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Original Research

How Environmental Signals Affect Frequency of Three-Needle Dwarf Shoots on *Pinus mugo*

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Abstract

The main aim of our study was to verify the influence of climatic factors on the formation of abnormal 3-needle dwarf shoots in the two-needle *Pinus mugo*. Twenty individuals of the species, which had at least one abnormal brachyblast in 2002, have been studied in the Tatra Mountains (Carpathians) and an additional 20 in the Giant Mountains (Sudetes) over a period of 11 years. The number of atypical dwarf shoots in both populations in particular years was correlated to temperatures during the period of initiation and determination of apical meristems. Three-needle dwarf shoots appeared to occur every year in most of the studied individuals. It also showed positive correlation with (1) average, (2) absolute maximum, and (3) minimum average monthly temperatures of late autumn two years, and early winter one year, before emergence from the bud.

Keywords: gymnosperms, plant ecology, plant variation, climate influence, shoot apical meristem

Introduction

Pinus mugo Turra belongs to the subgenus *Pinus* (=*Diploxylon*), section *Pinus*, subsection *Sylvestres* (=*Pinus*) of the genus *Pinus* [1]. The subsection in Europe, except the dwarf mountain pine, also includes *Pinus sylvestris* L., *P. uncinata* Ramond, and *P. nigra* Arnold [1, 2], and is characterized by two-needle dwarf shoots and two vascular bundles within the needle. Seven of the fifteen species of subsection *Sylvestres* have the three-needle and/or two- and three-needle dwarf shoots, most of them occuring in southeast Asia [1]. The number of needles on the dwarf shoot is an important character to understand the evolution of the pines from subgenus *Pinus*. The oldest Cretaceous fossil leaves of pines containing two vascular bundles were reported from Japan. Interestingly, these leaves were found growing on the three- or four-needle dwarf shoots [3]. This finding and occurrence of three-needle pines in East Asia suggests evolution by reduction of number of leaves on dwarf shoots during the settlement of Europe, as taxa of subgenus *Pinus* arrived there from East Asia [3-5]. The occurrence of anomalous, mostly three- but sometimes even up to six-needle dwarf shoots on the European two-needle pines was reported as exceptional [6-19]. It is considered as (1) an occasionally manifested, primitive character inherited from the ancestral taxa [9, 14] or (2) a reaction to mechanical injuries of buds [11, 15]. The reaction of some seedlings of *P. sylvestris* to bud elimination was, *inter alia*, the formation of three-needle dwarf shoots in the following year [11]. Similarly, the three-needle dwarf shoots on *P. sylvestris* appeared as a reaction to the damage of buds by insects [15]. The occurrence of three-needle dwarf shoots in natural conditions on *Pinus mugo* and the related *P. uncinata* was reported from a dozen

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Table 1. Development of long shoot of *Pinus sylvestris* (on the basis of data of Hejnowicz [20]).

Years	Month	Development of terminal bud										
		Terminal scales	Dormancy	Bud scales	Bud elongation	Scales supporting dwarf shoots	Dwarf shoot buds	Scales supporting lateral buds	Lateral buds	Needle primordia	Dormancy	Bud elongation (shoot emergence)
Year of shoot emergence from the bud	V											■
	IV											■
	III										■	
	II										■	
	I										■	
Year before shoot emergence from the bud	XII										■	
	XI									■		
	X									■		
	IX						■		■	■		
	VIII				■		■	■	■			
	VII				■	■	■					
	VI				■	■	■					
	V			■	■	■						
	IV			■								
	III		■									
	II		■									
	I		■									
Two years before shoot emergence from the bud	XII		■									
	XI	■										
	X	■										
	IX	■										
	VIII											

locations within their natural ranges [6, 7, 9, 10, 12-14, 17-19]. Around 18% of *P. mugo* and about 19% of *P. uncinata* individuals had at least one three-needle dwarf shoot [7].

The greatest numbers of individuals with three-needle dwarf shoots were found in the upper portion of the vertical range of *P. mugo*, close to their altitudinal limit [7, 9]. The two populations of *P. mugo* sampled twice in different years in the Sudety Mts. had high but different frequencies of individuals with three-needle dwarf shoots every year [6, 7]. This seems to indicate the possible genetically determined potential to form three-needle dwarf shoots in response to specific environmental conditions, probably year-to-year climate changes.

The formation of abnormal dwarf shoots takes place during bud formation resulting from the shoot apical meristem (SAM) activity. Development of SAM and time of initiation of dwarf shoot meristems on *P. mugo* have not been investigated, and we adopted data concerning the closely related *P. sylvestris* [20]. The apical meristem of dwarf shoots on *P. sylvestris* is initiated during bud formation (Table 1), about sixteen to eighteen months before their emergence from the bud [20, 21]. We hypothesize that the number of anomalous dwarf shoots shall probably be modified by an environmental factor within that time.

The aim of the present study was to verify the hypotheses that:

(1) the presence of three-needle dwarf shoots is exhibited by individuals for a number of consecutive years, and
(2) the percentage of three-needle dwarf shoots in the same population in a particular year partly depends on the climatic conditions of the period, when the dwarf shoot meristem is determined and initiated.

Table 2. Characteristics of investigated populations of *Pinus mugo*.

Acronym	Location	Altitude [m]	Time-span of investigation	Number of individuals	Climate data source/altitude [m]
SUD	Sudetes, Giant Mountains (Karkonosze Mts)., Równia below Śnieżka	1,400-1,420	(1996) 1998-2002	20	Śnieżka/1603
			2003-06		
			2007-08		
TATRA	Carpathians, Tatra Mts., N slope of Grześ-Wołowiec	1,600-1,700	(1996) 1998-2002	20	Kasprowy Wierch/1987
			2003-06		
			2007-08		

Material and Methods

Plant Material

We studied two populations of *Pinus mugo*, the first in the Tatra Mountains (West Carpathians), the second in the Karkonosze (Giant Mountains, Sudetes) (Fig. 1, Table 2), both recognized as containing numerous individuals with three-needle dwarf shoots [7]. Twenty individuals in each population manifesting several three-needle dwarf shoots on the youngest long shoot were chosen in the field. The individuals chosen were at least 40 m apart to avoid possible sampling of the same genet twice [22, 23].

One apical, upright shoot containing longitudinal increments from 1998/2002, 2003/06, and 2007/08 was examined from the illuminated canopy part of every individual. The live span of *Pinus mugo* needles lasts more than 4 years in the Karkonosze and even more than 5 years in the Tatra Mountains [24]. This allows us to verify the presence/absence of atypical dwarf shoots retrospectively, up to 4-5 years ago (Fig. 2). The field investigations were conducted in September 2002, 2006, and 2008.

Fig. 1. Location of: – examined populations of *Pinus mugo* (dots) in the Karkonosze (Giant) (1) and in the Tatra Mountains (2); – related meteorological stations (triangles) on the Śnieżka (1) and Kasprowy Wierch (2).

Following the different time of determination and initiation of dwarf shoot primordia on the lower, central and apical parts of the long shoot during bud formation [20], the expected period of environmental factor influencing the formation of atypical dwarf shoots on these parts shall also be earlier on the low, and later at the apical part of the long shoot. For this reason the dwarf shoots were examined on the basal, central, and apical part of long shoots separately, for every year longitudinal increment. Consequently, 60 dwarf shoots were examined to describe the long shoot of each of 11 years on every individual. The basal and apical parts of yearly increments of the long shoots were studied starting from the base and top of a yearly increment, respectively. The 20 dwarf shoots were examined in turn, and three-needle dwarf shoots were counted. Afterward, the central part of a yearly increment was determined and the next 20 dwarf shoots were examined (Fig. 2B). The limits of yearly increments were detected using a branch ramification and by searching for lower bud scales or their traces (Fig. 2A, D). In total, 418 yearly increments of long shoots and 26,280 dwarf shoots were examined in both populations, among them 4,618 atypical, mostly three-needle ones (Fig. 2C).

Climatic Data

The influence of average monthly temperature (T) and sum of monthly precipitation (PR) as potential long-lasting stress sources was assessed. Additionally, the possibility of short duration impact was tested using average maximum monthly temperature (TMAX), absolute maximum monthly temperature (ATMAX), average minimum monthly temperature (TMIN) and absolute minimal monthly temperature (ATMIN). The climatic data for the Giant Mountains came from the Mt Śnieżka (E15º44'23", N50º44'11", 1602 m alt.), and for the Tatra from the Kasprowy Wierch (E19º58'58", N49º13'56", 1,940 m alt.) climatic stations (Fig. 1). The influence of climatic factors was tested during the two years preceding the emergence of dwarf shoots from the bud.

Statistical Treatment

Data covering a period of 11 years permit a statistical examination of the results. The statistical verifications, carried out after the first and second series in 2002 and 2006, gave approximately similar results.

The influence of individual trees, part of a long shoot and years of emergence of needles from the bud on the number of three-needle dwarf shoots, was tested using analysis of variance (ANOVA). The interaction of the year of dwarf shoot emergence with the number of anomalous dwarf shoots was also verified using analysis of frequencies in Chi^2 distribution [25].

The possible influence of five climatic factors (T, TMAX, ATMAX, TMIN, ATMIN, and PR) for particular months of two and one years before the emergence of yearly increment from the bud to the number of abnormal dwarf shoot was analyzed using Pearson's correlation coefficient [25].

The mathematical comparisons and calculations were made using STATISTICA and JMP software.

Table 3. Results of ANOVA test.

Source	DF	F Ratio	Prob>F
Year	10	6.34	<0.0001
Population	1	2.43	0.1197
Year * population	10	2.89	0.0014
Level of long shoot	2	125.19	<0.0001
Year * level of long shoot	20	5.07	<0.0001
Population * level of long shoot	2	3.05	0.0477
Year * population * level of long shoot	20	0.46	0.9806

Results

Occurrence of Abnormal Dwarf Shoots in Particular Years

Every individual formed three-needle dwarf shoots in more than six or seven years during the eleven years of observation of both tested populations. The occurrence of three-needle dwarf shoots between 1998 and 2008 on particular individuals, independent of amount, fluctuated between 54.5 and 100% in the Tatra, and 72.7 and 100% in the Karkonosze (Giant) Mountains, and on average was 88.2 and 87.3%, respectively.

The average percentages of three-needle dwarf shoots was not stable, and differed between years at a statistically significant level in both studied populations (Table 3). Interaction between year and population was statistically significant, but the changes of percentages of three-needle dwarf shoots in subsequent years have a similar character in the Karkonosze (Giant) and Tatra Mountains, and were correlated at a statistically significant level (Fig. 3).

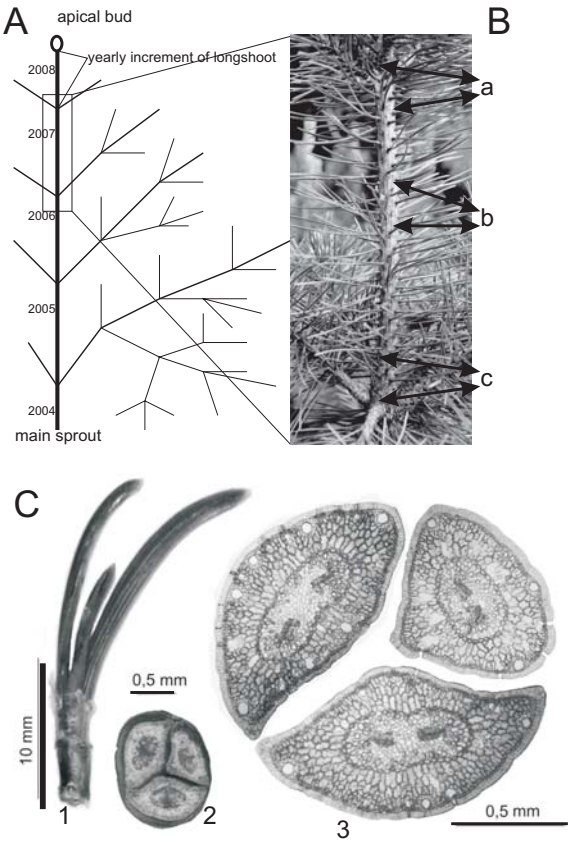

Fig. 2. Scheme of main shoot of *Pinus mugo* (A) with marked longitudinal yearly increments during the last four years of field studies (2005-08); (B) – longitudinal increment of *P. mugo* individual from 2007 with description of dwarf shoot counting from apical (a), central (b), and basal parts (c); (C) – atypical, three-needle dwarf shoots of *Pinus mugo* (after Boratyńska and Jasińska [44]): 1 – dwarf shoot, 2 – cross-section of basal part, 3 – cross-section of central part of the needles.

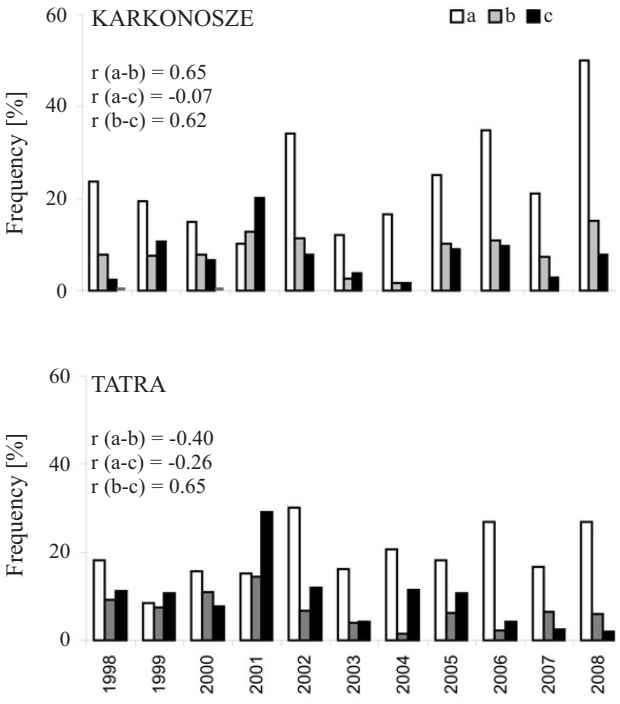

Fig. 3. Frequencies of three-needle dwarf shoots of *Pinus mugo* in the Tatra and Karkonosze (Giant) Mountains from 1998 to 2008: a – apical, b – central, c – basal parts of yearly increments; r – correlation coefficients between frequencies of three-needle dwarf shoots from apical, central, and basal parts of yearly increments.

Allocation of Abnormal Dwarf Shoots on Yearly Increment

The percentages of abnormal dwarf shoots on the basal, central and apical regions of long shoots differed for particular individuals. Also, dependences of the number of three-needle dwarf shoots on population and allocation on the long shoot were statistically significant, but at a lower level (Table 3). Generally, the highest numbers of three-needle dwarf shoots were found on the apical parts of the long shoots in both the Tatra and Karkonosze (Giant) Mountains (Figs. 3 and 4). Only a few individuals in the Tatra Mts. have the highest or at least a high number of three-needle dwarf shoots at the basal part of the yearly increment for some of the years (data not shown). The exception was the year 2001, when the percentages of three-needle dwarf shoots on the basal part of the yearly increment were higher than at the apical in both populations (Fig. 4).

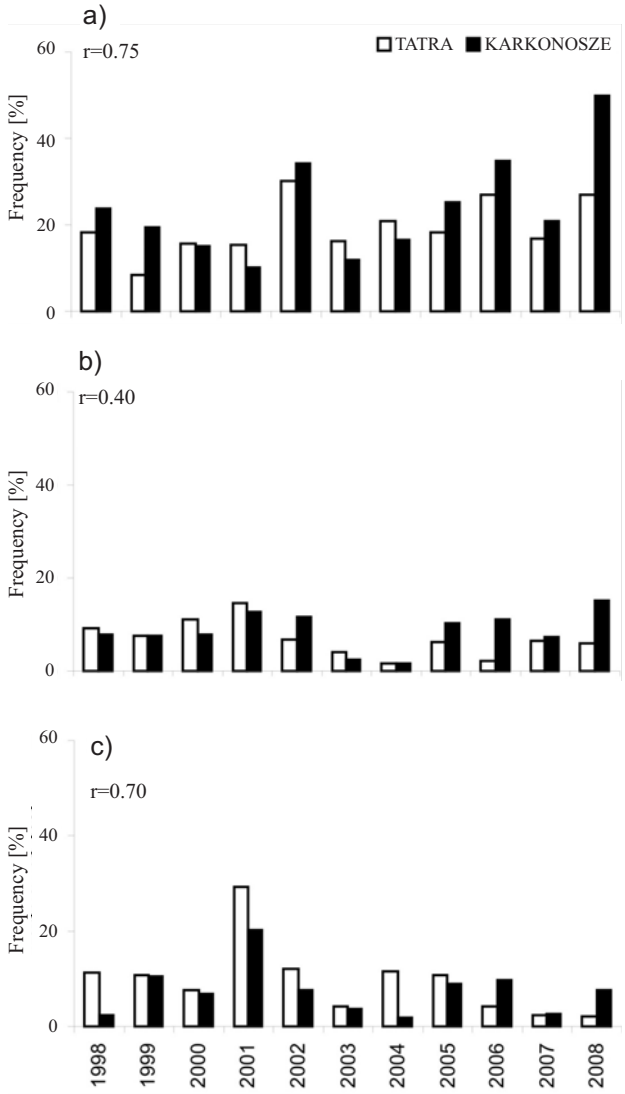

Fig. 4. Frequencies of three-needle dwarf shoots in apical (a), central (b), and basal (c) parts of yearly increments of *Pinus mugo* in the Tatra and Karkonosze (Giant) Mountains from 1998 to 2008; r – correlation coefficients between data from the Tatra and Karkonosze Mts.

The percentages of three-needle dwarf shoots from the apical and central, as well as from basal and central parts of the yearly increment, correlated at a statistically significant level (Fig. 4), but the latter were more closely connected. For that reason the data sets for the basal and central parts of the yearly increment were merged for subsequent analyses.

Climatic Factors

The percentage of three-needle dwarf shoots at the apical part of the yearly increment in the Karkonosze (Giant) Mountains is positively correlated with average (T), average maximum (TMAX), and average minimum (TMIN) temperatures of November and December two years before emergence from the bud (Fig. 5). In the Tatra this dependence is not as clear. The percentages of abnormal dwarf shoots on the apical part of long shoots were correlated there at a statistically significant level with average (T), average maximum (TMAN), and average minimum (TMIN) monthly temperatures of December two years before emergence from the bud (Fig. 5).

The second temperature signal in the Karkonosze Mountains appears in April and October of the year preceding the year of emergence from the bud, and concerns only one of the percentages of three-needle dwarf shoots at the basal and central parts of the yearly increment. This signal is not observed in the population from the Tatra Mountains, where a negative influence of average (T) and average minimum (TMIN) temperatures of July of the preceding year (Fig. 5) is found. In the Karkonosze Mountains this tendency is also negative, but not significant (Fig. 5).

The absolute minimum temperatures (ATMIN) significantly correlated with the percentage of three-needle dwarf shoots only in the Karkonosze Mountains. The percentages of abnormal dwarf shoots at basal and central parts of the yearly increment seem to depend on absolute minimum temperature (ATMIN) of November two years, and of October one year before emergence from the bud. The number of three-needle dwarf shoots at the apical part of the yearly increment is positively correlated with ATMIN of December two years and January one year before emergence from the bud. The negative correlation with ATMIN of May a year before emergence from the bud is also observed (Fig. 5).

Precipitation in March a year before emergence from the bud correlated positively with the percentage of three-needle dwarf shoots at basal and central parts of the yearly increment in both tested populations. Additionally, it was also connected with October precipitation, but in the Tatra Mountains only. The percentage of three-needle dwarf shoots at the apical part of the yearly increment correlated positively at a statistically significant level with September precipitation a year before, but only in the Karkonosze Mountains (Fig. 5).

Discussion

The high repeatability of the occurrence of three-needle dwarf shoots on the same individuals (Table 2) confirms the genetic ability to produce three-needle dwarf shoots, as an ancestral character [9, 14, 26]. However, in several pines reported from the Miocene and Pliocene of West and Central Europe, recognized as possible ancestors of *P. mugo* and *P. uncinata* [2, 5, 27, 28], mostly cones, pollen, and sometimes long shoots without dwarf shoots were reported. The lack of fossil materials does not allow the testing of this hypothesis. Nevertheless, the East-Asiatic origin of extant European pines [2, 3] suggests the possible contribution of an ancestor with three- and even four-needle dwarf shoots [3]. Additionally, East Asia currently maintains several pine species related to *P. mugo*, which have three, or two and three needles on their dwarf shoots [1, 4, 29].

In spite of high repeatability, the number of three-needle dwarf shoots is expressed with various intensities in particular years, as a reaction to more or less favourable conditions for their determination and initiation during organogenesis and bud formation by SAM. The coincidence between percentages of three-needle dwarf shoots on *P. mugo* in the Tatra and Karkonosze Mountains (Fig. 4) indicates a synchronized formation of highest numbers of three-needle dwarf shoots, which suggests a reaction of both populations to climate conditions, similar to the reaction of the annual growth of ring width, utilized in dendrochronological investigations [30-32]. The synchronized formation of highest numbers of three-needle dwarf shoots at basal and not apical parts of a

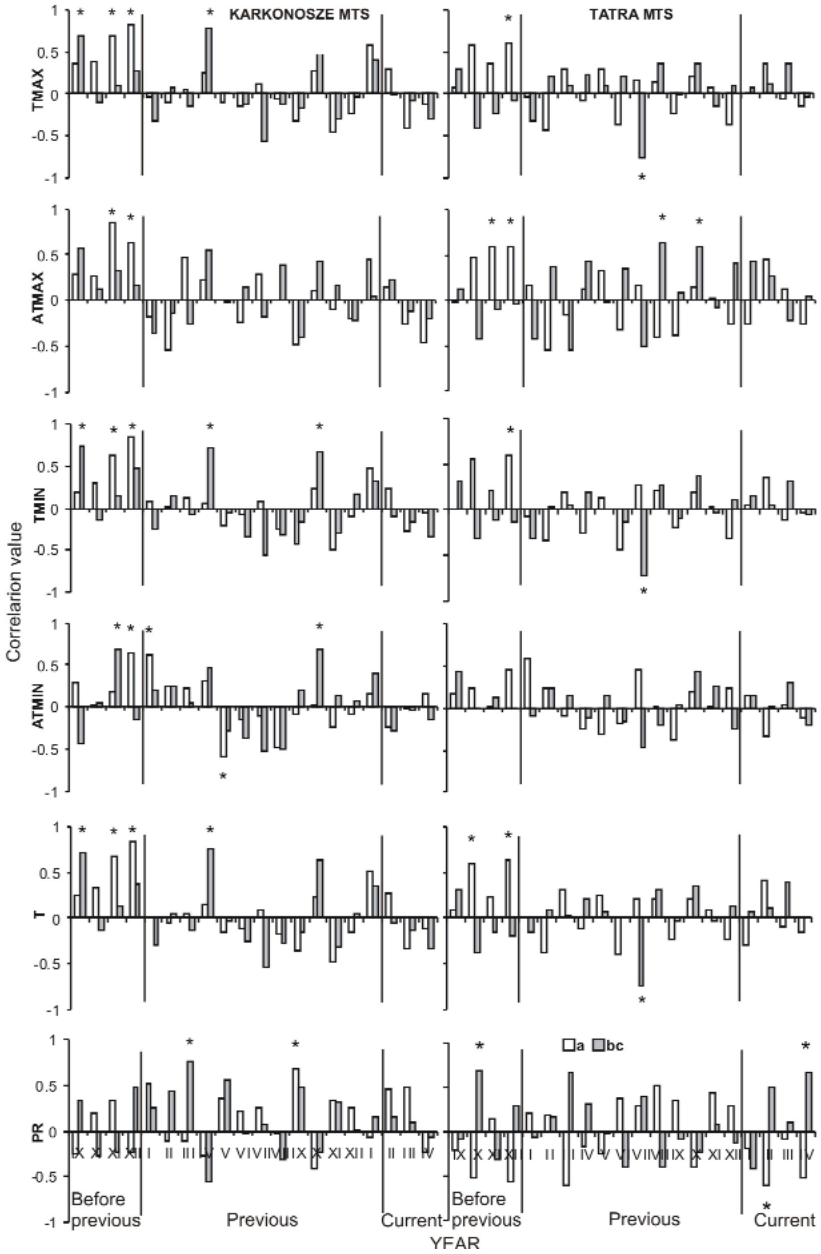

Fig. 5. Relations between frequencies of three-needle dwarf shoots on yearly increments of *Pinus mugo* in the Tatra and Karkonosze (Giant) Mountains with climate factors of before previous, previous, and current year of emergence from the buds; * – correlations statistically significant (p=00.1).

yearly increment emerged from the bud in 2001 by both populations confirms this suggestion (Fig. 4). In conclusion, we can state that the ability to produce the abnormal dwarf shoots could be a genetically determined ancestral character, but their expression in particular years is modified by environmental conditions during bud formation.

The organogenesis and formation of vegetative buds of coniferous trees of the Pinaceae take place during the preceding vegetation season [20, 21, 26, 33, 34]. We expected that climate conditions of this period could be a reason for abnormal dwarf shoot initiation, but surprisingly the high correlation of numbers of three-needle dwarf shoots with higher than normal temperatures of the late month of autumn and first months of winter 2/1 years before emergence of the needles from the bud seems to indicate that such temperatures are the most influential of the environmental factors (Fig. 5). During that period SAM in the most apical part of the bud is just in the deep dormancy stage (Table 1). It will start to form the apical bud of the next yearly increment in the spring and summer [20, 21, 35].

The higher temperatures of the winter two years before could also be treated as a climatic signal, similar to dendrochronological studies [30, 32, 36]. It seems, however, that this signal might not be received directly by SAM, which during the winter months is reduced to a small number of cells and characterized by dormancy and limited hormonal activity [20, 21, 35, 37]. The more probable hypothesis explanation seems to be the perception of signals by older parts of the bud and then transmission from mature tissues, as suggested in the case of phyllotaxis [38, 39]. The significant correlations of numbers of three-needle dwarf shoots with temperatures of October, November, and December two years before emergence of the sprouts from the bud can also suggest the possibility of predetermination by gene expression in the particular cells of SAM [34, 40-42], which will start to produce the primordia and dwarf shoot meristems about seven to eight months later, but both these last ideas are more speculations at present and shall be verified in a separate study.

The expected dependence of percentage of abnormal dwarf shoots on *P. mugo* to the thermic anomalies reflected with absolute and average monthly temperatures (TMAX, ATMAX, TMIN, and ATMIN), and to the precipitation (PR) of June or July of the year before emergence of the needles from the bud is not clear. The statistically significant negative dependence of number of dwarf shoots on the basal parts of the yearly longitudinal increment of the branches on average (T), average maximum (TMAX), and average minimum (TMIN) monthly temperatures of July is marked only in the population from the Tatra Mts. A similar tendency is also observed in the population in the Karkonosze Mts, but without statistical significance. This dependence could indicate that SAM reacts to the lower than normal temperatures, but we probably possess too short a data set, and during a period longer than 11 years clearer correlations might be reasonabily expected. Additionally, we can state that the period of initiation of dwarf shoot meristem inside the apical bud of *P. mugo* in the mountains is slightly delayed in comparison with *P. sylvestris* [20, 21].

The highest average percentages of abnormal dwarf shoots were observed at the apical part of the yearly increment of shoots during the years 1998/2008, except for 2001 (Fig. 3). The apical part of long shoots was also the place of the highest numbers of three- and four-needle (and even more than four-needle) dwarf shoots on *P. sylvestris* in France [10]. This suggests that:

(1) organogenesis of the apical part of a yearly increment takes place during a period with a higher possibility of occurrence of conditions promoting their determination and/or initiation,
(2) the environmental signal that takes place before organogenesis (see above) is predominantly not accepted in that part of SAM, when the basal and central parts of the yearly increment would be formed and transmitted to the apex.

The exceptional 2001 in our study period, when the highest frequency of three-needle dwarf shoots appeared at the basal part of long shoots, was also different from all the others in terms of climate conditions. Reviewing the climate data of the autumn/winter months two years preceding the needle emergence we found that September was characterized by high temperatures (T, TMAX, TMIN) when compared with other years. Afterwards, from October, the temperatures were significantly lower than the average for these months during other years. Additionally, the winter of 1999/2000 was colder than normal and with low precipitation and snow cover. All these events suggest the possible earlier influence on determination of dwarf shoots with three needles than in the other years and, consequently, their location at the basal parts of long shoots. It is also possible that the inverse position of abnormal dwarf shoots in 2001 results from high solar activity [43], but this shall be examined in a more detailed study on the observations overlapping periods of more solar cycles.

Conclusions

In summary:

(1) The individuals forming the abnormal dwarf shoots in one year would repeat this character over the next few years with high probability.
(2) The percentage of abnormal dwarf shoots on any individual in particular years depends on the higher temperatures of the winter before, and lower temperatures during the period of organogenesis of dwarf shoots.
(3) The apical parts of SAM are the most frequently exposed to the influence of temperatures that cause the formation of abnormal dwarf shoots during the winter before the period of organogenesis.

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