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Genome size in wild *Pisum* species

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Abstract Genome size was measured in 75 samples of the wild pea species *Pisum abyssinicum*, *P. elatius*, *P. fulvum* and *P. humile* by ethidium-bromide (EB) flow cytometry (internal standard: *Triticum monococcum*) and Feulgen densitometry (internal standard: *Pisum sativum* 'Kleine Rheinländerin'). Total variation of EB-DNA between samples covered 97.7% to 114.9% of the *P. sativum* value, and Feulgen DNA values were strongly correlated with EB-DNA values ($r = 0.9317$, $P < 0.001$). Only *P. fulvum* was homogeneous in genome size (108.9% of *P. sativum*). Wide variation was observed between samples in *P. abyssinicum* (100.9–109.7%), *P. elatius* (97.7–114.9%) and *P. humile* (98.3–111.1% of *P. sativum*). In view of the world-wide genome size constancy in *P. sativum*, the present data are interpreted to show that the pea taxa with variable genome size are genetically inhomogeneous and that the current classification is not sufficient to describe the biological species groups adequately.

Key words *Pisum* · Wild peas · Genome-size variation · Flow cytometry · Feulgen densitometry

Introduction

The wild pea species *Pisum abyssinicum*, *P. elatius*, *P. fulvum*, and *P. humile* have received relatively little attention by cytogeneticists in recent decades. For instance, no chromosome banding analyses have been done, and only limited evidence for karyotype variation (Conicella and Errico 1990; Errico et al. 1991) and genome-size variation (Schweizer and Davies 1972; Baranyi and Greilhuber 1995, 1996) is available. Using flow cytometry Baranyi and Greilhuber (1996) demonstrated genome-size constancy in *P. sativum* accessions of very different origins, including wild samples, landraces and high-bred cultivars, and confirmed the earlier results of Greilhuber and Ebert (1994), which were obtained with Feulgen densitometry. However, Baranyi and Greilhuber (1995, 1996) found larger genomes in some accessions of *P. elatius* (up to 119.5% of the *P. sativum* value) and *P. humile* (108.9%), while other accessions of these taxa were not different from *P. sativum*. *P. abyssinicum* and *P. fulvum* had about 107% of *P. sativum* in these studies. In view of the general usefulness of genome-size data in biosystematic work (Greilhuber and Ehrendorfer 1988), it appeared to us that a more thorough analysis of genome-size variation in wild peas could be a useful contribution to an improved understanding of the biological structure of the genus and the ancestry of cultivated *P. sativum*. In the present work genome size was analysed in 75 accessions of wild peas by ethidium-bromide (EB) flow cytometry, using Feulgen densitometry as a control.

Material and methods

Seventy-five seed samples were obtained from the *Pisum* Gene Bank, Laboratory of Pea Breeding and Collection, Plant Breeding Station, Wiatrowo, 62–100 Wagrowiec, Poland (see Table 1). Plants were grown and vouchers were made. Vouchers are also deposited at Wiatrowo. A revision by one of the authors (W.K.S.) modified the taxonomic affiliation of two accessions as indicated in Table 1. The taxonomic affiliation of the samples as listed in Table 1 adheres to the designation of the gene bank, but is not always consistent with all characters given in the artificial classification of Lehmann (1954).

Internal standards used were *Triticum monococcum* with flow cytometry and the cultivar. *P. sativum* 'Kleine Rheinländerin' with Feulgen densitometry.

Seeds were germinated on plates. In flow cytometry every nuclear isolation was jointly done for one individual of the test material and one of *T. monococcum*. Preparation of the nuclear suspension, staining, and conditions of measurement are described in Baranyi and

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Table 1 Ethidium-bromide (EB) flow cytometric and Feulgen densitometric data in *P. abyssinicum*, *P. elatius*, *P. fulvum*, and *P. humile*, numbered as given by the seed bank entries. The internal standard was *T. monococcum* for flow cytometry and *P. sativum* 'Kleine Rheinländerin' for Feulgen densitometry. EB and Feulgen data are presented as the ratio (%) of *Pisum* versus the internal standard. For EB data also the re-calibrated ratio (%) of *Pisum* species versus *P. sativum* 'Kleine Rheinländerin' (see Table 2) is given. EB data: For each accession the average ratio (mean) with the Scheffé groups ($P > 0.05$) indicated, its standard deviation (SD, with reference to N_r), the number of seedling pairs tested (N_s) and the number of total runs (N_r) are given. Feulgen data: ten telophase nuclei per primary root-tip meristem and slide were measured. Up to seven lines plus the standard were jointly processed and measured. The standard deviation (SD) refers to the number of nuclei (N) of the test sample and represents the relative weighted standard deviation obtained by combining the variation of the test material and the standard (for formula see Greilhuber and Ebert 1994). Origin of accessions: *Afg.* Afghanistan, *Ana.* Anatolia, *Eth.* Ethiopia, *Ind.* India, *Isr* Israel, *Kat.* Katmandu, *Pal.* Palestine, *Rus.* Russia, *Sud.* Sudan, *Syr.* Syria, *Tib.* Tibet, *Tur.* Turkey, ? unknown

WT no	Origin	EB, *Pisum* spp.					Feulgen, *Pisum* spp.		
		% of *T. monococcum*		% of *P. sativum*	N_s	N_r	% of *P. sativum*		N
		Mean$^{\text{Scheffe'group}}$	SD	Rel. EB			Mean	SD	
P. abyssinicum									
1	Eth.	78.50^{I-L}	0.68	108.05	3	9	107 85	5.62	150
2	Eth.	$73.55^{A-D(-G)}$	0.64	101.24	3	9	99.90	5.20	30
3	Eth.	78.09^{I-L}	1.22	107.49	4	10	107.35	4.55	30
4	Eth.	78.86^{I-L}	0.56	108.55	4	9	108.15	5.35	30
5	Sud.	78.92^{I-L}	0.80	108.63	3	9	104 39	5.32	30
6	Eth.	78.90^{I-L}	0.44	108.60	3	9	106.89	5.02	30
7[a]	Tib.	$73.85^{A-F(-G)}$	0.77	101.65	3	9	98.50	4.46	60
8	?	74.15^{B-H}	0.89	102.06	3	8	100.66	3.79	30
9	Eth.	76.37^{D-J}	0.56	105.12	3	9	102.93	4.48	30
10	Eth.	78.32^{I-L}	0 89	107.80	3	9	107.01	4.33	30
11	?	73.27^{A-C}	0.88	100.85	4	9	99.52	4.28	30
12	Eth.	78.24^{I-L}	1.35	107.69	4	10	105.52	4.39	30
13	Tur.	$73.72^{A-F(-G)}$	0.60	101.47	3	7	99.56	3.97	30
15[b]	Ind.	$73.44^{A-D(-G)}$	0.61	101.09	3	8	99.76	5.14	60
16	?	78.19^{I-L}	1.43	107.63	3	8	106.50	4.02	30
17	?	78.41^{I-L}	0.47	107 93	3	6	111.25	6.27	30
18	?	$76.93^{(F-)G-K}$	1 10	105.89	3	9	108.09	3.77	30
19	?	78.60^{I-L}	0.92	108.19	3	7	110.11	6.05	30
20	Eth.	79.64^{J-N}	1.38	109.62	3	8	111.31	5.51	30
21	Eth.	79.38^{I-L}	2.14	109.26	4	9	108.05	4.30	30
22	?	78.13^{I-L}	0.54	107.54	4	9	108.01	4.28	30
23	?	78.27^{I-L}	0.73	107.74	3	9	107.13	4.80	30
24	Eth.	79.71^{J-M}	0.66	109.72	5	9	107.61	4.35	30
26	Eth.	78.90^{I-L}	1.00	108.60	4	9	106.93	4.27	30
27	?	78.09^{I-L}	0.83	107.49	4	11	103.58	3.94	30
P. elatius									
101	Ana.	73.36^{A-C}	0.59	100.98	3	9	99.78	5.06	60
102	Pal.	73.29^{A-D}	0.80	100.88	3	7	99.77	5.21	60
103	?	74.16^{B-H}	0.73	102.08	3	8	97.83	6.26	30
104	Rus.	$73.70^{A-F(-G)}$	1.18	101.45	3	7	98.60	4.88	30
105	Rus.	80.29^{K-N}	0.67	110.52	4	8	106.31	7.56	30
106	Pal.	76.29^{C-J}	0.79	105.01	3	8	102.48	6.18	30
107	Pal.	76.10^{C-I}	0.92	104.75	4	10	102.67	6.45	30
108	?	$72.72^{A,B}$	0.53	100.10	4	8	98.89	5.92	30
109	?	74.07^{B-G}	0.59	101.95	4	9	102.85	5 49	30
110	?	80.48^{K-N}	0.44	110.78	3	7	110.80	5.72	30
111	Tur.	73.22^{A-C}	0.30	100.78	3	7	101.12	5.09	30
112	Eth.	74.08^{B-H}	1.06	101.97	3	8	101.76	4.94	30
113	?	$73.68^{A-E(-G)}$	0.30	101.42	3	9	102.26	5.34	30
114	Sud.	$73.59^{A-D(-G)}$	0.71	101.29	4	9	101.25	5.27	30
115	Eth.	$72.56^{A,B}$	0.43	99.88	3	9	100.81	5.29	30
116	?	$76.45^{(D-)E-J}$	0.70	105.23	4	11	102.63	5.22	30
117	?	$76.64^{(E-)F-J}$	0.45	105.49	3	9	103.76	6.17	30
118	?	77.63^{H-L}	0.61	106.85	3	9	105.08	5.99	30
120	?	70.96^{A}	0.67	97.67	3	9	98.24	5.35	30
121	?	$73 64^{A-F(-G)}$	0.52	101.36	3	8	101.88	4.80	30
122	?	83.38^{M-N}	0.36	114.77	3	7	110.32	5.60	30
123	Ana.	73.34^{A-C}	0.74	100.95	6	9	98.89	4.95	30
124	?	83.49^{N}	0.69	114.92	3	7	114.32	6.43	30
P. fulvum									
301	Pal.	78.79^{I-L}	1.21	108.45	5	9	105.73	6.25	30
302	?	$79 27^{J-L}$	1.23	109.11	8	14	107.37	5.35	30

Table 1 (Continued)

WT no.	Origin	EB, *Pisum* spp.					Feulgen, *Pisum* spp.		
		% of *T. monococcum*		% of *P. sativum*	N_s	N_r	% of *P. sativum*		N
		Mean^{Scheffegroup}	SD	Rel. EB			Mean	SD	
303	?	79.74^{I-N}	0.78	109.76	4	6	107.48	5.19	30
304	Isr.	79.04^{I-L}	1.11	108.80	3	9	104.43	5.09	60
11256	Tur.	79.02^{I-L}	0.68	108 77	4	9	106.82	3.99	30
P. humile									
401	Syr.	$73.22^{A,B}$	0 84	100.78	5	11	100.21	4.34	30
402	Isr.	$72.81^{A,B}$	0.76	100.22	5	13	98.34	3.91	30
403	Pal.	80.55^{L-N}	1.26	110.87	5	13	109.64	4.29	30
404	Syr.	$72.72^{A,B}$	0.71	100.10	3	8	100.26	4 52	30
405	Syr.	$72 78^{A,B}$	0.89	100.18	4	13	100.51	3 88	30
407	Ind.	$74.10^{B-G(-H)}$	0.96	102.00	4	9	101.10	4.31	30
410	Tur.	80.68^{L-N}	0.59	111.05	3	9	108.55	4.55	30
411	Afg.	$73.17^{A,B}$	0.63	100.72	4	15	97.77	4.77	30
412	Afg.	74.24^{B-H}	0.60	102.19	4	8	99.41	3.87	30
413	Tur.	$73.07^{A,B}$	0.82	100.58	3	10	100 55	2.99	30
415	Kat.	$73.43^{A-D(-G)}$	0.55	101.07	3	8	99 30	3.59	30
416	Rus.	$72.10^{A,B}$	0.41	99.24	3	7	100.38	3.95	30
417	Tur.	$72.16^{A,B}$	0.96	99.33	3	7	97.99	3.74	30
418	?	$72.93^{A,B}$	0.58	100 39	4	12	98.91	3.69	30
419	Rus.	$72.81^{A,B}$	0.99	100 22	5	12	98.89	3.61	30
420	?	$71.41^{A,B}$	0.71	98.29	4	11	97.97	3.92	30
421	?	73.30^{A-D}	0.64	100.89	3	7	97.34	4.21	30
422	Afg.	$72.74^{A,B}$	0 56	100.12	4	9	98.36	4.22	30
423	Ind.	$72.07^{A,B}$	0 78	99 20	5	15	98.73	3.96	30
424	?	$72.11^{A,B}$	0.88	99.26	5	12	98.38	3.96	30
425	Tur.	$73.11^{A,B}$	0.89	100.63	4	10	98.30	3.72	30
427	Ind.	$73.20^{A,B}$	0.81	100.76	3	10	99.08	3.73	30

[a] Sample shows affinities with *P. sativum*
[b] Sample shows affinities with *P. humile*

Greilhuber (1996). The coefficient of variation was on average 2.48%. Feulgen densitometry followed Greilhuber and Ebert (1994).

Single classification analysis of variance, the Scheffé test, and a correlation analysis were done with the SPSS for Windows 6.0 package (SPSS Inc., Chicago, Ill.) and nested analysis of variance with the NESTAN routine of the BIOM-pc Vers. 2.1. package (Rohlf 1992). Since the Scheffé test can only handle up to 50 samples, it was performed separately for the 50 lines ranking lowest and highest, respectively, in DNA amount. Resulting minor differences in affiliation to Scheffé groups are indicated by brackets in Table 1.

Results and discussion

All samples had 2n = 14, as seen from the Feulgen slides prepared for densitometry. An overall variation covering 97.7 to 114.9% of *P. sativum* 'Kleine Rheinländerin' was observed among the four taxa (Table 1, Fig. 1a). The data obtained with EB-flow cytometry and Feulgen densitometry were strongly correlated ($r = 0.9317$, $P < 0.001$; Fig. 1b).

The 25 accessions affiliated with *P. abyssinicum* varied from 100.85% to 109.72% of *P. sativum*. Of these, six accessions ranked low at 100.85%–102.06%, 17 ranked high from 107.49% to 109.72%, and only two were intermediate at 105.12% and 105.89% of *P. sativum* 'Kleine Rheinländerin' (Table 1, Fig. 1a). This taxon was previously measured by Schweizer and Davies (1972), who found 105.1% and by Baranyi and Greilhuber (1995, 1996), who found about 106.6% of *P. sativum*. The present sample of accessions was heterogeneous with respect to leaf serration. The low-ranking samples had no serrated leaves; whereas, with only one exception (WT 23, the only accession of *P. abyssinicum* with an anthocyanin ring in the leaf axil), the high-ranking samples had serrated leaves. Of the intermediate samples, one was serrated (WT 18), and the other one was heterogeneous (WT 9).

The 23 accessions of *P. elatius* varied from 97.67% to 114.92% of the *P. sativum* value (Table 1, Fig. 1a). The one accession ranking lowest (WT 120) was reproducibly lower than *P. sativum*, as shown by control tests (Table 2). Thirteen accessions ranked low with up to 102.08% of *P. sativum*, five ranked intermediate at 104.75–106.85%, two ranked high at 110.52% and 110.78%, and two ranked very high at 114.77% and 114.92% of *P. sativum*. *P. elatius* had been previously measured by Schweizer and Davies (1972), who found 105.1% of *P. sativum* in an accession for which Baranyi and Greilhuber (1996) later obtained a value of 118.3%. Greilhuber and Ebert (1994) measured *P. elatius* convar. palestinicum, which was not different from *P. sativum*.

In five accessions of *P. fulvum* a genome-size constancy, at on average 108.9% of *P. sativum* (EB-DNA),

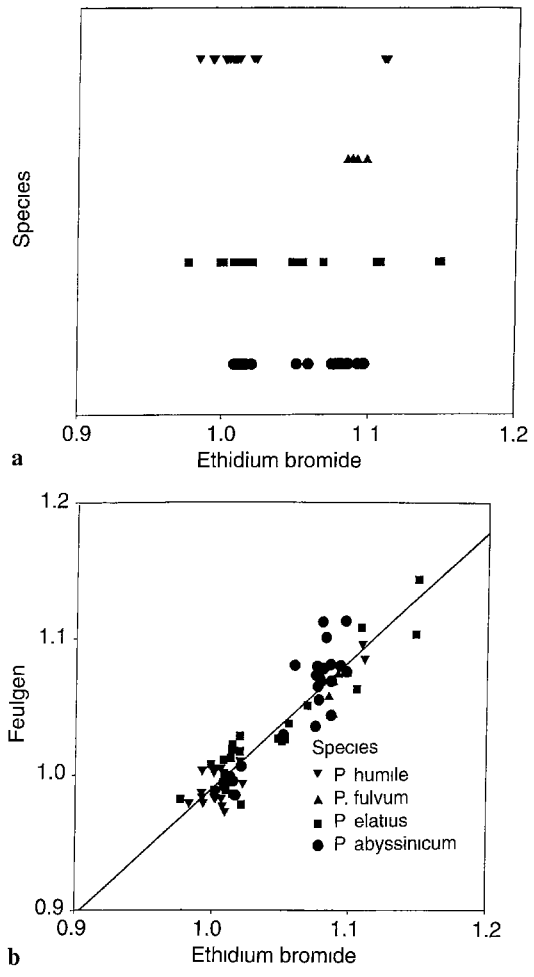

Fig. 1a,b Genome-size variation in four wild *Pisum* species (EB data re-calibrated versus *P. sativum* 'Kleine Rheinländerin'). **a** variation within taxa, **b** correlation of EB flow cytometric and Feulgen densitometric genome-size data ($r = .9317$, $P < 001$)

was obtained (Table 1, Fig. 1a). The small variation observed was non-significant. In other accessions of *P. fulvum* Baranyi and Greilhuber (1996) reported 107.0% of *P. sativum*, which is very similar. Previously, *P. fulvum* was measured only by Schweizer and Davies (1972) who, however, found less DNA than in *P. sativum*. Flower colour seems to be species-specific. Leaf shape, on the other hand, does not appear to be a constant and reliable character; thus, accession WT 301 and WT 11256 both had serrated leaves, WT 302 and WT 304 had indistinctly serrated leaves, while WT 303 was not serrated.

In *P. humile* the 22 accessions varied between 98.29 and 111.05% of *P. sativum* (Table 1, Fig. 1a). The lowest ranking accession (WT 420) was reproducibly lower than *P. sativum* (Table 2, Fig. 2a), though not different from most other accessions in respect of the Scheffé test (Table 1). Nineteen accessions varied between 99.20 and 102.19% of *P. sativum*, most of these being non-significantly different with the Scheffé test. Two accessions were strikingly higher at 110.87% (WT 403) and 111.05% (WT 410; Fig. 2b) of *P. sativum*. Of all *P. humile* samples analyzed here, only six had distinctly serrated leaflets (WT 403, WT 407, WT 422, WT 423, WT 425, WT 427), but nine had the diagnostic anthocyanin ring (WT 413, WT 416, WT 417, WT 418, WT 420, WT 422, WT 423, WT 427). No correlation of these characters with genome size was observed.

The species status of *P. fulvum* is acknowledged by most pea taxonomists (e.g. Smartt 1984). It is separated from the other taxa by sterility barriers (Lamprecht 1974), which are at least partly caused by chromosomal rearrangements (Lamprecht 1974; Conicella and Errico 1985, 1990; Errico et al. 1991). The species status of the other taxa is less clear and they have also been treated as subspecies or ecotypes. For instance, Davis (1970) in the Flora of Turkey treats *P. elatius* and *P. humile* at infraspecific levels (*P. sativum* subsp. *elatius* with the varieties elatius, pumilio and brevipedunculatum, the latter two representing the *P. humile* of other authors, e.g. Lehmann and Blixt 1984). Some evidence exists for the occurrence of chromosomal translocations between wild peas. Håkansson (1936) found a translocation and an inversion between *P. sativum* and *P. humile*. Ben Ze'ev and Zohary (1973) investigated meiotic configurations in *P. sativum*, *P. elatius*, *P. humile*, *P. fulvum* and their hybrids. In their material *P. elatius* was differentiated from *P. sativum* by one translocation. The same translocation as in *P. elatius* was also found in *P. humile*, but only in the southern accessions; northern accessions had no translocation relative to *P. sativum*. At least one further translocation was disclosed when crosses with *P. fulvum* were made. Lamprecht (1964) found three trans-

Table 2 Control tests for lower genome size in *P. elatius* WT 120 and *P. humile* WT 420 compared with *P sativum* 'Kleine Rheinländerin'. The internal standard was *T. monococcum*. Lines WT 120 and WT 420 were also run simultaneously with *P. sativum* 'Kleine Rheinländerin'; the peaks remained unimodal, but were shifted closer towards *T monococcum*

Line	N_s	N_r	% of *T monococcum*	% of *P. sativum*
'Kleine Rheinländerin'	6	24	72.65	100.00
WT 120 *P. elatius*	2	6	69.66	95.88
WT 120 + 'Kleine Rheinländerin'	3	9	70.39	96.89
WT 420 *P. humile*	2	4	71.22	98 03
WT 420 + 'Kleine Rheinländerin'	2	6	72.39	99.64

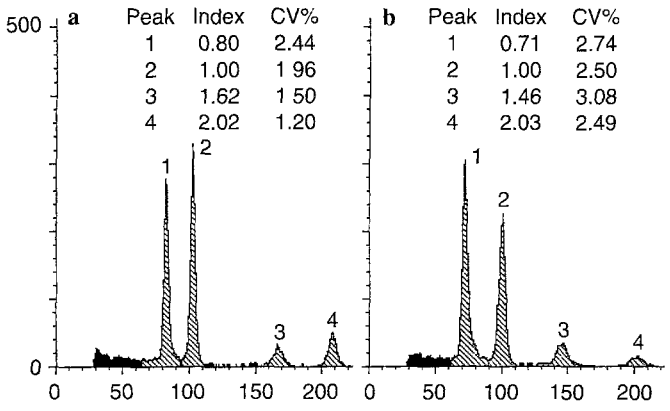

Fig. 2a,b EB flow cytograms of wild pea accessions using *T. monococcum* as a standard. **a** *P. humile*, WT 420. **b** *P. humile*, WT 410

locations in *P. fulvum* relative to *P. sativum* by genetic means, and Errico et al. (1991) observed two in hybrid meiosis. In *P. abyssinicum*, one or two translocations and inversions have been repeatedly seen in crosses with *P. sativum* (von Rosen 1944; Lamprecht 1964; Saccardo 1971; Conicella and Errico 1985, 1990), but the taxon is obviously not homogeneous in karyotype structure, and Conicella and Errico (1985, 1990) even describe a strain without a translocation.

The present genome-size data confirm that *P. abyssinicum*, *P. elatius* and *P. humile* are genetically non-homogeneous. Presently it is not known whether the variation found is correlated with re-patterned karyotypes. It is not apparent that there is a geographic differentiation in genome size, but the relevant information available is very sparse. Exact geographic data would be particularly important in *P. elatius*, the taxon with the widest distribution, which extends from the western Mediterranean to Tibet and India (Lehmann 1954). Moreover, it is questionable, whether the current system, which is based on allelic differences (Lehmann and Blixt 1984), is adequate to describe the biological species structure, as indicated by genome-size differences, in wild peas. We maintain that significant genome-size differences between populations provide evidence for profound genomic diversification and therefore biological separation. (This, of course, does not exclude the occurrence of transitory or hybrid populations). Therefore, the closest relatives, in terms of genomic similarity, of *P. sativum* among wild peas will not be found among those populations with genomes larger than those of *P. sativum*. This applies in particular to those specimens of *P. abyssinicum* and *P. humile* with larger genomes which are most certainly not candidates for the direct ancestry of *P. sativum* (compare Govorov 1937, cit. in Lehmann 1954 and Makasheva 1984). We assume that *P. sativum* has its closest relatives among those wild peas which are very similar in genome size to *P. sativum*. The present data do not allow us to decide between *P. elatius* and *P. humile*, which are considered as potential ancestors by Zohary and Hopf (1973), because both taxa include samples having the same genome size as *P. sativum* (see also Smartt 1984, here given as *P. sativum* var. elatius and *P. sativum* var. pumilio).

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