

## *Pinus pumila* growth at different altitudes in the Svyatoi Nos Peninsula (Russia)

R. GEBAUER<sup>1</sup>, D. VOLAŘÍK<sup>1</sup>, T. FUNDA<sup>2</sup>, I. FUNDOVÁ<sup>2</sup>, A. KOHUTKA<sup>2</sup>,  
V. Klapetek<sup>2</sup>, M. MARTINKOVÁ<sup>1</sup>, O. A. ANENKHONOV<sup>3</sup>, A. RAZUVAEV<sup>4</sup>

<sup>1</sup>Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

<sup>2</sup>Department of Dendrology and Forest Tree Breeding, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

<sup>3</sup>Institute of General and Experimental Biology in Ulan-Ude, Ulan-Ude, Russia

<sup>4</sup>Zabaikalsky National Park, Ust-Barguzin, Russia

**ABSTRACT:** Detailed research is necessary to better understand ecological adaptations of *Pinus pumila* (Pall.) Regel as a species, whose biological properties are vital for its survival. In the Svyatoi Nos Peninsula, three sites differing in altitude were selected. At all sites the growth form of *P. pumila* was determined. At the high and medium sites, the following parameters were measured: linear increment on terminal branches, leaf mass per area and the content of nitrogen per unit leaf area. Anatomical studies were carried out on shoots and four needle-year classes. It was found that needles were longer and narrower at the medium site when compared to the high site. Leaf mass per area was higher and a substantial increase in older needles occurred at the high site. Nitrogen content per unit leaf area served as an indicator of assimilation capacity and was higher at the high site. We can conclude that *P. pumila* has xeromorphic needles, higher assimilation capacity, better protection ability against pathogens and slower growth rate of terminal branches at the high site. Important is also a significant increment of the growth rate of terminal branches at the high site in recent years. Therefore, data obtained from sites at the upper forest limit are valuable in assessing the climate changes and are useful for the forest management practice in mountain areas.

**Keywords:** anatomy; assimilation capacity; climate changes; morphology; nitrogen content

*Pinus pumila* (Pall.) Regel is a slowly growing, long-lived (over 350 years) species of shrubby appearance (KHOMENTOVSKY 2004), which is physiognomically similar to mountain pine (*Pinus mugo* Turra). *P. pumila* occurs naturally from lowlands to the upper forest limit in eastern Siberia, Manchuria, Kamchatka and Japan (MOLOZHNIKOV 1975).

High-elevation sites are typical for having severe environmental conditions for plant growth and survival, where low temperatures, strong winds, the amount of snow and short growing seasons

(HADLEY, SMITH 1983; KÖRNER 1999; KAJIMOTO et al. 2002) are determining factors. These key abiotic factors controlling plant life in high-elevation sites are sensitive to the anthropogenic climate change and will alter the environmental conditions to a considerable extent by the end of this century (BENISTON et al. 1996; THEURILLAT, GUI SAN 2001; SCHÖB et al. 2009). It is thought that in future climatic changes will markedly affect plant communities at higher locations (HENRY, MOLAU 1997; CHAPIN et al. 2004; TAKAHASHI

Supported by the Ministry of Education, Youth and Sports of the Czech Republic, Project No. MSM 6215648902.

2005). The vegetation at high altitudes is believed to be particularly sensitive to the long-term climate change because abiotic factors, especially climate, dominate with respect to biotic interactions (KÖRNER 1994; GRABHERR et al. 1995; BENISTON et al. 1996; THEURILLAT, GUIBAN 2001). KAJIMOTO et al. (1996) reported a shift of its upper limit for *P. pumila* and explained its cause to be global warming. Mountains also provide life-sustaining water for most regions of the world. The critical function of mountains as seasonal and longer-term water storage implies that climatic and other environmental changes in the world's mountains will have a large impact not only on those immediate regions but also on a much greater area (DIAZ et al. 2003).

There is still a lack of information on whether mountains are intrinsically more sensitive than other ecosystems and on the influence of global climate changes on mountain regions (DIAZ et al. 2003). Therefore, the study of differences in the plant growth, anatomical and morphological strategies in various environmental conditions is useful for estimating the future processes.

The aim of this paper is to compare growth rate, anatomical and morphological variations of *P. pumila* between different altitudes in the Svyatoi Nos Peninsula (Russia). This study will also provide useful information about ecological adaptations of *P. pumila* as a species, which survives and is vigorous under unfavourable ecological conditions thanks to its biological properties.

## MATERIAL AND METHODS

### Study sites

The Svyatoi Nos Peninsula (area 596 km<sup>2</sup>, the Republic of Buryatia, Russia), situated within the distribution area of *P. pumila*, was selected for research purposes. This site is characterized by highly broken topography. The prevailing podzolic soils are most often sandy or loamy-sandy. Three sites were selected in the area that differed in their altitude. The first site (high site) occurred at an altitude of 1,815 m (53°38'15.9"N and 108°47'47"E), the second (medium site) at an altitude of 1,110 m (53°36'87"N and 108°49'73"E) and the third (low site) at 466 m (53°34'46.8"N and 108°47'10.8"E). The high site had sandy soil texture and the medium site had sandy-loamy soil texture. The soil depth was higher at medium site compared to high site. The soil profile at low site was not studied. All sites faced south. *P. pumila* was a dominant species at the high site.

*P. pumila* grew under the closed stand of Scots pine (600 trees.ha<sup>-1</sup>, mean stem girth 99 cm) at the medium site. In the mixed stand of *Pinus sylvestris* (L.), *Larix sibirica* Ledeb. and *Betula* sp. only the growth form of *P. pumila* was determined at the low site. Sample plots of 500 m<sup>2</sup> were established at all experimental sites.

### Temperature data

The temperature data were obtained from the weather data archives (found at <http://meteo.infospace.ru>) for weather station 30635 in Ust-Barguzin (Russia), (53°26'N 108°59'E; 461 m), situated about 60 km from the Svyatoi Nos Peninsula. Unfortunately, we could obtain only data from 2000 to 2008. The diurnal temperature measurements were taken at 0:00, 6:00, 12:00 and 18:00. The mean daily temperature was calculated as the arithmetic average of the diurnal temperature measurements. The mean monthly temperature was calculated as the arithmetic average of the mean daily temperatures. The mean July temperature was 17.1°C from 2000 to 2008.

### Growth form

The growth forms and maximum height of *P. pumila* shrubs were described at all sites. Growth form was characterized according to GROSSET (1959) and KHOVENTOVSKY (2004). For the purpose of this study two types of growth form are distinguished: globose (shrub height to width is  $\geq 1$ ) and creeping (shrub height to width is  $< 1$ ) (Fig. 1).

Table 1. Needle anatomical variables measured with an image analyzer. The measurements were performed according to JOKELA et al. (1998)

Variable	
Needle thickness ( $\mu\text{m}$ )	
Needle cross-section width ( $\mu\text{m}$ )	
Needle cross-section area ( $\mu\text{m}^2$ )	
Area of resin duct ( $\mu\text{m}^2$ )	
Area of the central part of needle ( $\mu\text{m}^2$ )	Areas of endodermis, transfusion tissue, vascular bundle and sclerenchyma tissue
Area of the central part of needle (%)	Area of the central part of needle/needle area (%)
Resin duct area (%)	Resin duct area/needle area (%)

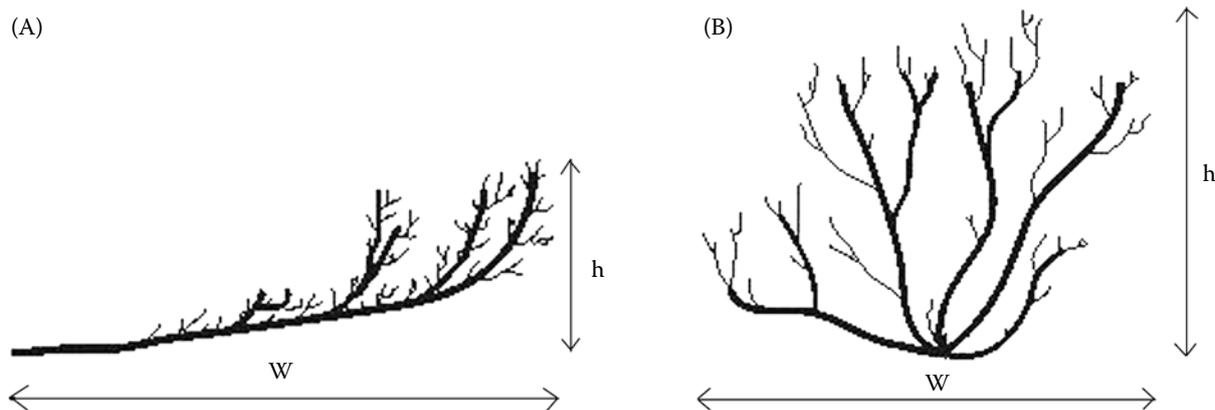


Fig. 1. Crown shape of *P. pumila* (Pall.) Regel. (A) – creeping shape ( $h/W < 1$ ); (B) – globose shape ( $h/W \geq 1$ )

### Mean linear increment of terminal branches

The mean annual linear increment of terminal branches (MLI; KHOMENTOVSKY 2004) was calculated from samples represented by 15 terminal branches from *P. pumila* shrubs at high and medium sites. The annual increment for terminal branches was determined on the basis of branch rings over the period of the last 20 years. Measured data were grouped into two decades (i.e. 1986–1995 and 1996–2005) for further calculations.

### Projected leaf area, length, width of needles and leaf mass per area

Four needle-year classes (i.e. 2002–2005) were sampled from high and medium sites. Needles grown during the current year were not fully developed yet and were not therefore sampled. Needle material was fixed in FAA (the solution of 90 ml 70% ethanol, 5 ml glacial acetic acid and 5 ml 40% formaldehyde, NĚMEC et al. 1962). Later, 20 needles were taken from each sample at the laboratory (Mendel University of Agriculture and Forestry, MUAUF). These needles were scanned using ImageTool 3.00 software (The University of Texas Health Science Center in San Antonio) and then dried (85°C, 48 h) to determine their dry matter (DM). Scanned needles were used for the determination of the projected area, length and width of particular needles. Leaf mass per area (LMA) ( $\text{g}\cdot\text{m}^{-2}$ ) was calculated from the projected area and DM of a mean needle (ČERMÁK 1998; TEMESGEN, WEISKITTEL 2006).

### Nitrogen content in needles

Samples from four different needle-year classes from high and medium sites were dried (85°C, 48 h)

and the total content of nitrogen ( $N_{\text{mass}}$ ) in g per kg DM was determined in the authorized laboratory (Ekola Bruzovice Ltd., Czech Republic). By means of LMA, the nitrogen content per unit leaf area ( $N_{\text{area}}$ ) was calculated (formula 1).

$$N_{\text{area}} = (N_{\text{mass}} \times \text{LMA}) / 1,000 \quad (1)$$

### Anatomical structure of needles and shoots

Samples of shoots and needles from particular needle-years were taken from selected trees at high and medium sites to characterize their histological structure. These samples were also fixed in FAA solution. Cross-sections of shoots and through the centre of particular needle-year classes were made for histological analysis. The microslides were stained with

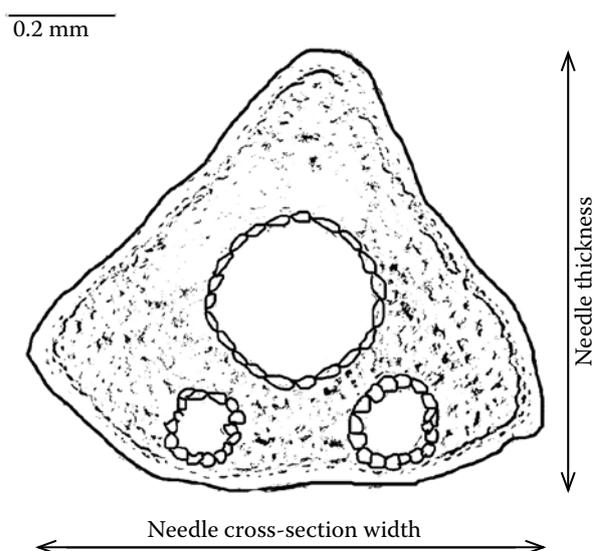


Fig. 2. Cross-section of *P. pumila* needle with two resin ducts shows the measurement of needle cross-section width and needle thickness

phloroglucinol + HCl to mark lignin (NĚMEC et al. 1962; PRASAD 1986; BHANDARI 1997). Stained sections were scanned by a microscope-digital camera-computer in the biometrical laboratory of MUAF.

The primary and secondary structure of stems was described according to photographs. We described the histological structure including the number of resin ducts in particular needle-years. Different needle anatomical variables were measured by an image analyzer program ImageTool 3.00 (The University of Texas Health Science Center in San Antonio) (Table 1 and Fig. 2). The area of the resin duct was measured with epithelium cells.

### Data analysis

We analyzed differences in needle area, needle length, needle width, needle thickness, needle cross-section width, needle cross-section area, area of resin duct and area of the central part of the needle among needles from different sites and needles of different age. Two-way analysis of variance (ANOVA) was used to assess each needle characteristic separately. Needle length was analyzed using the Kruskal-Wallis test as the nonparametric analysis of variance because of the violation of the assumptions of ANOVA. Statistical analyses were carried out using the program R (R Development Core Team 2007).

## RESULTS

### Growth form

The creeping crown shape dominated at the high site. There was no globose crown shape. The



Fig. 3. Procumbent branches are rooted at contact with soil. The oldest parts of the procumbent branches gradually died back (high site; Svyatoi Nos Peninsula, Russia)

maximum detected height was 1.9 m. The shape of *P. pumila* crowns was mostly globose (72% of all shrubs) at the medium site and reached a maximum height of 4.5 m. Individual trees did not create dense and extensive polycormons, as it is typical of the high site. At the medium site, one specimen of *P. pumila* was found that exhibited a stem 0.7 m in height. The globose crown shape dominated at the low site. There was no creeping crown shape. The highest specimen reached a height of 4.9 m.

Procumbent branches rooted at contact with soil and the oldest parts of procumbent branches gradually died back at the high site (Fig. 3). Individuals originating in this way separated gradually and it was then very difficult to determine the number of specimens originating generatively in extensive polycormons.

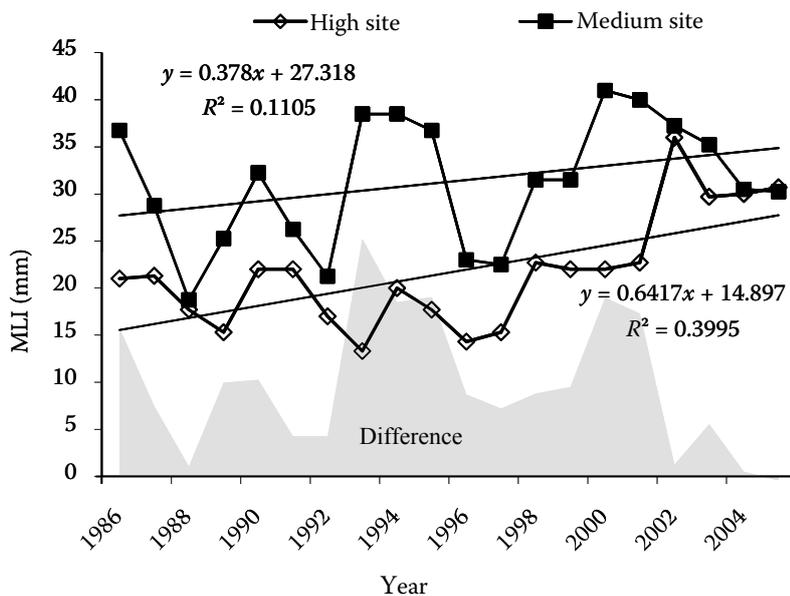


Fig. 4. Mean annual linear increment of terminal branches in *Pinus pumila* (Pall.) Regel in the period from 1986 to 2005 at various altitudes (Svyatoi Nos Peninsula, Russia)

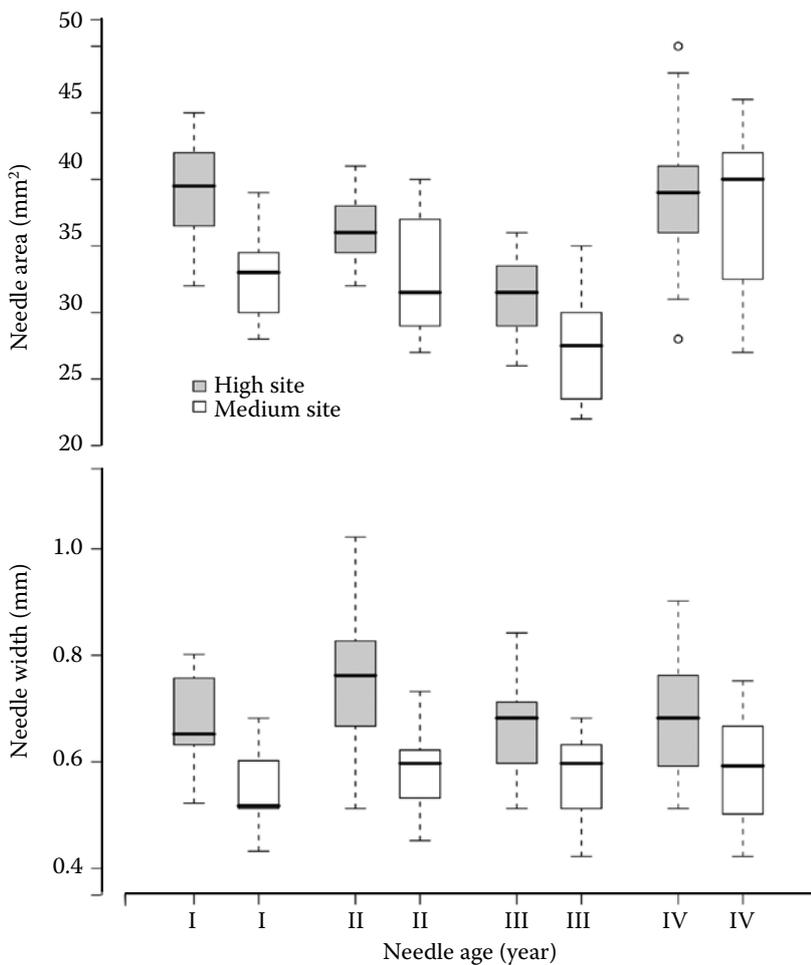


Fig. 5. Box plot of needle area and width from different sites according to needle age. The centre line and outside edge (hinges) of each box represent the median and range of the inner quartile around the median; vertical lines above and below the box (whiskers) represent values falling within 1.5 times the absolute value of the difference between the values of the two hinges; circles represent outlying values (Svyatoi Nos Peninsula, Russia)

#### Mean linear increment of terminal branches

We found that the mean increment based on the measurement of lengths of increments on terminal branches in particular years was 19 mm at the high site in the period from 1986 to 1995, increasing by 30% in the period 1996–2005. At the medium site, the mean linear increment of terminal branches reached

30 mm in the period 1986–1995 and increased by 7% in the period from 1996 to 2005 (Fig. 4).

#### Projected leaf area, length, width of needles and leaf mass per area

*P. pumila* needles were longer (about 10%), narrower (about 6%) and their projected area was

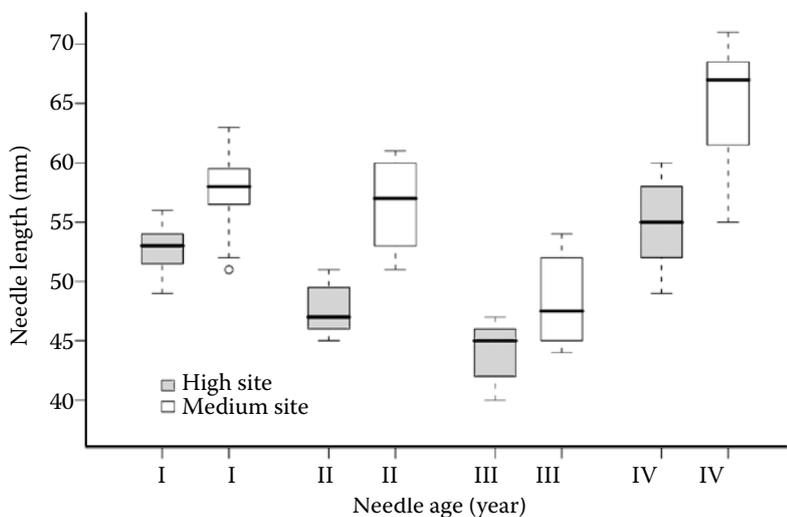


Fig. 6. Box plot of needle length from different sites according to needle age. The centre line and outside edge (hinges) of each box represent the median and range of inner quartile around the median; vertical lines above and below the box (whiskers) represent values falling within 1.5 times the absolute value of the difference between the values of the two hinges; the circle represents an outlying value (Svyatoi Nos Peninsula, Russia)

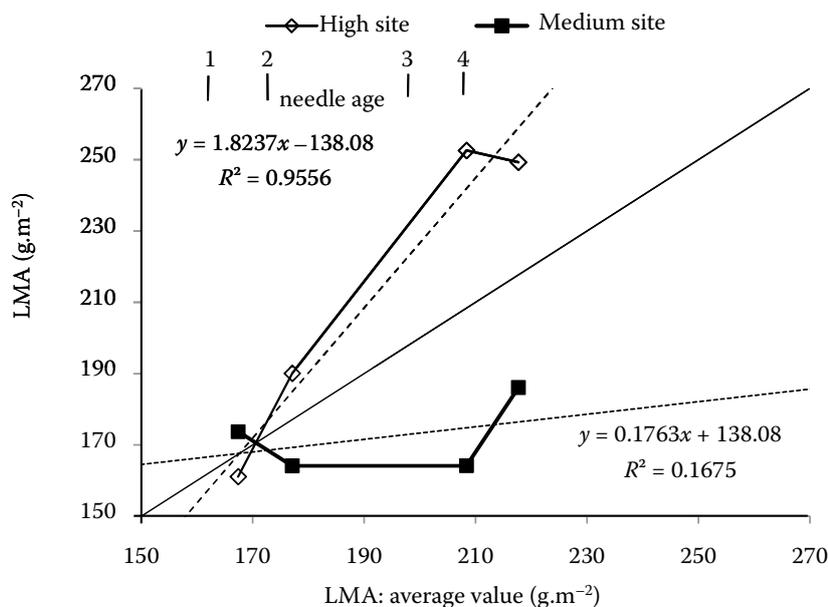


Fig. 7. Evaluation of four needle-year classes at two sites by comparing how leaf mass per area (LMA) relates to mean values (Svyatoi Nos Peninsula, Russia)

smaller (about 6%) at the medium site. When comparing the projected area and width of needles of particular needle-years, the differences were statistically significant between the high and medium sites ( $F = 29.9096$ ,  $df = 1$ ,  $P = 1.82e^{-07}$ ;  $F = 87.9083$ ,  $df = 3$ ,  $P = < 2.2e^{-16}$ ) and also between needle-years ( $F = 35.3623$ ,  $df = 3$ ,  $P = < 2.2e^{-16}$ ,  $F = 4.2940$ ,  $df = 3$ ,  $P = 0.006116$ ) (Fig. 5). The site and needle year were also statistically significant for needle length ( $\chi^2 = 0.535$ ,  $df = 3$ ,  $P < 2.2e^{-16}$ ) (Fig. 6).

LMA was roughly the same in all needle-years, ranging from 164 to 186  $g.m^{-2}$ , at the shaded medium site; in older needles, only a negligible increase

occurred. At the insulated high site, this value was higher, and a more substantial increase occurred in needles from older needle-years (from 161 to 249  $g.m^{-2}$ ) (Fig. 7).

#### Nitrogen content in the needles

Nitrogen content in g per kg DM ( $N_{mass}$ ) was about 25% higher at the high site.  $N_{mass}$  was lowering towards older needles in both sites. Nitrogen content per unit leaf area ( $N_{area}$ ) was also higher at the high site (Fig. 8). The difference in  $N_{area}$  in the first needle-year between the high and medium

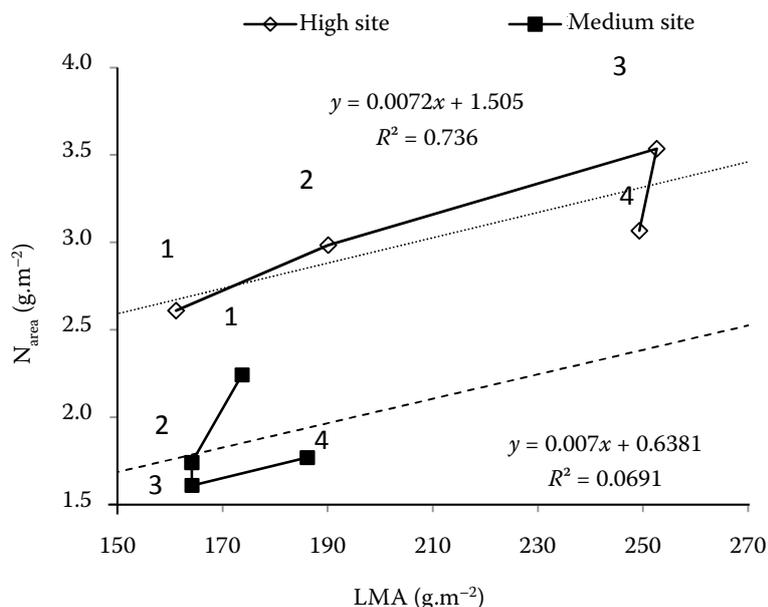


Fig. 8. Nitrogen content per leaf area unit in four needle-years (number in the graph) of *P. pumila* with respect to leaf mass per area (LMA). Values from the high and medium sites are smoothed by linear regression (Svyatoi Nos Peninsula, Russia)

Table 2. Anatomical measurements of needle cross-sections at high and medium site. Different letters within a row indicate statistically significant differences (*t*-test,  $\alpha < 0.05$ ) between variables within sites

Variable	Mean $\pm$ SD	
	high site	medium site
Needle thickness ( $\mu\text{m}$ )	787 $\pm$ 18 <sup>a</sup>	708 $\pm$ 25 <sup>b</sup>
Needle width ( $\mu\text{m}$ )	718 $\pm$ 23 <sup>a</sup>	619 $\pm$ 19 <sup>b</sup>
Needle area ( $\mu\text{m}^2$ )	334,400 $\pm$ 9,646 <sup>a</sup>	275,577 $\pm$ 9,396 <sup>b</sup>
Area of resin duct ( $\mu\text{m}^2$ )	7,294 $\pm$ 280	6,871 $\pm$ 335
Area of the central part of needle ( $\mu\text{m}^2$ )	60,009 $\pm$ 1,897 <sup>a</sup>	41,734 $\pm$ 1,446 <sup>b</sup>
Area of the central part of needle (%)	18.96 $\pm$ 0.33 <sup>a</sup>	15.16 $\pm$ 0.23 <sup>b</sup>
Resin duct area (%)	4.39 $\pm$ 0.23	4.95 $\pm$ 0.29

sites was not as marked (20%) as in other needle-years.

#### Anatomical structure of needles and shoots

Cross-sections through needles showed the presence of two large resin ducts at both sites. The finding of a single resin duct in some needles was of exceptional note. The cross-section area of the needle as well as the area of the central part of the needle (expressed in  $\mu\text{m}^2$ ) were statistically lower (about 26% and 34%, respectively) at the medium site compared to the high site (Table 2). The area of resin duct (expressed in  $\mu\text{m}^2$ ) was about 6% larger at the high site, but this difference was not statistically significant (Table 2). When the area of resin duct was expressed in % to cross-section area, the opposite trend was recorded, yet, this difference was not statistically significant either (Table 2).

## DISCUSSION

### Growth form

The crown shape reflects environmental conditions which affect shoot growth such as light, water, temperature, mineral supply, chemical properties, insects, other plants and various animals (KOZŁOWSKI 1971). The creeping shape of the crown at high site is typical of wide valleys where growth is affected by strong winds that can bring humidity, cool air and increasing evaporation (KHOMENTOVSKY 2004). The globose shape of the crown at medium and low site was classified as an indicator of the more favourable environment. It refers to the optimum construction for the maximum use of solar radiation for photosynthesis and, at the same time, for protection from overheating and excessive loss of water (LARCHER

1995; KHOMENTOVSKY 2004). According to OKITSU and ITO (1984) the height of *P. pumila* generally depends on the intensity of prevailing winds which cause differences in the accumulation of snow in winter. On shaded or poorly insolated locations, *P. pumila* can create a short stem (KHOMENTOVSKY 2004) as was found at medium site. Hence we confirm that the more favourable environment (higher snow accumulation, lower wind intensity, lower light intensity and higher temperature) is at medium and low sites.

*P. pumila* was described as a species that successfully regenerates due to the considerable production of adventitious roots from stems under the soil surface (KAJIMOTO 1992; DROZDOV 1998). Regeneration and spreading of adventitious roots were also described for the physiognomically similar mountain pine (*Pinus mugo* Turra) (ŠPINLEROVÁ, MARTINKOVÁ 2006). KHOMENTOVSKY (2004) stated that, theoretically, a specimen of the same genotype could possibly live for several thousand years in areas where fires did not take place.

### Mean linear increment of terminal branches

The method of mean linear increment measurement (MLI) showed good results, even when the species grew under unfavourable conditions (SANO et al. 1977; OKITSU 1988; KHOMENTOVSKY 2004; ŠPINLEROVÁ, MARTINKOVÁ 2006). KHOMENTOVSKY (2004) found that the MLI for *P. pumila* growing in Kamchatka at high altitudes is lower than for medium altitudes. It corresponds with our results and it also indicates the more favourable environment at lower altitudes. Interesting is a significant increase of MLI in the last decade, particularly in *P. pumila* growing at the high site. It could be caused by an increase in temperatures during the growing season as it is docu-

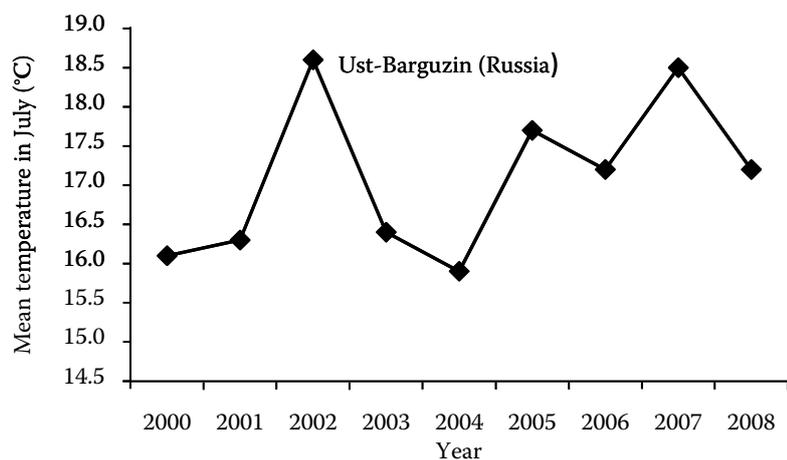


Fig. 9. July temperature for the meteorostation in Ust-Barguzin (Russia). Data obtained from the weather data archives (<http://meteo.infospace.ru>)

mented by the graph (Fig. 9). The graph shows mean July temperatures, since TAKAHASHI (2006) found there is a positive correlation between the growth of shoots and July temperatures for *P. pumila* growing in central Japan. Because we could not obtain data for a longer period, we analyzed the graph of July temperature dynamics since 1900 given for Irkutsk, the city situated 350 km SW from our sites (VORONIN 2008). There is a decrease in temperatures from 1969 to 1992, followed by a rapid increase in temperatures until the present. A slight change in MLI at medium site is caused by more favourable growth conditions. *P. pumila* growing at high site is exposed to extreme climate and, in such environment, trees respond to climatic changes much more sensitively.

#### Projected leaf area, length, and width of needles and leaf mass per area

Temperature and water availability have major effects on plant growth and carbon assimilation (TAIZ, ZEIGER 2006). Leaves that develop under conditions of low temperature and water supply are usually correspondingly smaller and have a smaller surface area (LARCHER 1995; FITTER, HAY 2002).

The relationship between the needle morphology and elevation that we observed in *P. pumila* (smaller and shorter needles at higher elevation) was consistent with other work on conifers in alpine regions (TRANQUILLINI 1964; DELUCIA, BERLYN 1984; RICHARDSON et al. 2001), although the opposite trend was observed in semi-arid regions at higher altitudes (CALLAWAY et al. 1994; POULOS, BERLYN 2007). In semi-arid regions are better climatic conditions at middle and upper elevations during the growing season and these factors are probably responsible for the greater needle length, needle mass and needle area in these regions at high elevations (POULOS, BERLYN 2007).

Leaf mass per area (LMA) in *P. pumila* growing in Japan at altitudes of 2,600 m and 2,665 m was higher

in older needles (190 and 187 g.m<sup>-2</sup>) compared to the first year of needle growth (161 and 121 g.m<sup>-2</sup>) and decreased with the decline of solar radiation (KAJIMOTO 1989). In our results LMA was roughly the same in all needle-years at the shaded medium site (in older needles, only a negligible increase occurred) and at the insolated high site, this value was higher and the more substantial increase also occurred in older needle-years. As mentioned by KAJIMOTO (1989), differences in the LMA indicate the potential for sun and shade to modify needles, a phenomenon generally valid in other tree species (TADAKI et al. 1970; OGAWA 1967 in KAJIMOTO 1989; ČERMÁK 1998) and also in herbs (ŠESTÁK 1985). Higher values of LMA at high site are related not only to the higher solar ratio but also to the needle anatomy (i.e. higher proportion of mechanical and conductive tissues) (SUTINEN et al. 2006) and hence increase of carbon investment per given leaf area (ZHANG, CREGG 2005).

#### Nitrogen content in needles

In deciduous broadleaves, it was found that the nitrogen content in leaves per unit area is a good indicator of the assimilation capacity of leaves because photosynthetic enzymes such as RuBP carboxylase/oxygenase contain a large amount of nitrogen (ELLSWORTH, REICH 1992, 1993; TAKAHASHI et al. 2005). The development of the palisade parenchyma is also associated with increasing light intensity, which improves the assimilation capacity of leaves per unit leaf area (JURIK 1986; GOULD 1993). The higher N<sub>area</sub> in open crowns increases the rate of net production per unit leaf area (TAKAHASHI et al. 2001, 2005). The relationship of increasing nitrogen content per unit leaf area with altitude that we observed was consistent with other studies (e.g. FRIEND et al. 1989; CORDELL et al. 1999; HIKOSAKA et al. 2002). The higher N<sub>area</sub> (i.e. better assimilation capacity) is one of the adaptations for

the most effective use of the shorter growing season at the high site.

### Anatomical structure of needles and shoots

In the needles of different species the number and distribution of resin ducts are variable (ESAU 1977). There is no trend in the number of resin ducts with increasing altitude. Generally *P. pumila* needles had two resin ducts, but needles with a single resin duct were also discovered. In some *P. pumila* needles, which grow on Kamchatka, four resin ducts were found (GEBAUER, unpublished data). The increasing area of the central part of the needle at a high elevation site can support transport or water reserves in individuals growing at higher altitudes as well as the faster removal of photosynthate from needles and its translocation to its sinks. The increase in the size of the area of the central cylinder indicates more xeromorphic characters of the needle at high site (SUTINEN et al. 2006). JOKELA et al. (1998) discovered smaller dimensions of resin ducts for *P. sylvestris* needles (4,300–6,300  $\mu\text{m}^2$ ) than we have found for *P. pumila* needles. Higher N concentration and smaller resin duct area when the resin duct area was calculated in relation to the whole needle area at high site as we have found correspond with results reported by KAINULAINEN et al. (1996) and JOKELA et al. (1998).

### CONCLUSION

Selected biometric parameters of the shoots and needles of *P. pumila* were compared at two sites of the Svyatoi Nos Peninsula differing in their altitude and solar radiation availability. Based on statistically significant differences in the anatomical characteristics of particular needle-years between the high and medium sites, we distinguished two different ecotypes of *P. pumila* (lowland ecotype and high-elevation ecotype). *Pinus pumila* has a creeping form of the crown, more xeromorphic needles, higher assimilation capacity and slower growth of terminal branches with increasing altitude. Important is also a significant increment of the growth rate of terminal branches in recent years at high site. Therefore, data obtained from sites at the upper forest limit are valuable in assessing the climate changes and are useful for the forest management practice in mountain areas.

### Acknowledgements

The authors of the paper thank WARMPEACE Co., the Zabaikalsky National Park, Project *Monitoring of*

*Pinus pumila* (Pall.) Regel in the Range of Its Natural Distribution.

### References

- BENINSTON M., FOX D.G., ADHIKARY S., ANDRESSEN R., GUISAN A., HOLTEN J.L., INNES J., MAITIMA J., PRICE M.F., TESSIER L. (1996): Impacts of climate change on mountain regions. In: WATSON R.T., ZINYOWERA M.C., MOSS R.H., DOKKEN D.J. (eds): *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change*. Cambridge, Cambridge University Press.
- BHANDARI N.N. (1997): *Staining Techniques Manual*. New Delhi, Ultimate Printers: 344.
- CALLAWAY R.M., DELUCIA E.H., SCHLESINGER W.H. (1994): Biomass allocation of montane and desert ponderosa pine: An analog for response to climate change. *Ecology*, **75**: 1474–1481.
- CHAPIN F.S., CALLAGHAN T.V., BERGERON Y., FUKUDA M., JOHNSTONE J.F., JUDAY G.P., ZIMOV S.A. (2004): Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio*, **33**: 361–365.
- CORDELL S., GOLDSTEIN G., MEIZER F.C., HANDLEY L.L. (1999): Allocation of nitrogen and carbon in leaves of *Metrosideros polymorpha* regulates carboxylation capacity and  $\delta^{13}\text{C}$  along an altitudinal gradient. *Functional Ecology*, **13**: 811–818.
- ČERMÁK J. (1998): Leaf distribution in large trees and stands of the floodplain forest in southern Moravia. *Tree Physiology*, **18**: 727–737.
- DELUCIA E.H., BERLYN G.P. (1984): The effect of increasing elevation on leaf cuticle thickness and cuticular transpiration in balsam fir. *Canadian Journal of Botany*, **62**: 2423–2431.
- DIAZ H.F., GROSJEAN M., GRAUMLICH L. (2003): Climate variability and change in high elevation regions: past, present, future. *Climatic Change*, **59**: 1–4.
- DROZDOV I.I. (1998): *Introduced Conifer Species in Forest Stands*. Moscow, MGUL. (in Russian)
- EIDE W., BIRKS H.H. (2005): Stomatal frequency of *Betula pubescens* and *Pinus sylvestris* shows no proportional relationship with atmospheric  $\text{CO}_2$  concentration. *Nordic Journal of Botany*, **24**: 327–339.
- ELLSWORTH D.S., REICH P.B. (1992): Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Functional Ecology*, **6**: 423–435.
- ELLSWORTH D.S., REICH P.B. (1993): Canopy structure and vertical patterns of photosynthesis and related leaf trans in a deciduous forest. *Oecologia*, **96**: 169–178.
- ESAU K. (1977): *Anatomy of Seed Plants*, 2<sup>nd</sup> Ed. New York, John Wiley and Sons.
- FITTER A.H., HAY R.K.M. (2002): *Environmental Physiology of Plants*. New York, Academic Press.

- FRIEND A.D., WOODWARD F.I., SWITZUR V.R. (1989): Field measurements of photosynthesis, stomatal conductance, leaf nitrogen, and  $\delta^{13}\text{C}$  along altitudinal gradients in Scotland. *Functional Ecology*, **3**: 117–122.
- GOULD K.S. (1993): Leaf heteroblasty in *Pseudopanax crassifolius*: functional significance of leaf morphology and anatomy. *Annals of Botany*, **71**: 61–70.
- GRABHERR G., GOTTFRIED M., GRUBER A., PAULI H. (1995): Patterns and current changes in alpine plant diversity. In: CHAPIN III F.S., KÖRNER C. (eds): Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies 113. Berlin, Springer: 167–181.
- GROSSET G.E. (1959): Siberian Dwarf Pine. Moscow, Moskovskoie Obshchestvo Ispytateley Prirody: 144. (in Russian)
- HADLEY J.L., SMITH W.K. (1983): Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming. *Arctic and Alpine Research*, **15**: 127–135.
- HENRY G.H.R., MOLAU U. (1997): Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, **3**: 1–9.
- HIKOSAKA K., NAGAMATSU D., ISHII S., HIROSE T. (2002): Photosynthesis – nitrogen relationships in species at different altitudes on Mount Kinabalu, Malaysia. *Ecological Research*, **17**: 305–313.
- JOKELA A., SARJALA T., KAUNISTO S., HUTTUNEN S. (1998): The structure and hardening status of Scots pine needles at different potassium availability levels. *Trees*, **12**: 490–498.
- JURIK T.W. (1986): Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *American Journal of Botany*, **73**: 1083–1092.
- KAINULAINEN P., HOLOPAINEN J.K., PALOMÄKI V., HOLOPAINEN T. (1996): Effect of nitrogen fertilization on secondary chemistry and ectomycorrhizal state of Scots pine seedlings and on growth of grey pine aphid. *Journal of Chemical Ecology*, **22**: 617–636.
- KAJIMOTO T. (1989): Aboveground biomass and litterfall of *Pinus pumila* scrubs growing on the Kiso mountain range in central Japan. *Ecological Research*, **4**: 55–69.
- KAJIMOTO T. (1992): Dynamics and dry matter production of belowground woody organs of *Pinus pumila* trees growing on the Kiso mountain range in central Japan. *Ecological Research*, **7**: 333–339.
- KAJIMOTO T., KURACHI N., CHIBA Y., UTSUGI H., ISHIZUKA M. (1996): Effects of external factors on growth and structure of *Pinus pumila* scrub in Mt. Kinpu, central Japan. In: KOMASA K. et al. (eds): Climate Change and Plants in East Asia. Tokyo, Springer: 149–156.
- KAJIMOTO T., SEKI T., IKEDA S., DAIMARU H., OKAMOTO T., ONODERA H. (2002): Effects of snowfall fluctuation on tree growth and establishment of subalpine *Abies mariesii* near upper forest-limit of Mt. Yumori, northern Japan. *Arctic, Antarctic, and Alpine Research*, **34**: 191–200.
- KHOMENTOVSKY P.A. (2004): Ecology of the Siberian Dwarf Pine (*Pinus pumila* (Pallas) Regel) on Kamchatka (General Survey). Enfield, Science Publisher: 226.
- KÖRNER C. (1994): Impact of atmospheric changes on high mountain vegetation. In: BENISTON M. (ed.): Mountain Environments in Changing Climates. London, Routledge: 155–166.
- KÖRNER C. (1999): Alpine Plant Life. Berlin, Springer: 338.
- KOZŁOWSKI T.T. (1971): Growth and Development of Trees. Volume I – Seed Germination, Ontogeny, and Shoot Growth. New York, London, Academic Press: 443.
- LARCHER W. (1995): Physiological Plant Ecology. Berlin, Springer-Verlag: 506.
- MOLOZHNIKOV V.N. (1975): *Pinus pumila* of Mountain Landscapes of Northern Part of the Western Coast of Lake Baikal. Moscow, Nauka: 203. (in Russian)
- NĚMEC B., BARTOŠ J., HRŠEL I., CHALOUPKA J., LHOTSKÝ O., LUXOVÁ M., MILOVIDOV P., NEČÁSEK J., PAZOURKOVÁ Z., PAZOUREK J., SOSNOVÁ V. (1962): Botanical Microtechnic. Praha, Nakladatelství Československé akademie věd. (in Czech)
- OKITSU S. (1988): Geographical variation of annual fluctuations in stem elongation of *Pinus pumila* Regel in the Taisetsu mountain range, Hokkaido, Japan. *Japanese Journal of Ecology*, **38**: 177–183.
- OKITSU S., ITO K. (1984): Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu mountain range, Hokkaido, Japan. *Vegetatio*, **58**: 105–113.
- POULOS H.M., BERLYN G.P. (2007): Variability in needle morphology and water status of *Pinus cembroides* across an elevational gradient in the Davis Mountains of west Texas, USA. *The Journal of the Torrey Botanical Society*, **134**: 281–288.
- PRASAD B.K. (1986): Staining Technique in Botany. Dehradun, International Book Distributors: 107.
- R Development Core Team (2007): R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org> (accessed January 5, 2009)
- RICHARDSON A.D., BERLYN G.P., GREGOIRE T.G. (2001): Spectral reflectance of *Picea rubens* (Pinaceae) and *Abies balsamea* (Pinaceae) needles along an elevational gradient, Mt. Moosilauke, New Hampshire, USA. *American Journal of Botany*, **88**: 667–676.
- SANO Y., MATANO T., UJHARA A. (1977): Growth of *Pinus pumila* and climate fluctuation in Japan. *Nature*, **266**: 159–161.
- SCHÖB CH., KAMMER P.M., CHOLER P., VEIT H. (2009): Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecology*, **200**: 91–104.
- SUTINEN S., VUORINEN M., RIKALA R. (2006): Developmental disorders in buds and needles of mature Norway spruce, *Picea abies* (L.) Karst., in relation to needle boron concentrations. *Trees*, **20**: 559–570.

- ŠESTÁK Z. (1985): Photosynthesis During Leaf Development. Praha, Academia; Dordrecht, Boston, Lancaster, Dr. W. Junk Publishers.
- ŠPINLEROVÁ Z., MARTINKOVÁ M. (2006): Growth of mountain pine (*Pinus mugo* Turra) in relation to the use of other tree species. Journal of Forest Science, **52**: 217–225.
- TADAKI Y., HATIYA K., MIYAUCHI H. (1970): Studies on production structure of forest 16. Primary productivity of *Abies veitchii* in the subalpine zone of Mt. Fuji. Bulletin of Government Forest Experiment Station (Tokyo), **229**: 1–12.
- TAIZ L., ZEIGER E. (2006): Plant Physiology. 4<sup>th</sup> Ed. Sunderland, MA Sinauer Associates Inc.: 705.
- TAKAHASHI K. (2005): Effects of artificial warming on shoot elongation of alpine dwarf pine (*Pinus pumila*) on Mount Shogigashira, central Japan. Arctic, Antarctic, and Alpine Research, **37**: 620–625.
- TAKAHASHI K. (2006): Shoot growth chronology of alpine dwarf pine (*Pinus pumila*) in relation to shoot size and climatic conditions: a reassessment. Polar Bioscience, **19**: 123–132.
- TAKAHASHI K., SEINO T., KOHYAMA T. (2001): Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species. Canadian Journal of Forest Research – Revue Canadienne De Recherche Forestière, **31**: 1336–1347.
- TAKAHASHI K., TATSUYUKI S., KAHYAMA T. (2005): Plastic changes of leaf mass per area and leaf nitrogen content in response to canopy openings in saplings of eight deciduous broad leaved tree species. Ecological Research, **20**: 17–23.
- TEMESGEN H., WEISKITTEL A.R. (2006): Leaf mass per area relationships across light gradients in hybrid spruce crowns. Tress, **20**: 522–530.
- THEURILLAT J.P., GUISAN A. (2001): Potential impact of climate change on vegetation in the European Alps: A review. Climatic Change, **50**: 77–109.
- TRANQUILLINI W. (1964): The physiology of plants at high altitudes. Annual Review of Plant Physiology and Plant Molecular Biology, **15**: 345–362.
- VORONIN V.I. (2008): Large-scale forest decline in east Siberia by industrial emissions at the end of XX century. In: Proceedings from the Conference Ecology and Diversity of Forest Ecosystems in the Asiatic Part of Russia. Praha, ČZU, FLD: 157–168.
- ZHANG J., CREGG B.M. (2005): Growth and physiological responses to varied environments among populations of *Pinus ponderosa*. Forest Ecology and Management, **219**: 1–12.

Received for publication May 27, 2009  
Accepted after corrections August 24, 2009

---

*Corresponding author:*

Ing. ROMAN GEBAUER, Ph.D., Mendelova univerzita v Brně, Lesnická a dřevařská fakulta, Zemědělská 3,  
613 00 Brno, Česká republika  
tel.: + 420 545 134 057, fax: + 420 545 211 422, e-mail: gebo@email.cz

---