of the rainfall at the three meteorological sites.

Figure 10.9.3. Monthly Rainfall at Finzean and Bush

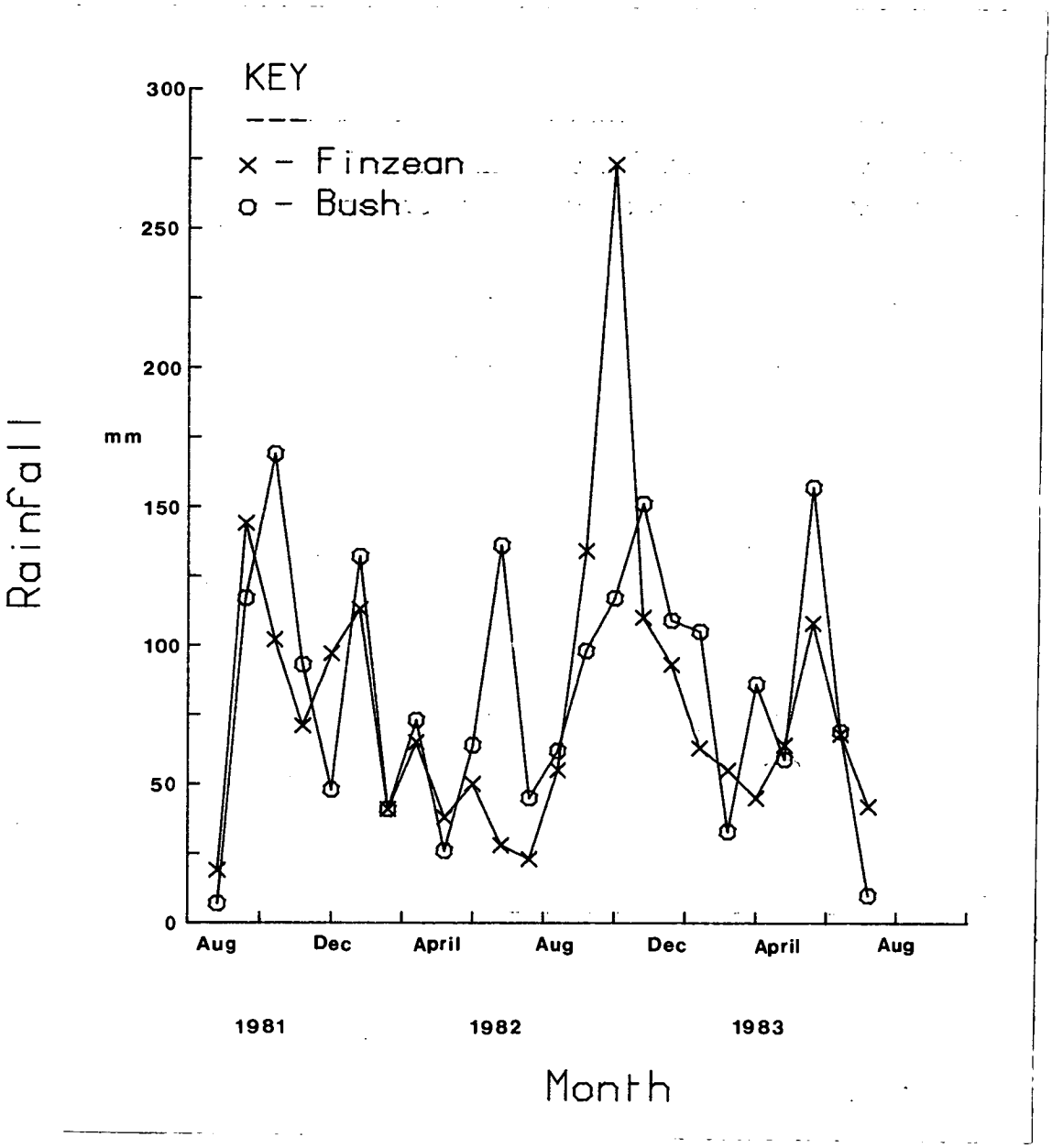
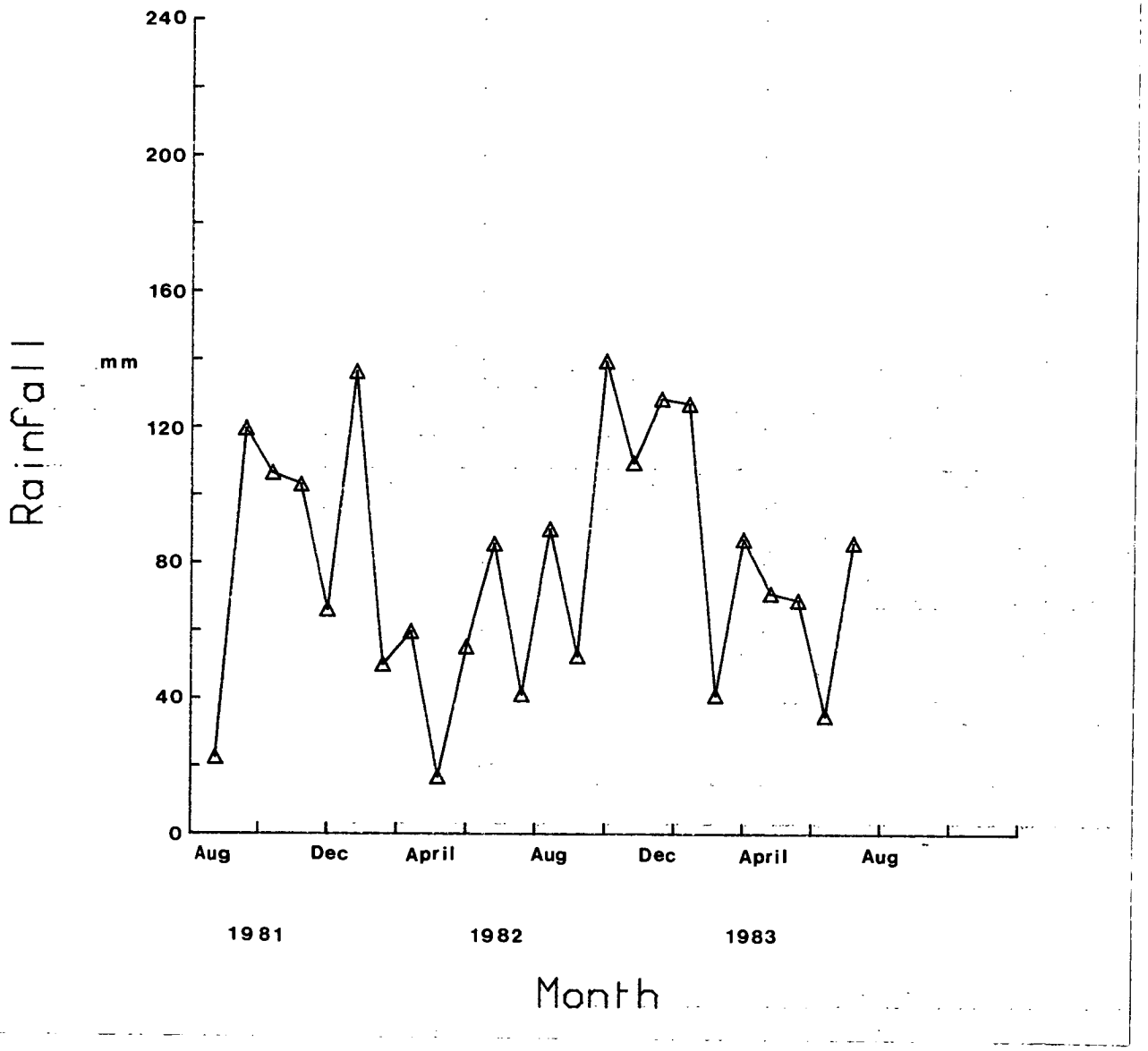


Figure 10.9.4. Monthly rainfall at Redesdale



The high rainfall in the second year at Aberdeen is largely due to the heavy rain here in October, 1982. The rainfall at the other two sites was not particularly heavy in October, 1982.

Again, this shows the greater environmental fluctuations encountered at Finzean, compared to Redesdale.

The number of days with snow lying is recorded at meteorological stations as the number of days with 1cm or more of snow on the ground at 9 a.m. This varies from site to site, as shown in Table 10.9.6.

Table 10.9.6. Number of days with snow lying

Site	1st Year	2nd Year	Total
Finzean	45	42	87
Bush	37	12	49
Redesdale	38	25	63

In the first year, the number of days with snow lying on the ground was fairly similar for all three sites, and the values were high, reflecting the cold winter of 1981/82. In the second year there was much less snow at Bush and Redesdale than in the first year, but at Finzean there was still a long period with the ground covered in snow.

On the whole, the results show that the winter of 1982/83 was milder than the previous winter.

The site at Dalmally, in Argyll, was only used from November, 1982 to July 1983. The nearest meteorological station is at Kilchrenan, 13km away. The climate here is fairly mild: over the nine months the mean maximum temperature at Kilchrenan was 10.5^{o}C, which is higher than at the other three sites. Also, over the winter

of 1982/83, there was never more than 0.5cm of snow at Kilchrenan, so there were no days with 'snow lying' (snow > 1cm deep), compared to between 12 and 42 days at the other sites (Table 10.9.6).

Kilchrenan was much wetter than the other sites. Between 1st November and 31st July, 1983, there was 1.7m of rain at Kilchrenan, compared to 0.78m at Bush, 0.76m at Redesdale and 0.65m at Finzean over the same period.

Generally, the meteorological data from the nearest meteorological station reflects fairly accurately the difference between the experimental sites. The climate at Aberdeen (nearest meteorological station Finzean) is relatively continental, with hot summers and a long period of snow cover in the winter. Bush is fairly frost free, and has less snow cover than Finzean or Redesdale. The climate at Sourhope (Redesdale) is more maritime, with relatively small temperature fluctuations. Dalmally (Kilchrenan) has a mild climate and has much more rain than the other sites.

There are several other factors that are likely to differ between the experimental sites, but unfortunately information on these is not available for most of the meteorological stations. These factors include mean annual accumulated temperature, amount of solar radiation, fog, and potential water deficit, all of which will affect plant growth [221]. It is likely that these factors will reinforce the climatic differences between the experimental sites, and will contribute to the different responses of the plants growing in different sites. The experimental sites therefore, cover a range of different climatic conditions, reflecting the diversity of environments found in Scotland.

10.10 Dalmally

The three main experimental sites were all in eastern Scotland, because an essential requirement for a cultivar in Scotland is good winter hardiness [38], and so only plants which perform well in the more severe climate of eastern Scotland are likely to make good cultivars. In order to check that plants that were successful in the other sites could also grow well in the milder, wetter climate of western Scotland, a small experimental plot was set up for nine months at Dalmally in Argyll. Six biotypes and two cultivars were planted out here in November 1982. The plants used were :

'Quanterness', 'New Cumnock', '9 Dalmelington', 'Lochans', 'Knapdale', 'Birsay', 'Baron', 'Arina'.

The first three biotypes mentioned above all performed well in the other experimental sites. 'Lochans' had good ground cover and dry matter production at Sourhope, but did not do well at Aberdeen or Bush. 'Knapdale' and 'Birsay' both performed relatively poorly at the other sites. 'Arina' and 'Baron' were respectively the most and least productive cultivars at Sourhope, which had a relatively maritime climate and acid soil, and might therefore be expected to be the best guide to possible performance at Dalmally.

At Dalmally, the metre square plots were arranged in a 4 x 4 block, with two plots per biotype and cultivar. The randomisation of the plots is shown in Table 10.10.1.

Table 10.10.1. Randomisation of the Plots at Dalmally

		Row A	B	C	D
Column	1	Lochans	9 Dal	Knap	Birsay
	2	Quant	Knap	N.Cum	Lochans
	3	Arina	Baron	9 Dal	Quant
	4	Birsay	N.Cum	Arina	Baron

All the plants of each biotype or cultivar were of the same clonal group. The clonal groups used were :

Quanterness : C9, New Cumnock : C11, 9 Dalmelington : C12

Lochans : C3, Knapdale : C12, Birsay : C3,

Baron : C1, Arina : C1

Six tillers were planted in each metre square plot on 16th November, 1982, in the same arrangement as shown in Figure 10.2.2. The soil pH at Dalmally was between 4.2 and 4.4, and the soil phosphate level was low (mean : 6 kg/ha). Before planting, the plots were fertilized with 50 kg/ha nitrogen, 110 kg/ha phosphate and 50 kg/ha potassium.

Six visits were made to the plots, on 23rd February, 1983, 15th March, 14th April, 5th May, 26th May and 24th June.

On 15th March, the plants that had died over the winter were replaced with material of the same clonal group as the original.

At each visit, the plant survival, dry matter production

and disease incidence and colour were noted. Ground cover was not recorded as the plants had only nine months in which to grow, and so the ground cover was too low to be accurately measured.

10.11. Seed Production

In April, 1982, twenty tillers of each of the biotypes and cultivars used in the experimental plots were planted out at the Botany Department, Edinburgh University (Map reference NT 268706, Altitude 70m). The tillers were arranged in four rows of five tillers, spaced 8cm apart, so that all 20 tillers of each biotype were in an area 32cm by 24cm. Very few plants flowered in 1982, but the tillers multiplied rapidly and by the summer of 1983 each biotype and cultivar had produced a fairly uniform sward about 25cm by 35cm. The plants were not cut at all over this period. In July, 1983, 10 panicles of each biotype and cultivar were collected and the number of seeds in each panicle was counted. Five biotypes - 'Wooler', 'Yetholm', 'Tomintoul', 'Stromness' and 'Knapdale' and the cultivar 'Primo' did not flower in 1983, so seed production could not be estimated for these plants.

10.12. Germination

Tillers from the biotypes and cultivars used in the experimental plots were planted in boxes containing Fisons 'Levington' compost. The boxes were kept in the greenhouse for eight weeks, and then transferred outside at the beginning of October, 1981. Seed was collected from the panicles at the end of July, 1982.

The biotype 'Port Patrick' and the cultivars 'Primo' and 'Fylking' did not flower in 1982, so no seed of these cultivars was available for the germination tests. Seed of the other biotypes and cultivars were cleaned to remove the glumes, and tested for germination in March 1983.

The standard germination test for Poa pratensis lasts 28 days, and an interim germination count is made on day 10, as well as the final germination count on day 28 [189]. The interim germination count is assumed to give an idea of the vigour of the seeds. In Lolium perenne, the interim germination count correlates better with seed establishment than the final germination count [220].

In this study, germination conditions were as specified in the International Rules for Seed Testing [189], but germination was recorded twice weekly to give a more accurate picture of the speed of germination. Germination was assumed to have commenced when the primary root had emerged from the caryopsis. Also, the number of seeds with primary shoots longer than 2.5mm was recorded. Seed of Poa pratensis is normally sown about 2.5mm deep, and so the time taken for the shoot to grow this distance gives an estimate of the minimum time before photosynthesis can commence.

Four hundred seeds of each biotype and cultivar were used for the germination test, with 100 seeds on each 7cm diameter Whatman No.3 filter paper. Seeds were initially watered with 0.2% potassium nitrate, and subsequently obtained distilled water from a wick attached to the base of the filter paper. Seeds were incubated in a Charles Hearson germination cabinet, with a 16 hour night at 20 ^{o}C, and 8 hour day at 30 ^{o}C. Illumination was provided by a Philips 'Daylight 33' 80W fluorescent light.

10.13 Analysis of Variance

Plot results were subjected to two Analyses of Variance, using the quantitative data assembled for percentage survival, percentage ground cover and dry matter production. These are among the most basic in any assessment of amenity value in a perennial grass.

The first analysis was of biotypes, sites and their interaction; the second of "biogroups", sites and their interaction. The "biogroups" (listed below) were largely geographic groups of biotypes and were studied to see if there was any possibility of predicting amenity qualities of plants native to particular areas.

Biogroup	Biotypes and areas of origin
1	1, 5, 10, 19 (coastal)
2	2, 3, 4 (Cheviots)
3	6, 7, 8, 9 (South West Scotland)
4	11, 12, 13, 14 (Grampians)
5	15 (Northern lowland)
6	16, 17, 18 (Orkney)
7	20, 21, 22, 23 (Barra - Western Isles)

CHAPTER 11. RESULTS FROM EXPERIMENTAL SITES

11.1. Introduction.

Twenty three biotypes and four cultivars were planted in experimental plots at Aberdeen, Bush (Edinburgh) and Sourhope (Cheviots) in July 1981, and studied for two years. About 20 visits were made to each site during this period (see Table 10.4), and record made of plant survival, dry matter production, ground cover, disease, plant colour and flowering time. Six biotypes and two cultivars studied for nine months at Dalmally (Argyll), were monitored for plant survival, dry matter production, disease and plant colour.

11.2. Results.

Analysis of variance results (see Appendix 2), which are referred to where appropriate, show some general findings. A significant difference in percentage survival of biotypes was shown in 1982 but not in 1983, probably due to an "establishment" component and the harsher weather of 1982. Other quantitative criteria differed significantly between biotypes in both years. The two years differed also in biotype-site interactions and site variance for percentage survival and ground cover (significant in 1982, not in 1983). This may reflect weather differences between the years. Biotype-site interactions for dry weight were highly significiant in both years. Ideally, more years of trial would be operated.

Partition of variance indicates that biotypes themselves were very significantly different from each other ($P<.001$) except for percentage survival over the relatively mild winter of 1982/83. Sites enjoyed generally more similar weather in 1983 than in 1982.

Residual variance of the site-replications stratum in these analyses is attributable to "between-replications-within-sites" variation. Only in dry weight gain was this component significant. Of the two explanations for this, i.e. genotypic variation or environmental heterogeneity over the plots, the latter is more likely, since care was taken in cloning the

plant material used. The environmental variation is unlikely to have been edaphic - soil within each site was level and fairly consistent at the outset, and would have become more so, given the fertiliser treatments described. Microclimatic variation is the likely cause. Insolation is less likely to vary significantly over an unshaded plot less than 11 x 8 m, than for there to have been minor variations in exposure, particularly as some biotypes grew up better than others. It was therefore prudent to have randomised biotype positions within plots.

Plant survival is summarised in Table 11.3. Mortality rates refer to the number of plants of each biotype that died within a given period. There were originally 12 plants of each biotype per site.

The total dry weight of cuttings from each biotype over the two years is shown in Table 11.4.1. Each site had two plots of each biotype. The mean result from these plots is shown in the table. Seasonal distribution of dry matter production is shown for each site in Figures 11.4.1. Table 11.4.2. shows first year dry matter production (July 1981 - July 1982). In tables of results in this chapter, the cultivars are asterisked. If a biotype and a cultivar have the same value, the cultivar is listed first.

Results for ground cover were converted to mean ground cover recorded per visit, because total ground cover measured depends on the number of visits made to each site. This is not true of dry matter production; if a visit to a site is missed, recorded ground cover will not increase, but dry matter produced in this period will be harvested at the next visit. Table 11.5.1. shows mean ground cover results from the three sites over the two year period. Seasonal variation in ground cover is illustrated in Figures 11.5.1. and 11.5.2., and Table 11.5.2. shows ground cover results after one year.

Results for disease are given in the order that the infections appeared in the plots: mildew first, then rust, and finally 'melting out' (Tables 11.6.1. to 11.6.8.).

Mean score for colour over the two years is shown in

Tables 11.7.1 to 11.7.4, and the results for colour over winter are shown in Tables 11.7.5 to 11.7.7.

Finally, the time of panicle production is shown in Table 11.8.1, and the final date at which panicles were noted at Sourhope in 1982 is shown in Table 11.8.2.

11.3. Plant Survival

The plant survival in each plot was recorded at every visit. In July 1982, one year after planting, all the plants that had died were replaced with material from the greenhouse. At Aberdeen and Sourhope, a few plants died between June and early September 1982, necessitating a second replanting at these sites in September. This replanting meant that all the plots had the same number of live plants (6) at the beginning of the winter of 1982/83. The highest plant mortality rate was at the Aberdeen site.

At Aberdeen, in the first year 53 plants died out of a total of 312. The winter of 1981/82 was a severe one. The mean daily 'grass minimum' temperatures recorded at Finzean in December 1981 and January 1982 were $-5.4^{o}C$ and $-4.5^{o}C$ respectively. This compares with $-2.6^{o}C$ in December 1982, and $-0.4^{o}C$ in January 1983. However only three plants died between 18th November and 21st May: the great majority died within 4 months of planting. This was probably due to the unusual weather in the two months immediately after planting. August 1981 was very dry (rainfall at Finzean was only 22% of the 1941 - 1970 average August rainfall), and was followed by a very

wet September (rainfall 208% of average). Plants of almost every cultivar and biotype died during this initial period, with only 'Newburgh', 'Airport' and the cultivar 'Primo' having 100% survival. The plants with the worst survival over this period are shown in Table 11.3.1.

Table 11.3.1. Initial mortality of plants at Aberdeen

D = The number of plants of that biotype that died between 20th July and 18th November, 1981

Biotype	D
Port Patrick	6
8 Dalmelington	4
9 Dalmelington	4
North Berwick	3
Yetholm	3
Tomintoul	3
Knapdale	3

These plants were collected predominantly from the south and west of Scotland, and presumably were not adapted to the more extreme climatic fluctuations found at Aberdeen. The notable exception was 'Tomintoul' which is from the north east of Scotland, and was collected 55km from the experimental plot at Aberdeen. However 'Tomintoul' was collected from an altitude of 530m, compared to only 50m for the experimental plot. The climate to which this biotype was presumably adapted is thus likely to be very different to that experienced in the experimental site, despite their relative geographical proximity. Sixteen plants died at Aberdeen between 15th July and 9th September 1982. The biotypes most affected were 'Ben Obe' (6 plants died) and 'Port Patrick' (4 plants died).

One plant each of the biotypes 'Wooler','Port Patrick'

and '8 Dalmelington' died between November 1981 and May 1982 at Aberdeen. The loss of only three plants over the winter is surprising considering the severity of the weather . The lowest daily 'grass minimum' temperature at Finzean over the winter of 1981/82 was - 23.7°C, compared to - 10.1°C the following winter. Laycock reported that winter hardiness was a problem with Poa pratensis cultivars grown in north east Scotland [161].

After replanting in September 1982, a further six plants died over the winter of 1982/83 : four of 'Port Patrick' and one each of 'Newburgh' and 'Ben Obe'. On the whole, contrary to expectations, plant survival at Aberdeen over the winter was very high, but many plants died in the late summer. This is surprising, as Poa pratensis is reported to have good drought resistance [31,41]. Possibly this relatively high mortality is an artefact of the method of planting. Individual tillers were planted rather than seeds or whole plants, and the number and length of the roots were often fairly low on each tiller initially. The fact that 'Ben Obe', which was only planted as tillers in July 1982, suffered high mortality in the summer of 1982, just as the other biotypes had high mortality in their first summer, suggests that individual tillers are more suceptible to drought than mature plants. The very dry period in 1981 immediately after planting was probably responsible for the majority of the plant deaths.

There is however a definite preponderance of biotypes from the south and west of Scotland amongst those with high mortality, which suggests that many of these biotypes are adapted to a more mild climate, and are therefore not tolerant of the dry summers in the north east of Scotland.

At Bush, only 10 plants died in the first year, and all of these died before the end of November. As at Aberdeen, August 1981 was very dry at Bush (7% of the normal rainfall), and presumably this drought was responsible for the plant mortality. One plant each of 'Lochans','8 Dalmelington','Fannich','Kinlochleven' and the cultivar 'Baron' were killed, and five plants of 'Ben Obe' died. 'Ben Obe' had fairly poor survival after planting at Aberdeen, and so apparently has relatively poor drought resistance, at least initially. This biotype was planted a year late at Aberdeen, due to its slow tillering, and the tillers planted in 1981 at Bush and Sourhope were relatively small, with correspondingly poor root growth. After replanting in the summer of 1982, no more plants died at Bush, suggesting that, once established, all the biotypes and cultivars are relatively hardy.

At Sourhope, 22 plants died between July and November 1981, and a further 6 died in the summer of 1982. The biotypes with the highest mortality rates are shown in Table 11.3.2.

Table 11.3.2. Summer mortality rates at Sourhope

D = Number of plants of that biotype that died between 24th July and 24th November, 1981, and between 25th June and 31st August, 1982

Biotype	D
Stromness	5
Port Patrick	4
Fylking *	3
8 Dalmelington	3
Newburgh	3
Birsay	3
North Berwick	2

Several of these biotypes - 'Port Patrick','8 Dalmelington' and 'North Berwick' - had relatively high mortality over the summer at Aberdeen, and this suggests that they have fairly poor drought resistance. The other biotypes in Table 11.3.2 were all from the north of Scotland. This provides some evidence that plants are adapted to the climatic conditions in the area in which they grow: generally the plants with poor survival when grown in northern Scotland originated in the south, and those with high mortality rates when grown in the south often originated in the north.

Over the winter of 1981/82, thirteen plants died at Sourhope, the worst affected being 'West Cheviots' (3 plants died), 'Birsay' (3 died) and 'Baron' (2 died). The mean daily 'grass minimum' temperature in the Cheviots in December 1981 (- 6.9^{o}C) was slightly lower than at either Bush or Aberdeen. The minimum temperature in January 1982 (-4.5^{o}C) is very close to that at the other two sites. No plants at Sourhope died over the winter of 1982/83.

At Dalmally, a total of 17 plants died over the nine months that the plot was used. The mortality rates are shown in Table 11.3.3.

Table 11.3.3. Mortality rates at Dalmally

D = Number of plants that died between 16th November, 1982 and 24th June, 1983.

Biotype		D
Arina	*	5
Baron	*	3
New Cumnock		3
Lochans		3
Quanterness		1
9 Dalmelington		1
Birsay		1
Knapdale		0

The two cultivars had high plant mortality at Dalmally (Table 11.3.3.). Both 'Arina' and 'Baron' had survived well at the other experimental sites; the higher mortality at Dalmally is unlikely to be due to extreme cold, as the climate at Dalmally is relatively mild. However Dalmally is much wetter than the other sites : the rainfall recorded at Kilchrenan over the nine month period was over twice as much as that recorded at the meteorological stations near the other experimental sites. Over winter, plant mortality may be caused by dull, wet weather, possibly because with low irradiance and mild temperatures, respiratory losses are high, and carbohydrate levels may be severely depleted [155].

It is interesting that 'Knapdale', which was collected from the west of Scotland, had relatively high mortality at Aberdeen, but survived very well at Dalmally. This provides further evidence that plants tend to be adapted to the climatic conditions in the areas where they are growing.

11.4. DRY MATTER PRODUCTION

The plots were cut at approximately fortnightly intervals over the summer, and less frequently in the winter (see Table 10.4). Dry matter production refers to the total growth (leaves and culms) above 2.5cm. In Table 11.4.1, the total dry matter production over the two year period is shown.

In the tables below, cultivars are marked with an asterisk to show clearly the relative positions of the cultivars compared to the biotypes.

Table 11.4.1.i. Dry Matter Production, Aberdeen

Dry matter = Dry matter production in grams

Biotype	Dry Matter	Biotype	Dry Matter
Quant	457	8 Dal	230
Cumnock	451	N.Ber	229
Fylking *	411	Airport	225
9 Dal	342	Knap	220
Baron *	329	Newbur	204
Aviemore	327	Braemar	185
Cairn	326	Tomin	176
Lochans	316	W.Coast	172
Arina *	298	Wooler	146
Fannich	287	Ben Obe	140
Yetholm	280	Kinloch	130
Primo *	279	Birsay	107
Strom	268	Port P	98
W.Chev	266		

Table 11.4.1.ii. Dry Matter Production, Bush

Dry matter = Dry matter production in grams

Biotype		Dry Matter	Biotype		Dry Matter
Quant		934	Port P		600
9 Dal		832	8 Dal		590
Cairn		828	Newbur		589
W.Chev		808	Airport		524
Lochans		758	Arina	*	521
Fylking	*	754	Yetholm		513
Primo	*	750	Fannich		488
Cumnock		733	Strom		479
Braemar		683	N.Ber		467
W.Coast		680	Knap		390
Tomin		667	Birsay		345
Baron	*	651	Kinloch		281
Aviemore		622	Ben Obe		214
Wooler		600			

Table 11.4.1.iii. Dry Matter Production, Sourhope

Dry matter = Dry matter production in grams

Biotype		Dry Matter	Biotype		Dry Matter
Braemar		283	Wooler		178
Quant		251	Port P		176
Yetholm		248	Fylking	*	175
N.Ber		246	9 Dal		167
Lochans		243	Strom		166
Knap		242	Ben Obe		162
Arina	*	230	Fannich		161
Aviemore		229	W.Coast		161
Cumnock		215	8 Dal		155
Primo	*	210	Baron	*	153
Cairn		206	Kinloch		134
Tomin		197	Newbur		127
Airport		193	Birsay		47
W.Chev		191			

Comparing the results in Table 11.4.1. from different sites, the values are generally highest at Bush (mean of all the plants : 604g), and lowest at Sourhope (mean 191g). This must be due to climatic and edaphic differences between the sites. At both Aberdeen and Sourhope, available soil phosphate was low after a year; soil phosphate has a significant effect on grass yield in Scotland [222], and so low phosphate levels could reduce the dry matter production in these two sites.

Also the soil at Sourhope is fairly acid (pH 5.0). Although Poa pratensis is reported to be less sensitive to pH than Lolium perenne L. and Dactylis glomerata L. [205], the growth of Poa pratensis is affected by pH, with maximum yield reported to be between pH 6 and pH 7 [148]. It was interesting that 'Baron' is reported to be relatively intolerant of acid conditions compared with other cultivars [203], as in this study the pH was highest at Aberdeen and lowest at Sourhope, and 'Baron' was the second most productive cultivar at Aberdeen, third most productive at Bush, and least productive at Sourhope.

The high productivity of 'Fylking' at Aberdeen and Bush was surprising, as this is primarily regarded as an amenity grass , rather than a forage grass. Amenity grasses are usually not very productive. In contrast, 'Arina' and 'Primo' are specifically dual purpose cultivars for both amenity and forage use, and so were expected to be very productive. However not even at Sourhope, where their yield was higher than the other two cultivars, did they produce significantly greater dry matter than the other cultivars. At Bush, which had the highest yield of all three sites on average, the cuttings from 'Arina' were significantly lower in weight than

those of both 'Primo' and 'Fylking'. None of the four cultivars was either more productive or less productive than the other three at all three sites; different cultivars perform better at different sites, although 'Fylking' seems to have the best overall performance.

At every site, two or more biotypes exceed the production of all the cultivars, although in no case did the best biotype have a significantly higher yield than the best cultivar. 'Quanterness' produced more than any cultivar at all three sites, and at Bush it was significantly more productive than all the biotypes except 'New Cumnock' and 'Fylking'. In contrast to the apparently wide climatic tolerance shown by 'Quanterness', some biotypes such as 'Braemar' and 'Yetholm' only perform well at one site, while others such as '9 Dalmelington' are productive at two sites but not at the third. At the other end of the scale, 'Birsay' and 'Kinlochleven' are both amongst the three least productive biotypes at every site.

There is very little evidence that plants growing in plots geographically close to their site of origin tend to be productive there; 'Yetholm' produces a lot of dry matter at Sourhope, only a few miles from where it was collected, but 'Wooler' - also from near Sourhope - does not perform well there, 'Newburgh' and 'Tomintoul' were not particularly productive at Aberdeen, and 'North Berwick' has a disappointing yield at Bush.

There is also a large degree of variation between plants from a similar geographical area; 'Ben Obe' and 'Airport' were originally growing only 3.5 km apart, yet at Bush, 'Airport' is significantly higher yielding than 'Ben Obe'. This parallels the results in Chapter 5, which showed that plants within a small area

could be morphologically very different.

The results above are the mean results over the two year period, but there were some differences in performance during this time. The results for the only the first year are shown below. The six most productive biotypes at each site after one year (from July 1981 to July 1982) are shown in Table 11.4.2.

Table 11.4.2. Dry matter production in the first year

Aberdeen

Biotype	Yield
New Cumnock	133g
Quanterness	88g
9 Dalmelington	71g
Baron *	69g
Lochans	69g
Cairngorm	58g

Bush

Biotype	Yield
Quanterness	151g
Fylking *	128g
West Cheviot	117g
New Cumnock	111g
Aviemore	108g
Primo *	103g

Sourhope

Biotype	Yield
Quanterness	61g
Lochans	55g
Knapdale	49g
9 Dalmelington	47g
North Berwick	46g
Arina *	43g

Most of the biotypes retain approximately the same relative position over the two years, with some exceptions. The results after one year suggested that 'New Cumnock' was a fairly productive biotype : it had a significantly higher yield than any other biotype at Aberdeen. However after two years its performance at all three sites was poorer than expected. This is shown in Figure

11.4.1.. In contrast, '9 Dalmelington' at Bush was less productive than 'Fylking' during the first year, but more productive in the second year (Figure 11.4.2.). Similarly 'Braemar' and 'Yetholm' produced higher yields in the second year at Sourhope than would be predicted from their initial performance (Figure 11.4.3.). So there is some variation not only in the total yield of each biotype, but also in the distribution of the yield over the two year period.

Figure 11.4.1. Dry matter production at Aberdeen

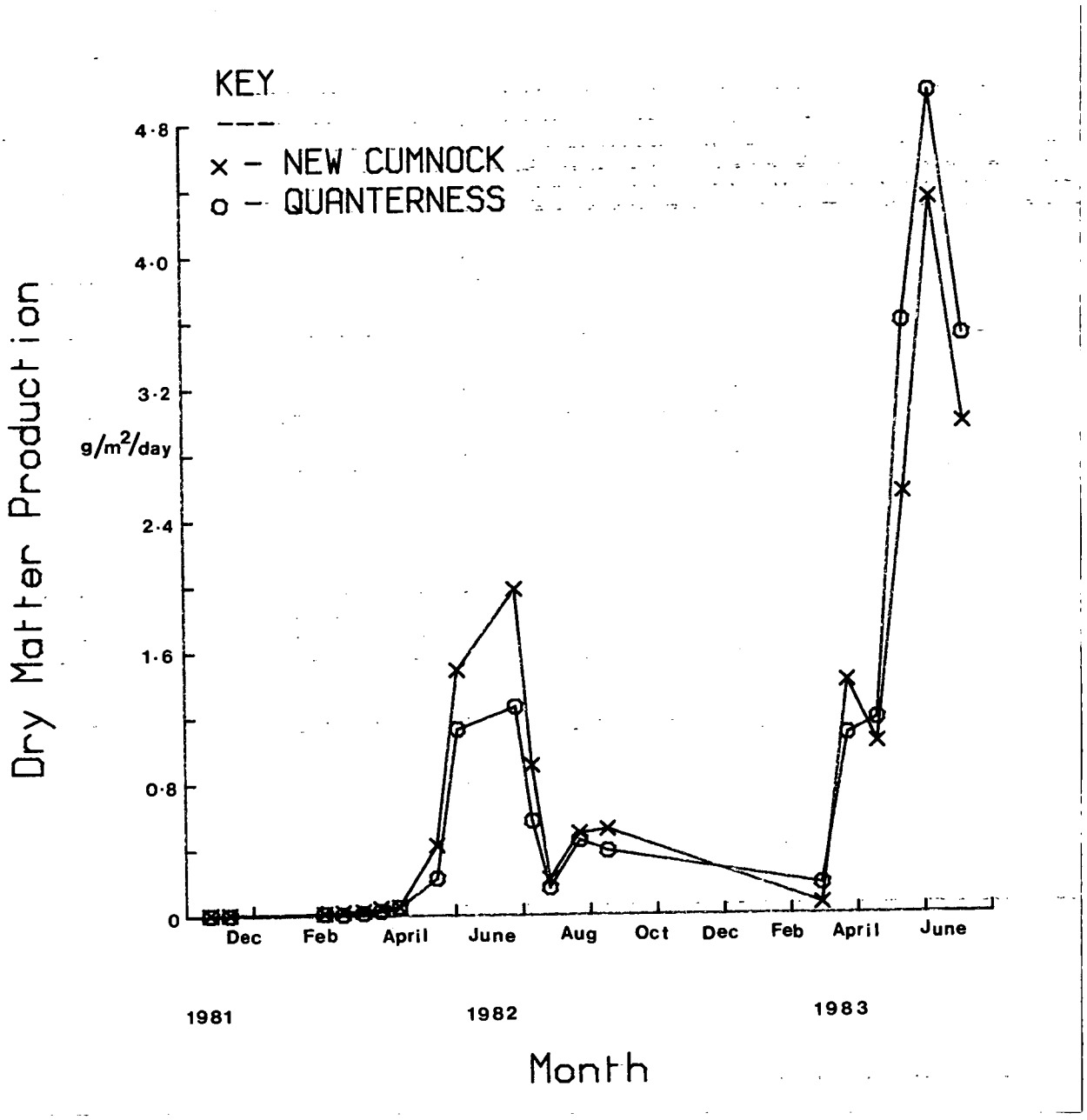


Figure 11.4.2. Dry Matter Production at Bush

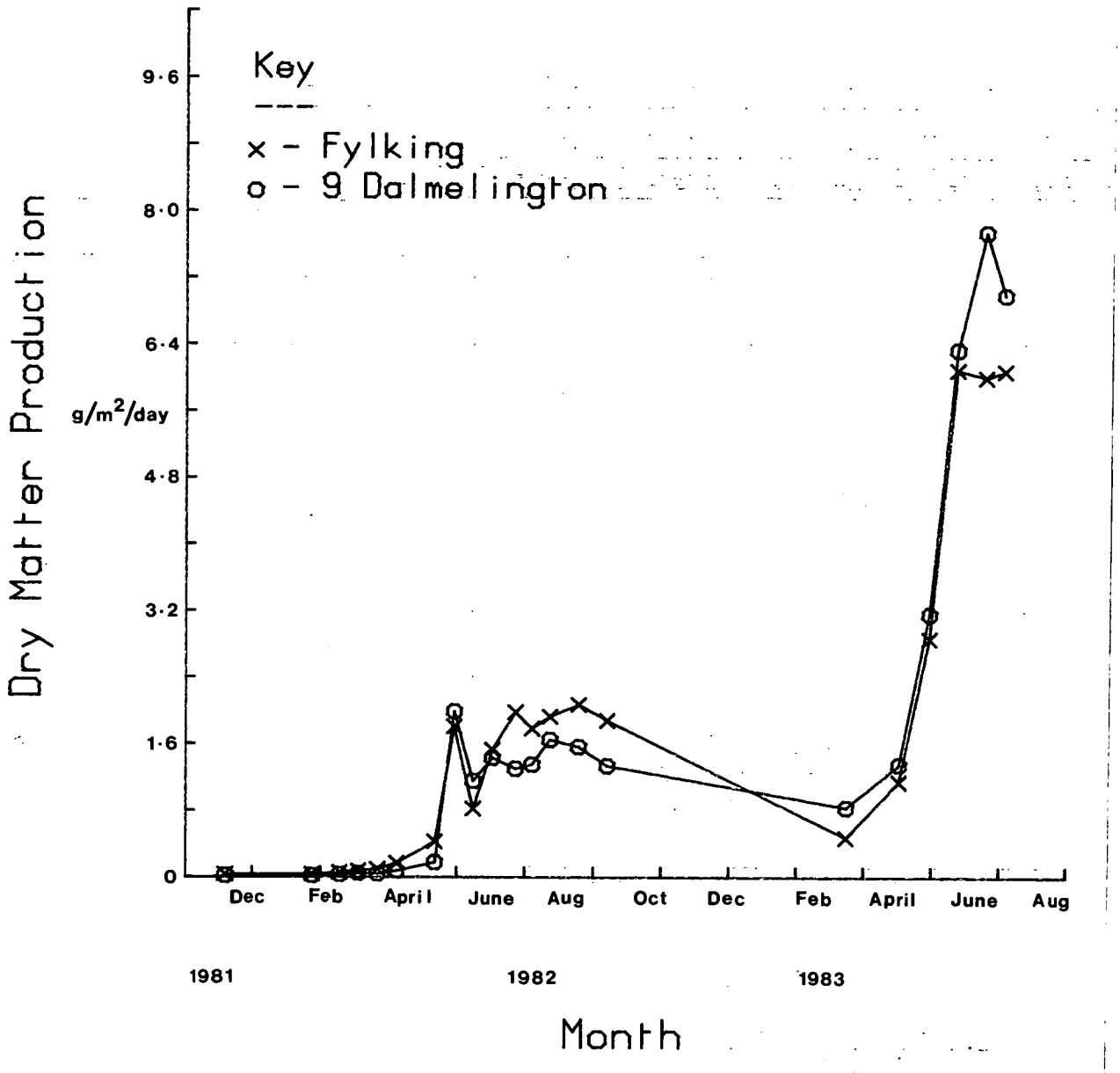
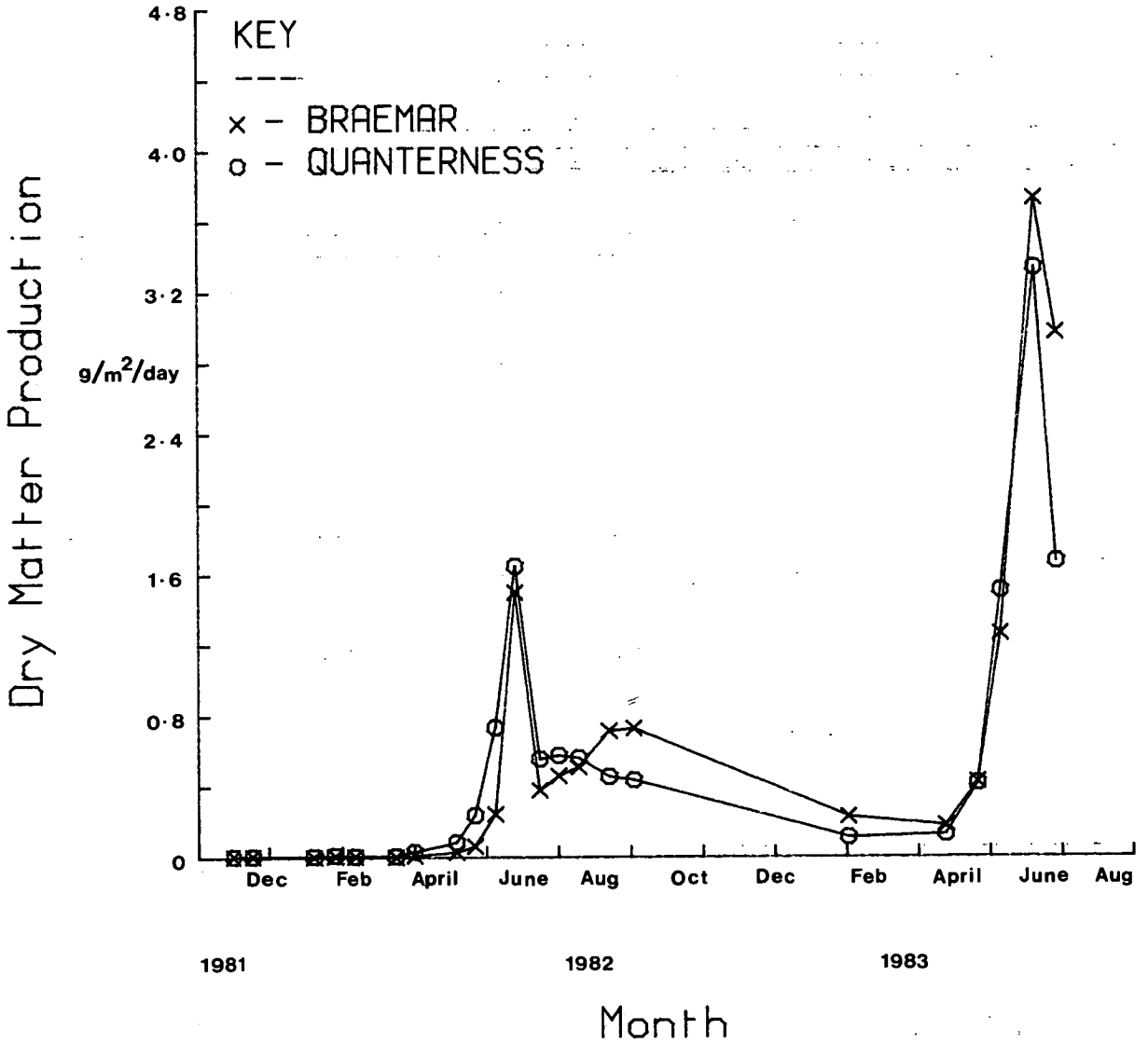
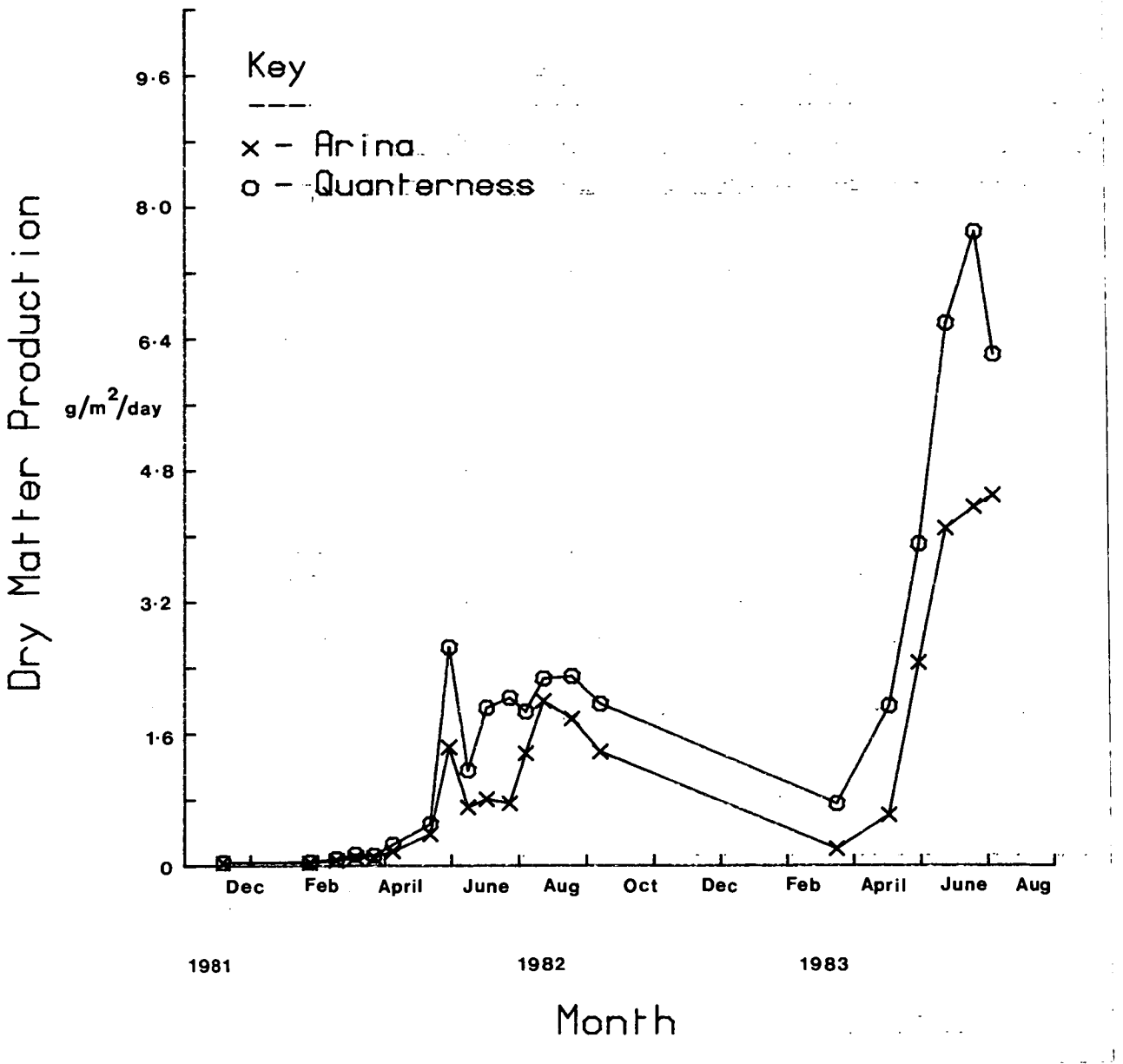


Figure 11.4.3. Dry Matter Production at Sourhope



In the majority of cases, however, the distribution of yield is similar for the different biotypes at the same site. For example, 'Quanterness' always had a higher dry matter production than 'Arina' at Bush (Figure 11.4.4.).

Figure 11.4.4. Dry Matter Production at Bush



In all the sites the dry matter production peaks during flowering, between late May and early June, then falls back to a fairly steady level over the rest of the summer, and declines over winter. The general pattern of dry matter production is similar for different biotypes at the same site (Figures 11.4.2. and 11.4.4.), but there are variations between sites.

At Aberdeen (Figure 11.4.1.), the broad peak in the summer of 1982 is probably not a true representation of the distribution of dry matter production. Unfortunately, due to difficulties with transport, this site was not visited at all in June, when the yield is at its peak. This meant that the dry matter produced then was not harvested until the beginning of July, so giving an artificially high value for this time of year. In 1983, when the plot was visited regularly, the peak in the summer is much more abrupt.

The relatively low dry matter production of both cultivars recorded on 30th April (Figure 11.4.1.), may have been caused by bad weather. Normally, maximum and minimum temperature increase over March and April, but at Aberdeen, the mean maximum and mean 'grass minimum' temperatures are both lower in April 1983 than in March 1983 (see Figures 10.9.1. and 10.9.2.). The low dry matter production is presumably caused by this unusual cold spell.

At Bush, the fall in production following flowering is less pronounced than at the other two sites (Figures 11.4.2 and 11.4.4). The soil at Bush is more fertile than that at Aberdeen and Sourhope, with a much higher phosphate content. This may partly explain the more constant yield at this site.

The general dry matter production at Sourhope is low

(Figure 11.4.3), which is probably due to a combination of climatic and edaphic factors. Consequently the peak caused by panicle production is very obvious, as even in the summer the yield of vegetative leaves is low.

The total dry matter production at Dalmally is much lower than at the other sites, because the plants were growing here for a shorter period. The dry matter production over the nine month period is shown in Table 11.4.3.

Table 11.4.3. Dry Matter Production at Dalmally

Dry Matter = Dry matter production in grams

Biotype	Dry Matter	Biotype	Dry Matter
Quanterness	1.53	Knapdale	0.60
Baron *	0.97	New Cumnock	0.57
Lochans	0.66	Arina *	0.40
9 Dalmelington	0.61	Birsay	0.39

As expected, the results are fairly similar to the results at Sourhope after one year's growth (Table 11.4.2). 'Quanterness' is the most productive plant at Dalmally, as well as at Bush and Sourhope, showing the wide climatic tolerance of this biotype. 'Baron' has a relatively higher dry matter production at Dalmally than at Sourhope, and 'Knapdale' and 'Arina' perform slightly worse at Dalmally than at Sourhope. The poor performance of 'Birsay' at Dalmally confirms the implication from the dry matter results from the other experimental sites that this biotype is very unproductive.

11.5. Ground Cover

Ground cover results were not recorded over winter, and the total number of results obtained per site were :

Aberdeen : 12, Bush : 15, Sourhope : 13

The total results over the two year period have been divided by the number of visits, to produce a mean value per visit.

As Goodall points out [216], estimates of percentage ground cover do not have a normal distribution, but the function: (arc sin %ground cover/100) is distributed approximately normally. This angular transformation is necessary before the results can be statistically analysed. In Table 11.5.1, the mean ground cover is shown, and also the mean ground cover after angular transformation. The latter was used for statistical analysis.

Table 11.5.1.i. Ground Cover, Aberdeen

Cover = Mean Percentage Ground Cover

Tran = Mean Percentage Ground Cover after angular transformation

Biotype		Cover	Tran	Biotype		Cover	Tran
Quant		15.2	23.0	Aviemore		8.82	17.3
Baron	*	14.1	22.1	Braemar		8.47	17.0
Fylking	*	14.0	22.0	Primo	*	8.38	16.8
9 Dal		12.3	20.5	Knap		7.59	16.0
Newbur		11.6	19.9	Arina	*	7.20	15.6
Cairn		11.4	19.7	W.Coast		7.04	15.4
Strom		11.4	19.7	Kinloch		7.02	15.3
Lochans		11.3	19.6	Birsay		7.00	15.3
Cumnock		10.9	19.3	Tomin		6.91	15.2
8 Dal		10.7	19.1	N.Ber		6.83	15.1
Airport		10.6	19.0	Wooler		6.83	15.1
Fannich		10.4	18.8	Port P		5.11	13.0
Yetholm		9.79	18.2	Ben Obe		3.03	10.0
W.Chev		9.17	17.6				

Table 11.5.1.ii. Ground Cover, Bush

Cover = Mean Percentage Ground Cover

Tran = Mean Percentage Ground Cover after angular transformation

Biotype		Cover	Tran	Biotype		Cover	Tran
9 Dal		25.3	30.2	Tomin		17.3	24.6
W.Coast		21.0	27.3	Primo	*	16.7	24.1
Baron	*	20.9	27.2	Lochans		16.6	24.0
Cairn		20.6	27.0	Fannich		15.2	23.0
Fylking	*	20.1	26.6	Strom		15.1	22.9
Wooler		20.0	26.6	Cumnock		14.0	22.0
Braemar		20.0	26.6	Knap		12.4	20.6
Newbur		19.5	26.2	Kinloch		12.3	20.5
Airport		18.2	25.3	Ben Obe		11.8	20.1
Birsay		18.1	25.2	N.Ber		11.6	19.9
Port P		18.0	25.1	Avie		11.6	19.9
8 Dal		17.5	24.7	Yetholm		10.4	18.8
W.Chev		17.4	24.7	Arina	*	9.87	18.3
Quant		17.4	24.7				

Table 11.5.1.iii. Ground Cover, Sourhope

Cover = Mean Percentage Ground Cover

Tran = Mean Percentage Ground Cover after angular transformation

Biotype		Cover	Tran	Biotype		Cover	Tran
Lochans		15.5	23.2	Tomin		9.73	18.2
Braemar		14.0	22.0	Wooler		9.42	17.9
Arina	*	13.4	21.5	Avie		9.42	17.9
Ben Obe		12.5	20.7	Port P		9.35	17.8
Cairn		11.7	20.0	Newbur		9.05	17.5
Quant		11.7	20.0	Strom		9.04	17.5
Airport		10.8	19.2	Fylking	*	8.96	17.4
Primo	*	10.6	19.0	W.Chev		8.78	17.2
W.Coast		10.5	18.9	Baron	*	8.68	17.1
N.Ber		10.3	18.7	8 Dal		8.46	16.9
9 Dal		10.3	18.7	Yetholm		8.08	16.5
Kinloch		10.2	18.6	Cumnock		7.09	15.4
Knap		10.1	18.5	Birsay		3.72	11.1
Fannich		9.81	18.2				

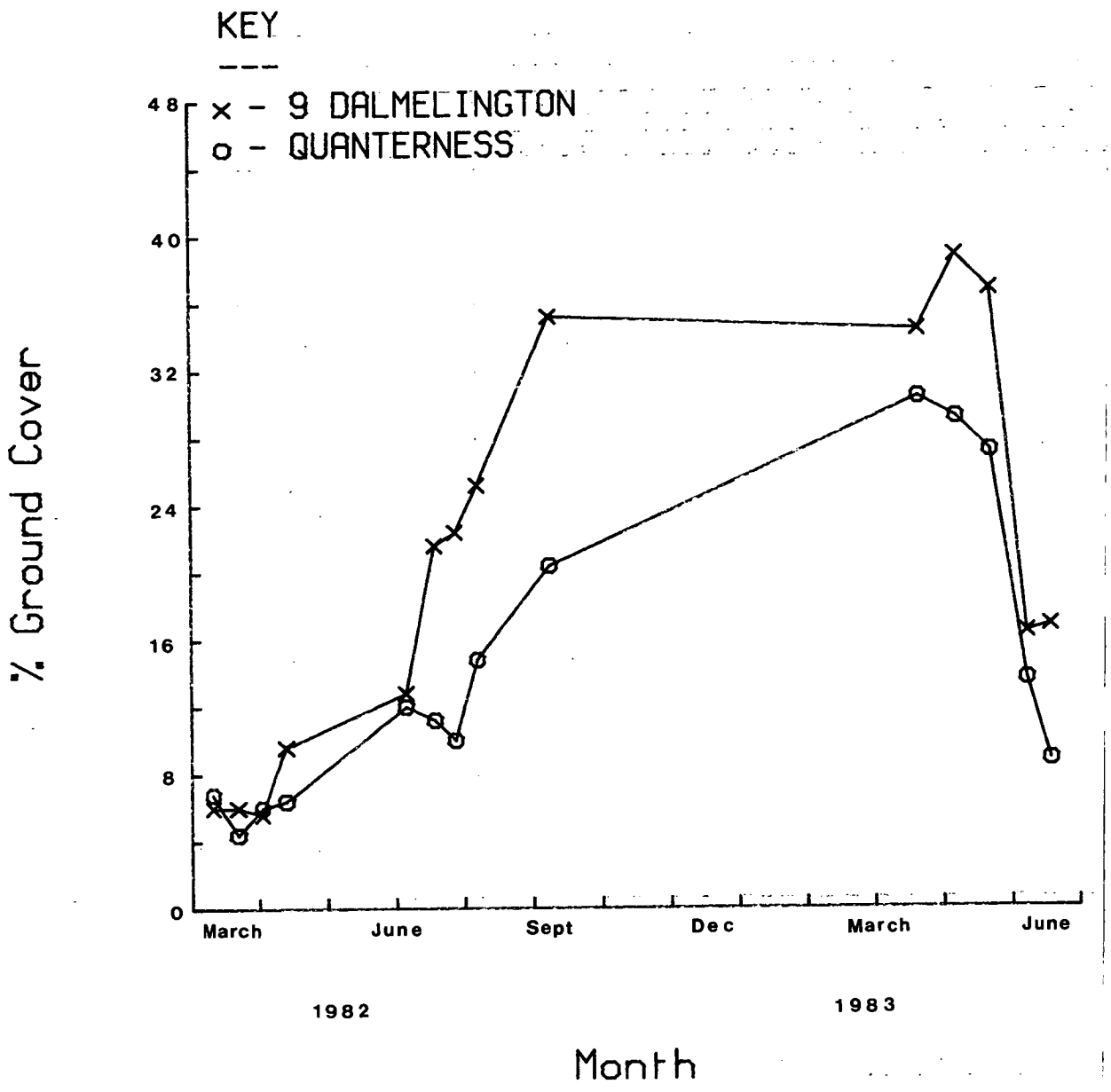
The results in Table 11.5.1. are generally highest at Bush (mean result 16.6), intermediate at Aberdeen (mean 11.7) and lowest at Sourhope (mean 10.0). As with the results for dry matter production, this may be due to the low phosphate levels at Sourhope and Aberdeen, and the acidity of the soil at Sourhope.

At Aberdeen, 'Quanterness' - which was the most productive biotype - had the highest ground cover. 'Fylking', '9 Dalmelington' and 'Baron' also had good ground cover as well as high dry matter production. Similarly, plants that had a low yield, such as 'Port Patrick' and 'Ben Obe', usually also had low ground cover. Not all the biotypes, however, occur in a similar position in Tables 11.4.1.i and 11.5.1.i. 'Newburgh' had a fairly low yield, but high ground cover, indicating that it is a relatively short grass that

spreads fairly rapidly. Similarly 'New Cumnock' is a more erect grass, with proportionally low ground cover compared to its dry matter production.

At Bush, '9 Dalmelington' has a significantly higher ground cover than all the other plants except for 'West Coast' and 'Baron'. The yield of '9 Dalmelington' was high at Bush, but 'Quanterness', which had the highest dry matter production, had a disappointing ground cover at Bush. This is shown in Figure 11.5.1.

Figure 11.5.1. Ground Cover at Bush



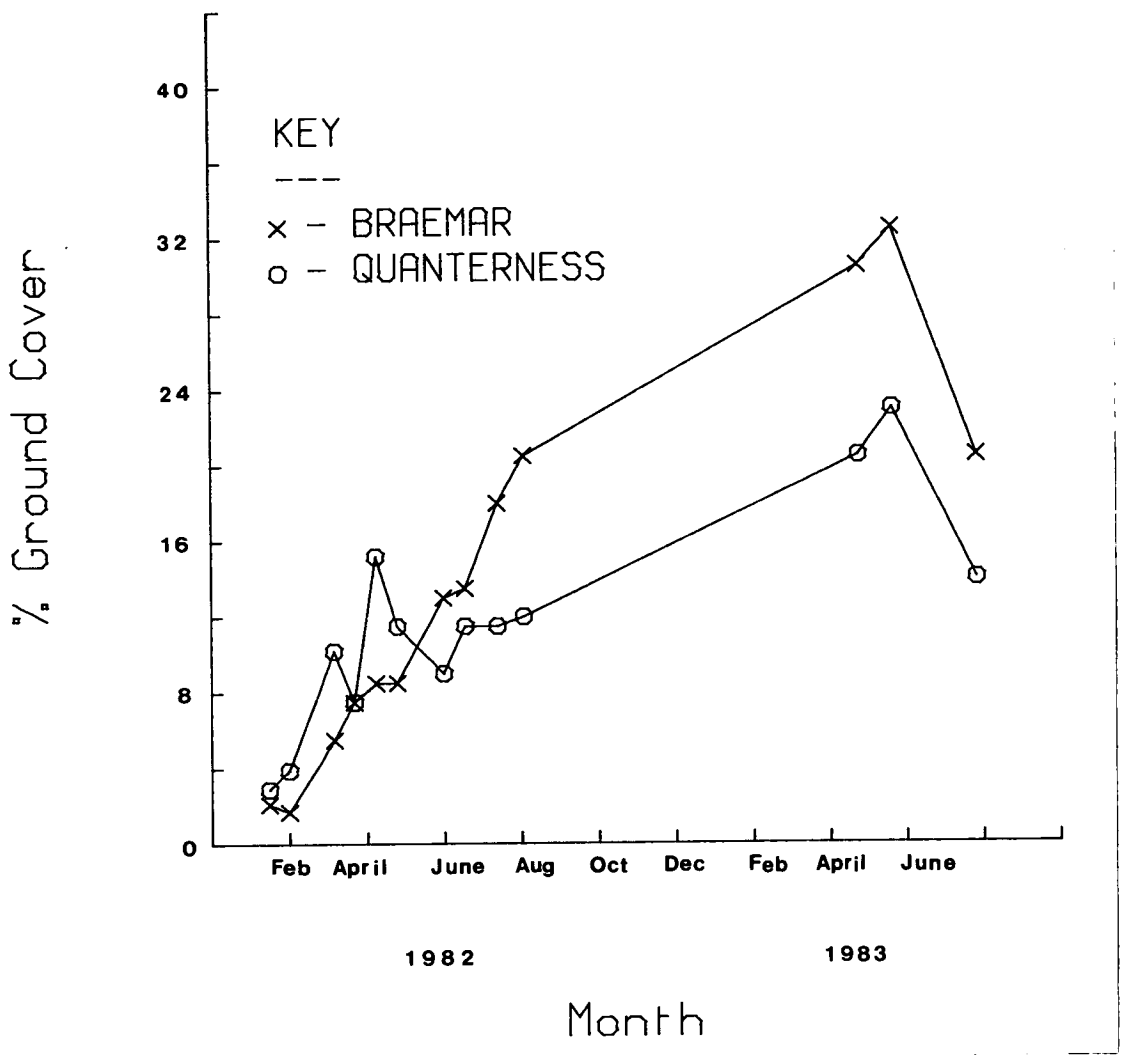
The ground cover of '9 Dalmelington' rises rapidly in the summer of 1982, and stays constant over winter, whereas 'Quanterness' increases fairly steadily throughout 1982 (Figure 11.5.1). Both biotypes suffer a large decrease in ground cover after

flowering in 1983. This may be partly due to the death of flowering culms which have been cut. The lower leaves, and bases of the flowering stems make an important contribution to the ground cover in the early summer. The number of culms produced in 1983 was considerably higher than in 1982, and so there is little evidence of a similar decline in the previous year. Another contributory factor was infection with Drechslera poae. This fungus causes leaf necrosis, and in all sites the disease increased rapidly during June (Section 11.6.3). As 'ground cover' refers only to green tissue, the death of leaves and tillers caused by this infection would result in a decrease in the recorded ground cover.

It is interesting that 'Arina' has the lowest ground cover at Bush. Forage grasses, such as 'Arina', are usually erect and therefore would be expected to have a relatively low ground cover compared to more prostrate forms.

At Sourhope, biotypes that were undistinguished in performance at the other sites, such as 'Braemar','Lochans' and 'Ben Obe' have a high ground cover. Both 'Braemar' and 'Lochans' also had relatively high dry matter yields at Sourhope. A few of the biotypes that did well at other sites, such as 'Quanterness' and 'Cairngorm' also perform fairly well at Sourhope (Fig. 11.5.2.). This indicates that these biotypes are adapted to a wider range of conditions than the biotypes that grow well at only one site.

Figure 11.5.2. Ground Cover at Sourhope



At Sourhope the pattern is broadly similar to that at Bush. There is stronger evidence here for a decline in ground cover following flowering in 1982. This could be due to the low yield in

the summer of 1982 - the corresponding drop at Bush may be concealed by a more vigorous vegetative growth immediately following flowering. At Sourhope both 'Quanterness' and 'Braemar' increase in ground cover over the winter, despite the low dry matter production at this time (Figure 11.4.3.). During the winter the plants here seem to be spreading horizontally rather than growing erect.

'Baron' is regarded as a low growing grass that forms a thick turf suitable for amenity purposes [148]. At both Aberdeen and Bush, 'Baron' has a higher ground cover than would be predicted from the dry matter production results. Some idea about the uses to which biotypes are suited can therefore be obtained from the combination of dry matter production and ground cover data. The result of (mean ground cover/total dry matter production X 100) should give a higher value for 'amenity' than for 'forage' grasses. The results at Bush, where both dry matter production and ground cover were highest, for the cultivars are :

Baron 3.2, Fylking 2.7, Primo 2.2, Arina 1.9

This agrees with the recommended uses of the cultivars outlined in Chapter 9. The values for the three biotypes with the highest ground cover at Bush are :

West Coast 3.1, 9 Dalmelington 3.0, Cairngorm 2.5

In contrast, 'Quanterness', which has the highest dry matter production at Bush, gives a value of 1.9 . This indicates that at Bush, '9 Dalmelington' and 'West Coast' have the characteristics of amenity grass, while 'Quanterness' is more like a forage grass. The range of values for the biotypes is very similar to that of the cultivars, showing that the range of growth habit of both cultivars and biotypes are identical.

The plants with the highest ground cover after one year are shown in Table 11.5.2.

Table 11.5.2. Ground Cover in the first year

G = Mean Percentage Ground Cover between July 1981, and July 1982.

Aberdeen

Biotype		G
Quanterness		10.4
New Cumnock		9.5
9 Dalmelington		8.4
Fylking	*	7.8
Cairngorm		7.7
8 Dalmelington		7.4

Bush

Biotype		G
9 Dalmelington		12.1
West Cheviots		9.4
New Cumnock		9.1
Fylking	*	8.7
Quanterness		8.4
West Coast		7.7

Sourhope

Biotype		G
Lochans		9.4
Quanterness		8.6
Arina	*	8.5
Cairngorm		7.6
9 Dalmelington		7.4
Braemar		6.7

The results after one year's growth show, like the dry matter production results, that several biotypes stay at about the same relative position over the second year. Unlike the results for dry matter production, the biotype that had the highest ground cover at each site after one year also had the highest ground cover after two years.

At Aberdeen, 'New Cumnock' did not have as high a ground cover after 2 years as would be expected from the first year results. A similar pattern was shown in the dry matter production

results for this biotype. This suggests that after a high initial growth rate, in the second year the relative performance of this biotype declines. Similarly at Bush, 'West Cheviots','New Cumnock' and 'Quanterness' do not maintain their initial high results, and '9 Dalmelington' and 'Quanterness' at Sourhope do not perform as well in the second year as in the first (Figure 11.5.2.).

Considering the generally low values after one year, it is perhaps surprising that there is such a correlation between the results for ground cover after one year and the results after two years. When ground cover is either very low or very high, estimates of the percentage ground cover become increasingly inaccurate. Best results are achieved when the ground cover is between 40 % and 60 % [169]. This was the case towards the end of the two year period. It should be stressed that the results shown in table 11.5.1 are mean values over the whole two years : the maximum value recorded at Bush, for example, was 59 %, but the highest mean result was only 25 %.

The reasons for the differences between the biotypes in terms of dry matter production and ground cover are unclear, but the amount of tillering is likely to be an important factor. The number of tillers of the plants at the experimental site at Bush, where dry matter production and ground cover were highest, was counted on 31st August, 1981: 41 days after planting. The mean results are shown in Table 11.5.3.

Table 11.5.3. Number of Tillers per Plant at Bush

T = Mean number of tillers per plant, on 31.8.1981.

Biotype	T	Biotype	T
New Cumnock	67.0	Yetholm	11.3
Quanterness	39.2	Fannich	11.2
Fylking *	22.7	West Coast	11.0
Arina *	22.7	Airport	9.6
Cairngorm	19.4	Wooler	9.5
9 Dalmelington	19.3	Port Patrick	8.5
Primo *	19.2	Stromness	8.2
Lochans	15.4	Newburgh	7.5
Aviemore	15.0	Braemar	7.0
Tomintoul	14.8	Knapdale	6.3
North Berwick	14.7	Kinlochleven	5.8
West Cheviots	14.5	Birsay	5.5
Baron *	14.3	Ben Obe	1.0
8 Dalmelington	11.8		

The mean number of tillers shown in Table 11.5.3. correlates significantly with the results from Bush for dry matter production after one year ($r=0.64$, $p<0.01$) and also after two year ($r=0.55$, $p<0.01$). The tillering also correlates significantly with the ground cover results from Bush after one year ($r=0.54$, $p<0.01$), but the correlation with ground cover after two years ($r=0.20$) is not significant.

11.6. Disease

11.6.1 Mildew

The first disease noted on the plants was mildew on 22nd February 1982 at Bush. Mildew, which is caused by Erysiphe graminis, was present almost continuously at Bush from then on until the end of the experiment in July 1983. At Sourhope, mildew first appeared on 9th June 1982, but none was recorded after 14th August 1982. Mildew was first apparent at Aberdeen on 3rd July 1982 and was present in low amounts over the next year.

The greatest mildew infection occurred at Bush - the mean score for mildew per site per visit was 28.2 for Bush, 5.9 for Aberdeen and 1.3 for Sourhope. At both Aberdeen and Sourhope, the majority of the biotypes and cultivars were free from mildew over the whole two year period. However at Bush, only the biotype 'Wooler' was entirely free from mildew.

The plants most susceptible to mildew at Aberdeen are shown in table 11.6.1.i. The 'score' is the number used to indicate disease severity (see page 127). A high score indicates high disease incidence, and therefore low resistance to that disease. Not all the plants that were infected are shown in the table, but only the most susceptible plants.

Table 11.6.1.i. Mildew infection at Aberdeen

M = Total score for mildew over the two years for that biotype

Biotype	M
Kinlochleven	19
Fannich	17
Lochans	9
Newburgh	8
Airport	7
North Berwick	6
Fylking *	6
Cairngorm	4

A dense sward of grass provides a more favourable environment for fungal infection than thinly scattered individuals [149]. Light intensity is lower inside a dense sward, and air circulation is also reduced compared to that in a thin sward. Together with the relatively high humidity in a dense sward, this provides an excellent environment for mildew [149]. It would therefore be expected, if all the plants had the same level of resistance to mildew, that those with higher dry matter production would also have the greatest mildew infection. However the biotypes worst affected by mildew at Aberdeen are not amongst the high yielding plants. It is therefore unlikely that variation in the microenvironment between plants is entirely responsible for the different amounts of mildew on each biotype. It seems that 'Kinlochleven' and 'Fannich' are more susceptible to mildew than the other biotypes, although the severity of infection is not very great on any of the biotypes at this site.

Mildew is much more of a problem at Bush. The score for mildew infection is shown in Table 11.6.1.ii.

Table 11.6.1.ii. Mildew infection at Bush

M = Total score for mildew over the two years for that biotype.

Biotype	M	Biotype	M
Kinlochleven	98	Yetholm	9
Quanterness	67	New Cumnock	8
Fylking *	56	Aviemore	8
Fannich	55	West Cheviots	7
Birsay	47	8 Dalmelington	6
Stromness	33	Braemar	6
North Berwick	26	Knapdale	6
Baron *	21	West Coast	6
Lochans	19	9 Dalmelington	3
Tomintoul	19	Ben Obe	2
Cairngorm	18	Primo *	1
Arina *	14	Port Patrick	1
Airport	14	Wooler	0
Newburgh	13		

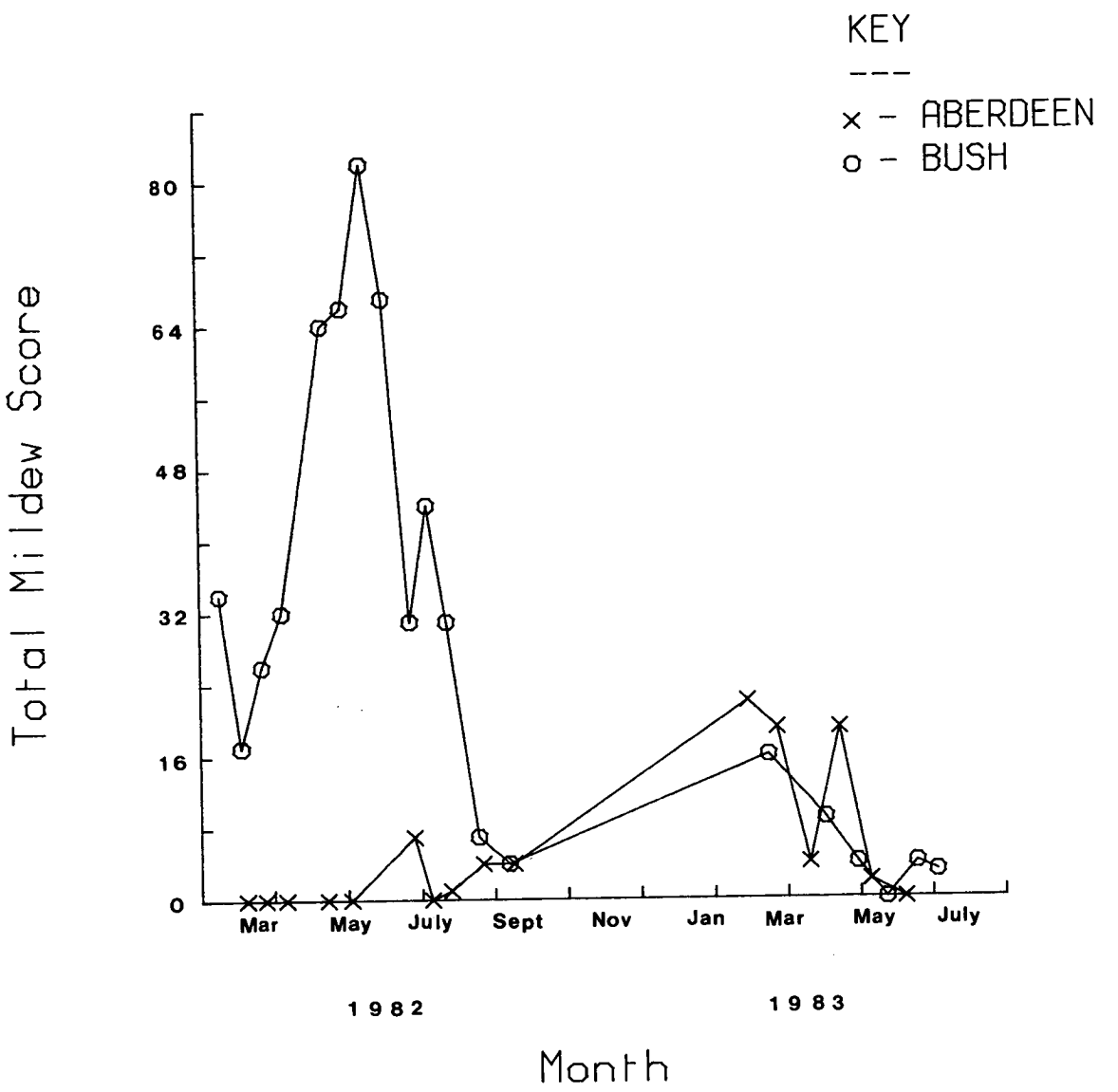
'Kinlochleven' and 'Fannich' are badly affected by mildew at Bush, despite their low dry matter production. 'Quanterness' and 'Fylking' also have high infection rates, and this may be partly due to their high yield. Within a tall dense plant, light intensity and air circulation are reduced, and humidity is high, which are ideal conditions for mildew [149]. It is very hard to assess the relative contribution of high dry matter production to increased susceptibility to infection.

At the other end of the scale, 'Ben Obe', which has very low dry matter production, also shows very little mildew infection. However there are still some obvious differences in the susceptibility of different cultivars and biotypes to mildew. 'Wooler', '9 Dalmelington' and 'Primo', for example, all have reasonable dry matter production but very low infection rates, and so resistance of these plants to mildew is obviously high. Disease resistance is affected by the environment, and also by the fungal

spore count of the particular area where the plants are growing. The great majority of fungal spores are deposited very close to their point of release. Close to infected plants, spore counts of 10,000 spores per cubic metre of air are found, whereas in areas distant from local sources fewer than 50 spores per cubic metre is the normal concentration [223]. This means that trials in different areas do not always give the same results. However Smith [204] tested several cultivars of Poa pratensis for resistance to mildew and found that 'Primo' was more resistant than 'Baron', and 'Fylking' was more susceptible than 'Baron', which agrees with the results in Table 11.6.1.ii.

The seasonal variation in incidence of mildew infection at Bush and Aberdeen is shown in Figure 11.6.1

Figure 11.6.1. Mildew infection at Bush and Aberdeen



At Bush mildew reaches a peak in June 1982, and declines over the summer. The infection in 1983 is much less severe than in the previous year. In contrast there is very little mildew at Aberdeen in 1982, but slightly more in 1983, reaching a peak in late

May and declining in July. The peak in mildew infection occurs at the same time as the peak in dry matter production, providing further evidence that there is a correlation between disease incidence and yield.

At Sourhope there was very little mildew infection. The biotype worst infected was 'Lochans'. The total score over the two years for 'Lochans' was only 3, compared to 98 for the most susceptible biotype at Bush. Over 60% of the biotypes and cultivars were entirely free from mildew at Sourhope.

11.6.2. Rust Infection

Rust, caused by Puccinia graminis, appeared at Aberdeen in July 1982. No rust was recorded here in February 1983, but it reappeared in April, and was present until July 1983. At Bush, rust was first noted on 30th May 1982, and it was present here until the end of the experimental period in July 1983. At Sourhope, rust initially infected the plants in June 1982, but after April 1983 very little rust infection occurred.

Rust infections were generally greatest at Bush (mean score per site 36.9), less at Aberdeen (mean 20.9) and lowest at Sourhope (mean 7.8). The mean scores for rust are higher than those for mildew at all three sites, showing that plants were on the whole more susceptible to rust. The total results for the three sites are shown in Tables 11.6.2.i. to 11.6.2.iii. High scores indicate high susceptibility to the disease.

Table 11.6.2.i. Rust infection at Aberdeen

R = Total score for Rust over the two years

Biotype	R	Biotype	R
Quanterness	51	Newburgh	5
Fylking *	29	Lochans	5
Baron *	27	Wooler	4
Airport	25	Braemar	4
Cairngorm	18	Fannich	4
Stromness	18	Kinlochleven	3
Knapdale	18	Yetholm	3
Tomintoul	17	West Cheviots	2
New Cumnock	16	West Coast	2
North Berwick	11	Primo *	2
Port Patrick	8	Ben Obe	1
9 Dalmelington	8	Aviemore	0
8 Dalmelington	6	Arina *	0
Birsay	5		

'Quanterness' and the cultivars 'Fylking' and 'Baron' were the plants most susceptible to rust at Aberdeen. All three also had high ground cover here, and the two cultivars had a high dry matter yield. Rust infections are known to be more severe where plant density is high [218]. However other plants which had high dry matter production, such as Aviemore, or both high dry matter production and high ground cover, such as '9 Dalmelington', were less affected by rust. Therefore as well as differences due to different densities of the individual plants, there are differences between the biotypes in resistance to rust. 'Quanterness', 'Fylking' and 'Baron' seem to have relatively low resistance to rust, whereas 'Primo', 'Aviemore' and 'Arina' have high resistance.

'Airport', which was susceptible to mildew at Aberdeen, is also susceptible to rust. However the other biotypes which were

very susceptible to mildew, such as 'Kinlochleven' and 'Fannich' were resistant to rust. There is no correlation between resistance to the two diseases.

Table 11.6.2.ii.. Rust Infection at Bush

R = Total Score for Rust Infection over the two years

Biotype	R	Biotype	R
Lochans	51	North Berwick	23
Quanterness	51	Arina *	22
Cairngorm	49	Fannich	22
Kinlochleven	47	Aviemore	21
Baron *	45	Ben Obe	18
Tomintoul	45	Wooler	17
New Cumnock	42	Newburgh	16
Braemar	42	Birsay	14
Fylking *	39	8 Dalmelington	9
Port Patrick	28	Primo *	8
Stromness	28	West Cheviots	8
Airport	28	West Coast	8
Yetholm	26	9 Dalmelington	6
Knapdale	26		

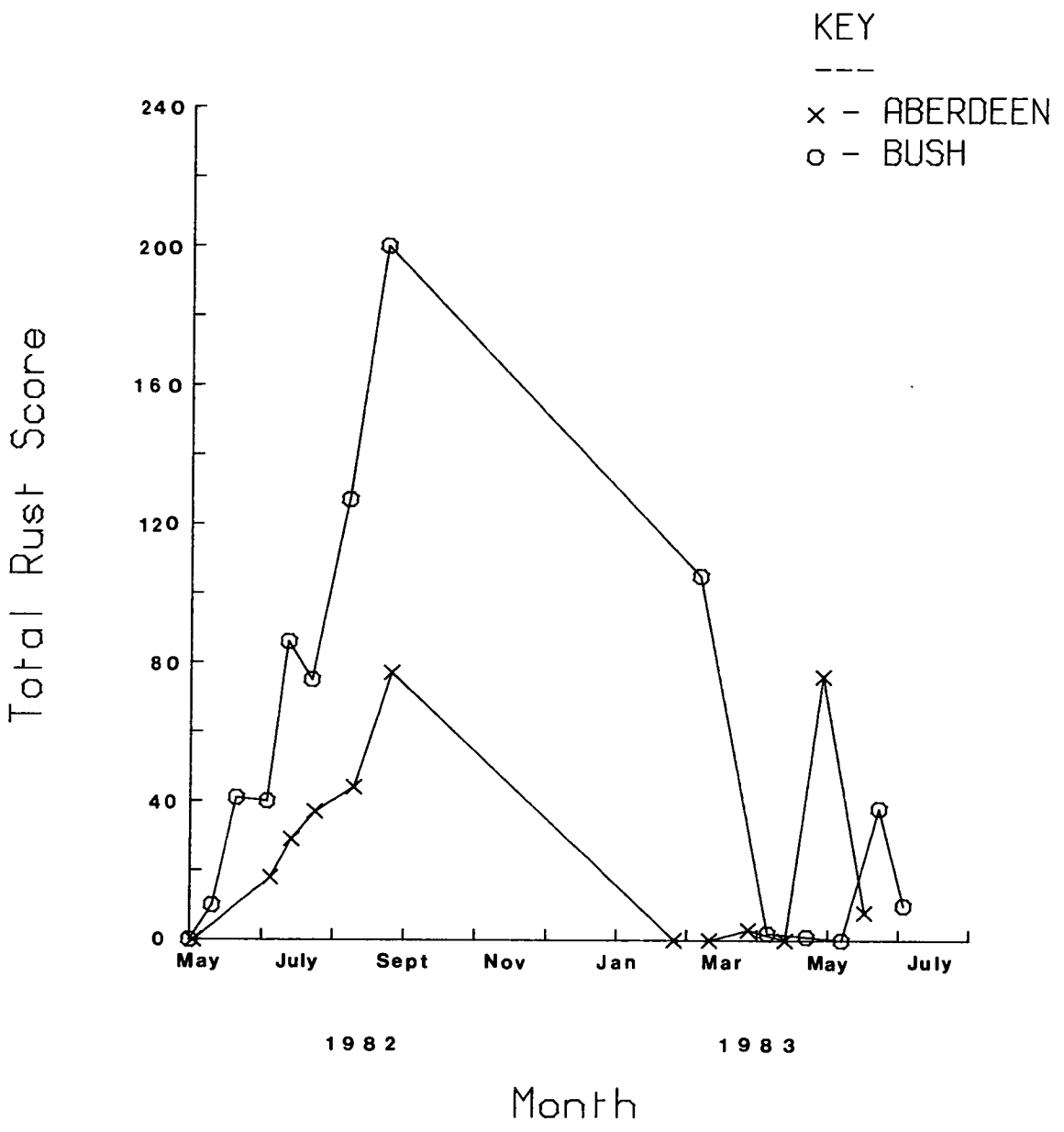
As at Aberdeen, there is a tendency for plants with high dry matter production to have the highest score for rust infection. The apparently increased susceptibility of 'Lochans' compared to the results from Aberdeen could be due to the high dry matter production of this biotype at Bush. Again there are exceptions to this : 'West Cheviots' has high dry matter production but very little rust infection, and '9 Dalmelington' which was one of the most productive plants has the lowest score for rust.

'Kinlochleven', which has a low dry matter yield, has a high susceptibility to rust at Bush. 'Kinlochleven' was also susceptible to mildew at Bush, but was relatively resistant to rust

at Aberdeen. Elliott [46], has reported that rust infection can reduce the yield of Poa pratensis, and so from Elliott's results one could speculate that the rust infection on 'Kinlochleven' was a major cause of the low dry matter production of this biotype. This, however, is unlikely for two reasons. Although it is possible that infection may have contributed slightly to the low yield, the fact that 'Kinlochleven' was unproductive at Aberdeen, where it was relatively unaffected by rust, suggests that low dry matter production is a general characteristic of this biotype. Also 'Quanterness', which had the highest level of rust infection, had the highest dry matter yield at Bush. Therefore there is no obvious relationship between susceptibility to rust and dry matter production.

The level of rust infection at Aberdeen and Bush is shown in Figure 11.6.2.1.

Figure 11.6.2.1. Rust infection at Aberdeen and Bush



At both Aberdeen and Bush, rust infection reaches a peak in late summer, and declines rapidly during the winter (Figure 11.6.2.1). Unlike mildew, which is present on the plants in low amounts over the winter (Figure 11.6.1), there were periods when no

rust was visible at all during the winter.

The rust infection at Sourhope is shown in Table 11.6.2.iii.

Table 11.6.2.iii. Rust Infection at Sourhope

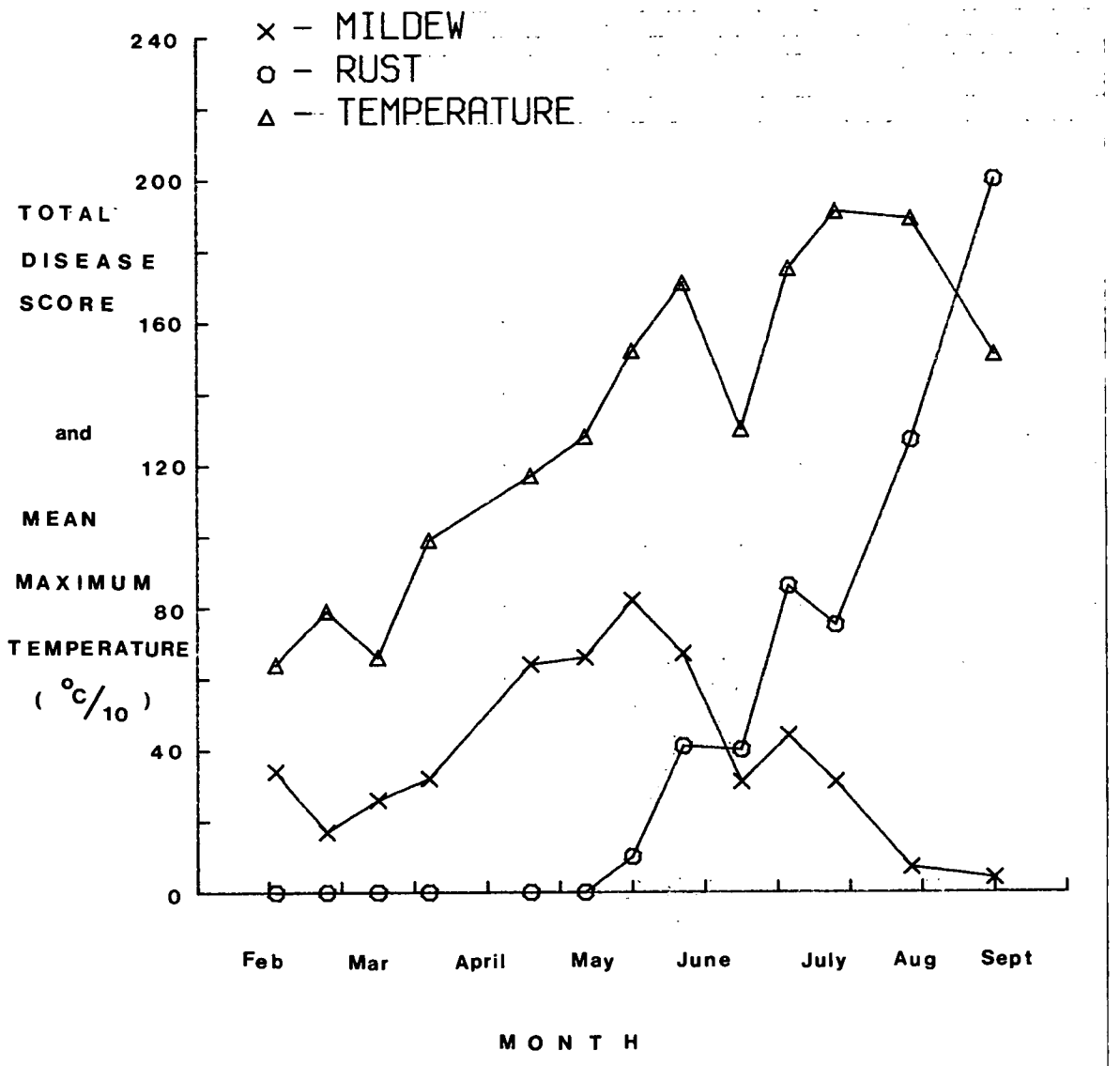
R = Total score for Rust over the two years

Biotype	R	Biotype	R
Fylking *	36	Quanterness	2
Kinlochleven	14	Baron *	1
Braemar	12	Arina *	1
Airport	11	Port Patrick	1
North Berwick	10	Newburgh	1
Stromness	6	Tomintoul	1
9 Dalmelington	5	Aviemore	1
Ben Obe	5	Primo *	0
Fannich	4	Wooler	0
Birsay	4	Yetholm	0
Lochans	3	New Cumnock	0
Knapdale	3	Cairngorm	0
West Cheviots	2	West Coast	0
8 Dalmelington	2		

These results are similar to those at the other two sites for several of the biotypes : 'Kinlochleven' and 'Airport' are fairly susceptible to rust, whereas 'Wooler', 'West Coast' and 'Primo' have high resistance. There are also some differences between the results here and in the other sites. 'Fylking' which was only moderately susceptible in the other sites is apparently very susceptible at Sourhope. 'Cairngorm' which was previously susceptible, has high resistance at Sourhope, despite having higher dry matter production and ground cover than 'Fylking'. Probably these differences are due to the different climatic and edaphic conditions at Sourhope. Disease resistance in Poa pratensis is altered by both climate [161] and soil fertility [172].

On the whole, rust infection was worst in the late summer, whereas mildew appeared fairly early in the year. The optimum temperature for mildew is reported to be lower than that for rust [149]. Some evidence for this is obtained from the results from Bush, where both mildew and rust infections were most widespread. The total 'score' for the two diseases at each visit over the summer of 1982, together with the mean maximum temperature recorded at Bush meteorological station are shown in Figure 11.6.2.2.

Figure 11.6.2.2. Disease incidence at Bush



The mildew infection increases gradually as the temperature increases, and then declines as the temperature exceeds about 12°C. No rust infection occurs until the temperature is above 12°C, and the rust spreads rapidly when the temperature is above

16°C. Thus mildew is the dominant disease when temperatures are fairly low, but at higher temperatures rust tends to predominate.

11.6.3. Drechslera poae infection

'Melting out', caused by Drechslera poae, appeared very late compared to mildew and rust. The initial symptoms - violet lesions on the leaves - were noted at Bush on 11th April and at Sourhope on 27th April, 1983. The level of infection remained fairly low initially: only 5 plots were infected at Bush on 23rd May, but there was a rapid spread of the disease in all sites in June. By 27th June, 53 plots at Bush were infected; at the other sites the number of infected plots rose from 10 on 6th June to 48 on 22nd June at Sourhope, and from 15 on 11th June to 40 on 5th July at Aberdeen. These were the last days that the sites were visited, and by this time the disease had caused high leaf mortality in several plots, resulting in a drop in the ground cover (Figures 11.5.1 and 11.5.2).

The worst Drechslera poae infection occurred at Bush (mean score 7.7), followed by Sourhope (mean 5.6) and Aberdeen (mean 4.4). The relatively low result for Aberdeen is probably due to the short infection time. The disease was not found here until June, but appeared at the other two sites in April. As with mildew and rust, the high infection rate at Bush is probably due to the rapid growth of most of the biotypes here, resulting in a denser sward and hence a better micro-environment for fungal growth than at

the other sites.

The total score for 'melting out' in the three sites is shown in Tables 11.6.3.i. to 11.6.3.iii.

Table 11.6.3.i. 'Melting out' at Aberdeen

D = Total score for Drechslera poae infection

Biotype	D	Biotype	D
Quanterness	11	Braemar	4
West Cheviots	10	Birsay	4
9 Dalmelington	9	Airport	4
Baron *	8	Port Patrick	3
Kinlochleven	8	Cairngorm	3
8 Dalmelington	7	Yetholm	2
Newburgh	6	Aviemore	2
Stromness	6	Fylking *	1
West Coast	6	North Berwick	1
Ben Obe	6	Knapdale	1
Fannich	5	Arina *	0
Primo *	4	New Cumnock	0
Wooler	4	Tomintoul	0
Lochans	4		

The correlation between dry matter production and infection rate at Aberdeen does not seem to be as strong for Drechslera poae infection as for the other diseases. Some plants with high dry matter yield, such as 'Quanterness', '9 Dalmelington' and 'Baron', also had large amounts of Drechslera poae. Other plants, however, such as 'New Cumnock' and 'Fylking' for example, had high yields and low infection rates. 'West Cheviots', which had low dry matter production, and showed very little infection with rust and mildew, seems very susceptible to Drechslera poae. The cultivars 'Fylking' and 'Arina' seem resistant to 'melting out'.

Table 11.6.3.ii. 'Melting out' at Bush

D = Total score for Drechslera poae infection

Biotype	D	Biotype	D
Primo *	29	Newburgh	6
Airport	23	Tomintoul	6
West Cheviot	13	Cairngorm	5
Baron *	12	Ben Obe	5
West Coast	11	Arina *	4
Knapdale	10	Port Patrick	4
9 Dalmelington	9	Aviemore	4
Quanterness	9	Birsay	4
Fannich	8	Fylking *	3
8 Dalmelington	7	Yetholm	3
Lochans	7	New Cumnock	3
Stromness	7	Kinlochleven	3
Wooler	6	North Berwick	2
Braemar	6		

At Bush, the relatively high yielding cultivar 'Primo' is the most susceptible to infection by Drechslera poae. 'Airport', which had mediocre dry matter production and ground cover at this site, also had a high infection rate. 'West Cheviots' and 'Baron', which were susceptible to 'melting out' at Aberdeen, were also susceptible at Bush. Similarly, 'Fylking', 'New Cumnock' and 'North Berwick' all show some resistance to the disease at both sites.

Table 11.6.3.iii. 'Melting out' at Sourhope

D = Total score for Drechslera poae infection

Biotype	D	Biotype	D
8 Dalmelington	13	Port Patrick	5
West Cheviots	9	Birsay	5
Ben Obe	9	Quanterness	5
Braemar	8	Airport	5
Newburgh	8	Arina *	4
Fannich	8	North Berwick	3
Wooler	7	Wooler	3
Lochans	7	Cairngorm	3
9 Dalmelington	7	Stromness	3
Tomintoul	7	Fylking *	2
Kinlochleven	7	New Cumnock	2
West Coast	6	Aviemore	2
Baron *	6	Knapdale	2
Primo *	5		

'8 Dalmelington', which was fairly susceptible at Aberdeen, is the plant most affected by 'melting out' at Sourhope. 'Baron' is the most susceptible cultivar at this site. Results from Sourhope confirm that 'West Cheviots' is susceptible to Drechslera poae, and that 'Fylking', 'New Cumnock' and 'North Berwick' have generally high resistance. 'Braemar' which has a high yield at Sourhope, has a relatively high infection rate here compared to the other sites.

On the whole, the results show that several of the biotypes have a similar level of resistance to Drechslera poae as that shown by the cultivar 'Fylking', and most biotypes have greater resistance than the widely used cultivar 'Baron'. A few biotypes such as 'West Cheviots' seem to have low resistance to Drechslera poae.

None of the plants at Dalmally showed any symptoms of

disease. This was probably because of the relatively small size of the plants here. Small plants will not make a suitable micro-environment for fungal growth, and also have a smaller surface area on which spores can land.

11.7. COLOUR

Colour is an important character for amenity grasses, but is not a character selected for in forage grasses [31,177]. The colour of each plot was scored at every visit, and the mean results for each site are shown in Tables 11.7.1 to 11.7.3. The mean result for the plants at Bush was 6.2, which was higher than both Sourhope (mean 5.7) and Aberdeen (mean 5.5). The scale used ranged from 1 to 8, with high scores denoting a high proportion of green leaf. Any dead, senescent or discoloured leaf reduced the score for colour.

Table 11.7.1. Colour at Aberdeen

C = Mean score for colour over two years

Biotype	C	Biotype	C
New Cumnock	6.10	Lochans	5.60
Baron *	6.07	Tomintoul	5.60
9 Dalmelington	6.07	Wooler	5.43
North Berwick	6.03	West Cheviots	5.37
Fylking *	6.00	Newburgh	5.37
Yetholm	5.90	Fannich	5.37
Quanterness	5.90	Kinlochleven	5.16
8 Dalmelington	5.86	Birsay	5.10
Cairngorm	5.86	Airport	5.10
Primo *	5.83	Knapdale	5.03
Arina *	5.80	Port Patrick	4.83
Braemar	5.80	West Coast	4.83
Aviemore	5.73	Ben Obe	3.69
Stromness	5.73		

The plants with the highest score for colour at Aberdeen, 'New Cumnock', 'Baron' and '9 Dalmelington' all had a high yield at this site. A high score for colour indicates that the plants have a high proportion of green leaves, and few senescent leaves, and so

there is likely to be some correlation between the colour scores and dry matter production. Generally the plants with low scores for colour were unproductive biotypes. However high dry matter yield is not essential for good colour: 'North Berwick' has a fairly low yield but scores well for colour.

Table 11.7.2. Colour at Bush

C = Mean score for colour over two years

Biotype	C	Biotype	C
Fylking *	6.79	New Cumnock	6.24
Quanterness	6.74	Cairngorm	6.24
Aviemore	6.71	Newburgh	6.18
9 Dalmelington	6.63	Baron *	6.13
Arina *	6.47	Primo *	6.11
North Berwick	6.47	Fannich	6.00
Wooler	6.47	Birsay	6.00
Braemar	6.45	Airport	5.95
Stromness	6.45	Knapdale	5.92
Yetholm	6.45	West Cheviots	5.92
Lochans	6.45	Port Patrick	5.89
Tomintoul	6.37	Ben Obe	5.79
West Cheviots	6.34	Kinlochleven	5.34
8 Dalmelington	6.24		

At Bush, the high yielding 'Quanterness' and '9 Dalmelington' have high scores for colour, and the unproductive 'Kinlochleven' and 'Ben Obe' have a low proportion of green to non-green tissue. However 'Fylking', 'Aviemore', 'Arina' and 'North Berwick' score better for colour than would be expected from the dry matter production results. Also 'Primo', 'West Cheviots' and 'Cairngorm' had relatively low scores for colour.

Table 11.7.3. Colour at Sourhope

C = Mean score for colour over two years

Biotype	C	Biotype	C
North Berwick	6.54	West Cheviots	5.59
New Cumnock	6.13	9 Dalmelington	5.59
Braemar	6.12	Baron *	5.56
Knapdale	6.03	Arina *	5.56
Yetholm	6.00	Airport	5.56
Cairngorm	5.82	Ben Obe	5.53
Aviemore	5.82	8 Dalmelington	5.41
Fylking *	5.79	Newburgh	5.41
Lochans	5.79	West Coast	5.41
Wooler	5.76	Fannich	5.29
Stromness	5.71	Kinlochleven	5.26
Quanterness	5.68	Tomintoul	5.21
Port Patrick	5.68	Birsay	5.00
Primo *	5.59		

At Sourhope, the biotypes that had a relatively high yield here compared to their performance at the other sites - 'Braemar' and 'Knapdale' - also scored well for colour. 'Fylking' which had fairly low yield here again had better overall colour than the other cultivars. As 'Fylking' is intended for use as an amenity grass, it has presumably been selected to have good colour. The other amenity grass cultivar used here - 'Baron' - has relatively poor colour. This could be because it is intolerant of acid conditions [203], and has very low dry matter production at this site.

Any discolouration of the leaves caused by disease will affect the score for colour. However there is very little evidence for a high correlation between disease susceptibility and poor overall colour. At Bush, where disease incidence was highest, 'Quanterness' was infected with relatively large amounts of mildew

and rust, yet had a very high score for colour at this site. Also Ben Obe, which had very little disease, had a poor score here for colour. So disease does not seem to be a very important factor affecting colour. Other characters, such as vigorous growth indicated by a high dry matter yield, seem to have a more significant effect on colour.

Generally the plants at Dalmally had a lower proportion of green leaf than at the other sites, probably due to their low growth rate here (see Table 11.4.3). The mean results for the plants at Dalmally are shown in Table 11.7.4.

Table 11.7.4. Colour at Dalmally

Colour = Mean Score for colour over the nine months.

Biotypes	Colour	Biotypes	Colour
Quanterness	4.0	Knapdale	3.7
New Cumnock	4.0	Lochans	3.6
Baron *	3.8	Arina *	3.4
9 Dalmelington	3.7	Birsay	3.3

As at the other sites, plants with high dry matter production have good colour (see Table 11.4.3). 'Quanterness' has relatively good colour at Dalmally, compared to the result at Sourhope, and 'Baron' also does better at Dalmally than at Sourhope relative to the other plants. 'Birsay', which had poor colour at the other sites, has the worst colour at Dalmally.

The proportion of green to non-green leaf was at its lowest during the winter, so the scores for colour were lowest over winter. Good winter colour is one of the characteristics sought in amenity grass cultivars [177]. The mean score per biotype towards

the end of the winter in both 1982 and 1983 is shown in Tables 11.7.5. to 10.5.7.. Scores were recorded at Aberdeen on 24th February, 1982 and 16th February, 1983; at Bush on 3rd March, 1982 and 3rd March, 1983 ; and at Sourhope on 17th March, 1982 and 27th January, 1983. The minimum value recorded for each biotype is also shown. All scores are on the scale 1 - 8, with 8 representing the best colour.

Table 11.7.5. Winter colour at Aberdeen

C = Mean value for colour in winter

L = Lowest value recorded over two years

Biotype	C	L	Biotype	C	L
9 Dal	5.75	4.5	Strom	4.25	2.5
Lochans	5.00	4.0	Yetholm	4.00	2.5
Quant	5.00	3.5	Cumnock	4.00	1.0
8 Dal	4.75	3.5	Wooler	3.75	2.0
Baron *	4.50	3.0	Newburgh	3.75	3.0
N.Ber	4.50	2.5	Fannich	3.50	1.0
Braemar	4.50	3.0	Birsay	3.25	2.5
Tomin	4.50	3.0	Airport	3.25	1.5
Avie	4.50	2.5	Kinloch	3.00	1.0
Tomin	4.50	3.0	W.Coast	3.00	1.5
Primo *	4.25	2.5	Port P	2.75	2.5
Fylking*	4.25	2.5	Knap	2.75	2.0
Arina *	4.25	2.0	Ben Obe	1.00	1.0
W.Chev	4.25	2.5			

In terms of winter colour at Aberdeen, five biotypes achieved higher scores than the best cultivar, 'Baron'. Generally the cultivars came lower in the order for winter colour than they did for overall colour, indicating that several of the biotypes have more consistent colour than the cultivars. The biotype '9 Dalmelington' had extremely good winter colour at this site. 'Lochans', which had only a moderate score for overall colour, also did well over the winter. The biotype with best overall colour, 'New

Cumnock', had fairly poor winter colour. The lowest value recorded for 'New Cumnock' (1.0) indicates that at its worst point over the two years, only about 25% of the total leaf surface was green: this poor winter colour would be a disadvantage in an amenity grass.

All the biotypes with very poor winter colour at Aberdeen originated in the west of Scotland, and were all originally growing in maritime areas. The environment to which these biotypes are presumably adapted would be milder than at Aberdeen, and their low scores for colour reflect their inability to retain a high proportion of green leaf over the cold winters here.

Table 11.7.6. Winter Colour at Bush

C = Mean colour over winter

L = Lowest value recorded

Biotype	C	L	Biotype	C	L
Arina *	5.75	3.5	Braemar	4.00	2.0
Aviemore	5.50	4.0	Knap	4.00	3.5
Fylking *	5.25	2.5	Primo *	3.75	1.5
Wooler	4.75	3.5	Baron *	3.75	1.5
Quant	4.75	1.5	Newbur	3.75	2.5
9 Dal	4.50	3.0	Fannich	3.75	2.5
Strom	4.50	3.0	W.Coast	3.25	2.5
Lochans	4.25	2.5	Port P	2.75	2.5
Cumnock	4.25	2.5	N.Ber	2.50	2.0
Tomin	4.25	2.5	Yetholm	2.25	1.5
Cairn	4.25	2.5	Birsay	2.00	1.0
Airport	4.25	2.5	Ben Obe	1.75	2.0
W.Chev	4.00	2.0	Kinloch	1.50	1.0
8 Dal	4.00	2.0			

At Bush the cultivars 'Arina' and 'Fylking' and the biotypes 'Aviemore', 'Quanterness' and '9 Dalmelington' all had good winter colour as well as high overall scores for colour. Although 'Quanterness' had good winter colour, the lowest value recorded for

this biotype (1.5) is lower than for most other plants. This suggests that 'Quanterness' may not be ideal for use as an amenity grass, although the cultivar 'Baron', which is commonly used as an amenity grass, also has a minimum score of 1.5, and has poorer overall winter colour than 'Quanterness'.

Table 11.7.7. Winter Colour at Sourhope

C = Mean score for colour over winter

L = Lowest score over two years

Biotype	C	L	Biotype	C	L
N.Ber	5.00	3.5	Baron *	3.75	2.0
Avie	5.00	3.5	Arina *	3.75	1.5
Fylking *	4.75	3.0	Port P	3.75	2.0
Quant	4.75	2.5	8 Dal	3.75	2.5
9 Dal	4.50	2.5	Fannich	3.75	2.0
Braemar	4.50	2.5	Strom	3.75	2.5
Cumnock	4.30	2.5	Tomin	3.50	2.0
Wooler	4.25	2.5	Primo *	3.25	1.5
Yetholm	4.25	2.5	W.Coast	3.25	1.0
W.Chev	4.25	2.5	Newbur	3.0	2.0
Lochans	4.00	3.0	Kinloch	2.75	1.5
Cairn	4.00	2.5	Ben Obe	2.50	2.0
Knap	4.00	2.0	Birsay	2.00	1.5
Airport	4.00	2.0			

Results from Sourhope indicate, as at Bush, that 'Aviemore', 'Fylking', 'Quanterness' and '9 Dalmelington' have good winter colour. The biotype 'North Berwick', which had the best colour overall at Sourhope, also had the best winter colour. 'Baron' and 'Primo' have fairly poor winter colour.

The results as a whole show that the biotypes '9 Dalmelington', 'Quanterness' and 'Aviemore' generally have good winter colour. Of the four cultivars, the amenity grass 'Fylking' performs relatively well, but 'Baron' - which is also an amenity grass - has a fairly poor winter colour at Bush and Sourhope.

As well as the 'score' for colour, which shows the proportion of green leaf on the plants, obvious colour differences between the biotypes were noted. The results are summarised in Table 11.7.8.

Table 11.7.8. Differences in colour between the biotypes

Letters in brackets after a biotype indicate the site at which that colour was recorded. If no brackets follow the biotype name, the colour was present at all three sites.

A = Aberdeen, B = Bush, S = Sourhope

Light green	Dark green	Blue-green
North Berwick	9 Dalmelington (B,S)	Port Patrick (B,S)
Yetholm (S)	Birsay	8 Dalmelington
New Cumnock	Kinlochleven (B)	Fannich
Tomintoul (A,B)		West Coast
Aviemore		Airport
Quanterness		Ben Obe (B,S)
Knapdale		Baron
Fylking (B,S)		
Arina		

Colour in Poa pratensis is affected by both fertilization and cutting frequency [161]. Plants that are well fertilized and frequently cut tend to be dark green, and plants that are fertilized and cut infrequently are lighter in colour. It is therefore difficult to compare results for colour between different trials using different management techniques. Shildrick has reported that plants of Poa pratensis with high growth rates are usually light green [177]. Table 11.4.1. shows that some plants with normally high dry matter production, such as 'Quanterness', 'New Cumnock' and 'Fylking', are indeed light green. Others with fairly low dry matter yields, however, such as 'Knapdale' and 'Tomintoul' are also light

green. Also '9 Dalmelington' which had high dry matter production at Bush, also has dark green leaves at this site. The other two biotypes with dark leaves, 'Birsay' and 'Kinlochleven', have low dry matter production at all the sites. There is no obvious correlation between dry matter production and plants with blue-green leaves.

For amenity uses, normally a dark green grass is desirable [161]. None of the cultivars used here were dark green, however, and the widely used amenity grass 'Fylking' was generally light green. Possibly this is because the grass in this experiment was not cut as frequently, or fertilized as much as is the case in some trials [161], which tend to show 'Fylking' and 'Baron' as having dark green colour.

11.8. FLOWERING

During the summer, a record was kept of the plots which were producing panicles, and the plots which were flowering (anthers dehisced). As visits to the plots were at about 2 or 3 weekly intervals, this gives only an approximation to the actual flowering time.

Flowering was later in 1983 than in 1982. For example, panicles were first noted in 1982 at Sourhope on 29th April, but no panicles were visible here on 13th May in 1983. The dates of initial panicle production and flowering are shown in Table 11.8.1

Table 11.8.1. Time of panicle production and Flowering

Panicle = date on which the first panicle was noted at that site

Flowering = date at which the first flower with anthers dehisced was noted

	1982		1983	
Site	Panicle	Flowering	Panicle	Flowering
Aberdeen	5th May	3rd July	21st May	5th July
Bush	3rd May	31st May	23rd May	27th June
Sourhope	29th April	9th June	3rd June	21st June

The apparently late date for flowering at Aberdeen in 1982 was caused by a delay in the normal schedule for visiting this site. No visit was made between 25th May and 3rd July, 1982, due to difficulties with transport. There is no evidence that plants at Aberdeen flower significantly later than at the other two sites.

In most cases, the interval between visits to each site was longer than any difference in flowering time between the biotypes. For example at Bush in 1983, no plants had flowered by 13th June, but at the next visit flowering had started in all the plants that flowered that year. However at Sourhope in 1982 some differences between the biotypes were apparent. All the biotypes and cultivars flowered here on 9th June, but the length of time that the plants carried on flowering after this varied form plant to plant. It should be recalled that the plants were cut at each visit, so panicles flowering at each visit after 9th June had grown since the last visit. This means that the regrowth capacity of the plants will affect the recorded flowering time. The last date on which flowering was recorded for each biotype in 1982 is shown in Table 11.8.2.

Table 11.8.2. Flowering period at Sourhope

Date = last date at which flowering panicles were noted

Biotype	Date	Biotype	Date
Primo *	9th June	Yetholm	8th July
Baron *	9th June	West Cheviots	8th July
Arina *	9th June	Lochans	8th July
New Cumnock	9th June	Fannich	8th July
Knapdale	9th June	Quanterness	8th July
North Berwick	25th June	Wooler	22nd July
9 Dalmelington	25th June	Stromness	22nd July
Newburgh	25th June	Fylking *	22nd July
Braemar	25th June	Port Patrick	14th August
Tomintoul	25th June	8 Dalmelington	14th August
Aviemore	25th June	Birsay	14th August
Cairngorm	25th June	Kinlochleven	14th August
Airport	25th June	West Coast	14th August
Ben Obe	25th June		

Generally, plants which flower for a long period at Sourhope originate from the west of Scotland. There is still

considerable variation between plants from a similar area - 'West Coast' and 'Ben Obe' were collected only 5 km apart, and yet differ considerably in the length of time that they flower. Some of these differences may be due to the fact that these plants were cut regularly at a height of 2.5cm, so plants with poor regrowth capacity will have their normal flowering period curtailed. Habjorg has found that Poa pratensis biotypes from northern Norway flower earlier than southern plants [224]. There is very little evidence in Table 10.6.ii. that this is true in Scotland, possibly because the maximum latitudinal difference between collection sites was only $4^{o}20'$, compared to $15^{o}45'$ in the Norwegian study.

CHAPTER 12. SEED PRODUCTION AND GERMINATION

12.1. Seed Production

The biotypes and cultivars that were used in the experimental plots (see Table 10.2.3) were planted out at the Botany Department, Edinburgh and were left uncut so that their seed production could be estimated.

Seeds were collected from the biotypes and cultivars that flowered in 1982 and used in the standard germination test [189] in order to compare the germination percentage and germination vigour of the cultivars and biotypes.

12.2. Seed Production Results

Tillers were planted out in April, 1982, and seed production estimated by counting the number of seeds per panicle on 10 panicles per biotype in July, 1983. The cultivar 'Primo' and biotypes 'Wooler', 'Yetholm', Tomintoul', 'Knapdale' and 'Stromness' did not flower in 1983. Results of seed production by the other biotypes and cultivars are shown in Table 12.2.1.. Some of the biotypes, and the cultivar 'Fylking' produced less than 10 panicles. The number of panicles counted is also shown in the table.

Table 12.2.1. Seed production

N = Number of panicles examined

Seed = Mean seed production per panicle

Biotype		N	Seed	Biotype	N	Seed
Quanterness		2	380	Lochans	8	185
Fylking	*	2	333	West Coast	10	185
Baron	*	10	276	Cairngorm	10	182
Fannich		10	254	Ben Obe	10	179
New Cumnock		5	223	Port Patrick	10	161
West Cheviots		10	220	Newburgh	7	148
Arina	*	10	215	8 Dalmelington	10	146
Braemar		10	211	Airport	10	140
9 Dalmelington		10	208	Kinlochleven	10	136
North Berwick		10	206			

Although 'Quanterness' has the highest number of seeds per panicle, the mean for all the biotypes is 194 seeds per panicle, compared to a mean of 275 seeds for the cultivars. So the biotypes generally produce fewer seeds that the cultivars. More important than this difference, however is the variation in the number of panicles produced.

Although 'Quanterness' had a large number of seeds per panicle, only 2 panicles of this biotype were produced. Several other plants, including the cultivar 'Fylking', produced less than 10 panicles, and five biotypes and the cultivar 'Primo' did not flower at all. Generally, seed production is a problem with Poa pratensis: several cultivars that flower well in one area will flower very poorly or not at all in another [150]. Normally this occurs when plants are grown at very different latitudes for where they originated, but this is not always so: 'Fylking' which was collected in southern Sweden does not flower well in southern Norway [225]. The plants that flowered poorly at Edinburgh did not come

from a specific geographical or climatic area. For example, three biotypes were collected from Orkney: 'Birsay' did not flower at all, 'Quanterness' only produced two panicles, but 'Stromness' flowered well.

Poa pratensis has a dual requirement for flower initiation and development. Low temperatures and short photoperiods are required to initiate floral primordia, but high temperatures and long photoperiods are required for the development of flowers [225], As Heide points out, this complex dual induction pattern means that complications may arise at several stages, when plants are growing different areas, resulting in poor flowering [225]. The balance between flowering and non-flowering is very delicate: this is illustrated by the fact that plants of the biotypes that did not flower in this experiment - 'Wooler', 'Yetholm', 'Tomintoul', 'Knapdale' and 'Stromness' - all flowered at Edinburgh in 1982 when placed outside in boxes (see Chapter 12.3.).

12.3. Germination Tests

Germination tests were carried out on seed from the 22 biotypes and 2 cultivars that flowered in 1982. Plants of 'Port Patrick' and the cultiars 'Primo' and 'Fylking' did not flower in 1982. Habjorg has also found that 'Fylking' flowers very rarely [225]. Poa pratensis does not normally flower in the first year after being sown as seed [226]. By using tillers instead of seed, it was hoped that this problem could be overcome. Possibly the plants that did not flower were not exposed to low temperatures for long enough to induce primordial initiation. The vernalization requirement for 'Fylking' seems to be longer than for most cultivars [225].

The number of germinated seeds, and 'grown' (primary shoot over 2.5mm long) seeds were recorded twice weekly for four weeks. A computer program was written which worked out the mean results at each count for the four replicates of a hundred seeds of each biotype. The program also worked out the mean daily increase in the germinated and 'grown' seeds, and from this estimated the time taken for 50% of the seeds to germinate and 50% of the seeds to 'grow'. The difference between these two times shows the time for the average seed to progress from germination to potential photosynthesis. This was thought to be a more accurate measure of the vigour of the seeds than the normal estimate of 'germination vigour' which is:

{(Germination at day 10/Germination at day 28) X 100 } [177].

12.4. Germination results

In this experiment, 'vigour' is calculated by taking the inverse of the time for the average seed to progress from germination to potential photosynthesis (primary shoot over 2.5mm long). This was thought to give a more accurate measure of the vigour of the seeds than the normal 'germination vigour'. To illustrate this, the germination of 'Cairngorm' and 'Arina' is shown in Figure 12.4.1.

Figure 12.4.1. Germination of 'Cairngorm' and 'Arina'

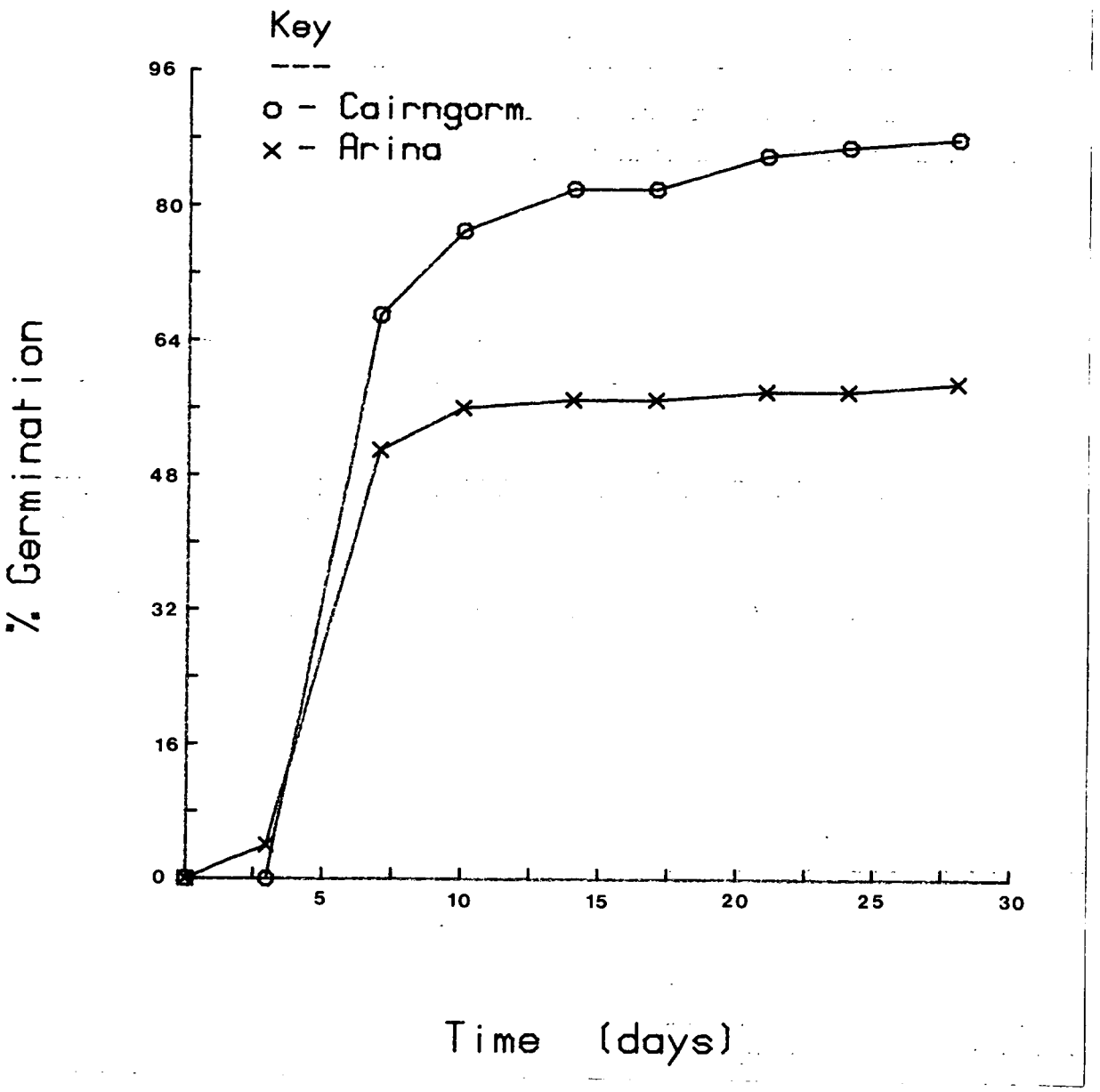


Figure 12.4.1. shows that 'Cairngorm' germinates faster than 'Arina', and 'Cairngorm' also reaches a higher final germination. Therefore any measure of germination vigour should give 'Cairngorm' a higher value than 'Arina'. This is not so: the

traditional calculation of germination vigour [177] gives values of 94 for 'Arina' and 87 for 'Cairngorm'. In contrast, the calculation of vigour used in this study gives values of 0.27 for 'Arina' and 0.32 for 'Cairngorm'. This latter calculation requires more frequent recording of germination than normal (twice weekly instead of fortnightly), but this seems worthwhile considering the increased accuracy of the results.

The results for final germination (day 28), and estimated time for 50% of the seeds to germinate and 'grow', for all the biotypes and cultivars tested, are shown in Table 12.4.1.

Table 12.4.1. Germination of Biotypes and Cultivars

F = Final percentage germination

G = Estimated time in days for 50% of the seeds to germinate

S = Estimated time in days for 50% of the seeds to 'grow' (shoot length exceeding 2.5mm)

V = Vigour (1/[S - G])

Biotype		F	G	S	V
Baron	*	90	8.5	11.7	0.31
9 Dalmelington		89	5.8	6.8	1.00
Cairngorm		88	6.8	9.9	0.32
Fannich		86	6.0	6.6	1.67
Quanterness		85	6.6	8.8	0.45
Wooler		85	7.0	11.1	0.24
Tomintoul		83	6.8	10.7	0.26
Birsay		83	8.0	12.8	0.21
Knapdale		82	8.2	12.7	0.22
Ben Obe		82	6.4	11.2	0.21
New Cumnock		80	6.3	7.0	1.43
Kinlochleven		78	7.2	13.2	0.17
West Cheviots		77	6.5	9.3	0.36
Aviemore		76	6.5	7.9	0.71
Newburgh		75	6.5	10.1	0.28
Yetholm		74	6.8	12.2	0.19
West Coast		72	6.2	11.0	0.21
North Berwick		71	6.1	9.1	0.34
Airport		70	9.0	13.2	0.24
Braemar		69	8.5	13.2	0.21
8 Dalmelington		68	6.6	9.9	0.30
Stromness		68	7.2	12.0	0.21
Lochans		68	10.7	13.7	0.33
Arina	*	60	6.9	10.6	0.27

The final germination of most biotypes was above the 75% minimum required for certification [190]. The lowest final germination was for the cultivar 'Arina'. Seed of all cultivars must have at least 75% germination before it can be certified and sold, and the original seed from which the plants of 'Arina' were obtained for this study had over 80% germination in this test. The low

germination result subsequently may be because fresh seed was used in this experiment. Seed dormancy is prolonged in Poa pratensis [227], and dormancy is deeper than in most other grass species [50]. Although the alternating temperatures and potassium nitrate used in this germination test will tend to break dormancy in Poa pratensis [228], it is possible that there was still some residual dormancy which reduced the total germination of 'Arina', and possibly also several of the biotypes.

The estimated time for 50% of the seeds to germinate varies widely from 5.8 days for '9 Dalmelington' to 10.7 days for 'Lochans'. Although 'Baron' has the highest final germination, it germinates fairly slowly - the estimated time for 50% of the seeds to germinate (8.5 days) is later than the mean time for all the biotypes and cultivars (7.1 days). Seeds of 'Baron' also take a long time to 'grow' (shoots > 2.5mm long) compared to the biotypes with highest germination.

It is interesting that several of the biotypes with high seed 'vigour' - '9 Dalmelington', 'New Cumnock', 'Cairngorm' and 'Quanterness' - tend to perform relatively well in the experimental plots in terms of dry matter production and ground cover. Also the plants that do relatively poorly in the plots, such as 'Ben Obe', 'Birsay' and 'Kinlochleven', tend to have low 'vigour'. The main exception to this is 'Fannich' with very high seed 'vigour' but mediocre performance in the plots. Plants of soyabean with rapidly germinating seeds and high 'vigour' have greater dry matter yields than plants with low 'vigour' [229]. However with grasses, the initial differences in vigour between seeds of the same species are reported to be short lived [230], so it is possible that this

apparent correlation is fortuitous. The results do however suggest that many biotypes have greater initial 'vigour' than the cultivars, so there is no evidence that the cultivars are exceptional in terms of speed of germination.

CHAPTER 13. DISCUSSION OF SECTION B.

13.1. Discussion

In Section B, the performances of twenty three biotypes and four cultivars were compared in experimental plots. The parameters recorded were: plant survival, dry matter production, ground cover, disease resistance, colour, and flowering time. Three main experimental sites were used: Aberdeen, Bush and Sourhope. These experimental sites differ in both climate and soil.

The results for all the biotypes and cultivars were treated identically, except for the biotype 'Ben Obe' in the experimental plot at Aberdeen. This biotype was grown here for only one year, and so the results for dry matter production and ground cover presented in Section B are estimates of the results after two years growth, based on the first year's performance. This is discussed below. Analysis of Variance results are in Appendix 2.

A small experimental plot at Dalmally was also used, to enable a comparison to be made, for some of the biotypes and cultivars, between the results when grown in eastern Scotland (the main experimental sites), and western Scotland (Dalmally). The significance of the Dalmally results are discussed in this chapter. Next, the significance of some of the results are discussed in terms of the objectives of plant breeders. Finally, the results from the experimental plots are compared with the results obtained by other authors who have worked on Poa pratensis, and the biotypes which show potential for possible development as cultivars are indicated.

The biotype 'Ben Obe' was grown at the experimental site at Aberdeen for only one year (see pages 116-117), whereas the other biotypes and cultivars were grown here for two years. The results for dry matter production and ground cover for this biotype were therefore estimated at Aberdeen by multiplying the results for 'Ben Obe' after one year by the mean percentage increase of the other plants between year one and year two. This assumes that 'Ben Obe' is an average plant. It is theoretically possible that this biotype would perform much better than average during its second year at Aberdeen, which would mean that the actual results have been underestimated. However the results from Bush and Sourhope for the dry matter production of this biotype are fairly low (see Table 11.4.1), and suggest that this is not a vigorously growing biotype. It is therefore more likely that the dry matter production results for this biotype at Aberdeen have been overestimated. 'Ben Obe' has good ground cover at Sourhope (Table 11.5.1), but the estimated ground cover at Aberdeen, which is derived from the results after one year, is so low that this biotype would have had to spread spectacularly well in the second year merely to achieve moderate ground cover. On the whole, therefore, it is unlikely that the estimation of results for 'Ben Obe' at Aberdeen has meant that a potentially useful biotype has been overlooked.

At Dalmally, the two cultivars grown there , ('Baron' and 'Arina'), did not survive well, and the biotypes 'Lochans' and 'New Cumnock' also had relatively high mortality. However the plant survival at Dalmally was generally fairly high compared to that at Aberdeen (see pages 150-151) and, considering the acidity of the

soil at Dalmally (pH 4.3), the plant survival results suggest that most biotypes should be able to endure well in this climate.

The ranking of the biotypes and cultivars in terms of dry matter production at Dalmally is very similar to the results from Sourhope after one year of growth (Table 11.4.2). At Dalmally, however, 'Quanterness' produces more than twice as much dry matter as the next most productive biotype ('Lochans'), whereas at Sourhope after one year 'Quanterness' produced only about 10 % more than 'Lochans'. As at the other sites, the results for colour at Dalmally show that, generally, plants with high dry matter production have better colour (a higher proportion of green leaf) than plants with low dry matter production.

On the whole, the results from Dalmally agree fairly well with the results from the other sites. 'Quanterness' performs well in all four experimental sites, whereas 'Birsay' is a uniformly unproductive biotype. This shows that the results from the main experimental sites are not biased in favour of plants from eastern Scotland; even when grown in western Scotland, the performances of 'Knapdale' and 'Birsay' are unimpressive.

As the biotypes used in the experimental plots were specifically collected for this work, obviously no other data on these biotypes has been published. However other workers have used the same cultivars as controls as were used in this study. The performance of the cultivars in this study was similar in several cases to the results reported by other authors. For example, 'Arina' has relatively good resistance to rust (Table 11.6.2), which agrees with the results of Jensen [173]. Also, other authors have found

that 'Primo' is susceptible to 'melting out' [148], and 'Fylking' is resistant to 'melting out' [204]. Table 11.6.3 provides further evidence for these statements.

However some of the results presented here differ from the results of other workers. 'Fylking' in this study was fairly susceptible to rust (see Table 11.6.2), whereas this cultivar has elsewhere been reported to have good resistance to rust [31]. This difference may be due to exposure to different concentrations of spores : the number of spores varies greatly with the distance from the nearest infected plant [223]. An alternative explanation is that although 'Fylking' is relatively susceptible compared to the biotypes and cultivars used in this study, it may be much more resistant to rust than the majority of Poa pratensis cultivars. One of the problems with comparing disease resistance in different trials is that results are expressed relative to the other plants used in that particular trial. Obviously if different plants are used in a second trial , the relative performance of a particular cultivar may be completely different. This is also a problem with the results for colour, which are also to some extent subjective. It would be obviously advantageous to have an absolute, quantitative measure for both these characters, to enable comparisons to be made between trials conducted in different areas. However it is very hard to devise an accurate, rapid method of assessing disease and colour in a quantitative and objective way. At the moment, the only practicable way of comparing different trials is if the same cultivars are used as contols in both trials. It would therefore be beneficial if certain cultivars could be used as standards - to be included in all trials of that particular species - by the different

testing stations.

Murray [203], compared the dry matter production of several cultivars of Poa pratensis grown in the greenhouse in soil at pH 5.7 and pH 4.6. The yield of 'Baron' was considerably less at pH 4.6, and Murray concluded that 'Baron' was intolerant of acid soils. The initial results from the study reported here seemed to confirm this view: the dry matter production of 'Baron' was indeed lower, compared to the other cultivars, at Sourhope (pH 5.0) than at Aberdeen (pH 6.6). However in the acid soil at Dalmally (pH 4.3), 'Baron' had relatively high dry matter production (see Table 11.4.3). Thus in the experimental plots, several different factors can affect the dry matter production of a particular biotype or cultivar, and so the results cannot be predicted simply on the basis of one factor in isolation. The conditions in experimental plots are much closer to conditions to which the plants would be exposed if they were used as amenity or forage grasses. This allows the effective performance of potential cultivars to be predicted more accurately than by using greenhouse experiments.

On the whole, the results from the experimental plots show that the biotypes display a wider range of variation for any character than the cultivars. There are biotypes at every experimental plot, for example, with higher dry matter production than the cultivars, and others with lower dry matter production. This large degree of variability suggests that there is considerable scope for producing improved cultivars from wild biotypes.

Winter survival, of both cultivars and biotypes, was surprisingly high. Laycock [161] reported considerable winterkill of

Poa pratensis cultivars - including 'Fylking' and 'Baron' - grown at Aberdeen. One possible reason for this difference could be that in the trial conducted by Laycock, the plots were fertilized with large amounts (280 kg/ha) of nitrogen, and cut every three or four days [161]. The hardiness of Poa pratensis is decreased by large inputs of fertilizer [156,157], and in other grass species frequent cutting reduces winter hardiness [158]. Trials conducted by Laycock using less fertilizer and less frequent cutting had much lower levels of winterkill [166].

The results in Table 11.3.1 and 11.3.2 show that the initial plant mortality was much higher than mortality over winter. This result is probably mainly due to the unusually dry weather immediately after planting (see pages 149 and 152). The biotypes and cultivars were initially planted out as individual tillers, and tillers - with their relatively short roots - seem to be much more susceptible to drought than established plants: mortality of established plants was much lower than that of newly planted tillers (Section 11.3).

The results from experimental plots show that several characters seem to be correlated. For example, plants with high dry matter production generally show higher amounts of fungal infection. From the point of view of the plant breeder, such correlations may not be advantageous. For forage grass, where dry matter is very important [146,152], the plant breeder may aim to combine high dry matter production with high disease resistance. This may be possible - the plants in this study definitely varied in their resistance to disease - but the fact that vigorously growing plants make a

favourable micro-environment for fungal growth means that very high levels of resistance are required.

Plants in the experimental plots that had high dry matter production also tended to have a high proportion of green leaves. A uniform green sward is desirable in amenity grass (31, 153), but high dry matter production may be a disadvantage. So here is another example where the plant breeder may have conflicting aims. However given the range of variation displayed by the biotypes, it is likely that, given a large enough sample, plants can be found with the characteristics required.

Several of the biotypes perform better than the cultivars in terms of one particular character, or at one experimental site. For example, 'West Coast' has good resistance to rust; 'Braemar' has good dry matter production and ground cover at Sourhope.

The analysis of variance of the results shows this clearly. The analysis reveals several significant site X biotype interactions for all the objective, quantitative characters: plant survival in 1982 ($p < 0.01$), % ground cover ($p < .05$ – $p < .001$) and dry matter production ($p < .001$). This indicates that different biotypes are varying in their performance in the different sites - some having their best performance at a site where other biotypes perform badly. This illustrates the great genetic variability of the plants growing in the wild; plants growing only a few miles apart respond differently to the same environment. It may be possible to incorporate such characters into promising biotypes using a large scale crossing programme, but given the facultative apomixis of Poa pratensis this is likely to be a long term, and expensive, process. Initially cultivar development should rely on the selection of genotypes that are already present in wild plants. There are four biotypes that warrant further investigation from this point of view: 'Quanterness', 'New Cumnock', '9 Dalmelington'

and 'Cairngorm'.

'Quanterness' has better dry matter production than any of the cultivars at all four experimental sites. It has fairly good ground cover and good colour. It therefore shows potential as a possible dual purpose cultivar, for both 'amenity' and 'forage' use. One possible problem with 'Quanterness' is that it seems to be fairly susceptible to 'melting out' (Tables 11.6.6 to 11.6.8). As 'melting out' only appeared at the end of the experimental period, the results in Tables 11.6.6 to 11.6.8 are tentative: it would be very useful to investigate resistance to Drechslera poae over a longer period. However, from the results in these Tables, 'Quanterness' seems to have a similar level of resistance to 'melting out' as does the widely used cultivar 'Baron', and so this level of susceptibility may not be an impediment to developing a cultivar from 'Quaterness'.

Although the seed production per panicle of 'Quanterness' is high (Table 12.2.1), relatively few panicles were formed. This suggests a possible problem with seed multiplication of this biotype. It has been reported in Poa pratensis that plants with otherwise promising performance have a low seed yield (147, 150). However perhaps not too much emphasis should be placed on the results from only one year, as the flowering of Poa pratensis varies from year to year: some biotypes that flowered in Edinburgh in 1982 did not flower in 1983 (pages 208-211). Presumably this is due to the complex dual induction requirement of Poa pratensis (225) (see pages 209-210). The plants that were scored for seed production in this study were left uncut. Evans (127) has reported that seed yield of Poa pratensis is increased by occasional cutting, and so it is possible that cutting could be used to stimulate the flowering of 'Quanterness'.

'New Cumnock' is another biotype which has potential for development

as a cultivar. It has dry matter production comparable to that of 'Primo' and 'Arina', which are both dual purpose cultivars. The great advantage that 'New Cumnock' has, however, is good resistance to 'melting out' (see Table 11.6.3). This disease can be a severe problem in Poa pratensis, and can kill large areas of turf (161). Any plant with increased resistance to Drechslera poae will have a considerable long term advantage.

The other two potentially useful biotypes are '9 Dalmelington' and 'Cairngorm'. Both of these would be more suited to amenity rather than forage use. '9 Dalmelington' has high dry matter production at Aberdeen and Bush, and good ground cover, especially at Bush. It has a high level of resistance to mildew and rust, and is moderately resistant to Drechslera poae. It has a high proportion of green leaf during winter, and a dark green colour.

'Cairngorm' has good ground cover, and fairly high dry matter production. It is moderately resistant to Drechslera poae but is fairly susceptible to rust. It has good winter colour. Seed production per panicle is about average, but many panicles are produced, and so seed multiplication should not be a problem. The work that would be required in the future in order to develop cultivars from these biotypes is outlined in Chapter 14.

Having completed the initial stage of cultivar development, some recommendations can be made as to how, with hindsight, the collection and initial selection procedure could be modified.

One possible improvement of the collection method would be to select the habitat from which the biotypes that performed best in the experimental plots originated, and then to collect plants preferentially from this habitat. Unfortunately, in this study, the most promising biotypes ('Quanterness', 'New Cumnock', 'Cairngorm' and '9 Dalmelington') grew in a variety of different habitats (see Table 10.1.), and there

was no factor that clearly linked the habitats. Further, although some plants, such as 'Newburgh' and 'Airport', from the same habitat responded in a similar way in the experimental plots, others which were growing in the same habitat differed in their performance. For example, 'Cairngorm' generally did very well in the experimental plots, but '8 Delmelington', which was also collected from a hillside, performed relatively poorly. Obviously, with such a limited sample of biotypes, it is very hard to accurately assess any apparent correlation between habitat and subsequent performance of the plants. The only correlation that seems to exist is that, on the whole, plants collected close to the sea performed poorly in the experimental plots. This applies only to those plants that were growing very close to the sea; some biotypes, such as 'Quanterness',which was growing about 500m from the sea, performed very well. The biotypes that were growing within about 30m, or less, of the high tide marks were: 'Port Patrick', 'Newburgh', 'Stromness', 'Birsay', 'West Coast' and 'Airport'. Generally, these plants did not grow particularly well in the experimental plots, and so by avoiding plants growing very close to the sea, the proportion of useful biotypes amongst those collected should be increased.

Some evidence that, on the whole, plants from particular geographic areas are very variable in their performance comes from analysis of variance of the plot results. In years when biotype-site interactions were significant, biogroup-site interactions were not always so (see Appendix 2). Thus there was no biogroups-site interaction for % survival 1982, % ground cover 1982 or 1983, but such interactions were demonstrable for dry weight in both years. Thus, while there can be no assurance that geographical area of origin can be used reliably as a guide to biotype performance, it may be more predictive for some characters than others.

The main collection sites used in this study were all in eastern Scotland, as lack of winter hardiness was reported to be a problem in Poa pratensis grown in Scotland (161), and only the biotypes that can survive the colder winters of eastern Scotland will make good cultivars. However, despite the unusually cold winter of 1981/82, winter survival was generally fairly high (Section 11.3.), and so in retrospect it seems that winter hardiness is less of a problem that anticipated. Therefore it would perhaps be useful, assuming the number of experimental sites was kept constant, in future to have one of the main experimental plots in western Scotland, where the climate is milder, but wetter. The small experimental plot used at Dalmally was in the west of Scotland, but had a more acid soil than that normally encountered by grass cultivars (148). This could not be immediately rectified, because liming takes some time to affect soil pH (205). If one of the main experimental plots was situated in western Scotland, the problem of acid soil, which is more common there than in the east (223), would have to be taken into account.

Infection of the plants in the experimental plots by Drechslera poae occurred towards the end of the experimental period (Section 11.6.3.). This meant that there was insufficient time to assess accurately the impact of this disease: the reduction in ground cover (Figure 11.5.1.), for example, could have continued, or levelled off in some of the biotypes. It would be very interesting to measure the rate of recovery of the plants from this infection. A separate experiment, with the biotypes and cultivars grown outside but deliberately infected with Drechslera poae, would provide evidence on the recovery rates of the plants.

Finally, the plots were not visited frequently enough to measure accurately the flowering time of the biotypes and cultivars (see page 206). Ideally the experimental sites should all be visited daily, during the flowering period, to record the number of plants flowering, but this

was obviously not possible in this study. In future, either the flowering could be recorded by other workers at each site, or all the plants could be grown at a central site which would be visited daily. Another problem with the flowering was that some of the biotypes and cultivars grown at Edinburgh did not flower at all in one year, so the data for seed production and germination are incomplete (Chapter 12). With hindsight, several plants of each biotype could have been given artificial vernalization treatment for several months, and then transferred to a growth room with a high temperature and long photoperiod to stimulate flowering (225). This would have provided seed for germination tests, but the results for seed production in such an artificial environment would possibly be very different from the results had the plants been growing outside. Therefore the results for seed production would be of very dubious validity.

CHAPTER 14. GENERAL DISCUSSION AND CONCLUSIONS.

14.1. Discussion

Several of the characters examined in this study are relevant both to the taxonomy and to the cultivar development of Poa pratensis. In this chapter some of these common links between the taxonomy and cultivar development are discussed, and a brief outline is given of future work that could be done in this field. There are some important questions related to the present work, such as the taxonomic position of potential cultivars - where should one look in the taxonomic spectrum of Poa pratensis, to find biotypes that are likely to perform well as cultivars ? Are there characters which might be used to predict cultivar value, which might be detectable in a taxonomic survey ? Is there any correlation between the geographical or ecological sites where the biotypes were collected, and their likely performance in experimental plots ? Which of the characters used in taxonomy are important for cultivar development ? These questions are discussed in this chapter. First, the characters which are useful both taxonomically and in cultivar development are examined, and then the predictive value , in terms of likely performance as cultivars, of some of the characters is discussed.

Some of the authors working on the taxonomy of Poa pratensis have used differences in the colour of the leaves, such as

light green or dark green leaves, as characters to distinguish inter-specific groups [87,89]. Leaf colour is also important in the development of amenity grass cultivars [31,153], and therefore this character is of interest both in taxonomy and in cultivar development. In this study, the leaf colour of the biotypes and cultivars was examined as an important character for amenity grass, so the results are presented in Section B, whereas the taxonomic results are in Section A. A comparison of the differences in leaf colour (see Table 11.7.8.), showed that the three biotypes with distinctly dark green leaves were: '9 Dalmelington', 'Birsay' and 'Kinlochleven'. These biotypes, however, did not form a distinct morphological group (Table 7.2.1.). For example, '9 Dalmelington' had tall culms, long, wide leaves, and long florets and glumes. In contrast 'Birsay' had short culms, short, narrow leaves and short florets and glumes. Similarly, the biotype 'Yetholm' and the cultivar 'Arina' both had light green leaves in the experimental plots (Table 11.7.8.), but differ morphologically (Table 7.2.1.). This character, leaf colour, thus does not correlate well with other taxonomic characters, and the fact that the colour of Poa pratensis depends upon dry matter production [177], and the amount of fertilizer provided [178], means that colour is of very limited use as a taxonomic character. It is suggested that its use in the taxonomy of this species should be discounted altogether.

One common link between the results in Section A and those in Section B is the great variability displayed by Poa pratensis. In Chapter 4 it was shown that plants from similar areas may differ morphologically (page 41), and the considerable

morphological variability of plants within the same population was apparent from the results in Chapter 5. Further, the analysis of herbarium material revealed that the range of form demonstrated in plants from Britain was in many cases comparable to that displayed by plants growing in completely different geographical areas - sometimes many thousands of kilometres apart (Table 6.2.3.). The biotypes collected from Scotland also displayed a range of different morphological characters (Table 7.2.1.). There is therefore morphological polymorphism both over large geographical areas (Figures 6.2.1 and 6.2.2), and within local populations (Figures 5.2.1 and 5.2.2). These results were mirrored by the diversity of the performance of different biotypes in the experimental plots. For example, the dry matter production and ground cover of the biotypes often differed by a factor of four or more (Chapter 11). As with the taxonomic results, plants growing relatively close together were frequently very different. For example, 'Quanterness' was amongst the most productive plants at all four experimental sites, but 'Birsay' - which was collected only 20 km from 'Quanterness' - had a very low dry matter production (Table 11.4.1.). This high variability is partly the result of the facultatively apomictic reproduction of Poa pratensis. The ability of plants with unbalanced chromosome complements to reproduce apomictically means that genotypic variability within a large population is high [20]. The occasional resumption of some sexual reproduction will ensure that populations are in a continual state of flux, which greatly complicates the taxonomic treatment of facultative apomicts [21]. However a high degree of variability in wild populations is an advantage for cultivar development, as it means that there is a wide

range of genotypes available, which have different combinations of characters.

The fact that plants growing within the same geographical area often differ physiologically (such as 'Birsay' and 'Quanterness'), implies that in many cases adaptation to local conditions is low. If the biotypes had all been well adapted to local conditions, strong correlations would be expected between the geographical origin of the plants and their performance in experimental plots. For example, the plants from the north of Scotland would all be expected to have excellent winter hardiness. There was a general tendency for the least hardy plants to have originated in southern or western Scotland (pages 151-153), but this was by no means always true. For example, 'Newburgh', which was from north-east Scotland, was one of only three biotypes which suffered plant mortality over the winter of 1982/83 at Aberdeen (page 151). Further, at Sourhope, 'Birsay' - which was the most northerly plant collected (page 102) - had very poor survival over the winter of 1981/82 (page 153).

Similarly, the mild, wet climate of western Scotland is an excellent environment for mildew growth [149], and so plants from this area would all be expected to have very high resistance to mildew - assuming that biotypes are all well adapted to the local conditions. This is not the case: 'Kinlochleven', collected from western Scotland, has extremely low resistance to mildew (Table 11.6.1). Therefore there are biotypes in which adaptation to local conditions is low, and so the pattern of physiological variation is to some extent random. The correlation between plants growing very close to the sea and poor performance in experimental plots, is an

example of an ecological factor which can be used to predict which biotypes are likely to have potential as cultivars. However, this does seem to be the only ecological character which is useful for predicting the future performance of the plants (page 226-227). Obviously, in some situations, climatic or ecological selection pressures will be sufficiently strong to exclude unadapted biotypes, but the existence of some biotypes that are not well suited to their environment, means that it is harder to use the geographical origin of the plants to predict their potential value. This has important implications for the initial selection of biotypes. In order to genuinely sample the plants from a particular geographical area, a whole range of local biotypes would have to be collected. If only one biotype were chosen, it may be relatively poorly adapted to that particular climate. So this is a disadvantage from the point of view of cultivar development, as it means that larger samples of the population from a particular area are required than would normally be the case.

This lack of adaptation is largely due to the predominantly apomictic reproduction of Poa pratensis. If one or two seeds of an apomictic species are dispersed to a new area, the plants will spread vegetatively, and also produce apomictic seeds. Therefore a population can rapidly be built up of only one or two genotypes [59]. This means that there is very little variability on which selection can act, and, further, means that the genotype of the original colonizing plants - which may well not be adapted to local conditions - may be maintained through the production of apomictic seed. Even if the original genotype is well adapted, occasional sexual reproduction of the facultative apomicts will

produce a wide range of new, often poorly adapted, genotypes, which may become fixed in the population by subsequent apomictic reproduction [59]. This results in an element of randomness in the variation pattern. Thus biotypes which do not grow vigorously, such as 'Birsay', may still survive for long periods within a population, and owe their survival more to accident than natural selection. In contrast, the genotypes of the initial colonizing plants of amphimictic species will not remain intact from one generation to the next, and selection pressure will ensure that those genotypes not adapted to the local environment will be rapidly lost from the gene pool.

In other grass species, plants have been found that are not well adapted to their environment. For example, Harberd [132], analysing a population of Festuca rubra L. in Scotland, found that in a closed sward seed survival was very low, and so the established genotypes were protected from the immigration of better adapted genotypes [132]. Festuca rubra, like Poa pratensis, spreads vegetatively as well as through seed dispersal, and Harberd speculated that vegetative reproduction may be sufficient to overcome a considerable genetic advantage of newer generations [132]. Only when established genotypes are very poorly suited to their environment will they easily be replaced by new seedlings.

This lack of adaptation to local conditions means that a wide range of genotypes, and phenotypes, may be present within a small area. Other workers investigating the taxonomy of Poa pratensis have mentioned the high morphological polymorphism exhibited by plants collected from a wide area [18,60,93], but often no mention is made of the local pattern of variation. A wild plant

of Poa pratensis from Sweden, examined by Muntzing [12], turned out to be two morphologically different biotypes growing very close together, which shows polymorphism within a very small area. Shutova found considerable intra-population variation in the morphology of Poa pratensis in Russia [5], and so this seems to be a widespread phenomenon in this species.

The morphological variation pattern of Poa pratensis, with a great diversity of genotypes, both within the local populations and on a larger scale - such as throughout Britain - can be compared with the variation pattern in other apomictic groups. Generally, apomictic species in other genera, such as Crepis, Taraxacum and Rubus, all exhibit great morphological polymorphism [59]. In Crepis, there are several diploid species in north America, which all reproduce sexually, and also a larger number of species which are obligate apomicts, and have a distribution overlapping that of the sexual plants [59]. The apomictic species are probably produced by hybridization between the sexual species [59]. The variation pattern here differs from the situation in Poa pratensis, because in Crepis, morphological diversity of the apomictic species is very great in areas where they are sympatric with the sexual species, but due to the obligate nature of the apomixis, populations growing away from the sexual species are very uniform [59]. In contrast, many species of Rubus are facultatively apomictic, like Poa pratensis, and so the variation is much more evenly spread throughout the geographical range [59]. Thus, unlike the situation in Crepis, there are no regions in which morphological diversity is concentrated. This is because new genotypes are continually being produced by occasional crossing between different biotypes in the

facultatively apomictic species. Again, as in Poa pratensis, apomixis will allow the retention of unadapted genotypes within a population, and so part of this variation is random.

Another of the characters that is of interest both to the taxonomist and the plant breeder is seed production. The number of spikelets per panicle, which will obviously affect the seed production, was one of the taxonomic characters used by Barling [11] in his study of Poa pratensis. Seed production is important to the plant breeder [147,150], because a low reproductive capacity would greatly increase the difficulty and time of seed multiplication. In this study, the number of spikelets per panicle was measured in several of the biotypes (Table 7.2.1.), and, in a separate experiment, the seed production of the biotypes was estimated (Table 12.2.1.). A comparison of the sixteen biotypes common to both experiments shows that the results for these two parameters were significantly correlated ($r=0.73$, $p<0.01$). This suggests a possible shortcut in cultivar development. If the characters that are sought in a cultivar correlate well with taxonomic characters, then, by concentrating on a particular taxonomic group within the species, a high proportion of the plants should have the characters desired. Unfortunately the biotypes that perform well in the experimental plots - 'Quanterness', 'New Cumnock', '9 Dalmelington' and 'Cairngorm' did not form a distinct morphological group (Table 7.2.1). For example, '9 Dalmelington' had tall culms, and long florets and glumes, but 'Cairngorm' had short culms, and very short florets and glumes. There is therefore no morphological character, amongst those used in Table 7.2.1., that will enable plants to be

selected that have particular characteristics when grown in experimental plots.

The results in Table 5.2.1. indicate that the degree of tufting (number of flowering culms per basal node), varies between plants. The amount of tufting in herbarium specimens also varies (Table 6.2.5.), and several authors have used the number of culms per tuft as a taxonomic character [4,7,11,72]. From the point of view of the plant breeder, the amount of tillering of individual plants is important. Although the breeder is interested in the number of vegetative tillers, whereas the taxonomist concentrates on flowering tillers, there is likely to be a correlation between the two. Table 11.5.3. shows the number of vegetative tillers of the biotypes and cultivars, in the experimental plot at Bush, 41 days after planting. The results in Table 11.5.3. correlate well with the dry matter production and ground cover of the biotypes and cultivars after one year's growth (see page 177). The number of tillers is also significantly correlated with the dry matter production after two years, implying that the initial differences between the plants in their tillering rates are maintained. The low correlation between the results in Table 11.5.3. and ground cover after two years (page 177), may be due to the fact that when the tillering was recorded, the plants had not been growing long enough for any tillers to be produced from rhizomes. However rhizome spread, and the subsequent production of tillers some distance from the original plant, will contribute greatly to the final ground cover. The initial tillering rate is a useful guide, however, to the future dry matter production of the plants. It is interesting that the four biotypes that show potential as possible cultivars ('Quanterness', 'New Cumnock', '9

Dalmelington', and 'Cairngorm') are the four biotypes with the highest initial rates of tillering (Table 11.5.3.). Also the biotypes that tillered slowly ('Knapdale', 'Kinlochleven', 'Birsay' and 'Ben Obe') generally performed poorly in the experimental plots, not only in dry matter production, but also in terms of survival (page 152), ground cover (Table 11.5.1.) and colour (Tables 11.7.1. to 11.7.3.). Although the amount of tillering in grasses is influenced by environmental factors, there is also a large genetic component [231]. It therefore seems possible that the initial rate of tillering could be used to screen biotypes, and by selecting those that tiller rapidly, the likelihood of obtaining potentially useful plants would be increased. Given that the degree of tufting of the plants varies between the intraspecific taxa of Poa pratensis (Table 6.2.5.), this suggests that biotypes from the pratensis or angustifolia part of the species should provide better cultivars than subcaerulea, which is less tufted. However there are several problems with this. Firstly, as demonstrated in Chapter 6, many plants have a mixture of taxonomic characters, so plants that are, on balance, closest to the angustifolia type may not be tufted, whereas plants like subcaerulea may have several culms per tuft (Table 6.2.5.). Therefore to restrict collection to one particular taxonomic group would risk missing some very useful plants. The fact that the four most useful biotypes in the present study were morphologically different confirms this point. Secondly, although plants of the type subcaerulea have a low degree of tufting, they often spread well by rhizomes [4], which would be an equally useful characteristic in terms of ground cover. The low correlation between the final ground cover results and the tillering rates shown in

Table 11.5.3. is presumably due to the plants spreading rhizomatously. Further, the rolled leaves of angustifolia are likely to be disadvantagous in an amenity grass, where a smooth sward of flat leaves is preferred. Finally, before plant breeding rights are granted for a new cultivar, the independent testing authority has to satisfy itself that the new cultivar is distinct from present cultivars [234]. Normally, this is taken to mean a morphological distinction, and so limiting the collection of biotypes to a narrow taxonomic range of the species may cause problems in that the biotypes will be morphologically very similar. The granting of plant breeding rights is a legal prerequisite before seed of that cultivar is marketed in Britain [234].

It would be extremely useful if a quantitative index could be produced to show the value of a particular cultivar or biotype as an amenity or forage grass. This could be used to compare and rank the biotypes in a trial using a single number to represent their potential value. This index would take into account several different factors, such as winter hardiness, disease resistance, ground cover, and so on. Unfortunately, however, there are two main problems in making such an index. Firstly, the importance of the different characters would have to be assessed, and this would be very subjective. One worker might rank the characters in a quite different way to another, and the score given to the same cultivar, derived from identical results, would therefore vary due to the different weightings given to the characters by different workers. The other problem is that the importance of the different characters will vary according to where the grass is to be grown, and what the turf will be used for. A character such as winter hardiness may be

of the utmost importance in one region, but not a selection criterion in another. Therefore an index produced using a standard procedure, where the relative weightings to be given to each character are predetermined, is likely to be of little use in many areas. Conversely, if different weightings are used by different testing stations, the results will only be of relevance to the local area, so the ability to compare results from different areas will be lost. Further, amenity grass is used in a variety of situations, and in each of these different characters are important. For example, wear tolerance, which is essential in sports turf [219], is of much less importance in grass that will be used for roadside verges [154]. So again, it is not possible to reduce the 'value' of a cultivar or biotype to a single index, because a plant that may be very useful for one particular situation, may be useless in another. Therefore, on balance, the present system, of producing a separate measure of the relative performance of cultivars for every character measured, is the most advantageous, as it allows plants to be selected that have the particular range of characters required.

14.2. Conclusions

The conclusions drawn from this study can be summarised as follows :

Local populations of *Poa pratensis s.l.* in Scotland display great morphological variability, and this phenotypic diversity is also found in herbarium specimens from Britain as a whole, and the other main areas of distribution of the species. The pattern of variation shows very considerable morphological overlap between the three putative intraspecific taxa found in Britain, viz. subsp *pratensis*, subsp *subcaerulea* and subsp *angustifolia*. Neither in Britain, nor abroad, do any of these three taxa have a geographical distribution distinct from the other two, and therefore the use of either specific or subspecific rank for *subcaerulea* and *angustifolia* is considered inappropriate. These two taxa should be treated as part of the single species *Poa pratensis* L.

Biotypes of *Poa pratensis* collected from around Scotland were grown in experimental plots. Measurements of plant survival, dry matter production, ground cover, disease resistance and colour, showed that morphological variability is at least paralleled by considerable physiological diversity within the species. There is much scope for improving upon the cultivars of *Poa pratensis* which are used at present. The current cultivars were all outperformed, in all the physiological characters examined, by one or other

of the wild biotypes, and four of the biotypes collected showed considerable potential as possible future cultivars.

There was no correlation between the taxonomic position within Poa pratensis and the performance of the plants in experimental plots. The taxonomic and physiological variability of the species is partly the result of facultative apomixis, which allows unadapted genotypes to be passed on to the next generation, and therefore introduces a random element into the variation pattern. This means that plants may not be adapted to the local conditions, and so the geographical situation, or ecological conditions of the collection site cannot be used to predict accurately their value as potential cultivars. The best single predictive character found was the initial tillering rate, which correlated significantly with the dry matter production of the plants after two years, and could be used as a general guide to the relative vigour of the established plants.

14.3. Future work

None of the plants in the populations studied in Chapter 5, nor the biotypes used in the experimental plots (Chapter 11), were typical specimens of 'subsp angustifolia'. Therefore although the lack of any morphological discontinuity between 'subsp pratensis' and 'subsp subcaerulea' was shown, the morphological overlap between 'subsp angustifolia' and the other subspecies was demonstrated only from herbarium specimens. It would therefore be interesting to examine populations and biotypes from the wild that included some 'subsp angustifolia', to confirm that this taxon is not sufficiently distinct to be considered a separate subspecies.

Similarly, there was a dearth of herbarium specimens of Poa pratensis subsp alpigena - which does not grow wild in Britain. A much larger sample of material would be required for the pattern of variation, between this subspecies and the rest of Poa pratensis s.l. to be revealed. Further investigation would indicate whether or not subspecific rank is appropriate for this taxon.

Although the sample of biotypes of Poa pratensis collected from Scotland was morphologically similar to herbarium specimens from Scotland (see Table 7.2.2.), a more extensive collection of wild material would offer useful further confirmation that there is no bias in the collection of herbarium material.

A larger sample of biotypes, including what are notionally alpigena and angustifolia, would also be of great benefit

from the point of view of general cultivar development. This study was to be on the resources of wild Poa pratensis specifically in Scotland, so neither were incorporated in the trials. Many of the biotypes collected have promising performance in the experimental plots, and some an overall excellence, even though 23 biotypes is not an extensive sample of the total population of wild Poa pratensis in Scotland. The discussion in Chapter 13 demonstrates that not all habitats contain biotypes that perform well in experimental plots. Therefore any subsequent collection could be more selective - for example by not collecting plants that are growing very close to the sea. It had been thought originally that maritime sites might contain particularly hardy, robust genotypes, but the results from the experimental plots showed that in fact these plants generally do not grow well in inland sites.

The biotypes and cultivars were grown in the experimental plots from individual tillers (page 113), whereas normally both amenity and forage grasses would be grown from seed. Although, in the laboratory, the final germination, and germination vigour, of the four potentially useful biotypes was good (Table 12.4.1.)., a field test of the germination and early establishment of these biotypes would be necessary to confirm that these plants could make successful cultivars.

Further, the seed production of these biotypes should now be tested on a larger scale than that used in this study, both to ensure that sufficient seed is produced to make seed multiplication economically viable, and also to provide seed for further testing. Some of this seed could be used to estimate the percentage of apomictic seed produced by each biotype. This is normally done by

planting out rows, or single spaced plants, of seed from each biotype and counting the number of seedlings that differ morphologically from the parental type [232]. Seedlings that are identical to the parent plant are assumed to have developed from apomictic seeds.

The rest of the seeds of the biotypes would be used in trials conducted by independent bodies, such as the Welsh Plant Breeding Station, which would enable the performance of the biotypes to be compared over a wide geographical area and against a large range of cultivars. Finally, if the results so far are promising, the seed could be entered for certification, and National List trials, which would result in the granting of breeding rights for the new cultivar.

BIBLIOGRAPHY

1] R.A.Cross. Distribution of sub-families of Gramineae in the Old World. Kew Bull. 35, 279-289 (1980)

2] W.Hartley. Studies on the Origin, Evolution and Distribution of the Gramineae. Aust.J.Bot. 9, 152-161 (1961)

3] M.S.Mani. The Vegetation of Highlands. Herbage Abstr. 52(3), 159 (1982)

4] C.E.Hubbard. Grasses. 188-193 (Penguin Books Ltd., 1978)

5] Z.P.Shutova. Intrapopulational and varietal variation under cultivation in Poa pratensis. Pl.Breed.Abstr. 51, 858 (1981)

6] W.L.Brown. Chromosome complements of five species of Poa, with an analysis of variation in Poa pratensis. Am.J.Bot. 26, 717-723 (1939)

7] A.R.Clapham, T.G.Tutin and E.Warburg. Excursion Flora of the British Isles. 451-455 (Cambridge Univ.Press, 1981)

8] J.R.Edmondson, (in T.G.Tutin et al. Eds.), Flora Europaea 5, 161-162 (Cambridge Univ. Press, 1980)

9] N.Tzvelev. The genus Poa in the USSR. Nov. Sist. Vyssh. Rast., 11, 24-41 (1974)

10] W.G.Dore and J.McNeill. Grasses of Ontario. 114-125 (Canadian Govt. Publ. Centre, 1980)

11] D.M.Barling. Studies in the biology of Poa subcaerulea Sm. Watsonia. 5(3), 163-173 (1962)

12] A.Muntzing. Further studies on apomixis and sexuality in Poa. Hereditas. 26, 115-190 (1940)

13] W.Brittingham. Types of seed formation as indicated by the nature and extent of variation in Kentucky bluegrass, and its practical implication. J.Agric.Res.. 67, 225-264 (1943)

14] F.W.Tinney. Cytology of parthenogenesis in Poa pratensis. J.Agric.Res.. 60, 351-360 (1940)

15] A.Nygren. Apomixis in the Angiosperms. Bot.Rev. 20, 577-649 (1954)

16] E.Akerburg. Apomictic and sexual seed formation in Poa pratensis. Hereditas. 25, 359-370 (1939)

17] A.W.Hovin et al. Effects of geographic origin and seed production environments on apomixis in Kentucky bluegrass. Crop Sci.. 16, 635-638 (1976)

18] G.Pommer. Investigation of breeding Poa pratensis with particular regard to the type of seed formation. Z.PflZuchtg. 67, 279-304 (1972)

19] C.J.Williamson. Light regimes and reproduction in Poa species. New Phytol. 87, 769-783 (1981)

20] S.Asker. Progress in Apomixis research. Hereditas. 91, 231-240 (1979)

21] P.H.Davis and V.H.Heywood. Principles of Angiosperm Taxonomy (Oliver and Boyd, 1963)

22] A.Nygren. How to breed Kentucky bluegrass, (Poa pratensis L.). Hereditas. 39, 51-56 (1953)

23] J.Clausen. Introgression facilitated by apomixis in polyploid Poas. Euphytica. 10, 87-94 (1961)

24] C.A.Stace. Hybridization and the Flora of the British Isles. 561-563 (Academic Press, 1975)

25] C.A.Stace. Plant Taxonomy and Biosystematics. 140-166 (Edward Arnold, 1980)

26] E.L.Core. Plant Taxonomy. 97 (Prentice Hall, 1962)

27] S.B.Jones and A.Luchsinger. Plant Systematics. (McGraw-Hill, 1979)

28] J.Symon. Scottish Farming. (Oliver and Boyd, 1959)

29] Anonymous. The Farmer. Feb 23rd, 244-246 (1870)

30] J.Frame et al. The effect of companion grasses on Timothy production in swards cut for conservation. J.Br.Grassld.Soc. 28, 213-218 (1973)

31] R.Hawthorn. Dawson's Practical Lawncraft. (Granada, 1977)

32] G.H.Jonassen and H.Faeste. Experiments with grass and green fodder in a mountain region. Herb.Abstr. 47, 21 (1977)

33] M.Jetne. Forkning og Forsok I Landbruket. 27, 601-613 (1976)

34] M.Noshiro. Frost hardiness of grasses. Herb. Abstr. 47, 38 (1977)

35] A.Habjorg. The effect of artificial heating on winter survival and turf quality of selected varieties of Poa pratensis L. Meld. Norg. LandbrHoisk 56, No 25 (1977)

36] A.Larsen. Freezing tolerance in grasses. Meld. Norg. LandbrHoisk 57, No 23 (1978)

37] A.Habjorg. Vegetative growth of selected latitudinal and altitudinal distant varieties of Poa pratensis L. cultivated at six localities in Norway. Meld. Norg. LandbrHoisk 58, No 27 (1979)

38] Anonymous. Advisory work : Grassland. Ann.Rep.Edin.Sch.Agric. 73 (1977)

39] J.P.Shildrick. Turfgrasses under intensive management. J.Sports Turf Res.Inst. 53, 95 (1977)

40] A.J.P.Gore, R.Cox and T.Davies. Wear tolerance of turfgrass mixtures. J.Sports Turf Res.Inst. 55, 45-68 (1979)

41] P.Van der Horst. Sports Turf Research in the Netherlands. J.Sports Turf Res.Inst. 46, 46-57 (1970)

42] D.J.Wehner and D.Watschke. Heat tolerance of Kentucky bluegrass, perennial ryegrass and annual bluegrass. Agron.J. 73, 79-84 (1981)

43] H.M.Bischoff et al, The suitability of grass species and cultivars for temporarily flooded riverside sites in the GDR. Herb. Abstr. 51, 650 (1981)

44] P.T.Thomas. Fifty years of progress at the Welsh Plant Breeding Station. Ann.Rep.Welsh.Pl.Breed.Stat. 5-10 (1969)

45] I.Moore. Grass and Grasslands. (Collins, 1966)

46] E.S.Elliott. Susceptibility of Kentucky bluegrass selections to some fungal diseases. Proc.W.Va.Acad.Sci. 35, 29-32 (1963)

47] P.A.Lubenets. Results of a study of perennial herbage crops and fodder root crops. Pl.Breed.Abstr. 47, 551 (1977)

48] G.E.van Dijk. Grass breeding in the Netherlands. Euphytica. 15, 163-170 (1966)

49] A.Habjorg. Effects of photoperiod and temperature on vegetative growth of different Norwegian ecotypes of Poa pratensis. Meld. Norges LandbrHoisk. 55, No 16 (1976)

50] S.Nakamura. Germination of grass seeds. Proc.Int.Seed Test.Assoc. 27 (3), 710-729 (1962)

51] R.Lutynska et al. Plant associations of meadow and pasture as sources of initial material for grass breeding. Pl.Breed.Abstr. 49, 838 (1979)

52] G.Almgard. Experiments with Poa. Kungl. lantbrHogsk. Annr. 26, 77-119 (1960)

53] F.H.Perring and S.M.Walters. Atlas of the British Flora. 381. (Nelson and Sons, 1962)

54] A.G.Tansley. The British Isles and their Vegetation (Cambridge Univ. Press, 1965)

55] P.J.Grime and P.S.Lloyd. An Ecological Atlas of Grassland Plants. (Edward Arnold, 1973)

56] E.Akerberg. Cytogenetic studies in Poa pratensis and its hybrid with Poa alpina. Hereditas 28, 1-126 (1942)

57] E.Miroshnichenko. Characters of Poa pratensis biotypes. Herb. Abstr. 49, 182 (1979)

58] J.Martusewicz. Analysis of the variation between ecotypes and forms of Poa pratensis L., Poa palustris L., and Poa compressa L. Herb. Abstr. 46, 292 (1976)

59] G.L.Stebbins. Variation and Evolution in Plants. (Columbia Univ. Press, 1950)

60] V.Regal. Synekologika Charakteristika Lipnice Lucni. Sb. vys. Sk. zemed. Praze, 123-130 (1967)

61] F.H.Perring. Critical Supplement to the Atlas of the British Flora. (Nelson Sons, 1968)

62] G.C.Druce. The Comital Flora of the British Isles 361 (Bungle and Co., Arbroath, 1932)

63] A.R.Clapham, T.G.Tutin and E.F.Warburg. Flora of the British Isles. 1435-1441 (Cambridge Univ. Press, 1952)

64] W.A.Weber. Rocky Mountain Flora. 360-362 (Colorado Associated Univ. Press, 1972)

65] L.Hitchcock and A.Cronquist. Flora of the Pacific Northwest 661 (Univ. Washington Press, Seattle, 1973)

66] J.E.Smith. Poa subcaerulea. English Botany. 14, 1004 (1802)

67] J.Lindley. A Synopsis of the British Flora. 317 (Longman,Rees,Orme,Brown and Green, 1829)

68] W.J.Hooker and G.Walker-Arnott. The British Flora. 551 (Longman, Green, Longman and Roberts, 1860)

69] G.Bentham. Handbook of the British Flora. II. 1001-1007 (Lovell Reeve and Co, 1865)

70] S.A.Stewart and T.H.Corry. A Flora of the North East of Ireland. 260 (Quota Press, Belfast, 1938)

71] R.Butcher. A New Illustrated British Flora. 951-952 (Leonard Hill Ltd., London, 1961)

72] A.R.Clapham, T.G.Tutin and E.F.Warburg. Flora of the British Isles. (Cambridge University Press, 1962)

73] M.Wigginton and G.Graham. Guide to the Identification of some Difficult Plant Groups. 139 (Nature Conservancy Council, 1981)

74] C.Linnaeus. Species Plantarum. 4th Edition, 1, 385-388. (Stockholm, 1797)

75] C.Hartman. Skandinaviens Flora. 35 (Zacharias Haeggstrom, Stockholm, 1843)

76] J.M.Norman. Norges Arktiske Flora. 1, 1276-1280 (O.Andersens Bogtrykkeri, 1894)

77] I.Hiitonen. Suomen Kasvio. 1, 202-206 (Kustannusosakeyhtio, Otava, 1933)

78] J.Grontved. The Botany of Iceland. IV, 149 (V.Pedersens Bogtrykkeri, Denmark, 1941)

79] J.Lid. Norsk Flora. 102-103 (Det Norske Samlaget,Oslo, 1952)

80] N.Hylander. Nordisk Karlvaxtflora. 256-258 (Almqvist et Wiksell, Stockholm, 1953)

81] E.Hulten. The Circumpolar Plants. 1, 14 (Almqvist et Wiksell, Stockholm, 1962)

82] C.A.M.Lindman. Nordens Flora. 1, 78-79 (Wahlstrom and Widstrand, Stockholm, 1964)

83] A.Love. Islenzk Ferdaflora. 100-109 (Almenna Bokafelagid, Reykjavik, 1977)

84] P.Andersson. Flora over Dal. 116 (Stockholm, 1981)

85] J.R.Suter. Flora Helvetica. 1, 52-64 (Orell, Fussli and Co., Zurich, 1821)

86] M.Willkomm and J.Lange. Florae Hispanicae. 80-82 (Stuttgart, 1861)

87] P.Ascherson and P.Graebner. Synopsis der Mitteleuropaischen Flora. 2(1), 428-431 (W.Engelmann, Leipzig. 1902)

88] H.Coste. Flore de la France. 3, 609-612 (Librairie des Sciences Naturelles, 1906)

89] G.Hegi. Illustrierte Flora von Mittel-Europa. 1, 299-307 (Lehmann, Munchen, 1907)

90] R.Douin (in G.Bonnier Ed.) Flore Complete. 12, 27-29 (Librairie de l'Enseignement, 1934)

91] P.Fournier. Les Quatre Flores de la France, 65-68 (Lechevalier, Paris. 1940)

92] A.Caballero. Flora Analytica de Espana. 97 (S.A.E.T.A., Madrid, 1940)

93] V.Jirasek. Einige taxonomische Probleme im Komplex der Poa pratensis s.l. Acta. Horti. Bot. Pragensis. 60-68 (1964)

94] E.Lopez and C.Jimenez. Elenco de la Flora Vascular Espanola. 385-386 (ICONA, Madrid, 1974)

95] M.Guinochet and R.de Vilmorin. Flore de France. 3, 911-914 (Centre National de la Recherche Scientifique, 1978)

96] C.J.Maximowicz. Primitiae Florae Amurensis. 319 (Kaiserlichen Akademie der Wissenschaften, 1859)

97] R.Y.Rozhevits and B.Shishkin (in V.Komarov. Ed.) Flora of the U.S.S.R. 2, 292-315 (Israel Program for Sci. Transl., 1935)

98] A.A.Kolakovski. Flora Abkhazian. 1, 149-154 (Abkhazian Crop Institute, 1938)

99] E.Lavrenko (in Bordzilovski. Ed.) Flora of the Republic of Ukraine. (Academy of Sciences, Kiev, 1940)

100] A.K.Makashvili and D.Sosnowsky. Flora Georgiae. 1, 247-256 (Botanical Institute, Tphilsiense, 1941)

101] B.N.Gorodikov. Flora Murmanskoi Oblasti. 203-205 (Academy of Sciences, Moscow, 1953)

102] N.V.Pavlov. Flora Kazakhstana. 1, 221,230 (Kazakhstan Academy of Sciences, 1956)

103] M.Koie and K.H. Rechinger. Symbolae Afghanicae. 6, 67-71 (Copenhagen, 1958)

104] J.Ohwi. Flora of Japan. 165 (Smithsonian Institue, Washington, 1965)

105] A.Gray. Gray's Manual of Botany. Revised by M.Fernald. 115-118 (American Book Co., 1950)

106] R.H.Mohlenbrock and J.W.Voigt. A Flora of Southern Illinois. 70-72 (Southern Illinois Univ. Press, 1959).

107] E.H.Moss. Flora of Alberta. 86-92 (Univ. Toronto Press, 1959)

108] I.L.Wiggins and J.H.Thomas. A Flora of the Alaskan Arctic Slope. 64-71 (Univ. Toronto Press, 1962)

109] A.E.Roland and E.C.Smith. The Flora of Nova Scotia. Proc. Nova Scotia Inst. Sci. 26, 82-85 (1963)

110] J.A.Steyermark. Flora of Missouri. 100 (Iowa State Univ. Press, 1963)

111] O.Lakela. A Flora of Northeastern Minnesota. 46-47 (Univ. of Minnesota Press, 1965)

112] E.Lucy Braun. The Vascular Flora of Ohio. (Ohio State Univ. Press, 1967)

113] E.Hulten. Flora of Alaska and the neighbouring Territories. 134-135 (Stanford University Press, 1968)

114] P.D.Strausbaugh and E.Core. Flora of West Virginia. 130-133 (Seneca Books, Virginia, 1970)

115] E.G.Voss. Michigan Flora. 124-129 (Cranbrook Institute of Science, 1972)

116] S.Welsh. Flora of Alaska. 588-596 (Brigham Young University Press, Utah, 1974)

117] F.W.Gould. The Grasses of Texas. 110-119 (Texas A+M Univ. Press, 1975)

118] H.Scoggan. The Flora of Canada. 2, 316 (National Museums of Canada, 1978)

119] D.M.Barling. Poa pratensis subsp subcaerulea in N.Glamorgan and S.Brecon. Nature in Wales. 3, 429-433 (1957)

120] D.M.Barling. Leaf measurements and epidermis in Poa pratensis. Watsonia. 6(2), 109-113 (1962)

121] A.R.Clapham. T.G.Tutin and E.F.Warburg. Excursion Flora of the British Isles. 1136-1141 (Cambridge Univ. Press, 1968)

122] C.Linnaeus. Species Plantarum 1st Edition, 67. (Stockholm, 1753)

123] C.Linnaeus. Species Plantarum 2nd Edition. 1, 99 (Stockholm, 1762)

124] D.M.Barling. Biological studies in Poa angustifolia. Watsonia. 4, 147-168 (1959)

125] G.W.Pepin and C.R.Funk. Evaluation of turf, reproductive, and disease response characteristics in crossed and selfed progenies of Kentucky bluegrass. Crop Sci. 14, 356-359 (1974)

126] M.A.Maun et al. Effect of soil temperature on the reproductive processes of Kentucky bluegrass (Poa pratensis L. 'Newport'). Agron. J. 60, 666-668 (1968)

127] D.W.Evans. 'Cougar' Kentucky bluegrass seed production as affected by clipping to simulate grazing. Crop Sci. 15, 601-602 (1975)

128] E.Mayr. Populations, Species and Evolution. (The Belknap Press, 1970)

129] R.MacArthur and J.Connell. The Biology of Populations. (Wiley International, 1966)

130] T.Dobzhansky et al. Evolution. 30-31 (Freeman and Co., 1977)

131] V.Heywood. Taxonomy and Ecology. (Academic Press, 1973)

132] D.J.Harberd. Observations on population structure and longevity of Festuca rubra. New Phytol. 60, 184-206 (1961)

133] J.L.Harper. Population Biology of Plants. (Academic Press, 1977)

134] D.J.Griffiths. The liability of seed crops of perennial ryegrass (Lolium perenne) to contamination by wind-borne pollen. J. Agric. Sci., Camb., 40, 19-38 (1950)

135] J.R.Edmondson. Taxonomic Studies in the genus Poa (Gramineae) Ph.D. Thesis. Univ. of Leicester. (1976)

136] R.C.Campbell. Statistics for Biologists (Cambridge Univ Press, 1967)

137] R.G.D.Steel and J.H.Torrie. Principles and Procedures of Statistics (McGraw-Hill, 1960)

138] D.H.Valentine. The treatment of apomictic groups in Flora Europaea. Feddes Rep., 63, 119-127 (1960)

139] L.N.Balaam. Fundamentals of Biometry. (George Allen and Unwin, 1972)

140] S.K.Jain and A.D.Bradshaw. Evolutionary divergence among adjacent plant populations. Heredity. 21, 407-441 (1966)

141] D.Briggs and S.M.Walters. Plant Variation and Evolution (McGraw-Hill, 1972)

142] R.W.Snaydon in V.Heywood (Ed.). Taxonomy and Ecology. (Academic Press, 1973)

143] K.K.Wu. Minimum sample size for estimating progeny mean and variance. Crop Sci. 18, 57-62 (1978)

144] G.Clifford Evans. The Quantitative Analysis of Plant Growth (Blackwell Sci. Publ., 1972)

145] E.Krannich and K.Muller. Continuous supply of forage from montane grassland for a specialist cattle-rearing enterprize. Herb. Abstr. 51, 301 (1981)

146] J.P.Cooper. Strategies in herbage plant breeding. Ann. Rep. Scot. Pl. Breed. Stat. 126-134 (1978)

147] D.J.Van der Have. Grasses. Plant Breeding Perspectives. 174-189. (Centre for Agric. Publ. and Documentation, Wageningen, 1979)

148] J.Beard. Turfgrass - Science and Culture. 62-64 (Prentice-Hall, 1973)

149] H.B.Couch. Diseases of Turfgrasses. (Reinhold Publ. Corp., 1962)

150] A.Habjorg. Seed production studies in latitudinal and altitudinal distant types of Poa pratensis L. cultivated at nine localities in Norway. Meld. Norg. LandbrHoisk. 58, No 28 (1979)

151] M.Humphreys. Amenity Grass Breeding. Ann. Rep. Welsh Pl. Breed. Stat. 44-46 (1979)

152] R.Gracan. Contribution to the study of correlations between some characters of the Yugoslav cultivars of Poa pratensis. Herb. Abstr. 50, (1980)

153] M.O.Humphreys. Amenity Grass Breeding. Ann. Rep. Welsh Pl. Breed. Stat. 37-38 (1978)

154] P.Boeker. Turf for roadsides and slopes in Germany. J. Sports Turf Res. Inst. 46, 58-62 (1970)

155] M.P.Fuller. The winter-hardiness of grasses - a review. J. Sports Turf Res. Inst. 56, 116-127 (1980)

156] J.C.Carroll and F.A.Welton. Effect of heavy and late applications of nitrogenous fertilizer on the cold resistance of Kentucky bluegrass. Pl. Physiol. 14, 297-308 (1939)

157] J.F.Wilkinson and D.T.Duff. Effects of fall fertilization on cold resistance, colour and growth of Kentucky bluegrass. Agron. J. 64, 345-348 (1972)

158] M.Azzaroli and A.Skjelvag. Influences of fertilization and cutting times on the freezing tolerance of four grass species. Meld. Norg. LandbrHoisk. 60, No 23 (1981)

159] D.H.Hides. Winter hardiness in Lolium multiflorum Lam. J. Brit. Grassld. Soc. 33, 175-179 (1978)

160] D.Wilson. Breeding herbage varieties adapted to environmental stresses. Ann. Rep. Welsh Pl. Breed. Stat. 160-177 (1976)

161] R.W.Laycock. Multi-centre trials of turfgrass cultivars in the U.K. J. Sports Turf Res. Inst. 56, 18-55 (1980)

162] C.J.Tucker. A critical review of remote sensing and other non-destructive methods of estimation of standing crop biomass. Grass and Forage Sci. 35, 177-183 (1980)

163] C.J.Williamson. Breeding interspecific hybrids of Poa for use in upland pastures. Ann. Rep. Scot. Pl. Breed. Stat. 38-41 (1978)

164] V.B.Youngner and F.J.Nudge. Soil temperature, air temperature and defoliation effects on growth and non-structural carbohydrates of Kentucky bluegrass. Agron J. 68, 257-260 (1976)

165] B.S.Baker and G.A.Jung. Effect of environmental conditions on the growth of four perennial grasses: I. Response to controlled temperatures. Agron J. 60, 155-158 (1968)

166] R.W.Duell and R.J.Trout. Quantitative removal of major nutrients by three pasture grasses. Agron J. 64, 739-743 (1972)

167] B.S.Baker and G.A.Jung. Effect of environmental conditions on the growth of four perennial grasses: II. Response to fertility, water and temperature. Agron J. 60, 159-162 (1968)

168] K.A.Kershaw. Quantitative and Dynamic Ecology (Edward Arnold, 1966)

169] A.R.Woolhouse. Estimation of ground cover in turfgrass communities. J. Sports Turf Res. Inst. 52, 64-76 (1976)

170] P.Grieg-Smith. Quantitative Plant Ecology. 41-46 (Butterworths Sci. Publ., 1957)

171] C.J.Williamson. Interspecific hybrids of Poa pratensis as perennial, rhizomatous grasses for hill land. Ann. Rep. Scot. Pl. Breed. Stat. 19-20 (1975)

172] A.J.Hull et al. Influence of nutrition on Stripe Smut severity in Kentucky bluegrass turf. Agron J. 71, 553-555 (1979)

173] A.Jensen. Sorter af Engrapgraes. (Meddelelse, Statens Planteavlsforsog, 1978)

174] J.D.Smith. Resistance of turfgrasses to LTB snow mould and recovery from damage. Can. Pl. Dis. Surv. 55, 147-154 (1975)

175] C.F.Hodges and J.Madson. The competitive and synergistic interactions of Drechslera sorokiniana and Curvaria geniculata on leaf spot development in Poa pratensis. Can. J. Bot. 56, 1240-1247 (1978)

176] O.R.Jewiss. Physiological reasons for differences in yield and persistency between grass cultivars. Ann. Rep. Grassld. Res. Inst. 32-33 (1975)

177] J.Shildrick. Grass variety trials, 1971. J. Sports Turf Res. Inst. 47, 88-108 (1971)

178] S.H.Nelson. Summer colour and fall colour retention of Kentucky bluegrass receiving varying amounts and timing of nitrogen. Can. J. Pl. Sci. 60, 1015-1021 (1980)

179] K.Sato. The germination of temperate turf grasses as influenced by temperature and gibberelic acid. Chem. Abstr. 88, No 5, 129-130 (1977)

180] R.D.B.Whalley et al. Seedling vigour and the early nonphotosynthetic stage of seedling growth in grasses. Crop Sci. 6, 147-150 (1966)

181] R.A.Arnott and L.Jones. The development and morphology of seedling grasses. Ann. Rep. Grassld. Res. Inst. 147-157 (1970)

182] E.M.Vincent and E.H.Roberts. The interaction of light, nitrate and alternating temperature in promoting the germination of dormant seeds of common weed species. Seed Sci. Technol. 5, 659-670 (1977)

183] I.V.Vainagy. Effect of temperature and light on grass seed germination. Ukr. Bot. Zh. 29, 482-491 (1972)

184] H.Wiberg and H.Kolk. Effect of gibberellin on the germination of seeds. Proc. Int. Seed Test. Assoc. 25, 440-443 (1960)

185] K.Thompson et al. Seed germination in response to diurnal fluctuations of temperature. Nature. 267, 147-149 (1977)

186] B.R.Phaneendranath and C.R.Funk. Germination stimulation of Kentucky bluegrass seed permeated with plant-growth regulators dissolved in Acetone. Crop Sci. 18, 1037-1039 (1978)

187] V.K.Toole and H.A.Borthwick. Effect of light, temperature, and their interactions on germination of seeds of Kentucky bluegrass. J. Amer. Soc. Hort. Sci. 11, 48-50 (1971)

188] J.D.Maguire and M.Stein. Effects of potassium nitrate on germination and respiration of dormant and non-dormant Kentucky bluegrass seed. Crop Sci. 11, 48-50 (1971)

189] Anonymous. International Rules for Seed Testing. Seed Sci. Technol. 4, 3-177 (1976)

190] P.D.Hebblethwaite and M.H Ahmed. Optimum time of combine harvesting for amenity grasses grown for seed. J. Brit. Grassld. Soc. 33, 35-40 (1978)

191] J.Clausen and W.M.Hiesey. Phenotypic expression of genotypes in contrasting environments. Rep. Scot. Pl. Breed. Stat. 41-52 (1958)

192] W.M.Hiesey and M.Nobs. Preparation of a monograph on the Poa investigations. Ann. Rep. Carnegie Inst. Dept. Pl. Biol. 169-171 (1972)

193] N.W.Simmonds. Forage Crop Investigations. Ann. Rep. Scot. Pl. Breed. Stat. 15-27 (1972)

194] C.J.Williamson in (E.Sanchez-Monge and F.Garcia-Olmedo. Eds) Interspecific Hybridization in Plant Breeding. 289-299 (Ciudad Universitaria, Madrid. 1978)

195] C.J.Williamson. Breeding interspecific hybrids of Poa for use in upland pastures. Ann. Rep. Scot. Pl. Breed. Stat. 39-40 (1977)

196] C.R.Funk et al. Registration of 'Bonnieblue' Kentucky bluegrass. Pl. Breed. Abstr. 46, 118 (1976)

197] R.J.Peterson et al. Registration of 'Majestic' Kentucky bluegrass. Pl. Breed. Abstr. 46, 685 (1976)

198] A.W.Jacklin et al. Registration of 'Glade' Kentucky bluegrass. Pl. Breed. Abstr. 47, 809 (1977)

199] T.F.Rewinski et al. Registration of 'Touchdown' Kentucky bluegrass. Pl. Breed. Abstr. 48, 707 (1978)

200] R.H.Bailey et al. Registration of 'Brunswick' Kentucky bluegrass. Pl. Breed. Abstr, 49, 484 (1979)

201] A.M.Radco et al. Registration of 'Ram I' Kentucky bluegrass. Pl. Breed. Abstr. 50, 266 (1980)

202] M.S.Wolfe and E.Schwarzbach. Patterns of race changes in powdery mildews. Ann. Rev. Phytopath. 16, 159-180 (1978)

203] J.Murray. Differential tolerances of turfgrass cultivars to an acid soil high in exchangeable aluminium. Agron J. 70, 769-774 (1978)

204] J.D.Smith. Powdery mildew on Poa pratensis cultivars and selections. J. Sports Turf Res. Inst. 54, 48-52 (1978)

205] H.W.Gardner and H.V.Gardner. The Use of Lime in British Agriculture. (Farmer and Stockbreeder Publ., 1953)

206] A.J.Powell et al. Physiological and colour aspects of turgrasses with fall and winter nitrogen. Agron. J. 59, 303-307 (1967)

207] O.L.Bennett et al. Effects of slope on yield of Kentucky bluegrass with variable rate and time of nitrogen application. Agron. J. 64, 630-634 (1972)

208] S.Kozlowski. Nitrate nitrogen concentration in Dactylis glomerata and Poa pratensis depending on application rate and form of nitrogen fertilizers. Chem. Abstr. 84 No 11, 349 (1975)

209] G.W.Cooke. Fertilizing for Maximum Yield. 120-122. (Crosby, Lockwood and Son, 1972)

210] D.Domska et al. Effect of high fertilizer doses on yield, content of nitrogen compounds, and protein quality of Kentucky bluegrass (Poa pratensis) and red fescue (Festuca rubra). Chem. Abstr. 83 No 13, 437 (1974)

211] M.Kubota et al. Relationship between level of nitrogen fertilizer and growth of grass mixtures. Herb. Abstr. 47, 163 (1977)

212] R.W.Fairbridge and C.W.Finkl. The Encyclopedia of Soil Science. 165 (Dowden, Hutchinson and Ross, 1979)

213] D.O.Erickson et al. Seasonal nutritional variations of three selected cool season forage species. Herb. Abstr. 52, 24 (1982)

214] I.A.Nicholson. Plant community ecology. Ann. Rep. Inst. Terr. Ecology. 92-95 (1980)

215] H.Mayland. Effect of drying methods on losses of carbon, nitrogen and dry matter production from alfalfa. Agron. J. 60, 658-659 (1968)

216] D.W.Goodall. Some considerations in the use of point quadrats for the analysis of vegetation. Aust. J. Scient. Res. 5, 1-41 (1952)

217] S.B.Chapman. Methods in Plant Ecology. (Blackwell Sci. Publ., 1976)

218] D.A.Roberts and C.W.Boothroyd. Fundamentals of Plant Pathology. (Freeman and Co., 1972)

219] P.M.Canaway. Wear tolerance of turfgrass species. J. Sports Turf. Res. Inst. 57, 65-83 (1980)

220] J.Shildrick and R.W.Laycock. Correlations between seed characters and initial establishment in Lolium perenne. J. Sports Turf Res. Inst. 55, 69-82 (1979)

221] F.H.Green (in J.Burnett. Ed.) The Climate of Scotland. The Vegetation of Scotland 15-35 (Oliver and Boyd, 1964)

222] F.Beavington. Upland grass production in NE Scotland in relation to soil and site conditions. J.Br.Grassld.Soc. 24, 31-39 (1969)

223] V.A.Gibeault et al. Mixing turfgrasses controls Fusarium blight. Rev. Pl. Pathol. 60, 337 (1981)

224] A.Habjorg. Floral differentiation and development of selected ecotypes of Poa pratensis L. cultivated at six localities in Norway. Meld. Norg. LandbrHoisk 58, No 4 (1979)

225] O.Heide. Studies on flowering in Poa pratensis ecotypes and cultivars. Meld. Norg. LandbrHoisk 59, No 14 (1980)

226] C.L.Kiellander. A subhaploid Poa pratensis L. with 18 chromosomes, and its progeny. Svensk. Bot. Tidskr. 36, 200-220 (1942)

227] B.R.Phaneendranath et al. Dormancy of Kentucky bluegrass seed in relation to the colour of spikelets and panicle branches at harvest. Crop Sci. 18, 683-684 (1978)

228] A.A.Khan. The Physiology and Biochemistry of Seed Dormancy and Germination. (North Holland Publ., 1977)

229] M.J.Pinthus and U.Kinnel. Crop Sci. 19, 291-293 (1979)

230] D.L.Kittock and J.Patterson. Seed size effects on performance of dryland grasses. Agron J. 54, 277-278 (1962)

231] G.J.Ryle. The growth of the grass plant. Grassld.Res.Inst. Silver Jubilee Report 1947-74 62-71 (1974)

232] C.J.Williamson. Interspecific hybrids of Poa pratensis as perennial, rhizomatous grasses for hill land. Ann.Rep.Scot.Pl.Breed.Stat. 17-18 (1976)

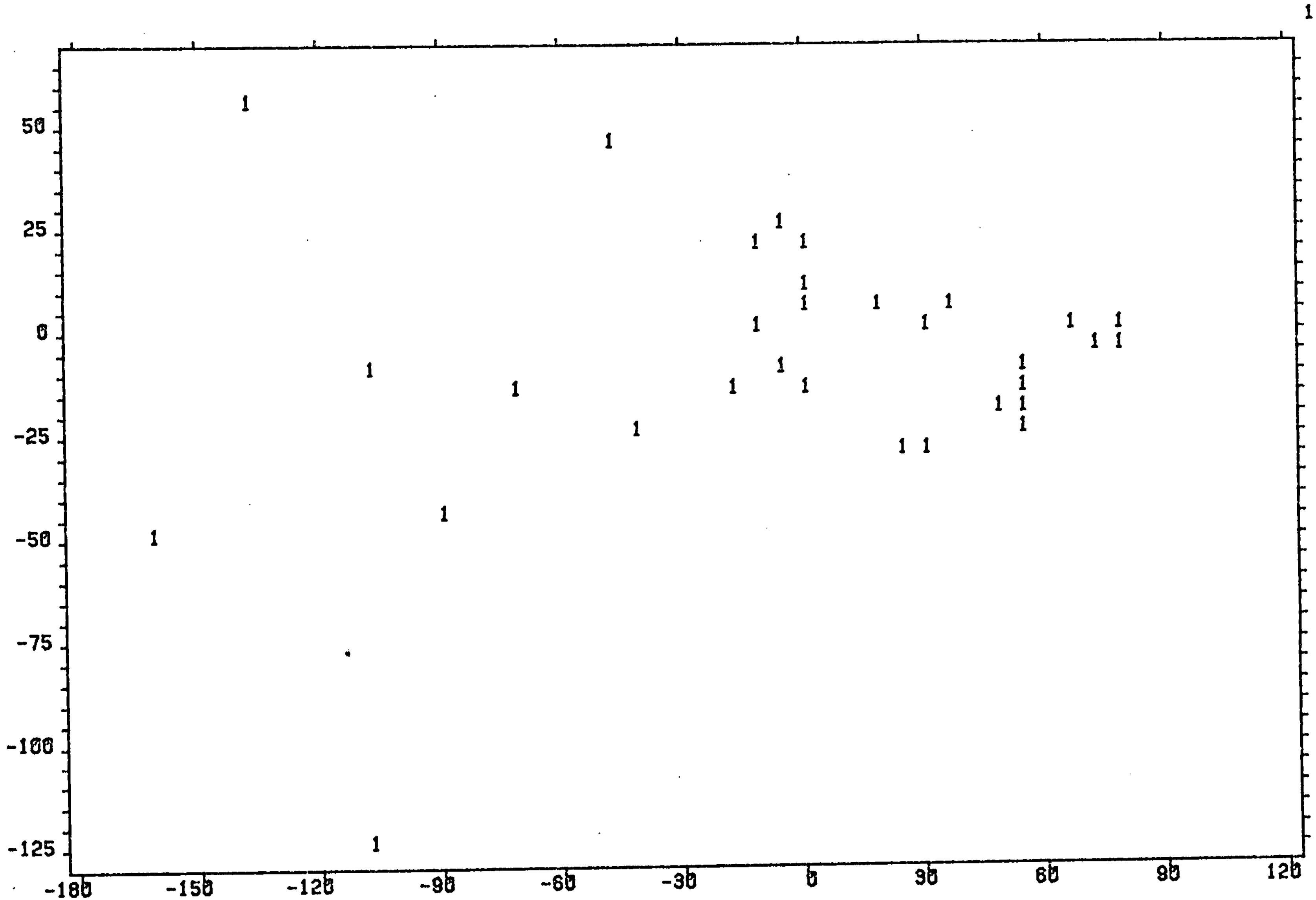
233] E.A. Fitzpatrick (in J. Burnett, Ed.). The soils of Scotland. The Vegetation of Scotland. 36-63 (Oliver and Boyd, 1964).

234] J.R. Thompson. An Introduction to Seed Technology. (Leonard Hill, 1979).

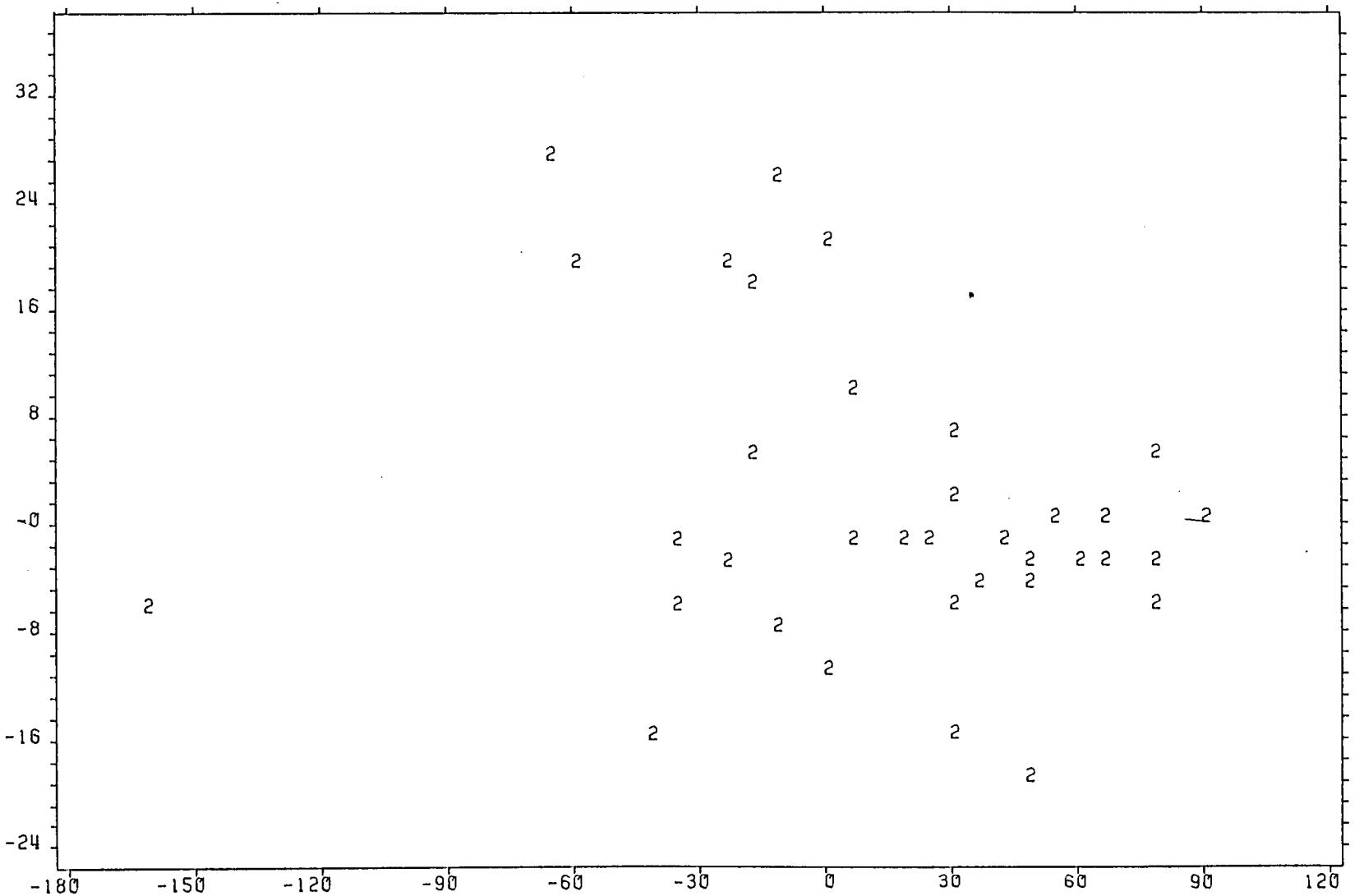
235] Clifford, H.T. and Stephenson, W. An Introduction to Numerical Classification. Academic Press, New York, 1975.

236] Parker, R.E. Introductory Statistics for Biology. Arnold, London, 1973.

APPENDIX 1

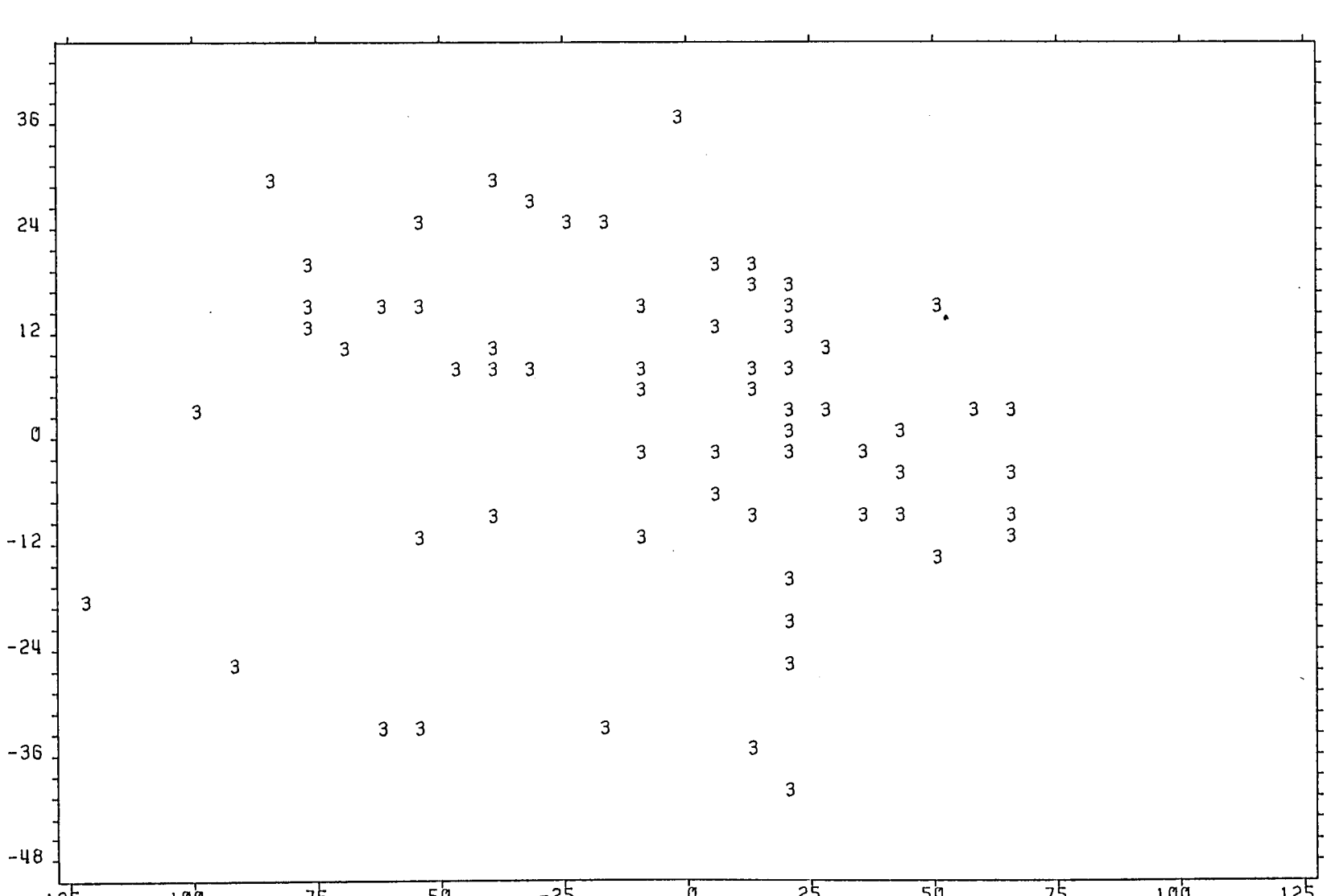


POINTS COINCIDING WITH POINT 1
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1



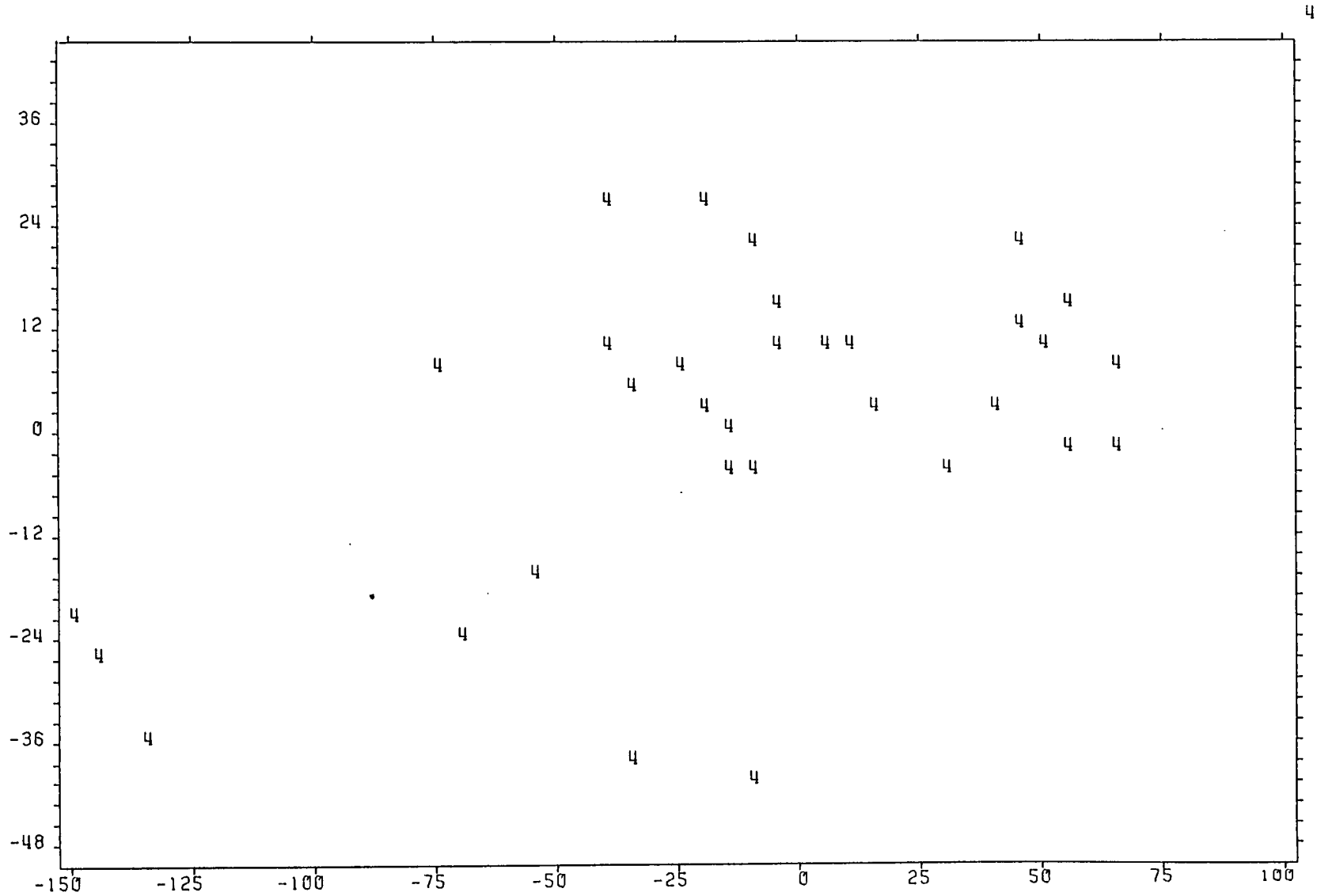
POINTS COINCIDING WITH POINT 2

2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2



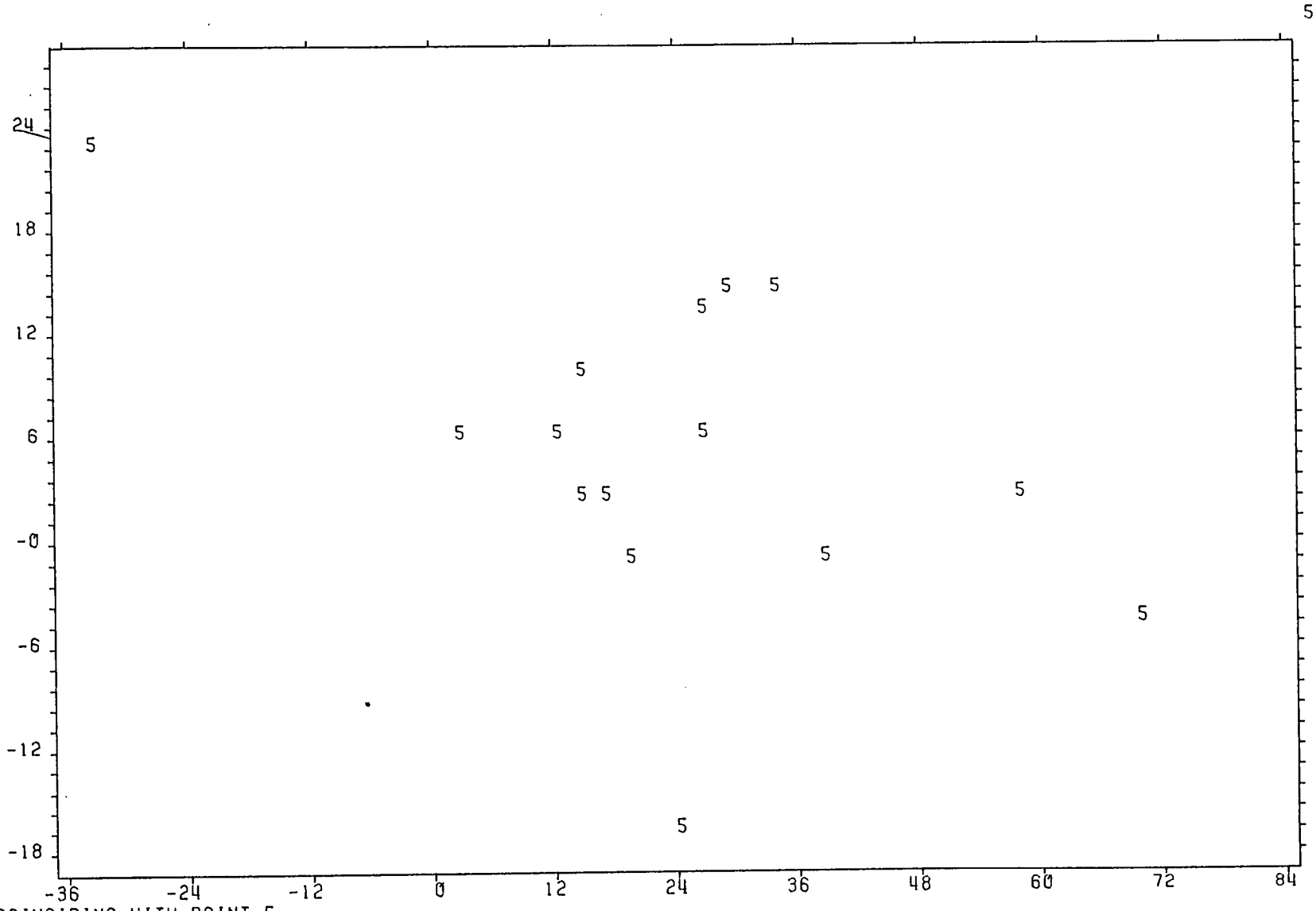
POINTS COINCIDING WITH POINT 3

3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3

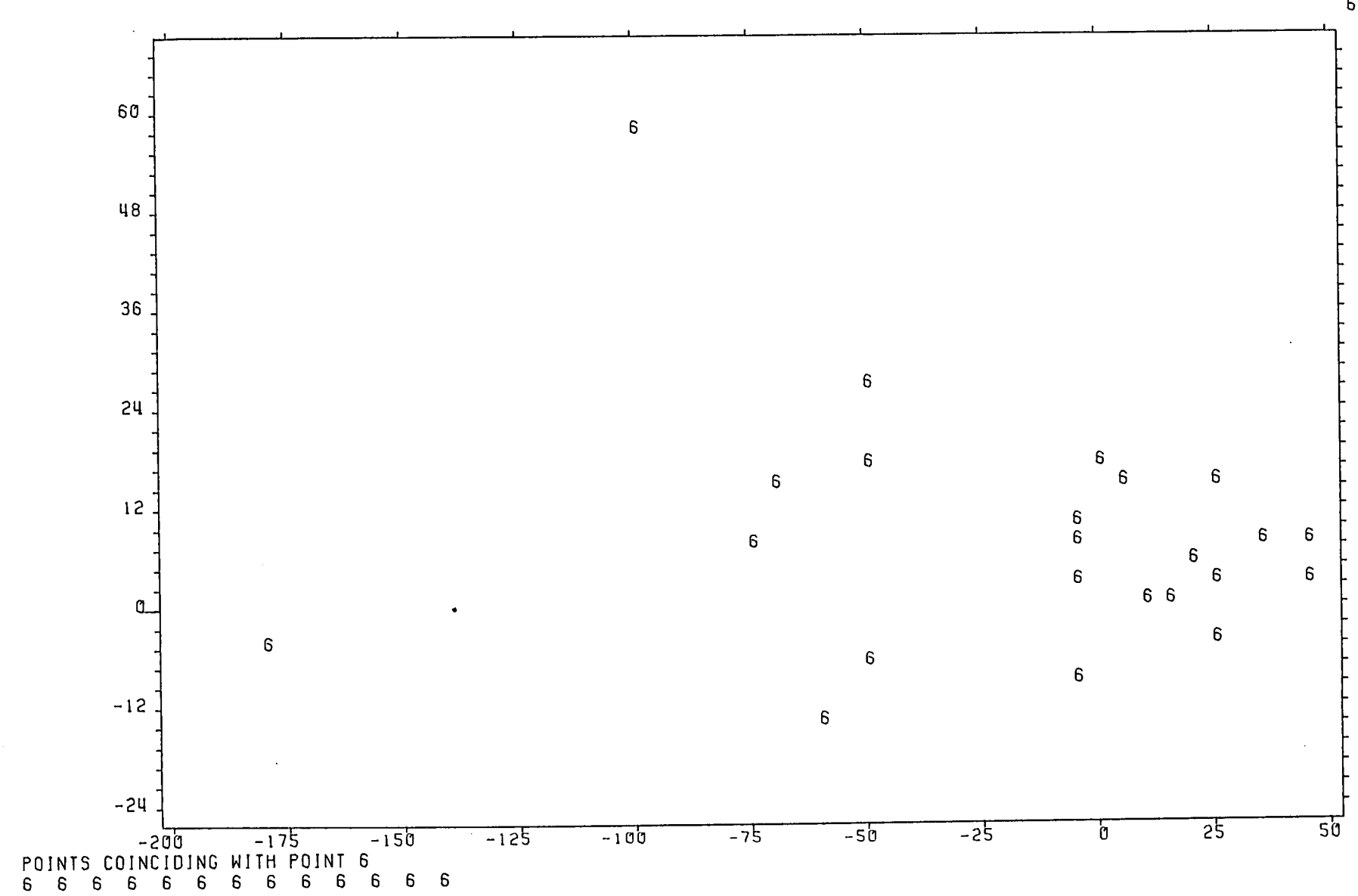


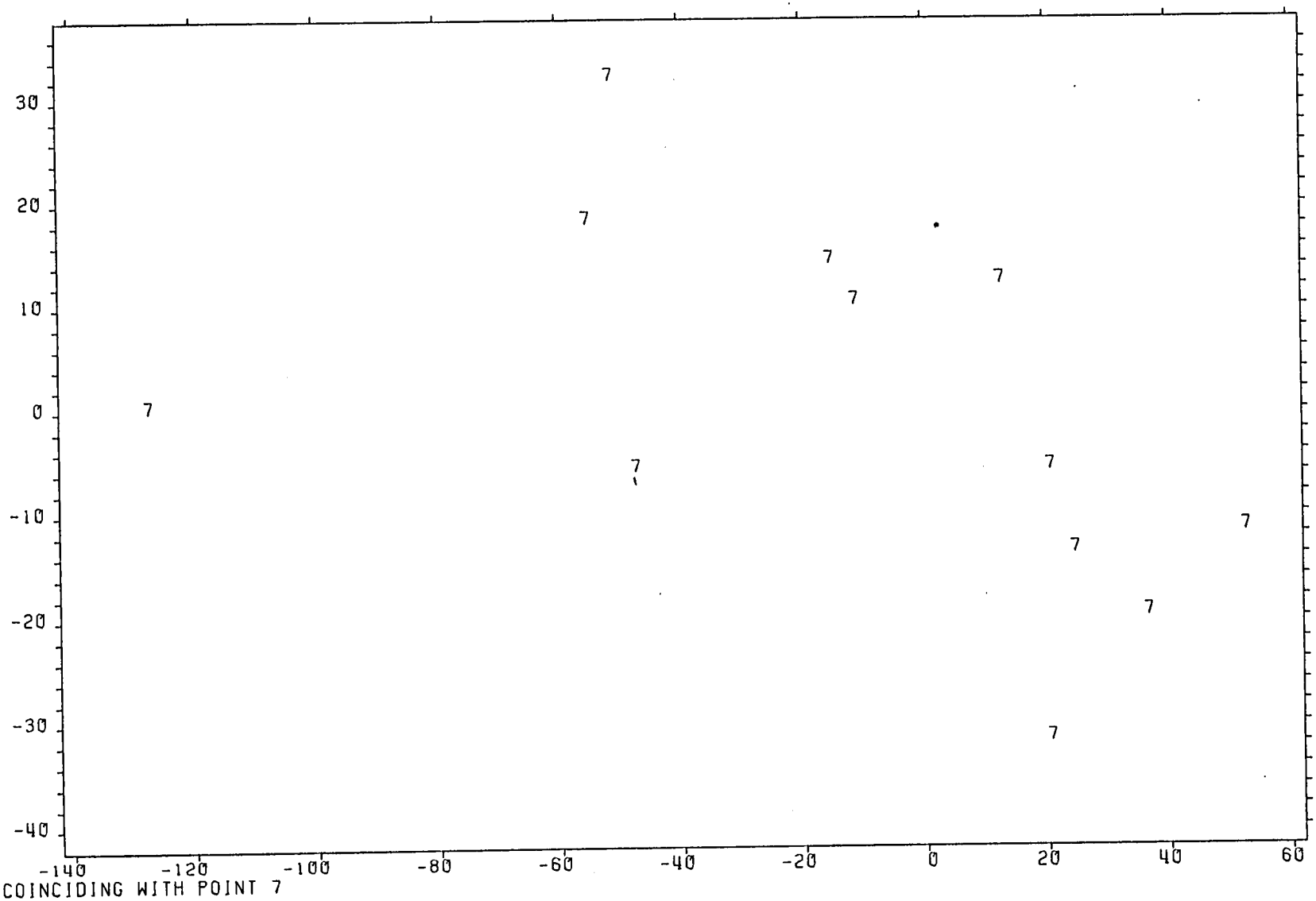
POINTS COINCIDING WITH POINT 4

4 4 4 4 4 4 4 4 4 4 4 4 4 4



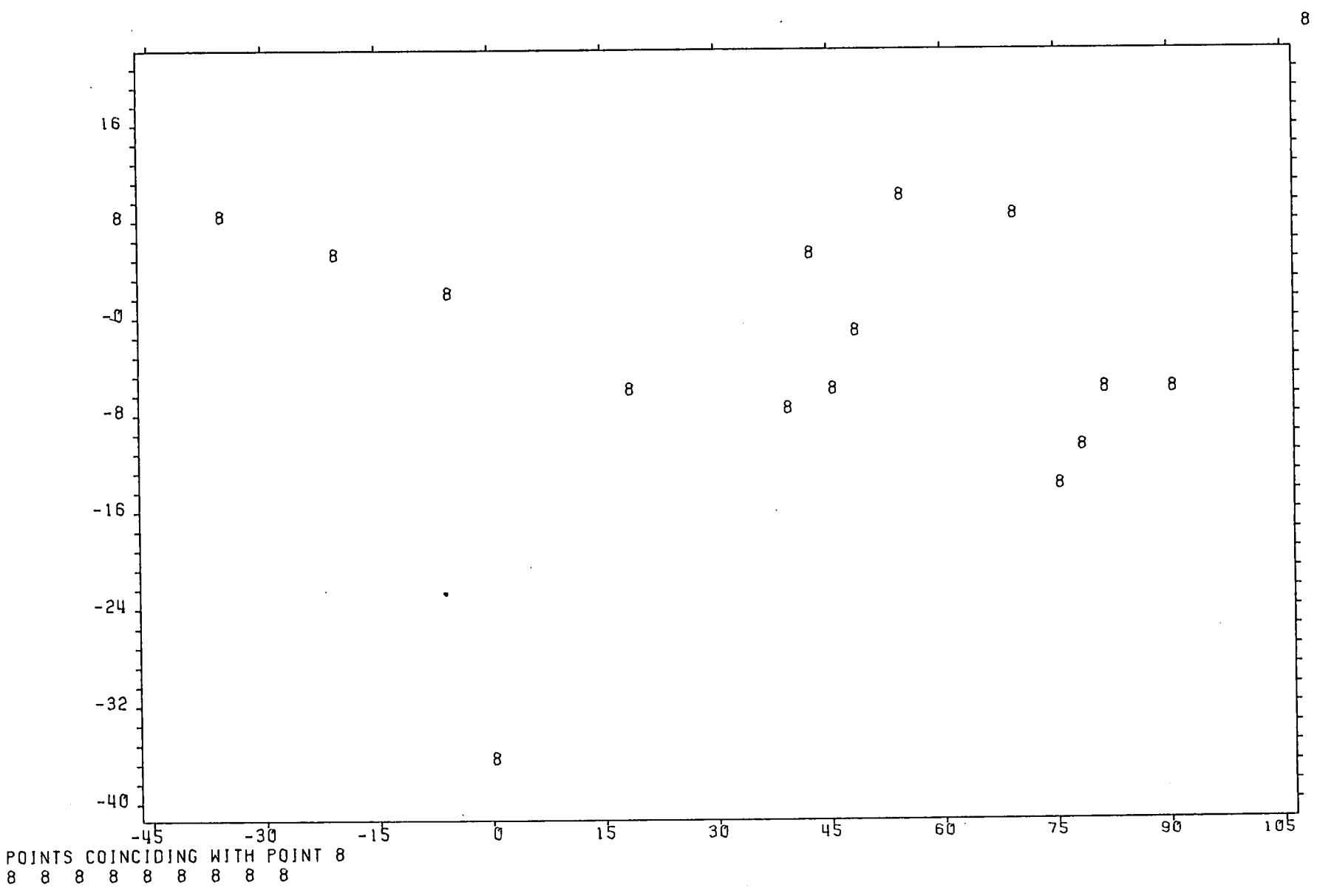
POINTS COINCIDING WITH POINT 5
5 5 5 5 5


6
60
48
36
24
12
0
-12
-24
-200
-175
-150
-125
-100
-75
-50
-25
0
25
50
POINTS COINCIDING WITH POINT 6
6 6 6 6 6 6 6 6 6 6 6 6 6



POINTS COINCIDING WITH POINT 7

7 7 7 7 7 7 7 7



POINTS COINCIDING WITH POINT 8

8 8 8 8 8 8 8 8 8

Appendix 2: Analysis of Variance of Plot Data (Part 2)

(a) Analysis of Variance of Biotypes and Sites

1. Percentage Survival 1982

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	818.59	5.09	409.29	266.249	***
Residual	3	4.61	0.03	1.54	0.025	NS
Total	5	823.20	5.12	164.64	2.680	
Site Reps *Units* Stratum						
Biotype	26	5335.57	33.16	205.21	3.341	***
Site Biotype	52	5141.97	31.95	98.88	1.610	**
Residual	78	4791.70	29.78	61.43		
Total	156	15269.23	94.88	97.88		
GRAND TOTAL	161	16092.43	100.00			

2. Percentage Survival 1983

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	130.79	3.20	65.39	1.000	NS
Residual	3	196.18	4.79	65.39	2.710	NS
Total	5	326.96	7.99	65.39	2.710	
Site Reps *Units* Stratum						
Biotype	26	627.46	15.33	24.13	1.000	NS
Site Biotype	52	1254.92	30.67	24.13	1.000	NS
Residual	78	1882.38	46.00	24.13		
Total	156	3764.75	92.01	24.13		
GRAND TOTAL	161	4091.72	100.00			

3. Percentage Ground Cover 1982

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	3608.08	48.00	1804.04	62.137	**
Residual	3	87.10	1.16	29.03	2.591	NS
Total	5	3695.18	49.16	739.04	65.942	
Site Reps *Units* Stratum						
Biotype	26	1266.94	16.86	48.73	4.348	***
Site Biotype	52	1680.33	22.35	32.31	2.883	**
Residual	78	874.18	11.63	11.21		
Total	156	3821.45	50.84	24.50		
GRAND TOTAL	161	7516.62	100.00			

. Percentage Ground Cover 1983

ource of Variation	DF	SS	SS%	MS	VR	
ite Reps Stratum						
Site	2	1175.82	15.15	587.91	8.837	NS
Residual	3	199.58	2.57	66.53	2.692	NS
otal	5	1375.41	17.72	275.08	11.130	
ite Reps *Units* Stratum						
Biotype	26	2562.66	33.01	98.56	3.988	**
Site Biotype	52	1897.57	24.44	36.49	1.476	**
Residual	78	1927.84	24.83	24.72		
otal	156	6388.07	82.28	40.95		
RAND TOTAL	161	7763.47	100.00			

. Dry Matter Production 1982

ource of Variation	DF	SS	SS%	MS	VR	
ite Reps Stratum						
Site	2	44619216	81.50	22309600	134.487	**
Residual	3	497661	0.91	165887	6.482	**
otal	5	45116864	82.41	9023372	352.593	
ite Reps *Units* Stratum						
Biotype	26	2896259	5.29	111395	4.353	**
Site Biotype	52	4737301	8.65	91102	3.560	**
Residual	78	1996137	3.65	25592		
otal	156	9629697	17.59	61729		
RAND TOTAL	161	54746560	100.00			

. Dry Matter Production 1983

ource of Variation	DF	SS	SS%	MS	VR	
ite Reps Stratum						
Site	2	16100617	47.89	8050308	11.848	*
Residual	3	2038369	6.06	679456	18.413	**
otal	5	18138976	53.95	3627795	98.313	
ite Reps *Units* Stratum						
Biotype	26	4252161	12.65	163545	4.432	**
Site Biotype	52	8349663	24.84	160570	4.351	**
Residual	78	2878226	8.56	36900		
otal	156	15480050	46.05	99231		
RAND TOTAL	161	33619024	100.00			

4. Percentage Ground Cover 1983

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	1100.74	15.55	530.37	6.817	NS
Residual	3	242.19	3.42	80.73	1.849	NS
Total	5	1342.93	18.97	268.59	6.151	
Site Reps *Units* Stratum						
Biogrp	6	420.76	5.94	70.13	1.606	NS
Site Biogrp	12	336.88	4.76	28.07	0.643	NS
Residual	114	4977.76	70.32	43.66		
Total	132	5735.39	81.03	43.45		
GRAND TOTAL	137	7078.32	100.00			

5. Dry Matter Production 1982

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	36155072	80.11	18077536	129.130	**
Residual	3	419985	0.93	139995	2.496	NS
Total	5	36575056	81.04	7315011	130.404	
Site Reps *Units* Stratum						
Biogrp	6	626726	1.39	104454	1.862	NS
Site Biogrp	12	1533983	3.40	127832	2.279	*
Residual	114	6394849	14.17	56095		
Total	132	8555558	18.96	64815		
GRAND TOTAL	137	45130608	100.00			

6. Dry Matter Production 1983

Source of Variation	DF	SS	SS%	MS	VR	
Site Reps Stratum						
Site	2	11902821	44.41	5951410	10.780	*
Residual	3	1656226	6.18	552075	6.642	**
Total	5	13559047	50.59	2711809	32.624	
Site Reps *Units* Stratum						
Biogrp	6	1238344	4.62	206391	2.483	*
Site Biogrp	12	2530993	9.44	210916	2.537	**
Residual	114	9476044	35.35	83123		
Total	132	13245381	49.41	100344		
GRAND TOTAL	137	26804416	100.00			

(b) Analysis of Variance of Biogroups and Sites

1. Percentage Survival 1982

Source of Variation	DF	SS	SS%	MS	VR
Site Reps Stratum					
Site	2	931.7	6.04	465.8	125.035
Residual	3	11.2	0.07	3.7	0.035
Total	5	942.9	6.11	188.6	1.756
Site Reps *Units* Stratum					
Biogrp	6	1149.5	7.45	191.6	1.784
Site Biogrp	12	1084.0	7.03	90.3	0.841
Residual	114	12244.6	79.40	107.4	
Total	132	14478.1	93.89	109.7	
GRAND TOTAL	137	15421.0	100.00		

2. Percentage Survival 1983

Source of Variation	DF	SS	SS%	MS	VR
Site Reps Stratum					
Site	2	153.53	3.76	76.77	1.000
Residual	3	230.30	5.64	76.77	2.568
Total	5	383.83	9.41	76.77	2.568
Site Reps *Units* Stratum					
Biogrp	6	96.45	2.36	16.07	0.538
Site Biogrp	12	192.90	4.73	16.07	0.538
Residual	114	3407.18	83.50	29.89	
Total	132	3696.52	90.59	28.00	
GRAND TOTAL	137	4080.34	100.00		

3. Percentage Ground Cover 1982

Source of Variation	DF	SS	SS%	MS	VR
Site Reps Stratum					
Site	2	3164.66	47.32	1582.33	44.654
Residual	3	106.31	1.59	35.44	1.398
Total	5	3270.97	48.91	654.19	25.810
Site Reps *Units* Stratum					
Biogrp	6	48.86	0.73	8.14	0.321
Site Biogrp	12	478.14	7.15	39.85	1.572
Residual	114	2889.48	43.21	25.35	
Total	132	3416.48	51.09	25.88	
GRAND TOTAL	137	6687.45	100.00		