Timberline Paleoecology in the Alps

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Holocene Timberline Fluctuations and Climate Variability

Alpine life and landscapes are exposed to extreme environmental conditions. Avalanches, landslides and floods, due to extreme climatic events such as heavy snow and rain storms, can impact both wild and managed landscapes. Above timberline, climatic conditions are so harsh that they impede the growth of trees. According to one recent hypothesis (the "growth-limitation hypothesis"), low temperatures reduce production of plant tissues (Körner, 1999). Therefore, trees become victims of their strategy to accumulate large amounts of biomass in order to overgrow other vegetational life forms. Because the upper boundary of tree growth is temperature controlled, it can be used as a proxy for estimation of past temperatures, assuming that today's occurrence of trees is in equilibrium with local climate. Similar assumptions are made to derive paleo-temperature estimations from other organisms. Many recent paleoecological studies in the Alps have focused on climate reconstruction, but relatively few studies have addressed basic past relationships between organisms and their biotic and abiotic environments. One of the reasons for avoiding the latter topic may be that accurate studies require independent environmental proxies and high temporal resolution (years to decades), especially if the goal is to reconstruct past responses of short-lived organisms to climatic change. Moreover, concerns about global warming have focused much effort on the reconstruction of past climatic changes and their forcing mechanisms, but the response of organisms and biomes seems - at least from an ecological and economical point of view - of similar relevance (e.g. collapse, migration or adaptation of boreal and alpine life).

The above-mentioned assumption that today's distribution of trees is in equilibrium with climate may not necessarily be true. Over the past several thousands years, human activities in the Alps have resulted in lowering of timberlines by 200-300 altitudinal meters. Nevertheless, single trees in remote

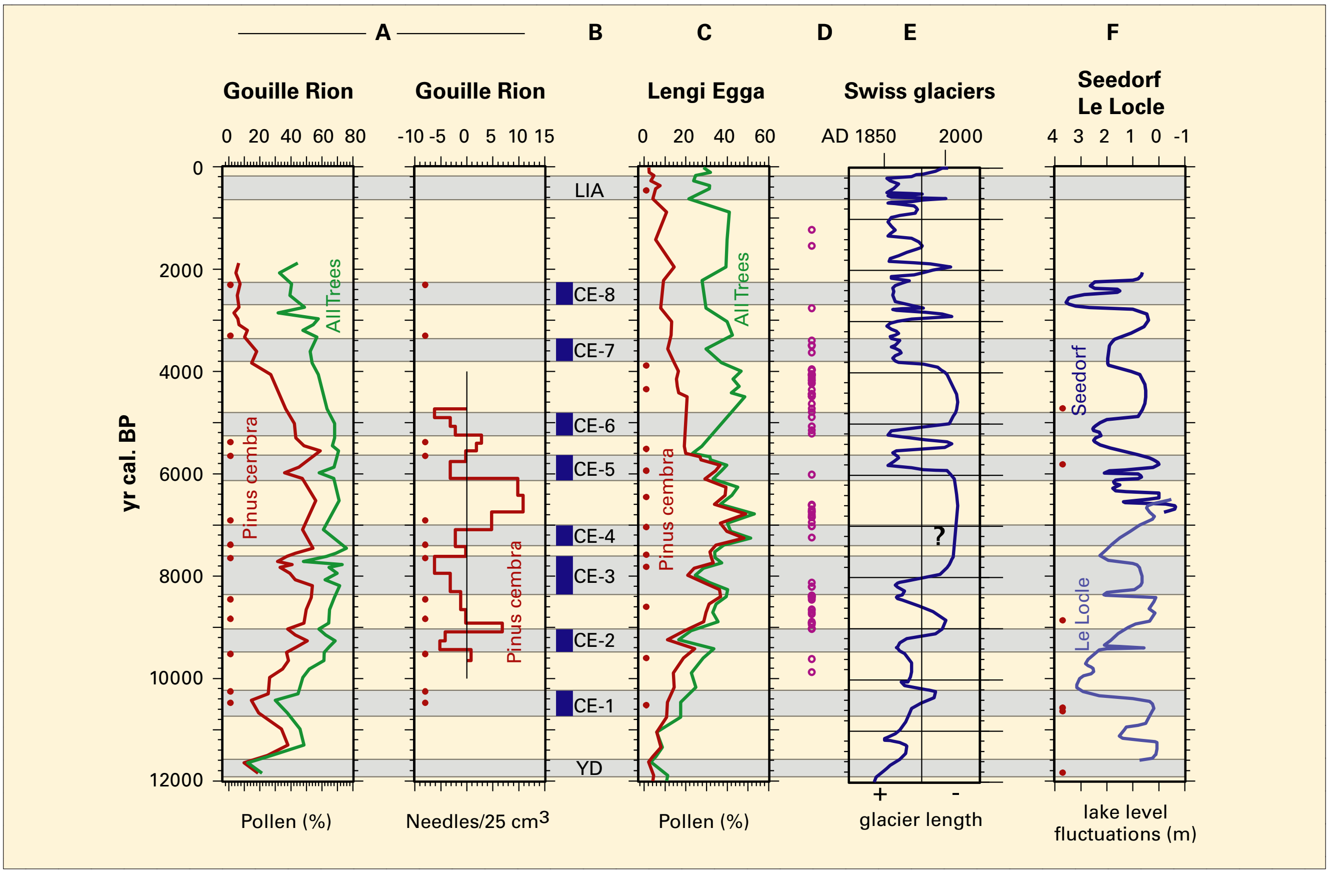

Fig. 1. Comparison between timberline vegetation, glaciers, and lake level fluctuations during the past 12,000 cal. yr BP. ***A***: *Pollen percentages (Pinus cembra, sum of trees) and macrofossil concentrations (Pinus cembra needles) at Gouillé Rion (Swiss Alps) (Tinner et al., 1996; Tinner and Wick, 1997). The pollen sum includes only subalpine and alpine taxa.* ***B***: *Central European cold-humid phases (Haas et al., 1998).* ***C***: *Pollen percentages (Pinus cembra, sum of trees) at Lengi Egga (Swiss Alps) (Tinner, unpublished). The pollen sum includes only subalpine and alpine taxa.* ***D***: *Chronological position of radiocarbon dates of wood and organic debris collected in front of Alpine glaciers (Hormes et al., 2001).* ***E***: *Estimated length variation of Swiss glaciers (Maisch et al., 1999).* ***F***: *Lake level fluctuations in meters at Seedorf and Le Locle (Switzerland) (Magny and Richoz, 1998; Magny and Schoellammer, 1999). The dots in A, C, and F show the chronological position of radiocarbon dates used for the depth-age models.*

areas may still indicate the potential altitudinal limit of tree growth. Qualitative timberline-inferred temperature reconstructions in the Alps are based primarily on these uppermost survivors. No quantitative timberline-based temperature reconstructions are available for the Alps.

Producing qualitative Holocene temperature reconstructions requires records from today's timberline ecotone that reach back to the Late Glacial. Two factors are essential: 1) The chronology must be fixed to an absolute scale with sufficient ^{14}C-dates and 2) terrestrial macrofossils must be present in high amounts throughout the Holocene to demonstrate the local presence of trees or alpine herbaceous species. One example is the Gouillé Rion site (Tinner et al., 1996), situated in the Central Swiss Alps and lying exactly at the limit of today's tree growth (trees > 5m; 2,343 m a.s.l.). Macrofossil analysis shows that the site was forested by coniferous species (*Larix decidua*, *Pinus cembra*) between 10,500 and 3,900 cal. yr BP indicating that during the early and middle Holocene growing season temperature was at least as high as today. Additional data from above today's tree limit indicate the uppermost limit of Holocene forest expansion and hence the range of Holocene temperature oscillations between 10,500 and 3,900 cal. yr BP (Tinner, unpubl.). Treeline was about 120-180 m higher than today in the warmest phases (9,000 - 8,200; 7,000 – 6,400; and 5,000 - 4,000 cal. yr BP.). Assuming a lapse rate of 0.7°C /100m, this suggests summer temperatures about 0.8-1.2°C higher than today. Between 10,500 and 3,900 cal. yr BP, treeline was always situated above the modern limit. Hence, the range of temperature oscillations was limited to 0.8-1.2°C and never fell below today's values. This amplitude of Holocene temperature changes is confirmed by a quantitative chironomid-based study from the northern Alps (Heiri, 2001) (about 80 km away). *Pinus cembra* pollen declines at Gouillé Rion are strongly correlated with negative temperature excursions, as estimated by chironomid-based transfer functions. Moreover, the new study allows a reconstruction of temperature oscillations after 4,000 cal. yr BP, when timberline position was influenced by prehistoric land-use (and hence less reliable for climatic reconstructions). In Figure 1, oscillations of treeline are illustrated by declines in the curves (macrofossils and pollen) of both *Pinus cembra* and all subalpine trees. After the local extinction of *Pinus cembra* at around 4,000 cal. yr BP, cold phases are recorded by tree species growing 200-300 m below the former *Pinus cembra* belt (e.g. *Picea abies*).

A recent systematic redefinition of Holocene climatic fluctuations in the Alps was attempted by Haas et al. (1998). Based on paleoecological data (pollen, macrofossils, sedimentology) as well as ^{14}C-dates, the authors introduced a numerical nomenclature (CE-1 to CE-8, see Fig. 1) for a series of century-scale cold periods during the Holocene. Some of the most severe oscillations seem synchronous with cool climatic periods recorded in the Northern Atlantic marine sediments and in Greenland ice cores.

Temperature, Precipitation or both?

Timberline fluctuations may be caused by changes in temperature, precipitation or both. Comparison with other proxies helps to disentangle temperature and precipitation effects. Timberline forests show oscillations similar to those of alpine glaciers during most of the Holocene. The most pronounced glacier minima were synchronous with uppermost timberline positions (Fig. 1) between 9,000 and 8,200 cal. yr BP, 7,000 and 6,400 cal. yr BP, as well as 5,000 and 4,000 cal. yr BP (Hormes et al., 2001). Maximum glacier advances (Maisch et al., 1999) occurred coincident with timberline depressions (CE-2 to CE-8). A further indication that high Holocene timberline positions reflect warm and dry conditions is provided by Holocene lake level changes across the Alps (e.g. Magny and Richoz, 1998; Magny and Schoellammer, 1999). For example, in the Swiss Jura and on the Swiss plateau (e.g. Le Locle and Seedorf, Fig. 1), lake levels were at a minimum during the Holocene warm phases (9,000 - 8,200; 7,000 – 6,400; 5,000 - 4,000 cal. yr BP.) and at a maximum during most cold phases (Fig. 1). Hence middle- and late-Holocene climatic reversals may have been comparable to the Little Ice Age climatic cooling around AD 1850, when cool summers where accompanied by increased precipitation. However, overall early Holocene climatic conditions in the Alps were more continental than today, with warm and dry summers and cold winters. The transition to today's climatic regimes was not synchronous. For example, in the southern Alps (between Aosta and Garda in Italy and southern Switzerland), the continental climatic regime came to an abrupt end at about 9,100 cal. yr BP, allowing the establishment of the so called Insubrian vegetation (Tinner et al., 1999). In the northern Alps and Central Europe, a similar sudden transition occurred at 8,200 cal. yr BP (Tinner and Lotter, 2001). This latter transition was probably caused by increased inflow of humid air masses from the west and north-west, leading to lower summer and higher winter temperatures and a general increase in the amount of precipitation. Because of the special orographic situation, the continental climate mode has persisted in some valleys of the central Alps until today.

Towards a paleoecological approach

The temporal resolution of the above-mentioned studies (50-300 years) is sufficient to indicate major Holocene climatic oscillations and trends. However, it is insufficient to address how, and how fast, organisms react to environmental changes. In and around the Alps, two recent studies (Ammann et al., 2000; Tinner and Lotter, 2001) follow a new approach to address this question. Based on highly reliable calendar chronologies (varves, calendar years), they compared independent climatic (oxygen isotopes) and biotic proxies. These studies suggest that different organisms (e.g. plants, cladocera, chironomidae) responded very fast to climate change during the Late Glacial and the Holocene (i.e. within 0-20 years). In the case of the Holocene study, vegetational responses to climate change were highly complex and related to physiological characteristics and life histories of the species involved. The resulting interspecific competition patterns were so complex that the response signal was not recognized as climatically driven in numerous previous studies, although it occurred on a subcontinental scale.

We conclude that because of the complex orographic situation and the resulting highly differentiated biome belts in the Alps, high temporal and spatial precision and resolution are required to provide a clear understanding of past climate changes and ecosystem responses. Such high resolution studies are also essential to overcome seeming differences between modern ecological and paleoecological paradigms of ecosystem functioning.

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Paleoenvironmental Reconstructions for Mountains in the Eurasian Mid-Continent

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Paleoenvironmental reconstructions for the Pirin Mountains (southwestern Bulgaria) and the Altai Mountains (southern Siberia, Fig.1) provide insight into the relationships between long-term vegetation dynamics and orbital forcing at two high-elevation sites in the Eurasian mid-continent. The topography of mountain regions constrains vegetation into distinct altitudinal bands, and these bands are sensitive to changes in both temperature and effective moisture through time. The sequence of late-glacial and early-Holocene vegetational change and the vertical displacement of vegetational bands are reconstructed for these mountains by pollen analyses at multiple sites along altitudinal gradients. However, the complexities associated with the dry early-Holocene conditions at these mid-continent sites require additional studies in order to disentangle the various responses of taxa to long-term regional climatic changes.

Fig.1: Location of the two case-study areas in the Eurasian mid-continent

Long-term vegetation dynamics in the Pirin Mountains, Bulgaria

The Pirin Mountains are situated in the eastern part of the Balkan Peninsula. The climate is more continental and significantly drier than in the Alps. Temperate deciduous trees occur at low elevation, followed by beech and then various conifers extending up to the tree line at about 2,200 m. Of particular biogeographic interest in the Pirin Mountains is the common occurrence of the Balkan endemic *Pinus peuce* and (on calcareous soils) the Balkan sub-endemic *Pinus heldreichii*.

Pollen analysis of lake sediments, recovered from several sites near tree line, reveals an unusual sequence of changes in forest composition. After a late-glacial sequence dating back to 13,000 ^{14}C-yr BP at lake Kremensko, the early-Holocene tree line was formed by birch which did not reach as high as the modern tree line (Fig. 2). At Dalgoto Lake close to modern tree line, the early-Holocene pollen assemblage of oak, elm, linden and

* The investigations in the Pirin Mountains were undertaken by Ivanka Stefanova, and those in the Altai Mountains by Tatiana Bliakhartchouk. H.E. Wright and Brigitta Ammann participated in the field work and aided in the interpretation of the pollen stratigraphy in both areas.