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Pinus mugo Turra geographic differentiation based on needle characters

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Abstract: The needles of 17 samples representing 15 populations of *Pinus mugo* Turra from the Alps, Apennines, Sudethians, Carpathians and Rhodopes were analysed in respect to 15 morphological and anatomical characters. The results of measurements were analysed statistically. The variation of the samples was generally not to large. Populations from the East Carpathians appeared different from all other examined. Two formed groups of analysed populations are separated mainly by thickness of epidermal cells, width/thickness of epidermal cell ratio, needle width and needle thickness. The differences between two groups of populations suggest their longer separation during Pleistocene.

Additional key words: dwarf mountain pine, plant variation, plant taxonomy, plant migration

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Introduction

The variation of *P. mugo* Turra and its relations with other taxa of the "*Pinus mugo* complex" (Christensen 1987a) were examined several times on the base of morphological, anatomical, biochemical and genetic investigations (Marcet 1967; Szweykowski 1969; Staszkiewicz and Tyszkiewicz 1969, 1972; Musill 1977; Szweykowski and Bobowicz 1977; Prus-Głowacki and Szweykowski 1983; Christensen 1987a, b; Fillpula et al. 1992; Siedlewska and Prus-Głowacki 1994; Lewandowski et al. 2000; Bobowicz et al. 2000; Wachowiak et al. 2000; Boratyńska and Bobowicz 2001; Odrzykowski 2001; Bobowicz et al. 2001; Lewandowski et al. 2002; Korszikov and Pirko 2002; Goncharenko 2002). In spite of that the detailed range of the variation of dwarf mountain pine was described only for a several local populations. As concerns of the needle characters it was lately examined on samples from the Alps (Minghetti 1997), the Tatra Mts (Bobowicz and Krzakowa 1986, 1988; Boratyńska 2002), the Karkonosze Mts (Boratyńska et al. 2003), the Góry Izerskie Mts (Szweykowski et al. 1976; Bobowicz et al. 1983), the East Carpathians (Boratyńska and Pashkevich 2001) and the Abruzzian Apennines (Boratyńska et al. 2004). Variation of the taxon in the whole area of distribution has not been verified.

P. mugo occurs in the mountains of the Central and southern Europe. It has a disjunctive range divided into several islands (Fig. 1). The largest of them covers the Alps, the other ones exists in particular, most elevated mountain ranges of Carpathians, Sudethians, Dynarian Alps and other massifs of the Balkan Peninsula, which have sufficiently well developed sub-alpine vegetation zone.

In the Alps the dwarf mountain pine grows between (450) 1500 and 2500 m alt, with the maximum at 2700 m (Hegi 1936; Bono et al. 1967; Montacchini and Caramiello 1968; Montacchini 1968; Fenaroli

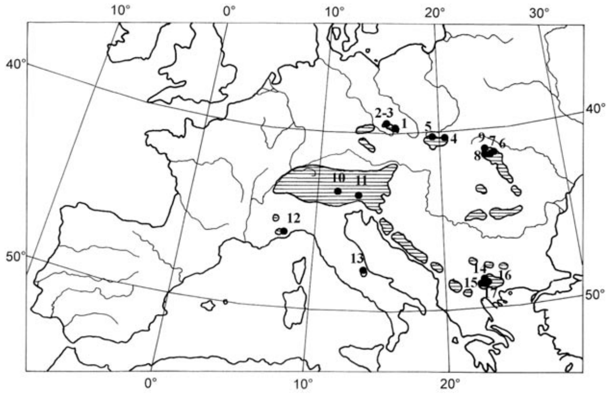

Fig. 1. Range of *Pinus mugo* (after Meusel et al. 1965 and Jalas, Suominen 1973, modified) with mark position of samples studied (1–17 as in Table 1)

and Gambi 1976; Polatschek 1997). The altitudinal range of the species differs significantly in the particular mountains: (800) 1200–1450 (1550) m in the Karkonosze (Boratyński 1994), (940) 1550–1800 (2140) m in the Tatra (Pawłowski 1972, Hantz 1979), 1300–2000 m in the Chornokhora (Czopik 1976; Boratyński et al. 2004), (1400) 1700–2300 (2500) m in the particular mountains of the Balkan Peninsula (Stojanov 1963; Cekov 1969).

The contemporary range of *Pinus mugo* was formed during postglacial, by reduction of the probably much larger area from the glacial period (Willis 1994; Willis et al. 2000; Berglund et al. 1996; Obidowicz 1996; Farcas et al. 1999; Wohlfarth et al. 2001). The isolation of particular populations of the species in the most elevated mountains started probably before 8000–9000 years. That separation (at least 150–200 generations) can lead to the differentiation of the species. It is also very probably, that the contemporary range of the species was formed from two or more glacial centres and that the samples from that populations, isolated for much longer period, would show the greater differences. The main aim of the study was verification of that hypothesis on base of the needle characters.

Material and methods

The present study is based on the 10 samples from 9 natural populations of typical *Pinus mugo* (=*P. mugo* subsp. *mugo* sensu Christensen 1987a), from outside the *P. uncinata* (=*P. mugo* subsp. *uncinata* sensu Christensen 1987a) range to avoid the possible influence of this taxon. The additional 7 populations were characterized in the previous publications (Boratyńska and Pashkevich 2001; Boratyńska 2002; Boratyńska et al. 2003; Boratyńska et al. 2004). The total material includes 17 samples from 16 populations and cover quite whole range of the species (Table 1). Every samples, except of two, was represented by at least 30 individuals. The samples were gathered on special way to avoid the possibility of duplicate collection from the same genet (Boratyńska et al. 2004). A total 622 individuals were sampled, each by collecting of 10 two-year old dwarf shoots from the central part of one long-shoot, from the southern part of crown. Every individual was characterized on the basis of 10 needles, and 6220 needles were analysed totally. Each needle was examined separately for 15 characters (Table 2), following the methods used in the previous studies (Boratyńska and Bobowicz 2000, 2001). The minimal and maximal values of characters were found, the arithmetical means, standard deviation and coefficients of variation were calculated and analysed (Appendix 1).

The discriminant analysis was performed and the position of the populations along the first three discriminant variables was examined to find differences among them. Then the shortest Mahalanobis distances were calculated and the minimum spanning tree was constructed on the squares of Mahalanobis distances to examine relationships among populations. Dendrogram of the shortest Euclidean distances among the populations was constructed to verify the relations among them (Marek 1989; Morrison 1990; Watała 2002).

Results

The discriminant analysis shows that the needle length (character 1), the width and thickness of epidermal cells (characters 11 and 10, respectively) and width/thickness ratio of epidermal cells (character 15) have the highest discriminant power with Wilk's lambda at level between 0.61 and 0.74. The numbers of stomatal rows on abaxial and adaxial needle sides (characters 2 and 3, respectively), and their ratio (character 13) did not statistically differ in any of the populations studied. The analysed populations formed two separate groups in the space of the three first discriminant variables (Fig. 2), which covered 77.6% of the total variation. The separate group formed populations from the East Carpathians (samples 6–9). All other samples have been grouped into one, slightly differentiated group.

The differentiation is determined mostly by the first discrimanant variable (U_1), which is correlated with thickness of epidermal cell, width/thickness of epidermal cell ratio, needle width and needle thickness (characters 10, 15, 7 and 8, respectively). These needle traits are in the great instance responsible for differentiation of the East-Carpathian populations. The width/thickness ratio and thickness of epidermal cell (characters 15 and 10) are decisive also for the second discriminant variable (U_2), which covers 19% of variability (Table 3). The numbers of the stomata (characters 4 and 5) are responsible on the third discriminant (U_3) variable, covering only 8% of the total variation.

Table 1. Localization of studied samples of *Pinus mugo*

Number of sample	Localization	Longitude	Latitude	Altitude (m) n.p.m.	Number of tested specimens
1	Poland, Sudethians, Karkonosze Mts, Równia below Śnieżka	15°47'41''	50°44'44''	1400–1420	30
2	Poland, Sudethians, Karkonosze Mts, between Łabski Szczyt and Szrenica	18°33'15''	50°47'40''	1350–1450	26
3	Poland, Sudethians, Karkonosze Mts, between Łabski Szczyt and Szrenica	18°33'15''	50°47'40''	1350–1450	39
4	Poland, Carpathians, Tatry Mts, Dolina Pięciu Stawów	20°03'05''	49°13'09''	1680–1710	50
5	Poland, Carpathians, Tatry Mts, N slopes of Grześ-Wołowiec ridge	19°45'50''	49°13'07''	1600–1650	57
6	Ukraine, Carpathians, Charnokhora Mts, N slopes of Bresckulec	24°35'00''	48°06'25''	1600–1700	41
7	Ukraine, Carpathians, Charnokhora Mts, N slopes of Khoverla	24°37'30''	48°08'00''	1500–1600	40
8	Ukraine, Carpathians, Charnokhora Mts, S slopes of Pozhyezhevska	24°39'19''	48°05'36''	1600–1750	35
9	Ukraine, Carpathians, Gorgany Mts, Mt. Kanch near Sinevir	23°50'00''	48°33'16''	1550	20
10	Austria, Salzburgian Alps, SW slopes of Hochkonig	13°05'00''	47°26'00''	1500	40
11	Italy, Karnishe Alps, Passo di Pramollo	13°15'35''	46°32'45''	1530	44
12	Italy, Maritime Alps, Coll de Tende	7°22'30''	44°08'00''	2000	33
13	Italy, Appenines, Abruzzi Mts, La Maiella	13°58'30''	41°46'20"	2200	33
14	Bulgaria, Vitosha Mts, Dragalevci, Khizha Aleko, N slopes of Chrny Vrkh above Aleko	23°16'08''	42°34'01''	1900	31
15	Bulgaria, Rila Mts, Ribni Ezera above Rilski Manastir, valey of the strean in the direction toward Tikha Rila	23°26'24''	42°05'20''	2100	41
16	Bulgaria, Rila Mts, Belica, Semkovo, S slopes of Chemerna	23°30'00''	42°04'01''	2100	31
17	Bulgaria, Pirin Mts, Bansco, Ravnako above Khizha Vikhren, in Bynderiski Circus	23°25'22''	41°46'07''	2000	31

The spanning tree constructed on the basis of the squares of Mahalanobis distances confirm the separateness of the East-Carpathian populations (Fig. 3). The shortest Mahalanobis distance unit the populations from the Bresculec and Pozhyezhevska (samples 6 and 8, respectively) and is not statistically significant ($p>0.05$), while all other differentiated populations statistically significantly ($p<0.05$). The largest distances divide the sample from the Gorgan and Równia below Śnieżka, Gorgan and Coll de Tende and Gorgan and Abruzzian Apennines (samples 9, 1, 12 and 13, respectively). Dendrogram constructed on the shortest Euclidean distances (Fig. 4) also confirms the different character of the East-Carpathian populations described above.

Table 2. Needle characters analysed

No	Characters	Precision
1	Needle length	1 mm
2	Number of stomatal rows on convex (abaxial) side of needle	
3	Number of stomatal rows on flat (adaxial) side of needle	
4	Number of stomata on 2 mm long section of needle, on convex (abaxial) side	
5	Number of stomata on 2 mm long section of needle, on flat (adaxial) side	
6	Number of resin canals	
7	Width of needle	0.1 mm
8	Thickness of needle	0.1 mm
9	Distance between the vascular bundles	1 μm
10	Thickness of epidermis cells (with hypodermis cells)	1 μm
11	Width of epidermis cells	1 μm
12	Marcet's coefficient (=traits 9×7/8)	
13	Stomatal rows ratio (=traits 2/3)	
14	Needle thickness/width ratio (=traits 8/7)	
15	Cell of epidermis width/thickness ratio (=traits 11/10)	

Discussion

The variation of *Pinus mugo* appeared surprisingly not to large. Two groups of populations separated on the sufficiently high level were distinguished (Figs. 2–4). The separateness of the East-Carpathian populations of *Pinus mugo* has not been described till now on such broad material. The previous investigations on dwarf mountain pine variation signalled the slightly greater differences between singular samples from the Ukrainian East Carpathians as compared with samples from Poland on the basis of the cone characters (Staszkiewicz and Tyszkiewicz 1976; Marcysiak 2003).

The great morphological differences in the cone characters have been also found between West- and East-Carpathian populations of *Picea abies* (Staszkiewicz 1966; Boratyński 1998). The Norway spruce is a mountain plant with the disjunction in the range di-

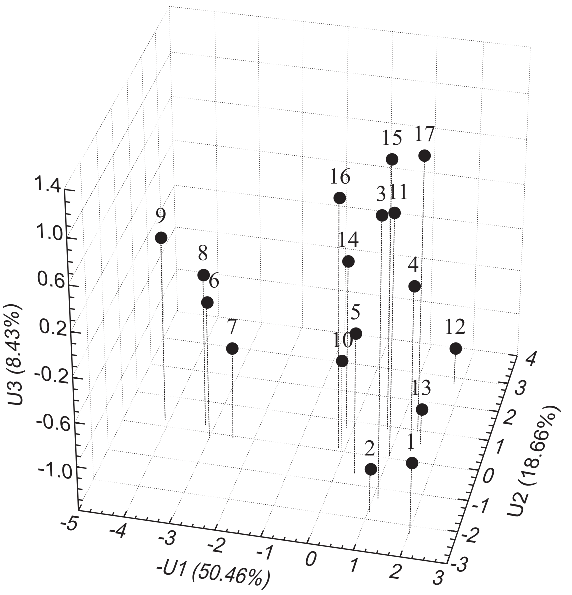

Fig. 2. Result of discriminant analysis based on 15 needle characters of 17 samples of *Pinus mugo* plotted along the three first discriminant variables U_1, U_2 and U_3 (samples numbers as in Table 1)

Table 3. The determination coefficients between discriminant variables U_1, U_2 and U_3 and 15 characters of needles (1–15 as in Table 2)

Characters	U_1	U_2	U_3
1	3.29	1.24	0.00
2	3.12	1.46	0.93
3	4.34	1.26	1.09
4	1.80	0.56	4.19
5	1.71	1.18	4.18
6	4.27	1.04	1.50
7	13.74	0.01	1.07
8	11.03	0.08	0.13
9	3.36	0.60	0.60
10	15.43	2.09	0.26
11	0.03	1.64	0.01
12	3.49	0.37	0.80
13	0.31	0.01	0.04
14	1.21	0.46	1.66
15	15.12	5.51	0.22

viding East and West Carpathians, which suggest origin from other Pleistocene refugia. The history of *P. abies* migration, however, was investigated much more detailed on the basis of the pollen data and on the morphological variation (Środoń and Tobolski 1998, Boratyński 1998).

The distinct differences between four samples of *Pinus mugo* from the East Carpathians and the rest of examined, suggests longer period of separation than Holocene. Thus, the dwarf mountain pine population should be expected to survive at the base of East Carpathians during the last glaciation period. The lack of great differences between populations sampled from the Alps, Sudethians, West Carpathians and mountains of Balkan Peninsula suggest the broad distribution of the species, at least during last glaciation, on the area to the South from the Alps – West Carpathians range through the Dynarian Alps to the Rodopy Mts. It has not been confirmed pallynologically, because of the insignificant differences between pollen grains of *P. mugo* and *P. sylvestris*, which did not allow distinguishing them. It is quite possible, that some of pallynological data, especially in the mountains southerly from Carpathians and Alps concern more pollen of *P. mugo*, than *P. sylvestris*, this, however, should be verified in future investigations. Nevertheless, the probably presence of *P. mugo* in the Nowy Targ basin at the northern foots of the Tatra Mts during the end of last glacial/preboreal peat sediments have been mentioned by Obidowicz (1996). The species was also mentioned from the same period in the lake sediments of the mountains of northern Romania (Wohlfarth et al. 2001), and in late glacial/preboreal peat sediments in the Orava Basin in Slovakia (Rybníček and Rybníčková 2002). *Pinus mugo* was also found in the mountain lake sediments from dryas/preboreal, in the Pirin mountains (Bulgaria) (Stefanova and Ammann 2003; Stefanova et al. 2003). All these and several other paleobotanical data seem to confirm the much larger area of distribution of

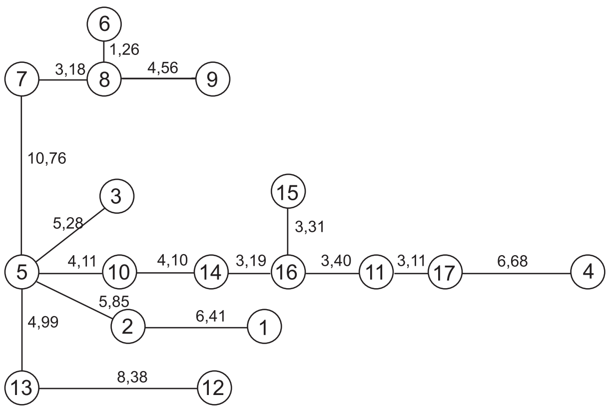

Fig. 3. Minimum spanning 17 samples of *P. mugo* constructed on the basis of the squares of Mahalanobis distances (samples numbers as in Table 1)

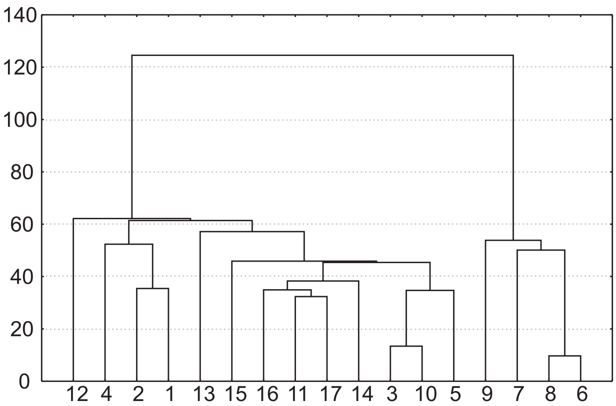

Fig. 4. Dendrograms of 17 samples of *Pinus mugo* constructed on the basis of the shortest Euclidean distances (samples number as in Table 1)

dwarf mountain pine in the late glacial period, with unrestricted gene flow between local populations, at least on the area surrounded by the Carpathians, Dynarian Alps, Alps and Rhodopes. The mountains, at least partly covered with glaciers, prevented the migration of the species from its local refuges.

Lately the possibility of existence of coniferous forest formations was also described at the eastern and south eastern bases of the East and South Carpathians (Tarasov et al. 2000). This justify statement, that *Pinus mugo* also survived the last glacial period in that center, isolated from its other populations. During late glacial it can migrate to the N and N–W, outside the arc of Carpathians, forming the present-day populations, examined in present study.

Conclusion

The dwarf mountain pine (*Pinus mugo*) is slightly variable on the area surrounded by the Alps, Sudethians, Carpathians, Rhodopes and Dynarian Alps. Only populations sampled in the East Carpathians differ from all other examined. It suggests their longer separation during last glacial period and probable origin from the coniferous forest refuge at south-east bases of East Carpathians.

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Appendix 1. Major needle characteristics of 11 analysed samples of *P. mugo*; date for sample number 5 in Boratyńska 2002, for number 6–9 in Boratyńska, Pashkevich 2001, for number 13 in Boratyńska et al. 2004 (full name characters as in Table 2, full name samples as in Table 1)

Analysed samples		Characters														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Arithmetic mean	1	40.92	10.89	8.29	18.45	17.61	5.06	1581.99	892.48	94.62	41.87	15.27	168.58	1.33	0.57	0.37
	2	40.95	10.93	8.13	19.41	19.43	4.83	1549.45	886.62	96.63	39.06	14.91	170.41	1.36	0.57	0.38
	3	38.87	9.43	7.07	17.17	16.77	4.31	1470.34	867.72	100.98	37.18	14.93	175.08	1.36	0.59	0.40
	4	45.21	10.14	7.82	18.96	18.69	4.40	1543.72	918.12	83.75	39.29	13.33	141.65	1.31	0.60	0.34
	10	48.10	9.33	6.75	20.04	19.77	4.46	1468.08	861.55	104.58	39.53	14.94	179.06	1.41	0.59	0.38
	11	45.47	8.84	6.54	17.92	17.74	4.13	1440.90	850.47	87.57	40.85	14.67	149.19	1.37	0.59	0.36
	12	48.69	9.31	7.13	19.85	19.75	4.41	1592.17	922.82	128.20	44.62	13.67	222.17	1.33	0.58	0.31
	14	45.92	9.08	6.84	19.65	19.63	3.56	1407.77	824.31	113.07	38.63	14.01	194.50	1.36	0.58	0.36
	15	50.89	9.60	7.07	17.74	17.63	3.61	1508.54	888.25	123.02	40.09	14.29	210.39	1.39	0.59	0.36
	16	50.33	9.03	6.79	18.10	18.15	3.54	1420.05	828.28	94.92	39.33	14.68	163.72	1.36	0.58	0.37
	17	40.25	8.44	6.36	18.15	18.18	3.52	1411.32	847.58	82.48	42.11	14.34	138.80	1.35	0.60	0.34
Minimum	1	28.00	7.00	5.00	14.33	13.33	2.00	850.00	680.00	29.97	33.30	11.09	53.36	0.78	0.42	0.25
	2	30.00	7.00	5.00	14.67	14.34	3.00	1275.00	658.75	13.32	29.97	10.82	20.58	1.00	0.49	0.23
	3	26.00	1.00	4.00	11.34	11.34	0.00	1168.75	637.50	13.32	26.64	9.99	23.09	0.14	0.42	0.25
	4	31.00	6.00	4.00	15.33	14.66	0.00	1253.75	765.00	16.65	29.30	9.99	26.73	0.86	0.51	0.25
	10	32.00	5.00	4.00	15.66	13.66	1.00	1105.00	680.00	16.65	29.97	10.46	26.82	0.78	0.48	0.26
	11	30.00	5.00	4.00	12.33	12.66	0.00	1168.75	680.00	13.32	33.30	10.82	22.83	0.75	0.51	0.24
	12	32.00	5.00	4.00	15.33	16.00	2.00	1296.26	796.88	36.63	31.64	9.16	61.81	0.62	0.50	0.20
	14	33.00	5.00	4.00	15.00	14.33	0.00	1041.25	616.25	39.96	26.64	9.99	59.94	0.78	0.45	0.24
	15	36.00	6.00	4.00	13.67	13.33	1.00	1168.75	658.75	33.30	29.97	9.99	52.45	0.87	0.46	0.27
	16	26.00	6.00	3.00	14.66	13.00	2.00	1083.75	658.75	3.00	29.97	9.99	4.56	0.89	0.47	0.25
	17	22.00	5.00	4.00	14.00	14.33	1.00	998.75	658.75	13.32	29.97	9.99	18.97	0.78	0.52	0.24
Maximum	1	54.00	16.00	12.00	26.33	23.66	8.00	2103.75	1083.75	196.56	59.94	23.31	365.69	2.00	0.87	0.54
	2	54.00	15.00	12.00	23.67	25.00	7.00	1870.00	1572.50	199.80	56.61	22.20	357.14	2.00	0.94	0.53
	3	62.00	15.00	11.00	26.34	23.67	7.00	1848.75	1126.25	176.49	56.61	21.09	321.58	2.33	0.73	0.53
	4	61.00	14.00	12.00	23.00	24.33	7.00	1827.50	1062.50	156.51	49.95	29.97	302.61	1.86	0.70	1.00
	10	70.00	15.00	11.00	25.00	24.66	8.00	1933.75	1147.50	206.46	49.95	19.98	389.45	2.25	0.72	0.52
	11	68.00	13.00	10.00	25.33	24.66	7.00	1763.75	1190.00	166.50	53.28	19.98	306.71	2.25	0.72	0.54
	12	67.00	14.00	11.00	24.33	24.00	7.00	1891.25	1190.00	259.74	59.94	19.98	477.06	2.00	0.69	0.48
	14	68.00	14.00	12.00	30.00	25.33	7.00	1912.50	1126.25	289.71	49.95	19.98	491.25	2.20	0.84	0.50
	15	71.00	15.00	11.00	22.00	22.67	7.00	1827.50	1168.75	243.09	49.95	18.87	403.31	2.50	0.70	0.50
	16	76.00	15.00	10.00	24.00	23.66	6.00	1785.50	1147.50	233.10	49.95	39.96	377.62	2.25	0.71	1.00
	17	61.00	13.00	10.00	22.33	22.33	7.00	1721.25	1020.00	199.80	53.28	19.98	364.63	2.20	0.70	0.47

Analysed samples		Characters														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Standard deviation	1	4.22	1.33	0.85	1.67	1.62	0.74	101.92	56.09	19.81	3.72	0.87	36.74	0.11	0.02	0.02
	2	4.80	1.02	0.71	1.43	1.50	0.73	89.62	52.93	31.72	2.72	1.05	58.70	0.07	0.02	0.03
	3	6.31	0.89	0.74	1.44	1.44	1.00	96.56	55.16	23.63	2.71	1.07	52.24	0.10	0.02	0.03
	4	4.51	1.15	0.98	1.22	1.20	1.09	92.13	44.80	19.35	2.77	0.60	34.83	0.07	0.02	0.03
	10	7.20	1.16	1.05	1.21	1.25	1.04	123.93	68.98	22.64	3.70	0.76	41.47	0.13	0.02	0.03
	11	6.21	1.18	0.80	1.73	1.67	0.86	104.21	65.12	22.54	3.08	0.83	40.58	0.11	0.01	0.03
	12	5.69	1.27	1.05	1.09	0.96	0.79	92.35	49.09	32.90	4.32	1.03	58.50	0.10	0.02	0.03
	14	6.90	1.23	1.06	1.53	1.49	0.92	139.46	78.77	28.13	2.92	1.09	50.98	0.14	0.03	0.03
	15	8.05	1.17	0.95	1.36	1.29	0.69	120.83	66.51	28.97	3.01	0.68	53.02	0.13	0.02	0.03
	16	10.60	1.35	0.95	1.44	1.43	0.75	122.54	61.74	31.52	2.24	1.04	56.68	0.15	0.02	0.03
	17	7.05	1.14	1.01	1.18	1.14	0.75	131.01	65.64	33.29	2.85	0.95	59.13	0.12	0.02	0.02
Variability coefficient	1	10.32	12.19	10.23	9.03	9.18	14.64	6.44	6.28	20.94	8.89	5.73	21.79	8.10	3.57	5.75
	2	11.73	9.38	8.75	7.36	7.71	15.07	5.78	5.97	32.82	6.96	7.02	34.44	5.45	3.28	7.28
	3	16.23	9.46	10.54	8.36	8.62	23.10	6.57	6.36	23.40	7.30	7.15	29.84	7.17	4.02	7.35
	4	9.98	11.32	12.53	6.44	6.41	24.86	5.97	4.88	23.11	7.06	4.54	24.59	5.52	2.62	9.74
	10	14.97	12.38	15.61	6.04	6.34	23.52	8.44	8.01	21.64	9.38	5.07	23.21	9.22	3.97	8.01
	11	13.65	13.35	12.26	9.66	9.42	20.89	7.23	7.66	25.74	7.55	5.67	27.20	8.20	3.18	8.02
	12	11.69	13.70	14.77	5.54	4.88	18.07	5.80	5.32	25.66	9.69	7.53	26.33	7.76	3.22	8.80
	14	15.02	13.50	15.42	7.80	7.62	25.76	9.91	9.56	24.88	7.56	7.81	26.21	10.55	5.33	6.97
	15	15.81	12.23	13.41	7.67	7.34	19.29	8.01	7.49	23.55	7.51	4.78	25.20	9.46	4.34	7.22
	16	21.07	14.93	14.05	7.96	7.90	21.22	8.63	7.45	33.20	5.68	7.07	34.62	10.99	3.85	8.10
	17	17.51	13.55	15.81	6.49	6.26	21.38	9.28	7.74	40.36	6.76	6.66	42.59	8.99	3.89	6.93