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Growth of plants on the Late Weichselian ice-sheet during Greenland interstadial-1?

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A B S T R A C T

Unglaciated forelands and summits protruding from ice-sheets are commonly portrayed as areas where plants first establish at the end of glacial cycles. But is this prevailing view of ice-free refugia too simplistic? Here, we present findings suggesting that surface debris supported plant communities far beyond the rim of the Late Weichselian Ice-sheet during Greenland interstadial 1 (GI-1 or Bølling-Allerød interstadial). We base our interpretations upon findings from terrigenous sediments largely resembling 'plant-trash' deposits in North America (known to form as vegetation established on stagnant ice became buried along with glacial debris during the deglaciation). In our studied deposit, we found macrofossils ($N = 10$) overlapping with the deglaciation period of the area (9.5–10 cal kyr BP) as well as samples ($N = 2$) with ages ranging between 12.9 and 13.3 cal kyr BP. The latter ages indicate growth of at least graminoids during the GI-1 interstadial when the site was near the geographic center of the degrading ice-sheet. We suggest that exposure of englacial material during GI-1 created patches of supraglacial debris capable of supporting vascular plants three millennia before deglaciation. The composition and resilience of this early plant community remain uncertain. Yet, the younger group of macrofossils, in combination with pollen and ancient DNA analyses of inclusions, imply that shrubs (*Salix* sp., *Betula* sp. and *Ericaceae sp*) and even tree species (*Larix*) were present in the debris during the final deglaciation stage.

1. Introduction

Knowing how and where plants survive during glacial stages is crucial for understanding selection pressures during Pleistocene glaciations and for understanding species resilience during deteriorating climatic conditions. In Europe, ice-free regions in the south as well as on summits (nunataks) protruding the Weichselian ice-sheet have served as the most discussed glacial refugia for plant and animals (Ives, 1974). The notion that plants could have survived in isolated populations in northern microrefugia during the Weichselian glaciation has gained support from plant dispersion models (Feurdean et al., 2013), tree megafossils with ^{14}C ages predating the deglaciation (Kullman, 2002), and more recently from genetic analyses of ancient herbivore remains (Lagerholm et al., 2014) and plants (spruce) preserved in lake sediments (Parducci et al., 2012). So far, searches for refugia have focused on ice-free areas, including coastal zones of northern Norway (e.g., Andøya) (Parducci et al., 2012) or ice-free nunataks in the Scandinavian mountains (Dahl, 1987; Kullman, 2008).

A more peripheral hypothesis regarding glacial refugia is that shrub or even tree communities were able to grow in debris deposited on top of the Weichselian ice-sheet (Fickert et al., 2007). This "debris-covered glacier hypothesis" is not yet supported by any palaeoecological data, but is based on contemporary observations of terrestrial ecosystems (including forests) developing on potentially thin layers (>0.1 m) of supraglacial debris (Stephens, 1969; Birks, 1980; Caccianiga et al., 2011; Pelfini et al., 2012). Exposure of englacial material and accumulation of surface debris on cold based ice (frozen bed) glaciers have been shown to respond positively to historical increases in solar radiation (Mackay and

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Marchant, 2017). However, the presence of surface debris on the Weichselian Ice-sheet during warmer periods (interstadial) with high solar radiations are not self-evident. While many modern glaciers accumulate surface debris by exposing englacial material derived from surrounding slopes, such processes are intuitively expected to be of limited importance during glacial cycles when these slopes are covered by kilometers of ice. During conditions when summits protruding to the ice-sheet is lacking, surface debris is expected to be derived from aeolian dust or from uplifted basal material (basal thrusting) (Hambrey and Huddart, 1995; Fickert et al., 2007). Development of a mature plant community on supraglacial debris requires areas where no net accumulation of surface ice occurs, which constrains establishment of supraglacial vegetation to ablation zones. Yet, observation from the contemporary environment indicate that ablation zones can extend hundred kilometers into the Greenland ice-sheet during periods of warmer climates (van den Broeke et al., 2009); hence, areas that can host supraglacial plants can be extensive during interstadials if debris is present.

It is a challenging task to find traces of ancient supraglacial ecosystems, as the remnants of plants growing on degrading ice becomes mixed into debris deposited during the physical collapse of the ice-sheet and are thus 'diluted' by a mineral matrix (Wright, 1980). Despite the difficulties, remnants of ancient vegetation, so called 'plant-trash', that grew on the stagnant, outermost parts of the Wisconsin ice-sheet have been found within inclusions (clasts) in terrigenous sediment from North America (Florin and Wright, 1969; Wright and Stefanova, 2004; Wright et al., 2004). None have yet been found in Scandinavia, but the tundra communities that were most likely to have colonized European ice-sheets would have left relatively little physical trace compared with the *Picea* forests from which the North American plant-trash deposits are derived (Wright and Stefanova, 2004). Here, we present results from a palaeoecological study of a kettle-hole system located near the former center of the Late Weichselian ice-sheet in Scandinavia. The geomorphic setting of the study site, in combination with macrofossil, ancient DNA (aDNA), pollen and diatom analyses, indicate presence of a former supraglacial ecosystem. The deposits resemble well known plant-trash deposits found in North America, but have one important difference: their age and geographical positon appears to reflect an ecosystem that existed near the center of the Late Weichselian Ice-sheet, rather than on stagnant ice near the ice-sheet margin.

2. Materials and methods

2.1. Site description

The study sites are located in central parts of northern Sweden and consist of two kettle holes adjacent to an esker (Fig. 1A). One kettle hole is currently covered by Lake Stora Blåsjön (up to 13-m deep) (N64°; 25"; 21′, E18°; 35"; 45′, WGS 84) and the other one is covered by a 3- to 4-m thick mire deposit (N64°; 25″, 24′, E18°; 35"; 35′, WGS 84). Frozen-bed conditions are believed to have prevailed in the area during the Late Weichselian Glaciation (Kleman and Hattestrand, 1999). The relict character of the landscape in the area makes it possible that the kettle hole system is relict and pre-date the last Weichselian advancement in similar to previous described systems from northern Sweden (Lagerback and Robertsson, 1988). The study area is estimated to be deglaciated about 9–10 cal kyr BP (Hughes et al., 2016; Stroeven et al., 2016; Patton et al., 2017). The lowest inlet points to the studied kettle hole basins (228 m a.s.l.) have been above the highest position of the former coastline, as evident by meltwater channels existing down to an altitude of 226 m a.s.l. in the valley. Carbonates and other carbonaceous rocks are lacking not only in the study area but also in a larger regional perspective making the expected impact from geologic carbon on ^{14}C dating minute.

2.2. Field sampling

Both the north (8-m deep) and the south basins (13-m deep) of Lake Stora Blåsjön were sampled with a modified Livingstone corer (Zale, 1994) in 2014. Glacial material underlying the mire was taken with a percussion corer. Three and five cores were taken from the north and south basin (separated about 220 m apart) of Lake Stora Blåsjön, respectively. Eight cores were collected from the mire. The stratigraphy of the two lake basins are summarized in Fig. 1E. The material underlying the lake sediments and peat deposits consists of diamict as indicated by fine-grained organic inclusions buried in sand along with pebbles covered with silt and clay coatings (indicating limited sorting by fluvial processes) and tilted structures of gravel and stones. Macrofossils and organic inclusions (humus) were mainly found in the upper 30 cm without any apparent chronology.

2.3. Radiocarbon dating

Macrofossils (woody or fibrous plant remains) suitable for accelerator mass spectrometry (AMS) dating (i.e., having a carbon mass of >5 mg) were dated by Beta Analytic (4985 S.W. 74th Court Miami, FL USA 33155). Dating was only carried out when a single macrofossil was large enough to be dated to avoid mixing of material with variable age. Two inclusions found near the base of the core and at the outermost part, both suspected of being from smearing during coring, were excluded from the dataset as ^{14}C measurements validated our suspicion of a Holocene origin. Remaining samples used for bulk dating were taken from well-isolated inclusions found within the mineral matrix of cores to avoid effects from smearing. All inclusions of organic sediments were sampled and AMS-dated by Beta Analytic after acid treatment (Supporting Table 1). All dates were calibrated using the IntCal13 calibration curve (Reimer et al., 2013).

2.4. Ancient DNA analyses

One core from the southern basin was handled according to clean sampling techniques to allow ancient DNA (aDNA) analysis. The subsampling for aDNA analysis was carried out in a dedicated lab space with a sampling hood, developed following the concept of a sampling box according to (Wood and Wilmshurst, 2016), and constructed from thick Perspex and PVC film ($210 \times 60 \times 50\ cm^3$). The latter sterilized with bleach and UV prior to subsampling. The surface of a core was firstly coated with artificial DNA of pCR 4-TOPO vector (Invitrogen) as a contamination tracer (Paus et al., 2015) and the core surface (at least 1 cm) was removed by working across (never down or up) the stratigraphy using sterile disposal spoons. Separate inclusions from the inner core (dated using bulk ^{14}C measurements) were analyzed together with multiple environmental blanks from hood, working bench, gloves, and sampling suits.

All aDNA extractions and pre-PCR preparations were performed in the aDNA facility at the Swedish Museum of Natural History, Stockholm. The work bench was cleaned with bleach before DNA extractions, and DNA extractions from environmental blanks ($N = 3$; one from the suit, one from the bench, and one from the hood) were first performed prior to samples using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, CA), along with two extraction blanks to examine potential contamination from the extraction kit and the laboratory environment. We processed only