ANOMALOUS NEEDLE NUMBERS ON DWARF SHOOTS OF *PINUS MUGO* AND *P. UNCINATA* (PINACEAE)

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ABSTRACT

The frequency of occurrence of abnormal, three- (or more) needle dwarf shoots of most southern and central European two-needle pine (*Pinus*) species were studied. No specimens with more than two-needle dwarf shoots were found in a population of *P. nigra* Arnold subsp. *salzmannii* (Dunal) Franco from the Iberian Peninsula and in two populations of *P. uliginosa* Neumann from the Sudeten Mountains in Central Europe. Single specimens were found within one population of *P. pinaster* Aiton from the Iberian Peninsula and among six populations of *P. sylvestris* L. from the Iberian Peninsula and Central Europe. Abnormal dwarf shoots mostly with three, but also four, five or six needles were found among 24 of 25 surveyed populations of *P. mugo* Turra and *P. uncinata* Ramond. The average frequency of specimens with at least one three-needle dwarf shoot was 24% for *P. mugo* and 20% for *P. uncinata*. The frequencies of occurrence varied significantly among studied populations and were highest in samples collected from the upper elevational range limits of the species in the mountains and near the northern limits of their ranges. The frequency of abnormal dwarf shoots in the same populations was significantly high in 2-3 consecutive years. Needles from three-needle dwarf shoots were not significantly shorter than those of two-needle shoots.

KEY WORDS: *Pinus mugo*, *Pinus uncinata*, Central and Southern Europe, morphological variation, abnormal dwarf shoots, brachyblasts.

INTRODUCTION

Pinus mugo Turra and *P. uncinata* Ramond are closely related species, treated recently as subspecies of *P. mugo sensu lato* (= *P. mugo* complex, see Christensen 1987a). Both taxa and other pines belonging to subsection *Sylvestres* (*Pinus sylvestris* L. and *P. uliginosa* Neumann in Central Europe) normally have two needles per dwarf shoot. For this taxa abnormal dwarf shoots with more than two needles have been found rarely and are regarded as an exception. Among them, three-needle dwarf shoots have been reported most frequently. Such shoots have been described for several localities of *Pinus mugo* and *P. uncinata* (Schneider 1913; Penzig 1922; Györffy 1932; Debazac 1962; Jähring 1962; Skawiński 1975; Klaus and Zetter 1978; Boratyński et al. 2000).

The occurrence of specimens of the *Pinus mugo* complex (*P. mugo*, *P. uncinata* and intermediate taxa) with three-needle dwarf shoots has recently been reviewed by Christensen (1987b). On the basis of herbarium materials, he concluded that three-needle dwarf shoots may be found throughout the natural range of the species, but mainly at the upper limit of their altitudinal range. He found 27 specimens with abnormal number of needles among 249 examined herbarium sheets.

The occurrence of three-needle dwarf shoots on *Pinus sylvestris* is also known from the literature (Penzig 1922; Rettich 1932; Przybylski 1970). Abnormal dwarf shoots in *P. sylvestris* may form as a result of mechanical injury to individual trees (mostly seedlings) (Szymański 1958; Król 1983/1984). The formation of dwarf shoots with three or more needles on *P. sylvestris* was also observed after experimental removal of buds from seedlings (Giertych 1968).

The presence of more than two needles on the dwarf shoots of a two-needle pine species is considered an ancestral state of the trait (Klaus and Zetter 1978).

The main goal of this study was to analyze on random samples the geographical variation of the frequency of occurrence individuals with three-needle dwarf shoots among populations of *Pinus mugo* and *P. uncinata* throughout their natural range in the mountains of Central and Southern Europe. The abnormal dwarf shoots were reported from these two species and from other pines, but nobody has compared frequencies among the species. For this reason the aim of the study was also the comparison of three-needle dwarf shoots frequencies among *P. mugo*, *P.*

TABLE 1. Location of populations and numbers of specimens tested.

Sample number	Species	Locality	Year of collection	Number of specimens	Altitude [m]	Vertical range	Source of information	Recalculated altitude [m]
1	*Pinus mugo*	Poland, Sudethians, Karkonosze Mts., Równia pod Śnieżką	1999	30	1400-1420	1200-1450 (1500)	Boratyński 1994	1770
2			2000	39				
3			2001	31				
4		Poland, Sudethians, Karkonosze Mts., between Łabski Szczyt and Szrenica	1999	26	1350-1450			1750
5			2000	39				
6		Poland, Carpathians, Tatra Mts., Dolina Pięciu Stawów Polskich	1999	50	1680-1710	1550-1800	Pawłowski 1958	1710
7		Poland, Carpathians, Tatra Mts., N slopes of Grześ-Wołowiec ridge	1999	57				1670
8		Ukraine, Carpathians, Charnokhora Mts., N slopes of Breskulec	1997	41	1600-1700	1500-1850	Środoń 1948; Chopik 1976; Boratyński et al. 2003a	1678
9		Ukraine, Carpathians, Charnokhora Mts., N slopes of Khoverla	1997	40	1500-1600			1592
10		Ukraine, Carpathians, Charnokhora Mts., S slopes of Pogygevska	1998	35	1600-1750			1704
11		Ukraine, Carpathians, Gorgany Mts., Mt Kanch near Sinevir	1998	20	1550			1592
12		Germany, Bavarian Alps, NW slopes of Kreuzspitze	2001	31	1800	1500-2300	Meusel et al. 1965	1550
13		Austria, Salzburgian Alps, SW slopes of Hochkonig	2001	40				1550
14		Italy, Karnishe Alps, Passo di Pramollo	2001	44	1530	1500-2200	Fenaroli and Gambi 1976	1560
15		Italy, Maritime Alps, Coll de Tende	2001	33	2000	1700-2100	Bono et al. 1967	1775
16		Italy, Appenines, Abruzzi Mts., La Maiella	2001	33	2200	2000-2600	Fenaroli and Gambi 1976	1650
17		Italy, Prealpi Venete, Gruppo di Brenta, Lago di Tovel	2001	30	1170-1200	1500-2200	Minghetti 1997	1421
18		Italy, Prealpi Venete, Monte Baldo, Mt Altissimo di Nago	2001	30	1700-1800			1657
19		Bulgaria, Vitosha Mts., Mt Aleko	2000	45	1500	1500-1700	Stoyanov 1963	1550
20	*Pinus uncinata*	Spain, Eastern Pyrenees, Vall de Nuria	1999	42	2100-2200	1300-2300	Vigo i Bonada J. 1983	2150
21			2001	33				2150
22		Andorra, Eastern Pyrenees, Vall de Ransol	1999	40	2000-2050	1300-2200	Boratynski et al. 2003b	2133
23			2000	30				
24		Spain, Central Pyrenees, Pico de Aneto	2001	32	2000-2100	1400-2400	Amaral Franco 1984	1950
25		Spain, Central Pyrenees, Port de la Bonaiqua	2001	34	2050-2100	1600-2400	Carrillo and Ninot 1992	1888
26		France, Eastern Pyrenees, Col de Jau	2001	32	1510-1520	1300-2200	Amaral Franco 1984	1320
27		Spain, Western Pyrenees, Belagoa	1000	40	1700	1600-2000	Villar 1980; Amaral Franco 1984	1550 1350
28		Spain, Sierra de Gudar, Vall de Linares	2001	31	2000	1950-2000	Amaral Franco 1984	1300
29		France, Massif Central, Col de la Croix de Morand	1999	31	1350-1400	1200-1400	Meusel et al. 1965	1300
30		France, Massif Central, Soulzet	2001	31	1200			
31	*Pinus uliginosa*	Poland, Bory Dolnośląskie, Węgliniec	1999	52	200			
32		Poland, Sudethians, Stołowe Mts., Batorów Moor	1998	50	750			
33	*Pinus sylvestris*	Spain, Sierra de Baza, below the top of Baza	2001	32	1950-2000			
34		Poland, Bory Dolnośląskie, Węgliniec	1999	33	200			
35		Poland, Sudethians, Stołowe Mts., Mt Szczeliniec	2000	35	900			
36		Spain, Eastern Pyrenees, Col del Canto	1999	40	1500-1600			
37		Spain, Central Pyrenees, Pena de Oroel	1999	35	1750			
38		Spain, Sierra de Guadarrama, Puerto de los Cotos	1999	41	1900			
39	*Pinus pinaster*	Spain, Cabezas Altas near Quintanar de la Sierra	1999	29	900			
40	*Pinus nigra*	Spain, above Noves de Segre near Seu d'Urgel	1999	42	1100			

uncinata, *P. sylvestris*, *P. uliginosa*, *P. nigra* and *P. pinaster* coming from the mountains, mostly from the areas close to *P. mugo* and *P. uliginosa* range.

MATERIAL AND METHODS

Plant material was collected in native populations of *Pinus mugo*, *P. uncinata*, *P. uliginosa* and *P. sylvestris*, in 1997-2001. All four pine species belong to the Section *Pinus* subsection *Sylvestres* and are common in Europe (Little and Critchfield 1969; Boratyński 1993). Single populations of *Pinus nigra* and *P. pinaster* from the Iberian Peninsula were analyzed as comparative material.

The samples were gathered from individuals without visible symptoms of injury and exclusively from cone-bearing branches. The shoots of the prostrate *Pinus mugo* were sampled from specimens in distance no less than 30 meters from each other to avoid the possibility of collecting multiple samples from the same individual. In each analyzed population, the two-year-old long shoots were collected from 26-57 individuals (38 on average), always on the sunny, south-facing (SE and SW) side of the crown. Ten two-year-old dwarf shoots were removed from the mid length of the long shoots, and absence or presence of atypical, mostly three-needle, but also four- to six-needle dwarf shoots was reported for each individual separately.

For the individuals with abnormal dwarf shoots, the frequency of dwarf shoot occurrence was calculated as ratio of numbers of abnormal to normal + abnormal dwarf shoots and was presented in %.

The populations were characterized by:
– number of individuals with at least one abnormal dwarf shoot,
– frequency of abnormal dwarf shoots in the sample, calculated as ratio of abnormal to normal + abnormal dwarf shoots.

In total, 1454 individuals were sampled from all taxa (Table 1). The distribution of samples of *Pinus mugo* and *Pinus uncinata* covered the geographic ranges of these species (Fig. 1). Four samples of *P. sylvestris* came from the south-western limit of its range, while two others, as well as two samples of *P. uliginosa*, were collected in the and near the northern limit of the Sudeten Mts. (Fig. 1).

The length of needles from typical and atypical dwarf shoots was measured on 25 specimens in two populations of *Pinus mugo* and on 51 specimens in five populations of *P. uncinata* on fresh material, directly after sampling. Then central portion of the needles (about 2-3 cm long) were cut out and preserved in 70% alcohol for further anatomical studies.

One of the *Pinus uncinata* populations was sampled in each of two years (Table 1, samples 20 and 21). Similarly one population of *P. mugo* was studied in two and another in three consecutive years (Table 1, samples 1-5). Each year random samples of shoots were collected from different or the same individual, depending on the presence of cones.

Dependence of occurrence of specimens bearing abnormal dwarf shoots and frequency of abnormal dwarf shoots in sampled populations with their latitude, altitude and position in vertical range were tested using Pearson's correlation coefficient.

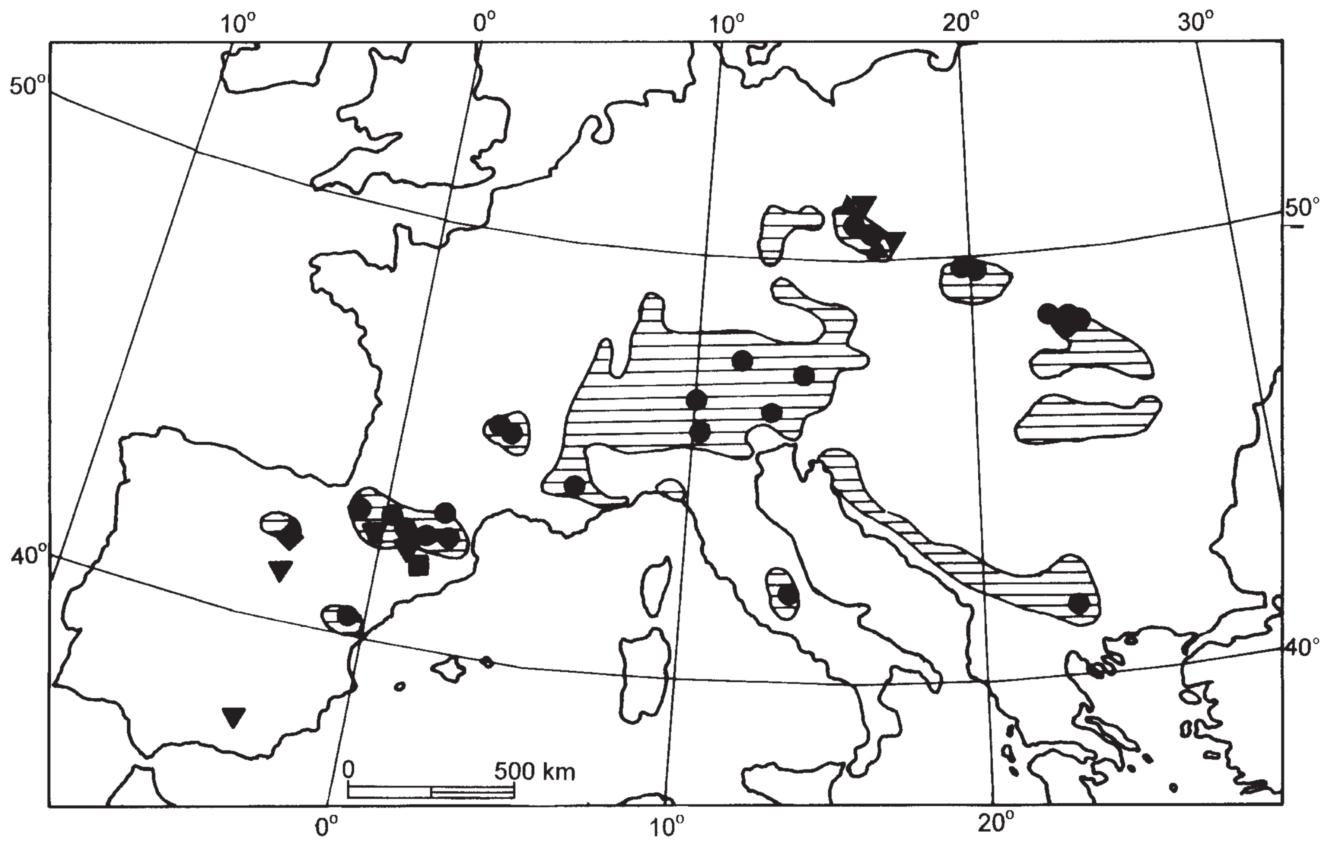

Fig. 1. Distribution of sampled populations against the background of the range of *Pinus mugo* complex: ● – *Pinus mugo* and *Pinus uncinata*; ▲ – *Pinus uliginosa*; ▼ – *Pinus sylvestris*; ■ – *Pinus nigra*; ◆ – *Pinus pinaster*.

Altitudinal range of the species is different in particular mountain ranges (see Table 1). For this reason statistical comparison among the sampled populations of *P. mugo* are done on altitudes recalculated relative to altitudes at the Tatra Mts. (Table 1, samples 1-19), and among *P. uncinata* to altitudes at the Vall de Nuria in the East Pyrenees (Table 1, samples 20-30). Recalculations were done according to the formula:

[1]

$$ALT_{xrecT} = ALT_{Tmin} + \frac{ALT_x - ALT_{xmin}}{ALT_{xmax} - ALT_{xmin}} * (ALT_{Tmax} - ALT_{Tmin})$$

ALT_{xrecT} – Altitude of population x after recalculation
ALT_x – Real altitude of population x
ALT_{xmin} – Minimal altitude of *P. mugo* (or *P. uncinata*) range in the mountain where sample x were collected
ALT_{xmax} – maximum altitude of *P. mugo* (or *P. uncinata*) in the mountain range where sample x was collected
ALT_{Tmin} – Minimal altitude of *P. mugo* range in the Tatra Mts. (or *P. uncinata* in the Vall de Nuria)
ALT_{Tmax} – Maximal altitude of *P. mugo* range in the Tatra Mts. (or *P. uncinata* in the Vall de Nuria)

The interaction of frequency of abnormal dwarf shoots within particular populations depends also on their position in altitudinal local range. This includes all environmental influences. For this reason all sampled populations were also analyzed in respect to their position in:
– low (low 25%),
– central (central 50%),
– top part of altitudinal range (upper 25%).

The correlations were analyzed with average recalculated altitudes (see formula 1) of all samples of particular portion of altitudinal species ranges (Table 1).

The lengths of two- and three-needle dwarf shoots were compared using Student's t-test for unpaired data (Underwood 1997; Zar 1999). Calculations and comparisons were made using STATISTICA 5.1.

RESULTS

Frequencies of abnormal dwarf shoots among taxa

Dwarf shoots with more than two needles are found on *Pinus mugo*, *P. uncinata*, *P. sylvestris* and *P. pinaster* (Table 2). The samples of *P. uliginosa* and *P. nigra* do not contain specimens with more than two-needle dwarf shoots.

Only one three-needle dwarf shoot is found on one sample of *Pinus sylvestris* in the Sierra de Baza, at the southern limit of the range of this species. For *P. pinaster* only one three-needle dwarf shoot is found (Table 2). Occurrence of more than two-needled dwarf shoots on *Pinus sylvestris* is very rare, when compared with frequency of occurrence of atypical dwarf shoots on *P. mugo* and *P. uncinata*. For this reason more detailed analyses are possible for last species only.

Abnormal dwarf shoots among populations of Pinus mugo

Geographic differentiation

Pinus mugo has the greatest number of individuals with atypical dwarf shoots. More than 10% of the specimens examined have more than 10% three-needle dwarf shoots and nine specimens have more than 50% of dwarf shoots with three needles. Two specimens from the Sudeten (Karkonosze Mts., samples 1 and 4) have single five-needle dwarf shoots.

Among the analyzed samples of *Pinus mugo* only one from the Vitosha Mts. in Bulgaria do not contain abnormal dwarf shoots (Table 3). Most of the samples contain 8-15% specimens with at least one three-needle dwarf shoot, although two populations are characterized with frequency of 50% or more (Fig. 2).

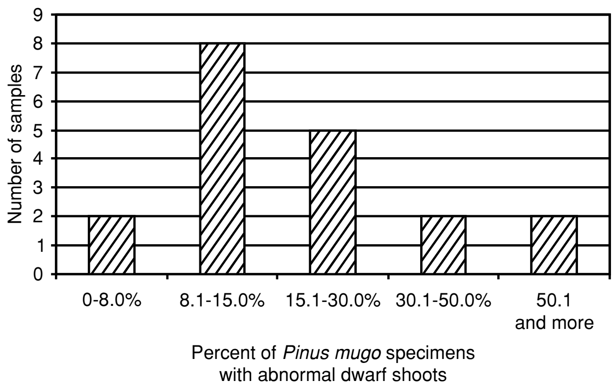

Fig. 2. Numbers of *Pinus mugo* samples in classes of percentage of individuals with three-needle dwarf shoots.

A geographical analysis of the phenomenon shows that populations from the Tatra Mts. (West Carpathians) and Karkonosze Mts. (Sudeten Mts.) have the highest frequency of specimens with three-needle dwarf shoots. Only one population from the Maritime Alps has a comparatively high frequency of specimens with abnormal dwarf shoots. All other populations located south of the Sudeten Mts. and West. Carpathians have a considerably lower frequency of such specimens (Table 3). Nevertheless, the frequency of specimens with abnormal dwarf shoots in particular popu-

TABLE 2. Percentage of abnormal dwarf shoots witnin *Pinus mugo*, *P. uncinata*, *P. uliginosa*, *P. sylvestris*, *P. nigra* and *P. pinaster*.

Species	Total number of specimens examined	Percentage of specimens with various % of 3-needle dwarf shoots						Percentage of specimens with 3-needle dwarf shoots [%%]	Specimens with more than 3-needle dwarf shoots [%%]
		To 10%	11-20%	21-30%	31-40%	41-50%	51% and more		
Pinus mugo	694	13.7	4.2	1.7	1.9	1.3	1.3	24.1	0.3
Pinus uncinata	376	8.5	3.2	2.1	0.8	1.6	4.3	20.2	1.3
Pinus uliginosa	102							0.0	0.0
Pinus sylvestris	213	0.5						0.5	0.0
Pinus nigra	42							0.0	0.0
Pinus pinaster	29	3.4						3.4	0.0

TABLE 3. Percentage of abnormal dwarf shoots withnin studied populations of *Pinus mugo* and *P. uncinata*.

Sample number [refer to Table 1]	Number of specimens within sample	Frequency of specimens with various percentage of 3-needle dwarf shoots						Percentage of specimens with 3-needle dwarf shoots [%%]	Specimens with more than 3-needle dwarf shoots [no]	Percentage of 3-needle dwarf shoots in sample [%%]	Remarks
		To 10%	11-20%	21-30%	31-40%	41-50%	51% and more				
1	30	36.7	13.3	3.3			3.3	56.7	1	9.7	one 5-needle dwarf shoot
2	39	15.4	5.1	5.1	2.6			28.2		5.1	
3	31	19.4	6.5					25.8		3.2	
4	26	15.4					3.8	19.2	1	4.2	one 5-needle dwarf shoot
5	39	12.8	2.6	2.6	7.7			25.6		5.6	
6	50	22.0	10.0	10.0	10.0	10.0	4.0	66.0		19.0	2 specimens with 60% of 3-needle dwarf shoots
7	57	24.6	8.8	1.8		3.5	5.3	43.9		10.2	3 specimens with 60% of 3-needle dwarf shoots
8	41	19.5	9.8					29.3		3.9	
9	40	7.5						7.5		0.8	
10	35	8.6	2.9		2.9			14.3		2.6	
11	20	0.0	10.0					10.0		2.0	
12	31	9.7					3.2	12.9		3.2	1 specimen with 70% of 3-needle dwarf shoots
13	40	7.5		2.5				10.0		1.5	
14	44	6.8				2.3		9.1		1.8	
15	33	15.2	9.1	3.0	9.1	3.0	3.0	42.4		11.5	1 specimen with 95% of 3-needle dwarf shoots
16	33	12.1						12.1		1.2	
17	30	10.0						10.0		1.0	
18	30	10.0						10.0		1.0	
19	45							0.0			
20	42		4.8			2.4	14.3	21.4	1	12.1	one 5-needle dwarf shoot
21	33	15.2	3.0	3.0	3.0	6.1		30.3		7.3	
22	40	10.0	10.0	7.5	5.0	2.5	10.0	45.0		15.5	
24	32	3.1	6.3				3.1	12.5		3.8	1 specimen with 70% of 3-needle dwarf shoots
25	34	11.8	2.9	2.9			5.9	23.5		6.8	2 specimens with 60% of 3-needle dwarf shoots
26	32	15.6						15.6		1.6	
27	40	2.5						2.5	1	0.3	one 4-needle dwarf shoot
28	31	9.7						9.7		1.0	1 specimen with 70% and 1 with 80% of 3-needle dwarf shoots; 2 4-needle and 1 6-needle dwarf shoot
29	31	19.4	9.7	9.7		6.5	6.5	45.2	3	14.5	
30	31	9.7					3.2	12.9		3.2	1 specimens with 70% of 3-needle dwarf shoots

lations is not strongly correlated with latitude of origin (Pearson's r = 0.4371).

The frequency of abnormal dwarf shoots in populations in relation to all dwarf shoots varied even more strongly among the populations, but the ranking of the populations is unchanged (Table 3). The correlation of the frequency of abnormal dwarf shoots in populations with latitude of origin is weak (r = 0.381).

Influence of altitude

The highest frequencies of three-needle dwarf shoots and frequencies of specimens with three-needle dwarf shoots among *Pinus mugo* populations are found in the samples from the top portion of altitudinal ranges of the species (Fig. 3). The frequency of specimens with abnormal dwarf shoots and frequency of abnormal dwarf shoots are both positively, strongly statistically significantly correlated with position in the altitudinal range of the species (Pearson's r = 0.9923 and r = 0.9744 respectively). They are also positively but weak correlated with recalculated altitudes (r = 0.5855 and r = 0.5010).

The percentage of individuals with abnormal dwarf shoots and the frequency of abnormal dwarf shoots among studied samples of *P. mugo* exhibit rather non-linear, polynomial relationship with altitude (Figs 4A and B). The correlations appear to be slightly more significant at higher elevations.

Variation in time

Two populations of *Pinus mugo* from the Karkonosze Mts. were examined for 2 and 3 years (see Table 1). The frequency of specimens with three-needle dwarf shoots in samples collected in the same populations varied from year to year, but was relatively high each year in comparison to the other sampled populations of the species (Table 3, samples 1-3 and 4-5).

Abnormal dwarf shoots among populations of Pinus uncinata

Geographic differentiation

The frequency of trees with at least one three-needle dwarf shoot exceeded 20% among the 376 specimens of *Pinus uncinata*. The frequency of trees exhibiting more than 50% abnormally developed dwarf shoots per specimen are greater in this taxon than in *P. mugo* (Table 2). Consequently, the probability of finding of three-needle dwarf shoots on *P. uncinata* is greater than *P. mugo* (Table 2).

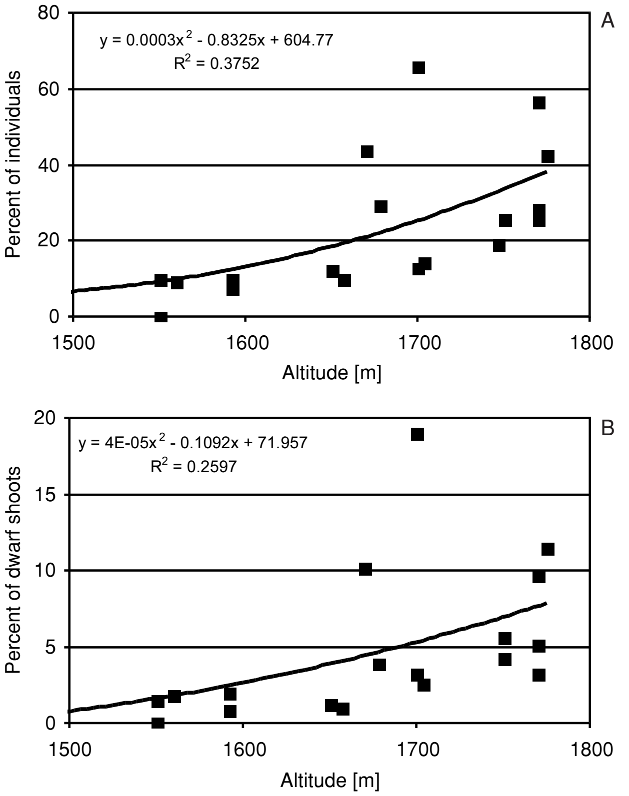

Fig. 4. Relationships of the frequency of *Pinus mugo* individuals with three-needle dwarf shoots (A) and three needle dwarf shoot (B) in particular populations and its altitudinal origin.

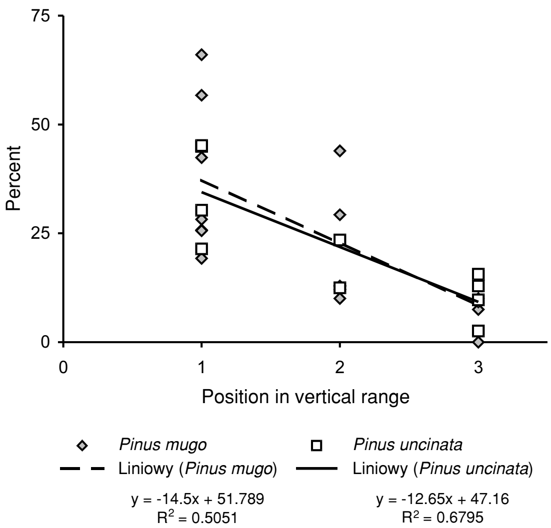

Fig. 3. Frequency of specimens with three-needle dwarf shoots of *Pinus mugo* and *P. uncinata* from the upper (1), central (2) and lower (3) parts of the altitudinal range of the species.

Samples of all the analyzed populations of *Pinus uncinata* contain at least a few specimens with an atypical number of needles on dwarf shoots. The lowest frequency of such trees is found in Belagoa in the West Pyrenees and Vall de Linares in the Sierra de Gudar (Table 3). The highest frequencies of trees with abnormal dwarf shoots are found in the Central Massif and in the East Pyrenees, with a maximum at 45% in Coll de Croix de Morand in France and in Vall de Ransol in Andorra (Table 3). The highest frequencies of three-needle dwarf shoots in the samples are recorded at the northern limit of the range of this species, as in the case of *P. mugo*. The southernmost and westernmost populations were characterized by a significantly lower number of specimens with abnormally developed dwarf shoots. Neither the frequency of specimens with abnormal dwarf shoots nor the presence of abnormal dwarf shoots among samples correlate strongly with latitude (Pearson's r = 0.2789 and r = 0.2987, respectively).

Influence of altitude

The populations of *Pinus uncinata* from the upper limit of the species have greater numbers of specimens with three- (or more)needle dwarf shoots than populations at lower altitudes (Fig. 3). The frequency of specimens containing abnormal dwarf shoots and the frequency of abnormal dwarf shoots in the population with position in altitudinal range correlates positively and strongly statistically significantly (Pearson's r = 0.8602 and r = 0.9205, respectively). The frequency of specimens containing abnormal dwarf shoots and the frequency of abnormal dwarf shoots in the population are each strongly correlated with the recalculated altitudes of the sampled populations (r = 0.7538 and r = 0.8288 respectively). The relationships are non-linear (polynomial), and for the lower altitudes are slightly negatively correlated, whereas for the mid and upper portions of the altitudinal range the correlations were strongly positive (Figs 5A and B).

Variation in time

The population of *Pinus uncinata* from Vall de Nuria in the East Pyrenees was examined in 1999 and 2001 (Table 1, samples no 21 and 22). The frequency of three-needle dwarf shoots varied between years, but was significantly higher compared to the other studied populations of the species (Table 3).

Morphological characteristics of needles from more than two-needle dwarf shoots

Needle length

As compared to two-needle dwarf shoots, the length of needles from the three-needle dwarf shoots are more variable (variation coefficient 12-21%). The needles from three-needle dwarf shoots are generally somewhat shorter. The average difference between the lengths of the needles from two- and three-needled dwarf shoots is at about 1-2 mm and is statistically insignificant (Table 4). Also needles from four-needle dwarf shoots are shorter than those of two-needle dwarf shoots, but the number of such dwarf shoots was to small to be compared statistically.

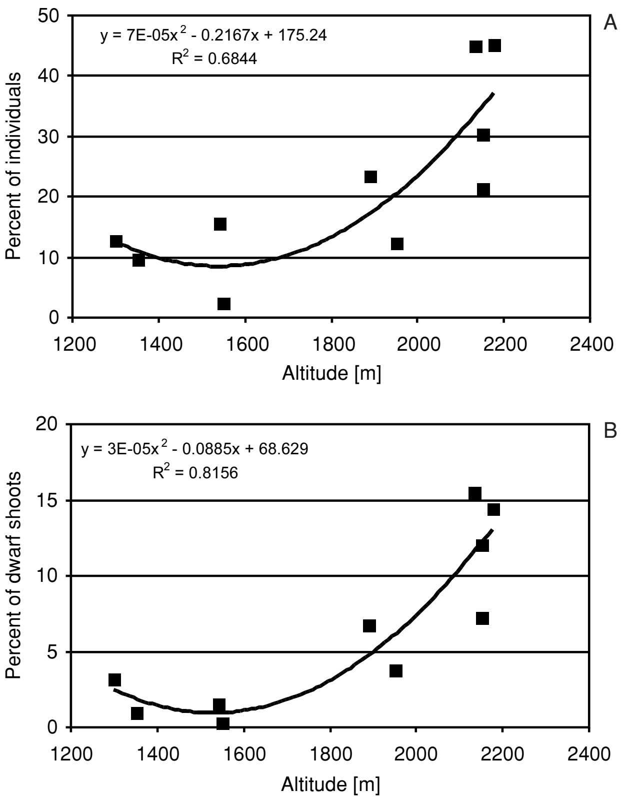

Fig. 5. Relationships of the frequency of *Pinus uncinata* individuals with three-needle dwarf shoots (A) and three needle dwarf shoots (B) in particular populations and its altitudinal origin.

TABLE 4. Length of needles from two- and three-needle dwarf shoots of *Pinus mugo* and *Pinus uncinata*.

Species	Population	Two-needle dwarf shoots / Three-nedle dwarf shoots			t	p
		X [mm]	δ	V		
Pinus mugo	10	54.3	6.8138	12.54	0.9414	0.3567
		51.3	8.1172	15.81		
	15	48.7	6.1733	12.67	0.5017	0.6205
		47.4	6.8773	14.51		
Pinus uncinata	20	76.7	12.9861	16.93	0.3437	0.7356
		74.4	13.8910	18.68		
	21	57.9	6.8178	11.78	0.6015	0.5537
		56.2	6.4983	11.57		
	22	62.7	7.8.091	12.46	0.5667	0.5746
		61.2	7.4494	12.17		
	24	61.4	13.4710	21.96	0.0324	0.9752
		61.0	12.9637	21.26		
	25	63.5	9.2336	14.55	0.5574	0.5861
		61.0	7.0702	11.59		

X – average length (arithmetic mean)
δ – standard deviation
V – variation coefficient
t – Student's t-test value
p – probability level

Needle cross-section

Morphological and anatomical differences between needles from two- and three-needle dwarf shoots are observed in the shape of the cross-section. The needles from two-needle dwarf shoots are semicircular in cross-section, whereas the needles from three-needle dwarf shoots are nearly triangular.

Each of the needles within the four-needle dwarf shoots is of the same length or the two marginal needles are significantly longer than the central ones. In the first type of four-needle dwarf shoot, needles are nearly triangular in cross-section, so that the four needles together form a circle (Fig. 6A). In the second type (with needles of different length), the larger marginal needles are crescent-shaped in cross-section, whereas the shorter central needles are semicircular to triangular (Fig. 6B).

The needles from five-needle dwarf shoots vary considerably in length, thickness and shape of cross-section even within the same dwarf shoot. The marginal needles are usually longer and semicircular, whereas the central needles are significantly shorter, more slender and have various shapes of cross-sections: from triangular to quadrangular or somewhat ovate (Figs 6C and 6D). The needles from the only six-needle dwarf shoot (found on *Pinus uncinata* in Central Massif) also vary in length, thickness and shape of cross-section (Fig. 6E).

DISCUSSION AND CONCLUSIONS

The analysis of the frequency of dwarf shoots with more than two needles among the taxa studied shows that they

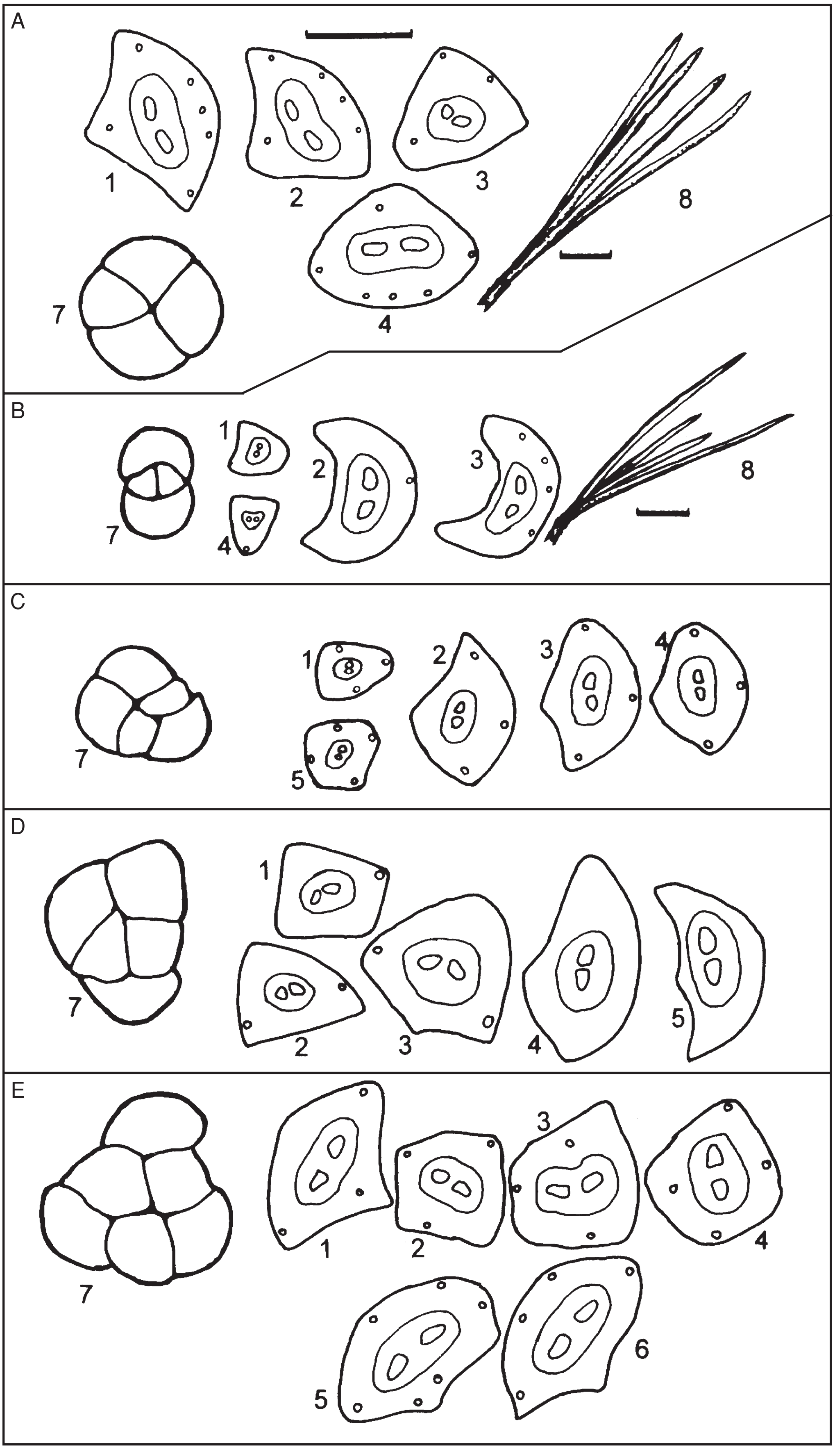

Fig. 6. The shape of cross-section of the needles and its composition on the dwarf shoot: A – 4-needle dwarf shoot with the needles of the same length (*Pinus uncinata* from population No 29); B – 4-needle dwarf shoot with needles of various length (*Pinus uncinata* from population No 27); C – 5-needle dwarf shoot (*Pinus mugo* from population No 1); D – 5-needle dwarf shoot (*Pinus uncinata* from population No 20); E – 6-needle dwarf shoot (*Pinus uncinata* from population No 29); 1-6 needles; 7 – scheme of the needles composition on dwarf shoot; 8 – scheme of dwarf shoot.

appear in *Pinus mugo* and *P. uncinata*. All the other taxa either do not have three-needle dwarf shoots at all, as in the case of *P. nigra* (1 population) and *P. uliginosa* (2 populations), or the frequency of three-needle dwarf shoots is to low to be detected, as in *P. sylvestris* (1 specimen in 6 populations) and *P. pinaster* (1 specimen in 1 population). However, even single specimens with three-needle dwarf shoots confirm literature records of the occurrence of abnormal shoot on normally two-needle pine species in Europe (Penzig 1922; Klaus and Zetter 1978).

It can be also concluded, that the three- to six-needle dwarf shoots are formed most frequently on specimens of the *Pinus mugo* complex, including *P. mugo*, *P. uncinata* and *P. uliginosa* (Christensen 1987a). Abnormal dwarf shoots have been found on specimens of *P. mugo* and *P. uncinata*, but not on *P. uliginosa*. Perhaps this is related to the low altitude of the studied populations of *P. uliginosa* (about 200 and 700 m), as compared with the studied populations of *P. mugo* and *P. uncinata* (see Table 1). The taxonomic relationship to *P. sylvestris* may also possibly explain the lack of abnormal numbers of needles in dwarf shoots on *P. uliginosa*. This taxon shows intermediate characteristics between *P. mugo* and *P. sylvestris* (see for example Staszkiewicz and Tyszkiewicz 1972; Bobowicz 1990; Staszkiewicz 1994; Siedlewska and Prus-Głowacki 1995; Prus-Głowacki et al. 1998; Lewandowski et al. 2000).

The majority of specimens with abnormal dwarf shoots on *Pinus mugo* and *P. uncinata* are found at the upper limits of the ranges of these species in the mountains, which is in consistent with observations of Christensen from herbaria review (1987b). High frequencies of abnormal dwarf shoots are also found in the northernmost populations of the *P. mugo* complex in the Carpathians and the Sudeten Mts. However, both populations of *P. uliginosa* are exceptions to this rule, although they are the northernmost among the studied populations of the *P. mugo* complex.

The three-needle specimens of *Pinus mugo* have not been reported from the Dynarian Alps and from the southern part of Balkan Peninsula (Christensen 1987b). They have not been found in the Vitosha Mts. in the present study. Our material from Balkan Peninsula is insufficient to state that specimens with abnormal numbers of needles in dwarf shoots are absent in Balkan portion of the species range. It should be noted, however, that the frequency of specimens bearing three-needle dwarf shoots is significantly lower in the south-eastern portion of the range of *P. mugo* than in the northern portion. In the Abruzzi Mts. specimens with three-needle dwarf shoots are also not so frequent as in the Carpathians – Sudeten range (Table 3).

The high frequencies of abnormal dwarf shoots have repeated in samples collected over 2-3 years in the same populations. This may indicate that formation of three-needle dwarf shoots is genetically conditioned and perhaps characteristic for local populations of *Pinus mugo* and/or *P. uncinata*. The differences among frequencies of abnormal dwarf shoots in particular years in the populations analyzed may be due to collecting samples from different individuals. Also the impact of environmental conditions should be taken into consideration, but this issue should be the subject of more detailed research on permanent plots and marked individuals in the future.

The three-needle dwarf shoots on *Pinus sylvestris* seedlings result from regeneration after mechanical damage (Szymański 1958; Giertych 1968). This should be checked experimentally in the case of *P. mugo* and *P. uncinata*. All individuals of these species from which the material for the present study was collected had no visible injuries or symptoms of disease.

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WYSTĘPOWANIE KRÓTKOPĘDÓW *PINUS MUGO* I *P. UNCINATA* O NIETYPOWEJ LICZBIE IGIEŁ

STRESZCZENIE

Badano częstotliwość występowania nietypowych, trzyigłowych (lub więcej) krótkopędów na naturalnych stanowiskach południowo- i środkowoeuropejskich gatunków sosen dwuigłowych. Nie znaleziono okazów z nietypowymi krótkopędami w analizowanej populacji *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco z Półwyspu Iberyjskiego, ani w dwóch populacjach *P. uliginosa* Neumann (= *P. rotundata* Link) z Sudetów i ich przedpola w środkowej Europie. Pojedyncze osobniki z trzyigłowymi krótkopędami znaleziono w jednej analizowanej pod tym względem populacji *P. pinaster* Aiton z Półwyspu Iberyjskiego oraz sześciu populacjach *P. sylvestris* L. z Półwyspu Iberyjskiego i środkowej Europy. Nietypowe brachyblasty, najczęściej z trzema, ale także z czterema, pięciu lub sześciu igłami, znaleziono na wielu okazach w 24 na 25 badanych pod tym względem populacjach *P. mugo* Turra i *P. uncinata* Ramond. Przeciętny udział osobników z przynajmniej jednym trzyigłowym krótkopędem na jeden długopęd wynosił 24% w grupie 694 badanych okazów *P. mugo* i 20% w grupie 376 okazów *P. uncinata*. Analizowane populacje różniły się istotnie pod względem częstotliwości występowania osobników z nietypowymi krótkopędami. Największym udziałem takich osobników odznaczały się populacje pochodzące z górnych partii zasięgów gatunków. Częstość występowania nietypowych krótkopędów utrzymywała się na wysokim poziomie w kolejnych 2-3 latach obserwacji w jednej badanej pod tym względem populacji *P. uncinata* i w 2 populacjach *P. mugo*. Igły z trzyigłowych krótkopędów były przeciętnie krótsze (statystycznie nieistotnie) od igieł z krótkopędów typowych, niezależnie od gatunku.

SŁOWA KLUCZOWE: *Pinus mugo*, *Pinus uncinata*, zróżnicowanie morfologiczne, zmienność morfologiczna, nietypowe krótkopędy, brachyblasty, Europa.