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LATE PLEISTOCENE DEGLACIATION IN THE VOSGES AND THE KRKONOŠE MOUNTAINS: CORRELATION OF COSMOGENIC ¹⁰Be EXPOSURE AGES

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The paper is focused on correlation of Late Pleistocene deglaciation of the Vosges in Eastern France and the Krkonoše Mountains in the Bohemian Massif through measurements of in situ-produced cosmogenic ^{10}Be ages of glacial landforms. The minimum ^{10}Be exposure ages of deglaciation after the last glacial expansion in the eastern flank of the Vosges range from 19.2 ± 2.09 ka to 5.11 ± 1.25 ka and in the Krkonoše Mountains from 27.17 ± 2.26 ka to 4.41 ± 0.52 ka. The results indicate a rapid retreat of glaciers in the Vosges at 10.2 ± 0.45 ka and they do not evidence of significant ^{10}Be exposure ages variations with altitude. In the Krkonoše Mountains the most recent glacial expansion was completed before 13.81 ± 1.29 ka and 12.45 ± 1.68 ka respectively for the Labský důl Valley and the Obří důl Valley. Labský důl Valley deglaciation began on south facing slopes at 995 m a. s. l. 14.37 ± 1.37 ka ago, near terminal moraines at 820 m 13.81 ± 1.29 ka ago and reached the upper end of the cirque (1 275 m) at 10.3 ± 0.86 ka. In the Obří důl Valley cirque, the deglaciation started at 990 m around 12.45 ± 1.68 ka and was

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extensive amount of relevant publications has been summarized by Mercier et al. (1999). It also includes a description of sampling, laboratory and interpretation steps of ¹⁰Be method of dating and considerations about topographic, snow cover or vegetation shielding and possibilities of rock surface weathering and small-scale erosion.

¹⁰Be analyses of samples were performed by accelerator mass spectrometry (AMS) at the Tandétron AMS facility of Gif (France) from a purified 0.25-1 mm granulometric quartz fraction spiked with 0.3 mg of ⁹Be carrier. NIST ¹⁰Be standard (Standard Reference Material 4325, ¹⁰Be/⁹Be = 2.68×10⁻¹¹, 1986 August) was used to calculate ¹⁰Be concentrations. This work uses a calibrated regional production rate, allowing significant reduction of uncertainties in exposure age calculations. Since there is still no agreement, ages are reported as "¹⁰Be exposure ages" and were not corrected for potential variability of the paleomagnetic field intensity.

Spatial and temporal variability of the production rate is the most significant source of error for exposure age estimates from cosmonuclide concentration measurements (Gosse and Phillips 2001). To calculate exposure ages from the measured ¹⁰Be concentrations, we utilized a production rate determined for material from the well-dated Köfels landslide in Austria (Kubik and Ivy-Ochs 2004). Köfels production rate was normalized to the latitude and altitude of our samples using the scaling factors of Stone (2000) and an atmospheric attenuation length of 130 g/cm² (Brown et al. 2000). The production rates were not only scaled to the sampling latitudes and altitudes but were also corrected for shielding by surrounding obstructions using image analysis of wide-angle photographs.

In the studied areas, episodic winter burial of the samples by snow also affects the ¹⁰Be production rate. Even if in the past snowfall was most likely different from that of today, a first order estimate of the reduction of the production rate by snow overburden was calculated for each sample. ¹⁰Be production rate corrections induced by the snow cover range from 1 to 15 %, most of them being lower than 5 %.

Radiometric dating using in-situ production rates of ¹⁰Be is a relatively young method, and, therefore, it should be testified in different environmental conditions and also compared with results of other radiometric methods of dating relating to geomorphology.

DESCRIPTION OF REGIONS AND SITES OF SAMPLES

The Vosges

The horst massif of the Vosges in Eastern France is located on the collision zone of the Hercynian orogen and it was uplifted during the Neogene. The westward slope is gentle and the plateau is derived from pre-Miocene peneplain (B. Etlicher in Koster et al. 2005). On the contrary, the Vosges shows a steep eastern side towards the Rhine Graben. The main ridge is oriented NNE – SSW (Fig. 2), with higher elevations in the south (Grand Ballon 1 424 m a. s. l.) and moderate plateau around 700 m a. s. l. in the north. During the maximum extent of Pleistocene glaciers the Vosges were completely covered by a local ice cap

(Mercier and Jeser 2004), with valley glaciers descending on both sides of the mountains. The lenghts of these glaciers were upto 40 km on the western side and 15 km on the eastern side of the Vosges.

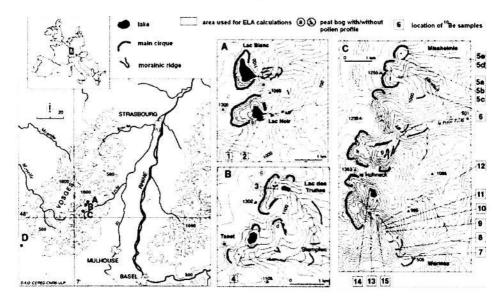


Fig. 2. Location of ¹⁰Be dated samples and peat bogs on a simplified geomorphological map in the Vosges

A – Lac Noir cirque; B – Lac des Truites cirque; C – Missheimle cirque and Wormsa valley. D – "La Grande Pile" pollen profile. The other peat bogs studied in the publications are: a = Tockensee, b = Lac Noir, c = Gazon de Faing, d = Stillenbach, e = Tanet, f = Hirschensteinried, g = Rothried, h = Frankenthal.

During the last glacial period, the Vosges massif in Eastern France is thought to have been affected by steep climatic gradients due to: (i) its location within the discontinuously glaciated corridor extending from 48° N to 53° N between the edges of the Scandinavian ice sheet to the north and the alpine ice sheet to the south; (ii) its topographic lee position with respect to west-east general circulation, and (iii) its topography generating a significant precipitation gradient from west to east (200 mm/km). These make the Vosges particularly well-suited to study the climatic oscillations in Europe. During the last glacial cycle, while a plateau glacier developed in the western Vosges, in the eastern Vosges, precipitation and temperature gradients as well the pronounced topography of the eastern flank induced development of deep valley glaciers anchored in well shaped cirques which remain visible to the present day.

In the western Vosges, the ¹⁴C ages of peat bogs (Fig. 2D) associated with the three terminal moraines correspond to the marine isotopic stage 3 age (30 to 45 ka). By contrast, the upper valleys of the eastern flank of the Vosges Massif exhibit numerous late recessional moraine deposits corresponding to climatic oscillations. Although this deposits remain undated, till and outwash sediments

have therefore been estimated as Würmian. However, palynological studies of bogs located on the cirque floor at the heads of some eastern valleys (Fig. 2D) suggest a Preboreal for their development (Woillard 1978, Woillard and Mook 1982).

Twenty boulders (2-3 m diameter) were sampled for this study (Fig. 2A, B, C). From north to south, the 5 studied sites are: 1) The Lac Noir cirque (Fig. 2A) contains a lake in its overdeepened part. Both cirque and lake are surrounded by a ~30 m high moraine lobe. Sample 1 is a roche moutonnée located between the lake and the upper cirque while sample 2 was taken from a ~28 m³ granitic boulder lying on the inner part of the south side of the moraine's lobe. 2) Sample 3 comes from the central upper roche moutonnée located in the Lac des Truites cirque (Fig. 2B). 3) Sample 4 was taken from a boulder of a small recession moraine's ridge limiting a peat bog within the Tanet cirque. 4) The Missheimle cirque (Fig. 2C) is one of the four upper cirques of the Altenbach valley. Five boulders (5a-b-c-d-e) were sampled on the two moraines formed on the lip of the Missheimle cirque, in front of a steep slope: 5b, 5e come from the inner moraine whilst 5a, 5c the outer and 5d is an angular boulder lying on the outer moraine, near the cirque wall. One 20 m³ erratic boulder (sample 6) from a recessional moraine was sampled 2 km beyond the Missheimle cirque. At this location, the glacier most likely became a hanging glacier above the Petite Fecht valley. 5) Morainic samples 7 and 8, and roches moutonnées samples (9, 10, 11, 12, 15, 13 and 14) come from the Wormsa valley.

The Krkonoše Mountains

The general relief patterns of the main Krkonoše Mountains ridge (1 400-1 600 m) are large plateaus limited to the north by a NW - SE oriented abrupt slope of 700-800 m, and to the south by a parallel lower ridge. The whole area is inclined to the south, which has strongly influenced the development of the river network. The northern rivers flow directly from the main divide to the north while the upper courses of the southern ones begin on the summit plateaus. The principal evidences for Pleistocene glaciation in the Krkonoše Mountains is the presence of cirques, glacier accumulations and fluvioglacial sediments. Valley and cirque glaciers were formed in at least twelve regions of the Krkonoše Mountains during the last glaciation. Most of these glacial features are preserved in the Obří důl Valley and in the Labský důl Valley (Fig. 3) where one can find evidence of two of the largest glaciers of the Krkonoše Mountains. During the last (Wűrm) glaciation the lowest snow line position was situated at approximately 1 000 - 1 100 m a. s. l. The present-day (theoretical) position of the permanent snow line in the Krkonoše Mountains is considered to be about 1 600-1 700 m higher.

The Obří důl Valley

Crystalline rock samples were taken at sites G01 and G02 in the western and the best developed part of the bottom of the Úpská jáma Pit cirque (Fig. 3A). This part is separated from the northern part of the cirque by an inexpressive crest forming the watershed line between the Úpa River and its left-side affluent

Lavinový potok Brook. The Úpa river steps down into the cirque from the summit etchplain (~1 400 m) by a pronounced erosional notch below which it flows through a glacially transformed valley deepened into the granite. Sample G03 was taken at the foot of the northern wall's erosional ravine. Sample G04 was taken from a rock block and slight slope movement of this block cannot be excluded. Rock samples G05 and G06 were taken from rounded granite surfaces in the lower part of the Čertův hřebínek Crest in the southern part of the Úpská jáma Pit. The sampling sites G07 and G08 are situated in the upper part of the lower cirque step of the Úpská jáma Pit and the site G09 in its lower part. This cirque step (960-1 050 m) is the place where the ancient glacier fell in the form of an icefall into the trough of the Obří důl Valley.

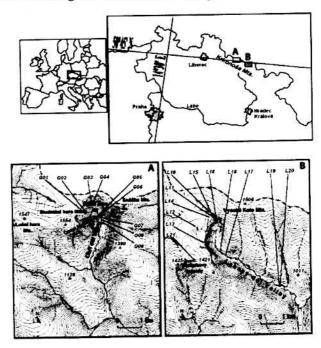


Fig. 3. Location of ¹⁰Be dated samples in the Krkonoše Mountains. A refers to the Obří důl Valley and B refers to the Labský důl Valley and neighbouring areas.

The Labský důl Valley and neighbouring areas

The highest part of the Labský důl Valley (Fig 3B) evidences the erosional Labská rokle Ravine. The over-200 m long and 30 to 50 m wide defile is oriented and open to the SE. Its bottom is covered mainly by debris. The upper part of this Labe River defile is limited by a pronounced edge of rock slopes which, higher up, link to a slightly inclined planation surface. The Labe River, springing on an uplifted peneplain probably of Tertiary age, overcomes the mentioned edge by a waterfall and continues through the Labská rokle Ravine. Rock sample L10 has been taken from a rock outcrop in the upper part of the

ravine. Sample L11 originates from a site above the upper edge of the waterfall. Rock sample L12 comes from the watershed plateau Labská louka, a relic of an uplifted graded surface, qualified as an etchplain. The slightly undulated surface results from the long-term influence of denudational processes continuing from the Mesozoic up to the end of the Palaeogene. This planation surface has been uplifted to its present position (1 300 to 1 400 m) by Neogenic tectonic activity, manifested in the Krkonoše Mountains region mainly by block uplifts. The site of the rock sample L13 is situated on the upper cirque edge of the Pančavská jáma Pit, in the immediate proximity of the Pančavský Vodopád Waterfall. This rock edge forms the boundary line between the relic of the etchplain of the Pančavská louka Meadow and the composed cirque of the Labský důl Valley, above its largest cirque-in-cirque landform, the so-called Pančavská jáma Pit. Rock samples L14, L15 and L16 were taken from the upper closure of the Labský důl Valley. Samples L17 and L18 represent rock outcrops of the cirque step of the Labský důl Valley which evidenced a morphostructural increase in inclination (8-9° compared to 1-3° of the cirque) of the valley bottom between 920 m and 1 010 m. This valley step is an area where a tongue of the ancient Labský ledovec Glacier used to flow away from the cirque and passed to the trough bottom by an icefall. The lower part of the Labský důl Valley is represented by rock samples L19 and L20, taken from granite blocks on the ridge of terminal moraine, situated nearly 100 m above the mouthing of the Medvědí potok Brook into the Labe River. The moraine accumulation rises from flat valley bottom (820 m) and covers the slope up to an altitude of about 855 m with a total length of more than 600 m. Rock sample L21 was taken from a denuded bedrock near the Harrachovy kameny Stones (1 421 m) situated on the southwestern ridge of the Krkonoše Mountains. This torso type summit, partially covered by eluvial and slope sediments, is part of a group of rock outcrops and tors forming the southern margin of large plateaus of the Labská and the Pančavská louka Meadows. These plateaus are relics of an uplifted planation surface probably of Tertiary age.

RESULTS

The Vosges

The presence of preserved striations on several roche moutonnée, yields us to assume that losses due to rock weathering and erosion are minor. Interplay of local topography with the climatic perturbations is evidenced by the occurrence of 6 different Holocene push moraines at low altitude (Tab. 1 and Fig. 2C).

When plotted as a function of altitude (Fig. 4), minimum 10 Be exposure ages ranging from ~5 to ~19 ka (Tab. 1) do not evidence any significant variations with altitude. This suggests that rapid retreat occurred after the most recent glacial expansion in the eastern flank of the Vosges Massif around a mean weighed 10 Be age of 10.2 ± 0.45 ka. The oldest sample, 6a,b and the two youngest, 1, 5d have been excluded from this mean. Due to its position near the lake sample 1 may have been buried; sample 5d, the youngest age among the 5 ages obtained for the Missheimle moraine, may have undergone a displacement since its emplacement.

Tab. 1. Sample details and ¹⁰Be results for the Vosges samples. The calculated production of ¹⁰Be is corrected to account for burial by seasonal snow cover and for topographic shielding

| Sample | Altitude (m) | Dip ¹ (°) | Production rate (at/g/yr) | ¹⁰ Be concentration (10 ⁵ at/g) | ¹⁰ Be error (10 ⁵ at/g) | T _{min} . (10 ³ yrs) | T _{min} error (10 ³ yrs) |
|--------|--------------|-------------------------|------------------------------|---|--|---|--|
| 1* | 971 | 21 | 13.2 | 0.68 | 0.16 | 5.11 | 1.25 |
| 2* | 1 001 | 1 | 13.6 | 1.31 | 0.13 | 10.63 | 1.25 |
| 3* | 1 110 | 19 | 14.5 | 1.37 | 0.13 | 10.55 | 1.20 |
| 4* | 1 100 | 31 | 14.4 | 1.34 | 2.30 | 10.80 | 1.96 |
| 4bis* | 1 100 | 31 | 14.4 | 1.40 | 1.39 | 11.30 | 1.31 |
| 5a* | 1 102 | 28 | 14.0 | 1.60 | 1.14 | 12.90 | 1.21 |
| 5b# | 1 102 | 15 | 14.0 | 1.49 | 1.24 | 11.60 | 1.19 |
| 5c* | 1 102 | 30 | 14.0 | 1.60 | 1.31 | 13.00 | 1.33 |
| 5d# | 1 102 | 0 | 14.0 | 0.75 | 1.49 | 5.80 | 1.21 |
| 5e# | 1 102 | 16 | 14.0 | 1.48 | 1.38 | 11.60 | 1.29 |
| 6a§ | 850 | 0 | 11.9 | 1.71 | 1.23 | 15.90 | 1.49 |
| 6b§ | 850 | 43 | 11.6 | 1.77 | 1.61 | 19.20 | 2.09 |
| 7# | 537 | 10 | 9.4 | 0.85 | 0.09 | 10.30 | 1.32 |
| 8# | 572 | 8 | 9.7 | 0.81 | 0.09 | 9.20 | 1.24 |
| 9* | 620 | 21 | 10.0 | 0.76 | 0.18 | 8.70 | 2.19 |
| 10* | 628 | 16 | 10.1 | 1.01 | 0.12 | 11.50 | 1.56 |
| 11* | 645 | 0 | 10.3 | 0.94 | 0.10 | 10.60 | 1.29 |
| 12* | 699 | 38 | 10.2 | 0.64 | 0.07 | 7.60 | 1.02 |
| 13* | 816 | 0 | 11.7 | 1.02 | 0.11 | 9.80 | 1.18 |
| 14* | 951 | 8 | 12.9 | 1.16 | 0.11 | 10.20 | 1.18 |
| 15* | 773 | 21 | 11.2 | 1.04 | 0.12 | 10.60 | 1.37 |

Dip angles measured with reference to the horizon. * refers to roche moutonnée; * to boulder from moraines, and § to an erratic boulder.

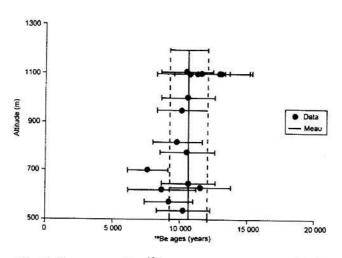


Fig. 4. Vosges samples: ¹⁰Be exposure ages versus altitude

The Krkonoše Mountains

The exposure ages of 21 samples from rock slopes of cirques, tors, roche moutonnée, moraines and boulders collected for 10 Be dating (Tab. 2) in the dissected relief of the Krkonoše Mountains range from 27.17 ± 2.26 to 4.41 ± 0.52 ka. The oldest 10 Be exposure age was found for the tor sample L21, 27.17 ± 2.26 ka, located at 1 420 m on the southwestern ridge of the Labe plateau. The second oldest sample, boulder L12, 22.88 ± 1.86 ka, is located in a mild saddle area of the central part of this high plateau. This lower part of high plateau was covered by a table glacier somewhat longer than group of tors on the ridge with sample L21. Four youngest samples 10 Be ages for samples L10, L11, G04 and G09 can be explained by cryogenic and/or fluvial erosion combined with temporary burial or slope movements.

Tab. 2. Sample details and 10 Be results for the Krkonoše Mountains samples. The calculated production of 10 Be is corrected to account for burial by seasonal snow cover and for topographic shielding

| Sample | Altitude (m) | Dip ¹ (°) | Production rate (at/g/yr) | ¹⁰ Be concentration (10 ⁵ at/g) | ¹⁰ Be error (10 ⁵ at/g) | T_{min} . (10^3 yrs) | T _{min} . error (10 ³ yrs) |
|--------|--------------|-------------------------|------------------------------|---|---|----------------------------------|---|
| G01 | 1 200 | 20.0 | 13.0 | 1.15 | 0.13 | 8.85 | 0.94 |
| G02* | 1 180 | 17.0 | 12.9 | 1.24 | 0.14 | 9.58 | 1.14 |
| G03* | 1 250 | 36.5 | 13.2 | 1.39 | 0.17 | 10.58 | 1.25 |
| G04* | 1 200 | 0.0 | 13.6 | 0.72 | 0.11 | 5.28 | 0.69 |
| G05* | 1 060 | 26.5 | 11.9 | 1.30 | 0.13 | 10.96 | 1.17 |
| G06* | 1 040 | 14.0 | 12.1 | 0.81 | 0.16 | 6.74 | 1.13 |
| G07* | 1 020 | 11.0 | 11.9 | 1.06 | 0.12 | 8.90 | 1.00 |
| G08* | 990 | 15.0 | 11.6 | 1.44 | 0.19 | 12.45 | 1.68 |
| G09* | 970 | 25.0 | 11.2 | 0.62 | 0.10 | 5.52 | 0.78 |
| L10* | 1 280 | 0.0 | 14.5 | 0.64 | 0.07 | 4.41 | 0.52 |
| L11* | 1 290 | 11.0 | 14.9 | 1.01 | 0.09 | 6.73 | 0.63 |
| L128 | 1 335 | 4.0 | 15.3 | 3.49 | 0.24 | 22.88 | 1.86 |
| L13 | 1 300 | 8.0 | 15.0 | 1.96 | 0.14 | 13.11 | 1.09 |
| L14* | 1 275 | 11.0 | 14.3 | 1.47 | 0.11 | 10.30 | 0.86 |
| L15* | 1 098 | 12.0 | 12.4 | 1.43 | 0.12 | 11.52 | 1.11 |
| L16* | 1 095 | 19.0 | 12.3 | 1.32 | 0.12 | 10.75 | 1.03 |
| L17* | 995 | 0.0 | 11.4 | 1.63 | 0.14 | 14.37 | 1.37 |
| L18 | 970 | 0.0 | . 11.4 | 1.18 | 0.11 | 10.35 | 0.98 |
| L19* | 830 | 0.0 | 10.0 | 1.44 | 0.12 | 14.42 | 1.35 |
| L20# | 828 | 0.0 | 10.0 | 1.37 | 0.12 | 13.81 | 1.29 |
| L 21 | 1 425 | 0.0 | 16.7 | 4.50 | 0.31 | 27.17 | 2.26 |

¹ Dip angles measured with reference to the horizon. * refers to roche moutonnée; * to boulder from moraines, and § to an erratic boulder.

When plotted as a function of altitude (Fig. 5), the calculated 10 Be cosmic ray exposure ages for both Krkonoše Mountains systems (except the oldest and youngest samples) are more scattered than those previously discussed for the Vosges. The most recent glacial expansion was completed before 13.81 ± 1.29 and 12.45 ± 1.68 ka respectively for the Labský důl Valley and the Obří důl Valley. Labský důl Valley deglaciation began on south facing slopes at 995 m 14.37 ± 1.37 ka ago and near terminal moraines at 820 m 13.81 ± 1.29 ka ago and reached the upper end of the cirque 1 275 m at 10.3 ± 0.86 ka. In the Obří důl Valley cirque, the deglaciation started at 990 m around 12.45 ± 1.68 ka and was completed in the main cirque (1 180 m) at 9.58 ± 1.14 ka. Permanent ice and firn fields were still present in the upper parts of cirques and on high plateaus up to the Middle Holocene.

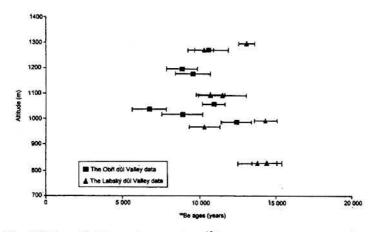


Fig. 5. Krkonoše Mountains samples: ¹⁰Be exposure ages versus altitude

CONCLUSIONS

The minimum 10 Be exposure ages of deglaciation after the last glacial expansion in the eastern flank of the Vosges range from 19.2 ± 2.09 ka to 5.11 ± 1.25 ka and in the Krkonoše Mountains from 27.17 ± 2.26 ka to 4.41 ± 0.52 ka. The results indicate a rapid retreat of glaciers in the Vosges at 10.2 ± 0.45 ka and they do not evidence of significant exposure ages variations with altitude. The wide range of exposure ages in the Krkonoše Mountains evidences the time of deglaciation on particular localities was depending not only on altitude but also on the landforms pattern and very local topography which, in turn can have major impacts on local climate. The exposure ages of deglaciation for both the Vosges and the Krkonoše Mountains appears to be related to the Younger Dryas climate event. These results are in good agreement with recent paper by Rinterknecht et al. (2004) about 10 Be chronology of a sequence of prominent Weichselian moraines of the Scandinavian Ice Sheet in northeastern Europe.

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work and analyses were supported by INSU through the DBT II Program. Tandétron operation is supported by the CNRS, CEA and IN2P3. Interpretation of ¹⁰Be exposure ages of samples Lecture is based on published results of the long-term geomorphological research in the Vosges and the Krkonoše Mountains (e. g. Mercier et al. 2001 and 2002, Carr et al. 2002 and Bourlès et al. 2004). The paper was prepared in the framework of research project of the Faculty of Science, Charles University in Prague, MSM 0021620831.

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ODLEDŇOVÁNÍ VOGÉZ A KRKONOŠ V POZDNÍM PLEISTOCÉNU: KORELACE DATOVÁNÍ EXPOZICÍ KOSMOGENNÍM ¹⁰Be

Práce se zabývá průběhem pozdně pleistocénního odledňování Vogéz ve východní Francii a Krkonoš v Českém masivu. Byla provedena geomorfologická analýza reliéfu těchto pohoří a korelace datování vybraných glacigenních tvarů radiometrickou metodou 10Be. Minimální stáří expozice in-situ produkovaným 10Be je indikátorem ústupu zalednění po poslední expanzi ledovců na východních svazích Vogéz od 19,2 ± 2,09 ka do $5,11\pm1,25$ ka a v Krkonoších od $27,17\pm2,26$ ka do $4,41\pm0,52$ ka. Výsledky tohoto radiometrického datování metodou ¹⁰Be svědčí o rychlém ústupu ledovců ve Vogézách před 10,2 ± 0,45 ka, přičemž neukazují na jejich podstatnou závislost na nadmořské výšce. V Krkonoších byl poslední postup ledovců dokončen v Labském dole před 13,81 ± 1,29 ka a v Obřím dole před 12,45 ± 1,68 ka. Odledňování Labského dolu začalo na svazích s jižní expozicí v 995 m n. m. před 14,37 ± 1,37 ka, u terminálních morén v 820 m před 13,81 \pm 1,29 ka a dosáhlo horní konec karu (1 275 m) před 10.3 ± 0.86 ka. Ústup zalednění v Obřím dole začal v 990 m před 12,45 ± 1,68 ka a byl dovršen v hlavním karu (1 180 m) před 9,58 ± 1,14 ka. Odlednění Vogéz a Krkonoš proběhlo v období mladšího dryasu, avšak stálá ledová a firnová pole existovala v horních částech karů a na vysoko položených plošinách ještě ve středním holocénu. Větší rozpětí výsledků radiometrického datování metodou ¹⁰Be v Krkonoších nasvědčuje, že odlednění bylo na některých lokalitách závislé zejména na konfiguraci povrchových tvarů a topografii reliéfu, což se projevilo na místních klimato-morfogenetických podmínkách.