

Biosystematic studies on *Dactylis* L. 1. Review of previous studies. 1.1. Systematics, variability, ecology, biology and cultivation problems

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Abstract

In this paper the author presents a review of previous studies on *Dactylis* L. This review deals with systematics, variability, ecology, biology and cultivation problems.

Key words: *Dactylis*, review, systematics, variability, ecology, cultivation

INTRODUCTION

The species, subspecies and other taxa of the genus *Dactylis* are characterized by great variability of morphological, anatomical, physiological, cytological and other characteristics. Such great variability is typical of many representatives of the grass family.

The genus *Dactylis* is represented by perennial species. This complex contains both taxa which occupy very large territories (*D. glomerata*, *D. hispanica*, *D. marina* and *D. polygama*), and others of restricted geographical distribution (Figs. 1 and 2). The latter are usually classified as subspecies of *D. glomerata* or taxa of lower rank. For example: ssp. *reichenbachii*, ssp. *judaica*, ssp. *santai*, ssp. *mairei*, ssp. *smithii*. Some taxa are frequently classified as endemics: ssp. *ibizensis*, ssp. *juncinella*, ssp. *rigida*. Taxa of restricted distribution are separated from each other not only geographically but also ecologically. It is interesting that *D. glomerata* ssp. *himalayensis* Dom. has a disjunctive distribution. Its first area is in the western Himalayas-Kashmir, and Nepal, the second is southeastern China (Stebbins and Zohary 1959, Grigoryev 1962).

D. glomerata has long been used as a fodder plant and is cultivated beyond the limits of its natural distribution. It has been noted on Sakhalin and Kurile islands (Sokolovskaya and Probatova 1976, Voroshilov

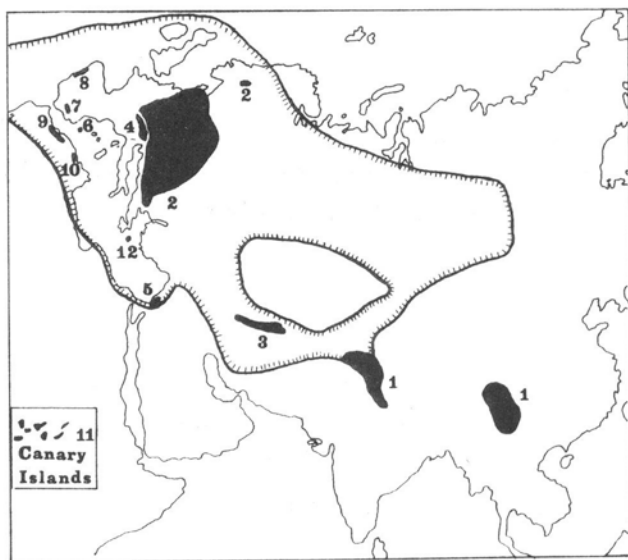


Fig. 1. Generalized distribution of native forms of *Dactylis* (according to: Hylander 1936, Domin 1943, Stebbins 1956, Stebbins and Zohary 1959, Jones et al. 1961). Hatched boundaries of *D. glomerata*, 1 — *D. glom.* ssp. *himalayensis*, 2 — *D. polygama*, 3 — *D. glom.* ssp. *woronowii*, 4 — *D. glom.* ssp. *reichenbachii*, 5 — *D. glom.* ssp. *judaica*, 6 — *D. glom.* ssp. *ibizensis*, 7 — *D. glom.* ssp. *juncinella*, 8 — *D. glom.* ssp. *lusitanica*, 9 — *D. glom.* ssp. *santai*, 10 — *D. glom.* ssp. *mairei*, 11 — *D. glom.* ssp. *smithii*, 12 — *D. glom.* ssp. *rigida*

1982), China (Li-Yun Chang et al. 1977), North America (Eaton 1958), Australia (Sambo 1983), New Zealand (Jacques and Edmond 1952) and Greenland (Pedersen 1965/66). *D. glomerata* has a very wide ecological amplitude (Grigoryev 1962, Pavlova 1981) and may grow in different habitats.

A xerophytic *D. hispanica* Roth was quite unexpectedly found by Scannell (1964) in Ireland (Fig. 2). Her determination was later confirmed by Borrill and in this way *D. glomerata* ssp. *hispanica* was listed among the flora of Ireland (Scannell and Synnott 1972).

D. marina Borrill is also of a xerophytic nature. It is easily recognized because of the structure of the leaf epidermis. This species was distinguished by Borrill (1957) as a variety of *D. glomerata* and later raised by him to the rank of a species (Borrill 1961c).

D. polygama Horvátovski is a species with quite different environmental requirements than those of the two mentioned above. It is of mezophytic character and grows mostly in the deciduous forests of central Europe. Hylander (1936) and Jones et al. (1961) mention this taxon from Sweden (Fig. 1).

The classical taxonomy of the genus *Dactylis* is very difficult as there

is no distinct morphological border between recognized taxonomical units. This is the result of great variability of morphological characters. In addition, the discrimination of modifiatory from genetic variability presents many difficulties. Moreover some characters are gradually changing (both topocline and ecocline — Gregor 1939).

D. glomerata was described for the first time by Linnaeus (1753). In his paper, Linnaeus cited three older synonyms for this species with the appropriate literature. Horvátovski (1774) described *D. polygama* from

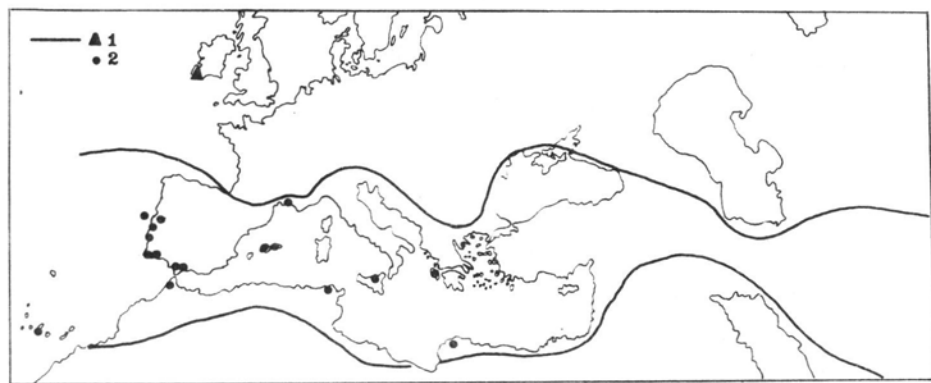


Fig. 2. Distribution of *D. hispanica* and *D. marina* (according to: Borrill 1961a and c, Jones et al. 1961, Scannell 1964, Borrill and Carroll 1969, Scannell and Synnott 1972). 1 — *D. hispanica* (generalized distribution — continuous line; locality in Ireland — triangle), 2 — *D. marina*

the Slovakian Little Carpathians. In 1797 Roth recognized *D. hispanica* as a Mediterranean taxon. Graebner (in Ascherson and Graebner 1898-1902) described *D. aschersoniana*, which corresponded to the earlier *D. polygama* distinguished by Horvátovski. Thellung (1911) classified this taxon as a subspecies of *D. glomerata* and named it: *D. glomerata* ssp. *aschersoniana*. Here it should be mentioned that, according to the current International Code of Botanical Nomenclature (1983), the above-mentioned taxon has two correct epithets (according to the rank in which it occurs). When the taxon is determined as a species the correct name is *D. polygama* Horvat., whereas in the case of the subspecies, it is *D. glomerata* ssp. *aschersoniana* (Graebner) Thell., as *aschersoniana* and not *polygama* was the name first given it as a subspecies. This is mentioned because much misunderstanding arises from the use of these two names for the same taxon.

The complexities in the systematics and nomenclature are presented by Domin (1943) in his monograph on the genus *Dactylis*. He recognized only one species *D. glomerata* with seven subspecies: ssp. *euglomerata* Hayek, ssp. *slovenica* Dom., ssp. *altaica* (Bess) Dom., ssp. *polygama* (Horvátovski) Dom., ssp. *himalayensis* Dom., ssp. *hispanica* (Roth) Nym.,

ssp. *rigida* (Boiss. et Heldr.) Hayek. The subspecies were divided into numerous varieties and forms. After 1943, further new taxa of the genus *Dactylis* were described. Stebbins and Zohary (1959) described five new subspecies of *D. glomerata*. They are as follows: ssp. *judaica*, ssp. *ibizensis*, ssp. *lusitanica*, ssp. *santai*, ssp. *mairei*. Parker (1972) also distinguished a new taxon: *D. smithii* ssp. *hylodes* as well as Tzvelev (1976) *D. glomerata* ssp. *hyrcana*. At present this genus is treated differently in several floras (Table 1). From the previous studies on *Dactylis* it is evident that researchers do not hold definite opinions as to the rank of particular taxa.

Detailed investigations on the variability of the systematic units of *Dactylis* have been carried out by numerous authors.

Borrill (1961a) compared the *Dactylis* populations from the Mediterranean region with populations from north Europe. He studied the variability, heredity and correlation of the following characters: the length of the panicle, the length of the leaf blade and the morphology of the lemma apex. These three characters have great taxonomical significance and are genetically controlled. From the studies it is evident that the length of the panicle is negatively correlated with the lobed condition of the lemma apex (a typical character of ssp. *hispanica*) and positively correlated with the length of the leaf blade. In the Mediterranean area, Borrill (1961a) observed a tendency in *Dactylis* to decrease the plant size, the occurrence of shorter and narrower leaves and shorter, ovate panicles as well as the occurrence of flowers with a lobate lemma apex. Plants with extreme characters are identified as *D. glomerata* ssp. *hispanica* (Roth) Nym. The structure of the lemma apex depends on the latitude. A lobate lemma apex is much more distinctly formed in the Mediterranean area while to the North this character gradually declines. Comparative studies show that ssp. *hispanica* is not a clearly distinct taxon. Intermediate forms between *D. glomerata* ssp. *glomerata* and *D. glomerata* ssp. *hispanica* have been observed.

Cenci (1982) studied the geographical variability of *D. glomerata* populations from Italy. The populations of northern Italy differ considerably from those of southern Italy. Cenci l. c. identified the latter as ssp. *hispanica*.

Cooper's (1964) studies also confirmed climatic selection and clinal variability in the genus *Dactylis* from the Mediterranean area through the Atlantic coast of Europe to central and northern Europe.

Eagles and Östgård (1971) and Östgård and Eagles (1971) indicated differences in the adaptation capacity (temperature, photoperiod) between populations of *D. glomerata* from Norway and Portugal.

Stapledon (1928) studied morphological variability of *D. glomerata* from 458 localities (Sweden, England, Scotland, Wales, Denmark, France,

Table 1

Systematics of the genus *Dactylis* according to various authors (taxa lower than subspecies have been omitted)

Author, year	Taxa				
	<i>glomerata</i>	<i>polygama</i> (<i>aschersoniana</i>)	<i>hispanica</i>	<i>slovenica</i>	other
Hubbard 1968	<i>D. glomerata</i>	<i>D. polygama</i>			
Klemm 1974	<i>D. glomerata</i>	<i>D. polygama</i>			
Mullenders 1967	<i>D. glomerata</i>	<i>D. polygama</i>			
Rothmaler 1963	<i>D. glomerata</i>	<i>D. polygama</i>			
Pedersen 1974	<i>D. glomerata</i>	<i>D. aschersoniana</i>			
Josifović 1976	<i>D. glomerata</i>	<i>D. polygama</i>	<i>D. hispanica</i>		
Oberdorfer 1970	<i>D. glomerata</i>	<i>D. polygama</i>	<i>D. hispanica</i>		
Pignatti 1982	<i>D. glomerata</i>	<i>D. polygama</i>	<i>D. hispanica</i>		
Prokudin et al. 1977	<i>D. glomerata</i>	<i>D. polygama</i>	<i>D. hispanica</i>	<i>D. slovenica</i>	
Garcke 1972	<i>D. glomerata</i> ssp. <i>glom.</i>	<i>D. polygama</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>		
Dimitrov 1962	<i>D. glomerata</i>	<i>D. aschersoniana</i>			<i>D. glaucescens</i> and <i>D. ciliata</i>
Smejkal 1980	<i>D. glomerata</i> ssp. <i>glom.</i>	<i>D. polygama</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>	<i>D. glomerata</i> ssp. <i>slov.</i>	
Kárpáti et al. 1955	<i>D. glomerata</i> ssp. <i>glom.</i>	<i>D. glomerata</i> ssp. <i>ascherson.</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>	<i>D. glomerata</i> ssp. <i>slov.</i>	
Hegi 1965	<i>D. glomerata</i>	<i>D. glomerata</i> ssp. <i>ascherson.</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>		
Christiansen 1953	<i>D. glomerata</i>	<i>D. glomerata</i> ssp. <i>ascherson.</i>			
Jordanov 1963	<i>D. glomerata</i> ssp. <i>euglom.</i>	<i>D. glomerata</i> ssp. <i>ascherson.</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>		
Tzvelev 1976	<i>D. glomerata</i> ssp. <i>glom.</i>	<i>D. glomerata</i> ssp. <i>lobata</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>	<i>D. glomerata</i> ssp. <i>slov.</i>	<i>D. glomerata</i> ssp. <i>himalayensis</i> , ssp. <i>woronowii</i> , ssp. <i>hyrcana</i> , ssp. <i>altaica</i>
Flora Europaea 1980	<i>D. glomerata</i> ssp. <i>glomerata</i>	<i>D. glomerata</i> ssp. <i>ascherson.</i>	<i>D. glomerata</i> ssp. <i>hispanica</i>	<i>D. glomerata</i> ssp. <i>slov.</i>	<i>D. glomerata</i> ssp. <i>woronowii</i> , ssp. <i>reichenbachii</i> , ssp. <i>ibizensis</i> , ssp. <i>juncinella</i> , ssp. <i>lusitanica</i>

U.S.A., New Zealand). He stated that *D. glomerata* is characterized by ecotypic differentiation.

Stebbins and Zohary (1959) in their studies of *Dactylis* variability from the Mediterranean and Middle East territories (i. e. from the area where the variability of this genus is greatest) stated that populations in the southern part of the distribution area differ from the typical *D. glomerata* in having narrower, shorter and stiffer leaves and more compact panicles. They are included in *D. glomerata* ssp. *hispanica* or *D. hispanica*. But the taxon *hispanica* is not uniform either. Populations from the eastern part of the distribution area (Greece, Turkey) differ from the typical *D. hispanica* growing in the western part (Spain, France). The authors mentioned 11 diploid subspecies of *D. glomerata* and 3 tetraploids. They did not decide the rank of the last 3 cytotypes. The authors' detailed consideration concerning chromosome numbers, evolutionary connections and systematic classification reflecting the relationships within the genus *Dactylis* will be discussed in the next paper of this cycle (Mizianty a — in preparation).

Turesson (1929) investigated populations of *D. glomerata* from Altai. He noted the variability of Siberian populations. Then he compared them with the populations from other (non-Siberian) areas. The Siberian populations were distinguishable by their adaptability to the Siberian environment (winter hardiness, suitable time of flowering).

Tomov (1973) studied the morphological variability (time of heading, leafiness, habit) in 711 clones of *D. glomerata* from Bulgaria, England and Australia. According to the time of heading these clones were classified into six groups: from very early to very late. He stated that variability of heading time is of a geographical character.

The variability of smaller taxonomical units of the genus *Dactylis* in smaller areas has been studied by several authors.

Benson and Borrill (1969) reported the occurrence of topoclines within *D. marina* in Portugal.

From Borrill's (1961d) studies it appears that in Crete, *D. hispanica*, *D. rigida* occur along with a number of intermediate populations between them. According to Borrill (1961d), *D. rigida* is an adaptive line deriving from *D. hispanica* and should not be ranked as a separate species. It should be pointed out that *D. rigida* was recognized by Boissier and Heldrich (Boissier 1855) as a species but Hayek (Hayek and Markgraf 1932) reduced its rank to that of ssp. of *D. hispanica*.

Vierhapper (1915) in his investigation on the variability in Cretan *Dactylis*, stressed that plants growing there form a series from ssp. *glomerata* through ssp. *hispanica* to ssp. *rigida*.

Parker (1972) found morphological differentiation of *D. smithii* from

Madera and other Atlantic islands. The inland populations differed from the sea cliff populations. In spite of this polymorphism, Parker l.c. considered *D. smithii* a very uniform group that should be distinguished as a species.

Wetschnig (1984) studied the distribution and morphology of two Carinthian ssp. of *D. glomerata* (ssp. *glomerata* and ssp. *aschersoniana*). According to him, these taxa are not morphologically differentiated. He held the opinion that only cytological characters (number and morphology of chromosomes) and length of stomata and diameter of pollen grains are helpful in distinguishing these subspecies.

In Poland according to previous data, *D. glomerata* and *D. polygama* (Raciborski and Szafer 1919, Szafer et al. 1967) occur. Jasiewicz (1965) also mentioned *D. glomerata* ssp. *slovenica* Domin from the Bieszczady Mts. This taxon was described by Domin (1929) from the Belanske Tatry massif as a species and in 1943 degraded by him to the rank of a subspecies. It is a mountain taxon, occurring in the Carpathians.

Doroszewska (1961) compared Polish populations of *D. glomerata* (mountain and lowland) with the populations of *D. slovenica* from the Belanske Tatry (Czechoslovakia). She investigated morphological, cytological and physiological characters. During her studies she found a series of intermediate forms between these two taxa. The question whether *D. slovenica* may be treated as an independent species or ssp. of *D. glomerata* is still open. In the opinion of Doroszewska (1961) if other taxa of *Dactylis* e.g. *D. marina* Borrill are classified as species, then *D. slovenica* also should definitely rank as an independent species.

The author of the present paper discovered *D. slovenica* in several localities in the Polish Carpathians. The occurrence and distribution of *D. slovenica* in Poland will be the subject of a separate paper (Mizianty b—in preparation).

Cytological studies on the *Dactylis* species in Poland were carried out by Doroszewska (1963), Rurka (1974) and Mizianty (1985).

Popova (1963) studied the anatomy of leaves and stems of *Dactylis* from Bulgaria. She investigated in detail the arrangement of sclerenchyma and vascular bundles.

Koryakina and Shilova (1962) investigated the anatomical and morphological variability of the *D. glomerata* inflorescence. They mentioned that under favourable environmental conditions, panicles are well branched and florets are well developed. Disturbances in the normal morphological structure of florets and branching panicles are caused by prolonged deviations in air temperature and humidity, soil moisture and photoperiod. The structure of floral glumes under unfavourable conditions changes and occupies an intermediate position between the normal floral glumes and leaves (i.e. s.n. proliferation).

A detailed study of the flowering of *D. glomerata* is presented by Petrova and Nikolayevskaya (1972).

Nikolayevskaya in a series of papers described: the development of the inflorescence (1979), development of the caryopsis (1974) and the influence of frosts on the reproductive organs of *D. glomerata* (1973).

Elvers' (1980) observations indicate that *Dactylis* flowers (although grasses are wind fertilized plants) are often visited by *Thricops semicinerea* (Diptera, Muscidae) and *Misumena vatia* (Thomisidae).

In the present short review mention should be made of an electron microscope investigation of the epidermis cells of *D. glomerata*. The study of the epidermis outer cell wall's structure confirmed the mezophytic character of *D. glomerata* (Miroslavov and Zhigar 1973).

Borrill (1961b) studied the nature of the leaf epidermis of the eight diploid subspecies of *Dactylis* (ssp. *smithii*, *ibizensis*, *juncinella*, *judaica*, *woronowii*, *lusitanica*, *aschersoniana* and *santai*). The following measurements were made: cell length, width of cell at the centre, width of cell at the end, stomatal length, number of stomata per unit area. In addition to the differences shown by the numerical data, there were others, mainly qualitative in character, which are of value in separating the diploid *Dactylis* groups. These are: 1) the extent to which the cell wall is smooth, sinuous, or beaded; 2) the type of stomatal distribution; 3) the extent to which the cells are hexagonal or square. When the subspecies are placed in groups based on these characters, the arrangement conforms with their geographical distribution. The above mentioned papers deserve special attention because it is generally accepted that epidermal characters are of significance in grass classification (Prat 1932).

D. glomerata is a useful grass and has been studied because of its economic importance. Paper dealing with this subject should not be omitted in the present short review. Our aim is to give only an outline of the main problems:

- The effect of fertilization on the growth, development and yield of *Dactylis* (Stuczyński et al. 1971, Rais and Kráľovec 1973, Tomka and Kulichova 1973, Rutkowska 1976, Habovštiak and Páter 1977, Kráľovec et al. 1978, Mika 1978, Davies 1979, Falkowski and Łyduch 1982, Kern and Baryła 1983, Stoicovici 1983).
- The reaction of *D. glomerata* to certain environmental factors (humidity, temperature, winter hardiness, day length, insolation). The references deal with cultivated varieties, as well as those growing in natural habitats (Forde 1966a and b, Broué et al. 1967, Eagles 1967, 1971, Korohoda and Zawisza 1967a and b, Stuczyński et al. 1971, Abe 1980a and b, Duda and Kacperska 1983, Golovko 1983, Roy and Berger 1983, Stoyanova and Kostov 1983).
- The influence of some agrotechnical and chemical factors on the growth,

development and biology of *D. glomerata* (Stapledon and Milton 1930, Tincker 1930, Nelson and Robins 1957, Jameson 1963, Bochniarz et al. 1983, Rutkowska et al. 1983, Etherington 1984).
 — The effect of SO₂ and NO₂ on *D. glomerata* (Ashenden 1978, 1979, Crittenden and Read 1979).

In the present paper, cytological and genetical problems as well as experimental studies and evolutionary relationships in the genus *Dactylis* are omitted. They will be the subject of the next paper in this cycle (Mizianty a — in preparation).

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Biosystematyczne studia Dactylis L. 1. Przegląd dotychczasowych badań.
1.1. Systematyka, zmienność, ekologia, biologia i zagadnienia hodowlane

Streszczenie

Niniejsza praca stanowi przegląd dotychczasowych badań przeprowadzonych w rodzaju *Dactylis L.* z zakresu systematyki, zmienności, ekologii, biologii i problemów dotyczących uprawy. Wyniki niektórych prac zostały krótko omówione a inne prace zostały tylko wymienione w obrębie poruszanych zagadnień.