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TRABAJOS CIENTÍFICOS

DIFFERENTIAL ADAPTABILITY OF ONE POPULATION OF *DACTYLIS GLOMERATA* SUBSP. *MARINA* AND THE HYBRID BETWEEN *"MARINA x GLOMERATA"*.

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SUMMARY

One natural population of cocksfoot (*Dactylis glomerata*) of subsp. *marina* (Mm504) and the natural hybrid between subsp. *marina* and subsp. *glomerata* (Mm794), were clonally replicated as spaced plants in two environments in the same locality, to detect differential genetic responses to the soil environment. Environment 1 had a less acid soil with more nutrients, less sand and less drought than environment 2. Morphological and agronomic traits were recorded, and most of them showed significant differences between populations, between environments and between plants (within populations). Mm794 had more erect plants and higher reproductive output than Mm504, but less biomass production in general. Environment 2 was stressful for several characters (e.g. there was no winter growth and some plants of Mm504 did not flower in both years, 1998 and 1999), but there was significant genotype x environment interaction in many traits. Leaf biomass at the reproductive stage (which presented crossover interaction) and growth habit were the traits with highest phenotypic plasticity, but each population showed plasticity for different traits. The effect of the environment on the differences between populations depended on the trait considered. Seed production was positively correlated with flag leaf length (r=0.63***).

Key words: Clon, cocksfoot, environment, hybrids

INTRODUCTION

Dactylis glomerata L. (cocksfoot) is a forage grass that includes many subspecies, with diploid (2x), tetraploid (4x) and hexaploid (6x) cytotypes. The tetraploids display

wide ecological tolerance (Borrill, 1978). The tetraploid subspecies *glomerata* is more productive than the diploid and shows genotype x environment interaction in fresh weight (Breese, 1969). Santen and Casler (1987) evaluated clones of 2x and 4x subspecies and concluded that tetraploid subspecies *glomerata* had higher IVDMD and correspondingly lower cell wall fraction than diploid clones, but for N, diploids exceeded the tetraploids. Other clonal studies have differentiated genetically 2x and 4x cytotypes of subsp. *izcoi* (Lindner and García, 1997a; Bretagnolle and Thompson, 1996). Reciprocal clonal transplants in the Alps showed differential adaptive differentiation and phenotypic plasticity between subsp. *glomerata* and the tetraploid subspecies *reichenbachii*, mainly due to soil nutrient status (Gauthier *et al.*, 1998).

D. glomerata subsp. *marina* is a tetraploid with small, bluish plants growing on subtropical coasts including Galicia (Spain), occuring on sea cliffs with epidermal leaf papillae. It is an interesting subspecies, due to it's quality and it's salinity and drought tolerance. It can easily hybridize with tetraploid subsp. *glomerata* (Lindner and García, 1997b).

The objective of the present study was to determine differential genetic responses to the soil environment (norms of reaction), of one natural population of subsp. *marina* and the natural hybrid population between subspecies *marina* and *glomerata*.

MATERIALS AND METHODS

Two natural *D. glomerata* populations, chosen by their performance in a sloping field with acid sandy loam soil and summer drought, were used in the present work: Mm504 (subsp. *marina)* and Mm794 (a natural hybrid between subsp. *marina* and subsp. *glomerata* with an erect habit). Mm504 was collected in Cabo Touriñán (Coruña), on a sea cliff co-existing with scarce and short gorse, 100 m above sea level. It is prostrate, with good soil cover. Mm794 was collected in Cíes islands (Pontevedra), at the edge of a pinewood and the beach.

Seeds from both populations were germinated and seedlings were transplanted in spring 1997, with a 40 cm x 40 cm spacing, in 10-plant rows, in the sloping field with sandy loam soil with summer drought, in Salcedo, Pontevedra (Galicia, Northwest Spain). Plants were randomized inside populations: 368 Mm504 and 150 Mm794.

In March 1998, the plants were vegetatively cloned in two halves. The first half was planted in a flat field in the same locality (Salcedo), with good soil and some shade (environment 1=E1), minimizing summer drought, while the second half was replanted in the original sloping field (environment 2=E2), which was more acid soil, and with less nutrients, and less organic matter and more sandy, and with full sun exposure. In each environment, plants of both populations were arranged in a single block. No fertilization,

herbicides, pesticides, or fungicides were applied. Average temperature in Salcedo in 1998 was 14.5° C and total precipitation 1370.8 mm and in 1999, the average temperature was 14.2° C and 1690 mm total rainfall.

The following traits were recorded in both environments:

- heading date as days from 25 April in 1998 and 1999 (HD98, HD99, respectively).

- summer regrowth (29 June 1998), after cutting all plants at 5 cm the 18 June (SR98) (six visual classes from 1=little to 6=abundant)

- autumn growth in 1998 (AG98) and in 1999 (AG99), measured the 28th October 1998 (after cutting plants at 5 cm the 8th September) and the 22 September 1999 (after a cut the 9th August) (nine visual classes from 1=little to 9=abundant).

- plant height in cm (10 November 1998) (PH98).

- growth habit (30 April 1999) (GH99).

- leaf biomass at the reproductive stage (1 June 1999) (LB99) (nine visual classes from 1=little to 9=abundant).

- rust infection (1 June 1999) (RI99) (nine visual classes from 1=little to 9=abundant).

- flag leaf length (FLL99), width (FLW99) and ligule length (LL99), at heading 1999, in cm.

- number of flowering stems (24 June 1999) (NFS99).

- seed production in 1999, in g/plant (SP99).

Winter growth (WG) was only scored in environment 1 (nine visual classes from 1=little to 9=abundant), the 1st March 1999, due to lack of growth in environment 2. Between December 1998 and February 1999, there were 30 days with mean minimal temperatures below 0° C.

Mortality and flowering proportions were statistically analysed by independence χ^2 tests. The rest of the traits were submitted to hierarchical analyses of variance, with plants nested within populations. Pearson=s correlation coefficients between traits were also calculated.

RESULTS

χ^2 tests of independence showed that a significantly higher proportion of plants died in population Mm794 than in Mm504, both before clonal replication and after it, in both environments (Table 1). There were no significant differences in mortality between environments 1 and 2 within population Mm794 nor globally (when both populations were pooled).

TABLA 1

Mortality and flowering proportions in two populations and envirnments

Mortandad y proporciones florales en las dos poblaciones y ambientes

	Populations		
	Mm504	Mm794	$\chi^2_{1\dagger}$ (P)
E 0			
Alive	363	136	19.2***
Dead	5	14	
E 1			
Alive	360	120	25.0***
Dead	2	12	
E 2			
Alive	357	125	12.6**
Dead	6	11	
$\chi^2_{1\dagger}$ (E)	#	0.1 n.s	
Total! $^2_{1\dagger}$ (E)	0.3 n.s		

	1998 Population			1999 Population	
	Mm504	Mm794	$\chi^2_{1\dagger}$ (P)	Mm504	Mm794
E 1					
Flowering	352	134	#	359	122
Non-flowering	10	1		1	0
E 2					
Flowering	335	136	5.2*	354	125
Non-flowering	28	3		3	2
$\chi^2_{1\dagger}$ (E)	1.8 n.s.	#	$\chi^2_{1\dagger}$(P) 6.9**	#	
Total χ^2	$\chi^2_{1\dagger}$(E)11.3**				

E0, before clonal replication; E1 and E2, environment 1 and 2, respectively.

E, environmental homogenity between E1 and E2 ; P, population homogenity

† degrees of freedom.

not calculated due to expected values of class < 5.

P≥0.05*; P≥0.01**; P≥0.001*** level of significant

The proportion of non-flowering plants was higher in 1998 than in 1999. In 1998, population Mm504 flowered significantly less than Mm794 in environment 2 and globally (when both envirnments were pooled) (Table 1). Five Mm504 plants did not flower in environment 2 in any year. There were no significant differences between environments in the flowering of Mm504, but environment 2 had significantly less flowering plants than environment 1 when both populations were pooled. The only case in which all plants flowered was population Mm794 in environment 1 in 1999, but 1999 data can not be statistically analysed, due precisely of small expected values of non-flowering plants.

TABLE 2

ANOVA mean squares of characteres of two *D. glomerata* populations in two environments

ANOVA de los cuadrados medios de los caracteres de dos poblaciones de D. glomerata en dos ambientes.

Source of variation+	HD98	SR98	AG98	PH98	GH99	LB99	RI99	HD99	FLL99	FLW99	LL99	NFS99	SP99	AG99
Population	3180.3***	127.8***	147.6***	664.3***	755.7***	0.4NS	107.6***	7654.0***	9547.9***	1.2*	38.2***	11278.2***	593.1***	36.9***
Environment=E	262.1***	155.0***	449.5***	17963.7***	295.7***	197.1***	37.3***	78.1*	4566.5***	1.3*	4.8***	140714.5***	2076.2***	64.8***
Plant(Population)	34.9***	1.5***	2.7***	37.7***	3.7***	1.2***	2.5***	37.9***	17.0***	0.2NS	0.08***	264.5***	4.2***	1.6***
Population x E	173.8***	11.2***	11.9***	0.3NS	180.0***	10.0***	2.1NS	5.4NS	298.0***	0.4NS	1.1***	1251.2**	240.2***	12.3***
Error	10.8	0.6	1.0	21.4	2.2	0.5	1.5	17.2	9.8	0.2	0.05	145.7	3.0	0.8
R^2	0.81	0.80	0.80	0.84	0.75	0.79	0.67	0.78	0.85	0.52	0.80	0.83	0.80	0.72
CV(%)	17.4	28.6	24.1	30.2	22.0	18.3	29.4	23.4	37.4	61.4	28.1	50.1	71.5	23.5

HD98, HD99 = heading date; SR98 = summer regrowth 1998; AG98 and AG99 = autumn growth 1998 and 1999, respectively; PH98 = plant heigth 1998; GH99 = growth habit 1999; LB99 = leaf biomass at reproductive stage 1999; RI99 = rust infection 1999; FLL99, FLW, LL99 = flag leaf length, flag leaf width and ligule length, respectively; NFS99 = number of flowering stems 1999; SP99 = seed production 1999.

+ df: Population =1; Environment = 1; Population x Environment = 1; Plant (Population): 489(HD98); 498(SR98, AG98); 497(PH98); 495(GH99, LB99,RI99); 494(HD99, FLL99, FLW99, LL99, NFS99);

Error: 453(HD98); 492(SR98); 493(AG98); 475(PH98); 462(APE98); 465(GH99); 464(LB99, RI99, AG99); 432(HD99, FLL99, FLW99); 434(NFS99); 422(SP99).

All quantitative traits showed significant differences at P≥0.001 and P≥0.05 level between environments in analyses of variance (Table 2). In environment 1, plants headed earlier in both years and were taller and produced more biomass in all seasons (in environment 2, winter growth was so small that it was not scored, but there was no dormancy) (Tables 3 and 4). Here plants also showed less brown rust (*Puccinia graminis*) symptoms, had longer and broader leaves, more flowering stems and seed production than in environment 2. Plants in environment 1 were more erect than those in environment 2.

All quantitative traits were also significantly different at P≥0.001 level between populations, except for leaf biomass (LB99) (Table 2). Mm794 had taller plants, were more susceptible to rust, had a later heading date in both years, were generally less productive, with more flowering stems, more seed production, longer and broader flag leaves than Mm504 (Tables 3 and 4). Mm794 plants were more erect.

Statistic differences at P≥ 0.001 level between plants (within populations) were also detected in all traits except for flag leaf width (FLW99) (Table 2). No significant differences in population x environment interaction were found in plant height (PH98), rust infection (RI99), heading date in 1999 (HD99) and flag leaf width (FLW99).

Vigour reduction in environment 2 was more pronounced in Mm504 than in Mm794, ligule length and seed production were more reduced in Mm504 (Table 4). Differences between populations were higher in environment 2 for HD98, GH99, LB99, FLL99 and NFS99. They were higher in environment 1 for SR98, AG98, AG99, LL99 and SP99 (Table 3 and 4).

TABLE 3

Means of traits without significant population x environment interaction

Media de los caracteres sin interacción significativa población x ambiente

	Environment		
	E 1	**E 2**	**Overall mean**
Plant height 98			
Mm504	19.7	9.9	14.8
Mm794	21.7	11.7	16.7
Overall mean	20.7	10.8	15.8
Heading date 99			
Mm504	15.8	16.2	16.0
Mm794	22.3	23.2	22.8
Overall mean	19.1	19.7	19.4
Rust infection 99			
Mm504	3.8	4.2	4.0
Mm794	4.4	5.1	4.8
Overall mean	4.1	4.7	4.4
Flag leaf width 99			
Mm504	0.8	0.7	0.8
Mm794	0.7	0.6	0.7
Overall mean	0.8	0.7	0.8

In 1998, Mm504 headed at the same average date in both environments: it was less plastic phenotypically than Mm794. Growth habit showed a high genotype x environment interaction: it was very plastic phenotypically. The difference of growth habit between environments was also higher in Mm794. However, the most plastic trait was leaf biomass at the reproductive stage, the only trait that showed crossover interaction: in environment 1 it was higher in Mm504, while in environment 2 it was higher in Mm794 (Table 4). This resulted in no global differences between populations. Breese (1969) also found genotype x environment crossover interaction in fresh weight of spaced cocksfoot plants. In the present study, seed production was positively correlated with flag leaf length, in the whole experiment (r=0.63***), within Mm504 (r=0.53***) and within Mm794 (r=0.64***).

TABLE 4

Mean of traits with significant population x environment interaction

Media de los caracteres con interacción significatuva población x ambiente

	Environment		
HD 98	**E1**	**E2**	**Overall mean**
Mm504	22.6	22.7	22.7
Mm794	25.9	27.9	26.9
Overall mean	24.3	25.3	24.8
AG 98			
Mm504	5.3	3.5	4.4
Mm794	4.2	2.9	3.6
Overall mean	4.8	3.2	4.0
SR 98			
Mm504	3.4	2.3	2.9
Mm794	2.4	1.7	2.1
Overall mean	2.9	2.0	2.5
AG 99			
Mm504	4.4	3.6	4.0
Mm794	3.8	3.4	3.6
Overall mean	4.1	3.5	3.8
LB 99			
Mm504	4.6	3.3	4.0
Mm794	4.5	3.6	4.1
Overall mean	4.6	3.5	4.0
LL 99			
Mm504	0.7	0.6	0.7
Mm794	1.3	1.0	1.2
Overall mean	1.0	0.8	0.9
FLL 99			
Mm504	8.3	4.4	6.4
Mm794	17.2	10.6	13.9
Overall mean	12.8	7.5	10.2
NFS 99			
Mm504	31.2	8.9	21.6
Mm794	45.2	14.1	29.7
Overall mean	39.7	11.5	25.7
SP 99			
Mm504	3.0	0.8	1.9
Mm794	6.1	1.4	3.8
Overall mean	4.6	1.1	2.9
GH 99			
Mm504	7.4	7.1	7.3
Mm794	6.3	4.0	5.2
Overall mean	6.9	5.6	6.3

HD 98=heading date 1998; SR 98=summer regrowth 1998; AG 98, AG 99=autumn growth 1998 and 1999; LB 99=leaf biomass at reproductive stage 1999; FLL 99, LL 99=flag leaf length and ligule length 1999, respectively; NF 99=number of flowering stems 199; SP 99=seed production 1999; GH 99=growth habit 1999.

DISCUSSION

The significant genotype x environment interaction found in this study in numbers of flowering stems and seed production was also recorded by Gauthier *et al.* (1998) in cocksfoot. The positive association found here between seed production and flag leaf length may be comparable to the association between panicle size and large flag leaves in cereals (Yan and Wallace, 1995), used in wheat and barley as a selection criterium.

In the present study, flower induction was higher in the second year, and globally higher in environment 1 (with more fertile soil) than in environment 2. More flowering in the second year is not unfrequent in Galician cocksfoot (unpublished results), and low fertility conditions can depress floral induction in *D. glomerata* (Gauthier *et al.*, 1998).

Variation between clones is genetic (nuclear and cytoplasmic) (Hayward, 1985). Therefore, in our study, significant differences between populations have a genetic origin. Mm504 showed good ground cover, important against erosion in sloping sandy soils. Mm794 had more mortality, less production, in general, and more rust infection in summer, taller plants and they headed later in spring.

The effect of the environment on the difference between populations depended on the trait considered. In addition, each population showed plasticity in different traits with genotype x environment interaction. Mm794 was more plastic in growth habit, ligule length, seed production and heading date in 1998, which was later in environment 2, probably by slow establishment on a soil with low nutrient content. Mm504 was more plastic in number of flowering stems, summer regrowth, autumn growth and flag leaf length (Tables 1 and 4). Populations adapted to low productive habitats have generally less morphological plasticity (Gauthier *et al.*, 1998), but in the present study there is no clear association.

Clonal stratified selection will be applied to the data of this study and a yield trial will be sown with seed from selected plants of each population, together with commercial checks.

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ADAPTABILIDAD DIFERENCIAL DE UNA POBLACIÓN DE *DACTYLIS GLOMERATA* SUBSP. *MARINA* Y EL HÍBRIDO ENTRE "MARINA *x* GLOMERATA"

RESUMEN

Una población natural de *Dactylis glomerata* subsp. *marina* (Mm504) y el híbrido natural entre ésta subespecie y la subespecie *glomerata* (Mm794), se multiplicaron vegetativamente y se plantaron en dos ambientes diferentes dentro de la misma localidad, para detectar respuestas diferenciales genéticas en aspectos ambientales de distinto suelo. El ambiente 1 era un suelo menos ácido y con mayor cantidad de nutrientes, menos arenoso que el suelo del ambiente 2. Se evaluaron caracteres morfológicos y agronómicos, y la mayor parte de ellos mostraron diferencias significativas entre poblaciones, entre ambientes y entre plantas (dentro de poblaciones). Mm794 fue una población más erecta y más productiva que Mm504, pero en general con menos biomasa. El ambiente 2 fue más extremo para varios caracteres (p. ej. no se percibió crecimiento invernal y cinco plantas de la población Mm504 no florecieron en 1998 ni en 1999), pero hubo una interacción significativa genotipo x ambiente en muchos caracteres. La biomasa en estadio reproductivo y el hábito de crecimiento fueron

los caracteres con mayor plasticidad fenotípica, pero cada población mostró plasticidad para distintos caracteres. El efecto ambiental sobre las diferencias entre las poblaciones dependió del carácter en consideración. La producción de semilla estuvo correlacionada positivamente con la longitud de la hoja bandera (r=0,63***).

Palabras clave: Clon, dactilo, ambiente, híbridos.