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An investigation on the diploid and tetraploid forms of *Dactylis glomerata* L. ssp. *Woronowii* (Ovczinn.) Stebbins et Zohary

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INTRODUCTION

In 1955 seeds were obtained from two natural stands of *Dactylis* in the mountains of Soviet Armenia. These seeds were collected by Professor W. Gajewski in the neighbourhood of Lake Sewan and of the town Erivan in Armenia, USSR. The seeds were planted in 1956 and the plants that grew out of them flowered the next year.

Cytological examinations showed that the plants from the neighbourhood of Erivan were tetraploids, whereas those from the neighbourhood of Lake Sewan were diploids. The two groups of plants were morphologically very similar and corresponded to the description of *Dactylis Woronowii* Ovczinn. in the Flora SSSR (1934). In accordance with the systematics of the genus *Dactylis* advanced by Domin (1943) and Stebbins and Zohary (1959), who consider that this genus consists of one common species *D. glomerata*, the plants from Armenia were classified as the subspecies *D. glomerata* L. ssp. *Woronowii* (Ovczinn.) Stebbins et Zohary.

Similarly, the other forms of *Dactylis* covered by this investigation were classified as subspecies — i.e. ssp. *slovenica* and ssp. *Aschersoniana* — though in the previous work they were defined as independent species (Doroszewska 1961).

The preliminary examinations of the plants from Armenia showed that they could be an interesting object for investigation since the tetraploid form of ssp. *Woronowii* had not been known before.

MATERIAL AND METHODS

The plants covered by this investigation were originally obtained from natural stands:

ssp. *Woronowii* Ovczinn. $2n = 28$ (4x)

plants No. 71—90 came from an arid, mountain steppe in the neighbourhood of Erivan, Armenia, altitude over 1500 metres above sea level,

ssp. *Woronowii* Ovczinn. 2n = 14 (2x)
plant No. 91—110 came from an arid mountain steppe near Lake Sewan, Armenia, altitude about 2000 metres above sea level.

The plants of *D. glomerata* used for comparison and for making the necessary crosses came from various parts of Poland. Among them were plants of ssp. *Aschersoniana* from the Białowieża Forest and from Zalesie, and ssp. *slovenica* from the Belanske Tatry Mts. The detailed list of these plants and of the stands from which they were collected was given in an earlier report (Doroszewska 1961).

All the experimental plants were grown for several years at the Botanical Garden in Warsaw. Every year the plants were measured and records were made of their blooming season, the general condition, pollen fertility etc. The size of the plants was established from measurements of 20 culms, 20 leaves, and 20 panicles of each plant; in the case of less vigorous tufts only ten or all the culms of a plant were measured.

Cytological observations were made on fresh smear preparations; for fixing 3 : 1 absolute alcohol with glacial acetic acid was used. Cells in the course of meiosis were stained in propiocarmine this stain giving better results than acetocarmine. For pollen fertility counts 1 : 1 acetocarmine with glycerine was used. Two slides were prepared from each plant and 200 pollen grains were counted on each slide.

Ssp. *Woronowii* (4x) and ssp. *Woronowii* (2x)

In Armenia ssp. *Woronowii* (4x) as well as ssp. *Woronowii* (2x) grow on unsheltered stands of arid, high mountain steppes where the vegetation cover is very scarce. The growth habit of both these forms is in very tight tufts of a greyish blue-green colour and with stiff culms and leaves, which reflects the xeromorphic adaptation of the plants. The growth habit of the tufs, which owing to the straight culms and leaves look like plumes, is entirely different from the growth habit of *D. glomerata* from Poland (Doroszewska 1961). The leaves of ssp. *Woronowii* are usually folded along the central vein which makes them appear less wide than they really are. Before anthesis and after blooming the panicles are stiff and erect. Sometimes the branches of the panicles may be appressed to the main axis, which makes them more compact and dense (Fig. 1, 2). The spikelets on the panicles form compact and fairly large bunches; the ciliation of the spikelets usually is scarce.

The lemma may be incised at the tip, the incision varying so that in some cases the end of the lemma may be obtuse. Some of the well developed glumes also have a similar incision. In both forms of ssp. *Woronowii* the glumes are usually well developed and their length may almost equal the length of the spikelet.

Fig. 1. *Dactylis glomerata* ssp. *Woronowii* 2n=28

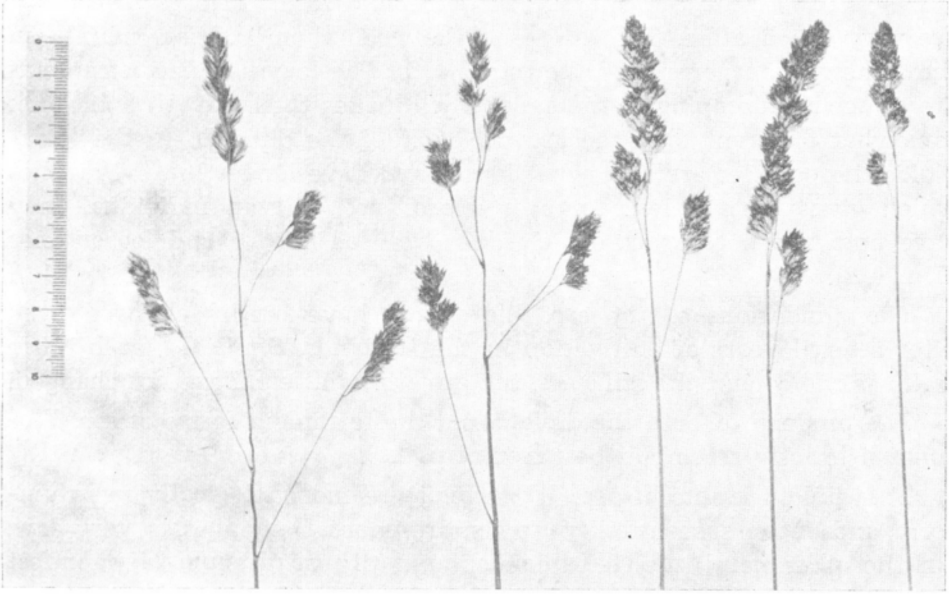

Fig. 2. *Dactylis glomerata* ssp. *Woronowii* 2n=14

The general traits of the diploid and tetraploid forms of ssp. *Woronowii* are compared in the following list:

	2x	4x
Growth habit	culms, leaves, and panicles straight	culms and panicles straight, leaves slightly drooping at ends
Colour	greyish blue-green	greyish blue-green
Maximum length of culms	61.0—88.0 cm.	66.0—112.0 cm.
Maximum length of leaves	34.1—53.0 cm.	44.0—70.1 cm.
Width of leaves	3—7 mm.	4—8 mm.
Length of ligule	3—4 mm.	3—4 mm.
Range of panicle lengths	3.0—18.0 cm.	4.0—20.0 cm.
Average length of internodes	2.0—6.2 cm.	2.5—4.8 cm.
Number of branches	1—3	1—3
Length of spikelets	6—9 mm.	6—9 mm.
Number of florets in a spikelet	2—7	2—9
Ciliation of spikelets	glabrous to medium ciliated	glabrous to medium ciliated
Tip of lemma	incised to obtuse	incised to obtuse
Blooming season in Warsaw	late June	late June

As is to be seen the diploid and tetraploid forms of ssp. *Woronowii* are very much alike. The difference between them consists mainly in the somewhat larger size of the tetraploids. The leaves of the tetraploids are somewhat drooping at the ends which makes their growth habit look somewhat different than the growth habit of the diploids. In the tetraploids the panicles are somewhat larger and have longer lower branches which gives them a less compact appearance; but an individual may have both short, compact panicles as well as longer and looser ones (Fig. 1, 2).

The dimensions of the ssp. *Woronowii* have hardly changed even after several years of cultivation in the lowlands. Similarly, such other traits as the colour, the stiffness, the growth habit etc. have not changed.

The progeny of both the diploid and the tetraploid forms of ssp. *Woronowii* exactly resemble the parental plants.

The diploid plants of ssp. *Woronowii* are morphologically very uniform and their susceptibility to environmental changes is very low. On the other hand the tetraploid plants of ssp. *Woronowii* manifest a slight variability between the particular individuals and are more susceptible to the changes of environmental conditions.

In spite of this the similarity between the diploid and tetraploid plants of ssp. *Woronowii* is so great that it is difficult to distinguish one from the other without checking the chromosome number.

Crosses

Ssp. *slovenica* (4x) × ssp. *Woronowii* (4x)

In 1958 a cross was made between the tetraploid plants of ssp. *slovenica* and ssp. *Woronowii:* castrated flowers of ssp. *slovenica* (4x) were pollinated with the pollen from ssp. *Woronowii* (4x). The F_1 progeny consisted of 12 individuals; these plants were vigorous, phenotypically rather uniform and intermediate between the parental plants. The characteristic traits of the parental and the F_1 plants are compared in Table 1.

Generally speaking the culms, the leaves, and the panicles in the hybrids were larger than in ssp. *Woronowii* (4x) and almost as large as in ssp. *slovenica* (4x). The traits characteristic for ssp. *slovenica*, such as the drooping panicles and the swelling at the base of the culms, were intermediately developed in the crosses and there was some variability in these traits between the particular individuals, but the differences were small and on the whole the F_1 generation was uniform.

The F_1 progeny manifested some traits that did not appear in the parental plants; the culms of the parents were smooth whereas in the progeny they were moderately harsh and the hybrids flowered two weeks earlier. Both ssp. *slovenica* and *Woronowii* flowered late in June and the crosses flowered early in that month (Table 1).

The F_2 generation was composed of only 51 plants, which made it impossible to investigate how some of the characteristic traits of the experimental plants were inherited. Among the 51 F_2 plants there were three with the same traits as ssp. *slovenica* but not one was found which morphologically resembled the ssp. *Woronowii* (4x). On the whole the F_2 generation resembled the tetraploid *D. glomerata* plants from open stands of the Polish lowlands.

The F_1 and F_2 plants grew vigorously, flowered profusely, and produced many seeds from free pollination. As is to be seen the hybrids were fully viable and their vigour was even greater than of the ssp. *Woronowii* (4x) parent.

D. glomerata (4x) × ssp. *Woronowii* (2x)

In 1958 a cross was made by additionally pollinating a tetraploid plant of *D. glomerata* coming from a forest stand near Warsaw with pollen of a diploid plant of ssp. *Woronowii*. The progeny from this cross consisted of 15 seedlings of which 12 were triploids containing 21 chromosomes. This domination of the hybrids in the progeny reflected the high

Table 1

Comparison the parental plants ssp. slovenica (4×) and ssp. *Woronowii* (4x) with their F_1 hybrids

	Max. height in cm	Max. length of leaves in cm	Width of leaves in mm	Length of panicles cm	Number of panicle branches	Colour	Habit of panicles	Swelling of the culm base	Harshness of plants	Blooming season	Pollen fertility %
Ssp. *slovenica* (4×)	191,0	110,0	8—12	13,2—25,7	5—6	bright green	drooping	bulbed	smooth	middle of June	79,0—86,0
Ssp. *Woronowii* (4×)	112,0	70,1	4—8	4,0—20,0	1—3	grayish green	erect	without bulb	smooth	middle of June	74,0—98,0
F_1 hybrids (4×)	173,0	74,8	7—9	7,4—27,6	4—5	bluish green	semidrooping	without bulb interm. bulbed	harsh	first days of June	68,0—96,0

Table 2

Comparison of the triploid F_1 hybrids with their parental plants

	Max. height cm	Max. lenght of leaves cm	Width of leaves mm	Length of panicles cm	Number of panicle branches	Colour	Harshness of plants	Blooming season	Pollen fertility %
D. glomerata (4×)	123,0	56,5	7—8	9,3—14,0	3—5	bright green	harsh	end of May	80,0—96,0
Ssp. *Woronowii* (2×)	78,0	47,0	3—6	6,0—18,4	1—3	grayish green	smooth	middle of June	74,0—85,0
F_1 hybrids (3×)	153,0	49,0	5—9	4,3—20,3	1—4	bright green, grayish green	slightly harsh	first days of June	11,6—41,0

self-sterility of the maternal plant in which the setting of seeds was much easier after pollination with alien haploid pollen that with its own diploid pollen.

In the first year of growth the triploids formed small tufts; their growth habit rather resembled ssp. *Woronowii* (2x). The majority of the plants did not flower and the few panicles were small, compact, and as if malformed.

In the next year the growth of the triploids was much more vigorous and large tufts with numerous culms developed. The panicles resembled those of *D. glomerata*; they flowered profusely but few seeds were developed from free pollination; on the 12 F_1 individuals about 400 seeds were collected. The seeds were sown out soon after they were gathered but about 1/3 of the thus obtained seedlings did not survive the winter of 1960/1961. The plants that survived grew with much vigour but did not flower in 1961.

The vigorously growing triploids very closely resembled the tetraploid plants of *D. glomerata*, so much so that it was impossible to distinguish between them without counting the chromosome number. The malformation and the failure to burst of the anthers characteristic for the *Dactylis* triploids (Müntzing 1937, Zohary and Nur 1959) was very seldom observed and only in some panicles, this could not be, therefore a distinguishing trait. On the other hand the greatly reduced pollen fertility could be of assistance in identifying the triploids.

Table 2 lists some of the traits of these parental plants and of their triploid F_1 progeny. As is to be seen the size of the triploids greatly exceeded the ssp. *Woronowii* (2x) and almost equalled *D. glomerata* (4x). The other traits of the triploids, e.g. the growth habit and the shape of the panicles etc., were intermediate and the particular individuals somewhat differed from each other.

Cytological Examinations

Meiosis in ssp. *Woronowii* (2x)

The course of meiosis was wholly regular and well developed tetrads were formed. At diakinesis the chromosomes conjugated with each other forming seven bivalents in each cell and at anaphase their parting was wholly regular seven of them going to each of the poles. The second meiotic division was also unobstructed no irregularities in the parting of the chromosomes having been observed.

Out of the 600 PMCs examined at the stage of diakinesis only seven had 6 bivalents and 2 univalents in each of the cells instead of the usual seven bivalents (Table 3): thus about one per cent of the PMC's had two univalents in the cells. The irregular parting of these univalents at anaphase I or their division, a behaviour rather frequent in the *Dactylis* tetraploids, was not observed.

Table 3

Chromosome conjugation in diakinesis in ssp. *Woronowii* 2n = 14

Cult. No	Number of counted PMC	7_{II}	$6_{II} + 2_{I}$
91	100	100	—
92	100	99	1
93	100	99	1
94	100	100	—
97	100	96	4
99	100	99	1

At diakinesis the chromosomes of the diploids were connected with one or two, usually terminal chiasmata, which made the bivalents shaped like rods or rings. The chiasmata of 638 bivalents having been counted it was found that they averaged 0.681 to one chromosome (Table 4).

Table 4

Chiasmata formation in diakinesis in ssp. *Woronowii* 2n = 14

Cult. No.	Number of counted PMC	chiasmata number in one cell					Average number of chiasmata per one chromosome
		8	9	10	11	12	
92	20	2	2	9	5	2	0,725
94	30	—	10	10	4	—	0,557
97	22	—	7	10	3	2	0,711
99	16	—	2	7	6	1	0,741
Total	88	2	17	36	24	9	0,681

Meiosis in ssp. *Woronowii* (4x)

The course of the meiotic division in this form was on the whole regular and typical for the *D. glomerata* tetraploids. At diakinesis there were bivalents, tetravalents, and a few univalents, but trivalents were very rare. The shape of the tetravalents did not differ in any detail from the tetravalents in other plants of *D. glomerata*.

The average number of tetravalents per one PMC of the particular

Table 5

Chromosome conjugation in diakinesis in tetraploid plants

Cult. No.	2n	Number of counted PMC	14_{II}	$13_{II} + 2_{I}$	$12_{II} + 1_{III} + 1_{I}$	$1_{IV} + 12_{II}$	$1_{IV} + 11_{II} + 2_{I}$	$1_{IV} + 10_{II} + 1_{III} + 1_{I}$	$2_{IV} + 10_{II}$	$3_{IV} + 8_{II}$	$3_{IV} + 7_{II} + 2_{I}$	$4_{IV} + 6_{II}$	$5_{IV} + 4_{II}$	$6_{IV} + 2_{II}$	7_{IV}	Average number of tetravalents per 1 PMC	PMC with bivalents only %
Ssp. *slovenica*																	
45	28	115	19	1	—	50	—	—	38	6	—	1	—	—	—	1,29	16,9
Ssp. *Woronowii*																	
71	28	105	4	1	—	24	1	—	41	25	—	7	2	—	—	2,20	3,8
81	28	68	5	—	—	21	1	2	19	13	—	6	1	—	—	1,90	7,3
82	28	100	8	—	—	26	—	—	36	15	1	8	4	2	—	2,10	8,0
83	28	85	4	—	—	11	1	2	28	23	—	13	3	—	—	2,40	4,7
F_1 Hybrids																	
114/1	28	100	5	—	—	27	—	—	34	21	—	10	2	1	—	2,14	5,0
114/2	28	61	4	—	—	25	1	—	20	7	1	2	1	—	—	1,78	6,5
114/3	28	101	7	—	—	21	—	—	46	20	—	5	2	—	—	2,01	7,0
114/5	28	100	5	—	—	16	—	—	38	29	1	8	3	—	—	2,21	5,0
114/6	28	69	9	—	—	33	2	—	32	15	—	7	2	1	—	1,86	13,0
114/7	28	104	12	—	—	30	—	—	38	13	—	8	3	—	—	1,84	11,5
114/8	28	100	4	—	—	27	—	—	43	17	—	6	2	—	1	2,05	4,0
114/9	28	100	4	—	—	23	—	—	44	21	—	6	2	—	—	2,08	4,0
114/10	28	100	3	—	—	23	—	—	43	22	—	8	1	—	—	2,12	3,0
114/11	28	103	4	—	—	24	1	1	39	24	—	6	3	1	—	2,15	4,0
114/12	28	101	3	—	—	14	3	—	41	26	—	10	3	—	1	2,36	3,0

plants of ssp. *Woronowii* (4x) ranged 1.9 to 2.4 and the cells with bivalents only amounted to between 3.8 and 8.0 per cent (Table 5).

The characteristic irregularities of meiosis in tetraploid *D. glomerata*, such as the occurrence of univalents, the lagging of chromosomes in the cytoplasm at anaphase I, and the formation of additional micronuclei in the tetrads, were relatively rare in ssp. *Woronowii* (4x): the meiotic divisions in this subspecies were almost entirely regular.

Meiosis in the F_1 cross ssp. *slovenica* (4x) × ssp. *Woronowii* (4x)

In the F_1 hybrids the course of meiosis was similar as in the parental plants; however, two cells with seven tetravalents each were found, whereas in the parental plants the highest number of tetravalents was six in a cell (Table 3). The average number of tetravalents to the PMC was 1.7 to 2.4 in the particular individuals and the cells with bivalents only ranged 3.0 to 13.0 per cent. In ssp. *Woronowii* (4x) these values were similar, whereas in the other parental plant, ssp. *slovenica*, the level of tetravalents was lower and the proportion of cells with bivalents only was higher (Table 5).

The level of tetravalents at diakinesis of the crosses showed that the chromosomes of ssp. *slovenica* (4x) and of ssp. *Woronowii* (4x) were partly homologous. The number of homologous or partly homologous chromosomes capable of forming tetravalents was higher in the F_1 hybrids than in the ssp. *slovenica* (4x) and approximately equalled the number of these chromosomes in ssp. *Woronowii* (4x).

The few irregularities observed in the course of meiosis in the F_1 crosses were of the same kind as in the parental plants.

Meiosis in the triploid hybrids *D. glomerata* (4x) × ssp. *Woronowii* (2x)

In the genus Dactylis the meiotic divisions of the PMC's of one floret are all very accurately synchronized so that all the cells in the pollen sacs divide simultaneously and have the same rate of division: in this way only one stage of division can be found in each floret. This refers to tetraploid as well as to diploid plants. In the pollen sacs of the triploids cells at different stages were found. The stages ranged e.g. from prophase I to metaphase II or from anaphase I to anaphase II. Likewise, in the particular anthers of a floret different stages of meiosis could occur simultaneously.

Meiosis in the triploid hybrids was always irregular the disturbances being of different kinds.

The diakinesis of nine triploids was analysed 50 PMC's being examined from each plant. At this stage of meiosis trivalents, bivalents, and univalents were found. The trivalents usually were V-shaped or rod-

-shaped; their number in one cell could range from zero to seven. The numbers of univalents and bivalents were usually the same, but the univalents could also be more numerous, e.g. the following proportions were recorded: $6_{II} + 9_I$ and $6_{III} + 3_I$.

The arrangement found most often was $7_{II} + 7_I$; the conjugation according to this pattern was found in 125 out of the 420 PMC's in which chromosome counts were made. The arrangement 7_{III} was recorded in four cells only. The number of trivalents in the cells varied between these extreme values the cells with 1, 2, and 3 trivalents occurring in approximately equal numbers (Table 6). The average number of trivalents in a cell for all the examined individuals was 2.06.

The presence of trivalents at diakinesis showed that the chromosome set of the triploids consisted of three groups each composed of seven homologous or partly homologous chromosomes. The chromosomes from each group were capable of mutual conjugation and could form as many as seven trivalents in one PMC.

Table 6

The diakinesis in triploid plants

Cult. No.	2n	Number of counted PMC	Chromosome conjugation										Average number of trivalents per one PMC
			$7_{II} + 7_I$	$1_{III}+6_{II}+6_I$	$2_{III}+5_{II}+5_I$	$3_{III}+4_{II}+4_I$	$4_{III}+3_{II}+3_I$	$5_{III}+2_{II}+2_I$	$6_{III}+1_{II}+1_I$	7_{III}	$6_{III}+3_I$	$6_{II}+9_I$	
1	21	50	6	7	9	6	8	9	4	1	—	—	3,80
2	21	50	3	2	1	10	20	9	3	2	—	—	3,00
3	21	50	25	13	6	3	1	—	—	—	—	—	0,76
4	21	50	25	17	4	1	—	—	—	—	—	3	0,56
5	21	20	—	—	3	5	7	3	1	—	1	—	3,80
6	21	50	12	7	14	13	2	2	—	—	—	—	1,80
7	21	50	19	12	8	5	2	3	1	—	—	—	1,44
8	21	50	15	5	9	13	4	3	—	1	—	—	2,00
9	21	50	21	5	9	10	4	1	—	—	—	—	1,48
Total		420	126	68	63	66	48	30	9	4	1	3	2,06

The meiotic irregularities mainly consisted in the uneven distribution of the chromosome material. The triploids having 21 chromosomes they could not be evenly distributed in the first division. This was clearly visible in many instances; e.g. at anaphase I almost all the chromosomes were groupped at one pole while not more than three or four remained at the other. A still more uneven distribution could be observed at metaphase II when as many as 20 chromosomes were clearly visible in one cell whereas in the other daughter cell there was only one chromosome.

Very often in the course of the first as well as the second division some of the chromosomes were left behind in the cellular cytoplasm and were not included in the telophase nuclei; the chromosomes which remained in the cytoplasm later formed an additional micronucleus. An instance was observed when such an addition micronucleus was separated together with a small amount of cytoplasm by a membrane from the two daughter cells, which were then at anaphase II.

Out of the 482 tetrads, which were examined, 302 contained either additional micronuclei or additional cells thus forming pentads or even hexads. The remaining 180 tetrads contained no additional micronuclei and were composed of four cells, but considerable differences in the size of the particular nuclei in a tetrad were apparent: this must have been caused by the uneven distribution of chromosomes at meiosis.

Irregularities were also observed in the formation of division spindles: in many cells at anaphase I the spindles were arched and placed in a peripheral position. Spindles with three poles were also found both in the first and in the second divisions.

Pollen fertility

Pollen fertility counts were made every year from 1958 to 1961 and no significant differences between the particular years were observed. Pollen fertility ranged 73.5 to 94.7 per cent in ssp. *Woronowii* (4x) and 74.5 to 98.0 per cent in ssp. *Woronowii* (2x).

In the tetraploid crosses pollen fertility was not reduced. In F_1 of F_2 of the cross ssp. *slovenica* (4x) × ssp. *Woronowii* (4x) the pollen fertility ranged 68.0 to 96.0 per cent, i.e. it essentially was the same as in the parental plants (Table 1).

The pollen fertility of the triploids from the cross *D. glomerata* (4x) × ssp. *Woronowii* (2x) was considerably reduced ranging in the particular individuals from 11.6 to 41.0 per cent (Table 2).

DISCUSSION

Dactylis Woronowii Ovczinn. was described for the first time in the »Flora SSSR (1934)«. According to this description the species grows on rocks and in arid areas in the mountains of Crimea, Caucasus, Turkmen and Amu Darya. This new species was discriminated on the ground of the morphological traits without accounting for the chromosome number.

The next description was made by Stebbins and Zohary (1959) who defined this taxon as the diploid subspecies *D. glomerata* L. ssp. *Woronowii* (Ovczinn.) Stebbins and Zohary. The specimens described by these two workers came from Elbruz Mountains and Province Khorassan in Iran, i.e. from a region neighbouring with the areas mentioned in »Flora SSSR«. The plants from both stands in Iran were diploid. Plants morphologically similar but all with the tetraploid chromosome numbers were also reported from Turkish Armenia by Stebbins and Zohary (1959) who thought it extremely unlikely for the diploid form of ssp. *Woronowii* to occur in that area.

The plants brought to Warsaw from Soviet Armenia correspond by their morphology to the description of *D. Woronowii* in the Flora SSSR (1934) and to the description of ssp. *Woronowii* by Stebbins and Zohary (1959).

The only differences that were found concerned the ciliation of the spikelets and the variably lobed tip of the lemma. In both of the above mentioned descriptions the *Woronowii* form is stated to have a dense ciliation of the spikelets and lemmas with deeply lobed tips. In the here described diploid and the tetraploid plants from Armenia the spikelets range from glabrous to moderately ciliated and the lemmas from distinctly lobed to obtuse.

A similar variability in the ciliation of spikelets is manifested by ssp. *slovenica* and because of this trait Domin discriminated in the subspecies the variety subglabra forma trichosantha and forma atrichosantha. In the tetraploid *Dactylis* plants from Poland the ciliation of spikelets also manifests a similar variability. The trait is probably polygenic, which would account for the considerable differences between the plants.

The same can be said of the lobed tip of the lemma. According to Stebbins and Zohary (1959) in ssp. *judaica* the tip of the lemma may range from pointed to shallow lobed (attenuate-weakly lobed), whereas in ssp. *ibizensis* the lemma tip may range from shallow to deeply lobed (weakly-strongly lobed): the trait must be, therefore, determined by more than a pair of genes. All this makes highly probable the variability of this trait in ssp. *Woronowii*.

The above mentioned differences seem to consist in a variability within the ssp.*Woronowii*. This was to be expected in view of the large distribution area of the subspecies in regions which have no geographic isolation from the other *Dactylis* forms, but on the contrary are situated in the very middle of the distribution of this genus.

The specimens of this investigation coming from only two stands in Soviet Armenia it is to be expected that elsewhere plants with strongly ciliated spikelets and with deeply lobed lemmas would be found.

A separate question is the occurrence in the genus Dactylis of individuals which, though differing by the degree of polyploidy, are so similar that it is difficult to distinguish between them without checking the chromosome number. This question has not been given sufficient attention but more and more data are being assembled showing that the phenomenon is not an exception.

Zohary and Nur (1959) found in Palestine di-, tri-, and tetraploid populations of *D. glomerata* occurring together, which were morphologically indistinguishable.

A very close resemblence between di- and tetraploid individuals was reported in ssp. *Reichenbachii*, ssp. *judaica*, and ssp. *Santai* (Stebbins and Zohary 1959). Borrill and Johnes (1959) found in Cirenaica and in Egypt natural hexaploids which morphologically did not differ from the tetraploids. This is also the case with the diploid and the tetraploid ssp. *Woronowii* from Soviet Armenia. In the forests of eastern and central Poland tetraploid individuals have been found which morphologically were exactly like ssp. *Aschersoniana* (Doroszewska 1961) and Böcher (1961) found in Yougoslavia tetraploid plants which morphologically resembled the diploid ssp. *Aschersoniana* from Denmark.

In spite of the many researches on *Dactylis* there is much disaccord in the systematic treatment of this genus by the particular authors. The whole question is highly complicated by the occurrence of plants which for all their morphological similarity have different levels of polyploidy.

It seems, however, that the best approach would be to assign the plants with different chromosome numbers but the same morphologal traits to the same systematic units noting after the name of the plant its level of polyploidy, i.e. 2x 3x, 4x, etc. This is how the difference between ssp. *Woronowii* (4x) and ssp. *Woronowii* (2x) was marked in the present report. This classification seems to be the simplest and very convenient, since it conveys the information about the morphology of a plant as well as about its chromosome number.

The occurrence in the same areas of diploid and tetraploid plants morphologically indistinguishable points to the autotetraploid origin of the tetraploids.

It seems that ssp. *Woroonwii* (4x) developed as an autotetraploid of ssp. *Woronowii* (2x).

An entirely different question arises in connection with the tetraploid ssp. *Aschersoniana* found in different parts of Poland. Some of the populations of *D. glomerata* occurring in the forests of central and eastern Poland are composed of small, rather frail, light coloured plants; the spikelets of these plants are weakly ciliated or glabrous and distinctly differ from the spikelets of *D. glomerata* individuals growing outside the forests on stretches of open ground. Phenotypically they approach in a varying degree the ssp. *Aschersoniana*. Because of their tetraploid chromosome number they could not be taken for hybrids between ssp. *Aschersoniana* (2x) and ssp. *euglomerata* (4x). Among these forest populations individuals have been found which had all the traits of ssp. *Aschersoniana* and as such have been brought to the Botanical Garden in Warsaw; however, when their chromosome number was counted it was found that they were tetraploids. These individuals must have arisen in the course of the segregation of the particular traits in the forest populations of *D. glomerata*. On the ground of the morphological traits these plants ought to be classified as *D. glomerata* L. ssp. *Aschersoniana* (4x) (Graebn.) Thellung.

Even if the correctness of this classification is questioned it is to be remembered that for no other than morphological reasons the florists give the distribution area of ssp. *Aschersoniana* as extending over the whole of Poland and reaching to the western territories of the USSR. In central and eastern Poland diploid plants of ssp. *Aschersoniana* were not found: it seems that ssp. *Aschersoniana* reported by florists from these areas is a tetraploid form growing in forest associations and resembling the plants found in Zalesie and the Białowieża Forest. More detailed researches are, however, necessary before a final solution to this question will be found.

Cytological observations of meiosis in the diploid and tetraploid ssp. *Woronowii* bring no new information. The course of meiosis in ssp. *Woronowii* (2x) is similar to meiosis in the other diploid subspecies of *Dactylis* and does not differ from what has been reported by Katterman (1931) and Müntzing (1937) for *D. Aschersoniana* and by Mc Collumn (1958) for ssp. *lusitania*, ssp. *ibizensis*, ssp. *Smithii*, and ssp. *Aschersoniana*.

Meiosis in ssp. *Woronowii* (4x) follows the same typical pattern of all the *Dactylis* tetraploids. The average number of teravalents per one PMC in this subspecies ranged 1.9 to 2.4. The number of tetravalents reported by other workers for the tetraploids *Dactylis* have usually been somewhat higher, but Myers and Hill (1942) found in *D. glomerata* an average of 2.42 to 4.39 tetravalents per one PMC. The lower of the values reported by these workers for *D. glomerata* approximately corresponds to the number of tetravalents found in ssp. *Woronowii* (4x).

The observations of meiosis in the examined triploids have revealed some interesting details and the results differ somewhat from what was reported by Müntzing (1937) for the crosses between *D. glomerata* and *D. Aschersoniana*.

The observations of this investigation concerning the shape of the trivalents and the irregularities of meiosis are on the whole in agreement with Müntzing's results. He also noted the uneven distribution of the chromosomes in the course of meiosis and the development of additional micronuclei which were formed by the elimination of chromosomes during either of the meiotic divisions. Having analysed 53 cells at anaphase I Müntzing found that the number of trivalents in a cell varied from one to seven, but he never found the arrangement $7_{II} + 7_{I}$. In the F_1 triploids of the cross *D. glomerata* (4x) × ssp. *Woro-*

nowii (2x) there were about 30 per cent of cells with the arrangement $7_{II} + 7_{I}$. In Müntzing's (1937) triploids the average number of trivalents per one PMC was 4.58 whereas in this investigation there were 2.06 trivalents per one PMC, i.e. less than a half of the number given by Müntzing.

The reason of these differences probably was that the chromosomes of ssp. *Woronowii* (2x) from Armenia and of *D. glomerata* from Poland were more differentiated than the chromosomes of *D. Aschersoniana* and *D. glomerata* from Denmark, which were the parental plants of Müntzing's triploids.

Müntzing counted the chromosomes at anaphase II of triploids and found 7 to 13 chromosomes per one cell. From such cells pollen with either the haploid (7) or almost the diploid (13) chromosome number could develop, but according to his observations the triploids manifested a complete male sterility, though they could produce partly fertile egg-cells, which could contain the unreduced chromosome number 21. Owing to this the progeny of the triploids consisted among others also of tetraploids and pentaploids, which developed from the fertilization of the unreduced egg-cells by haploid and diploid pollen (Müntzing 1937, Zohary and Nur 1959). In the progeny of the triploids Müntzing also obtained plants with a higher chromosome number than 5x: in his opinion such plants must have developed from the egg-cells of the triploids with a chromosome number higher than 3x.

In the investigated F_1 triploids from the cross *D. glomerata* (4x) × ssp. *Woronowii* (2x) some of the anthers were well developed and contained small amounts of pollen. Fertility counts made in acetocarmine showed that the fertility of this pollen amounted to 41 per cent and it seems wholly probable that at least a part of this pollen was capable to fertilize egg-cells. At metaphase II of the meiotic division a cell was found which in one plate had 20 chromosomes and in the other only one. From such a cell a pollen grain with nearly the triploid chromosome number may arise and, thus, in self-pollination the triploids could give an aneuploid as well as an euploid progeny with the maximum chromosome number of 42, which was found by Müntzing (1937). In view of the number of chromosomes found in the plates at metaphase II the self-pollination of the triploids seems more probable than the interpretation advanced by Müntzing.

SUMMARY AND CONCLUSIONS

1. Plants of ssp. *Woronowii* collected from two stands in Soviet Armenia differed by the degree of polyploidy but morphologically closely resembled each other.

2. The specimens from the neighbourhood of Lake Sewan had the chromosome number $2n = 14$ and those from near Erivan had $2n = 28$

chromosomes. The two forms were discriminated as ssp. *Woronowii* (2x) and ssp. *Woronowii* (4x).

3. Ssp. *Woronowii* (4x) probably developed as an autoteraploid from ssp. *Woronowii* (2x).

4. This author is of the opinion that plants with different chromosome numbers but morphologically indistinguishable, should be classified as one subspecies and that their chromosome numbers should be noted after the name, i.e. 2x, 3x, 4x etc.

5. Ssp. *Woronowii* (4x) could be crossed with ssp. *slovenica* (4x) giving a fertile F_1 and F_2 progeny.

6. The triploids obtained by crossing *D. glomerata* (4x) with ssp. *Woronowii* (2x) were partly fertile. The average number of trivalents at diakinesis of these triploids was 2.06 per one PMC.

7. Meiosis in ssp. *Woronowii* (2x) was regular with seven bivalents per one cell at diakinesis. Meiosis in ssp. *Woronowii* (4x) had the same course as in the other tetraploids of *Dactylis*: in this subspecies the average number of tetravalents per one PMC ranged 1.9 to 2.4. A similar proportion of tetravalents was found in the F_1 cross ssp. *slovenica* (4x) × ssp. *Woronowii* (4x).

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