Dactylis glomerata subsp. izcoi, a new subspecies from Galicia NW Iberian Peninsula

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A new subspecies of *Dactylis glomerata* L. from Galicia NW Iberian peninsula is described. Diploid (2n = 14) populations of the new subspecies are confined to surviving patches of climax *Quercus robur* L. woodland in central Galicia, whilst tetraploid populations of autopolyploid origin are widely distributed, with broad ecological range, throughout the region. We compare the characters of the new taxon with those of the most similar subspecies, and we justify the taxonomic approach taken.

Key words: Dactylis glomerata, Galicia, Iberian Peninsula, taxonomy

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INTRODUCTION

In 1977, in the course of studies in Galicia NW Iberian peninsula, Chorton and Young (1980) discovered a native diploid (2n = 14) Dactylis glomerata L. occurring sympatrically with an almost indistinguishable tetraploid cytotype (Tyler & Chorton 1979). Since that time, various aspects of the biology of this taxon have been studied in some depth, with authors always on the lookout for possible differences between the two ploidal forms: its germination was studied by Pannangpetch and Bean (1984); its genetics by Barrientos (1985); its enzymatic composition by Ardouin et al. (1987); its phenolic composition by Ardouin et al. (1987, 1988) and Fiasson et al. (1987); its ecophysiology and autoecology by Lumaret et al. (1987a, b); and various morphological, physiological and biochemical aspects by Selbmann (1989). Borrill (1977) included the taxon amongst the Eurosiberian temperate subspecies, whilst more recently Ardouin et al. (1987, 1988) and Fiasson

et al. (1987) referred to it as the "galician" subspecies. However, no formal description of the subspecies has ever been published; in this paper we hope to make good this omission.

DESCRIPTION

Dactylis glomerata L. subsp. izcoi Ortiz & Rodríguez–Oubiña, subsp. nova

Culmi caespitosi e basi erecto-patentes usque ad decumbentes in base, glabri vel glabrescentes. Folia lucide viridis lucida 6–15 mm lata. Ligula foliorum culmeorum 2–8(10) mm longa. Panicula 2.50–12(15) cm longa cum 1–3 ramis lateralibus, plerumque adnatis praecipuo axi. Spiculae (3)3.50–6 mm longae, (1)2–4(6) florae. Lemma (2)3–4.5(5) mm longum. Stamina 3; antherae (1.20)1.50–2(2.30) mm longae. Numerus chromosomaticus: 2n = 14, 28. Magistro nostro Prof. Dr. Jesús Izco Sevillano dedicata.

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Type: prope Silleda (Pontevedra province). 14.VII.1989. *Ortiz & Rodriguez–Oubiña 300*. 2n = 14. Holotype in SANT (Fig. 1). Isotype in SANT, COI, MA, LISE, K and G.

Culm tuft spread, with stems erecto-patent to decumbent at the base. Culms (37)60-100(127) cm. Basal part of the culm covered with sheaths of a papery texture. Both culms and sheahts may be glabrescent or covered with very short hairs. Leaves light green, 6–15 mm wide, acuminate, with lamina of (4)7-25(29) x (0.15)0.20-0.55(0.70) cm, conduplicated or flat, borders and keel scabrous. Ligule of the culm leaves 2–8(10) mm long, generally papery, truncate-rounded to acute, entire or lacerate, the outer face covered with small, generally reflexed, basally thickened hairs, the inner face glabrous and glossy. Panicle 2.50-12(15) x 1-2.50(3.50) cm, with peduncle and pedicle scabrous; 1-3 stalked basal branches of 1.50- $5(8) \times 0.50-1.30$ cm, generally adnate to the principal axis. Spikelets (3)3.50-6 x 1-3(4) mm with (1)2-4(6) flowers. Glumes navicular, (1)1.50-4.50(5) x 0.30-1.50(2) mm, covered with small adpressed hairs thickened at the base and sessile minute glands, ciliate or non-ciliate along borders and on keel, often with an apical arista of 0.20-1.20(1.70) mm, lower glume generally from 1/4 to near equal length with the upper glume. Lemma navicular, (2)3–4.50(5) x 1.30–1.80 mm, with similar pilosity to the glumes and a generally sub-apical arista 0.30-1.50(2) mm long. Palea membranous, similar in dimensions to the lemma, covered with small erect hairs, ciliate to scabrous on the green keels. Stamens 3, with anthers (1.20)1.50-2(2.30) mm long. Caryopsis ellipsoid, 1.70–2.30(2.50) x 0.50-0.80(1) mm. Chromosome number 2n =14, 28; triploid individuals (3x = 21) are unlikely to occur since the flowering periods of diploid and tetraploid plants do not overlap. Lumaret and Barrientos (1990) collected seed which gave rise to triploid seedlings, but did not find adult triploid individuals in the wild; this suggests that, even if this cytotype occurs naturally, it has very low vigour (Fig. 1).

DISTRIBUTION

Populations of the new subspecies have been found at various sites in Galicia (NW Iberian peninsula), at altitudes of between 15 and 1 120 m a.s.l. The diploid cytotype generally occurs

between 400 and 650 m a.s.l. in central Galicia (Lumaret et al. 1987b, Selbmann 1989), whilst the tetraploid is distributed throughout most of the territory (Fig. 2).

ECOLOGY

The new subspecies is abundant in open seminatural *Quercus robur* L. woodlands, heavily influenced by man and reflecting the original climax vegetation of the region, in the interior of Galicia. In these environments the new subspecies occurs largely as the diploid cytotype, whilst the tetraploid cytotype occurs in a wide range of open habitats, particularly those subject to disturbance and in which, conversely, the diploid cytotype is much less frequent (Ardouin et al. 1987, Lumaret et al. 1987a, b).

PHENOLOGY

Flowering of the tetraploid cytotype generally starts at the beginning of June and finishes in the middle of the same month, shortly after the flowering peak. Flowering of the diploid cytotype generally starts in early July and finishes in September, with the peak occurring towards the end of July. In some years flowering may be delayed especially in tetraploid populations, leading to flowering period overlap with diploid populations; generally, however, there is a period of about eight days between the last tetraploid flower and the earliest diploid flower (Selbmann 1989, Lumaret & Barrientos 1990). This is related to the habitat preferences of the two forms and to the existence of a major summer drought period in Galicia: the tetraploids, occurring in more open sites, bring forward and reduce their flowering period so that it takes place before the drought, whilst the diploids, growing in more or less shady environments, withstand the dry period without significant problems (Lumaret et al. 1987a, b).

BIOCHEMISTRY

Ardouin et al. (1987) reported that enzyme polymorphism is greater in the tetraploid cytotype than in the diploid cytotype (specifically at the loci GOT-1, AcPH-1, PX-1, MDH-1 and PG-1-2), indicating greater heterozygosity in the tretraploid. The same

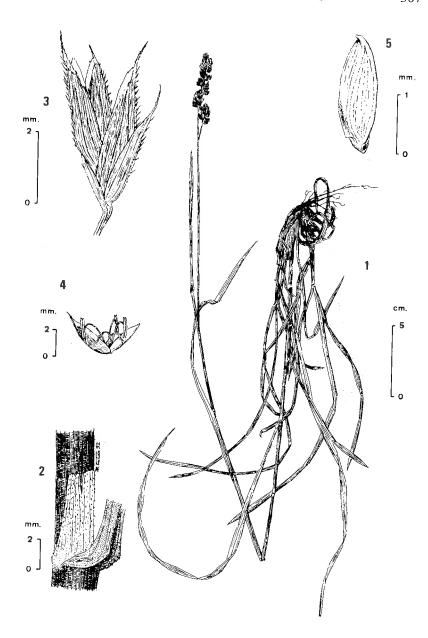


Fig. 1. Dactylis glomerata subsp. izcoi, holotype. 1 = Habit, 2 = Ligule, 3 = Spikelet, 4 = Flower, 5 = Fruit.

authors also reported differences in flavonoid concentrations: leaf extracts from the diploid cytotype contained relatively high concentrations of C-glycosyl flavones and glycosilated derivatives (mono-O-glycosides) of tricin, whilst leaf extracts from the tetraploid cytotype contained relatively high concentrations of free tricin. The authors suggested that these differences might be related to the better adap-

tation of the tetraploid cytotype to open sunny habitats with a more marked summer drought.

DISCUSSION

Table 1 shows the series of morphological, biogeographical and ecological characters which distinguish *Dactylis glomerata* subsp. *izcoi* from the introduced taxon *D. glomerata* L. subsp.

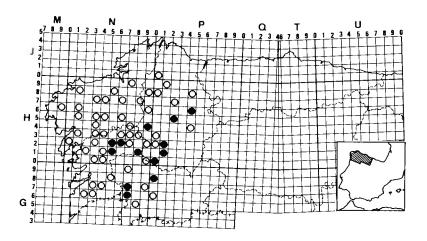


Fig. 2. Distribution D. glomerata subsizcoi. (Chorton Young 1980, Lumar & Barrientos 199 and own data). ● Diploid and tetraplo cytotypes. ○ Tetraploid cytotype

glomerata, with which it co-occurs and has, in recent years, hybridized; from D. glomerata subsp. lusitanica Stebbins and Zohary, a subspecies with a geographically close range and considered by Lumaret et al. 1987b to be closely related; from D. glomerata subsp. aschersoniana (Graebner) Thell., recently reported from the NW Iberian peninsula by Acedo and Llamas (1991), and which some authors (Stebbins & Zohary 1959, Borrill 1961, Stebbins 1961) consider related to the more northerly populations, i.e. those closest to Galicia, of D. glomerata subsp. lusitanica; and finally, from D. glomerata subsp. hispanica (Roth) Nyman, also present in the NW Iberian peninsula (Acedo & Llamas 1991) but restricted to areas of Mediterranean climate and thus not in contact with D. glomerata subsp. izcoi except perhaps at the south-western limit of the latter's distribution.

There are at least two biochemical characters of the new subspecies which clearly differentiate it from other members of the species. Firstly, diploid populations carry the 0.50 allele at the enzyme-controlling locus GOT-1; this allele is probably limited to this subspecies (Lumaret & Barrientos 1990). Secondly, leaf extracts from tetraploid individuals of the new subspecies generally contain high concentrations of free tricin, and those from diploid individuals various mono-O-glycosides of tricin (Fiasson et al. 1987, Ardouin et al. 1988).

The taxonomy of the various *D. glomerata* cytotypes has been the subject of considerable debate, especially where the diploid and tetra-

ploid forms co-exist and which, whilst almost indistinguishable on morphological grounds display some differences in their autoecology such a situation has been reported for sympatri cytotypes of D. glomerata subsp. santai Stebbin and Zohary (Stebbins & Zohary 1959), D glomerata subsp. mairei Stebbins and Zohar (Stebbins & Zohary 1959, Borrill & Lindne 1971, Lumaret et al. 1987b), D. glomerate subsp. aschersoniana (Graebner) Thell. (Borril 1977, Lumaret et al. 1987b) and D. glomerate subsp. judaica Stebbins & Zohary (Borrill & Lindner 1971). The case of the *izcoi* cytotype is similar: they exhibit certain differences in their autoecology and, although several authors (Tyles & Chorton 1979, Lumaret et al. 1987a, b, Selbmann 1989) have reported certain morphological differences between the two cytotypes (in the number and height of shoots, the number of leaves, stomatal size and cell size), probably many of these differences are environmentally determined, and in practice they are almost indistinguishable on morphological grounds.

Stebbins and Zohary (1959), in accordance with the hypothesis of Löve (1950, 1951), recognize two series of subspecies of *D. glomerata*, one diploid and the other tetraploid: according to Love's hypothesis, 2x–4x sympatric complexes (such as the complex occurring in Galicia) should be split into two subspecies even when morphologically they are almost homogenous. Borrill (1977), on the other hand, in accordance with the hypothesis of Camp and Gilly (1943) and Valentine (1949), considers, as do Domin (1943) and Borrill and Lindner

Table 1. Differences between *D. glomerata* subsp. *izcoi* and other subspecies of *Dactylis glomerata* L., showing the most important diagnostic characters.

	D. glomerata subsp.				
Character	izcoi	glomerata	lusitanica	aschersoniana	hispanica
Appearance	Spread	Erect to spread	Erect	Erect	Erect
Culm length (cm)	60–100	60-140	70-130	60–100	10-80
Chromosome number	2n = 14, 28	2n = 28	2n = 14	2n = 14, 28	$2n = \dot{2}8$
Leaf colour	Light green	Deep green to subglaucous	Deep green	Yellowish green to bright green	Glaucous
Leaf width (mm)	7–15	4–12	6–12	5–7	4–8
Ligule length (mm)	2–8	8–15	5–17	5–10	4–8
Panicle length (cm)	2.5–12	9–25	9–27	15–25	2–10
Number of panicle branches	1–3	3–7	2–5	3–5	0–1
Spikelet length (mm)	3.5–6	6–10	5–9	5–8	3–6
Number of florets per spikelet	2–4	2–9	2–8	5–6	3-5
Lemma length (mm)	3–4.5	6.5–8	5–6	5–6	3–8
Distribution	Galicia (NW Iberian peninsula)	Temperate regions of Europe. Central Portugal and East Asia. Present in the N Iberian Peninsula	North and Central	Central Europe. Recently cited from the N Iberian type	Mediterranean region. Present ir Mediterranean- climate in the N Iberian Penin- sula
Ecology	Open <i>Quercus</i> robur woodland and others open habitats	Wide range of habitats. Cultivated land	Open <i>Pinus</i> pinaster wood- land, scrub	Deciduous woodland, especially beech woods	Wide range of habitats
Sources	Own data Lumaret et al. (1987b)	Domin (1943) Borrill (1977) Borrill (1961) Doroszewska (1961)	Own data Stebbins & Zohary (1959) Stebbins (1961) Ardouin et al. (1988) Acedo & Llamas (1991)	Domin (1943) Stebbins & Zohary (1959) Borrill (1961) Ardouin et al. (1988)	Domin (1943) Borrill (1961) Cenci (1982) Pignatti (1982) Acedo & Llamas (1991)

(1971), that in such cases the two cytotypes should be treated as belonging to a single subspecies.

In the present case, in which the tetraploid cytotypes arise from autopolyploidy in the absence of gametic reduction (Barrientos 1985, Ardouin et al. 1987, Lumaret et al. 1987a, b,) the latter of these taxonomic approaches seems more appropriate, particularly if it is also borne in mind that no other native tetraploid cytotypes,

other than those of autopolyploid origin already mentioned, occur within the area of distribution of *D. glomerata* subsp. *izcoi*. As was pointed out above, *D. glomerata* subsp. *hispanica* only comes into marginal contact with the new subspecies, at the south-western limit of the latter's distribution. Furthermore, *D. glomerata* subsp. *glomerata* was introduced as a fodder crop only in 1965 (Yepes & Piñeiro 1972), and the spread of the subspecies throughout Galicia

has probably occurred only over the last 15 years or less, as reported by Lumaret et al. (1987b). This allows us to rule out the possibility which arises, for example, in the case of *D. glomerata* subsp. *marei*, which occurs in the same geographical area as the native tetraploid *D. glomerata* subsp. *hispanica*; those workers who support the taxonomic interpretation proposed by Stebbins and Zohary (1959) assign all tetraploid populations in this area to *hispanica*, including those morphologically identical with *marei*.

Borrill (1977) has suggested that cytotypes of the same subspecies, in cases where these can be discriminated on morphological grounds, should be treated as varieties. Since the two cytotypes of *D. glomerata* subsp. *izcoi* are often indistinguishable on morphological grounds, we have dismissed this possibility.

In view of the proposals of Stebbins and Zohary (1959) concerning the origin of the various subspecies of *D. glomerata*, it would seem reasonable to suppose that the diploid cytotype of the subspecies *izcoi*, associated with semi-natural *Quercus robur* L. woodland of ancient origin, is one of the oldest representatives of the genus, of Tertiary origin,

alongside the diploid cytotypes of *D. glomerata* subsp. *aschersoniana* and *D. glomerata* subsp. *himalayensis* Domin, the only other nemorose taxonh of this species, and the Macaronesian subspecies *smithii* (Link) Stebbins and Zohary. It seems likely that, with the gradual deforestation of the Holocene, the 4x cytotypes of autopolyploid origin, which are of much greater adaptive potential as a result of their larger cell size, higher heterozygosity and greater potential for metabolic diversification (Lumaret et al. 1987a), gradually colonized new habitats and eventually attained their current ubiquitous distribution. While the 2x cytotypes were virtually relegated to their primitive habitat.

However, in the phylogenetic proposal of Fiasson et al. (1987), it is postulated that *D. glomerata* subsp. *izcoi* is one of the more recently differentiated taxa of the species.

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REFERENCES

- Acedo, C. & Llamas, F. 1991: Revisión del género Dactylis L. (Poaceae) en el N.O. de la Península Ibérica. — Bull. Soc. Bot. France Lettres Bot. 138(4/5): 329–338.
- Ardouin, P., Fiasson, J.-L. & Jay, M. 1988: La composante diploïde du complexe specifique Dactylis glomerata L. (Graminees): organisation sur la base de son metabolisme phénolique. — Taxon 37(2): 272-281.
- Ardouin, P., Jay, M. & Lumaret, R. 1987: Etude d'une situation de sympatrie entre diploïdes et tétraploïdes de Dactylis glomerata (Gramineae), sur la base du polymorphisme enzymatique et phénolique. Can. J. Bot. 65:526–531.
- Barrientos, E. 1985: Evolution dans les complexes autopolyploïdes: exemple de Dactylis glomerata L. Etude comparative de la structure génétique des populations dans deux situations de contact entre diploïdes et tétraploïdes: 35–54. Ph. D. Thesis Univ. Sci. Tech. Languedoc, Montpellier, France.
- Borrill, M. 1961: The pattern of morphological variation in diploid and tetraploid Dactylis. J. Linn. Soc. (Bot.) 56:441-452.
- Borrill, M. 1977: Evolution and genetic resources in coksfoot. Report Welsh Plant Breeding Station: 190-209.

- Borrill, M. & Lindner, R. 1971: Diploid-tetraploid sympatry in Dactylis (Gramineae). New Phytol. 70:111-1124.
- Camp, W.H. & Gilly, C.L. 1943: The structure and origin of species. Brittonia 4:323–385.
- Cenci, A.C. 1982: Caratteristiche biometriche e morfologiche di popolazioni naturali tetraploidi di Dactylis glomerata L. — Webbia 36(1): 135–159.
- Chorton, K.H. & Young, N.R. 1980: List of grass ecotypes collected in July and August 1977 in Galicia, NW. Spain. Report Welsh Plant Breeding Station: 1-23.
- Domin, K. 1943: Monograficka studie o rodu Dactylis L. — Acta Bot Bohem 14:3–147.
- Doroszewska, A. 1961: A comparative study on Dactylis slovenica Dom. and D. glomerata L. Acta Soc. Bot. Pol. 30(3–4): 775–803.
- Fiasson, J.L., Ardouin, P. & Jay, M. 1987: A phylogenetic groundplan of the specific complex Dactylis glomerata. — Biochem. Syst. and Ecol. 15(2): 225– 229.
- Löve, A. 1950: The taxonomical evaluation of types with different chromosome numbers. — Proc. Seventh Int. Bot. Congress, Stockholm: 283–284.
- Löve, A. 1951: Taxonomic evaluation of polyploids. Caryologia 3:263–284.

- Lumaret, R. & Barrientos, E. 1990: Phylogenetic relationships and gene flow between sympatric diploid and tetraploid palts of Dactylis glomerata (Gramineae). — Pl. Syst. Evol. 169:61–96.
- Lumaret, R., Barrientos, E., Guillerm, J.-L., Jay, M., Fiasson, J.L., Ardouin, P., Delay, J., Ait Lhaj Loutfi, A., Izco, J. & Amigo, J. 1987a: Signification adaptativa et évolutiva de la polyploïdie infraspécifique: cas des dactyles diploïdes et tetraploïdes de Galice. In: Legay, J.M. (ed.), Biologie des populations, évaluation et prospective. Université Claude Bernard. Lyon I: 129–133.
- Lumaret, R., Guillerm, J.-L., Delay, J., Ait Lhaj Loutfi, A., Izco, J. & Jay, M. 1987b: Polyploidy and habitat differentiation in Dactylis glomerata L. from Galicia (Spain). — Oecologia (Berlin) 73:436–446.
- Pannangpetch, K. & Bean, E.W. 1984: Effects of temperature on germination in populations of Dactylis glomerata from N W. Spain and Central Italy. Ann. Bot.-London 53:633-639.

- Pignatti, S. 1982: Flora d'Italia. Edagricole. Bologna.
 Selbmann, R.L. 1989: Estudio comparativo entre dos citotipos de Dactylis (Gramineae). Pastos 18–19(1/2): 147–157.
- Stebbins, G.L. 1961: A diploid subspecies of the Dactylis glomerata complex from Portugal. — Agronomia Lusit. 23:9–15.
- Stebbins, G.L. & Zohary, D. 1959: Cytogenetic and evolutionary studies in the genus Dactylis. I: Morphology, distribution, and interrelationships of the diploid subspecies. Univ. Calif. Publ. Bot. 31(1): 1-140.
- Tyler, B.F. & Chorton, K.H. 1979: Diploid and tetraploid Dactylis from N.W. Spain. — Rep. (Annual) Welsh Pl. Breed. Sta. 1979;34–37.
- Valentine, D.H. 1949: The units of experimental taxonomy. Acta Biotheoretica 9:75–88.
- Yepes, V. & Piñeiro, J. 1972: Distribución estacional de la producción de algunas especies pratenses en Galicia. — Pastos 2:63-76.

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