

STUDIES IN *DACTYLIS*

II. NATURAL VARIATION, DISTRIBUTION AND SYSTEMATICS OF THE *DACTYLIS SMITHII* LINK. COMPLEX IN MADEIRA AND OTHER ATLANTIC ISLANDS

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SUMMARY

Samples of populations of *Dactylis smithii* native to Madeira were collected for studying seed set and morphological characteristics. The analysed data showed two main groupings, the reasons for these groupings and the resultant classification are discussed.

INTRODUCTION

During an extensive study of diploid *Dactylis* (Parker, 1965) it was found that the taxon *Dactylis smithii* Link. had been recorded from the Canary and Cape Verde islands but not from Madeira.

A study of herbarium sheets of a number of *Dactylis* collections from the Atlantic islands including Madeira, showed a range of material so variable, and with so little of the diploid *D. smithii* subsp. *smithii* present, that I undertook a trip to Madeira to collect a wide range of local populations for further study.

MATERIALS AND METHODS

Thirty-three populations were sampled in the field as ripe panicles with stem and flag-leaf attached. Representative herbarium specimens were also collected. The seed fertility figures were collected, and chromosome check counts were made at the Welsh Plant Breeding Station, Aberystwyth. All subsequent characters from both panicles and herbarium specimens were measured and analysed at Leicester.

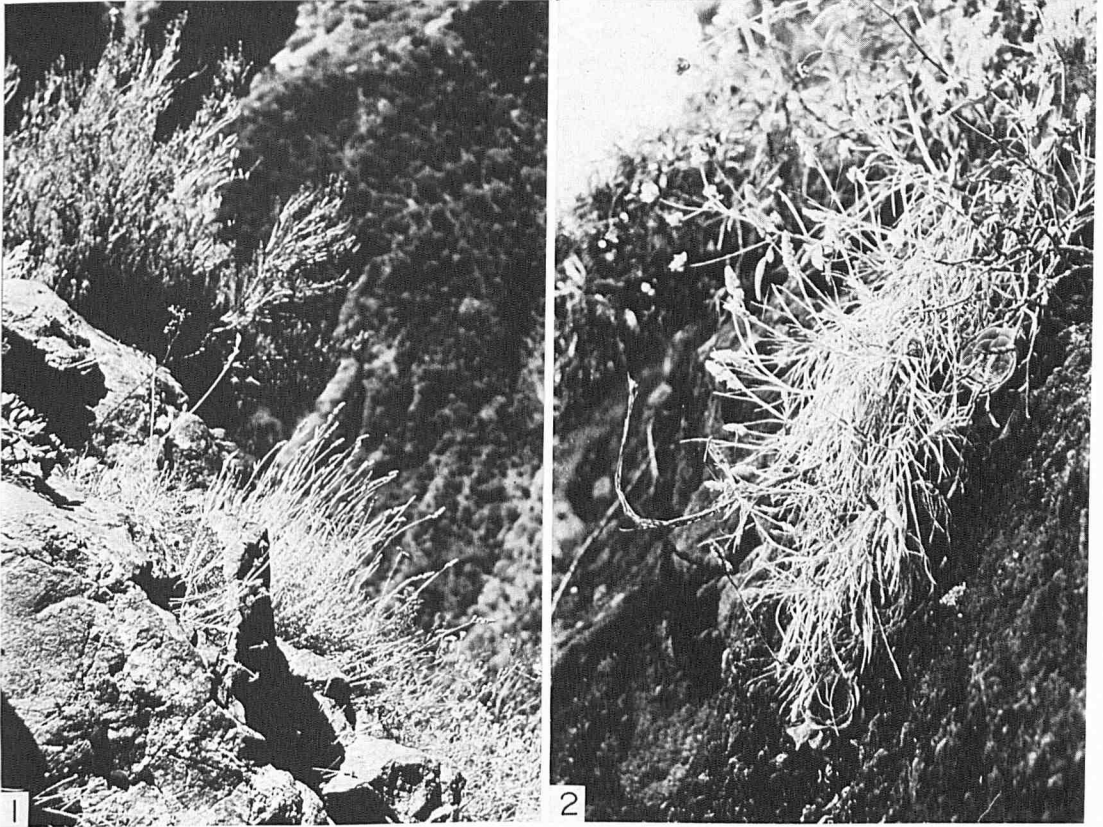
RESULTS

Habitat and distribution

The list of localities and habitats (Table 1) shows very clearly that the *Dactylis smithii* Link. subspecies in Madeira are by preference either chasmophyte or saxatile forms. The cliff habitat is a very old and relatively permanent 'pioneer habitat', chasmophyte associations of vertical rock generally being the climax vegetation, particularly in the dry climates of the Atlantic islands. Such a habitat offers little competition from other species and this is often reflected in the growth form of the plants (Plate 1, Nos. 1 and 2).

Table 1. *Localities and habitats of the populations sampled: all collections comprised samples of five plants each except 7, 46 and 51 (six plants), 27 (eight plants), and 48 (two plants)*

Locality	Altitude (m)	Habitat	Coll. No.
(a) Coastal sites			
Cabo Girao	550	Vertical south-coast cliff, growing in scattered clumps	1
Porto do Moniz	6	Steep north-coast cliff just above beach	7
Porto do Moniz	10	As above	8
Ribero do Janela	3	As above	9
Ribero do Janela	4	Cliff by road between two tunnels, north coast	10
Between Ribero do Janela and Seixal	7	By waterfall on north-facing cliff	11
Ribeira das Furnas ou d'Alto	7	Hanging from bare cliffs sprayed by waterfall	12
Ribeira da Pedra	55	Damp sea cliff, north aspect	13
Quebradas, between Sao Vicent and Ponta Delgada	20	Barren sea cliff, north aspect	14
Road above Ponta Delgada	50	Cliff, north aspect	15
Lombadenha	109	Cliff, north aspect	16
Porto da Cruz	10	Scree and loose earth at edge of track by sea, north aspect	18
Porto da Cruz	10	Bare sea cliff	19
Sao Vicente, by river bridge	7	Steep bare cliffs, north-west aspect	49A
Sao Vicente, Seixal side	2	Low cliffs just above beach	50
Ribeiro do Inferno between S. Vicente and Seixal	30	Cliff facing sea	51
(b) Inland sites			
Eira do Serrado, just below viewpoint	1026	Steep north-west-facing rock face, with <i>Erica</i> and various composites	22
Eira do Serrado	1040	Vertical cliff north of 22 with <i>Laurus</i> , <i>Erica Vaccinium</i>	23
Curral Das Freiras Rd just above tunnel	950	Bare cliffs with no other vegetation, west aspect	24
Eira do Serrado-Funchal Road by E.D.S. turning	1000	Dry rock face near a spring, west aspect	25
Eira do Serrado-Funchal Road	950	Damp cliff face, with <i>Erica</i> , <i>Holcus</i> , <i>Festuca</i> , west aspect	26
Eira do Serrado-Funchal Road	850	Dry rock wall facing south on sharp bend	27
Encumeada-Serra D'Agua path	560	Sheer rock face, sheltered by trees, only three plants, west aspect	36
Serra D'Agua, Ribeira Brava Valley	300	Rock face beside river, south-east aspect	37
Ribeira Brava Valley	200	Cliff by roadside, east aspect	38
Ribeira Brava Valley	100	Cliff face by Carpenter's cave house	39
Ribeira Brava Valley	20	Cliff by schoolhouse	40
Ribeira Brava Valley	10	South end of causeway on rocks beside Levada	41
Encumeada-Estreito path, near Pico Diabolo	1200	Steep, hot, rock face, scanty vegetation, west aspect	45
As 45, near Pico da Pocinha	1200	As 45, south west aspect	46
As 45, near Pico Grande	1300	As 45, with <i>Erica</i> , <i>Cytisus</i> , <i>Laurus</i> , west aspect	47
As 45, near Pico das Pedras	1182	Steep rock face, surrounded by grassy slopes, two plants only	48
Hells Bridge, Estreito de Camara de Lobos	580	Dry shaded cliff by roadside, east aspect	49



No. 1. Plant of subspecies *hylodes* Eira do Serrada, just below viewpoint, 1026 m.
No. 2. Plant of subspecies *marina*, beach cliff Porto Moniz.

The distribution of the native *Dactylis* of Madeira, although following the distribution of maritime and inland cliff formations, is not uniform. The species is restricted apparently by lack of water on the eastern and south-eastern coastal cliffs, and by competition from the native *Laurus* and *Erica* shrubs on the inland cliffs of the wetter northern side of the island. On the south coast the species is found at Estreito de Camara de lobos (49) and Cabo Girao (1). There is then an apparent gap until the high cliffs at Paul do Mar are reached further west (C), and distribution is then continuous around the west and northern coasts as far as Porto da Cruz (18, 19). Inland, the species favours the cliffs to the south of the central mountain ridge. The dotted line on the map (Fig. 1) gives an approximate limit to the south eastern distribution of the species, being as accurate as a preliminary investigation will allow.

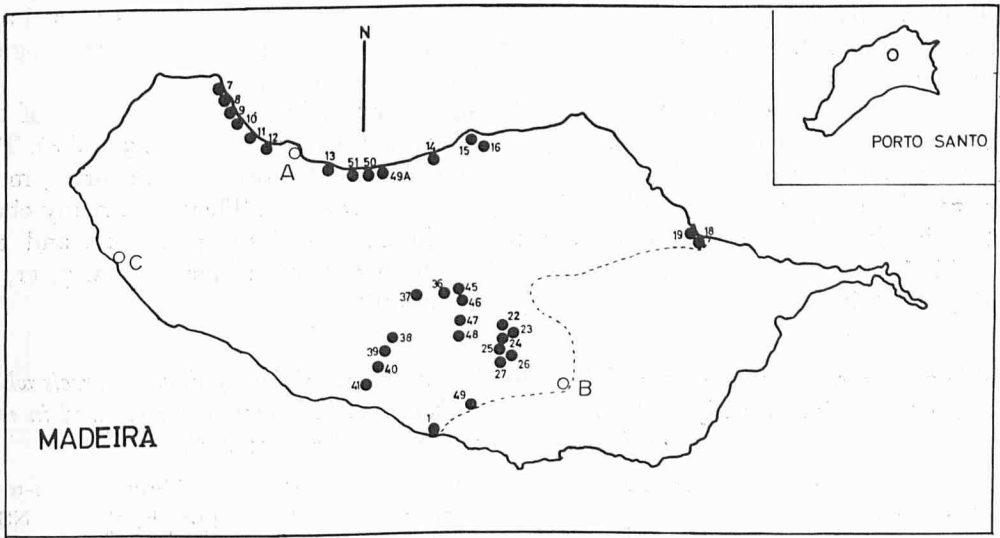


Fig. 1. Map of Madeira showing collection sites and approximate limit of distribution of the subspecies. A and B herbarium specimens of R. P. Murray. A, Seixal; B, Ribero da Santa Luzia, inland form; C, J. Malato Beliz, sea cliffs Paul do Mar.

Population size and seed fertility

The size of individual populations is often difficult to assess. Where the plant is common, large areas of cliff support populations of plants spaced irregularly over their surfaces. In areas of low frequency, plants occur singly or in small groups of two or three together, spatially isolated from other groups. Inland populations are usually smaller and more isolated from each other than those on the coast; however, neither seed set nor germination percentage of the two groups show a statistically significant difference (Table 2 and Fig. 2). Differences in germination between the two population groups are the larger, and this may well be related to an increased level of inbreeding in the smaller populations.

Morphology

In the Madeiran populations of *Dactylis smithii* sens. lat., as well as in populations of this species in certain areas of the Mediterranean, the selective forces operating in a cliff habitat have resulted in increased lignification and longevity of the aerial stems. This

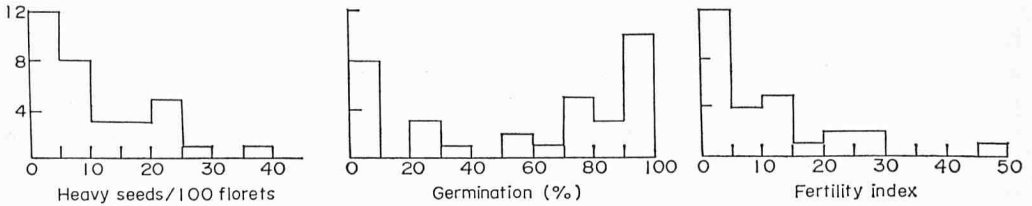


Fig. 2. Seed fertility histograms of the tetraploid populations (pooled data, $N = 33$).

gives the inland populations, and to a lesser extent the maritime populations, a lax shrubby habit quite different from that of the typical *D. glomerata* sens. lat. (Plate 1, Nos. 1 and 2).

Table 2 gives the mean, variance and standard error of the mean for both coastal and inland populations. Because there were clear visual differences in the field, morphological characteristics were compared on the basis of these two groupings.

It can be seen that there are statistically significant differences in nearly all of the morphological characteristics measured, both in variance and mean (Figs. 3 and 4). The coastal populations have a shallower lemma apex lobe and shorter awn, shorter, more hexagonal, mainly papillose epidermal cells, and shorter stems. They have many characteristics in common with both the tetraploid *D. smithii* subsp. *marina* and the diploid *F. smithii* subsp. *smithii*, however, chromosome counts of populations 7, 11, 18 and 51 established that this form is tetraploid ($2n = 28$).

Table 2. The mean and variance of the characters measured, giving significance levels where the two populations are different (all gross morphological characters are measured in mm, cell characters in micrometer eyepiece units at $\times 400$)

Character	Population	N	Variance	F	Mean	t-test
Panicle length	Coast	82	938.25	*	51.21 ± 3.38	NS
	Mountain	84	603.26		58.58 ± 2.68	
Basal Glomerulus length	C	82	70.01	**	15.71 ± 0.92	NS
	M	84	37.05		16.31 ± 0.66	
Florets/spikelet	C	82	0.223	**	3.18 ± 0.05	***
	M	84	0.373		2.73 ± 0.07	
Spikelet length	C	82	0.370	NS	4.83 ± 0.07	**
	M	84	0.406		4.54 ± 0.07	
Lemma length	C	82	0.332	***	4.05 ± 0.06	*
	M	84	0.597		4.08 ± 0.08	
Awn length	C	82	0.0279	**	0.39 ± 0.02	***
	M	84	0.0769		0.50 ± 0.03	
Apical notch	C	82	0.0064	***	0.108 ± 0.009	***
	M	84	0.0127		0.167 ± 0.012	
Cell length	C 10 PL	200	1.5671	***	3.768 ± 0.088	***
	M 15 PL	300	4.2118		5.305 ± 0.102	
Cell median width	C	200	0.1662	***	1.811 ± 0.029	***
	M	300	0.0685		1.353 ± 0.015	
Cell length/median width	C	200	0.6717	***	2.14 ± 0.058	***
	M	300	1.3450		4.05 ± 0.067	
Heavy seed set		33	83.2	-	10.90 ± 1.2	-
Germination (%)		33	949.27	-	46.45 ± 7.45	-
Fertility index		33	105.97	-	9.78 ± 2.47	-

* $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$.

The inland forms are very similar to the diploid *D. smithii* subsp. *smithii*, having the same pale green non-glaucous leaves, but differing in that the long numerous-noded stems produce many fewer secondary branches at any one time; the ligule of the upper culm leaves is shorter, and the number of florets per spikelet is fewer. The chromosome number, counted on seedling root-tips of populations 23, 26, 27, 37 and 49 is uniformly tetraploid.

Nomenclature

During this survey, it became apparent that there existed in the Atlantic islands a

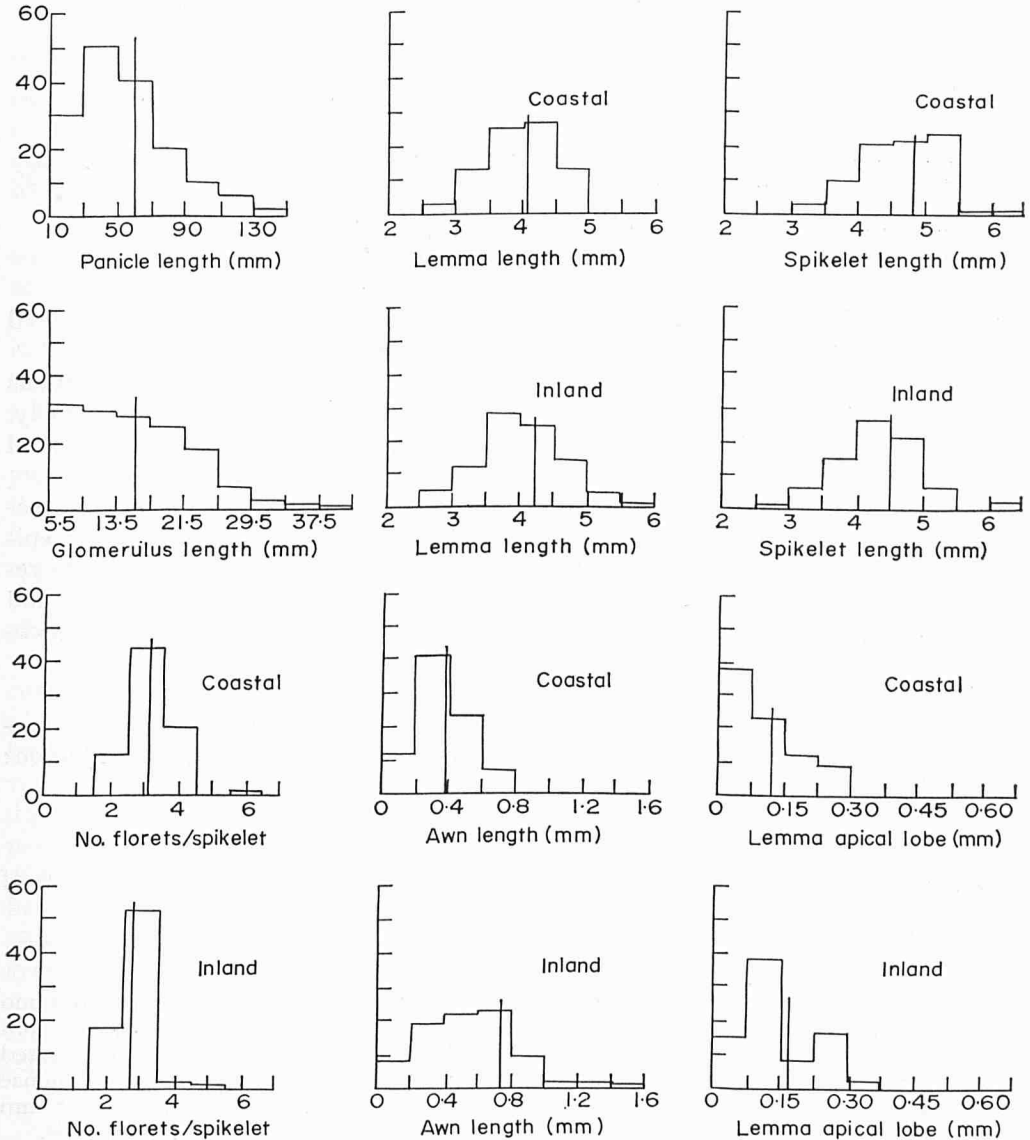


Fig. 3. Distribution and range of the morphological characters measured. $N = 166$ for pooled data, 82 and 84 respectively for the separate coastal and inland populations.

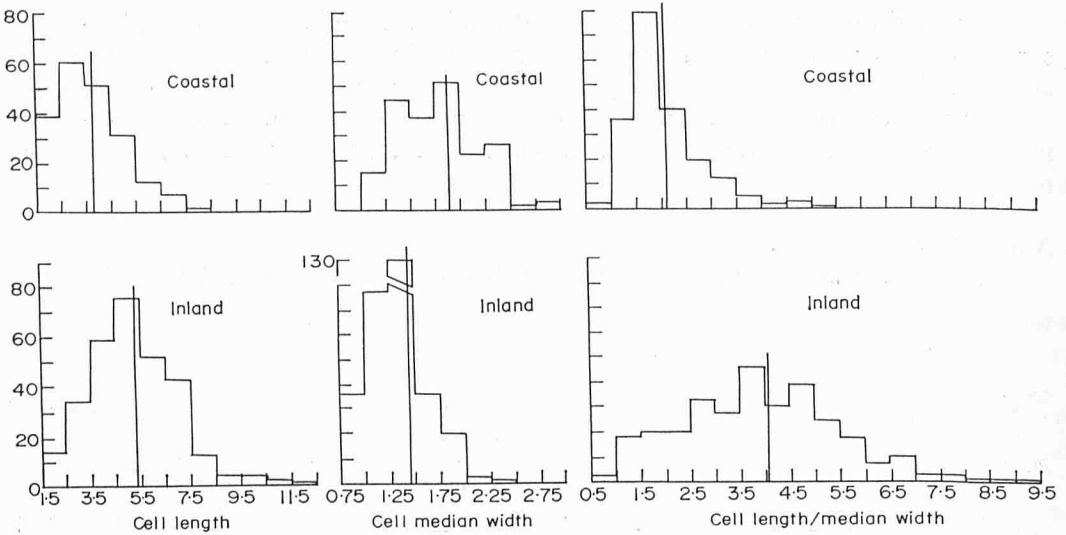


Fig. 4. Distribution and range of the cell characters measured. $N = 200$ cells (ten plants) for the inland population, and 300 cells (fifteen plants) for the maritime population.

number of variants with either non-papillose or papillose leaves, and these were all grouped without differentiation under the common species name *D. smithii*.

This investigation has revealed that there are distinct tetraploid island populations which are recognizably different from the diploid, and can be grouped separately. Furthermore, the morphological characteristics of the maritime form of the tetraploid from Madeira fall within the range of the species *D. marina* Borrill.

Previous work (Borrill, 1962), has also shown that diploid *D. smithii* Link., characterized by a lax shrubby habit, and in some populations, a slightly papillose leaf epidermis, shares several characters with *D. marina* Borrill. The logical step was to reinstate *D. smithii* Link. from the sub-specific status imposed upon it by Stebbins and Zohary (1959) and place the diploid and the tetraploid populations together as a coherent group of related sub-species.

D. smithii Link. subsp. *smithii*

D. smithii Link in Buch, Physic. Beschreib. Canar. Inseln 139, 1825; and, Barker-Webb and Sabin Berthelot, *Hist. Nat. Iles Canar.* 3(2): 417 tab. 249, 1836. Distribution: Canary islands only. Type specimen at the British Museum (Nat. Hist.).

D. smithii Link. subsp. *marina* (Borrill) Parker. Comb. et stat. nov.

D. Marina Borrill, in *J. Linn. Soc. (Bot.)*, 56, 368, p. 431 1962.

Further distribution: Madeira, north, west and south western coastal cliffs. Coasts of Cape Verde islands. Type specimen at Kew.

D. smithii Link. subsp. *hylodes* Parker subsp. nov.

Plantae fruticosae, plerumque multis surculis e basi procedentibus, curvate et erecto culmo ligne in basi, biennes. Ligula frondium superiorum culmi 3–6 mm longa, frondes aridae anni anterioris nec spiratae nec pendulae, epidermis frondis haud papillosa. Paniculae variabiles, sed vulgo breves, 28–60 (120) mm longae. Spiculae compactae (3) 4–5 (6.5) mm longae. Glumae et lemmata breves, apex lemmatis semper fere mucronatus cum puneto aristae 0.2–0.7 mm longae. Subspecies variabilis. Habitat in scopulis non-maritimis et areis apertis et saxosis.

Bushy plants, usually densely tillering, and with curved erect culms woody at base. biennial. Ligule of upper culm leaves 3–6 mm long, dry leaves of last year's growth not

coiled, not pendulous, leaf epidermis not papillose. Panicles variable, but generally short 28–60 (120) mm long. Spikelets compact (3) 4–5 (6.5) mm long. Glumes and lemmas short, lemma apex nearly always mucronate with an awn point 0.2–0.7 mm long. A variable subspecies. Habitat: inland cliffs and open rocky areas.

Distribution: Madeira, widely distributed inland. Canary islands, Tenerife: E. Bourgeau No. 527 (C.G.E.) R. P. Murray (C.G.E.). Gran Canaria: 4000 ft R. T. Lowe (C.G.E.). La Palma: 700 m D. Bramwell 1901 (L.T.R.). Cape Verde islands, Covao: 700 m, Chevalier 13 (P). San Antao: Cova, Chevalier 45600 (P). Type specimen at British Museum (Nat. Hist.).

DISCUSSION

The tetraploid populations of *Dactylis smithii* found throughout the tropical Atlantic islands have clearly diversified into two distinct forms. The inland subspecies *hylodes* is confined to the non-maritime cliffs of these islands, whereas the coastal subspecies *marina* also occurs around the shores of the Mediterranean, Portugal, and probably the west coast of North Africa.

The natural fertility data are of interest in that the number of heavy seeds produced shows a skewed or 'Poisson' distribution. The data of Van Haverbeke (1968) for natural seed set per cone in *Juniperus* shows a similar pattern; here, as in *Dactylis smithii*, the plants are wind pollinated and often comprise small populations of spatially isolated individuals. It is probable that this spatial discontinuity alone makes successful pollination a rare event, although the likelihood of environmental pressures preventing full seed set must also be considered.

Although there are many quantitative differences between the characters of the two populations in Madeira, these mainly appear to be shifts in the optimum value, rather than a clear alteration in the shape of the distribution histogram. Only with awn length, lemma lobe length, cell length and cell length/width ratio in the coastal population do we apparently find directional selection against plants with higher values for those characters.

The separation of diploid *D. smithii* subsp. *smithii* and its close relatives from *D. glomerata*, divides the genus into two distinct parts, covering all the species diversity within the genus *Dactylis*. This diploid subspecies is sharply isolated by genetic incompatibility barriers as well as morphology (Parker and Borrill, 1968). Its closest tetraploid relative, subspecies *hylodes*, is morphologically very similar, although both hybridization (Parker, in preparation) and polyploidy have provided the physiological versatility which has enabled this subspecies to maintain a far wider distribution than the diploid. The tetraploid subspecies *marina*, which is also of hybrid origin (Parker, in preparation), shows a high degree of polymorphism of stem length throughout its distribution range. This is related partly to changes in the predominant foreshore habitat (cliffs on the islands, as opposed to sandy or shingly beaches on the mainland), partly to past gene flow from adjacent diploids, such as still occurs where cytodesmes are sympatric (Zohary and Nur, 1959).

Despite the polymorphisms present within this actively evolving genus, *D. Smithii* sens. lat. is a very distinctive and coherent group of populations. As such, it is worthy of recognition as a separate biological and taxonomic species group within the genus.

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