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Authors: Solár, Jaroslav, and Janiga, Marián

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Long-term Changes in Dwarf Pine (*Pinus mugo*) Cover in the High Tatra Mountains, Slovakia

Jaroslav Solár* and Marián Janiga
** Corresponding author: solar@uniza.sk*
Institute of High Mountain Biology, University of Zilina, Tatranska Javorina 7, Zilina 05956, Slovakia

The present article focuses on the distribution of Pinus mugo *under conditions in the central Tatra Mountains, the main mountain range of the Western Carpathians. We analyze the response of* P. mugo *distribution to selected abiotic habitat conditions in the eastern Tatra Mountains. The study also compares data on the distribution of* P. mugo *in the higher central Tatras and in the hills of the western Tatras published in previous studies. The source data for this study were aerial photographs from 3 periods (1955, 1986, and 2002). Mountain areas covered by mountain pine were identified and analyzed by ArcGIS 10, and pine fields were classified with the help of the gray scale mode. A strip of mountain pine above the upper limit of the forest represents an easily identifiable boundary on the aerial photographs: 25 well-recognized localities were selected to examine the changes in the tree line in the eastern Tatras. The distribution of mountain pine increased in the central granite and eastern limestone Tatra Mountains from 1955 to 2002 at all monitored sites. The percentage of total surface area covered in* P. mugo *increased from 28.11% in 1955 to 34.74% in 1986 and to 39.01% in 2002. The study also analyzes the dispersal of mountain pine over 40 years in relation to elevation, slope, radiation aspect, flow accumulation, and vertical and horizontal curvature. The results of this study explain ongoing vegetation changes and are of importance as a contribution to monitoring of climate change in the mid-European mountain areas.*

Keywords: Pinus mugo*; Abiotic habitat conditions; land use change; climate change; Carpathians; Slovakia; Poland.*

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Introduction

High mountain ecosystems are unique areas for detection of climate change and assessment of climate-related impacts (Beniston 2003). The main ecological driving force is climate, with temperature and the duration of the snow cover as key factors (Gottfried et al 1999). Climate change associated with global warming is more pronounced at higher elevations than at low elevations (Beniston and Rebetez 1996; Diaz and Bradley 1997; Giorgi et al 1997). The effect of elevation on surface warming is especially marked in the winter and spring seasons because it is mostly associated with a decrease in snowpack and is thus enhanced by the snow–albedo feedback (Giorgi et al 1997). Changes in air temperature can extend the length of the average annual growing season (Menzel and Fabian 1999) and can also cause a shift in phenology (Parmesan and Yohe 2003; Visser and Both 2005). Many studies show that high mountain ecosystems are vulnerable to climate change (eg Theurillat and Guisan 2001; Dullinger et al 2003a, 2003b; Dirnböck et al 2011). Climate change mainly affects the distribution of plant and animal communities (Beckage et al 2008), and, under expected climate scenarios, in the final perspective, results in the loss of rare species of alpine habitats (Dirnböck et al 2011). In global meta-analyses by Parmesan and Yohe (2003) and Root et al (2003), significant range shifts toward the poles or toward higher altitudes were documented for many organisms. Large parts of these changes may be attributed to increased global temperatures. In general, we expected that climate-related changes in mountain ecosystems would be most pronounced in the "ecoclines" (boundary ecosystem) or the ecotones (Theurillat and Guisan 2001).

Scenarios of upward plant species and vegetation shifts have been widely discussed in many research articles. Theurillat and Guisan (2001) published a review that discusses this matter and concludes that, although the alpine vegetation can tolerate an increase of 1–2°C of average air temperature, in the case of a sharper increase, we can expect major changes. Dullinger et al (2012) showed that projected extinctions of high-mountain plants under 21st century climate change have a significant long-term component, and they also believe that endemic Alpine species seem to face the highest range losses. Loss of diversity in alpine communities and fragmentation of plant populations caused by climate warming is expected for comparable high mountain areas around the world (Grabherr et al 1995; Saetersdal et al 1998). Results from Dirnböck et al (2003) support the hypothesis that alpine plant species above the forest line will be affected by heavy fragmentation and habitat loss but only if the average annual temperature increases by 2°C or more. The loss of most of these Alpine plant species habitats is expected to be caused by the expansion of *Pinus mugo* in the Alpine zone. The same species of alpine heaths are declining due to expanded dwarf pine, for example, *Carex sempervirens*, *Agrostis rupestris*, *Festuca supina,* and others. Growth and fertility of *P. mugo* is mostly controlled by temperature (Dullinger et al 2004). Thus, the main limiting factor of *P. mugo* growth at high altitudes could be the soil temperature (Smith et al 2003), although Rossi et al (2007) refer to varying soil temperature thresholds at different sites, which indicates that soil temperature may not be the main factor that limits xylogenesis of conifers and provides strong evidence that air temperature is a critical factor that limits xylem cell production and differentiation at high altitudes. However, the air temperature alone may not be the dominant factor that determines the tree-line position, because the direct influence of temperature may be masked by interactions with other factors, such as precipitation, cold-induced photoinhibition, disturbance, or plant–plant interactions (Harsch et al 2009). This evidence, therefore, is inconclusive. Differences in expert opinions on this matter have led Smith et al (2009) to formulate 6 current hypotheses about the causes of upper tree-limit movement: climatic stress, mechanical disturbance, insufficient carbon balance, limitations in cell growth and tissue formation, limited nutrient supply, and limited regeneration. In the global meta-analyses by Parmesan and Yohe (2003) and Root et al (2003), significant range shifts toward the poles or toward higher altitudes were documented for many organisms. Large parts of these changes may be attributed to increased global temperatures. The expansion of tree-line–forming species (subalpine zone) to higher altitudes is evident in the Pyrenees (Camarero and Gutiérrez 2004; Peñuelas et al 2007), in the Alps (Dullinger et al 2003a, 2003b; Gehrig-Fasel et al 2007; Vittoz et al 2008), in the Carpathians (Mihai et al 2007; Martazinova et al 2009; Švajda et al 2011), and also in Sweden (Kullman 2002) and Caucasus (Akatov 2009).

Generally, climate conditions and land use in high mountain areas have been shown to influence the distribution of mountain pine. The potential model of timberline is based on the assumption that climate change as a factor in forest regeneration is primarily responsible for moving the upper limit of the natural forest above the original climatically determined timberline, whereas the abandonment of farming in the country is assumed to be the dominant factor that determines forest regeneration below this line. The aim of this study was analysis of mountain pine cover in the central and eastern Tatra Mountains and of the abiotic conditions significantly related to *P. mugo* increments.

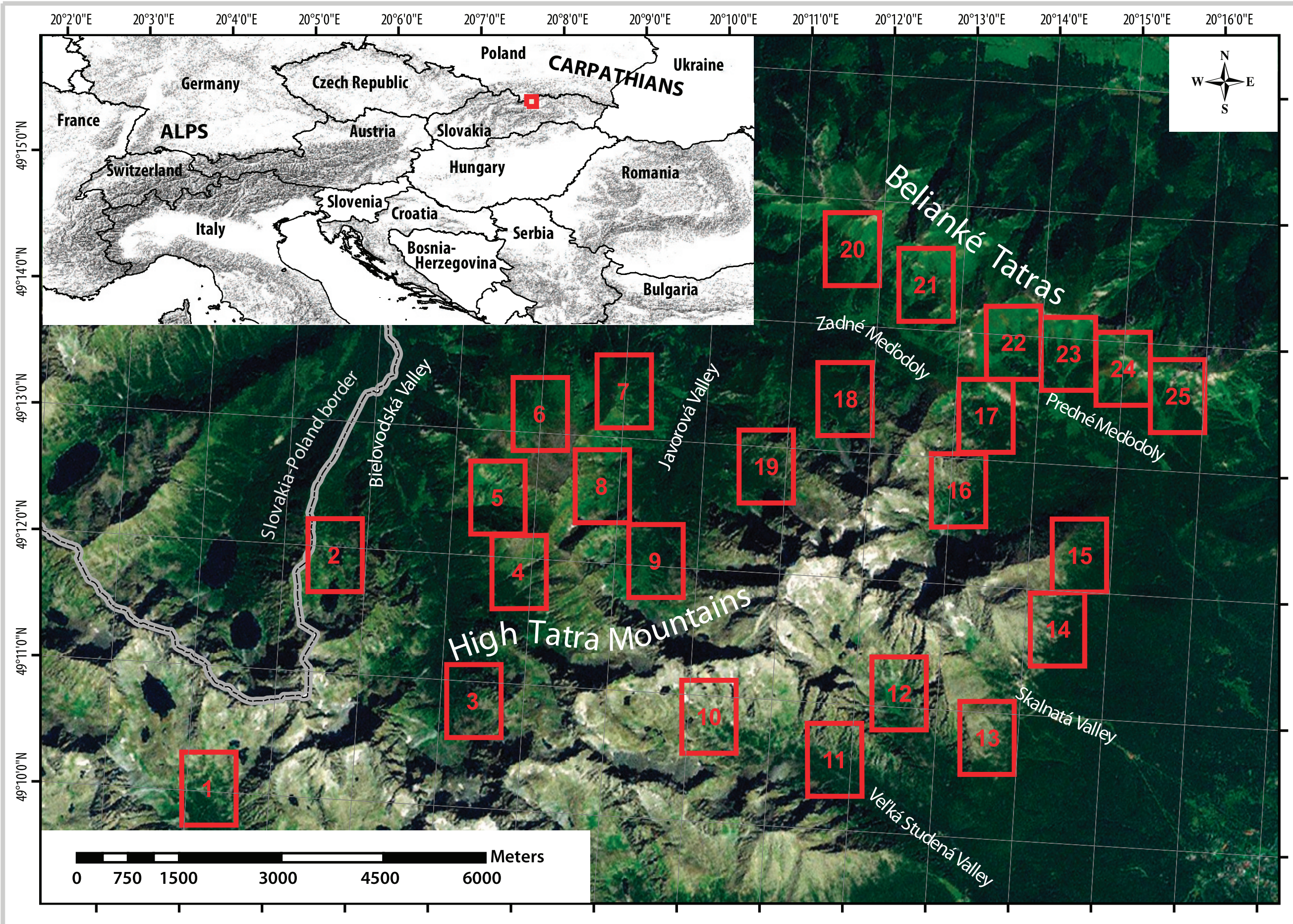
Study area

The Tatra Mountains are situated at the Slovak–Polish border (20°11′E; 49°11′N) and are the highest mountain massif within the Carpathian Range of Central Europe. The highest summit reaches 2656 m; the massif is classified as a high-mountain landscape covered by subalpine and alpine zones. The study area (Figure 1) is situated in the central and eastern Tatra Mountains, composed of the high Tatras and Belianské Tatras. The geology of the study area is based on crystalline bedrock. The high Tatra Mountains contain from significant biotite tonalities to granodiorites, and locally porphyritic and also porphyritic granodiorites to granites. The Belianské Tatras contain various shales, sandstones and dolomites, dark limestones, and quartzites (Biely et al 2002).

The vegetation of the Alpine zone is dominated by Alpine meadows (dry tundra with mostly *Festuca picturata*, *Luzula alpino-pilos*a, *Calamagrostis villosa*, and *Juncus trifidus*), with patches of dwarf pine (*P. mugo*) and an increasing percentage of rocks (bare or covered with lichens, commonly *Rhizocarpon*, *Acarospora oxytona*, and *Dermatocarpon luridum*) above the upper tree line of 1800 m (Vološčuk 1994).

The average annual air temperature decreases with elevation by 0.6°C per 100 m, being 1.6 and 23.8°C at elevations of 1778 and 2635 m, respectively (Konček and Orlicz 1974). The amount of precipitation increases as elevation rises, varying from approximately 1.0 to approximately 1.6 m/y between 1330 and 2635 m but reaching >2.00 m/y in some valleys (Chomitz and Šamaj 1974). Precipitation is generally higher in the northern part than in the southern part of the mountains, as is runoff, which averages 1.42 and 1.57 m/y for the south and north, respectively (Lajczak1996). Snow cover usually lasts from October to June at elevations >2000 m. The climate-driven tree line in the Tatra Mountains is located at approximately 1550 m and partly includes natural ecotones, with individual conifers that reach ages of 350–450 years (Büntgen et al 2007). *P. mugo* is an obligatory prostrate pine with adult canopy height that varies between 0.3 and 2.5 m in the study area. The typical dwarf pine altitudinal (subalpine) zone extends from 1500 to between 1850 and 1900 m. Mountain pine zone developed especially in the western Tatras with glacial–meadow relief, with great antierosion and water retention potential. Closed mountain-pine thickets stretch up to 300 m above the timberline, which reaches approximately 1600–1750 m in the Tatras and encompasses the upper part of the forest alpine tundra ecotone. Mountain pine plays a significant role in the natural environment: it protects the soil and stabilizes the snow cover, thus restricting the release of avalanches, and it provides habitats for many species of flora and fauna (Jodowski 2006).

FIGURE 1 Central and eastern Tatra Mountains in Slovakia and detailed view of the 25 sites in the study area (from west to east: Mengusovská, Bielovodská, Litvorová, Rovienková valleys, Litvorový žlab, Široká, Javorová, Veľká Studená, Malá Studená, Skalnatá, Huncovská, Kolová valleys, Dolina Bielych plies, Zadné and Predné Meďodoly). (Map by Jaroslav Solár)



Material and methods

The present analysis was carried out by using geographic information system (GIS) (ArcGIS 10), based on aerial photographs from 1955, 1986, and 2003. The aim of the analysis was to verify temporal trends in the distribution of *P. mugo* and to investigate which environmental variables best explain the changes in the growth and distribution of the mountain pine. The applied modeling approach is based on 3 major assumptions: (1) the abiotic factors are assumed to be the major driving force of species distribution changes as well as of postgrazing succession, (2) rhe models are calibrated by using field data and thus comprise any competitive constraint a species may force upon or experience from its neighbor, (3) the speed of plant migration is consistent with that of climate change so that plant communities are in a permanent equilibrium with their environment (Dirnböck et al 2003).

Aerial images from 2002 had a reference system (s-jtsk); aerial photographs from 1986 and 1955 (without reference system) were georeferenced on the basis of orthophotos (Table 1). For our analysis, we selected 25 localities from the study area. The main factor in selection of study localities was spatial distribution of *P. mugo* with respect to a variety of abiotic conditions and shadowed areas on the aerial photographs. Mountain pine fields were extracted according to Švajda et al (2011) from the aerial photos in gray scale and then reclassified into the range that represents mountain pine occurrence in the study area. Each photo was examined individually. If mountain pine on the slide was gray, with a value from 75 to 110, all such values in the range were reclassified as 1 (pine cover). The remaining values from 0 to 75 and 110 to 256 were reclassified as 0 (no pine cover). Intervals for segmentation were separately fixed for each image on the previous identification of pixel values that represented patches of mountain pine. We created a grid in which each pixel contained either the value 1 or the value 0. Then, the grid was automatically vectorized on the basis of the 2 values (Figure 2).

Habitat conditions were spatially simulated by using GIS, a digital elevation model, meteorological data, and existing maps. The most significant factors that explain

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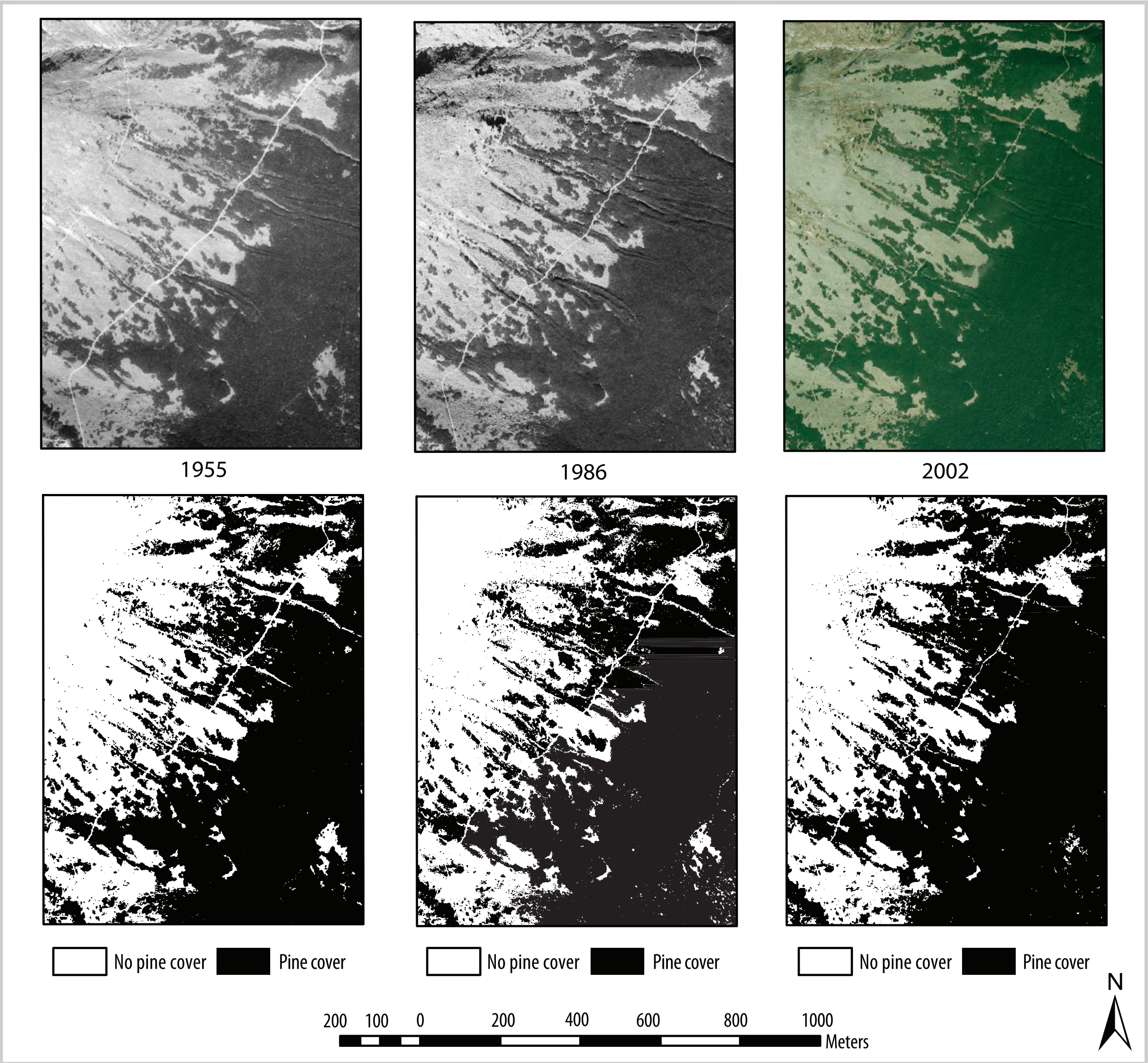
TABLE 1 Quality and resolution of data features (aerial imagery).[a)]

Year	Source	Type	Resolution	Width (px)	Height (px)	Format
2002	Eurosense Slovakia	Orthophoto	RGB 72 DPI	2500	2000	.jpg
1986	Topographical Institute	Aerial photo	Gray 1200 DPI	11,015	11,065	.tiff
1955	Topographical Institute	Aerial photo	Gray 1200 DPI	8805	8286	.tiff

[a)]DPI, dots per inch; RBG, red/blue/green.

FIGURE 2 Example of the comparison between aerial photographs: Changes between 1955, 1986, and 2002 in 1 analyzed valley (Site 14, Huncovská Valley; see Figure 1).



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the presence of *P. mugo* according to Dirnböck et al (2003) are the daily temperature, followed by slope, geology, solar radiation in September, and duration of snow cover. To test this hypothesis, it was necessary to create an explicit temporal and spatial model of the spread of mountain pine and to analyze their sensitivity to predicted climate change trends. The size of the pixels' (cell) grid was equivalent in all images, because each image was adjusted to the same cell size through the transformation of the grid as well as during georeferencing. Thus, all images and the grids had the same pixels. A digital elevation model of the study area was used for representation of selected abiotic habitat conditions. Finally, we created a grid (25 × 25 m) from raster maps of abiotic conditions overlaid with maps of mountain pine cover. Each square represented a row in the database, with unique values to identify number, site number, cover of mountain pine (1955, 1986, 2003), elevation, slope, orientation, radiation, water flow, and horizontal and vertical curvature. GIS intersection of study sites divided the sites studied into 23,526 smaller areas with unique characteristics related to pine increase. Two sites (nos. 3 and 11) (Table 2) were excluded due to the lack of data from 1986. A single matrix was analyzed. Independent variables were as follows: elevation (m); slope (degree); radiation as the whole energy of solar radiation in the vegetation period from May to November (watt hours per square meter); aspect (degree); flow accumulation, accumulated flow to each cell as determined by accumulating the weight for all cells that flow into each downslope cell; vertical curvature, curvature of the surface perpendicular to the slope direction (a positive value indicates that the surface is upwardly convex at that cell; a negative plan indicates that the surface is upwardly concave at that cell), horizontal curvature, and curvature of the surface in the direction of slope (a negative value indicates the surface is upwardly convex at that cell; a positive profile indicates the surface is upwardly concave at that cell). Dependent variables were expressed as relative increments of mountain pine during observed periods 1955–1986 (relative increments of mountain pine from 1955 to 1986 in m^2) and 1986–2002 (relative increments of mountain pine from 1986 to 2002 in m^2).

The increments in mountain pine were reported as means and standard deviations for potential comparison with other studies, but the values showed a highly skewed distribution in most sample groups. Therefore, a nonparametric approach to analysis of the data was necessary. The significance of differences between groups was tested by using the Kruskal–Wallis nonparametric test. When $P < 0.05$, the data were considered as significantly different. The principal component (PC) analysis, correlation matrix, a multivariate technique, was used to extract the potential relationships between the variables studied. Principal components are linear combinations of original variables (slope, elevation, radiation, flow accumulation, vertical curvature, horizontal curvature, and relative increase of pine during observed periods), each axis being statistically orthogonal to the others. Integration of the variables slope and elevation (m) in different periods enabled us to follow different processes of mountain colonization by mountain pine during the respective periods. Because this statistical technique produces statistically orthogonal axes, we were able to examine potentially independent biological phenomena. We used 8 variables; consequently, we evaluated 8 principal components. The proportions of the total variance accounted for by each component are shown in Table 3 (see results).

Results

Mountain pine cover in the Tatra Mountains in the period 1955–2002 increased permanently at all observed sites (Figure 3). The total surface area covered by mountain pine increased from 5,542,975 m^2 in 1955 to 6,850,096 m^2 in 1986 and 7,693,706 m^2 in 2002. The percentage of total surface area covered thus increased from 28.11% in 1955 to 34.74% in 1986 and 39.01% in 2002 (Table 2). The results also indicate that the mean increase in mountain pine surface cover for all periods was approximately 0.2% per year (0.21% first period, 0.27% second period) for the total surface area, but results in relation to selected abiotic conditions still showed some differences.

From 1955 to 1986, mountain pine cover probably increased in areas that were subject to grazing. It is likely that this is determined by the PC1 component (Table 3). Mountain pine in the earlier period expanded mainly at lower altitudes with lower slope and expanded in the ridge portions of these areas (vertical versus horizontal curvature). The effect of intensive growth of mountain pine occurred in the period 1955–1986. In the later period (1986–2002), this effect decreased (PC1) (Table 3). PC1 can be designated as a factor in the ingrowing of mountain pine areas in the lower parts of the mountains, mainly due to abandoned grazing (Figure 4A, B). PC2 (Table 3) is a factor that mainly describes the variability of dwarf pine growth rates in both periods. This happened in the ridge portions of the mountains. The phenomenon of scattering of mountain pine on ridges is especially significant on the western slopes of hills (Figure 5A). Therefore, we can conclude that mountain pine tended to spread very intensively, mainly on the western and southwestern ridges of the central and eastern Tatra Mountains. The spread of mountain pine on the western ridges is significantly different from that on the eastern ridges (Figure 5A). PC3 and PC4 are the factors that primarily reflect the mutual variability of the abiotic variables. PC5 (Figure 5B; Table 3) mainly describes the trend in the growth of mountain pine in the later period,

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TABLE 2 Overview of evaluated sites with different *P. mugo* cover for the period 1955–2002. (Table extended on next page.)

Site no.	Average altitude (m)	Average radiation (WH/m^2) a)	Average slope (%)	Average aspect	Average flow accumulation
1	1735	907629.89	21.24	S	212.38
2	1746	798794.24	27.03	SE	78.59
3 b)	–	–	–	–	–
4	1660	910550.80	29.32	SW	79.97
5	1692	881711.55	34.14	SW	30.60
6	1760	790060.64	26.73	S	51.83
7	1722	830735.81	32.97	S	7.76
8	1824	867867.65	30.96	SE	33.45
9	1623	735408.87	26.48	SW	169.72
10	1948	947361.80	22.41	SE	52.82
11 b)	–	–	–	–	–
12	1735	809751.40	30.06	S	222.63
13	1787	973826.05	31.89	SE	8.02
14	1717	979786.59	26.71	E	33.11
15	1765	927649.73	31.21	SE	11.95
16	1714	897250.13	28.50	SE	87.06
17	1731	899534.74	20.76	E	33.36
18	1663	866169.28	23.33	SW	42.90
19	1696	874048.11	29.96	SW	84.36
20	1666	949842.72	30.71	SW	15.91
21	1713	965495.43	29.78	SW	18.49
22	1743	914520.33	25.69	SE	26.59
23	1660	936022.74	24.51	S	74.05
24	1754	960325.66	29.56	S	13.20
25	1669	975446.08	27.43	S	18.37
All	1727	895643.05	27.89	S	61.18

a)WH/m^2, watt hours per square meter.

b)Excluded.

where the effect of mountain pine expansion is visible due to better conditions with enough water. This relates to expansion of mountain pine to territory with a higher altitude.

Component PC6 (Figure 5C) is relatively important for understanding of differential scattering of mountain pine in different periods. It shows the spread of mountain pine by slope, independent of altitude. For mountain pine, steeper places were more suitable in the earlier period, and, therefore, it expanded from more level areas onto steeper positions. In the later period, 1986–2002, mountain pine colonized more level places. This effect also differs according to the aspect (Figure 5C). The "steeper slope" strategy of pine growth known in the earlier period was southerly oriented (compare Figure 4C), whereas the "level strategy" from the years 1986–2002 was westerly oriented (compare Figure 4D). A combination of the necessary amounts of hours of daylight and proper temperatures is probably very important for the spread of pine. In the second period,

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TABLE 2 Extended. (First part of Table 2 on previous page.)

Site no.	Covered with *P. mugo* (%)			Difference (+ or −)
	1955	1986	2002	
1	42.79	47.01	47.17	+3.6 / +0.1
2	16.20	18.63	20.49	+2.1 / +1.5
3 b)	–	–	–	–
4	31.78	43.05	48.29	+9.6 / +4.4
5	10.57	15.58	23.08	+4.3 / +6.4
6	21.35	28.76	35.95	+6.3 / +6.1
7	37.11	42.99	48.87	+5.0 / +5.0
8	8.66	11.78	11.90	+2.6 / +0.1
9	42.93	46.91	51.00	+3.4 / +3.5
10	4.74	6.23	6.73	+1.2 / +0.4
11 b)	–	–	–	–
12	11.90	16.84	18.73	+4.2 / +1.6
13	26.40	32.83	36.71	+5.5 / +3.3
14	54.92	57.48	59.30	+2.1 / +1.5
15	39.52	48.43	51.53	+7.6 / +2.6
16	19.94	22.40	24.50	+2.1 / +1.8
17	31.75	41.38	46.83	+8.2 / +4.6
18	39.06	46.88	53.40	+6.7 / +5.5
19	43.82	47.78	54.43	+3.3 / +5.7
20	38.75	50.10	55.71	+9.7 / +4.8
21	17.76	31.79	43.83	+12 / +10
22	9.51	15.52	17.91	+5.1 / +2.0
23	34.29	48.95	54.39	+12. / +4.6
24	22.89	29.63	35.94	+5.7 / +5.4
25	39.92	47.95	50.64	+6.8 / +2.3
All	28.11	34.74	39.01	+5.6 / +3.6

when mountain pine extended to the north, northwest, and western areas, it was distributed mainly in the more level places. This effect is also independent of altitude. Obviously, north–west and westerly orientations once again play an important role, which allows the species to spread to less favorable habitats. The PC7 and PC8 components describe the intervariability among climatic factors, which is not significantly related to the growth of pine. We also tested regression analysis–related components with a dependent variable (*P. mugo* increments), but this regression analysis is not shown because it led to the same results.

Discussion and conclusion

At high altitudes, vegetation is under constant environmental stress and thus abiotic conditions become more important for community development than biotic relationships (Pauli et al 1996). Körner (2003) defined 3 components that affect the cold climate of alpine plants:

TABLE 3 Principal component (PC) vectors (loadings) and percentage variance associated with the components, which indicate the pattern of natural reforestation with mountain pine in the eastern and central Tatra Mountains (n = 13,594; snaps from aerial photographs).

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Eigenvalue	1.891	1.351	1.162	0.939	0.890	0.673	0.587	0.507
% Total variance	23.634	16.891	14.525	11.743	11.125	8.415	7.333	6.334
Cumulative eigenvalue	1.891	3.242	4.404	5.343	6.234	6.907	7.493	8.000
Cumulative %	23.634	40.525	55.050	66.793	77.919	86.333	93.666	100.000
Elevation	0.748	−0.233	−0.064	0.104	0.297	−0.095	0.129	−0.507
Radiation	0.464	0.111	0.214	0.802	−0.067	−0.122	0.055	0.248
Slope	0.446	−0.071	−0.695	−0.022	0.263	0.409	0.062	0.268
Flow accumulation	−0.393	−0.203	0.525	0.045	0.645	0.220	0.234	0.091
Vertical curvature	0.540	0.411	0.298	−0.386	−0.233	0.041	0.485	0.106
Horizontal curvature	−0.593	−0.300	−0.418	0.223	−0.194	−0.139	0.522	−0.066
Pine increment (1955–1986)	−0.316	0.728	−0.045	0.286	−0.066	0.439	0.019	−0.296
Pine increment (1986–2002)	−0.141	0.670	−0.295	−0.060	0.465	−0.468	0.029	0.066

solar radiation, slope and exposure, and plant stature. Additional components that modulate the interplay of the 3 main drivers are wind velocity; ambient air temperature above the vegetation; and soil properties such as surface structure, moisture, and thermal conductivity.

Dwarf pine is a tree species that is well adapted to high variability of climatic conditions in the high mountains. The most significant factors that explain the presence of *P. mugo* are the daily temperature, followed by slope, geology, solar radiation in September, and duration of snow cover (Dirnböck et al 2003). Dispersal of pine in the central and eastern Tatra Mountains is westerly oriented. The air temperature increases gradually during the day, and, by comparison with eastern slopes, when westerly oriented slopes are exposed to the sun, the temperature is usually high, the snow melts, and mountain pine have enough heat, water, and sunlight for photosynthesis. The onset of photosynthetic functions depends mainly on weather conditions in early spring (Lehner and Lütz 2003), when wood cell production starts in April and May, followed by maximum cell production in June–July (Büntgen et al 2007). The autumn effects (September) may also play an important role in pine development (Dirnböck et al 2003). A combination of precipitation, temperature, and the timing of snow melt is evidently responsible for early pine wood production. Water supply is important during the first part of the growing season (Büntgen et al 2007). In the main chain of the Tatra Mountains, the western aspect and westerly oriented slopes seem to be crucial for effective dispersal of this wood species.

Similar to other high mountains, the Carpathians can show climate change trends and possible shifts of vegetation types with altitude. Climate development can to some extent affect phenological trends (Bauer 2006; Škvareninová 2008), which reflect the changing climate conditions. The onset of individual phenological stages and their progress is mainly influenced by air temperature as well as temperature and humidity of soil and other meteorological variables (Škvareninová 2009). Over the past 50 years, summer temperatures in the Tatra Mountains have increased by 0.7°C at higher elevations and by 1.4°C at lower elevations. Winter temperatures have increased by 1.4°C at higher elevations and by 1.9°C at lower elevations (Melo 2005). The temperature limit of the mountain pine zone is determined by the biotemperature threshold in the range of 3.0 to 2.0°C (maximum °C to minimum °C) (Miňdáš et al 2003). When considering the rate of the current temperature change (2–3°C in 100 years), we can expect more changes in

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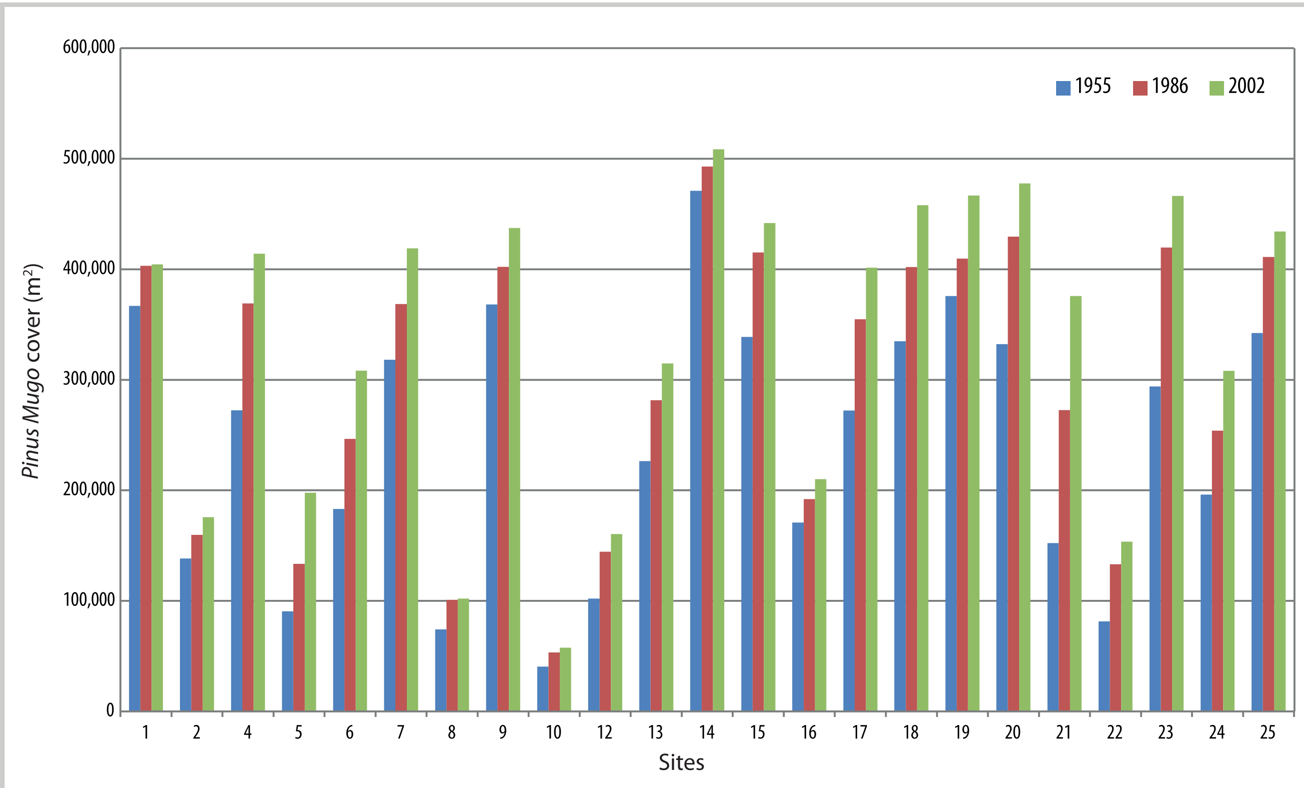
FIGURE 3 Comparison of area covered with *P. mugo* (23 sites) in 1955, 1986, and 2002, in m^2.



growth within a single generation of woody plants. According to Miňdáš et al (1996), a model scenario predicts complete extinction of conditions for some alpine communities and their replacement by subalpine forest bioclimatic conditions.

The results of our study confirm the results of previous research in the western Tatra Mountains (Švajda et al 2011). Mountain pine permanently increased throughout the Tatra Mountains. Statistical analysis of thematic maps of the Tatra Mountains from 1949 to 2003 by Boltižiar (2007) suggests extension of mountain pine cover, advance of forest, and reduction of grassland areas. Martazinova et al (2009) conducted research on grasslands above the upper forest limit in the Ukrainian Carpathians. Grass cover significantly decreased at the sites with conifers. Spruce stands moved to higher altitudes, mainly on the northern slopes, whereas the beech stands in the same area on the southern slopes did not show any significant movement. Apparently, the greatest changes were recorded at those sites where upper forest limit was marked at higher elevations. In a study of alpine, subalpine, and forest landscapes in the Iezer Mountains (Southern Carpathians), Mihai et al (2007) described how mountain pine–subalpine associations developed and gradually covered subalpine meadows and barren land (between 1986 and 2002, colonization averaged 0.14 km^2/y). However, the mountain pine area has lost some lower stands because of spruce forests, which increased in elevation. This is largely a feature of southern aspect slopes (sunny), where the natural timberline is higher under some local conditions. Another example from the Austrian Alps (Dullinger et al 2004), which ran a model with projections for 1000 years, predicted that the area covered by pines will increase from 10% to between 24% and 59% of the landscape studied. The shape of the dispersal curve and spatial patterns of competitively controlled recruitment suppression affect range size dynamics at least as much as does variation in assumed future mean annual temperature (between 0 and 2°C above the current mean). Moreover, invasibility and the shape of the dispersal curve interacted with each other due to the spatial patterns of vegetation cover in the region.

Upward pine shifts above the potential regional tree line will be primarily influenced by climate change (Gehrig-Fasel et al 2007), whereas upward shifts below the potential regional tree line are usually interpreted as primarily influenced by land abandonment. Dullinger et al (2003a) indicated that a shift of tree and shrub species caused by land use and expected climate change can be expected in the European Alps. Abandonment of pasture will allow invasive expansion of *P. mugo* scrubs to new areas. Our study clearly offers the field data for time scheme prognoses in the Alps, because pasturing in the central Tatras was forbidden and abandoned in the 1950s.

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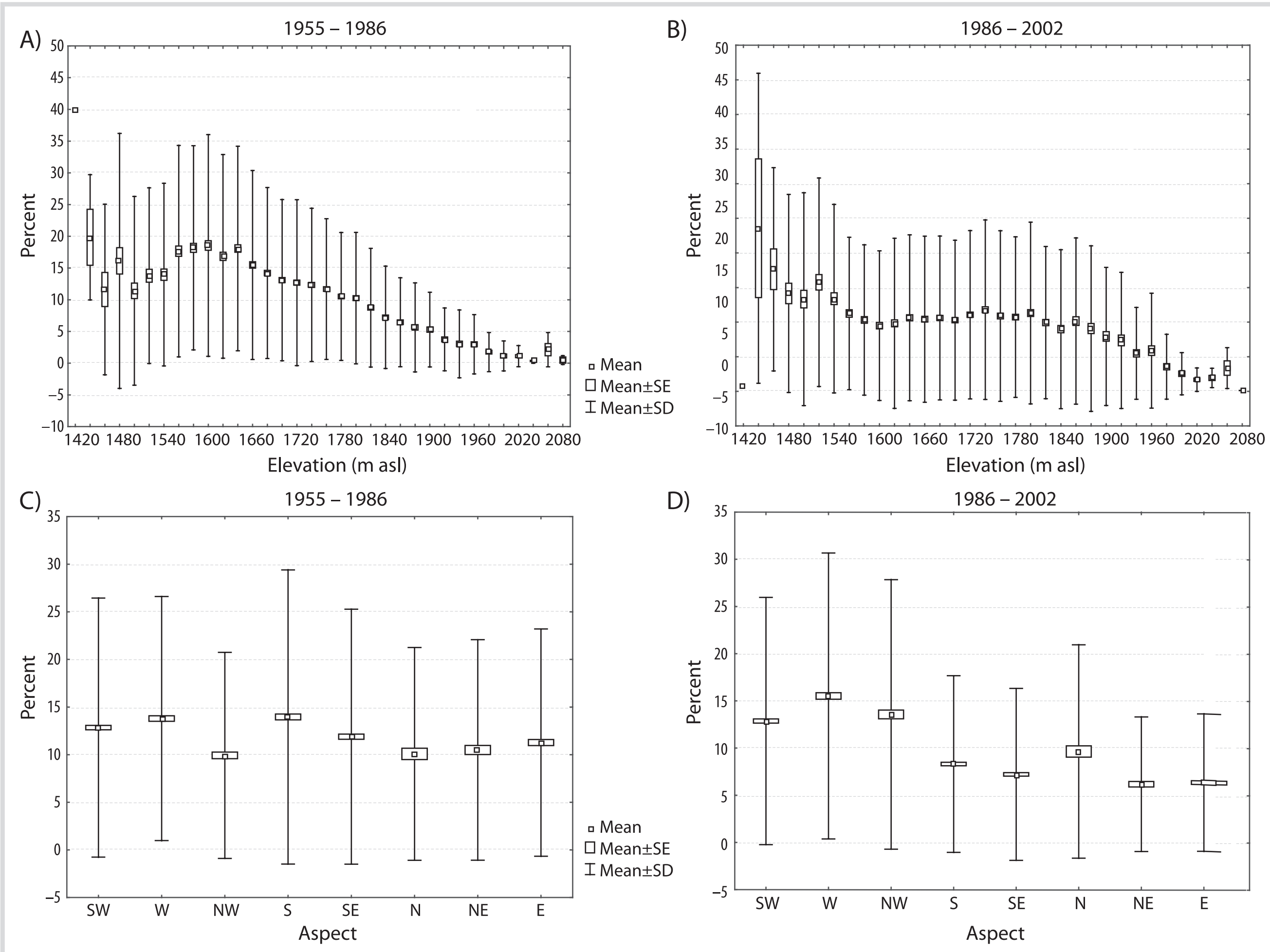
FIGURE 4 Increments in mountain pine cover in the Tatra Mountains in the periods 1955–1986 and 1986–2002, according to (A and B) elevation and (C and D) aspect. In both periods, the tempo of growth differed at the different elevations from the period 1955–1986: Kruskal–Wallis analysis of variance (ANOVA) nonparametric test at H (33, N = 13,594) = 1606.419, P = 0.000, 1986–2002: H (33, N = 13594) = 378.0978, P = 0.000. At lower elevations, *P. mugo* tended to grow more intensively in the earlier than in the later period (compare Figure 1A and 1B, PC1 in Table 3) (C) In the period 1955–1986, the groups did not differ according to aspect. Kruskal–Wallis ANOVA H (7, N = 13586) = 125.91, P = 0.000. (D) In the period 1986–2002, the westerly aspects were significant, Kruskal–Wallis ANOVA H (7, N = 13586) = 970.90, P = 0.000.

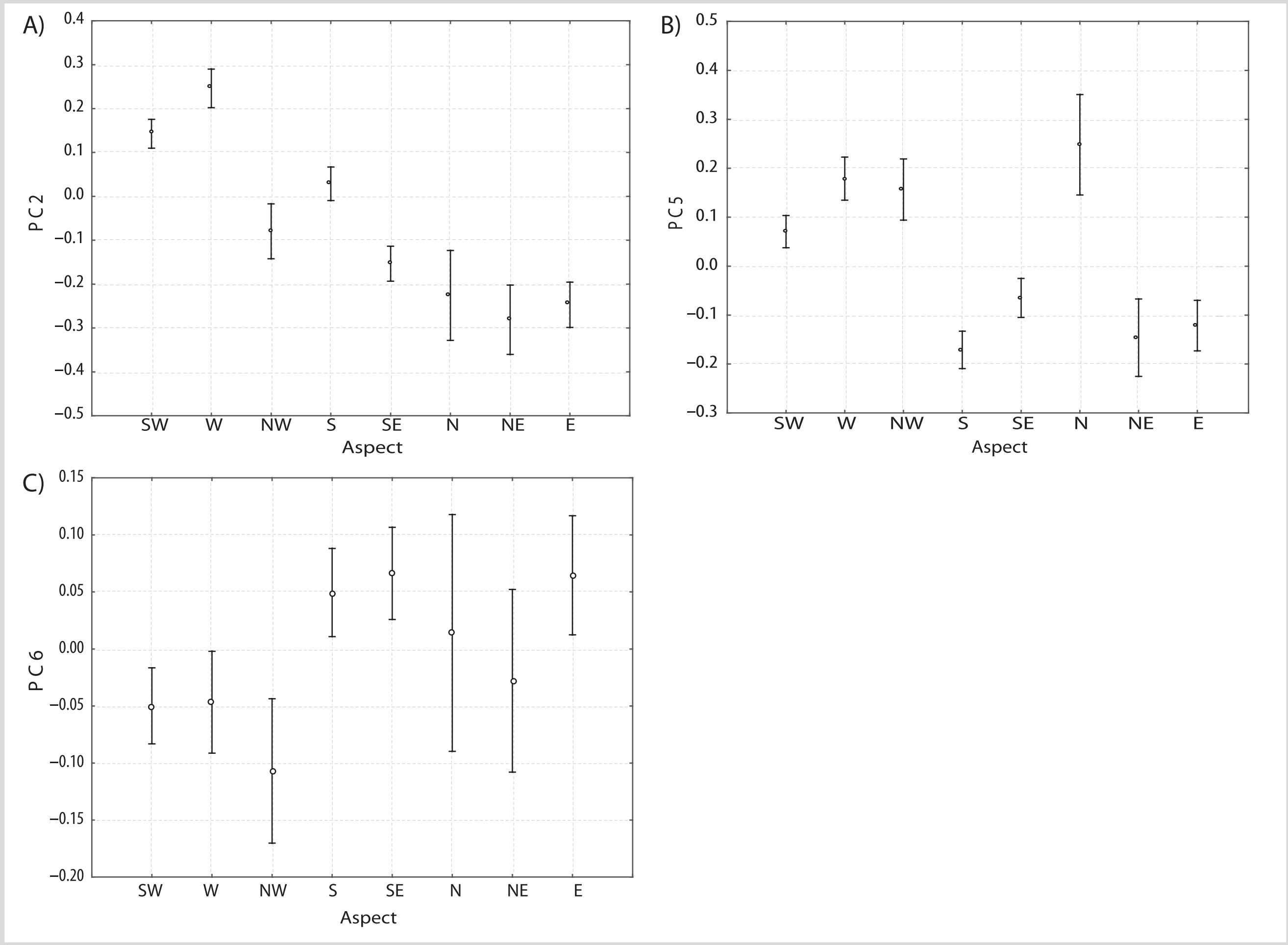


In peripheral areas, this process will be dependent on the competitive struggle with abandoned grasslands for light after grazing has ceased. In recent decades, dwarf pine forest has generally lost total surface area as the result of pressure from lower vegetation communities and even secondary pastures (Mihai et al 2007).

In addition to climate change, human land use may drive changes in the tree line. Land use in subalpine and alpine areas (grazing and extraction) affects the distribution of flora just as much as climate. Since the 13th and 14th centuries, anthropogenic land cover change has involved clearing mountain-pine thickets to obtain new pastures for sheep and cattle grazing, for extensive charcoal and oil production, and for copper and iron-ore mining, sometimes leading to degradation. Jodowski (2007) described how establishing national parks in the Tatras, Babia Góra, and Giant Mountains, enabled secondary succession, which has led to colonization of previously abandoned habitats. However, these processes have been hampered by harsh edaphic and climatic conditions as well as by avalanches and debris flows. Extensive planting of mountain pine in the former Czechoslovakia significantly facilitated the regeneration of mountain pine thickets. After the absolute restriction of grazing in some national parks, we observed progressive long-term trends in secondary succession and patterns of plant establishment driven by climate. Habitats in the peripheral or isolated mountain belts at or above the tree line are generally rich in diversity of endemic species. In these habitats, tree-line expansion disproportionally reduces the habitats of high-altitude species. Such legacies of climate history, which may aggravate extinction risks under future climate change, have to be expected for many temperate mountain ranges (Dirnböck et al 2011).

In the Tatras, mountain pine is westerly oriented. Longer growing seasons, milder winters, and shorter duration of snow cover create favorable conditions for the growth of mountain pine. This shift has not only had a

FIGURE 5 Influence of aspect on area increments of *P. mugo* in relation to (A) curvature, (B) potential water resources (flow accumulation), and (C) slope. (A) In the west and southwest areas, the mountain pine grew significantly more intensively than in the north and east areas (1-way ANOVA = F [7, 13578] = 59.016, $P = 0.000$). (B) The number of areas covered by mountain pine increased significantly in the areas of higher flow accumulation than in the areas of lower flow accumulation, especially in the period 1986–2002 (1-way ANOVA = F [7, 13578] = 35.606, $P = 0.0000$). (C) In 1955–1986, mountain pine occupied steeper areas on the south and southeast slopes. Then in the second period mountain pine extended to the north, northwest, and western areas, where it occupied the more level areas (1-way ANOVA = F [7, 13578] = 6.6930, $P = 0.0000$).



devastating effect on alpine plant communities due to habitat loss but also due to greater fragmentation, which ultimately may affect the population of different animal species dependent on these habitats. Further understanding of dispersal, persistence, and survival strategies of dwarf pine in the other mountain in Slovakia is also required. We will continue to monitor dispersal of *P. mugo* and extend our studies to the low Tatras. Continued research on vegetation dynamics in Slovakia's mountain areas is needed in light of the significance of vegetation in the context of global change. This work will help to characterize and evaluate the total tree surface area as a basis for the state Nature Conservancy's management of mountain national parks and protected areas in Slovakia.

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