Rapid Communication

Widespread, episodic decline of alder (Alnus) during the medieval period in the boreal forest of Europe

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ABSTRACT: We report pollen-stratigraphical evidence for an abrupt, episodic and widespread population decline of alder (Alnus), one of the most common boreal tree genera, during the medieval period in northern Europe. Decline of alder pollen values was observed both in forest hollow pollen records reflecting local vegetation of pristine forests and in pollen percentage and pollen accumulation data from lake sediments. The event began roughly at AD 600 and the recovery took place at AD 1000. Human impact is an unlikely cause because the decline is specific to alder and there is no evidence for a concurrent episode of human impact. It is possible that the decline was caused or influenced by a severe drought. Another potential cause is a sudden, widespread pathogen outbreak, especially as alder is known to be sensitive to the impacts of fungal pathogens such as the oomycete Phytophthora. Copyright © 2017 John Wiley & Sons, Ltd.

KEYWORDS: drought; human impact; macrocharcoal; pathogen; pollen.

Introduction

Few episodic declines of tree populations have been recognized in Holocene pollen records. The best documented decline in Europe is the sudden drop of elm (Ulmus) pollen values 6300–5800 years ago, probably caused by complex factors including Dutch elm disease (Peglar and Birks, 1993; Batchelor et al., 2014). In North America, pollen records demonstrate a sudden, widespread and simultaneous collapse of hemlock (Tsuga) populations 5500 years ago (Davis, 1981). Pathogen or insect outbreaks have been suggested as the causes of the collapse (Davis, 1981) but recent studies have instead stressed cooling and drought as the causes (Marsicek et al., 2013).

In northern Europe, Sarmaja-Korjonen (2003) and Saarse et al. (2010) were the first to notice a decline in alder (Alnus) pollen percentage values at about AD 600–900 or 1350–1050 cal a BP, and attributed the decline exclusively to anthropogenic activities. This decline was different from the typical gradual decreases or rises of tree pollen values during the Holocene, because it was sharp and episodic, and in most cases was followed by a recovery after <300 years. Moreover, other tree taxa showed no decreasing values during the event.

Here, we report consistent pollen evidence for an abrupt decline of the alder population during the medieval period (AD 600–1000) in the boreal forest in northern Europe. We demonstrate that this decline affected the alder population in forest regions with no evidence of human impact. We also show that the same population collapse can be seen over a large area in Europe. We discuss the likely causes of such an exceptional, episodic decline and suggest that a pathogen outbreak, possibly associated with a climate change, is the likeliest cause of the decline.

Study sites and background information

In the boreal forest, grey alder (Alnus incana) and black alder (Alnus glutinosa) belong to the most abundant tree species. Pollen of the two species is usually not separated in routine pollen analysis. We analysed pollen and macro charcoal (>150 μm) data from two small forest hollow sediment cores (Naava, Kämmekää) and one small lake sediment core (Valkea-Kotinen) from southern Finland (Fig. 1). The forest hollows are located 90 m from each other and the lake is situated 350 m from the forest hollows. Consecutive 1-cm samples were analysed from Kämmekää (125 cm) and Naava (127 cm) hollows, and 0.5-cm samples from lake Valkea-Kotinen (37 cm). The Naava core was additionally analysed for fungal spores and other non-pollen palynomorphs. Accelerator mass spectrometry 14C dating of samples was processed in Poznań, Poland (Supporting Information Table S1). 210Pb measurements were used to establish the modern age of the top of the lake sediment core. All 14C dates were calibrated using the IntCal13 calibration dataset (Reimer...
Results and discussion

In all three analysed sediment sequences, alder pollen percentages decline at AD 600 (Fig. 2). In both forest hollow records the alder percentages are above 20% before the event, decline to <5% suddenly at AD 600, stay at that level for about 300 years until an almost equally abrupt rise to over 10% in the Kämmekkä and 7–8% in the Naava hollow record. In the lake sediment pollen percentages decline from 6 to 10% before the event to 2–3% during the event and rise to almost the same level as before the decline. Pollen accumulation data from the lake indicate a rapid decrease in alder biomass (Fig. 2). Importantly, all records show that no other tree pollen types declined during this period (Fig. 3).

Our pollen data do not show increases in pollen types that would indicate human influence on the vegetation during the alder decline. The first Cerealia pollen appears in the pollen record as late as AD 1600 (Fig. 2). A charcoal peak in the Kämmekkä hollow core indicates a fire at the beginning of the alder decline, but no peak is present in the Naava hollow core, nor in the Valkea-Kotinen lake record (Fig. 2). Thus, the alder decline was not associated with an increase in crop cultivation, forest clearance, fires or other types of human activity.

In her pioneering paper, Sarmaja-Korjonen (2003) listed 41 pollen diagrams, of which 19 indicated the alder decline in Finland. In Estonia, Saarse et al. (2010) reported 30 sites with evidence for the event. It is thus clear that the alder decline represents a widespread event in the boreal forest. In Fig. 2 we show that the decline is present not only in Finland and Estonia, but occurred roughly synchronously over a large region in the boreal forest in North and Central Europe. A high-resolution study from a forest hollow in Russia indicates an alder decline at a time with no occurrence of local fire or agriculture (Kuosmanen et al., 2014) (Fig. 2). Likewise, in Latvia the decline in alder pollen can be observed at AD 700–900 (Stivrins et al., 2016). A laminated Lake Suminko sediment core in northern Poland (Pędziszewska et al., 2015) reveals a decline of alder pollen from 11 to 4% at AD 850–880. Alder percentage values at Lake Suminko stay low for 60 years with steady recovery to its former value at AD 1050, which is later than in other, more eastern sites (Fig. 2).

However, given the inherent chronological uncertainties of lake and peat sediment sequences, the changes in alder population in these records are roughly simultaneous and consistent. Our results show therefore that the local and regional alder population experienced a sudden decline at about AD 600 lasting roughly 400 years, and was followed by a recovery during which alder reached abundance levels comparable to the values before the event.

There are several potential causes that can explain the episodic alder decline. Any of these must account for the characteristic traits of the decline, in other words that (i) the event is specific to alder, (ii) the decline is episodic, i.e. it begins abruptly and is followed by a recovery, and (iii) the event can be observed in different environments, including boreal forest sites away from regions with intense medieval human impact.

Sarmaja-Korjonen (2003) and Saarse et al. (2010) explained the decline by human influence. They noted that fire frequency and Cerealia pollen increased during the decline. They further claimed that extensive slash-and-burn cultivation with the clearing of forest was necessary for agriculture purposes. In addition, alder wood was needed for specific constructions, as fuel for iron smelting or smoking fish and meat (Sarmaja-Korjonen, 2003). However, this explanation is incompatible with the absence of evidence of human influence at many boreal sites (Fig. 2). Moreover, a simultaneous decline and subsequent recovery of populations of one tree species or genus over a large region is an unlikely response to gradually increasing late Holocene human impact (Davis, 1981; Peglar and Birks, 1993).

Another potential factor that could have caused the alder decline is an abrupt climatic event. The best-documented episodic decline in Holocene pollen diagrams in northern Europe has been detected during the 8.2-ka event, a cold event 8200 cal a BP, when the pollen percentages of alder and other thermophilous tree species declined widely (Seppä et al., 2007). However, the high-resolution temperature reconstructions from boreal Europe do not indicate a particularly cold climate at AD 600–1000 (Helama et al., 2010; Esper et al., 2012). Büntgen et al. (2016) reported tree-ring-based evidence for a spatially synchronized cooling in some parts of Europe at AD 536–660. It is unclear whether this cold event occurred in boreal Europe (Helama et al., 2017). If it did, it still fails to explain why it would have influenced only the alder population and not the other, more thermophilous tree species. As black alder is a species that requires wet soils, a drought could cause its population decline. Water table reconstructions from the Baltic Sea region indicate a dry period during the alder decline (Väliranta et al., 2007; Galka et al., 2017), if one allows a minor offset due to uncertainties in radiocarbon-dated sediment sequences (Fig. 2). However, the fact that the decline is specific to alder does not support the climatic explanation because a major drought should have affected many other tree species as well. For example, spruce (Picea abies) is sensitive to drought and severe droughts cause high spruce mortality in the boreal forest (Aakala et al., 2011; Lévesque et al., 2013), but the spruce pollen values increase at the beginning of the alder decline (Fig. 3). Moreover, the soil moisture records show varying humidity and dryness throughout the late Holocene, and the
Figure 2. Alder pollen values from Valkea-Kotinen lake: (a) pollen accumulation rates (pollen cm$^{-2}$ a$^{-1}$) and (b) percentages, (c) Kämmekkä hollow (%), (d) Naava hollow (%), (e) Kiilaspere bog (%), (f) Trikätas lake (%), (g) Suminko lake (%) and (h) Olga hollow (%). Potential factors influencing the alder decline: charcoal records from (i) Valkea-Kotinen, (j) Kämmekkä hollow, (k) Naava hollow, (l) Kiilaspere bog and (m) Olga hollow; (n) circles indicate individual Cerealia pollen grains from Kämmekkä and Naava hollow; (o) water table variability from Kontolanrahka bog, southern Finland (Väkiranta et al., 2007). See Fig. 1 for the location of the sites.
dry conditions at AD 500–1000 are not exceptional (Galka et al., 2017).

A third possible factor that can explain the event is a pathogen outbreak. Such an outbreak would cause a widespread, synchronous and rapid (10–20 years) decline of a species influenced by the pathogen (Peglar and Birks, 1993). This is consistent with the evidence for alder decline in our data.

Alder species are sensitive to several fungal pathogens. An ongoing rapid alder population dieback has been observed since the 1990s in Europe and recently in North America. This dieback is caused by an infection of Phytophthora alni, a fungal disease causing lethal root and collar rot (Aguayo et al., 2013; Bjelke et al., 2016). In Sweden, a recent survey showed that 28% of 168 alder stands were infected by P. alni, with 45% of the trees in the infected stands showing symptoms of decline, often followed by trees dying within a few years to decade (Bjelke et al., 2016). P. alni is a new fungal pathogen complex, which has originated from a recent hybridization event (Bjelke et al., 2016) and is thus unlikely to be the cause of the medieval alder decline. However, Phytophthora are well-known plant pathogens causing diseases that can affect alder and other tree populations. It is thus possible that a fungal disease comparable with the ongoing Phytophthora outbreak may have caused the decline during the medieval period.

To firmly connect the cause of the decline with a pathogen would require finding direct evidence of the pathogen, such as remains of sexual or asexual propagules or ancient DNA of the pathogen causing the epidemic from the same sediment records as the pollen data. Our non-pollen palynomorph analysis of the Naava core did not show evidence for the pathogen causing the epidemic from the same sediment samples. We thus suggest that the episodic and widespread alder decline in the boreal forests was most likely caused either by a drought or pathogen or possibly by their combined effect, but the suggested explanations remain inconclusive in the absence of direct evidence.

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Supporting Information
Table S1. ¹⁴C accelerator mass spectrometry, ²¹⁰Pb radionuclide and biostratigraphic dates used in age–depth models of the Kämmekkä and Naava hollows, and Lake Valkea-Kotinen.

Figure S1. Age–depth models for (a) Kämmekkä hollow, (b) Naava hollow and (c) Valkea-Kotinen lake sediment sequence. Grey area indicates a reconstructed 95% chronological uncertainty band.

References


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