



Paleoclimatic implications of glacial and postglacial refugia for *Pinus pumila* in western Beringia

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ARTICLE INFO

Article history:

Received 21 May 2009

Available online 27 January 2010

Keywords:

Refugium

Seasonality

Pollen

Northeastern Siberia

Beringia

Late Quaternary

ABSTRACT

Palynological results from Julietta Lake currently provide the most direct evidence to support the existence of a glacial refugium for *Pinus pumila* in mountains of southwestern Beringia. Both percentages and accumulation rates indicate the evergreen shrub survived until at least ~19,000 ¹⁴C yr BP in the Upper Kolyma region. Percentage data suggest numbers dwindled into the late glaciation, whereas pollen accumulation rates point towards a more rapid demise shortly after ~19,000 ¹⁴C yr BP. *Pinus pumila* did not re-establish in any great numbers until ~8100 ¹⁴C yr BP, despite the local presence ~9800 ¹⁴C yr BP of *Larix dahurica*, which shares similar summer temperature requirements. The postglacial thermal maximum (in Beringia ~11,000–9000 ¹⁴C yr BP) provided *Pinus pumila* shrubs with equally harsh albeit different conditions for survival than those present during the LGM. Regional records indicate that in this time of maximum warmth *Pinus pumila* likely sheltered in a second, lower-elevation refugium. Paleoclimatic models and modern ecology suggest that shifts in the nature of seasonal transitions and not only seasonal extremes have played important roles in the history of *Pinus pumila* over the last ~21,000 ¹⁴C yr BP.

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Introduction

Understanding the dynamics of plant communities under changing climates has been fundamental to late Quaternary paleoecological studies since their inception. One of the earliest issues addressed was the survival of modern flora within harsh, glacial environments (Dahl, 1946; Heusser, 1955). While the concept of glacial refugia is well accepted (see Bennett and Provan, 2008 for discussion and history of the term), new research centered mostly in Europe has caused paleoecologists to rethink the nature of full- and late-glacial environments (e.g., Willis and Whittaker, 2000; Stewart and Lister, 2001; Kullman, 2000, 2008). Relying primarily on nonpalynological data, these investigations have brought into serious question the previously accepted paradigm that Northern Hemisphere refugia occurred in restricted southern locations, with virtually intact modern plant associations migrating northward with post-glacial amelioration. The new data suggest that thermophilous species survived in smaller “cryptic” refugia (Stewart and Lister, 2001), often containing non-analogous plant associations, scattered across glacial and periglacial landscapes, including areas such as northern Scandinavia (e.g., Kullman, 2002) and central and eastern Europe (e.g., Willis et al., 2000; Willis and van Andel, 2004).

Although details are emerging about locations of glacial refugia in Europe, the presence and settings of similar plant refuges in Siberia remain speculative. As in the early European studies, most conclusions about northern Asia are based on palynological data. Grichuk (1984) pioneered one of the first vegetation reconstructions for the last glacial maximum (LGM; ~25,000 to 12,500 ¹⁴C yr BP), using 187 pollen sections that spanned the Soviet Union. He concluded that a mosaic of tundra, steppe, and *Larix-Pinus-Betula* forest occupied areas to the south of the Scandinavian ice-sheet, extending to northern portions of northeastern Siberia. He further inferred the presence of an open *Larix-Betula* forest in areas bordering the northern and eastern Okhotsk Sea, the two forests being separated by tundra and mountain glaciers of central northeastern Siberia. Later studies (Anderson et al., 2002c; Sher et al., 2005; Kienast et al., 2005; Tarasov et al., 2007) supported the conclusion that the northern Siberian landscape was not treeless, although forests or woodlands were likely less extensive than inferred by Grichuk, being restricted to only the most protected and suitable sites. In an attempt to clarify the primarily palynological interpretations, Binney et al. (2009) compiled a comprehensive plant macrofossil database for northern Eurasia. Macrofossils dated to the LGM indicate the presence of *Picea*, *Larix*, *Pinus*, *Alnus*, and *Betula* species in areas of the two continents, but they are sufficiently rare to provide only limited insight into the full-glacial vegetation of Siberia. While macro- and megafossils remain the most definitive means for determining the presence of a plant taxon (Birks,

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1989), Brubaker et al. (2005) demonstrated that with a sufficient number of sites, spatial and temporal patterns in palynological data from the LGM and late glaciation (LG; 12,500–10,000 ^{14}C yr BP) can be used to infer the persistence of major woody species at northern high latitudes. Thus until the Siberian macrofossil database is enriched with additional studies, palynological data will provide the only immediate means for studying possible past refugia in far northern Asia.

Investigations of Siberian glacial refugia have given little attention to *Pinus pumila* (Pall.) Regel (Japanese stone pine). This conifer, a main component of the modern forest and tundra of northeastern Asia, exhibits the climatic hardiness and phenotypic plasticity needed to survive in marginal environments (Khomentovskii, 1995; Krementski et al., 2000; Moskalyuk, 2008). In Russia, the shrub currently is found from eastern Chukotka to the Lena basin and southward to Lake Baikal and the Kuril Islands. *Pinus pumila* takes prostrate form at its latitudinal range limits and is capable of vegetative reproduction. The conifer endures more frigid winters than other *Pinus* taxa because its prostrate habit during the cold season allows for burial of its branches within deep snow cover, thereby protecting the evergreen leaves from winter desiccation. Many of the shrubs take a cup-shaped form, which may enhance utilization of available solar radiation when branches are above snow level. *Pinus pumila* requires moderately warm summers, with its northern limit approximating the 12°C mean July isotherm (Andreev, 1980; Kozhevnikov, 1981). *Pinus pumila*, thus, is somewhat unique in that its paleo-data can be used for inferring conditions during both warm and cool seasons. Furthermore, *Pinus pumila* pollen, unlike other *Pinus* species, has large grains that are not carried long distances by wind, thereby simplifying interpretations of the fossil record (Lozhkin et al., 2001).

Krementski et al. (2000) postulated that the adaptive strategies of *Pinus pumila* make it a prime candidate for survival during the LGM throughout much of its modern range, including areas of northern China, Korea, Japan, eastern Siberia, and the Russian Far East. They cited the early Holocene appearance of *Pinus pumila* pollen in records from such widely separated areas as Lake Baikal, the Lena River valley,

Sakhalin Island, and Kamchatka as indirect evidence of *Pinus pumila* expansion from multiple refugia within Russia. They further noted that the vegetation history of northeastern Siberia (western Beringia, WB) differed from these other regions, with the earliest Holocene plant communities in the northeast lacking *Pinus pumila*. This pattern implies a later migration of the shrub into far northeastern Asia from distant LGM populations. In contrast, Brubaker et al. (2005) proposed that Beringia (northeastern Siberia to far western Canada) was an important locality where boreal trees and shrubs, including *Pinus pumila*, survived long intervals of adverse glacial climates in cryptic refugia. However, their argument for the presence of a *Pinus pumila* refugium in WB is one of the least strong for all described taxa. Although multiple LGM and LG sites in this study contain *Pinus pumila* pollen, only Lesnoye Lake (96 m a.s.l.; Anderson et al. 1997a; Fig. 1) consistently has >5% *Pinus* Haploxylon pollen, a presence/absence threshold suggested by modern pollen studies (Lozhkin et al., 2001). However, the spatial distribution of LG through early Holocene records with trace to 10% *Pinus pumila* pollen does suggest the northern Priokhot'ye–Upper Kolyma region as a possible refugium.

Shilo et al. (2007) recently reported the area near Julietta Lake (61°20.25'N, 153°93.33'E, 880 m a.s.l.; Fig. 1), located in the mountainous Kilgan Massif which separates the Okhotsk Sea coast from the Upper Kolyma drainage, as a probable area where *Pinus pumila* survived during glacial times. The Julietta core contains a pollen assemblage with typical LGM contributors, but it also displays unusually high percentages of *Pinus pumila* pollen (Fig. 2). These high pollen percentages persist into the LG, when they decrease to trace amounts. In the absence of macrofossils, the Shilo et al. (2007) study provides the strongest evidence to date for the continued presence of *Pinus pumila* in WB throughout the LGM, but the absence of radiocarbon dates prior to ~12,200 ^{14}C yr BP limit the certainty of this conclusion. Additional radiocarbon dates from Julietta Lake, reported herein, support the idea that *Pinus pumila* did survive in this area during glacial times in agreement with Grichuk (1984) and Brubaker et al. (2005). However, the modified chronology suggests a somewhat different late LGM–LG vegetation history. We present these

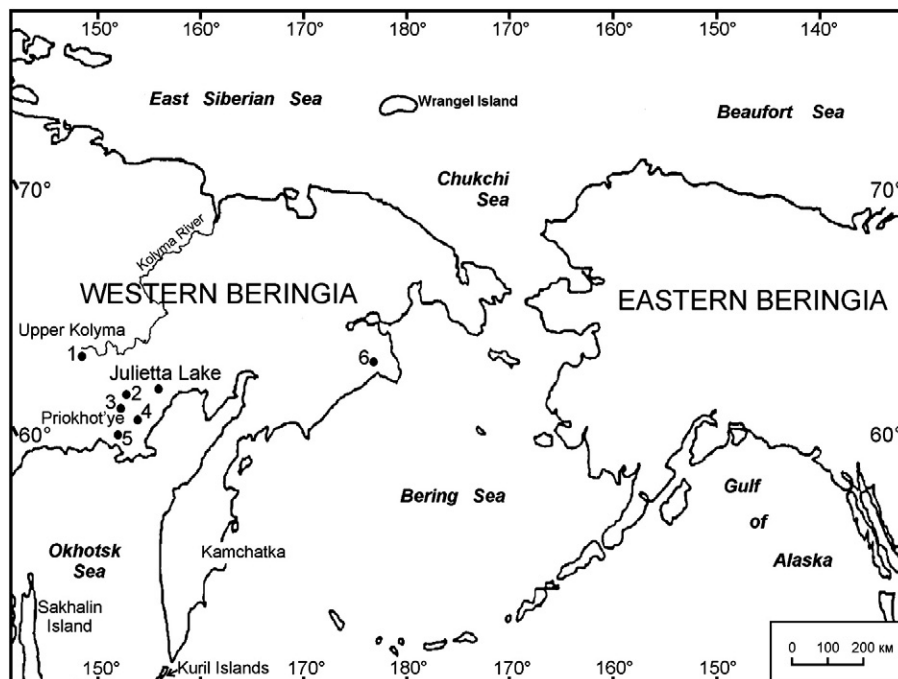


Figure 1. Map of Beringia with location of Julietta and other lake sites mentioned in the text: (1) Elgennya Lake; (2) Goluboye Lake; (3) Elikchan-4 Lake; (4) Lesnoye Lake; (5) Alut Lake; and (6) Gytgykai Lake.

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