Dwarf Pine (Pinus mugo) and Selected Abiotic Habitat Conditions in the Western Tatra Mountains

Authors: Švajda, Juraj, Solár, Jaroslav, Janiga, Marián, and Buliak, Martin

Source: Mountain Research and Development, 31(3) : 220-228

Published By: International Mountain Society

URL: https://doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

Mountain Research and Development (MRD)
An international, peer-reviewed open access journal
published by the International Mountain Society (IMS)
www.mrd-journal.org

MountainResearch
Systems knowledge

Dwarf Pine (*Pinus mugo*) and Selected Abiotic Habitat Conditions in the Western Tatra Mountains

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

The present paper focuses on the distribution of Pinus mugo *in the Carpathians, in an area on the border between Slovakia and Poland. We analyze the response of* P. mugo *distribution to abiotic habitat conditions in the western Tatra Mountains and discuss possible implications for research. The source data for this study were aerial photographs from 3 periods (1965, 1986, and 2002). Mountain areas covered by dwarf pine were identified and analyzed by ArcGIS 9.2, and pine fields were classified with the help of the gray scale mode. A strip of dwarf pine above the upper limit of the forest represents a well-identifiable boundary on the aerial photographs: 25 well-recognized localities were selected to examine the changes in the tree line in the western Tatras. The distribution of dwarf pine systematically increased in the western Tatra Mountains from 1965 to 2002 on all monitored sites. The percentage of total surface area covered in* P. mugo *increased from 41.8% in 1965 to 51.8% in 1986 and to 58.2% in 2002. The study also analyzes the dispersal of dwarf pine over 40 years in relation with slope and elevation. The results of this study explain ongoing and future vegetation changes and can be used as an important contribution to monitoring of climate change in the mid-European mountain areas.*

Keywords: *Abiotic habitat conditions; climate change; land use change;* Pinus mugo*; principal component analysis (PCA); Carpathians; Slovakia; Poland.*

Peer-reviewed: *August 2009* ***Accepted:*** *June 2011*

Introduction

High-mountain ecosystems are considered particularly vulnerable to climate change because productivity, composition, and diversity are directly limited by temperature. The European Alps experienced a 2°C increase in annual minimum temperatures during the 20th century, with a marked rise since the early 1980s (Beniston et al 1997). Alpine plants have moved upward, community composition has changed at high alpine sites, and tree line species have responded to climate warming by invasion of the alpine zone or increased growth rates during the last decades (Dirnböck et al 2003; Weżyk and Guzik 2004). The coniferous forest zone has a general tendency to increase in elevation (Mihai et al 2007; Sitko and Troll 2008). Recent changes of climate and land use are often considered to affect the European alpine region substantially and to trigger an increase in the elevation of the upper tree line (Bolli et al 2007). Although forest composition and geographic distributions of canopy trees are expected to shift with global warming, it is not clear what level of inertia—or time lag—forests will display to climatic forcing, nor how strong the relationship will be between warming and tree line rise (Beckage et al 2008). Grace et al (2002) have considered the possible effects of climate change on the advance of the tree line. Nicolussi and Patzelt (2006) describe the alpine timberline zone as very sensitive to climate variability. The rise of temperatures during the vegetation period over long periods also induces a rise of the tree line, with higher forest stand density. Vescovi et al (2007) suggest that the tree line ascended by about 800–1000 m in a few centuries at most, probably as a consequence of climatic warming.

Both forest management and pasture abandonment have also caused dramatic vegetation changes (Baur et al 2007). The historical effect of human use on vegetation in mountain areas greatly limits approaches based only on an assessment of current climatic change. The subalpine species *Pinus mugo* quickly establishes itself on areas modified by human use and transforms the vegetation cover from former pastureland to a 2-m-high “forest” (Dirnböck and Grabherr 2000). Among others, this has hydrological effects, as the strong root system of *P. mugo* increases soil pores and consequently increases water drainage (Dirnböck and Grabherr 2000). Becker et al (2007) have stated that human-driven land use and land cover changes affect important ecosystem services (vegetation shifts, biodiversity, phytomass production, carbon sequestration, and water relationships). Wieser (2008) warns that changes may have important implications on biogeochemical cycles and probably on biodiversity within the timberline ecotone. Climate change will impact rare and invasive species (Randin et al 2009). On the one hand, some invasive species have been introduced in multiple sites and subsequently dispersed to many other locations (Eliáš 2009). On the other hand, severe declines of several rare plant species have been documented in the western Swiss Alps (Parisod 2008). Therefore, priority in research has been given to monitoring activities for understanding processes and for modeling and validating concepts of natural and socioeconomic developments (Bugmann et al 2007). Such orientated research not only brings concrete statistical–spatial information about the structure of landscapes and changes in landscapes but also helps further predict human influence on a high-mountain landscape and its management (Kellerer-Pirklbauer 2002).

Clearly, it is important to consider climate in concert with land use when predicting vegetation change in the future. An array of models has been developed to cover aspects as diverse as biogeography, conservation biology, climate change research, and habitat or species management (Guisan and Zimmermann 2000). Potential responses of alpine plant species distribution to different future climatic and land use scenarios is a subject of much research. Dirnböck et al (2003) used ordinal regression models of 85 alpine plant species based on environmental constraints and land use to determine their abundance in the northeastern Calcareous Alps. Dullinger et al (2004) used a temporally and spatially explicit model of plant spread, parameterized and analyzed its sensitivity to variation in predicted climatic trends, and described the spatial distribution of vegetation in the northern Calcareous Alps in Austria, where the tree line is dominated by *P. mugo.* Gehrig-Fasel et al (2007) analyzed forest regeneration in the tree line ecotone in the Swiss Alps between 1985 and 1997, including possible drivers.

The approach presented in our study aimed to analyze the response—in terms of spatial distribution—of *P. mugo* influenced by abiotic habitat conditions in the western Tatra Mountains and to describe possible implications for research in the context of human and natural environmental change. As the highest mountain range in the Carpathians, the Tatra Mountains were selected as the study site. The strip of dwarf pine above the upper limit of the forest represents a well-identifiable boundary in aerial photographs. Jodłowski (2007) used the example of the dwarf pine line as a type of boundary timberline. Growth of dwarf pine *(P. mugo)* is affected by internal and external conditions; external conditions are climate, soil, height above sea level (asl), and historical human impact (Somora 1981). The appearance of dwarf pine is connected with site conditions, especially with soil, which segregates competition of shadow trees, mostly spruce *(Picea abies).* Another important factor is the intensity of light.

Apart from climatic effects, it is necessary to take into consideration factors including land use. The historical human effect on vegetation in the Tatra Mountains (Plesník 1978) greatly limits approaches toward trying to find equivalent indications of current climatic change. In the western Tatra Mountains, human use consisted mainly of grazing, which from the 16th century influenced the subalpine and alpine vegetal zones (Harvan 1965). Grazing was prohibited as of the early 1950s, when the Tatras became a national park. After this absolute restriction on grazing, we can observe a progressive long-term trend of secondary succession and climatic-related interaction of vegetal societies. This paper tries to verify trends in the spread of *P. mugo* and uses other variables to specify the method of expansion.

Study area and study species

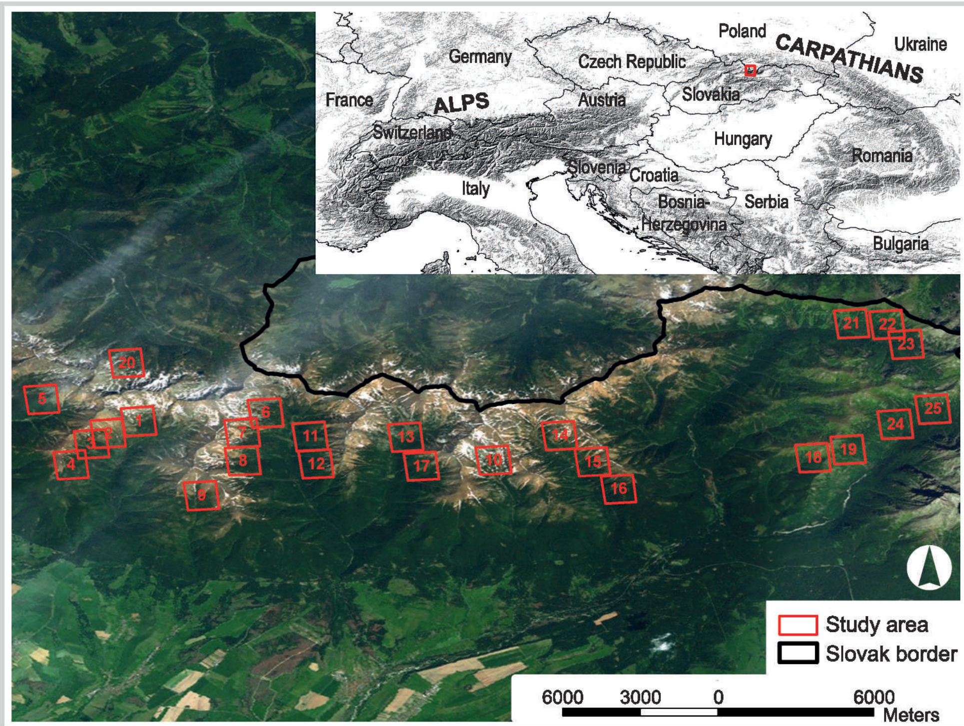
The Tatra Mountains are situated at the Slovak–Polish border (20°10′E, 49°10′N) and constitute the highest mountain massif within the Carpathian Range of Central Europe. The highest summit reaches 2656 m; the massif is classified as a high-mountain landscape. The study area (Figure 1) is situated in the western Tatra Mountains and covers the subalpine and alpine zones. The geology of the investigated area is based on crystalline bedrock. The western Tatra Mountains contain a significant amount of metamorphics (gneiss and mica schist), in addition to granodiorite (Nemčok et al 1993). The vegetation of the alpine zone is dominated by alpine meadows (dry tundra with mostly *Festuca picturata, Luzula alpino-pilosa, 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 masl (Vološčuk 1994).

The average annual air temperature decreases with elevation by 0.6°C per 100 m, being 1.6 and −3.8°C at elevations of 1778 and 2635 m, respectively (Konček and Orlicz 1974). The amount of precipitation increases with the rise in elevation, varying from ~1.0 to ~1.6 m yr^{-1} between 1330 and 2635 masl but reaching >2.00 m yr^{-1} 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 yr^{-1} for the south and north, respectively (Lajczak 1996). Snow cover usually lasts from October to June at elevations > 2000 masl.

The relationship between climatic conditions of the environment (microclimate and vertical climate) and phytocenosis is expressed in different altitudinal zones in the forest. Climatic conditions definitively influenced the natural distribution of forest species; they were constant from the sub-Atlantic period (around 2000 years ago), when the current altitudinal zones were formed. Significant changes in structure also have been conditioned by intense human activity since the 13th century. Ecologically, forest altitudinal zones represent vertical classification of vegetation. Horizontal classification is determined by growth condition of forest societies, differentiated especially according to soil

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

FIGURE 1 Western Tatra Mountains in Slovakia and detailed view of the 25 localities in the study area (from west to east: Roháče, Baníkov, Baranec, Bystrá, Jamnická, Račkova, Kamenistá, Tichá, Kôprová, and Špania valleys). (Map by Jaroslav Solár)



conditions, ecological rows, interrows, and hydric files of forest type groups. The climate-driven tree line in the Tatra Mountains is situated around 1550 masl and partly includes natural ecotones with individual conifers reaching ages of 350–450 years (Büntgen et al 2007).

P. mugo is an obligatory prostrate pine with adult canopy height varying 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 masl; it 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 timberline, reaching approximately 1600–1750 masl in the Tatras and encompassing the upper part of the forest alpine tundra ecotone. Mountain pine plays a significant role in the functioning of the natural environment: it protects the soil and stabilizes the snow cover, thus restricting the release of avalanches, and it provides habitat for many species of flora and fauna (Jodłowski 2006).

Material and methods

Aerial images from 2002 were acquired and georeferenced by Eurosense Ltd. and Geodis Slovakia on the basis of contour lines at a scale 1:10,000 (digital elevation model); we georeferenced aerial photographs from 1986 and 1965 on the basis of orthophotos (Table 1).

Dwarf pine fields were extracted as vectors. The orthophotos in gray scale and panchromatic aerial photos were reclassified according to the gray scale range that represented dwarf pine occurrence in the study area. Each photo was examined separately. If dwarf pine on the slide was gray, with a value from 75 to 110, all such values in the range were reclassified as 1. The remaining values from 0 to 75 and 110 to 256 were reclassified as 0. We created a grid where each pixel contained either the value 1 or the value 0. Then the grid was automatically vectorized on the basis of the 2 values. Histogram transformation because of misrepresentation of values

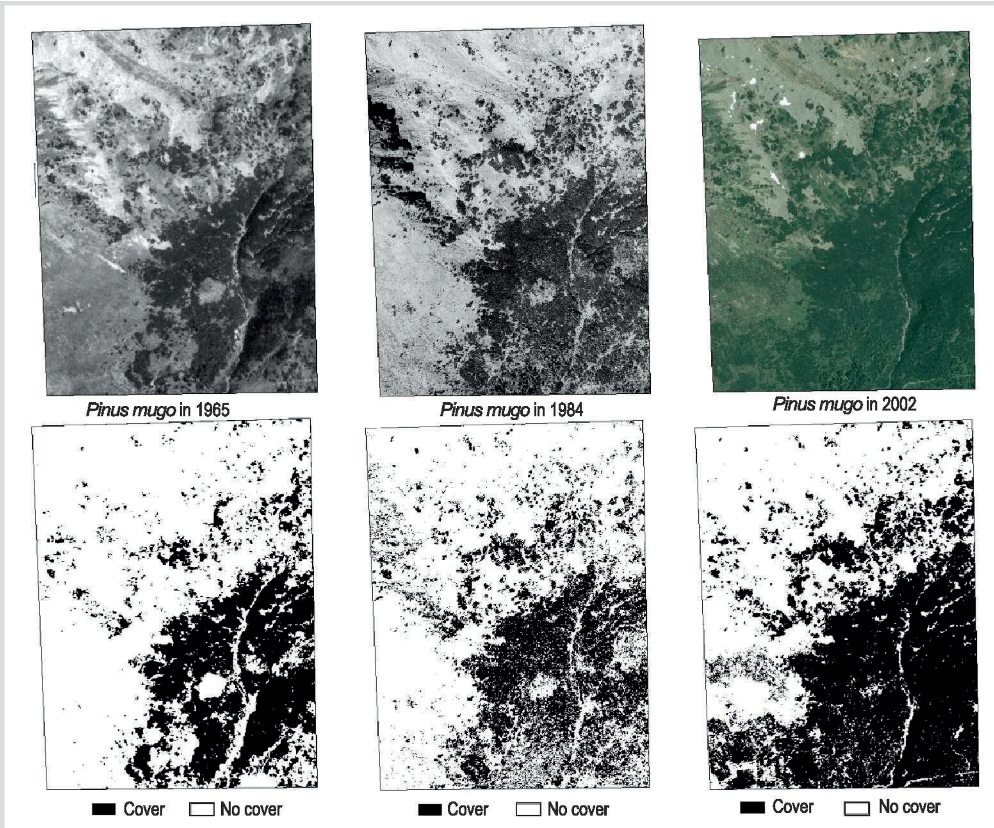
TABLE 1 Quality and resolution of data features (aerial imagery).

Year	Source	Type	Resolution	Width	Height	Format
2002	Eurosense Slovakia	Orthophoto	RBG 72 DPI	2500	2000	.jpg
1986	Topographical Institute	Aerial photo	Gray 2400 DPI	21,829	21,924	.tiff
1965	Kňazovický	Aerial photo	Gray 300 DPI	2164	2175	.jpg

DPI, dots per inch; RBG, red green blue.

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

FIGURE 2 Example of the comparison between aerial photographs: changes between 1965, 1986, and 2002 in 1 analyzed valley (locality 1, Baníkov valley; Figure 1).



was not realized. The size of the pixels' (cell) grid was equivalent, because each image was adjusted to the same size cell size in the transformation of the grid, as well as in the georeferencing; thus, all images and the grids had the same pixels (Figure 2).

Selection of the appropriate areas, which represented 25 localities from the study area, and analysis of imagery were realized in ArcGIS 9.2. Differences in the *P. mugo* surface cover between the 2 periods were calculated using Statistica 8. The increments in dwarf 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 the analysis of the data was necessary. The significance of difference between groups was tested using the Kruskal–Wallis nonparametric test. When $P < 0.05$, the data were considered as significantly different.

A digital elevation model served as the main input for the representation of a selection of abiotic habitat conditions. One matrix was analyzed. Intersecting of study areas with 3 parameters (slope, aspect, and height asl) created 325 small localities with characteristics related to pine increase. Two localities (nos. 5 and 9; Table 2) were excluded due to lack of data from 1986. A multivariate technique, principal component analysis (PCA)–correlation matrix, was used to extract the potential interdependence among mentioned variables. Principal components are linear combinations of original variables (slope, height asl, and relative increase of pine during observed periods), each axis being statistically orthogonal to the others. Integration of the variables slope and height asl to increase of pine in different periods enabled us to follow different processes of mountain colonization by pine during the different periods. Because the technique produces statistically orthogonal axes, we were able to examine potentially independent biological phenomena. We use 4 variables; consequently, we evaluated 4 principal components. We tabulated the proportion of the total variance accounted for by each component.

Results

Dwarf pine permanently increased in the western Tatra Mountains in the period 1965–2002 on all monitored sites. The total surface area covered by dwarf pine increased from 8,173,812 m^2 in 1965 to 10,141,505 m^2 in 1986 and 11,394,461 m^2 in 2002. The percentage of total surface area covered thus increased from 41.8% in 1965 to 51.8% in 1986 and 58.2% in 2002. Only in 1 case (no. 25) did surface area covered by dwarf pine decrease.

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

TABLE 2 Overview of evaluated localities with differences in *P. mugo* cover in the period.

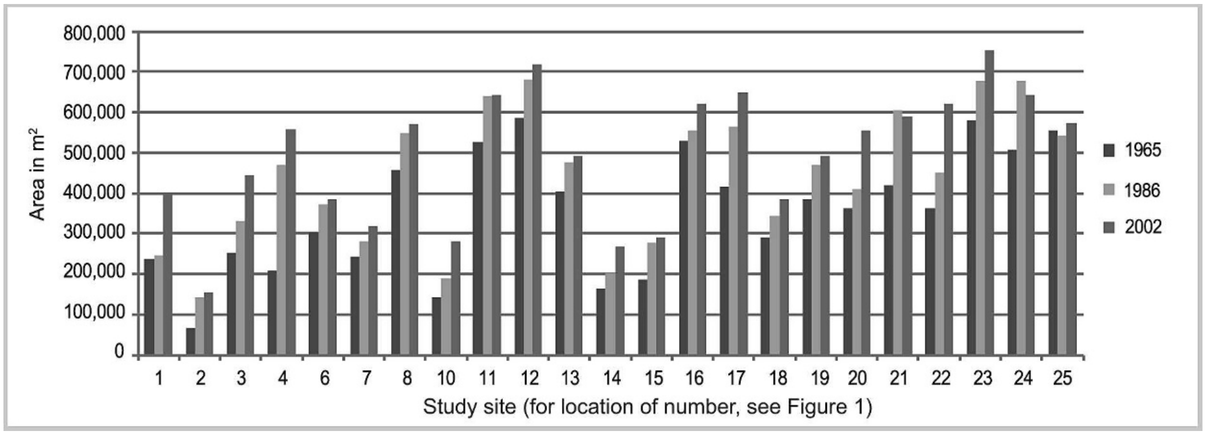
Site number	Average altitude (masl)	Average slope (%)	Covered with *Pinus* (%)	Difference (+/−)
1	1674	34	27	+1/+20
2	1670	46	7	+9/+11
3	1614	44	29	+9/+23
4	1675	36	24	+31/+41
5 (excluded)	1686	42	—	—
6	1614	33	35	+8/+10
7	1733	28	28	+4/+9
8	1604	40	53	+11/+13
9 (excluded)	1807	34	—	—
10	1825	22	16	+6/+16
11	1511	47	61	+14/+14
12	1533	43	68	+12/+16
13	1493	33	47	+8/+10
14	1684	40	19	+4/+12
15	1617	46	21	+11/+13
16	1561	43	62	+3/+10
17	1640	45	48	+18/+28
18	1777	35	34	+6/+11
19	1595	55	45	+10/+12
20	1627	30	42	+6/+23
21	1449	33	49	+21/+20
22	1632	45	42	+11/+31
23	1599	36	68	+11/+20
24	1428	31	59	+20/+16
25	1533	38	65	−2/+2

In 2 cases (nos. 21 and 24) the area decreased in the first and increased in the second period (Figure 3; Table 2). This was probably due to influence by human activities or avalanches.

From 1965 to 1986, dwarf pine tended to grow rapidly at the lower elevations (Figure 4A; Table 3—PC1). This indicates ability of pine to recolonize sites from previous periods. In the period from 1986 to 2002, pine grew rapidly on steeper slopes (Table 3—PC2), mainly at elevations from 1500 to 1700 m (Figure 4B). In the first period measured, dwarf pine was able to densify to such a level at elevations between 1300–1400 masl that in the second period it further filled the area and increments were minimal. The third factor (Table 3—PC3) is less important for explaining pine increments: it shows a positive relationship between slope and elevation. PC4 (Table 3) is a unipolar vector indicating that pine grew more rapidly in the earlier period (1965–1986) than the later period (1986–2002). In the earlier period it grew intensely at all locations (Figure 4C), whereas in the period 1986–2002 it mainly preferred northwest and northeast aspects on steeper slopes, probably the most suitable locations for plant development in the Tatra Mountains. In both periods, the increments in the areas covered by dwarf pine were very low at the elevation of 1900 m, reflecting its natural upper line of occurrence. In

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

FIGURE 3 Comparison of area covered in *P. mugo* (23 localities) in 1965, 1986, and 2002, in square meters.



the earlier monitored period the increments at 1900 m were 0%, whereas between 1986 and 2002 they were approximately 3% (Figure 4A, B). The trend is probably connected to warming in the region.

Discussion and conclusions

A multivariate technique, PCA, was used to extract the variability of real pine growth increment from the

FIGURE 4 Increments in dwarf pine cover in the western Tatra Mountains in the periods 1965–1986 and 1986–2002, according to (A and B) elevation and (C and D) aspect. In the earlier period, the groups did not differ according to aspect. (C) Kruskal–Wallis nonparametric test at $p = 0.05$. (D) In the period 1986–2002, the following aspects differed significantly: N:NE, N:SW, NE:W, NE:S, NE:SE, SE:SW, S:SW, and SW:W.

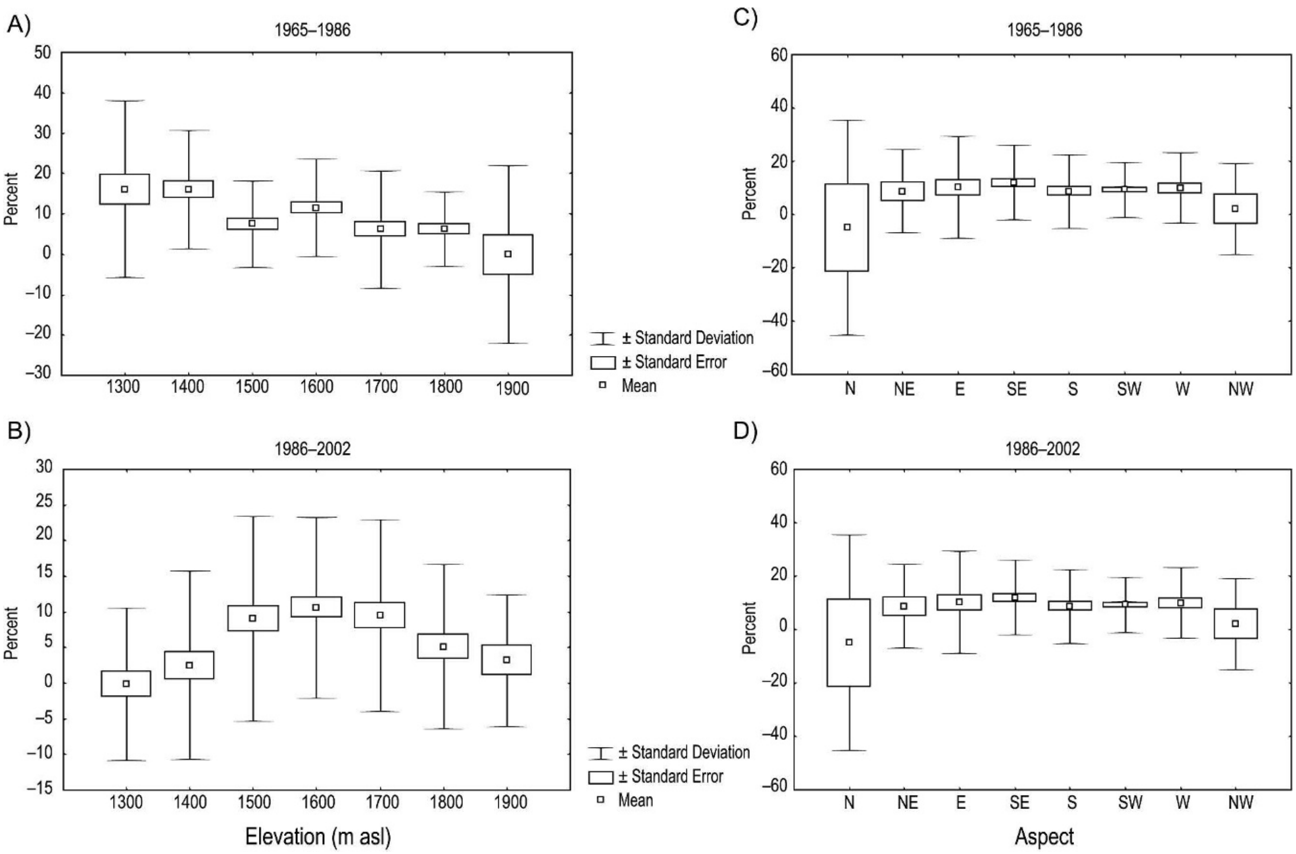


TABLE 3 Component vectors (loadings) and percent variance associated with the components indicating the pattern of natural reforestation with dwarf pine in the Tatra Mountains ($n = 325$; snaps from aerial photographs).

Variable	PC1	PC2	PC3	PC4
Slope	0.51	−0.64	−0.50	0.26
Elevation	−0.71	0.11	−0.63	−0.27
Pine increment (1965–1986)	0.73	0.14	−0.10	−0.64
Pine increment (1986–2002)	−0.38	−0.78	0.30	−0.37
Variability (%)	36.5	26.8	18.9	17.8

PC, principal component.

variability caused by geographic information system processing of samples. The main results of our case study confirm the results of previous research on mountain vegetation zones in the Slovak Tatras. Boltižiar (2007) analyzed spatiotemporal landscape structure change in the alpine environment of the Tatra Mountains. The landscape structure in 1949 in the study area showed dominant grass, which resulted mainly from human activity. Statistical analysis of thematic maps from 2003 suggests extension of dwarf pine surface, advance growth of forest, and reduction of grass areas.

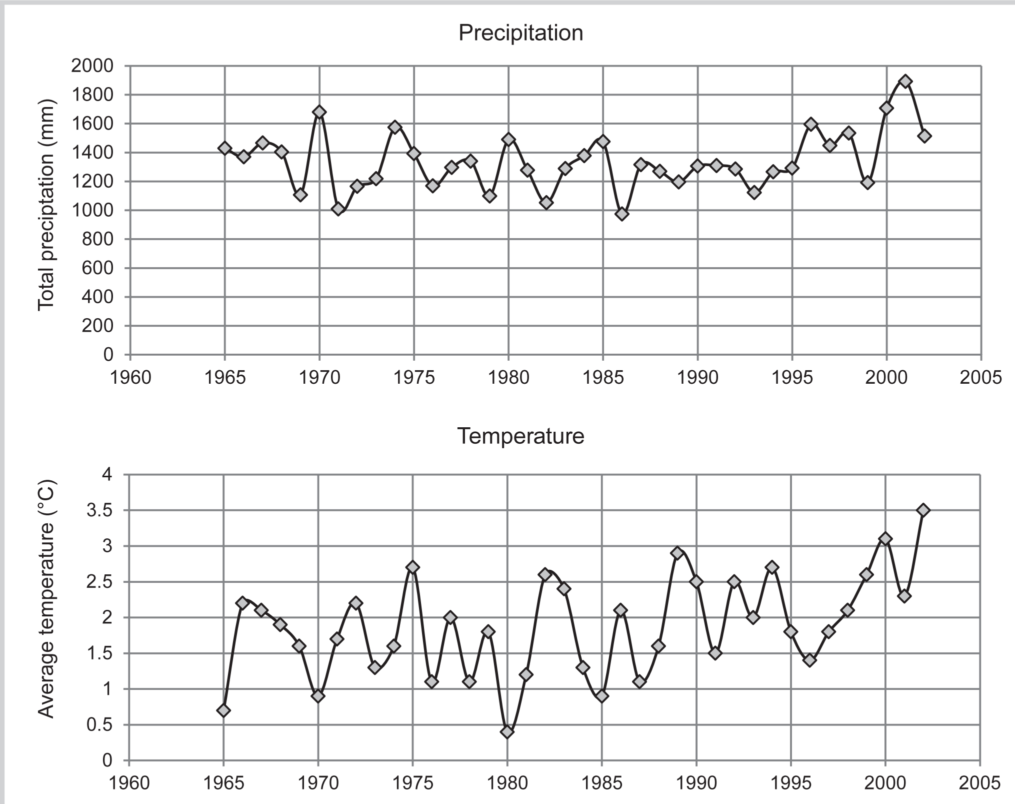
However, there are interesting comparisons with research in other European mountains. Examples from the Alps in Austria (Dullinger et al 2004), after running a model for 1000 years, predicted that the area covered by pines will increase from 10% to between 24% and 59% of the study landscape. The shape of the dispersal curve and spatial patterns of competitively controlled recruitment suppression affect range size dynamics at least as severely as does variation in assumed future mean annual temperature (between 0 and 2°C above the current mean). Moreover, invasibility and shape of the dispersal curve interacted with each other due to the spatial patterns of vegetation cover in the region. In their study of alpine, subalpine, and forest landscapes in the Iezer Mountains (southern Carpathians), Mihai et al (2007) describe how dwarf pine–subalpine associations developed and gradually covered subalpine meadows and barren land (between 1986 and 2002, colonization averaged 0.14 km^2/y). This might be important in the context of the surface of the subalpine and alpine zones in the mountains. However, dwarf pine area lost terrain because of spruce forests, which increased in elevation. This is largely a feature of southern aspect slopes (sunny), where the natural timberline is—under some local conditions—higher. Generally, dwarf pine forest lost a total surface area under pressure from lower vegetation communities and even secondary pastures (Mihai et al 2007).

Tree line is primarily considered to be thermally controlled, so increases in temperature should result in their upslope expansion (Moen 2006). Casty et al (2005) remark that in the European Alps, 1994, 2000, 2002, and particularly 2003 were the warmest years since 1500. Lapin et al (2005) detected similar climate changes in the Slovak mountains. The results showed a significant increase in temperature and a decrease in relative humidity in the April to August season after 1990. From 1901–2005, air temperature increased (annual mean) moderately and precipitation decreased (Melo 2007). This trend of warming is expected to continue in the Slovak mountains. The climate in the Slovak mountain region is thus becoming warmer. Figure 5 shows a general trend that could partially explain the dynamics of the vegetation zones. Results of 3 general circulation models show additional warming on this territory by the end of the 21st century. In Slovakia, we expect the annual average air temperature to increase by about 2–4°C by 2075 (Minďáš and Škvarenina 2003). Minďáš et al (2004) predict the following changes in an area of dwarf pine zone timberline: (1) an increase in the abundance of tree species, (2) dominant representation of spruce, (3) a decrease of dwarf pine, and (4) an increase of general production and biomass of about 200–300%. The results of the study conducted by Dirnböck et al (2003) support earlier hypotheses that alpine plant species on mountain ranges with restricted habitat availability above the tree line will experience severe fragmentation and habitat loss, but only if the mean annual temperature increases by 2°C or more. Even in temperate alpine regions, it is important to consider precipitation, in addition to temperature, when climate impacts are to be assessed.

In addition to climate change, human land use may drive changes in 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–14th century, 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. Jodłowski (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 former Czechoslovakia significantly facilitated the regeneration

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

FIGURE 5 Trends in annual average temperature (in degrees Celsius) and annual total precipitation (in millimeters) from 1965 to 2002 at the meteorological station of Skalnaté pleso (1751 masl), Slovak Institute of Hydrometeorology.



of dwarf 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. Closed mountain-pine thickets stretch up to 300 m above timberline, reaching approximately 1600–1750 masl in the Tatras and encompassing the upper part of the forest–alpine tundra ecotone. The maintenance of large summer farms may contribute to preventing the expected loss of nonforest habitats for alpine plant species (Dirnböck et al 2003).

Gehrig-Fasel et al (2007) compared upward shifts to the potential regional tree line by calculating the difference in elevation of the respective pixels. The altitude of the potential regional tree line was considered as a reference. Upward shifts above the potential regional tree line were considered to be influenced primarily by climate change, while upward shifts below the potential regional tree line were interpreted as primarily influenced by land abandonment. A significant increase in forest cover was found between 1650 and 2450 m. Above 1650 m, 10% of the new forest areas were identified as true upward shifts, whereas 90% represented ingrowth, and the authors identified both land use and climate change as likely drivers. Most upward shift activities were found to occur within a band that ran to 300 m below the potential regional tree line, indicating land use as the most likely driver. Only 4% of the upward shifts were identified to rise above the potential regional tree line, thus indicating climate change. Land abandonment was thus considered to be the most dominant driver for the establishment of new forest areas, even at the tree line ecotone (Gehrig-Fasel et al 2007).

More research on vegetation dynamics in Slovakia's mountain areas is needed in light of the significance of vegetation in the context of global change. The results of our study can be used not only as a baseline for future research to test possible climate change influences (resulting upward shifts compared to a potential surface size and trends in approach of dwarf pine extension) but also to compare trends in other mountainous areas. Further understanding of dispersal, persistence, and survival strategies of dwarf pine in the western Carpathians is also required. We will continue to monitor dispersal of *P. mugo* in Slovakia and extend our studies to the central Tatras. 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.

http://dx.doi.org/10.1659/MRD-JOURNAL-D-09-00032.1

ACKNOWLEDGMENTS

This research was partly supported by the European Economic Area and Norwegian financial mechanism grant SK-00061. We thank Dr L. Kňazovický for aerial photos from 1965.

REFERENCES

Baur P, Müller P, Herzog F. 2007. Land use of alpine pastures is changing. *Agrarforschung* 14(6):254–259.
Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the USA* 105:4197–4202.
Becker A, Körner CH, Brun JJ, Guisan A, Tappelner U. 2007. Ecological and land use studies along elevational gradients. *Mountain Research and Development* 27:58–65.
Beniston M, Diaz HF, Bradley RS. 1997. Climate change at high elevation sites: An overview. *Climatic Change* 36:233–251.
Bolli JC, Rigling A, Bugmann H. 2007. The influence of changes in climate and land use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. *Silva Fennica* 41(1):55–70.
Boltižiar M. 2007. *Structure of High Mountain Landscape of Tatra Mountains. Largescale Mapping, Analysis and Evaluation of Changes by Application of Data from Earth Remote Survey* [in Slovak]. Nitra, Slovakia: UKF [Univerzita Konštantína Filozofa] Nitra, ÚKE [Ústav Krajinnej Ekológie] SAV [Slovenská Akadémia Vied] Nitra.
Bugmann H, Björnsen Gurung A, Ewert F, Haeberli W, Guisan A, Fagre D, Kääb A, GLOCHAMORE [Global Change and Mountain Regions] participants. 2007. Modeling the biophysical impacts of global change in mountain Biosphere Reserves. *Mountain Research and Development* 27(1):66–77. http://dx.doi.org/10.1659/0276-4741(2007)27[66:MTBIOG]2.0.CO;2.
Büntgen U, Frank DC, Kaczka RJ, Verstege A, Zwijacz-Kozica T, Esper J. 2007. Growth responses to climate in a multi-species tree-ring network in the western Carpathian Tatra Mountains, Poland and Slovakia. *Tree Physiology* 27:689–702.
Casty C, Wanner H, Luterbacher J, Esper J, Böhm R. 2005. Temperature and precipitation variability in the European Alps since 1500. *International Journal of Climatology* 25:1855–1880.
Chomitz K, Šamaj F. 1974. Precipitation characteristics [in Slovak]. *In:* Konček M, Bohuš I, Briedoň V, Chomicz K, Intribus R, Kňazovický L, Kolodziejek M, Kurpelová M, Murinová G, Myczkowski Š, Orlicz M, Orliczowa J, Otruba J, Pacl J, Peterka V, et al, editors. *Climate of Tatras*. Bratislava, Slovakia: Veda, pp 443–536.
Dirnböck T, Dullinger S, Grabherr G. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography* 30: 401–417.
Dirnböck T, Grabherr G. 2000. GIS assessment of vegetation and hydrological change in a high mountain catchment of the northern limestone Alps. *Mountain Research and Development* 20:172–179.
Dullinger S, Dirnböck T, Grabherr G. 2004. Modelling climate change-driven treeline shifts: Relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* 92:241–252.
Eliáš P. 2009. Invasions of alien organisms as negative externalities. *Acta regionalia et environmentalica* 6(2):29–34.
Gehrig-Fasel J, Guisan A, Zimmermann NE. 2007. Treeline shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science* 18:571–582.
Grace J, Berninger F, Nagy L. 2002. Impacts of climate change on the treeline. *Annals of Botany* 90:537–544.
Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
Harvan L. 1965. *How Was the Grazing Solved in the Tatra National Park?* [in Slovak]. Treatises Concerning the Tatra National Park Nr. 8 Tatranská Lomnica, Slovakia: TANAP [Tatra National Park] Administration, pp 231–253.
Jodłowski M. 2006. Anthropogenic transformation of the krummholz-line in some mountain ranges in Central Europe. *In:* Price M, editor. *Global Change in Mountain Regions*. London, United Kingdom: Sapiens, pp 186–187.
Jodłowski M. 2007. *Krummholz-line in the Tatra Mts. Babia Góra and the Giant Mts. Ecotone Structure and Dynamics* [in Polish] [PhD dissertation]. Krakow, Poland: Institute of Geography and Spatial Management of the Jagiellonian University.
Kellerer-Pirklbauer A. 2002. The influence of landuse on the stability of slopes with examples from the European Alps. *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark* 132:43–62.
Konček M, Orlicz, M. 1974. Temperature characteristics [in Slovak]. *In:* Konček M, Bohuš I, Briedoň V, Chomicz K, Intribus R, Kňazovický L, Kolodziejek M, Kurpelová M, Murinová G, Myczkowski Š, Orlicz M, Orliczowa J, Otruba J, Pacl J, Peterka V, et al, editors. *Climate of Tatras*. Bratislava, Slovakia: Veda, pp 89–179.
Lajczak A. 1996. Hydrology [in Polish]. *In:* Mirek Z, Głowaciński Z, Klimek K, Piękoś-Mirkowa H, editors. *Nature of the Tatra National Park, Tatrzański Park Narodowy*. Zakopane-Krakow, Poland: Tatrzański Park Narodowy, pp 169–196.
Lapin M, Šťastný P, Chmelík M. 2005. Detection of climate change in the Slovak mountains. *Croatian Meteorological Journal* 40:101–104.
Melo M. 2007. *Regional Climatic Scenarios for Slovak Mountain Region Based on Three Global GCMs*. Bratislava, Slovakia: Comenius University Bratislava. http://www.cnrm.meteo.fr/icam2007/ICAM2007/extended/manuscript_158.pdf; accessed on 14 June 2011.
Mihai B, Savulescu I, Sandric I. 2007. Change detection analysis (1986–2002) of vegetation cover in Romania. *Mountain Research and Development* 27:250–258.
Minďáš J, Čaboun V, Priwitzer T. 2004. Timber line and expected climate changes [in Slovak]. Kadlečík J. editor. *Year-book Turiec and Fatra*. Vrútky, Slovakia: ŠOP SR, pp 17–23.
Minďáš J, Škvarenina J, editors. 2003. *Forests of Slovakia and Global Climate Changes* [in Slovak]. Zvolen, Slovakia: EFRA [Ecological and Forest Research Agency] Zvolen.
Moen J. 2006. Treeline dynamics in a changing climate. *In:* Price M, editor. *Global Change in Mountain Regions*. London, United Kingdom: Sapiens, pp 187–188.
Nemčok J, Bezák V, Janák M, Kahan Š, Ryja W, Kohút M, Lehotský I, Wieczorek J, Zelman J, Mello J, Halouzka R, Raczkowski W, Reichwalder P. 1993. *Explanation of the Geological Map of the Tatra Mountains* [in Slovak]. Bratislava, Slovakia: Geologický ústav Dionýza Štúra.
Nicolussi K, Patzelt G. 2006. Klimawandel und Veränderungen an der alpinen Waldgrenze—Aktuelle Entwicklungen im Vergleich zur Nacheiszeit. *BFW—Praxisinformation* 10:3–5.
Parisod C. 2008. Postglacial recolonisation of plants in the western Alps of Switzerland. *Botanica Helvetica* 118(1):1–12.
Plesník P. 1978. *Implication of Human Influence in Area of Timber Line and Above in Tatra National Park Territory* [in Slovak]. Treatises Concerning the Tatra National Park Nr. 20. Tatranská Lomnica, Slovakia: TANAP [Tatra National Park] Administration, pp 67–91.
Randin CH, Engeler R, Le Lay G, Pearman PB, Vittoz P, Guisan A. 2009. Ongoing and future vegetation changes in the western Swiss Alps. *Newsletter of the Mountain Research Initiative* 2:18–21.
Sitko A, Troll M. 2008. Timberline changes in relation to summer farming in the western Chornohora (Ukrainian Carpathians). *Mountain Research and Development* 28(3/4):263–271.
Somora J. 1981. *Dwarf Pine (*Pinus mugo Turra*) in Tatra National Park (Distribution, Growth Forms)* [in Slovak]. Treatises Concerning the Tatra National Park Nr. 22. Tatranská Lomnica, Slovakia: TANAP [Tatra National Park] Administration, pp 31–76.
Vescovi E, Ravazzi C, Arpenti E, Finsinger W, Pini R, Valsecchi V, Wick L, Ammann B, Tinner W. 2007. Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. *Quaternary Science Reviews* 26:1650–1669.
Vološčuk I, Bohuš I, Bublinec E, Bohušová-Hradiská H, Drdoš J, Dubravcová Z, Gáer J, Greguš C, Haková J, Chovancová B, Hindák F, Janiga M, Kocián Ľ, Korbel L, Koreň M, et al. 1994. *Tatra National Park—Biosphere Reserve* [in Slovak]. Martin, Slovakia: Gradus.
Wężyk P, Guzik M. 2004. The use of "Photogrammetry-GIS" (P-GIS) for the analysis of changes in the Tatra Mountains' natural environment. *In:* Widacki W, Bytnerowicz A, Riebau A, editors. *A Message from the Tatra: Geographical Information Systems and Remote Sensing in Mountain Environmental Research*. Riverside, CA: Institute of Geography and Spatial Management, Jagiellonian University, and U.S. Forest Service, pp 31–46.
Wieser G. 2008. Risks of climate change on high elevation forests in Central Europe? *In:* Jandl R, Borsdorf A, van Miegroet H, Lackner R, Psenner R, editors. *Global Change and Sustainable Development in Mountain Regions: Proceedings of the COST Strategic Workshop*. Innsbruck, Austria: Innsbruck University Press.